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Life history and habitat requirements of the Oregon forestsnail, *Allogona townsendiana* (Mollusca, Gastropoda, Pulmonata, Polygyridae), in a British Columbia population

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Abstract. Population size, reproductive timing and habitats, seasonal behaviors, and juvenile activity were assessed in a British Columbia population of the endangered Oregon forestsnail, *Allogona townsendiana,* over a period of 4 years. Adult snail population size ranged from seven to 47 snails in four × 24-m^2 sampling sites. The mating period peaked in March and April; adults aggregated in clusters of eight to 14 snails before mating. Pairs of snails were observed to mate for 225 min or more in close proximity to coarse woody debris and stinging nettle, *Urtica dioica*. Nesting peaked in April–May and resulted in a mean clutch size of 34 eggs (SD = 9). Hatching for two nests occurred at 63 and 64 d after oviposition. Within hours of hatching, juveniles began dispersing from the nest site; by 1 month most had disappeared. Snails tracked with harmonic radar became less active or aestivated from late July to early September and hibernated from early November to mid-March within leaf litter and soil. Preliminary measurements of growth rate indicate this species takes a minimum of 2 years to reach adulthood and has a typical life span of at least 5 years.

Additional key words: conservation, endangered species, harmonic radar, land snail

Conservation of terrestrial gastropods has become of increasing concern in recent years as population declines and disappearances continue to be documented (Lydeard et al. 2004; Steinitz et al. 2005). Urbanization, forestry practices, and other anthropogenic changes, including habitat destruction and introductions of exotic predators, can have strong negative effects on snails with a limited range and low-dispersal abilities (Strayer et al. 1986; Baur & Baur 1990; DellaSala et al. 1999; Prezio et al. 1999; Hylander et al. 2004). Terrestrial gastropod conservation is important for several reasons: (1) Land snails and slugs play a significant role in decomposition and other food web processes (Mason 1970; Richter 1979; Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2002); (2) they often serve as dispersers of plant seeds and important fungal spores (Richter 1980; Gervais et al. 1998); and (3) they contribute to the overall biodiversity and health of ecological communities (Richter 1979, 1980).

Studies in various habitats suggest that terrestrial gastropods may serve as critical indicator species for ecosystems (Prezio et al. 1999; Ovaska & Sopuck 2005). Understanding the life history of a gastropod species is therefore crucial not only for conservation of the particular species, but also for broader protection of the ecosystem. Ignorance of life cycles, food web roles, and other ecological features of molluscs leaves gaps in overall knowledge of entire ecosystems and their health, to the detriment of ecosystem management (Tilman et al. 1994; Poiani et al. 2000). Indeed, the connection between individual species, ecosystem health, and human health is an important point for public education regarding gastropods and other molluscs (Rapport et al. 1998; Horwitz et al. 2001; Lydeard et al. 2004).

The Oregon forestsnail, *Allogona townsendiana* Lea 1838 (Pulmonata, Polygyridae), is one of few large land snails endemic to Pacific Northwest coastal forests of North America (Forsyth 2004). The species has been documented from the Willamette Valley of Oregon, the Puget Trough of Washington State, and the lower Fraser Valley of British Columbia (BC) (COSEWIC 2002). The current global status of this species is G3G4 (rounded status: G3—vulnerable) (NatureServe 2008), and it was designated endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in

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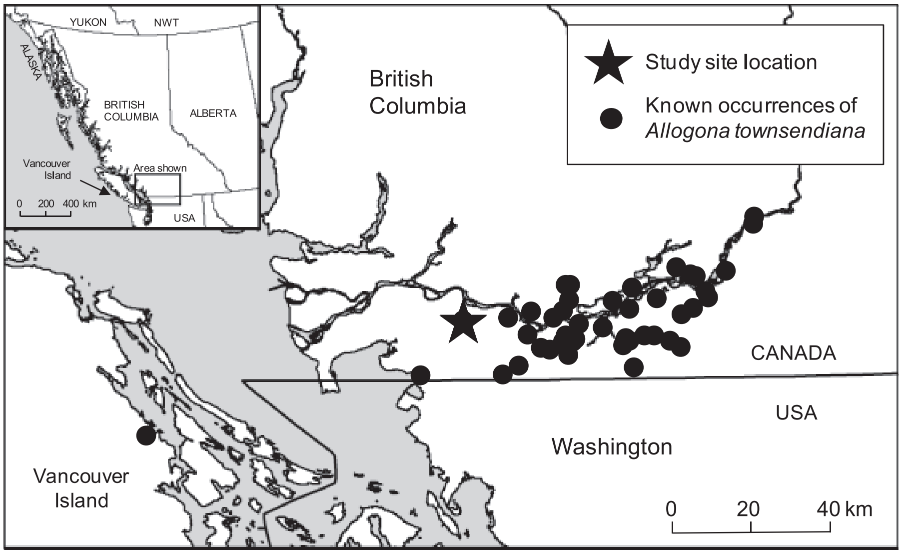

Fig. 1. Location of study site (Trinity Western University Ecosystem Study Area near Fort Langley, BC) and other known occurrences of populations of *Allogona townsendiana* in Canada (*Source:* British Columbia Conservation Data Centre).

November 2002. Remaining populations are highly fragmented and lie within heavily populated areas subject to urban and agricultural development. Conservation of *A. townsendiana* is particularly imperative in Canada, as BC populations of this species exist at the northern limits of their range, which may increase the likelihood that they are genetically distinct and possess unique ecological adaptations (Scudder 1989).

Despite its conservation status, the ecology of the Oregon forestsnail is poorly understood. Populations appear to exist primarily in remnant moist, mixed conifer–deciduous forests with open meadows. Further inland it exists only in sheltered ravines and riparian areas (Kozloff 1976). Members of *A. townsendiana* have also been associated with stinging nettle (*Urtica dioica*), although the exact nature of the relationship is unknown (Waldock 2002; Forsyth 2004). Distribution appears to be patchy throughout the range (COSEWIC 2002).

Current conservation planning for *A. townsendiana* is based on speculation about the habitat requirements at different life history stages. Though a Recovery Strategy is being prepared in compliance with Canada's Species at Risk Act (SARA), no previous work exists regarding mating, nesting, juveniles, or seasonal location. This information is a crucial precursor to understanding what factors limit population distribution and affect long-term viability. We sought to investigate key habitat requirements at important seasonal and life history stages including reproduction, migration, and hibernation. This article presents an overview of our findings on the life history of *A. townsendiana*.

Methods

Study area

Populations of *Allogona townsendiana* have been identified at several locations in southwestern BC, including the Ecosystem Study Area (ESA) of Trinity Western University (TWU) (Fig. 1). The TWU ESA near Langley, BC (49.14°N, 122.60°W) consists of ~ 50 ha of diverse habitats, including riparian areas, wet meadows, ponds, and mixed conifer–deciduous second-growth forests with large numbers of bigleaf maple (*Acer macrophyllum*). The presence of *A. townsendiana* was first documented at this site in the mid-1990s; the population appears to be relatively large (COSEWIC 2002; BC Conservation Data Centre 2008). The TWU population is well west of sizeable populations at Chilliwack and Agassiz, and is one of only a few populations that exist in protected areas (BC Conservation Data Centre 2008). The TWU population exists partially on land that is covenanted under the BC Ministry of Environment, due to the salmon-producing streams that run through the campus, thus shielding it from direct development impacts (K.M.M. Steensma & H.M. Silveira, unpubl. data).

Preliminary surveys, begun in 2000, led to mapping of the TWU snail populations using GIS in 2003 (Silveira 2004). Four areas separated by ≥ 50 m within ~ 10-ha area were identified for study during preliminary surveys. Field surveys took place from 2003 to 2007 and focused in habitats along existing trails and in previously identified off-trail areas, with care taken to limit damage to snails and their habitat.

Initial estimation of snail densities in four primary subpopulation sites in 2004 was followed up with studies of mating, nesting, and juvenile habitats and behavior through 2006. We tracked movements of snails using a harmonic direction finder from 2005 to 2007.

Population estimates and size distribution

Densities of individuals were assessed within four 24-m^2 sampling sites using the Jolly–Seber mark and recapture technique (Krebs 1989). Sites were searched for individuals for 30 min each on five consecutive days (June 8–12, 2004), with a 24-h interval between each sampling event. Each site was sampled at approximately the same time every day: site 1 at 09:00 hours, site 2 at 10:00 hours, site 3 at 11:30 hours, and site 4 at 13:30 hours. We measured the shell diameter of each snail found and on first capture marked them for individual recognition. We applied marks on the portion of shell furthest from the aperture, using black permanent marker and a coat of clear, quick-dry nail enamel to seal the ink. The snails were then returned to their original capture locations. The weather across the entire 5-d sampling period was consistently mild and dry. For each sample site, the computer program JOLLY (USGS Patuxent Wildlife Research Center, Laurel, MD, USA) (Pollock et al. 1990) was used to compute population size estimates. Assumptions for this program are as follows: all animals equally catchable, all with equal survivability, marks endure and are always seen if present, marked organisms released immediately, and sample processing time is extremely brief (Pollock et al. 1990).

Mating

Preliminary work in 2003 and 2004 showed snails to be active as early as February, with mating occurring as late as June (Kus 2005). Regular surveys for mating pairs began in January 2005, once every 2–3 weeks until mating pairs were first observed; surveys then continued at least weekly during the most active mating period of March 9 to May 4.

For all mating pairs, general location, air temperature, relative humidity, and day length were recorded. Three pairs were also assessed for additional habitat parameters, centered on the mating pair. These included soil moisture (%), pH, and soil temperature (5-cm depth), as well as distance to nearest stinging nettles and coarse woody debris (CWD) of diameter >3 cm. Soil moisture and pH were measured using a Kelway Soil Acidity and Moisture Tester (Model HB-2, Kel Instruments Co., Inc., Wyckoff, NJ, USA); relative humidity was measured using a Bacharach Sling Psychrometer (Model 12-9015, Bacharach Inc., New Kensington, PA, USA).

Nesting

Surveys for nesting snails were undertaken 2–3 × per week from the discovery of the first nest until nests were no longer located. Nests were located when snails were discovered in the process of ovipositing. For all nests, we recorded the general location and substrate. We also counted the number of eggs as soon after oviposition as possible.

Laboratory observations

Detailed observations of a single mating pair in captivity were made on August 10, 2005. Snails were kept in a 4.7-L Penn Plex aquarium with lid, set up to simulate natural habitat as closely as possible. Wet paper towels were used to retain moisture, and water was misted by spray bottle twice per day. Pieces of stinging nettle and other vegetative material were provided for food, and the enclosure was cleaned of excess food daily, with paper toweling replaced twice weekly. The aquarium was kept at 15°–18°C, and near a window to provide natural day length.

Snails were also monitored for oviposition in captivity. Eggs produced in captivity were measured with a ruler and examined at ×40 magnification.

Hatching and juveniles

In 2005, circular 50-cm^2 plots, centered on each of ten nest sites, were monitored 8 × from July 4 to August 10. Juveniles were detected by intensive and careful searches of each plot. Adult and juvenile snails, including other snail species posing potential predation threats to members of *A. townsendiana,* were counted in each plot search. The size and activity level of juveniles, and their microhabitat in terms of substrate, vegetation, and height above ground were noted, as were weather conditions.

Seasonal activity

From 2005 to 2007, we followed 18 adult snails using a harmonic direction finder. Individuals for tracking were chosen from widely dispersed locations in the study area and fitted with tags consisting of a small diode and antenna. Ten snails were tagged in the first season, and eight snails in the second. The diodes, ~1-mm diameter, were soldered to a thin wire antenna. The tags were secured to shells in a

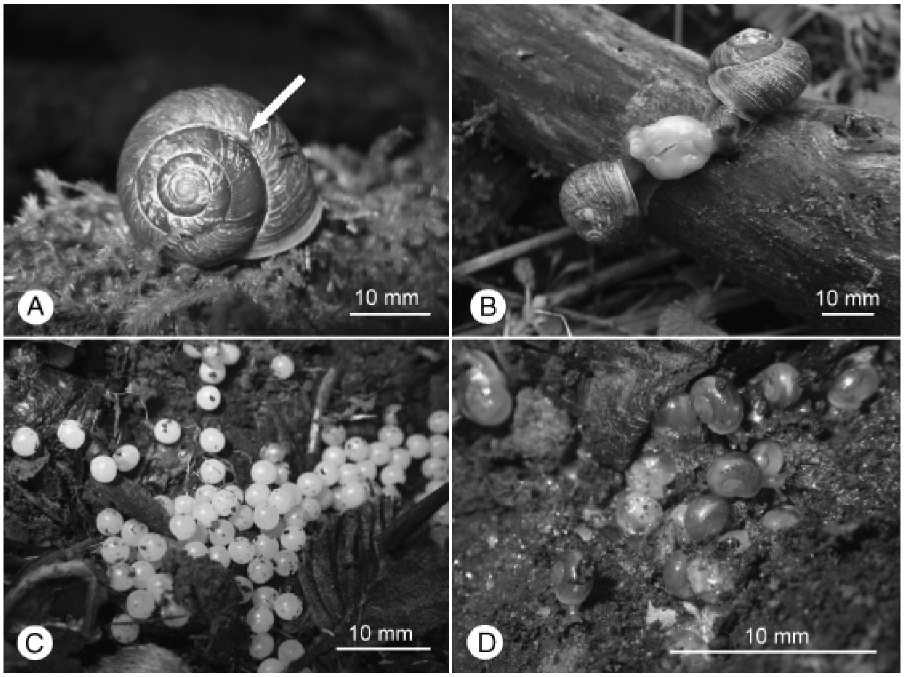

Fig. 2. Individuals of *Allogona townsendiana* at various life history stages. **A.** Adult snail, with tracking diode (arrow) and wire antenna attached to shell. **B.** Mating adult snails, shown on coarse woody debris. **C.** Eggs, shown in typical nesting substrate. **D.** Newly hatched juveniles.

spiral pattern using Super Glue™ (Super Glue Corp., Rancho Cucamonga, CA, USA) (Fig. 2A). Each snail was marked on its shell with a number and released where it had been found. A hand-held, battery-powered Recco® Harmonic Range Detector transceiver unit, Type R4P1A (Recco AB, Lidingö, Sweden), which emits a continuous microwave signal at 917 MHz, was used to follow movements of tagged snails (Lövei et al. 1997; Engelstoft et al. 1999). The signal bounces back to the transceiver from the diode as a harmonic frequency of the transmitted wavelength, providing an indication of diode location. Tracking was attempted at least once per week from March through August, once per 2 weeks from September through November, and once per month in December and January. More frequent tracking resumed in February as snails emerged from hibernation.

During tracking periods, searches began at the last known location and proceeded systematically outward by sweeping the detector back and forth across larger and larger concentric circles of ground. When detector receptivity indicated close proximity of a snail, the snail was located by visually searching the immediate area or, if the snail was not visually found, by careful digging in the leaf litter or forest duff layer. Once the snail was located, the site was flagged and data were collected on substrate type and activity level of the snail. Activity levels were classified as follows: (1) Hibernation/aestivation—withdrawn into shell, epiphragm present; (2) Inactive—withdrawn, no epiphragm; (3) Moderate—not withdrawn, little or no movement; (4) Active—out of shell, moving.

Results

Population estimates and size distribution

Estimates for the populations among the four sites ranged from seven to 47 snails (density 0.4–1.9 snails m^{-2}) (Fig. 3A). Overall mean population density was 1.0 snail m^{-2} (SD = 0.8 snails). Size distribution of 125 marked snails ranged 20–32 mm with an average size of 28 mm (SD = 2 mm) (Fig. 3B). Most snails were adults, and juveniles <20 mm in shell diameter were absent from the samples.

Mating

One mating pair of snails was found in 2004 and six in 2005. Snails were active as early as February, with mating occurring as late as June (Kus 2005), but most mating pairs were observed from March 9, to May 4. The pair in captivity was observed to mate on August 10, at 18°C with artificially elevated humidity.

Air temperature near mating pairs ranged 7.1°–17.0°C. No mating pairs were found below 76% relative humidity, with six of seven pairs mating at 81–100% humidity. Soil parameters (measured at

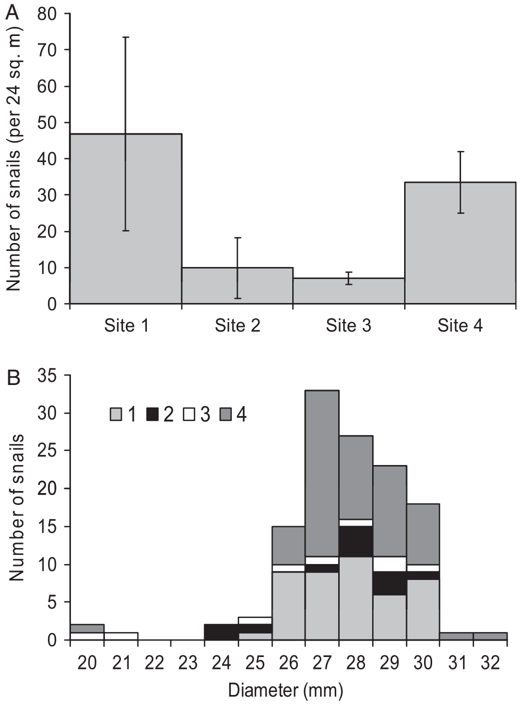

Fig. 3. Population size estimates and shell size distributions found in four 24-m^2 sampling sites. **A.** Estimates of population size (±95% confidence intervals) were determined through the Jolly–Seber mark–recapture method. Mean snail density across all sites was 1.0 snails m^{-2}. **B.** Histogram of shell diameters of snails ($n = 125$) found across four sampling sites (with bar colors showing distribution of sizes within each site). Mean shell diameter across all sites was 28 mm. Diameter was measured across the widest part of the snail.

three out of seven sites) showed that soil moisture at mating sites ranged 30–37%, soil pH 6.4–6.9, and soil temperature 9.9°–13.0°C. Mating first occurred at day length >11 h. Three out of three mating pairs assessed for additional parameters in 2005 were ≤1 m of stinging nettle and within 3 m of CWD, though stinging nettle and CWD were patchily distributed throughout the general mating habitat.

Mating was often observed directly on CWD (Fig. 2B) such as logs (4 of 7 times), with mating pairs usually (6 of 7 times) part of a prior aggregation of eight to 14 snails. Aggregating snails showed social behavior of shell and antenna touching. Mating times, partially observed for three pairs, ranged 225–395 min.

Nesting

Throughout the spring, adults of *Allogona townsendiana* were observed partially burrowed into the ground, which indicated nesting behavior. The stages of nesting consisted of digging nesting holes, ovipositing, and burying nests. Nesting peaked in mid-May, with earliest nesting over the 2005 and 2006 seasons seen on April 20, and latest on June 20 (Fig. 4). Fifty-three nests were surveyed in total, 26 in 2005 and 27 in 2006. Nesting occurred on multiple substrates, predominantly leaf litter and soil (Fig. 5A). A majority of nests were found in either edge or interior forest habitats in contrast to open field/meadow habitats (Fig. 5B).

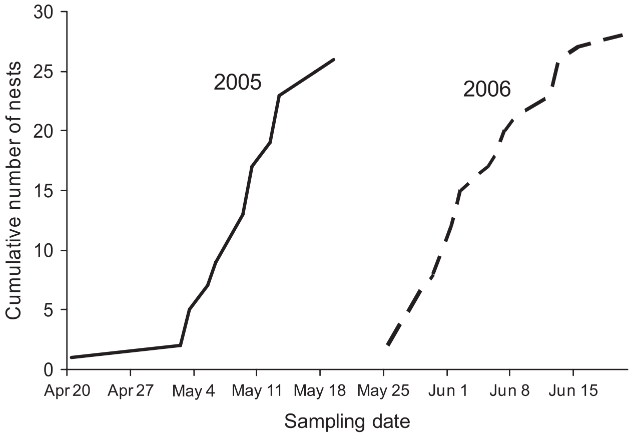

Fig. 4. Cumulative number of nests discovered during each of the 2005 (solid line) and 2006 (dotted line) nesting seasons. Nest searches were conducted using equal weekly effort (person-hours spent searching) in each year although searches for nests began ~1 month later in 2006 versus 2005.

Each snail usually dug a flask-shaped hole with the foot, often to a depth equivalent to the length of the entire snail, ~6–10 cm. Although the burrow was typically used for the nest, we also observed snails using pre-existing depressions under CWD, in moss, and in soil. On at least two occasions snails did not dig or use holes but laid eggs directly at the base of vegetation such as creeping buttercup (*Ranunculus repens*).

In three instances, it was observed that two snails oviposited simultaneously in the same burrow. The captive pair also exhibited this, producing a total of 63 eggs in the same burrow. One of the captive snails was directly observed to produce 13 eggs over the course of 40 min (11:40–12:20 hours) on June 2, 2005. These were removed and measured the same day; average egg diameter was 3.1 mm (SD = 0.4 mm), with size ranging 2.5–4.0 mm. Eggs were round, grayish-white in color and opaque, with a slightly grainy texture under magnification (Fig. 2C). It was observed that first eggs laid by the captive snails were generally larger than last eggs in the clutch. Average clutch size, measured in 2006, was 34 eggs clutch^{-1} (SD = 9, range = 18–54).

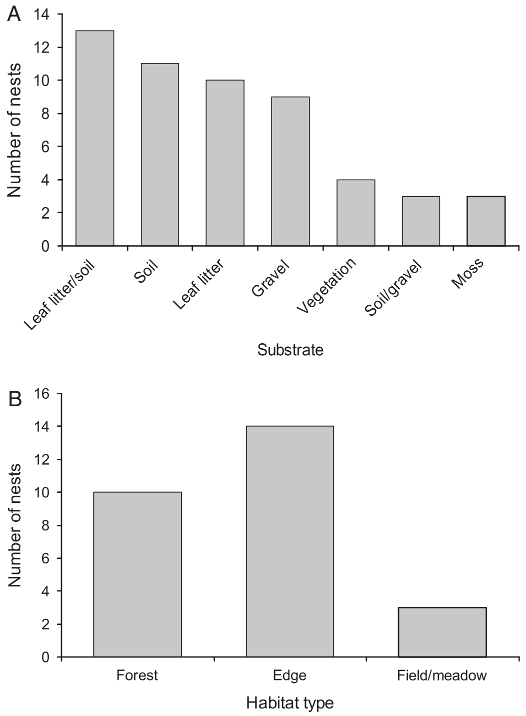

Fig. 5. Substrate and habitat use for nesting by forestsnails. **A.** Histogram of substrates used for nesting ($n = 53$). Eggs were usually found partially buried ~6–10 cm into the substrate. **B.** Histogram of habitat types used for nesting. Edge habitat was defined as ±2 m from the forest canopy drip line.

Hatching and juveniles

Newly hatched juvenile snails were seen in the vicinity of several nests 8–9 weeks after egg laying (Fig. 2D). Hatching was directly witnessed in two nests, at 63 and 64 d after oviposition. Incubation times appeared to vary for individual eggs within a single clutch in some cases. A total of 957 juveniles were sighted over the 2005 season. Most were found on the ground, largely on mixed soil and leaf litter or soil only, but also on a variety of other substrates (Fig. 6). Juveniles began visibly moving away from the nest within hours of hatching, but disappearance from nest sites occurred gradually over a 1-month period (Fig. 7).

Hatchlings found at nest sites were ~2 mm in shell width. After 6 weeks, juvenile shell size reached 3–3.5 mm. The shell was often transparent, particularly in the extremely delicate outermost whorl. The umbilicus was only partially visible. Juveniles were active and less easily stimulated to withdraw into their shells than adults, though by 4 mm they could form an epiphragm in dry weather.

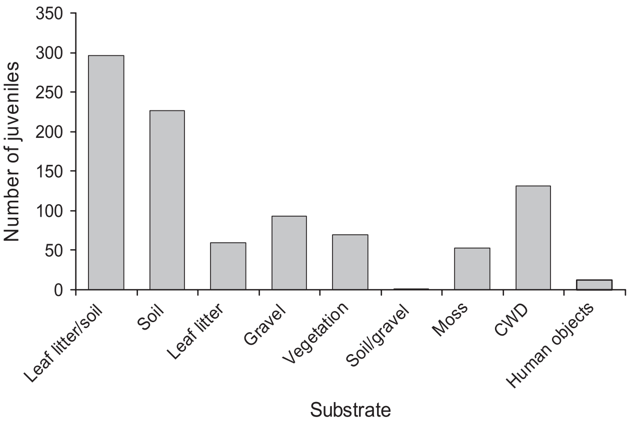

Fig. 6. Substrate use by newly hatched juveniles. Searches were conducted 8 × at ten nest sites ($n = 957$) over a 1-month period (July 11 to August 10) in 2005. CWD = coarse woody debris; human objects included wire stake flags, trail edging, and landscaping cloth.

Juveniles remained <5 mm in diameter ≤ 2 months after hatching. At this point, juveniles were seen migrating further away from the nest site, although they became more difficult to detect. Throughout the 2006 migration period, 5% were observed climbing ≤ 1 m on tall vegetation such as stinging nettle, reed canary grass (*Phalaris arundinacea*), Indian plum (*Oemleria cerasiformis*), and Himalayan balsam (*Impatiens glandulifera*). On any given sampling day, the percentage of climbing juvenile snails ranged 0–17%; however, on two occasions, $>60\%$ of the juveniles within a single plot were found climbing. No relationship was found between climbing behavior and temperature or humidity. Though hatchlings were not seen feeding, older juveniles fed on stinging nettle.

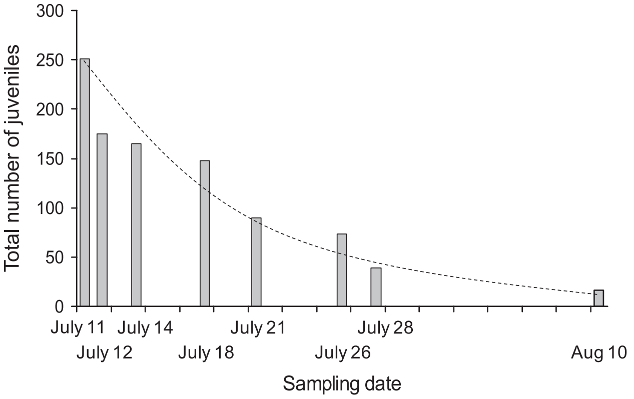

Fig. 7. Disappearance of juveniles from ten nest sites over a 1-month period (July 11 to August 10) in 2005. Loss of juveniles may have been due to dispersal out of the search area, burrowing into the ground, or to predation or other mortality factors.

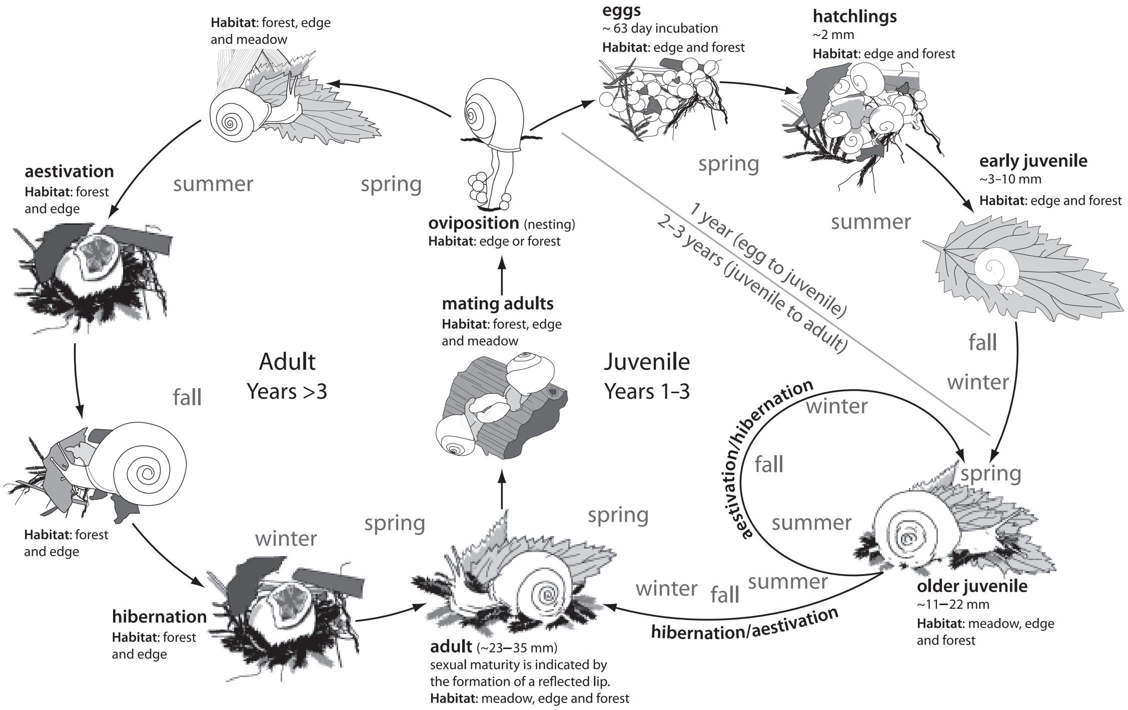

Fig. 8. Proposed life cycle and habitat requirements in *Allogona townsendiana*. Juveniles are thought to take a minimum of 2 and probably 3 years to reach sexual maturity, although little information exists for early to late juvenile stages. The substrate shown for each stage represents a major habitat requirement. More specific habitat requirements at each stage are: nesting, egg, and hatchling—soil, leaf litter, moss; early and late juvenile—stinging nettle; mating adult—coarse woody debris, stinging nettle; aestivation—moss, leaf litter; hibernation—leaf litter, soil, moss.

Hatchlings of *A. townsendiana* shared their habitat with other land snails, including *Haplotrema vancouverense, Monadenia fidelis, Cepaea nemoralis* (an introduced species), *Cryptomastix germana,* and *Vespericola columbiana,* as well as with various slugs including non-native *Arion* species. *Haplotrema vancouverense* was seen feeding on both eggs and juveniles of *A. townsendiana* in at least four instances.

Seasonal activity

Of the 18 adults tracked with the harmonic direction finder, five died within the 2-year tracking period, and several others were lost for periods ≤ 3 months. However, 15 were tracked for a minimum of 1 year, with seven of those tracked at least partially through 2 years. Searching continued for snails not detectable for days or even months at a time; all were relocated eventually.

A consistent pattern of hibernation during the winter was followed by an active season in spring and summer, with activity levels tapering off in late summer and fall (Fig. 8). The earliest date of emergence from hibernation occurred on February 9, 2006. By March 20, virtually all individuals increased frequency of moderate and active days, with peak activity during the April–June mating and nesting season.

The typical hibernation period was approximately November 5 to March 20, though hibernation sometimes began as early as late October. All snails were hibernating by November 26. During this period, mean daily high temperatures were 10.6°C (SD = 2.6°C), with below-freezing temperatures common overnight. Throughout hibernation, five of 15 tracked snails moved; distances averaged 14 cm (SD = 15 cm). Hibernating snails were found oriented with the aperture up. Hibernating snails had complete epiphragms; evidence of previous epiphragms was occasionally observed.

Hibernating snails buried themselves 2–7 cm down into leaf litter, or occasionally moss or soil. During periods with above-freezing temperatures, a few individuals showed activity breaks in which they appeared to briefly feed on dead leaf litter within reach of their hibernation sites. However, moderate to active behavior among individuals was rarely seen throughout the hibernation period. Juveniles were not seen during the hibernation period.

Shorter summer inactivity periods began for most snails by July 25. Snails continued with little or no activity, buried in moss, reed canary grass mats, or leaf litter, through the driest weeks, to August 10. Aestivation with epiphragm present was brief, often only a few days during the highest temperatures, but inactivity or low activity was common, sometimes as early as June 30. Moderate to active behavior resumed in September to early October.

Discussion

Demography

Population density of the TWU population of *Allogona townsendiana* appears low in comparison with densities of small, temperate forestsnail species (Grime & Blythe 1969; Hotopp 2002; Martin & Sommer 2004) but within normal range for larger species (Staikou 1998; Baur et al. 2000; Stringer & Montefiore 2000). Snail densities are positively correlated to soil moisture and other microclimate characteristics (Prior 1985), and densities observed here represent study sites selected because of their high suitability for this species.

The observed size distribution showing a paucity of juveniles could result from either lack of smaller juveniles due to mortality factors, or from survey methods that failed to capture these size classes. Snails >20 mm would have been difficult to overlook during the survey. However, it is possible that the searching technique and timing minimized chances of observing juveniles <20 mm for various reasons. With few juveniles being seen at any time of year, little is known of their fate. Their size and thinner shells may make them highly susceptible to desiccation and to predation by amphibians, reptiles, rodents, birds, and invertebrates (Stringer & Montefiore 2000), as well as human trampling. Further research is needed on density and survival of smaller juveniles.

Forsyth (2004) reports that sexual maturity of adults, indicated by the thickening and full reflection of the lip of the shell aperture, is reached by 23 mm. Our results support this expected size at maturity; several large snails ($\sim$20–23 mm) were seen without the thickened aperture lip. Given the growth rates observed in newly hatched juveniles in their first year, it is likely that sexual maturity thus takes at least 2, and quite probably 3 or more years.

Life history

The life cycle of *A. townsendiana* appears to be closely tied to seasonal temperature and humidity, with mating season beginning as early as February in some years (Fig. 8). Peak mating, typically in March and April, parallels the mild temperatures and moist spring conditions. Dependence of reproduction on moist, temperate conditions is typical of land snails (Solem & Christensen 1984), with activity levels in general being tied to a combination of day length, moisture, and temperature (Prior 1985). With spring-like temperature and humidity, the captive snail pair mated outside the observed mating dates for snails in the natural habitat, thus supporting this idea.

In order to choose a partner, many land snails aggregate in clusters as was observed for this species. Such social interaction may increase overall reproductive success, general fitness, and lifespan (Baur & Baur 2000). Genetic isolation of sub-populations, due to habitat fragmentation caused by roads and waterways, may lead to more instances of inbreeding and/or self-fertilization. Although it is currently unknown whether self-fertilization occurs in *A. townsendiana,* this could decrease fitness of populations as has been seen in other gastropods (Forsyth 2004). Further work on population genetics in *A. townsendiana* is needed in order to address these aspects of their conservation.

The mating process, observed to last ≥ 3 h 45 min, may often take longer. In some land snails, the mating process can last ≥ 24 h, such as in the Roman snail *Helix pomatia* (Baur 1998), or even several days, as in the rare New Zealand land snail *Paryphanta busbyi watti* (Stringer et al. 2003).

As with mating, the nesting season seemed to be strongly tied to temperature and humidity, with peak nesting occurring in May when conditions are still moist. Hatching likewise appeared to peak in June, with snails hatching over a period of several weeks. Asynchronous hatching, noted here, is seen in other land snails as well and may be a response to unfavorable environmental conditions or microclimate variations, or an adaptation to predation pressure (Baur 1994). Asynchronous hatching may also allow early hatchlings to cannibalize other eggs in the clutch. Though not witnessed in *A. townsendiana,* this behavior is seen in some herbivorous terrestrial gastropods (Baur 1988).

Other seasonal aspects of life history also appear to be tied to temperature and humidity. Midsummer aestivation serves to minimize desiccation stress and the onset of hibernation in late fall appears to correspond with colder weather. Temperature is likely more important to hibernation than day length, as brief activity has occasionally been seen on mild days (i.e., temperatures $>4°C$) regardless of day length (Rekers 2006). Additionally, moisture and osmotic requirements of the species probably play an instigating role in seasonal inactivity, which is typical of land gastropods (Prior 1985).

Habitat requirements

CWD appears to play an important role in mating. Snails mated on CWD $>50\%$ of the time. The wood likely provides the moisture crucial to terrestrial gastropods (Prior 1985), as well as a surface conducive to staging elaborate courtship rituals such as aggregation and shell and antenna touching, which may be a preliminary to mate choice (Locher & Baur 2000). Stinging nettle (*Urtica dioica*) may also be associated with mating habitat; all three mating pairs assessed for proximity to stinging nettle were $<1\,\mathrm{m}$ of the plant. Across the study area, stinging nettle stem density has been estimated to be $<0.02\,\mathrm{stems\,m^{-2}}$ ($\sim$1 stem per $50\,\mathrm{m}^2$) (K.M.M. Steensma, unpubl. data), suggesting these snails choose mating sites associated with stinging nettle. Waldock (2002) also found that stinging nettles were often associated with presence of adult snails. We propose that members of *U. dioica* are an important food source for older juveniles and adults, and may also be an aptly timed shade cover from summer heat and a cover from predation. The stinging nettle likely also provides some protection from human trampling, due to the skin reaction caused by contact with this plant.

Substrates most important to nesting and juveniles of *A. townsendiana* are soft and insulating soils and leaf litter. Eggs were laid individually in a burrow similar to that used by *H. pomatia* (Tompa 1984), usually dug in soil/leaf litter mixes, perhaps due to ease of digging and the thermal protection provided. When burrows are not used, the survival rate of eggs may be much lower due to exposure to the elements and to predators; further study is needed on this aspect of nesting. Soft nesting substrates are probably suitable for other terrestrial snails as it was common to encounter young juveniles of other species in close proximity to nests of *A. townsendiana*.

With large numbers of juveniles found climbing vegetation at times, the availability of tall vegetation such as stinging nettle or even non-native reed canary grass (*Phalaris arundinacea*) may be important as a vertical niche. Though we found no relationship between climbing and temperature or precipitation, this aspect warrants further study. Predation rates by ground-dwelling invertebrates such as carabid beetles or other snails is likely decreased with climbing, although it may increase chances of predation by birds. Climbing may also increase access to newer growth and higher quality food.

Within the general habitats of forest, edge, and open areas frequented by these forestsnails during the spring and summer reproductive season, two important microhabitats appeared: (1) leaf litter within the forest or at its edge, especially during winter hibernation, and (2) mossy areas or matted reed canary grass as refuge areas during summer aestivation. Leaf litter is likely to be critical year-round, as snails may feed on fungal mycelia colonizing this material (Pilsbry 1940), and it may provide low-disturbance areas during winter, sheltering snails from cold temperatures and low humidity. Moss and matted vegetation, especially within the forest and at the forest edge, may likewise provide short-term insulation and retention of moisture necessary to prevent desiccation during summer periods of heat. Further detail on seasonal activity level and use of habitats is needed.

Conservation implications

The life cycle in *A. townsendiana* is characterized by slow maturation and requirements for different habitats at different life history stages. Since juveniles appear to take ≥ 2 years to reach adulthood, and since some individual adult snails in this study (marked as adults at an unknown age) have been tracked for nearly 3 years, the life span of this species must be ≥ 5 years. Other similar species have been found to reach 7 years or more in age (Staikou 1998; Stringer et al. 2002; Forsyth 2004); *A. townsendiana* individuals may reach a higher maximum as well. Combined with suspected high egg and juvenile mortality, these life stage requirements make conservation of this species particularly challenging.

Because high-quality habitat for populations of *A. townsendiana* appears to consist of fertile lowland soils in riparian areas susceptible to development pressure throughout the region, conservation strategy requires minimization of loss of forest and meadow areas. Our recommended strategy would: (1) preserve mixed conifer–deciduous forests and forest–meadow edge habitats; (2) manage woodlots to avoid removal of fallen wood, stinging nettles (*U. dioica*), and other native vegetation; and (3) discourage roads, trails, and foot traffic through leaf litter and understory vegetation, especially under bigleaf maple (*Acer macrophyllum*). Further work on juvenile and adult mortality, and population genetics, is needed in order to inform future land management decisions and refine ongoing conservation efforts for this species.

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