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Coexistence of the endangered, endemic Chittenango ovate amber snail (*Novisuccinea chittenangoensis*) and a non-native competitor

Steven P. Campbell · Jacqueline L. Frair · James P. Gibbs · Rebecca J. Rundell

Abstract Distinguishing between non-native species that coexist with native species and those that threaten their persistence is critical for conservation and management. We investigated this distinction for a non-native terrestrial snail (*Succinea* sp.) (Sp. B) that occurs with the closely-related Chittenango ovate amber snail (*Novisuccinea chittenangoensis*) (COAS), an endangered species that is restricted to a single, known site. In 2008 and 2009, we performed ex situ competition experiments to examine the effects of density and body size of Sp. B on growth and mortality of COAS. We also conducted mark-recapture surveys from 2002 to 2009 to document trends of the in situ population of COAS and to identify spatio-temporal factors that may mitigate any competitive interactions between COAS and Sp. B. We observed lower growth rates and higher mortality rates of COAS at higher densities and larger sizes of Sp. B, indicating that the species compete. Nevertheless, population trends indicated that COAS population size was fluctuating but not in decline, and the spatial distribution, phenology, and size structure of each species indicated that there were enough mitigating factors to allow COAS to persist in the presence of Sp. B. Collectively, these results suggest that temporal niche partitioning resulting from a trade-off between growth and longevity of each species may enable their coexistence. Our results also suggest that control of Sp. B is unnecessary and, more generally, underscore the importance of conducting research aimed at understanding the effects of non-native species before instituting long-term, costly, and potentially unnecessary control measures.

Keywords Non-native species · Competition · Coexistence · Succineid snails · Endangered species · Endemic species

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Introduction

The contribution of non-native species to worldwide losses of biodiversity is second only to that of human-caused habitat loss and degradation (Wilcove et al. 1998; Pimental 2002). Non-native species have been estimated to account for the declines of 42 % of the species considered threatened and endangered in the United States (Nature Conservancy 1996; Wilcove et al. 1998) and 80 % of endangered species elsewhere

(Armstrong 1995). Despite the serious threat that non-native species collectively pose to biodiversity, 80–90 % of established non-native species around the world have minimal detectable effects on native biota and ecosystem functioning (Simberloff 1981; Williamson 1996). As such, distinguishing between non-native species causing damage (e.g., those driving native species to such low numbers that they are at risk of extinction) from those with negligible effects (e.g., those that can coexist with native species) is an important area of research for ecology and management (Shackelford et al. 2013).

Identifying non-native species that are highly destructive over short time scales is likely to be relatively straightforward through simple observational studies of abundance or distribution; however, when the negative effects of non-native species are more subtle and manifest over longer time scales (e.g., a protracted decline from exploitative competition) or when a non-native species takes many years to become a threat, it will be more difficult to distinguish these species from those that are innocuous. In these cases, more detailed information about each species demography, intra- and interspecific interactions, and habitat use is needed to determine the long-term consequences of the non-native species (Sakai et al. 2001). In particular, understanding mechanisms by which non-native species negatively affect or coexist with native species will help elucidate the relative risk posed by non-native species and facilitate more targeted and effective management actions (Byers et al. 2002).

Understanding the effects of non-native species is particularly important when narrowly endemic species are potentially affected because their high degree of ecological specialization and restricted ranges may make them especially susceptible to extinction (Drury 1980; Gaston and Kunin 1997). If endemic species are also weak competitors (Walck et al. 1999; Lloyd et al. 2002; Moora and Jõgar 2006), management actions will invariably be necessary because inaction in the face of negative effects can quickly threaten a species' persistence. However, narrowly endemic species may not always be vulnerable to non-native species; their level of specialization and evolved ability to persist in a limited geographic range may make endemic species good competitors and relatively resistant to the effects of non-native species (Rabinowitz et al. 1984; Snyder et al. 1994; Osunkoya and Swanborough 2001). In this case, management action to protect the endemic species from non-native competitors may be unnecessary.

In this paper, we examine the interactions between two snail species to assess their potential for coexistence: the Chittenango ovate amber snail (*Novisuccinea chittenangoensis*) (COAS), an endangered species that is endemic to the spray-zone of a single waterfall, and a closely-related non-native succineid snail (*Succinea* sp.) (Sp. B) that has invaded COAS's range. These two species have occurred together at the waterfall for over 30 years, but it is unknown if Sp. B is causing a protracted decline of COAS or if Sp. B is having a negligible effect on the persistence of COAS. To distinguish between these possibilities, we established ex situ experimental model systems to quantify the strength of competition between these two species, and we conducted population monitoring to document trends in the population size of COAS and to identify spatio-temporal factors that may mitigate the competitive interactions between these species.

Methods

Study system

The Chittenango ovate amber snail is a terrestrial succineid snail that is endemic to the cool, partially sunlit areas of herbaceous growth within the spray zone of Chittenango Falls (N 42.97869/W 75.84161) in central New York State in the United States. Due to its extremely limited range and small population size, COAS is listed as threatened by the United States Fish and Wildlife Service and as endangered by New York State (USFWS 2006). Because the entire range of COAS occurs within Chittenango Falls State Park, the snail and its habitat are currently protected from anthropogenic sources of loss, with the possible exception of human trampling, which remains a concern. Likewise, there are currently no imminent man-made threats with regard to upstream changes in water quantity or quality. However, natural threats exist in the form of rockslides that can bury habitat and periodic floods that can wash away vegetation in the spray zone where most COAS are found.

Chittenango ovate amber snails mate from May–July and oviposits clusters of 8–14 eggs (Molloy and

Norton [1993]) from June–July. Young snails hatch in 2–3 weeks when they are ∼2 mm in shell length and they are thought to reach maturity in 5–8 months (i.e., the spring following hatching; Grimm [1981]). Snails grow ∼10 mm per year and reach ∼21 mm length before they die, completing their life span of about 2.5 years (USFWS [2006]). They are thought to feed on microflora obtained from the surface of vegetation and other substrates and must obtain high levels of calcium carbonate from their environment for shell formation (USFWS [2006]).

Much less is known about Sp. B. It is thought to have been introduced from Europe (Hubricht [1985]) and to have arrived at Chittenango Falls by 1981. Initial attempts by Hoagland and Davis ([1987]) to identify the species, which they referred to as *Succinea* Sp. B, were unsuccessful, but based on electrophoresis, shell morphology, and internal anatomy they considered it to be closely related to, but distinct from, species of the *Succinea putris* (Linnaeus, 1758) complex in Europe. Due to the unresolved taxonomy of the species, USFWS and New York State conservation agencies adopted the moniker "Sp. B". To help with the biological interpretation of results from the present study, we attempted to identify Sp. B using a barcoding approach, which has shown promise for some land snails (e.g., using cytochrome oxidase I (COI) mitochondrial sequence data; Davison et al. [2009]). Because there were relatively few sequences from commonly introduced succineid species available on GenBank, we compared our Sp. B COI sequence data (GenBank Accession Number KM245556) with an unpublished alignment of 209 succineid COI sequences using MacClade (Maddison and Maddison [2001]) for alignment visualization, ClustalX (Thompson et al. [1997]) for alignment, and PAUP* (Swofford [2001]) for calculating genetic distances. Most of the sequences in the alignment were from introduced "tramp" succineid species obtained by the Oregon Department of Agriculture (B Holland, unpublished data), and thus represented a broad sampling of North America's introduced succineids, many of which have arrived through the gardening trade. Sp. B most closely aligned with *S. putris* collected from the Netherlands and differed from that COI sequence by only 1.8 %, which is within the range of intraspecific differences in the Succineidae (Rundell et al. [2004]). Nevertheless, given the taxonomic confusion present within the succineids

and specifically within *S. putris*, which may be a cryptic species complex, we continue to refer to the non-native snail in our study as Sp. B, pending detailed taxonomic work and comparisons with museum type material, both of which will be required for a full understanding of *S. putris*.

Following the introduction of Sp. B to Chittenango Falls around 1981, its population size at the falls increased rapidly from ∼300 snails in 1982 to >3000 in 1984 (USFWS [2006]). It is now the most abundant snail in the area, and based on its numerical dominance, Sp. B has been hypothesized to be an important limiting factor for COAS (USFWS [2006]). A comprehensive USFWS technical assessment suggests that other sympatric snail species are relatively rare within the emergent vegetation and rock habitat used by COAS and are unlikely to be having a significant effect on COAS (USFWS [2006]).

Although COAS and Sp. B look similar, the two species can be distinguished in the field using external morphological features (e.g., COAS has a deep, clearly defined suture on the whorls of the shell and a dark spot on the dorsal surface of the foot). These differences have been corroborated by mitochondrial and nuclear DNA sequences of COAS and Sp. B, which indicated large differences between the species and an absence of hybridization (T King, unpublished data).

We examined the interactions and population ecology of COAS and Sp. B within a 15 × 3 m area that extends eastward along the rock ledge away from the falls. While some COAS can be found just above this portion of the rock ledge, the study area encompassed nearly the entire known range of COAS. The portion of the study area farthest from the falls is covered by rocky debris and the remainder of the area is dominated by annual and perennial herbaceous vegetation: *Impatiens* spp. and *Eupatorium purpureum* in the central portion and *Nasturtium officinale* in the portion closest to the falls (Appendix A of ESM).

Field methods

Competition experiments

We assessed the intra- and interspecific competitive effects of Sp. B on growth and mortality of snails in ex situ experimental enclosures. Enclosures were constructed from 24 13.2-L (12-quart) rectangular plastic

containers with locking tops that had their side, top, and bottom panels removed so that only the containers' frames remained. Each container was divided in half (17L × 25 W × 15D cm = 6,375 cm^3) and lined with mosquito netting, yielding a total of 48 experimental enclosures. Mosquito netting may have altered shade and moisture conditions in enclosures, but all enclosures should have been affected equally. We placed 12 enclosures (6 containers) each on four floating platforms near the base of the falls and irrigated the enclosures with water from the falls to mimic conditions encountered on the rock ledge (Appendix B of ESM). Before the start of an experiment, we added approximately 125 g (wet mass) of *Nasturtium officinale* (a widely available plant on which both species occurred) and a roughly fist-sized rock to each enclosure. This experimental model system was used to perform two competition experiments.

The first experiment quantified Sp. B and COAS growth and mortality under increasing densities of Sp. B (i.e., density competition experiment). We used a randomized complete block design in which 3 replicates of 4 density levels were randomly distributed on each of the four floating platforms. Treatment levels consisted of 1 COAS with 0, 10, 25, or 50 individuals of Sp. B, which spanned the natural ratios of COAS and Sp. B densities observed in situ. We only varied the densities of Sp. B because the rarity of COAS limited the number we could use in the experiment.

We populated the enclosures with 1,068 snails (48 COAS and 1020 Sp. B) over a two-day period (9 and 10 July 2008). Ten Sp. B and a single COAS were uniquely marked and placed in each enclosure with the appropriate number of unmarked snails, except for enclosures with no Sp. B, into which only a single marked COAS was added. Before marked snails were put in the enclosures, one person (S Campbell) measured the lengths of shells along their longest axis (i.e., apex of the spire to the anterior-most part of the shell) using digital calipers. A single-blind test of measurement variation using 10 snails ranging in shell length from 8 to 17 mm indicated an average difference of 0.09 mm (CV = 0.98 %) among 5 repeated measurements per snail.

Each enclosure remained in the experiment for 15 days. This duration represented a balance between allowing enough snail growth to result in measurable differences in shell lengths (i.e., differences that exceeded measurement error) and minimizing the amount of time COAS was retained ex situ. To determine the duration, we assessed snail growth 1 week after the initiation of the experiment. By this time significant differences among some of the treatments were already present, so we let potential differences accrue for one more week before stopping the experiment.

A second experiment investigated the interaction between body size and density of Sp. B. on the growth and mortality of both COAS and Sp. B (i.e., size × density competition experiment). In this experiment, there were five size × density treatment combinations allocated among the 48 enclosures: 1 COAS and 0 Sp. B served as a control in 8 enclosures, and 1 COAS with 10 small (6–10 mm) Sp. B, 50 small Sp. B, 10 large (>13 mm) Sp. B, or 50 large Sp. B occurred in 10 enclosures each. The average sizes of "small" ($\bar{x}$ = 8.5 mm, SD = 1.1 mm) and "large" ($\bar{x}$ = 14.5 mm, SD = 1.7 mm) snails used in the experiment were significantly different and showed little overlap in their distributions. We populated the enclosures with 1,248 snails (48 COAS, 600 small Sp. B, and 600 large Sp. B) on 16 and 17 July 2009. Snails were marked and measured and placed into enclosures in the same manner as the density competition experiment. Block effects from the density competition experiment were not significant, so we distributed treatments among the four platforms according to a completely randomized design. Each enclosure remained in the experiment for 14 days.

At the end of each experiment, the same person (S. Campbell) measured the length of surviving marked snails and we counted all of the dead snails in each enclosure. Snails that died during the experiment were not measured because they were unable to grow for the full time period. After measurements were completed, COAS were released back into the study area and Sp. B were euthanized.

Population surveys

We conducted mark-recapture surveys to estimate the population size of COAS between 2002–2005 and 2007–2009 and to examine the phenology, size structure and spatial distribution of both species. Surveys were not conducted in 2006 due to researcher safety concerns associated with a major rockslide on site. Surveys occurred between 4 May and 15 October of each year and were conducted weekly for 16 weeks

in 2002 and for 10 weeks in 2007 and every 2 weeks for 20–24 weeks in 2003–2005 and 2008–2009 (Appendix C of ESM). The survey area occurred along a 15-m transect that extended east from the falls into the talus slope (Appendix A of ESM); the area was divided into 1-m wide blocks that ran perpendicular to the transect, with each block arbitrarily divided into lower, middle, and upper zones (based on terrain). Each block was searched for 15 min (5 min per zone). Surveys were started $\sim$9:30 h and continued until all blocks were sampled.

All snails encountered during a survey were placed in containers labeled with the respective block and zone. After the survey, snails were separated by species and tallied. We measured the shell length of each COAS and for those >8.5 mm we affixed a unique color-coded and numbered identifier (bee tags; www.beeworks. com) to the ventral surface of the shell's spire using a drop of cyanoacrylate gel adhesive. In 2008–2009, we also recorded shell lengths of Sp. B. Snails that could not be reliably identified to species, typically because they were too small (<5 mm), were measured and counted as unknown. All COAS and unknown snails were returned to the zones from which they were removed and Sp. B were euthanized.

Data analysis

Competition experiments

For each experiment, we compared growth rates (mm growth per duration of experiment [$\sim$2 weeks]) and mortality rates among treatment levels. (Although snail growth varies with body size, standardizing growth by initial size yielded results that were comparable to unadjusted growth rates, so we present the latter metric for ease of interpretation.) Because there was only one COAS per enclosure, growth rates for COAS were based on the surviving individual in each enclosure and mortality rate was calculated as the percentage of enclosures for a given treatment level in which a snail died (i.e., there was only one measure per treatment level). In contrast, for Sp. B, we calculated growth rate for each enclosure as the average growth of surviving marked individuals and mortality rate as the percentage of individuals (marked and unmarked) that died within a given enclosure.

For the density competition experiments, we used one-way ANOVAs to compare COAS growth rates

among the four density levels of Sp. B (1 COAS and 0, 10, 25, or 50 Sp. B) and to compare Sp. B growth and mortality rates among the three density levels where they were present. For the size × density competition experiment, we used a two-way ANOVA to examine the main and interactive effects of size and density of Sp. B on growth and mortality of Sp. B. For COAS, the additional control treatment (1 COAS and 0 Sp. B) created an incomplete factorial design. Consequently, we considered the five treatment combinations as levels of a one-way ANOVA and used contrasts to test for the main and interactive effects of size and density. Where variances were unequal we used the Welch's variance-weighted one-way ANOVA (SAS Institute Inc. 2008) and when ANOVAs indicated a significant difference ($\alpha < 0.05$) among more than two means we identified pair-wise differences using Fisher's LSD test.

Population surveys

We used Jolly–Seber models for open populations to estimate COAS population size each year. The population was assumed to be open because births, deaths, and movements between the sampled area of rock ledge and the part of the ledge that we could not readily sample were all possible during the surveys. We used the POPAN formulation of the Jolly–Seber model in Program MARK (White and Burnham 1999). Under this formulation, model parameters include apparent survival between occasions i and $i + 1$ (ϕ_i), probability of capture during sampling occasion i (p_i), and the probability of an animal entering the population between occasions i and $i + 1$ and surviving to occasion $i + 1$ (b_i) (Schwarz and Arnason 2008). Abundance (N) is derived from these parameters. For each year we built four a priori candidate models based on the combinations of p and ϕ being variable with time (t) or constant (.) and b being variable with time (i.e., $[p(t), \phi(t), b(t)]$, $[p(.), \phi(t), b(t)]$, $[p(t), \phi(.), b(t)]$, $[p(.), \phi(.), b(t)]$). Parameters were estimated via numerical likelihood and the best models were selected using the sample-size corrected AIC (AIC_c) or, when data were overdispersed, the quasi-likelihood adjusted AIC ($QAIC_c$). Before models were compared, we conducted goodness-of-fit tests on the most parameterized (i.e., saturated) models using the sub-module Release and adjusted the likelihood of the models if the data were overdispersed (i.e., if the variance inflation factor exceeded unity; Cooch and White 2008).

We also used the population survey data to graphically examine the phenology of the raw counts of COAS and Sp. B within each year, the distribution of snail sizes from the three earliest and three latest surveys in 2008 and 2009, and the spatial distribution of snail captures within the study area.

Results

Competition experiments

In the density competition experiment, the magnitude and trends of COAS and Sp. B growth rates were similar, with growth rates declining for both species at increasing densities of Sp. B (Fig. 1a). COAS growth rates with 0 and 10 Sp. B were not different. However, COAS growth rates were 73 and 83 % lower at densities of 25 and 50 Sp. B, respectively (Fig. 1a; Welch's ANOVA: $F_{3, 16.3} = 14.03$, $p < 0.01$). Growth rates of Sp. B showed no difference between treatments with densities of 10 and 25 conspecifics, but there was a 62 % reduction in growth rate at densities of 50 conspecifics (Fig. 1a; $F_{2, 30} = 10.71$, $p < 0.01$).

A total of seven COAS (14 %) died during the density competition experiment with a tendency for higher mortality at higher densities of Sp. B (Fig. 1b). Sp. B mortality rates did not differ with densities of conspecifics (ANOVA: $F_{2, 32} = 0.85$, $p = 0.44$); however, mortality rates at a given density were 1.3–5.5 times greater for Sp. B than COAS (Fig. 1b).

In the size × density competition experiment, COAS growth rates declined in the presence of both greater densities ($F_{1, 38} = 19.79$, $p < 0.01$) and larger sizes ($F_{1, 38} = 7.53$, $p < 0.01$) of Sp. B and the effects of Sp. B size were consistent across density treatments (i.e., there was no interaction between size and density). On average, large Sp. B depressed COAS growth rates (compared to small Sp. B) by 40 and 50 % at low and high densities, respectively (Fig. 2a). However, 50 small Sp. B had a similar effect on COAS growth rates as 10 large Sp. B. Growth rates of Sp. B were also lower at higher densities ($F_{1, 36} = 30.86$, $p < 0.01$) and larger sizes ($F_{1, 36} = 129.72$, $p < 0.01$) of conspecifics, and there was no interaction between density and size treatments. Large snails depressed the average growth rate of Sp. B by 56 and 75 % compared to small snails at low and high densities,
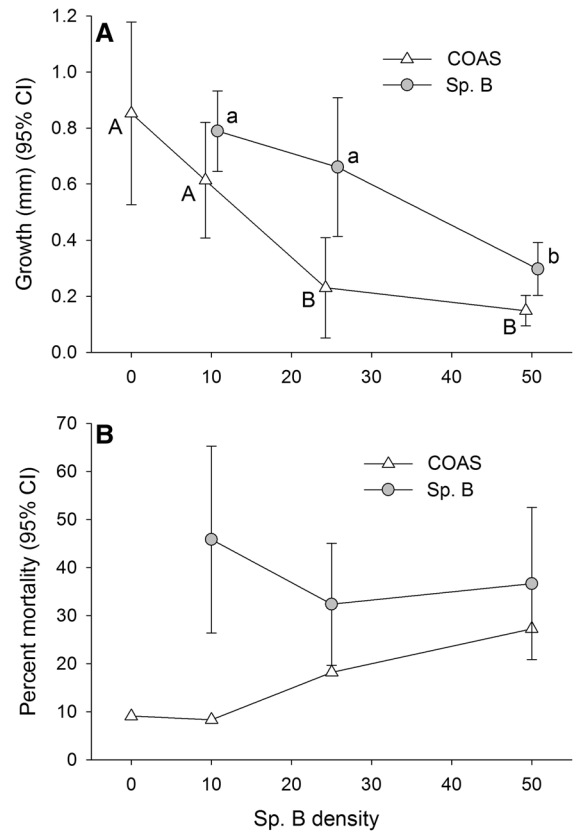

Fig. 1 Average growth (**a**) and percent mortality (**b**) of COAS and Sp. B at different densities of Sp. B. Growth of COAS is based on a single snail per enclosure and growth of Sp. B is based on the average of a maximum of 10 surviving snails per enclosure. Percent mortality of COAS is based on the percentage of enclosures in a treatment in which snails died and percent mortality of Sp. B represents the percentage of all snails that died in each enclosure. *Different uppercase* (COAS) and *lowercase* (Sp. B) *letters* indicate groups that are significantly different at α = 0.05. Note that some points are slightly offset from their actual values to prevent overlap of *error bars*

respectively (Fig. 2a). Growth rates of Sp. B were lower in treatments with 10 large snails than in treatments with 50 small snails. Although the growth rates of Sp. B and COAS followed similar patterns with respect to density and size, they differed in magnitude; Sp. B growth rates were 2.6-6.3 times greater on average than COAS growth rates (Fig. 2a).

Only four COAS died in the size × density competition experiment and there was no discernable pattern to their mortality (Fig. 2b). The intraspecific effects of Sp. B density on mortality rates were different when the population was comprised of large versus small individuals (density × size interaction:
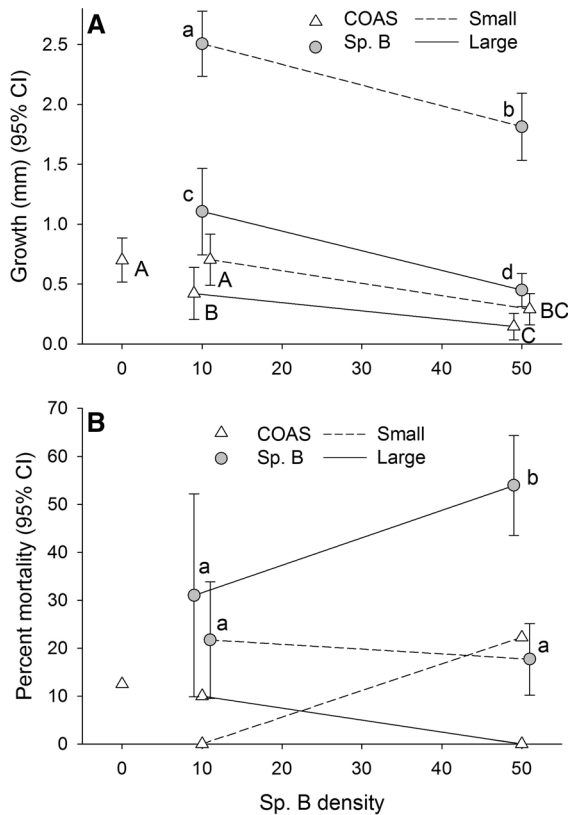
Fig. 2 Average growth (**a**) and percent mortality (**b**) of COAS and Sp. B at different combinations of size and density of Sp. B. Growth of COAS is based on a single snail per enclosure and growth of Sp. B is based on the average of a maximum of 10 surviving snails per enclosure. Percent mortality of COAS is based on the percentage of enclosures in a treatment in which snails died and percent mortality of Sp. B represents the percentage of all snails that died in each enclosure. *Different uppercase* (COAS) and *lowercase* (Sp. B) *letters* indicate groups that are significantly different at $\alpha = 0.05$. Note that some points are slightly offset from their actual values to prevent overlap of *error bars*

$F_{1,35} = 4.7$, $p = 0.04$). Mortality rates of Sp. B were similar in all treatments except for the treatment with 50 large Sp. B, which had higher mortality (Fig. 2b). In general, mortality rates of Sp. B were higher than those of COAS.

Population surveys

With the exception of a single survey year (2005), the best supported model for each year considered survival rates to be constant over the survey period (Table 1). In contrast, the probability of capture varied within four of the seven survey years. The best models indicate that

Table 1 COAS population estimates derived from the AIC_c- and $QAIC_c$-selected best models from 2002–2009

Year[a]	Best model[b]	Population estimate	SE
2002	$p(.), \phi(.), b(t)$	262.4	35.68
2003	$p(.), \phi(.), b(t)$	225.1	31.76
2004	$p(t), \phi(.), b(t)$	716.5	68.97
2005	$p(.), \phi(t), b(t)$	784.2	38.10
2007	$p(t), \phi(.), b(t)$	551.1	50.01
2008	$p(t), \phi(.), b(t)$	322.6	27.59
2009	$p(t), \phi(.), b(t)$	339.2	52.85

[a] In 2006, surveys were curtailed following a rock slide for safety reasons

[b] Model parameters include probability of capture (p), survival (ϕ), and probability of entering the population (b) that vary over sampling occasions within a year (t) or are constant (.)

COAS population size was lowest in 2003 at 225 snails, peaked in 2005 at 784 snails, declined in 2007, and stabilized around 330 snails in 2008 and 2009.

The phenology of each species of snail was relatively consistent among years (Fig. 3). Numbers of Sp. B in a survey peaked around mid-June and were lowest in mid-August before showing a smaller secondary peak in numbers in mid-September (Fig. 3b). This pattern corresponded with shifts in the size distribution of the population of Sp. B (Fig. 4b), such that early in the season most of the captured snails were large (>10 mm) and total counts were high, whereas late in the season most of the captured snails were small (<10 mm) and the total counts were low. In contrast, within each year the number of COAS collected fluctuated but remained more uniform and their size distributions remained fairly stable (Figs. 3a, 4a).

There were clear and consistent differences in the spatial distributions of COAS and Sp. B within the study area. Sp. B was more evenly distributed across this area, with a tendency in most years to occur closer to the falls than COAS, where conditions were wetter (Fig. 5b). In contrast, COAS tended to be concentrated around the center of its range (Block 8), with few snails occurring near the edge of its range (outside Blocks 3 and 13; Fig. 5a; Appendix D of ESM).

Discussion

Our study assessed the effects of a non-native snail on a highly range-restricted endemic snail that is
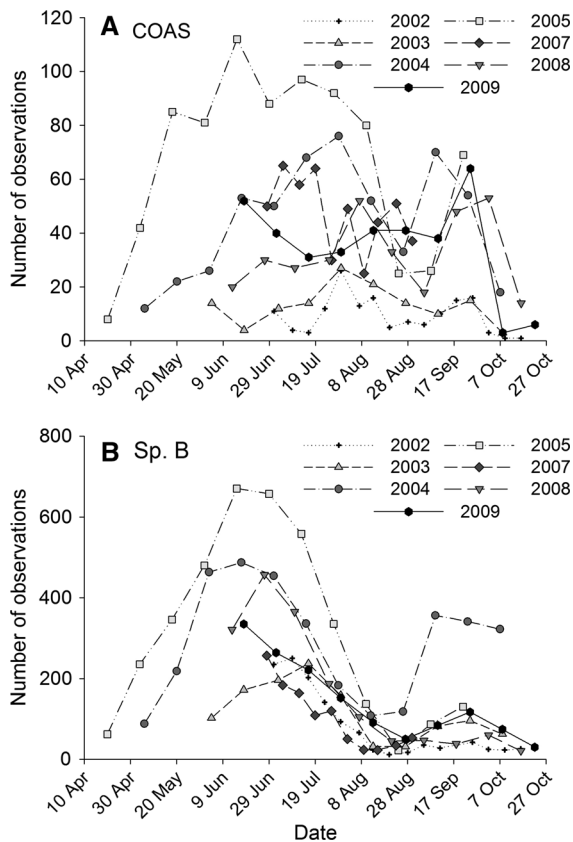
Fig. 3 Number of COAS and Sp. B collected in each mark-recapture survey in 2002–2005 and 2007–2009

Fig. 4 Size (shell length) frequencies of COAS and Sp. B from the first three and last three survey occasions in 2009

threatened with extinction. Collectively, the evidence from our competition experiments and our examination of population trends and life history patterns of COAS and Sp. B demonstrated that the introduction of a non-native competitor may not always result in the extirpation of threatened endemic species. However, the evidence was mixed. Our ex situ competition experiments indicated that these two species were competing, whereas our examination of population size, phenology, size structure, and spatial distributions indicated that there were enough mitigating factors to allow COAS to persist in the presence of Sp. B in situ.

Evidence for competition

Results from our competition experiments supported the contention that COAS and Sp. B are competitors (USFWS 2006). COAS had lower growth rates and higher mortality rates at higher densities and larger
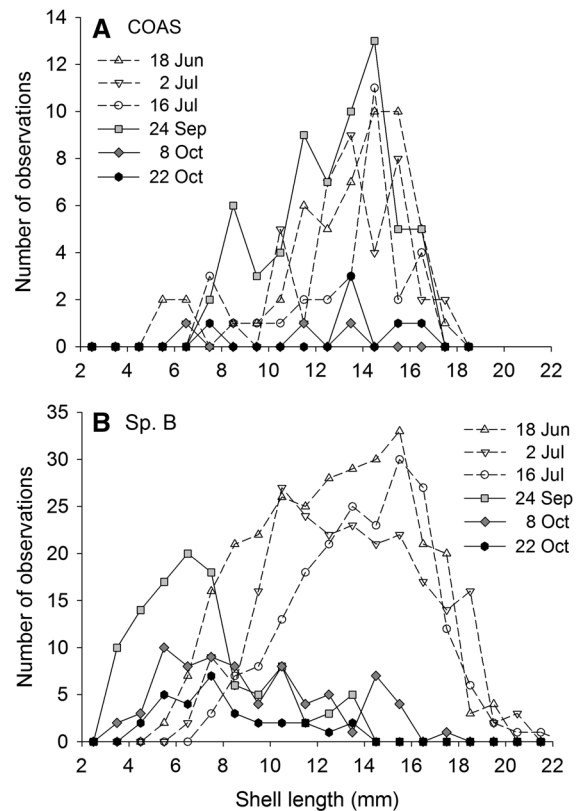
sizes of Sp. B (Figs. 1, 2). These effects were similar to those found by other studies of competition in terrestrial snails (e.g., Williamson et al. 1976; Cameron and Carter 1979; Smallridge and Kirby 1988; Baur and Baur 1990). We assumed that the patterns we observed in growth and mortality resulted from exploitation competition for limited food resources because COAS and Sp. B have coincident spatial distributions and use similar plants (Appendix D of ESM). However, our experiments did not allow us to definitively elucidate the mechanism of competition. For example, interference competition resulting from mucus trails could elicit similar patterns. At high densities mucus trails have been shown to reduce intra- and interspecific activity and inhibit growth directly through chemical compounds in the mucus (Williamson et al. 1976; Cameron and Carter 1979; Dan and Bailey 1982; Tattersfield 1981; Baur and Baur 1990, Pearce 1997). Further study is needed to quantify the relative importance of exploitative and
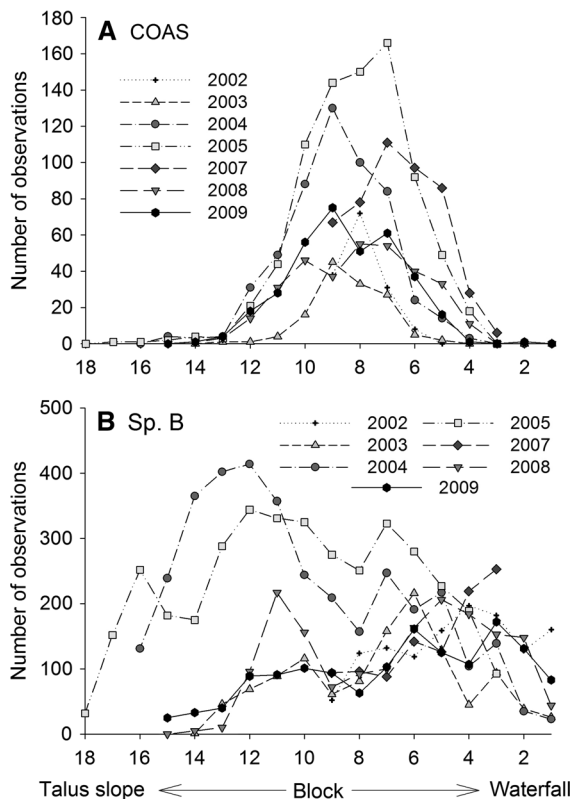
Fig. 5 Total captures per year of COAS and Sp. B in each block (1-m interval) of the mark-recapture survey transect

interference competition in these species in both experimental enclosures and natural populations.

The coincident spatial distributions of COAS and Sp. B at multiple spatial scales suggest that there is a high potential for interaction between these two species and thus some degree of competition under natural conditions (Ives 1988; Hartley and Shorrocks 2002). Sp. B was widespread across the study area and its range entirely encompassed the limited range of COAS (Fig. 5; Appendix D of ESM). Snails of both species also showed a high degree of overlap in their use of patches of dominant vegetation and substrate types, and within these patches, both species used many of the same plant species and substrates (Appendix D of ESM).

Further evidence for in situ competition is provided by the higher average growth rates of COAS that occurred alone in the experimental enclosures compared to the growth rates of naturally occurring COAS during similar time periods in each year (S Campbell, unpublished data). Although contributions of intra-

and interspecific competition to these differences are unknown, lower growth rates under natural conditions indicate that one or both types of competition are depressing in situ growth rates of COAS.

Evidence for coexistence

Despite the existence of some degree of competition between COAS and Sp. B, coexistence is possible if interspecific competition is weaker than intraspecific competition (Chesson 1991, 2000a; Kneitel and Chase 2004). Although our competition experiments allowed us to examine the interspecific effects of density of Sp. B on COAS growth rate and to a lesser extent the intraspecific effects of Sp. B on its own growth rate, the rarity of COAS prevented us from performing experiments with reciprocal treatment densities to observe the effects of COAS on itself and Sp. B. Thus, we were not able to determine coexistence directly by quantifying and comparing the relative strengths of intra- and interspecific competition (sensu Cross and Benke 2002).

There are, however, four lines of indirect evidence from our work that collectively suggest that the two species are coexisting. First, persistence of COAS for over 30 years in the presence of Sp. B is itself strong evidence for coexistence. If Sp. B were causing higher mortality and slower growth of individuals in natural populations of COAS, the effects would likely manifest as a population decline over a 30-year period through reductions in survival and fecundity (Oosterhoff 1977; Carter and Ashdown 1984; Baur 1988; Baur and Raboud 1988). Nevertheless, the recent trend in COAS population sizes suggests that the population size is fluctuating and that Sp. B is not causing a protracted extinction of COAS (Table 1). Second, the over three-fold increase in COAS population size from 2003 to 2004 showed that COAS retains a high capacity for population growth when conditions are suitable. There was also a high positive correlation between the total counts of snails of each species captured each year (Fig. 3), which suggests that COAS can increase even as the population of Sp. B grows. Third, natural populations of Sp. B rarely outnumbered COAS to the degree that caused the greatest reductions in the growth of COAS in our competition experiments. During the population surveys from 2002–2009, the ratio of the raw counts of Sp. B to COAS was less than 25:1 in 95 % of the

surveys and less than 10:1 in 80 % of the surveys. Finally, although there was a large degree of overlap in the use of plants and substrates, there were some fine-scale differences in resource use (Appendix D of ESM). Most notably, COAS tended to be found more often on decaying plant matter (e.g., detritus, dead leaves, wood) than Sp. B and Sp. B was more often found on living plant matter. Differences in habitat use on this scale could lead to coexistence because it would decrease the frequency of interaction between species and consequently reduce the intensity of inter- versus intraspecific competition (Ives 1988; Baur and Baur 1990; Ledergerber et al. 1997; Chesson 2000b; Hartley and Shorrocks 2002; Leisnham and Juliano 2009; Kimura and Chiba 2010).

Mechanism for coexistence

Niche differentiation is often proposed as a primary mechanism for coexistence of competitors (e.g., MacArthur and Levins 1967; Abrams 1984; Chesson 1991; Kneitel and Chase 2004) and it is usually manifested as a trade-off among ecological traits (e.g., higher growth vs. lower reproduction or efficient consumption of one resource vs. inefficient consumption of others; Stearns 1989; Zera and Harshman 2001; Kneitel and Chase 2004). At small spatial scales, such as those examined in this study, interspecific trade-offs are typically considered a prerequisite for species coexistence (Tilman 1982; Petraitis et al. 1989; Chesson and Huntly 1997; Grover 1997; Tilman 2000).

Based on a synthesis of results from the present study, we propose temporal niche partitioning based on a trade-off between growth and longevity of COAS and Sp. B as a mechanism for their coexistence. Namely, COAS is a slower growing and smaller biennial species and Sp. B is a faster growing and larger annual species. Evidence for this trade-off can be seen in the temporal patterns within each year of both the number of snails captured and the size distribution of snails. The bimodal distribution of the number of Sp. B captured (Fig. 3b) resulted from a size-dependent detection bias combined with a shift-ing size distribution of the population (Fig. 4b) due to its annual life cycle (Đatkauskienė 2005). The first peak in the distribution represents the cohort that hatched in the previous year. These individuals breed and then die in mid-August, completing their annual

life cycle. The low point in the distribution spans the time period when the new cohort of snails are in the egg stage or are recently hatched and thus difficult to detect. The second peak occurs in mid-September as the snails grow and their detectability increases. In mid-October, the numbers decrease again because the snails retreat to their overwintering areas. In contrast, COAS has a two-year life-cycle; overlapping gener-ations and two potential years of breeding allowed the simultaneous attrition of one cohort while the other cohort grew into larger, more detectable size classes, leading to a more uniform distribution of counts and more mixed size structure throughout the summer (Figs. 3a, 4a).

The temporal differences in size distributions may create a low competition environment for COAS at the end of every summer because COAS is exposed to a population of Sp. B composed of small individuals. This period may allow COAS to compensate for lower growth that it may have sustained earlier in the season when the population of Sp. B was composed of large individuals (see Baur and Baur 1992). Our second competition experiment, which was designed to test the idea that the effect on growth was less when COAS occurred with small (6–10 mm) individuals of Sp. B than with large (>13 mm) individuals, supported this supposition at lower densities (i.e., COAS growth rates were higher in the presence of small Sp. B). However, at high snail densities the results were more equivocal—the treatment with 50 small Sp. B had almost as strong of an effect on COAS growth as the treatment with 50 large Sp. B. This similarity may have occurred because small snails can be more efficient foragers than larger snails (Carlsson and Brönmark 2006). Although we did not directly mea-sure foraging efficiency in our study, small snails tended to grow faster than large snails. Alternatively, if interference competition is functioning (e.g., pre-sence of mucus trails) then the density of snails may be more important than body size.

Management implications

Our study has three practical implications for invasive species management. First, our study highlights the importance of identifying and responding with man-agement action to only non-native species that are having negative effects on native species and ecosys-tems. Managers may tend to favor the eradication or

control of non-native species to improve the status of a threatened species without first considering the root cause of the population decline, the effectiveness of removal methods, and the impacts of non-native species relative to the costs and efforts of its control (Choquenot and Parkes 2001; Grice 2009; Shackelford et al. 2013). However, eradication or control of the non-native species will not always be necessary or even benefit these types of at-risk species, and such efforts could be detrimental for conservation agencies already operating with limited financial resources. In our study, COAS appears to be coexisting with Sp. B, so the removal of Sp. B is unlikely to greatly improve the prospect of long-term persistence of COAS. Management actions are better directed toward recovery efforts that will increase the range and population size of COAS (e.g., captive breeding and establishment of additional populations).

Second, when non-native species are not having overtly deleterious effects, it is important for managers to consider multiple aspects of native and non-native species interactions when determining the impact of non-native species and prescribing management actions. For example, the results from our ex situ competition experiment suggested strong competitive effects and that control of Sp. B may be necessary. However, the additional consideration of population trends, phenology, size structure, spatial distribution, and habitat use indicated that there may be enough mitigating factors to favor coexistence in situ. These types of mixed results are likely to be common for non-native species whose negative effects on native species are more subtle.

Finally, in most cases there will be little to no research data for determining the necessity of management action for established non-native species. Our work suggests a three-staged approach to this problem. In the near term, hypotheses or anecdotal information may be used to justify attempts to eradicate or control non-native species; such precautionary measures may be especially prudent if endangered species are involved. Next, well-designed monitoring programs for both the native and non-native species should be conducted to collect basic information about population trends and life histories; this information leads to a better understanding of the species and can be used to determine if the initial actions are warranted (Campbell et al. 2002; Simberloff 2003). Finally, a more thorough mechanistic understanding of their interactions should

be acquired before long-term management plans are instituted. In short, we expect that there should be a reasonable relationship between the quality of the data and the implementation of management actions over the long-term (Strubbe et al. 2011).

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