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Research Article

Size-dependent desiccation tolerance in adult and juvenile introduced freshwater Japanese mystery snails (*Cipangopaludina japonica*, previously *Heterogen japonica*)

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Abstract

Freshwater Japanese mystery snails (*Cipangopaludina japonica*, previously *Heterogen japonica*) were introduced to North America from Asia in the early 1900s and have colonized many lake and river systems across the United States (US). Tolerance to environmental stressors, such as desiccation, plays a large role in species' invasion potential and persistence in novel environments. To characterize the desiccation tolerance of *C. japonica* snails, adults and juveniles from three eastern US populations were exposed to air for 13.5 weeks (adults, n = 650) or 48 hours (juveniles, n = 849) and their mortality assessed over time. Over 50% of adult snails from each population exposed to desiccation survived over 10 weeks of constant air exposure, while survival ranged from 10 to 64% at the end of the exposure experiment (13.5 weeks), depending on population, indicating exceedingly high resistance to desiccation mortality in adults of this species. In contrast, juvenile snails were much more vulnerable to desiccation, with over 70% mortality at just 24 hours of drying and only a single individual surviving 48 hours of desiccation stress. We found that the interaction between snail shell length and time affected survival for both adults and juveniles, where larger body sizes were associated with increased probability of survival as time of exposure increased ($p < 0.001$ for both juveniles and adults). Based on these data, juveniles cannot survive long-term air exposure, but the high desiccation tolerance of adults may facilitate survival and population persistence in stressful environments and allow for increased dispersal between water bodies. Therefore, both commercial and recreational users of water bodies containing introduced *C. japonica* should be aware of the risk of unintentional dispersal between water bodies via contaminated gear and/or boats, even if those materials are exposed to air for a significant amount of time.

Key words: Desiccation stress, management, mortality, invasive, shell length, Viviparidae

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Introduction

Invasive species are a global concern, threatening the biodiversity and function of many ecosystems (Crowl et al. 2008; Molnar et al. 2008; Gallardo et al. 2016). Controlling invasive species and their impacts on native flora and fauna has emerged as increasingly important for not only mitigating environmental and ecological impacts, but also economic and societal ones (Lovell et al. 2006; Holmes et al. 2009). For example, in the last 50 years, non-indigenous species have caused an estimated $1.288 trillion USD in economic damage (Zenni et al. 2021). And since the 1500s, approximately a quarter of plant species extinctions and a third of animal species extinctions were caused by invaders (Blackburn et al. 2019), highlighting the importance of not only managing invasions once they occur, but also identifying the mechanisms that govern a successful invasion to inform prevention measures. Understanding the biology of a known or potential invasive species to identify the traits that allow persistence in novel environments is a critical step towards invasive species management (Rejmánek and Richardson 1996; Whitney and Gabler 2008).

Many successful aquatic invasive species can tolerate a broad range of common stressors, such as salinity, desiccation, and temperature stress (Rahel and Olden 2008; Zerebecki and Sorte 2011; Havel et al. 2015; Thomaz et al. 2015). Many freshwater aquatic snail species, for example, are highly successful invaders due to certain adaptations that allow for persistence and acclimation to novel environments, such as an operculum to protect against predation and desiccation, or lungs to allow for respiration when in anoxic water or dry conditions (Mitchell and Brandt 2009; Spyra and Strzelec 2014). Management efforts thus depend heavily on understanding non-native snail species' vulnerabilities to these common stressors (Pyšek and Richardson 2010; Lennox et al. 2015).

Attempts to control invasive snails include a variety of strategies such as physical removal, molluscicides, or even biological control, with mixed results (Wong et al. 2009; Bernatis and Warren 2014; Olivier et al. 2016; Saglam et al. 2023). One such control method, water drawdown, attempts to cause high mortality rates from desiccation and has been used with varying success for both target invasive species and nontarget native species (Tucker et al. 1997; Hovingh 2004; Cheng and LeClair 2011). For example, extreme drought in a southeast Nebraska, USA, reservoir led to water drawdown and massive mortality of invasive Chinese mystery snails, *Cipangopaludina chinesis* (previously *Bellamya chinensis*) (Haak et al. 2013). Additionally, while recreational boats are a common vector that contributes to the spread of freshwater snails (Rothlisberger et al. 2010; Havel et al. 2014), the movement of boats between water bodies may also expose snails to air drying for days or weeks at a time, potentially mitigating meaningful dispersal.

However, many aquatic snails have the ability to enter estivation, or dormancy, to survive prolonged drying events (Sandland and Minchella 2004). Additionally, the ability to keep water loss at a minimum, via a carbonate operculum and/or burial in exposed, water-saturated soil, extends the time that individuals can stay in estivation (Mitchell and Brandt 2009; Unstad et al. 2013; Poznańska et al. 2015). With regard to species' invasions, resistance to desiccation stress can affect the invasion process in two ways: facilitating the spread of the species from one watershed to another (i.e., via vectors that present desiccation risk, such as boats), and/or by increasing the ability of invasive populations to resist local extinction in water bodies that are ephemeral or experience fluctuations in water levels (Facon et al. 2004).

Two invasive freshwater snail species, the Japanese mystery snail, *Cipangopaludina japonica* (previously *Heterogen* / *Bellamya* / *Viviparus japonica*) and the Chinese mystery snail, *Cipangopaludina chinensis* (previously *Bellamya chinensis*), are native to parts of Asia and were introduced to North America over 100 years ago as a food source (Clench and Fuller 1965; Wolfert and Hiltunen 1968). Due to repeated introductions and transport, both for food and in the aquarium trade (and possibly via recreational boating), mystery snails are now found in over 20 US states and eight Canadian provinces (Kingsbury et al. 2021a; United States Geological Survey 2022); Hall-Stratton unpublished data), representing a relatively large-scale and successful invasion. The two species are difficult to tell apart without genetic confirmation but are thought to have similar demographics and ecological impacts (Van Bocxlaer and Strong 2016; David and Cote 2019; Fowler et al. 2022a). Both mystery snail species are gill-breathing, with an operculum, and ovoviviparous; female snails often carry many young (over 100 juveniles, Van Bocxlaer and Strong 2016; Fowler et al. 2022a) at multiple different developmental stages internally in the brood pouch. Thus, single gravid females represent a large threat to aquatic ecosystems since one individual is sufficient to initiate a population (Van Bocxlaer and Strong 2016). Fairly little *in situ* work has been done to evaluate the specific impacts of mystery snails on aquatic ecosystems; however, recent work has shown that invasions may displace native gastropods (Johnson et al. 2009; Solomon et al. 2010; Fowler et al. 2022a; Wolfert and Hiltunen 1968) and potentially alter water clarity and nutrient content (Solomon et al. 2010; Schuler et al. 2020). Chinese mystery snails (*C. chinensis*) have been shown to decrease the abundance of native snails and reduce periphyton growth (Johnson et al. 2009), demonstrating that these snails are likely affecting invaded areas in diverse ways.

In spite of the extent of the mystery snail invasion in North American water bodies, there are few comprehensive studies identifying the specific aspects of their biology that afford them such success, and the mechanisms of dispersal between affected areas need further study (but see Kingsbury et al. 2021a for a review on Chinese mystery snail invasion ecology). Of the two species, more work has been done on snails morphologically identified as Chinese mystery snails, which has shown that adults can survive out of water for up to nine weeks (Havel 2011; Unstad et al. 2013) and in temperatures from < 0 °C to 45 °C for up to 33 hours (Soes et al. 2011; Burnett et al. 2018). Previous work has also demonstrated that adult Chinese mystery snails have higher survival rates when desiccated and are more tolerant of higher temperatures than juveniles (Havel 2011). Due to the morphological confusion between Chinese and Japanese mystery snails apparent in the literature (Burks et al. 2016; Abeyrathna and Davinack 2023), and the lack of genetic confirmation in most studies, some of this literature may in fact involve Japanese mystery snails that were misidentified as Chinese. However, to our knowledge the desiccation tolerance of confirmed Japanese mystery snails over their ontogeny has not been specifically measured in spite of its importance to developing feasible control strategies.

In this study we evaluated the desiccation tolerance of both adult and juvenile Japanese mystery snails in a laboratory environment by placing snails in a temperature-controlled incubator and measuring survival over time. Based on previous work on Chinese mystery snails, we expected snails to survive at least eight weeks out of water. We also tested if snail size predicted survival across the experiment, with the expectation that larger snails would have higher tolerance to desiccation due to the ability to retain more water within their shells. This study represents the first desiccation challenge for invasive populations of *C. japonica*.

Methods

Field collections

Adult Japanese mystery snails were collected in August and September of 2023 from three previously surveyed sites in central and northern Virginia, USA: Leesylvania State Park, on the Potomac River (38°35.1033'N, 77°15.7867'W), Lake Royal (38°48.2417'N, 77°17.455'W), a residential lake, and a stormwater pond in Maryland (39°10.6'N, 76°43.0467'W), hereafter designated "Maryland Pond". These three populations were chosen based on previous genetic identification using the barcoding gene cytochrome *c* oxidase subunit 1 (COI), which confirmed they were Japanese mystery snails (Fowler et al. 2022a). After collection, snails were separated by population and kept at room temperature in 5-gallon buckets on the floor in the laboratory with aerators and fluorescent lights on a natural light cycle (12 hours light:12 hours dark) at the Potomac Science Center, Woodbridge, Virginia, USA. Buckets were filled with water first from each respective collection site, with subsequent water changes (50% water change once per week) using dechlorinated tap water. Snails were placed into the experimental incubator 1–2 weeks after collection and were not fed before experimentation.

Juvenile experiment

Live, fully formed juveniles were removed from the female's brood-pouch, and only juveniles ≥ 3.8 mm shell length were used in experiments (n = 849, mean shell length = 5.64 mm, range = 3.8–8.2 mm; Table 1) to ensure juveniles were developed enough to survive outside the brood pouch (see Jaishanker et al. 2023). While we are unaware of any studies that have assessed the shell lengths of juveniles emerging naturally from *C. japonica* females, previous work by Edgar et al. (2022) found that the mean shell length of juveniles naturally emerging from female *C. chinensis* was 5.9 ± 1.6 mm. We took this approach because we needed to source juveniles as early in the development process as possible to avoid confounding environmental factors, and also to source enough juveniles for sufficient replication for the experiment. Either 20 (Leesylvania) or 10 (Lake Royal and Maryland Pond) juveniles were obtained from each female for each desiccation trial. Female snails from Leesylvania consistently had more juveniles in the brood pouch compared to the other two populations due to the larger sizes of these females, so we opportunistically took more juveniles per female. Trials were repeated either five (Lake Royal) or four (Leesylvania and Maryland Pond) times, depending on availability of adult female snails (n = 20 females from Leesylvania and Maryland Pond each; n = 25 from Lake Royal; total n = 65, mean female shell length = 52.3 mm, range = 38.0–62.0 mm).

For the experiment, juveniles were separated by population and all placed in the same incubator (daytime temperature = 32.2 °C; nighttime temperature = 21.1 °C; 12:12 light/dark cycle) on dry plates with moisture wicks immediately after removal from the female. Humidity was not explicitly measured during the experiment. After placement in the incubator, two (Maryland Pond and Lake Royal) or four (Leesylvania) juveniles per brood were randomly subsampled at 4-, 8-, 10-, 24-, and 48-hour time periods (for a total of 10 or 20 juveniles/brood/site sampled across five time periods = 50 or 100 juveniles per replicate experiment). At each time point after removal from the incubator, juveniles were individually placed in 60 mL of room temperature dechlorinated water in 18-well plastic bead boxes for a 24-hour rehydration period. After rehydration, juveniles were assessed for mortality by pushing the operculum with sharp forceps and looking under a dissecting microscope for movement

Table 1. Total number of adult and juvenile snails used in each experiment, with mean shell lengths in mm and standard deviations. Snails, both adults and juveniles, were significantly different in size between all three populations.

Population		Total snails used in experiment (n)	Shell length range (mm)	Mean shell length (mm) ± SD
LEESYLVANIA	Adults	234	17.8–63.0	52.16 ± 10.72
	Juveniles	400	3.8–7.8	5.46 ± 0.79
MARYLAND POND	Adults	207	15.2–55.5	40.06 ± 8.76
	Juveniles	200	4.3–8.1	5.98 ± 0.91
LAKE ROYAL	Adults	209	34.9–62.3	42.70 ± 4.84
	Juveniles	249	3.8–8.2	5.65 ± 0.90

within the shell. Juveniles were recorded as dead if they floated on the top of the water and/or if they had no response to their operculum being pushed in. The shell length of each juvenile was taken upon subsampling from the incubator. Snails were not fed before or during the experiment or during the rehydration period. One snail from Maryland Pond was accidentally crushed before being evaluated for survival or shell length, thus there are only 49 snails for that replicate trial rather than 50.

Adult experiment

A total of 650 adults were used for the experiment (Leesylvania State Park, n = 234; Lake Royal, n = 207; Maryland Pond, n = 209) and were exposed to air concurrently using the same conditions as the juvenile experiment. Leesylvania snails were placed in the incubator on August 28th, 2023, while snails from the Maryland Pond and Lake Royal were placed in the incubator one week later. All snails were placed in the same incubator for the entire experiment.

Snails were kept in dry bins with moisture wicks and high edges, to prevent movement and escape, for 13.5 weeks (95 days). Snails were separated into bins by site of origin and placed on the two middle shelves of the incubator (Suppl. material 1: fig. S1). Bins from two sites (Maryland Pond and Lake Royal) were placed on the lower middle shelf, while the bin for Leesylvania was placed on the upper middle shelf (Suppl. material 1: fig. S1). Identical fluorescent lighting systems were attached under each shelf such that each bin received the same light conditions. Thirteen adult snail replicates were randomly subsampled from each population once per week for the first four weeks of the experiment, and twice per week from week five through the end of the experiment to capture mortality rates on a finer scale later on in the experiment. After removal from the incubator, snails were kept separate by population and placed in five-gallon buckets with room temperature, dechlorinated tap water and aerators for a 24-hour rehydration period. After 24 hours submerged, the mortality of adult snails was assessed by manipulating the operculum and observing if the adult protruded out of the shell. If the operculum closed upon being touched, or any movement of the foot was observed, the snail was recorded as alive. If the operculum fell off or there was no resistance or movement, the snail was recorded as dead. Adult shell lengths were measured at the time of subsampling from the incubator. Due to the advanced state of decomposition of many deceased individuals, the sex of the snails was not determined.

Statistical methods

Data from adults and juveniles were analyzed separately. Statistical analyses and data wrangling were accomplished in the R programming environment (v4.4.0, R Core Team 2013). Data wrangling, visualization, and cleanup was

accomplished using the tidyverse (Wickham et al. 2019), ggplot2 (Wickham 2016), and dplyr (Wickham et al. 2020) packages. We first tested for significant differences in snail size distributions of the three sampled populations for each experiment by conducting unpaired Welch's t-tests using the stats package (R Core Team 2018), which accounted for uneven sample sizes and variances between the populations.

We then conducted two separate model-based analyses. The first approach focused on determining the impacts of source population and experimental timepoint on overall snail survival probability, and the second focused on the impact of shell length on individual snail survival over time. We conducted both analyses for the adult and juvenile experiments separately. For the first approach, we constructed generalized linear models (GLMs) or generalized linear mixed models (GLMMs) assuming binomial error distributions and logit link functions, where we modeled the number of live snails at each timepoint as the response and the number of dead snails as the binomial denominator. For both adult and juvenile experiments, we included timepoint (adults, week sampled; juveniles, hour sampled) and population (Leesylvania, Maryland Pond, or Lake Royal) as fixed effects. For the juvenile experiment, due to the replicate structure of the experiment (i.e., we conducted four or five independent trials), we also included replicate trial as a random effect.

For our second approach, to test for the impact of individual snail shell length on survival across time for both adults and juveniles, we constructed GLMMs treating each snail as an independent replicate with shell length (log scale) and timepoint (hours for juveniles, weeks for adults) as fixed effects. We also included population as a random effect in these models because we were primarily interested in determining the impact of shell size on individual survival across sites, which was not possible in our first approach. Additionally, there were site-level differences in shell size distributions (Table 1), and differences in survival between populations were already described directly via our first approach. We modeled individual snail survival as a binary response, treating each snail as a replicate sample, and fit Bernoulli-distributed GLMMs to these data. For the juvenile experiment only, we again included experimental replicate trial as an additional random effect along with population, and mother size (shell length in mm, log scale) as an additional fixed effect to explore the possibility that larger females may produce more robust offspring (i.e., Ribi and Gebhardt 1986).

We employed a model selection approach for both model-based analyses and tested all possible combinations of fixed effects. Models were selected based on the lowest AICc score. Models were fit using glmmTMB (Brooks et al. 2017; Magnusson et al. 2017), and model diagnostics were accomplished using DHARMa (Hartig 2022). Models were compared using the ICtab function in the bbmle package (Bolker 2017), and model predictions were generated using ggpredict in ggeffects (Lüdecke 2018). Figures were generated using ggplot2 (Wickham 2016).

Results

The three adult snail populations had significantly different mean snail shell lengths (in mm); snails sampled from the Leesylvania State Park were significantly larger than snails from the other two sites ($p < 0.001$, Table 1). Snails from Lake Royal were slightly larger on average than those collected from Maryland Pond ($p < 0.001$, Table 1), which had the smallest shell lengths on average ($p < 0.001$, Table 1). In contrast, juvenile snails extracted from females

of Maryland Pond were larger on average than Lake Royal juveniles ($p < 0.001$, Table 1) and those from Leesylvania ($p < 0.001$, Table 1), while Leesylvania juveniles were the smallest ($p = 0.009$, Table 1).

Juvenile experiment

As expected, the proportion of live juveniles decreased with increasing time of desiccation exposure ($p < 0.001$, Fig. 1, Suppl. material 1: table S1) for all populations. However, there were significant differences in overall juvenile survival between populations. Juveniles from Leesylvania and Maryland Pond populations were approximately two times more likely to survive over time than Lake Royal ($p < 0.001$, Fig. 1, Suppl. material 1: table S2), and there was no difference in juvenile survival between Leesylvania and Maryland Pond populations.

When we investigated individual juvenile survival probability, the most parsimonious model included the interaction between time exposed (in hours) and shell length (in mm). Concordant with our previous analysis, individual probability of survival decreased with increasing hour of exposure (estimate = -0.679, SE = 0.158, $p < 0.001$; Table 2), and larger shell lengths were associated with increasingly higher survival probabilities as time exposed increased ($p = 0.0014$, Fig. 2). The second-place model, which was < 2 AICc units from the top model (dAICc = 1.8, Suppl. material 1: table S3), also included shell length of the mother as an additional predictor. Therefore, we base our inference off the most parsimonious model but cannot rule out a potential effect of female size on offspring desiccation tolerance (although we note that the effect of female size was statistically equivocal, $p = 0.667$). At the end of the experiment at the 48-hour timepoint, all juveniles across all replicates were recorded dead except a single individual from Maryland Pond.

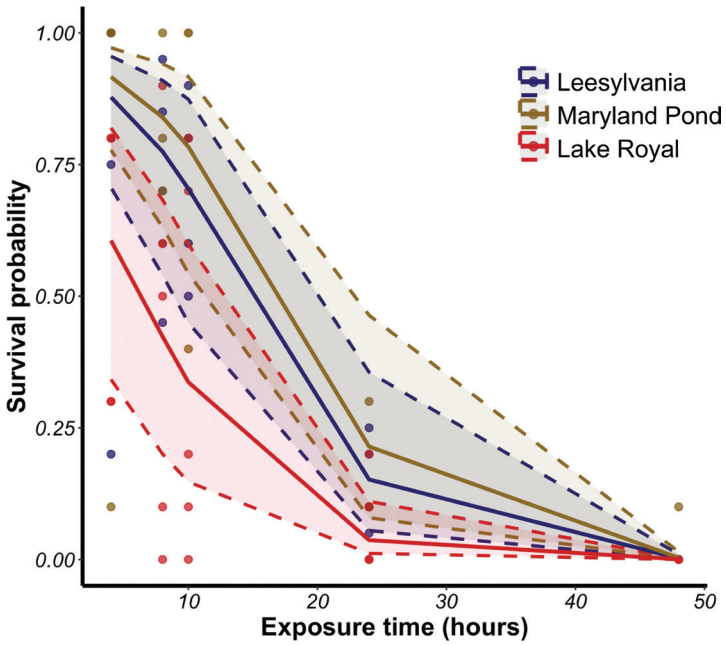

Figure 1. Survival probability of juvenile snails from three populations over a 48-hour period of desiccation stress. Plotted lines represent predicted values from a binomial generalized linear mixed model (GLMM), and shaded areas represent 95% confidence intervals plotted over raw data. Colors correspond to the population from which snails were collected.

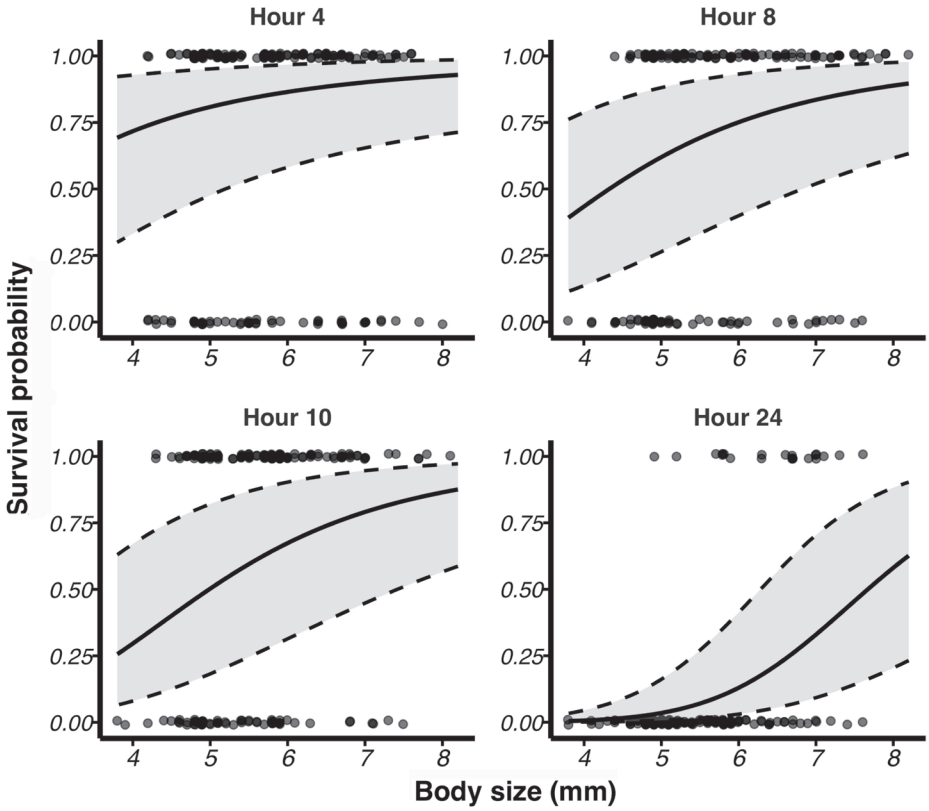

Figure 2. Interaction between juvenile snail body size (shell length in mm) and timepoint sampled (in hours) predicting individual survival probability over 24 hours of desiccation stress. Fitted lines are Bernoulli generalized linear mixed model (GLMM) predictions with 95% confidence envelopes plotted over raw data points. Only one individual snail survived at the final timepoint of 48 hours, so data from that timepoint is excluded from this figure.

Table 2. Juvenile individual survival table across all populations. Individual survival estimates and associated errors and confidence intervals are presented at all time points of the experiment. Predictions generated from a Bernoulli generalized linear mixed model (GLMM) with experimental replicate and population as random effects.

Time (hours)	Predicted survival probability	Standard error	Lower 95% CI	Upper 95% CI
4	84.7%	77.6%	54.8%	96.2%
8	70.9%	76.9%	35.1%	91.7%
10	61.8%	76.7%	26.5%	87.9%
24	8.4%	80.4%	1.9%	30.7%
48	0.1%	101.9%	<0.1%	0.5%

Adult experiment

Similar to results from our juvenile experiment, snail population and time exposed to desiccation (in weeks) interacted to determine adult snail overall survival (Fig. 3, Suppl. material 1: table S4). The proportion of snails alive decreased significantly over time depending on population; specifically, snails from Leesylvania had the highest proportion survive across time ($p < 0.001$) as compared to Maryland Pond ($p < 0.001$) or Lake Royal ($p = 0.0025$), the latter of which had the lowest survivorship over time (Suppl. material 1: table S5).

As for individual-level survival, predicted survival probabilities across populations ranged from 90–98% through five weeks of exposure, with many adults surviving

to the end of the experimental period at 13.5 weeks (Table 3). Consistent with what we observed in the juvenile experiment and the previous adult analysis, the most parsimonious model describing individual adult survival included the interaction between time exposed (in weeks) and shell length (in mm) (Suppl. material 1: table S6). Adult probability of survival decreased with weeks passed (-2.178, SE = 0.350, $p < 0.001$; Table 3), while larger shell lengths were again associated with higher survival probabilities as time exposed increased ($p < 0.001$, Fig. 4).

Discussion

Here we present the first study to our knowledge investigating the desiccation tolerance of invasive Japanese mystery snails (*Cipangopaludina japonica*). Mystery snails are likely to continue to spread to new waterbodies via anthropogenic (i.e., attachment to boats, equipment, or macrophytes) or "natural" (i.e., floating on the surface of the water, dispersal via bird or mammal predators, or flooding events) vectors (Van Leeuwen et al. 2013; Havel et al. 2014). Solomon et al. (2010) found that human dispersal means (i.e., the number of boat ramps and human population densities) were correlated with the occurrence of *C. chinensis* in Wisconsin, USA lakes. Kingsbury et al. (2021b) found similar patterns in Nova Scotia, Canada, where boat launches and lake connectivity were again associated with high probability of mystery snail invasion. Several of these vectors have a component of air exposure time and thus pose a risk of desiccation to snails, which in many cases may be sufficient to cause mortality for *C. japonica* juveniles but not adults. Indeed, here we show that large adult mystery snails specifically are highly resistant to desiccation stress, which is an adaptation that likely facilitates their dispersal via anthropogenic vectors and persistence as invaders. On average, over 50% of the snails in our study survived over 70 days out of water, with many individuals surviving 95 days of desiccation (Table 3). Survivorship was particularly high in snails from Leesylvania State Park, which demonstrated the highest tolerance to desiccation (i.e., > 75% survival rate at 95 days out of water) (Fig. 3). Since some snail individuals from all three sites remained alive at the end of our experiment, future research is needed to determine the absolute length of time exposed to air needed to reliably induce 100% mortality of adult mystery snails.

Desiccation-resistant snails like *C. japonica* (for example, *Pomacea* spp. apple snails and Chinese mystery snails) are found in their native range in ecosystems like rice paddies, which are characterized by fluctuations in water level and frequent drying (Nakanishi et al. 2014; Kingsbury et al. 2021a). Thus, *C. japonica* snails are likely capable of colonizing and persisting in novel environments of variable hydroperiods, as well as potentially accomplishing long-distance dispersal to other water bodies across dry-wet boundaries. The high resistance to desiccation seen in our study suggests that even if an effective chemical or biological control mechanism is deployed in a mystery snail population, individuals may be capable of closing their operculum and/or burrowing in sediment for long periods to survive such management methods (Poznańska et al. 2015; Burnett et al. 2018). Additionally, chemical management strategies applied to water bodies to control snails, such as niclosamide monohydrate (Abeyrathna and Davinack 2023), may similarly not persist in natural environments long enough to cause sufficient mortality due to half-lives of just hours to days, much lower than the tolerance period for desiccation we observed (Andrews et al. 1982; Graebing et al. 2004). One potential effective strategy may be to combine a period of water drawdown with molluscicides added once water levels are extremely low to cause a high mortality event, as suggested by Havel et al. (2014).

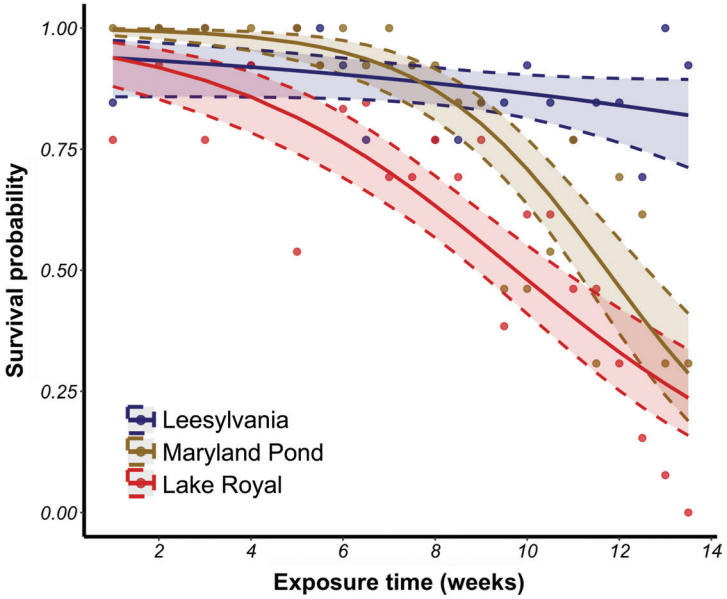

Figure 3. Survival probability of adult mystery snails from three populations over 13.5 weeks of desiccation stress. Trendlines represent predictions from a binomial generalized linear model (GLM) and shaded areas represent 95% confidence intervals, plotted over jittered raw data. Colors correspond to population.

Table 3. Adult individual survival table across all populations. Individual survival estimates and associated errors and confidence intervals are presented at every whole week of the experiment as well as at experiment end (13.5 weeks). Predictions generated from a Bernoulli generalized linear mixed model (GLMM) with population as a random effect.

Time (weeks)	Predicted survival probability	Standard error	Lower 95% CI	Upper 95% CI
1	98.5%	30.2%	94.3%	99.7%
2	97.8%	29.4%	92.4%	99.5%
3	96.7%	28.6%	90.0%	99.2%
4	95.3%	28.0%	87.1%	98.7%
5	93.4%	27.4%	83.5%	98.0%
6	91.1%	27.0%	79.4%	97.0%
7	88.2%	26.7%	74.6%	95.6%
8	84.6%	26.5%	69.2%	93.8%
9	80.4%	26.5%	63.2%	91.5%
10	75.5%	26.5%	56.8%	88.7%
11	70.1%	26.7%	50.1%	85.3%
12	64.1%	27.0%	43.3%	81.4%
13	57.8%	27.5%	36.7%	76.9%
13.5	54.6%	27.7%	33.4%	74.5%

We also observed a positive relationship between snail shell length and survival probability at later stages of the adult experiment (Fig. 4). Snail size became a stronger predictor of survival at long exposure times (in this experiment, approximately > 5 weeks) and was less impactful, if at all, at shorter exposure times (<5 weeks; Fig. 4). Snail body size correlates with increased ability to retain water in their tissues and survive desiccation (Poznańska et al. 2015), driving these patterns. Additionally, *C. japonica* have an operculum, which becomes more robust as they develop and is an important adaptation for protection against desiccation (Facon et al. 2004; Poznańska et al. 2015). It is important to note that this study did not include any

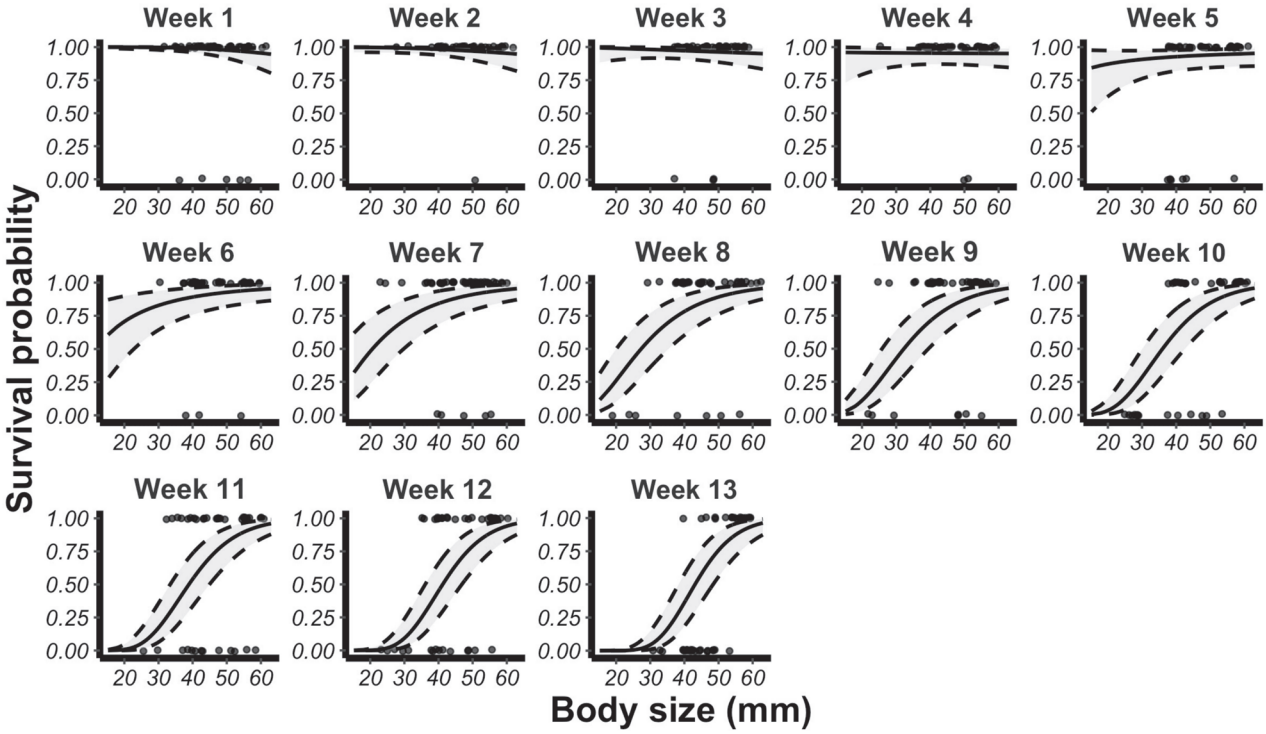

Figure 4. Interaction between body size (shell length in mm) and week sampled predicting survival probability of adult snails. Fitted lines are Bernoulli generalized linear mixed model (GLMM) predictions with 95% confidence envelopes plotted over raw data points. Whole weeks of the experiment (1 through 13) are represented.

naturally occurring substrates such as sand, leaf litter, cobble, etc., which could aid in extending survival over longer time periods by affording individuals with the opportunity to bury (Wood et al. 2011; Poznańska et al. 2015). Therefore, the data shown here are conservative estimates of survival under desiccation stress. Additional studies could explore if *C. japonica* responds behaviorally to air exposure by burying into different types of substrata with varying water retention capacities.

Our results are consistent with other studies that show high tolerance to desiccation for large freshwater snail species. For example, adults of the closely-related Chinese mystery snail (*C. chinensis*) can survive nine weeks of drying, and larger snails have higher survival rates than smaller snails, similar to our study (Havel 2011; Unstad et al. 2013). Additionally, Havel et al. (2014) found that *C. chinensis* not only survived over 63 days of desiccation, but still produced offspring at 54 days. Although we did not quantify the numbers of juveniles released by desiccated adults in our study, we noted that some adults released live juveniles upon rehydration after 13.5 weeks of desiccation stress. This ability to maintain reproductive output post-desiccation is likely an adaptation developed to resist drought, and has been seen in other species of snails inhabiting the same habitats as *C. japonica* (Havel et al. 2014; Glasheen et al. 2017; Kingsbury et al. 2021a). Desiccation tolerance of aquatic snails can even exceed hundreds of days, as seen in the invasive apple snail *Pomacea maculata* which has exceedingly high survival rates at 308 days out of water (Mueck et al. 2018). Apple snails are pulmonate snails, possessing lungs in addition to gills, which likely allows them to retain some metabolic activity while out of water and thus persist for such long periods (Mueck et al. 2018). Mystery snails, in comparison, do not have lungs and breathe with only gills, using retained water when exposed to air (Fowler et al. 2022a). Therefore, although many invasive snails exhibit similar biotic characteristics and tolerances, and may even be from similar habitats, it is critical to quantify these tolerances on a species-specific basis to inform management practices.

In contrast to our findings in the adults, juvenile snails had high mortality when desiccated, representing a much lower probability of survival in dry environments as compared to fully developed adult snails. Specifically, predicted juvenile mortality at 24 hours of desiccation was nearly 90% when estimated across populations, while mortality at 48 hours was essentially 100% (Fig. 1, Table 2). Even in the Maryland Pond and Leesylvania State Park populations, which had higher juvenile survivorship than Lake Royal, total survival at 24 hours was a maximum of ~30% or less in all replicates (Fig. 1). These results are consistent with other species of freshwater snail; for example, juveniles of *Melanoides tuberculata*, *M. amabilis*, and *Tarebia granifera* snails were less tolerant to drying stress than adults, with adult survival measured in the tens of days and juvenile survival limited to a matter of hours (Facon et al. 2004). Therefore, juvenile snails are much less likely than adults to succeed in dispersing across terrestrial landscapes, and likely have lower probability of survival in dynamic environments with high desiccation risk. In general, our results suggest that transportation of juvenile snails presents a much lower risk of invasion than transport of large adults due to their apparent vulnerability to desiccation stress, and thus management efforts must take alternate approaches to mitigating juvenile vs. adult colonization risk. For example, a desiccation-dependent approach such as drying boats and fishing equipment is likely to effectively control the spread of juvenile snails (e.g., "clean, drain, dry" approaches, Mohit et al. 2021, 2023).

In accordance with our adult experiment, we again observed an increasingly positive relationship between juvenile snail size and survival as time exposed increased (Fig. 2). Although juveniles have a less-developed operculum and are much more vulnerable to desiccation stress in general, we hypothesize that similar to adults, larger juveniles are able to retain more moisture than smaller snails and thus may tolerate short periods of desiccation better as compared to small juveniles. The relationship between snail survival and size became steeper as exposure time increased (Fig. 2), supporting this hypothesis.

The three populations from which we collected snails had significantly different size distributions and tolerance to desiccation, suggesting that geographically isolated invasive populations have varying abilities to survive environmental fluctuations and colonize new areas (e.g., Facon et al. 2004). There are many factors that can affect the population structure, fitness, and individual morphology of snail populations; for example, population density (Williamson et al. 1976), predator presence (Crowl and Schnell 1990), geochemical factors such as pH and calcium content (Watson and Ormerod 2004; Glass and Darby 2009), and resource availability (Crowl and Schnell 1990). During collection for this study, the population with the highest snail density was Lake Royal (Fowler and Lewis, personal observation), which was also the population with the lowest desiccation tolerance in both adults and juveniles (Figs 1, 3). In contrast, the Leesylvania State Park population, which exhibited the highest adult and juvenile survivorship (Figs 1, 3), had a high density of aquatic vegetation and was also the largest body of water we sampled due to its location on the Potomac River. Although we did not take advanced measures of environmental characteristics like water quality or food availability, nor was there reliable information on the biogeochemistry of any of the water bodies we sampled, we hypothesize that density-dependent environmental stressors (e.g., differences in resource availability) resulted in population-level differences in adult snail fitness and resistance to novel stressors such as desiccation (e.g., Moyle and Light 1996). It is possible that water bodies with fluctuating hydroperiods and frequent drying could select for snails with high desiccation tolerance, resulting in adaptation of the population over time (Chapuis and Ferdy 2012; Mizrahi et al. 2015; Levri et al. 2023). However, only one of our sites (Maryland Pond, a stormwater col-

lection pond) showed any potential for frequent drying, and also had moderate survivorship compared to the other two sites—a man-made lake in a residential community (Lake Royal) and a large, natural, slow-moving river (Leesylvania).

Further, we also hypothesize that effects of environmental stressors on adult snails likely cascaded to offspring, explaining the concurrent patterns we saw of low survival of both adults and juveniles from Lake Royal (Figs 1, 3). Additionally, desiccation tolerance is likely a heritable trait to some degree, as is tolerance to other types of stressors, further highlighting the importance of including multiple populations and cohorts of offspring from many females in studies of stress tolerance (Facon et al. 2004; Levri et al. 2023). For example, populations of the New Zealand mud snail (*Potamopyrgus antipodarum*) from the western US are more tolerant to desiccation than populations from the eastern US, which has been attributed to genetic differences (Levri et al. 2023). It is likely that populations of *C. japonica* are adapting independently to local conditions of invaded areas, which may drive differences in stress tolerance between populations (e.g., Facon et al. 2004); however, further study is required to disentangle the effects of adaptation and genetic differences from other population-level variables such as parasite infections, food availability, and/or population density.

An important factor in addition to survival probability when desiccated is the potential overhang effects of stress. That is, extended periods of desiccation and concurrent starvation likely have lasting impacts on snail fecundity, growth, and even future resistance to parasite infection (Vianey-Liaud 1984; Vianey-Liaud and Lancastre 1994; Sandland and Minchella 2004). For example, *Bulinus globosus* snails naturally encounter desiccation in their native range and are thus considered tolerant, but exhibit a decline in fecundity after desiccating for a similar amount of time as in our study (Kalinda and Chimbari 2022). If adult *C. japonica* also have lasting reproductive effects from desiccation stress, we expect that long term desiccation will likely limit the initial growth of new or restarting populations colonized by formerly stressed individuals with low fecundity. Future avenues of research include characterizing the long-term survivorship and fecundity of stressed female snails after rehydration to fully investigate if desiccation is a viable tool for future invasion management.

Lastly, the degree to which this desiccation advantage for *C. japonica* adults compares to other species of potential native gastropod competitors commonly found in the same habitats (such as *Elimia virginica*, *Physella/Physa* spp., *Campeloma decisum*, and *Planorbella trivolvis*; (Fowler et al. 2022b) requires further investigation. In general, native snails that share habitat with *C. japonica* exhibit lower desiccation stress tolerances than what we observed in the present study; for example, native *Physa gyrina* snails have extremely low desiccation tolerance as adults (less than 20% survival at only one day of desiccation and 0% survival at seven days) (Wood et al. 2011). Although there is a dearth of controlled laboratory tests of long-term desiccation stress of native planorbid (e.g., *Planorbella* spp.) and lymnaeid (e.g., *Lymnaea elodes*) snails, species in these families have variable tolerances to desiccation, surviving for several weeks up to a few months, depending on conditions (Cawston 1929; Jokinen 1978; Gallo et al. 1984).

Conclusion

This research highlights an important adaptation that facilitates *C. japonica* colonization of dynamic water bodies, dispersal to novel environments, and potential resistance to contemporary management methods. We found that large adult snails sourced from low-stress environments may represent a particularly high risk of spreading to other water bodies and may survive transport through dry, stressful conditions. Our

study suggests that due to their high desiccation tolerance and reproductive strategy of bearing live young, large gravid females specifically may be able to establish introduced populations in dynamic environments previously considered unfit for stable snail populations. This work suggests that management of *C. japonica* populations must accommodate their enhanced ability to survive out of water.

Author's Contribution

NTL conducted the experiment and collected the data, interpreted the data, wrote the first draft of the manuscript, and reviewed all subsequent drafts. SRG assisted in curating data, conducted statistical analyses, and assisted in co-writing and reviewing/editing all manuscript drafts. DHS assisted in conceptualizing the project, collecting specimens and data, and reviewed and edited all manuscript drafts. AEF conceptualized the project, supervised project design and resources, assisted in data curation and analysis, and reviewed and edited all drafts of the manuscript.

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Data accessibility statement

Data and statistical code have been deposited in a public Figshare repository (accessible at https://figshare.com/s/ffdff14a9ed8b6a8e75b).

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Supplementary material 1

Statistical tables and additional figure

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Explanation note: **fig. S1.** Diagram of snail spatial distribution in the incubator for the adult experiment. **table S1.** Top models and corresponding weights for overall juvenile survival analysis. **table S2.** Juvenile overall survival table separated by population. **table S3.** Top models and corresponding weights for individual juvenile survival analysis. **table S4.** Top models and corresponding weights for overall adult survival analysis. **table S5.** Adult overall survival table separated by population. **table S6.** Top models and corresponding weights for individual adult survival analysis.

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