Determining diet and establishing a captive population of a rare endemic detritivore, the endangered *Novisuccinea chittenangoensis* (Pilsbry, 1908) (Pulmonata: Succineidae)

Cody R. Gilbertson¹, Rebecca J. Rundell¹ and Robyn Niver²

¹State University of New York College of Environmental Science and Forestry, Department of Environmental and Forest Biology, 1 Forestry Drive, Syracuse, NY 13210, USA; and ²United States Fish and Wildlife Service, New York Field Office, 3817 Lake Road, Cortland, NY 13045, USA

Correspondence: C.R. Gilbertson; e-mail crgilber@syr.edu

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**ABSTRACT**

Land snails, particularly rare or narrow-range endemic species, are among the most threatened animals on Earth. For such species, captive-breeding programmes may be important for ensuring backup populations or for supplementing wild populations. However, establishing such programmes can be difficult, because natural history information on rare species is often scarce, and there are few potential ‘model’ captive-breeding programmes. Captive breeding is further complicated by wild diets that are poorly known and difficult to replicate. Furthermore, small populations can lead to official restrictions or reluctance to undertake dietary experimentation. Here we demonstrate how close captive observation of the target threatened species, combined with dietary experimentation and behavioural observation on a non-endangered but ecologically similar surrogate species, is an effective approach for determining the optimal captive diet. In order to establish a captive colony of the Chittenango ovate amber snail *Novisuccinea chittenangoensis*, which is known from only one side of a single waterfall in central New York State, we first performed dietary experiments on a common co-occurring succineid. This surrogate species grew and reproduced significantly better on certain types of leaf litter than on other diets. After failed initial attempts at raising *N. chittenangoensis*, we assessed leaf litter preferences and growth of a single captive *N. chittenangoensis*. This single-snail approach allowed us to gain information quickly with no impact on the wild population. Additional wild *N. chittenangoensis* were then brought into captivity for breeding and fine-tuning of the leaf-litter diet. Captive *N. chittenangoensis* thrived on the successful diet, which ultimately resulted in 632 F1 offspring with 0% mortality (compared with 80% mortality and significantly lower growth rate experienced in previous studies of *N. chittenangoensis*), some of which were released into the wild.

**INTRODUCTION**

An estimated 54% of North American land snails are threatened with extinction (Baillie, Hilton-Taylor & Stuart, 2004). Most of the snails included in this estimate are fungivores or detritivores; these break down leaf litter directly through ingestion, or passively by spreading fungi and other microbes to litter for additional decomposition via their movement or faeces (De Oliveira, Hattenschwiler & Handa, 2010; Meyer, Ostertag & Cowie, 2011). Extinction of detritivorous snails could thus potentially impact nutrient cycling in ecological communities. The difficulty of raising detritivorous land snails in captivity (Molloy, 1995; Rundell & Cowie, 2003) suggests that many species have dietary preferences. The suite of microbial species, particularly fungi, on which snails are feeding is just beginning to be discovered (O’Rorke et al., 2016). Increasing our knowledge of the specific diets of detritivorous snails increases our ability to raise these species in captivity, which will ultimately improve our knowledge of their biology. This is particularly important for improving the conservation prospects of endangered detritivorous snails, for which successful captive support can be critical for their survival.

The need for such captive breeding is likely to increase since, among animal species, nonmarine molluscs are the most threatened with extinction (Régnier, Fontaine & Bouchet, 2009). A large proportion of these are rare or narrow-range endemics (Lydeard et al., 2004), for which stochastic natural events (e.g. rockslides) or imminent human development may necessitate intervention *ex situ* to ensure their survival (Kobayashi & Hadfield, 1996). Some of the most imperilled snails are those restricted to freshwater springs or waterfalls (Lydeard et al., 2004; Perez et al., 2005) and these include succineids (e.g. *Succinea garrettiana*, a potentially extinct species known from Rainbow Falls, Hawai‘i; Cowie, Evenhuis & Christensen, 1995; Rundell, Holland & Cowie, 2004).

Captive breeding to augment wild populations or to provide backup populations in the case of stochastic extinction has proved useful in vertebrates (Bowkett, 2009; Conde et al., 2011), but is currently less common in terrestrial invertebrates, for which insects
are the primary models (e.g. Honan, 2008; Webb, 2010). The best-known captive breeding programmes of land snails have been focused on the mostly tree-dwelling tropical Pacific island partulids (Tonge & Bloxam, 1991) and achatinellines (Kobayashi & Hadfield, 1996). These precious few captive successes can be helpful for models for initiating a new snail captive-breeding programme. However these model systems can be less effective when the life history, habitat and diets of the target species diverge from those of the model species. For example, in contrast to our target species, partulids and achatinellines are tropical, slow-growing, live many years, give live birth to few young and primarily glean fungi from certain tropical trees and other native plants (Murray, Johnson & Clarke, 1982; Hadfield, 1986; Kobayashi & Hadfield, 1996; Gouveia, 2011).

The Chittenango ovate amber snail Novisuccinea chittenangoensis (Pilsbry, 1908) (Succinidae) is known only from a single population in the spray zone on one side of a waterfall at Chittenango Falls State Park (Madison County, NY). It lives within the leaf litter or on decaying emergent vegetation and limestone rocks, but its diet is poorly known. Novisuccinea chittenangoensis is federally listed as threatened and is endangered in NY (New York State Department of Environmental Conservation, NYSDEC). This site lies in a protected park with suitable habitat, so population augmentation and backup through captive management were prioritized over additional habitat conservation (United States Fish and Wildlife Service (USFWS), 2006). This strategy was considered particularly suitable because a 2006 roadside had destroyed a large portion of the N. chittenangoensis habitat, resulting in a 59% population decrease, from an estimated 784 (± 38) animals in 2005 to 322 (± 29) in 2008 (USFWS, 2012).

Because of the small number of snails remaining, bringing snails into captivity could be harmful to an already imperiled population, especially given limited knowledge on N. chittenangoensis husbandry. Although a previous captive breeding attempt resulted in reproduction, many of the hatchlings died before reaching adult size (Molloy, 1995). Captive-grown shells exhibited irregularities such as ridges and cracks, contrasting with the smooth shells of wild N. chittenangoensis, indicating that the captive diet was likely inadequate (E. Sullivan & J. Wyatt, personal communication). Proper diet is critical for the long-term success of captive populations of wild animals (Dierenfeld, 1997), including invertebrates (De Voe, 2009). We therefore sought to test new captive diets, including litter from different plant species and relevant habitat conditions, on an ecologically similar conchid species in order to reduce potential harm to N. chittenangoensis and to increase the possibility of establishing a captive population. Observations made on feeding, general health and behaviour with the surrogate were an important first step towards successful maintenance of N. chittenangoensis. The surrogate was Succinea putris (Linnaeus, 1758) and is an invasive European land snail that is short-lived (1–2 yr) and produces clusters of eggs, mirroring the relatively short lifespan (2.5 yr) and reproductive mode of N. chittenangoensis. This surrogate approach had proved successful in understanding achatinelline diets (O’Rorke et al., 2016). We selected S. putris as a surrogate since it is present in relatively large numbers and thus can be easily collected. Succinea putris also co-occurs with N. chittenangoensis in its habitat (Campbell et al., 2015), which initially suggested to us that there is a likelihood of dietary overlap between the two. An additional species, S. ovalis, is native to the area near the Chittenango Falls, but is not found within the habitat of N. chittenangoensis. In searches performed in nearby areas, 5 h of searching yielded only ten S. ovalis individuals. Although S. ovalis population numbers are not known, we decided not to use this species as the surrogate, in case numbers were inadequate for experimentation.

Initial observations of ‘normal’ health and behaviour of S. putris (i.e. ‘wild-like’ activity level, feeding, vibrancy or contrast of colours of body visible through shell), gave us a baseline of ‘normal’ features with which we could compare N. chittenangoensis, particularly when we first brought it into captivity. Because these first N. chittenangoensis captives initially failed to meet the baseline ‘normal’ standards, this gave us an early indication that conditions might not be suitable. Following an initial failure of captive establishment, we then refined the captive diet using observations of feeding and growth on a single N. chittenangoensis, followed by leaf-litter feeding trials of additional captive-bred individuals. Such close observations of few individuals proved effective in establishing captive breeding in the endangered Lord Howe Island stick insect (Honan, 2008).

MATERIAL AND METHODS

Initial feeding trials of surrogate species Succinea putris

Over 200 S. putris were captured at Chittenango Falls State Park on 14 September 2013, taken into captivity and reared on a common invertebrate zoo diet of romaine lettuce, fish food and calcium carbonate (see Supplementary Material for details of rearing methods). After wild-caught adults were found to suffer high mortality on this diet, a variety of other food items, including wild-collected leaf litter were placed in the terrariums and kept moist (Table 1). Leaf litter used in the initial diet trial was collected in December 2013 at Chittenango Falls along riparian zones where S. putris was commonly found. Leaf litter was then spread out and allowed to dry at room temperature for at least 2 weeks to keep leaves in their present state of decomposition, following which they could be stored for up to a year before rehydration and use (Supplementary Material). We also attempted to culture fungi from wild N. chittenangoensis substrates and N. chittenangoensis faeces on plates of potato dextrose agar (Kobayashi & Hadfield, 1996). Although little if any fungus grew, we still offered the agar to S. putris. Each week when all S. putris snails, including juveniles and eggs, were removed from terraria and counted, and leaf species and decomposition state were recorded. F2 snails were then removed for feeding trials.

S. putris feeding trials and data analyses

Survival was found to improve when S. putris hatchlings were raised with leaf litter, so F2 hatchlings were initially raised (for 2 months) on leaf litter and 0.25 ml calcium carbonate powder sprinkled evenly onto paper towel and food. Feeding trials were then undertaken to determine which diet was optimal for growth on plates of potato dextrose agar (Kobayashi & Hadfield, 1996). Although little if any fungus grew, we still offered the agar to S. putris. Each week when all S. putris snails, including juveniles and eggs, were removed from terraria and counted, and leaf species and decomposition state were recorded. F2 snails were then removed for feeding trials.

Wild Novisuccinea chittenangoensis acquisition

Capture of a limited number of N. chittenangoensis individuals, and their maintenance in captivity, were permitted through the USFWS, NYSDEC (permit no. 141) and New York State Office
Table 1. Food items offered to captive *Succinea putris* and *Novisuccinea chittenangoensis* and their feeding preferences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Type of food offered</th>
<th><em>N. chittenangoensis/S. putris</em> preferences and time of collection of litter (only shown for some leaf species)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer negundo</td>
<td>Boxelder</td>
<td>Dead leaves, pink to white</td>
<td>Collected in October and November.</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>Norway maple</td>
<td>Leaves, sun-bleached</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Acer saccharinum</td>
<td>Silver maple</td>
<td>Dead leaves, dark brown</td>
<td>Not preferred, but nibbled occasionally. Very little eaten.</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>Sugar maple</td>
<td>Dead leaves, light tan-white, top layer sun-bleached on both sides, thin, non-waxy</td>
<td>Moderately preferred. Green and tan to red leaves not eaten</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>Red maple</td>
<td>Dead leaves, collected early summer</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Agaricus bisporus</td>
<td>White mushroom</td>
<td>Sliced</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Avena sativa</td>
<td>Oats</td>
<td>Organic oat flour mixed with water from the waterfall, paste spread on sides of terrarium</td>
<td>Moderately preferred (quickly gets mouldy)</td>
</tr>
<tr>
<td>Beta vulgaris</td>
<td>Swiss chard</td>
<td>Dark green</td>
<td>Very little eaten</td>
</tr>
<tr>
<td>Brassica oleracea</td>
<td>Collard greens</td>
<td>Dark green</td>
<td>Very little eaten</td>
</tr>
<tr>
<td>Bryophyta</td>
<td>Moss</td>
<td>Green</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Carya cordiformis</td>
<td>Bitternut hickory</td>
<td>Dead leaves, brown</td>
<td>Moderately preferred</td>
</tr>
<tr>
<td>Celtis occidentalis</td>
<td>Hackberry</td>
<td>Dead leaves, brown</td>
<td>Low to moderately preferred</td>
</tr>
<tr>
<td><em>Cucumis sativus</em></td>
<td>Cucumber</td>
<td>Sliced</td>
<td><em>Not eaten (rotted quickly)</em></td>
</tr>
<tr>
<td>Daucus carota</td>
<td>Carrot</td>
<td>Shavings</td>
<td>Not preferred. Collected late October to mid-November. Very lightly misted leaves eaten more readily. Dry or soaked leaves not eaten. Green leaves not eaten</td>
</tr>
<tr>
<td>Eutrochium spp.</td>
<td>Joe pye weed (purple flowers)</td>
<td>Decaying, brown leaves, pulled off base of stem</td>
<td></td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>Beech</td>
<td>Dead leaves, collected early summer</td>
<td>Not eaten</td>
</tr>
<tr>
<td><em>Fungi</em></td>
<td></td>
<td>Wild-collected fungi from <em>N. chittenangoensis</em> substrates and faeces</td>
<td><em>Not preferred</em></td>
</tr>
<tr>
<td>Ipomoea batatas</td>
<td>Sweet potato</td>
<td>Sliced</td>
<td></td>
</tr>
<tr>
<td>Juglans regia</td>
<td>English walnut (non-native)</td>
<td>Dead leaves, brown</td>
<td>Highly preferred in right stage of decomposition</td>
</tr>
<tr>
<td>Lactuca sativa</td>
<td>Spring mix lettuce</td>
<td>Fresh (organic)</td>
<td>Not preferred</td>
</tr>
<tr>
<td>Lactuca sativa var.</td>
<td>Romaine lettuce</td>
<td>Dark green leaves</td>
<td>Eaten only when reproducing</td>
</tr>
<tr>
<td>longifolia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Malus domestica</td>
<td>Apple</td>
<td>Cut in slices</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Prunus spp.</td>
<td>Cherry</td>
<td>Dead leaves, transparent, thin, light tan</td>
<td></td>
</tr>
<tr>
<td>Quercus spp.</td>
<td>Oak</td>
<td>Dead leaves, dark brown to black, not waxy, thin</td>
<td>Collectively in March. Highly preferred.</td>
</tr>
<tr>
<td>Spinacia oleracea</td>
<td>Spinach</td>
<td>Blanched or raw</td>
<td>Not eaten</td>
</tr>
<tr>
<td>Tetramin fish food</td>
<td>Commercial fish flake food</td>
<td>Flakes</td>
<td>Moderately preferred. Eaten when thinly sprinkled onto romaine lettuce and lightly misted.</td>
</tr>
<tr>
<td>Tilia americana</td>
<td>Basswood</td>
<td>Dead leaves, light tan, thin</td>
<td>Collectively in December. Low preference of light, thin leaves. Darkly coloured or pubescent leaves not preferred</td>
</tr>
<tr>
<td>Trifolium spp.</td>
<td>Clover</td>
<td>Fresh</td>
<td>Not preferred. Nibbled occasionally</td>
</tr>
<tr>
<td>Triticum aestivum</td>
<td>Wheat grass</td>
<td>Powder</td>
<td>Moderately preferred (digestion questionable, green faeces)</td>
</tr>
<tr>
<td><em>Vitis spp.</em></td>
<td>Grapes</td>
<td>Cut in half</td>
<td>*Not eaten</td>
</tr>
</tbody>
</table>

Asterisks indicate leaf species offered only to *S. putris* and associated details.
of Parks, Recreation and Historic Preservation (NYSOPRHP). Ten *Novisuccinea chittenangoensis* were collected on 7 August 2014 and kept as described (Supplementary Material S1). *Novisuccinea chittenangoensis* individuals were fed a variety of diets, including a ‘partulid paste’ (Supplementary Material; Tonge & Bloxam, 1991; Gouveia, 2011). Snails that stopped feeding were returned to the wild on 3 September 2014, following tagging with bee tags (The Bee Works, Oro-Medonte, Ontario). Comparisons with previous observations of ‘normal’ *S. putris* behaviour enabled us to assess qualitatively the health of these ten individuals and to release them into the wild to prevent potential harm.

One month before the release, in August 2014, during the collection of vegetation for feeding *N. chittenangoensis*, we accidentally obtained a single 4 mm *N. chittenangoensis* juvenile as ‘by-catch’ from the *N. chittenangoensis* habitat. This single snail was tagged ‘G64’ (when it reached 9 mm) and was maintained using the described conditions (Supplementary Material), except for diet offered. G64 was presented with the foods described in Table 1. Observations of feeding and behaviour were recorded daily. New food items or types of leaf litter (i.e. tree species) were offered when the current food offered was not consumed. All food items consumed were continuously provided in the terrarium and therefore available during trials of other food items. Growth was measured as SL every 1–4 days.

Because G64 was growing, it was deemed safe to capture two more wild *N. chittenangoensis* (W10, W11) on 21 May 2015; the same methods were used for transportation, terrarium setup and care, except for leaf litter offered (Supplementary Material). We recorded growth, number of egg masses, number of eggs, number of hatchlings and hatching survival. F1 hatchlings were used in the subsequent feeding study, which was focused on identifying optimal diet among different wild leaf litter species.

*N. chittenangoensis* leaf litter preference

To quantify the preference of *N. chittenangoensis* for individual leaf species in the litter, we performed a set of feeding trials each lasting for 1 week, with multiple F1 offspring. These were offered selected leaf species that were found in litter adjacent to and within *N. chittenangoensis* habitat and for which G64 had shown a preference (Fig. 1). To reduce potential mortality resulting from snails being housed with an inedible litter, leaf litter species were grouped together within each terrarium to determine preferences (Supplementary Material). To determine which species of leaves were most consumed, each leaf was weighed before and after introduction to terraria. Leaf litter (dead, not green) species tested were: cherry (*Prunus virginiana*), divided into ‘thick cherry’ (light not visible through leaf) and thin cherry (translucent leaves); boxelder (*Acer negundo*), collected in October–November; sun-bleached hackberry (* Celtis occidentalis*); red oak (*Quercus spp.*) and sun-bleached sugar maple (*Acer saccharum*), collected in spring and summer. Species and types of leaves were weighed dry and recorded separately, then sets of multiple leaf species were grouped together within each snail terrarium, misted with stream water and introduced to the snails. This was repeated for 12 different terraria, each terrarium housing 8–30 hatching snails. The control group of leaves was saturated with water but was isolated from snails in order to obtain natural decomposition rates of each leaf species. After one week, leaves were separated from snails and air dried at room temperature for 3 weeks. Each leaf species was then weighed again. Differences in leaf weights were calculated and weight loss via decomposition was corrected for using the control. Descriptive statistics for leaf litter consumption were compiled (Fig. 1). Results of feeding trials dictated subsequent foods used for *N. chittenangoensis* rearing. Snails were then measured at intervals over a period of 5 months.

**RESULTS**

Preliminary study of surrogate species *Succinea putris*

Over the first 3 months of maintaining *S. putris* on the romaine-lettuce-based diet, mortality increased each month with 4, 15 and 34 snails dying in September, October and November 2013, respectively. The mortality of *S. putris* decreased by 85% on the mixed diet of leaf litter (mostly sugar maple) and romaine lettuce, compared with a diet of solely romaine lettuce, and only 6, 9, 4 and 5 snails died each month from December to March, respectively. In the absence of leaf litter, many snails crawled up to the top of the terrarium and became inactive or aestivated. With the addition of leaf litter, snails stayed active and within the leaves. Once leaf litter was introduced, reproduction occurred, with 100% of eggs hatching. F1 hatching survival was 100% during the first 2 weeks after hatching.

Rearing *S. putris* hatchlings on romaine lettuce compared with leaf litter

The mean SL of *S. putris* fed on leaf litter (6.70 mm; *N* = 61) for 6 weeks was significantly higher (*P* < 0.001) than that of snails fed solely on romaine lettuce (5.32 mm; *N* = 45) (Fig. 2). The mortality rate was greater on the romaine lettuce diet (4/45 snails died from February–March) compared with leaf litter (2/61 snails died from April–June). While reproduction started earlier (16 March 2014) in snails fed leaf litter than in those fed romaine lettuce (30 March 2014), the total number of eggs laid by the former (*N* = 352) were fewer than the latter (*N* = 465).

Diet of *S. putris*

*Succinea putris* showed a preference for sugar maple, basswood (*Tilia americana*), boxelder and English walnut (*Juglans regia*). However, if any of these species were not decomposed enough or still green, they were not consumed. The potato dextrose agar was partially consumed—resulting in clear gel-like facces—but did not...
elicit return feedings. The occurrence or lack of return feeding was also useful in determining *Novisuccinea chittenangoensis* preferences.

**Growth, food preferences and reproduction of N. chittenangoensis**

Between mid–late September 2014, growth of individual G64 continued despite a suboptimal diet (Fig. 3). This occurred possibly due to food consumption in the wild before capture, resulting in a delayed response in shell growth (Fig. 3A). There was zero growth from early October to late November. The diet at this time consisted of silver maple, basswood, live Joe pye weed (*Eutrochium* spp.), non-sun-bleached sugar maple, live watercress (*Nasturtium officinale*), burdock leaf (*Arctium lappa*) and boxelder with red to pink leaf colouration (Fig. 3B). Growth resumed when white to light pink boxelder collected in late October and November, cherry collected in November and yellowing leaves of watercress were offered (Fig. 3C). From late February to early June, the highest growth (1 mm/week) occurred; the diet at this time consisted primarily of cherry but included white boxelder, sun-bleached sugar maple collected in March and April, and red oak (Fig. 3D). Mating occurred on 27 May 2015 as soon as G64 and W10 (a new founder) were brought together. Growth of G64 slowed when it was reproducively active and on approaching its maximum SL (22 mm) (Fig. 3E). The first egg mass of about 60 eggs was laid by G64 7 days after mating on 3 June 2015. In two months (3 June to 31 July 2015), three individuals of *N. chittenangoensis* (G64, W10, W11) produced 669 eggs from 19 egg masses, of which 632 eggs hatched. The mean number of eggs in each mass was $35 \pm 4$ ($N = 19$) for *N. chittenangoensis*, compared with $41 \pm 2$ ($N = 46$) for *S. putris*.

**Leaf litter preference trials and subsequent captive diet of N. chittenangoensis**

*Novisuccinea chittenangoensis* consumed leaves from the following species: sun-bleached sugar maple collected in spring and summer, boxelder collected in October–November, sun-bleached hackberry, thin cherry and red oak. Multiple *N. chittenangoensis* trials demonstrated that thin cherry leaf litter was consumed significantly more than the other leaf species offered. There was no significant difference in consumption between sugar maple leaves collected in spring and in summer (Fig. 1).

**Successful rearing of N. chittenangoensis and release into the wild**

We performed the first ever release of captive-bred snails ($N = 270$) back into their wild habitat on 1 October 2015 (Supplementary Material). After 16 months over 200 *N. chittenangoensis* hatched and raised in captivity were still thriving in the laboratory, the majority of which had a smooth shell with no cracks or ridges. In total these snails laid more than 25,000 eggs.
DISCUSSION

Closely studied captive animals can help to address gaps in the knowledge of the life history, husbandry and management of threatened species (e.g. achatinelline snails, Kobayashi & Hadfield, 1996; cheetah, Bertsching, Melzer & Van Dyk, 2000). Such knowledge is lacking for most terrestrial invertebrates because so little is known of their captive requirements, particularly diet. Our successful captive colony of Nosiuscinea chittenanesis resulted from a stepwise approach of behavioural observation and dietary experimentation, first using the co-occurring confallal species Sucinea putris as a surrogate, followed by careful observation of a single N. chittenanesis individual, and culminating with leaf-litter feeding experiments on additional N. chittenanensis. There was minimal impact on the wild population. The captive N. chittenanensis colony has grown considerably from August 2014 to the present and this has enabled the establishment of a second colony at a separate location (Rosamond Gifford Zoo, Syracuse, NY), as well as the release of 270 individuals into the wild. Our study represents a major advance on an earlier rearing attempt in which N. chittenanensis was raised on a diet of romaine lettuce (Molloy, 1995). There were four key differences between the results of our study (in 2015) and those of Molloy (1995). First, whereas the mean number of eggs/egg mass was 16.9 ± 2.03 in 1995, in 2015 it was 35 ± 3.95. Second, while hatching mortality in the first 2 weeks was c. 80% in 1995, in 2015 it was zero and, even after 3 months, mortality was very low (0.008%). Third, egg production was markedly greater in 2015. Whereas six founders produced 130 eggs (from 13 egg masses) over the course of a year in 1995, the three founders in 2015 yielded 669 eggs (from 19 egg masses) in just 2 months, with 94.4% of eggs hatching. Fourth, growth rates were greater in 2015. The average growth of snails was 0.29 mm/week in 1995, but in 2015 snails feeding on leaf litter grew an average of 1.00 mm/week (measured over 5 months). Our results suggest that diets of romaine lettuce and partulid 'paste' were not suitable for captive snails and retarded growth and activity. Wild-based leaf-litter diets of thin (translucent) cherry leaf litter collected in March and sun-bleached, weathered sugar maple leaves were consistently consumed and supported high growth, reproduction and survival of hatchlings. Although collecting this diet is labour-intensive, its components can be successfully dried and stored for over one year and then rehydrated (Supplementary Material).

Surprisingly few captive-reared snails are fed leaf litter; instead they are generally raised on lettuce, carrots, oats, fish food or other ‘clean’ or synthetic diets (Orstan, 2006). Successful captive colonies of tropical partulids are maintained on a dietary paste based on oatmeal, lettuce/grass pellets, trout pellets, vitamins and calcium carbonate (Supplementary Material; Tonge & Bloxam, 1991; Gouveia, 2011), despite living on a variety of native plants in the wild (Murray et al., 1982). In contrast, captive tropical achatinelline glean microbes, particularly fungi, from ‘ōh‘ia lehua (Metrosideros polymorpha) branches and other native Hawaiian plants, as well as agar-plated fungi dominated by Cladosporium sp. (also part of the wild diet), but will also consume the high-caloric potato dextrose agar itself, likened to ‘junk food’ (O’Rorke et al., 2016). Natural diets are more efficiently assimilated by snails than are cultivated plants (Mason, 1970; Richardson, 1975; Staikou & Lazaridou-Dimitriadou, 1989) and snails do exhibit feeding preferences (O’Rorke et al., 2016). As shown by our study, these preferences can include the state of leaf decomposition. The evidence suggests that captive diets closer to wild diets might enhance survival, growth and reproduction in captivity. However, we note that Achatinella mustelina fed a cultured fungi and agar-supplemented diet, in addition to wild food, grew twice as fast as on wild food alone (Kobayashi & Hadfield, 1996). Having supplemented the romaine lettuce diet with leaf litter in our study, we noticed that N. chittenanensis ingested romaine lettuce sprinkled with fish food flakes most when reproducing, which could explain why S. putris fed on the romaine lettuce diet laid more eggs than those fed on leaf litter only. We do not know why romaine lettuce is eaten during egg laying, but it could be that snails are seeking additional water or sugar.

Rather than focussing on individual nutritional components, we used a holistic approach incorporating nutrient and mineral supplements and multiple wild leaf litter species collected near the N. chittenanensis habitat (also frequented by S. putris). These leaves were likely to harbour microbial, particularly fungal communities (O’Rorke et al., 2016) preferred by N. chittenanensis. Mixed species of dead leaves were offered to provide variety in palatability and/or nutrients, consumption of which might be reflected in the leaf litter preferences of snails. Mixed decomposition states were provided as well, to gain insight on preferences (Table 1). Maps & Krull (1951) showed that leached sugar maple leaves were preferred to brown or thick sugar maple leaves by the snail Cionella lubrica, which was also true for N. chittenanensis. Both S. putris and N. chittenanensis avoided leaves with pubescent or waxy cuticles. Two common European species, Cornu aspersum and Capasa nemoralis, are also known to consume similar leaf species (Grime et al., 1996). Such similarities in snail food preferences suggest that other endangered snail-breeding programmes might benefit from our characterization of preferred leaf litter, despite the apparent dietary specificity of N. chittenanensis. The dietary preferences of snails could also be taken into consideration when managing vegetation within the habitats of threatened species.

An irony facing captive breeding programmes of rare animals is that the very thing that makes captive breeding a desirable conservation strategy (i.e. few animals left in the wild) is what inhibits optimization of captive conditions, particularly diet. With few wild individuals remaining, risk can be reduced by experimenting initially on a few individuals. Successful captive colonies of endangered Lord Howe Island stick insects were established based on husbandry knowledge obtained through close observation and monitoring of just two captive individuals (Honan, 2008). In the present study, we had the benefit of using an ecologically similar, related surrogate species for initial experimental and behavioural observations. This, combined with observation of single individuals of the target species, proved successful—and culminated in the establishment of a captive breeding colony. Such observational work has the added benefit of providing natural history information on the most diverse, yet threatened animals on Earth—terrestrial invertebrates.

SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Molluscan Studies online

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