Dispersal, home-range size, and habitat use of an endangered land snail, the Oregon forestsnail (*Allogona townsendiana*)

A.B. Edworthy, K.M.M. Steensma, H.M. Zandberg, and P.L. Lilley

Abstract: Terrestrial molluscs have declined globally, often as a result of habitat loss and fragmentation. Many land snails are poor dispersers and exist in isolated habitat patches. The Oregon forestsnail (*Allogona townsendiana* (I. Lea, 1838)) coincides with the most densely populated region of British Columbia and is listed as endangered in Canada. To investigate the dispersal distances and habitat-use patterns of Oregon forestsnails, we tagged and tracked 21 adult snails at Langley, British Columbia, for up to 3 years (2005–2008). The maximum daily dispersal distance for a snail was 4.5 m and the maximum displacement that we observed for a snail was 32.2 m during 3 years. Snails occupied home-range areas of 18.4–404.4 m^2, often overlapping both forest and meadow habitat. Their home-range sizes were smaller in habitats with high availability of stinging nettle (*Urtica dioica* L.), which may be an indicator of high-quality habitat. Our results suggest that the Oregon forestsnail is a relatively sedentary species with limited dispersal ability in its adult stage. Although Oregon forestsnails are likely unable to colonize suitable habitat independently, remnant forest–meadow mosaic patches such as our study site provide valuable habitat for Oregon forestsnail, which are supplementary to large tracts of intact forest where most of their populations are found.

Key words: Allogona townsendiana, Oregon forestsnail, conservation, dispersal, endangered species, habitat use, harmonic radar, home range, movement.

Résumé : Les mollusques terrestres sont en déclin à l'échelle planétaire, en raison bien souvent de la perte ou de la fragmentation d'habitats. De nombreux escargots terrestres ne se dispersent pas bien et vivent dans des parcelles d'habitat isolées. L'aire de répartition de l'escargot forestier de Townsend (*Allogona townsendiana* (I. Lea, 1838)) coïncide avec la région la plus densément peuplée de la Colombie-Britannique, et l'espèce figure à la liste des espèces en voie de disparition au Canada. Pour étudier les distances de dispersion et les patrons d'utilisation d'habitat de l'escargot forestier de Townsend, nous avons marqué et suivi 21 escargots adultes à Langley (Colombie-Britannique) durant une période maximum de 3 ans (de 2005 à 2008). La distance de dispersion quotidienne maximum pour un escargot était de 4,5 m et le déplacement maximum observé était de 32,2 m sur trois ans. La superficie du domaine vital occupé par les escargots allait de 18,4 à 404,4 m^2, et chevauchait dans bien des cas des habitats forestiers et de pré. La taille du domaine vital était plus faible dans les habitats où la disponibilité de la grande ortie (*Urtica dioica* L.) était élevée, ce qui pourrait être un indicateur d'habitat de grande qualité. Nos résultats portent à croire que l'escargot forestier de Townsend est une espèce relativement sédentaire dont la capacité de dispersion au stade adulte est limitée. Bien que l'espèce soit vraisemblablement incapable de coloniser des habitats convenables de manière indépendante, des parcelles résiduelles d'une mosaïque de forêt–pré, comme le site de l'étude, constituent un habitat intéressant pour l'escargot forestier de Townsend, qui complémente les grandes étendues de forêt intacte où est concentrée la majorité des populations de cette espèce.

Mots-clés : Allogona townsendiana, escargot forestier de Townsend, conservation, dispersion, espèce en voie de disparition, utilisation d'habitat, radar harmonique, domaine vital, déplacement.

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Introduction

Nonmarine molluscs have declined globally because of cleared and fragmented habitat, introduced predators, and polluted environments (Lydeard et al. 2004). Although terrestrial gastropods are generally small, cryptic organisms, they provide important ecosystem functions, including dispersal of seeds and fungal spores, as well as decomposition of detri-

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tus (Richter 1979, 1980; Gervais et al. 1998). In fragmented habitats, species with poor dispersal may be unable to colonize neighbouring habitat patches, resulting in vulnerable and isolated populations (Fritz 1979). For example, Hall and Hadfield (2009) found that tree snails of the genus *Achatinella* Swainson, 1828 often moved within clumps of trees, but were unable to disperse to unconnected trees except when carried by wind gusts. They concluded that *Achatinella* spp. did not have the ability to disperse among isolated habitat patches without human intervention. To understand habitat-occupancy patterns and to conserve suitable habitat, information about dispersal, home-range size, and habitat use is required. Here, we investigate dispersal ability and habitat use of the Oregon forestsnail (*Allogona townsendiana* (I. Lea, 1838)) (Pulmonata, Polygyridae), an endangered species in Canada restricted to small and fragmented habitat patches at its northern range limit.

Movement patterns of snails range from sedentary (homing) to nomadic (wandering) (Tomiyama and Nakane 1993). Some limpet species return to an exact location each day, called a home scar (e.g., Cook 1971). Frank (1981) proposed that natural selection will favour animals which stay put if they (*i*) occupy patchy habitats with differences in quality and (*ii*) have no knowledge of the quality of surrounding habitat patches. These sedentary species may be poor dispersers, unable to colonize suitable habitat. However, a nomadic species adapted to continuous forest might suffer high mortality in habitat patches surrounded by human development, by wandering onto paved roads or edge environments (e.g., Spellerberg 1998). Thus, dispersal strategies can have an important impact on both habitat-colonization rates and survival rates of snail species. Habitat quality also determines whether a patch is colonized and supports a population (Franklin and Lindenmayer 2009). Long-term tracking studies enable us to determine both dispersal and habitat-use patterns.

The Oregon forestsnail was listed as Endangered under the Canadian *Species at Risk Act* in 2002 (SARA 2002). Population trends are unknown for the Oregon forestsnail, but development, agriculture, and logging have resulted in habitat loss and fragmentation throughout its range in Oregon, Washington, and British Columbia (COSEWIC 2002). At its northern range limit in southwestern British Columbia, scattered populations of Oregon forestsnail coincide with the most heavily populated region in the province (COSEWIC 2002). Many populations of Oregon forestsnail are isolated by high-traffic roads and cleared land. It is not known whether the Oregon forestsnail is nomadic and at risk of moving out of forest fragments into unsuitable habitat, or whether it is sedentary, with short dispersal distances. Staikou et al. (1989) hypothesized that species living in open habitats will be more exposed to extremes in temperature and evaporation rate and will travel farther to acquire shelter compared with species living in moderate forest environments. Because it lives in the mild, moist Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1991), we predicted the Oregon forestsnail to be a relatively sedentary species.

The Oregon forestsnail is primarily found in mixed-wood and deciduous forests dominated by bigleaf maple (*Acer macrophyllum* Pursh), western redcedar (*Thuja plicata* Donn ex D. Don), or balsam poplar (*Populus balsamifera* L.) (COSEWIC 2002). Individuals have also been found in open meadows dominated by reed canarygrass (*Phalaris arundinacea* L.) and creeping buttercup (*Ranunuculus repens* L.) (Silveira 2004). Consistent features of habitat of Oregon forestsnail include dense herbaceous ground cover, stinging nettle (*Urtica dioica* L.), and coarse woody debris (COSEWIC 2002; Steensma et al. 2009). Habitat-use patterns, especially at the microhabitat scale, and indicators of habitat quality are largely unknown. Home range reflects habitat quality for species that increase search effort in poor-quality habitat where resources are distantly spaced (Turchin 1991; Mitchell and Powell 2004). We hypothesized that forested habitat, stinging nettle, and coarse woody debris are indicators of high-quality habitat and that Oregon forestsnails living near high densities of these features have smaller home-range areas.

Past studies of movement patterns and habitat use of snails have employed methods including mark–recapture, spool–line tracking, radio-tracking, and time-lapse videography, none of which are ideal for tracking small animals for long periods of time (e.g., Baker 1988; Tomiyama and Nakane 1993; Murphy 2002; Coffin et al. 2008). We used a recently developed technique, harmonic radar, to tag and track 21 adult snails for up to 3 years (Lövei et al. 1997; Englestoft et al. 1999). Our objectives were (*i*) to estimate home-range sizes and long-term dispersal distances and (*ii*) to determine habitat-use patterns in a major population of Oregon forestsnail.

Materials and methods

Study area

Our study area was a mosaic of second-growth mixed-wood forest and wet meadow habitat, surrounded by agricultural land in Langley (49°8′25″N, 122°36′3″W), British Columbia, Canada. The study area was managed to maintain native plant species, but also contained disturbed meadow patches and gravel footpaths. Forest habitats were dominated by bigleaf maple and western redcedar and included streams with intact riparian zones. Meadow habitats were dominated by reed canarygrass and creeping buttercup, both of which are introduced species.

Tracking and habitat measures

We tracked the movements of 21 adult snails using harmonic radar technology for up to 3 years (May 2005 to Aug. 2008). Individual snails were chosen from both habitat types (forest and meadow) throughout the study area. Nine snails were tagged in the first season (2005), eight were tagged in the second season (2006), and four were tagged in the third season (2007) (Table 1). Each tag was a 1 mm Schottky detector diode soldered to a copper wire (4 cm long, 35 gauge), which functioned as an antenna. We attached tags to the snails' shells using Super Glue™ (Super Glue Corp., Rancho Cucamonga, California, USA), with the copper antenna glued in a spiral pattern on top of the shell (see Steensma et al. 2009). Individuals were marked on their shells with a number in permanent ink (sealed with clear nail polish) and then released back where they were found within several hours of capture. The tag reflects a microwave signal from the receiver within a range of 2–10 m, enabling searchers to pin-

Table 1. Summary of tracking effort, general habitat use, and fate for 21 Oregon forestsnails (*Allogona townsendiana*) in Langley, British Columbia, Canada.

					Proportion habitat occupancy		
Snail ID	Start date	End date	No. of days	No. of sightings	Forest	Meadow	Fate
H1	4 May 2005	6 Aug. 2008	1190	94	0.89	0.11	Alive
H2	4 May 2005	6 Aug. 2008	1190	101	1.00	0.00	Alive
H3	4 May 2005	5 May 2006	366	27	0.11	0.89	Dead
H4	4 May 2005	12 Sept. 2007	861	81	0.26	0.74	Dead
H5	4 May 2005	21 Aug. 2006	474	45	0.22	0.78	Dead
H6	5 July 2005	14 Nov. 2006	497	46	0.17	0.83	Dead
H7	5 July 2005	20 Mar. 2006	258	13	1.00	0.00	Dead
H8	5 July 2005	23 May 2007	687	59	0.42	0.58	Dead
H10	5 July 2005	18 May 2007	682	62	0.21	0.79	Dead
H11	12 July 2006	30 Apr. 2008	658	62	0.07	0.93	Alive
H12	12 July 2006	30 Apr. 2008	658	38	0.18	0.82	Alive
H13	12 July 2006	12 Sept. 2007	427	67	0.14	0.86	Dead
H14	12 July 2006	21 June 2007	344	41	1.00	0.00	Dead
H15	12 July 2006	4 July 2008	723	58	1.00	0.00	Dead
H16	12 July 2006	22 May 2007	314	36	0.83	0.17	Dead
H17	12 July 2006	24 Apr. 2007	286	31	1.00	0.00	Dead
H18	12 July 2006	6 Aug. 2008	756	67	0.70	0.30	Alive
H19	20 July 2007	12 Sept. 2007	54	12	0.58	0.42	Dead
F1	30 Aug. 2007	6 Aug. 2008	342	18	1.00	0.00	Alive
F3	17 Aug. 2007	22 Mar. 2008	218	8	1.00	0.00	Alive
F4	20 Aug. 2007	6 Aug. 2008	352	13	1.00	0.00	Alive
Mean ± SD			540±300	47±27			

point a tagged snail's location (for details see Steensma et al. 2009).

We attempted to locate each snail at least once every 2 weeks throughout the year, except during periods of high activity (Mar. to Aug.) when we tracked snails one to three times per week and during hibernation (Dec. and Jan.) when we tracked snails once per month. Most tracking attempts were successful (92%), though we briefly lost snails if reception was poor, for example, when the antenna was blocked by soil or coarse woody debris. We located snails multiple times during hibernation, but excluded these sightings from the habitat use analyses because the snails remained stationary and these sightings did not add any new information. At each sighting location of a tagged snail, we recorded the distance and direction to a fixed reference point. To compare movement across seasons, we calculated net distance travelled each month. To examine movement patterns throughout the year, we plotted the distance from initial location of each snail through time.

To investigate fine-scale habitat use by the Oregon forestsnail, we surveyed habitat type (forest or meadow), habitat attributes (stinging nettle and coarse woody debris), composition of plant species, and substrate type (e.g., leaf litter, soil, woody debris, dead vegetation, live vegetation). When a snail was found at the boundary of forest and meadow, we classified its location as meadow habitat. At each snail sighting point, we measured distance to the nearest live stinging nettle plant and nearest piece of coarse woody debris (here defined as down logs or sticks with diameter >3 cm).

We used minimum convex polygons (MCP) to estimate home-range area for each snail. Only snails with at least one full year of tracking data or 35 sightings were included in the home-range size analyses ($n = 15$), but the full sample of 21 snails was used in all other analyses. Because sightings were nonindependent, we could not use home-range estimates requiring statistical independence, such as kernel methods (Aebischer et al. 1993).We fit simple linear models to examine the relationship between snails' home-range size and mean proximity to (*i*) stinging nettle and (*ii*) coarse woody debris. Both home-range sizes and mean proximity to resources were based on all sightings during the period that we tracked the snails. There was no relationship between number of sightings and home-range size (Student's t test, $t = 0.83$, $p = 0.42$); nevertheless, to reduce any impact of differing number of sightings per individual snail, we weighted each observation in our linear models by the number of sightings that we had for the snail. Because we expected the relationship between home-range area (two dimensional) and distance variables (one dimensional) to be nonlinear, we transformed the home-range variable by taking its square root. To assess the difference in home-range size across habitat types, we compared mean home-range sizes for snails found primarily in forest habitat ($n = 6$) and snails found primarily in meadow habitat ($n = 9$), using a Student's t test (based on the subset of 15 snails for which we calculated home-range sizes). To assess the importance of coarse wood debris during peak mating season (Mar.–Apr.; Steensma et al. 2009), we averaged distance to coarse wood debris during mating and nonmating seasons for each snail. Then, we calculated the difference between distance to coarse wood debris for each snail during mating and nonmating seasons and used a paired-sample t test to determine the statistical significance of the mean of these differences.

To determine which plants (height <1 m) were present in the habitat of the Oregon forestsnail, we recorded the pres-

Table 2. Dispersal statistics for 21 Oregon forestsnails (*Allogona townsendiana*) in Langley, British Columbia, Canada.

			Net distance from initial location			
Snail ID	Maximum daily movement	Mean distance per month	After 1 year	After 2 years	After 3 years	Maximum distance from initial location
H1	3.28	2.75	10.97	27.40	28.90	32.20
H2	1.07	3.85	9.22	12.45	11.05	16.61
H3	3.09	3.08	5.37	na	na	12.10
H4	1.89	2.57	4.41	6.25	na	8.24
H5	4.45	5.21	4.68	na	na	7.07
H6	1.10	2.15	5.52	na	na	6.70
H7	0.93	1.99	na	na	na	5.05
H8	2.31	2.28	5.85	na	na	15.72
H10	1.50	2.15	10.82	na	na	11.39
H11	1.68	3.05	10.24	na	na	13.55
H12	2.66	3.85	15.05	18.32	na	18.99
H13	1.68	1.96	8.54	na	na	10.31
H14	1.19	2.00	1.13	na	na	5.83
H15	1.45	2.45	8.31	4.14	na	12.03
H16	2.21	2.68	na	na	na	12.29
H17	0.77	1.80	na	na	na	4.32
H18	0.92	1.53	3.20	3.97	na	7.59
H19	1.61	4.18	na	na	na	4.42
F1	0.90	2.60	6.31	na	na	7.41
F3	0.19	0.73	na	na	na	5.87
F4	0.55	1.70	0.74	na	na	10.22
Mean ± SD		2.60±1.02	6.90±3.84	12.09±9.34	19.98	

Note: na, not applicable.

ence of the three most dominant species (by cover) in a 1 m radius plot around each sighting location. We then calculated the frequency of presence of the plant species for each snail by dividing the number of sightings where a plant species was listed by the total number of sightings. We separated the vegetation analysis into snails found predominantly in forest habitat (n = 12) and snails found predominantly in meadow habitat (n = 9). Differences in plant use between habitat types were assessed using Student's t tests. All analyses were done using the "base" and "adehabitat" packages in the statistical program R (Calenge 2006; R Development Core Team 2010).

Results

We tracked 21 snails for 54–1190 days (540 ± 300 days, mean ± SD) with 12–101 sightings per snail (47 ± 27 sightings) between 4 May 2005 and 6 Aug. 2008 (Table 1). Thirteen of the 21 marked snails died during the study period (Table 1).

Snails stayed near their initial location, travelling a net distance of 6.9 m after 1 year (Table 2). The maximum daily dispersal distance was 4.5 m, which is less than the width of a paved road (Table 2). Mean monthly displacement was 2.6 m, but distance travelled peaked in May at 5.4 m (Fig. 1). The maximum displacement that we observed for any snail was 32.2 m from its initial location during 3 years of tracking. By examining graphs of the snails' distance from initial location across time, we found that snails were active travellers between hibernation periods, but their net displacement was small; they rarely travelled >15 m from their original location and often returned to locations within a few metres of their original location (Fig. 2). Snails strongly preferred gravel as a nesting substrate (Steensma et al. 2009), which was limited to footpaths. Thus, snails may have been returning to these preferred nesting sites. One of the snails tracked for the longest period (3 years) was an exception; it travelled farther from its initial location each year and had moved 28.9 m after 3 years.

Snails occupied home-range areas of 18.4–404.4 m^2 (117.0 ± 122.7 m^2; Fig. 3). Home-range area was smaller in

Fig. 1. Mean monthly dispersal distances for Oregon forestsnails (*Allogona townsendiana*) (n = 21) in Langley, British Columbia, Canada.

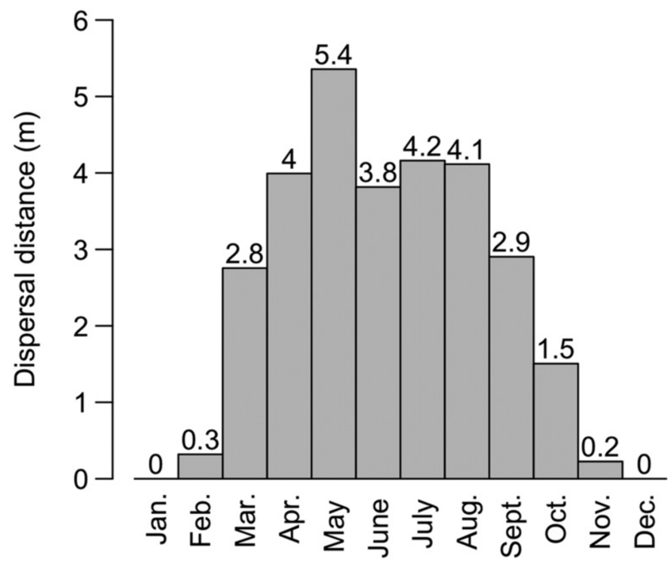
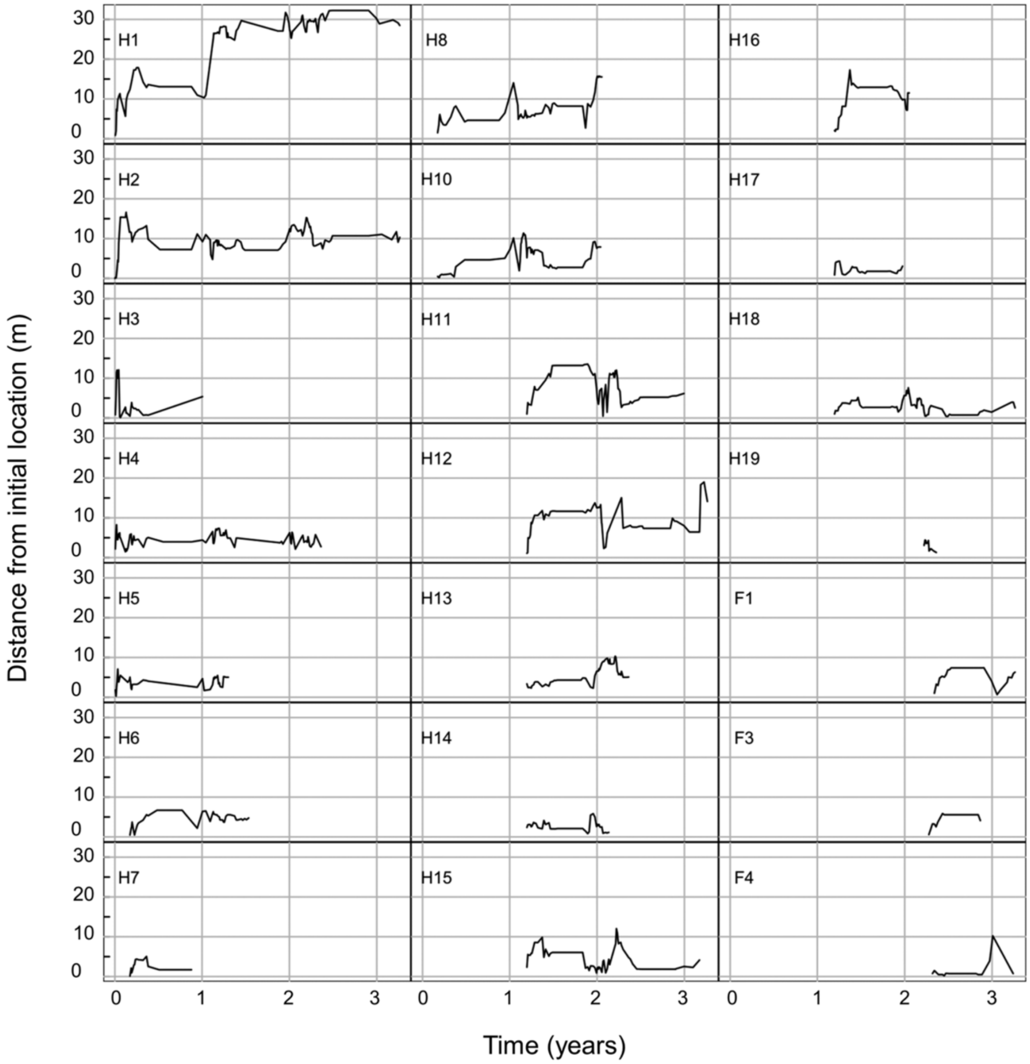


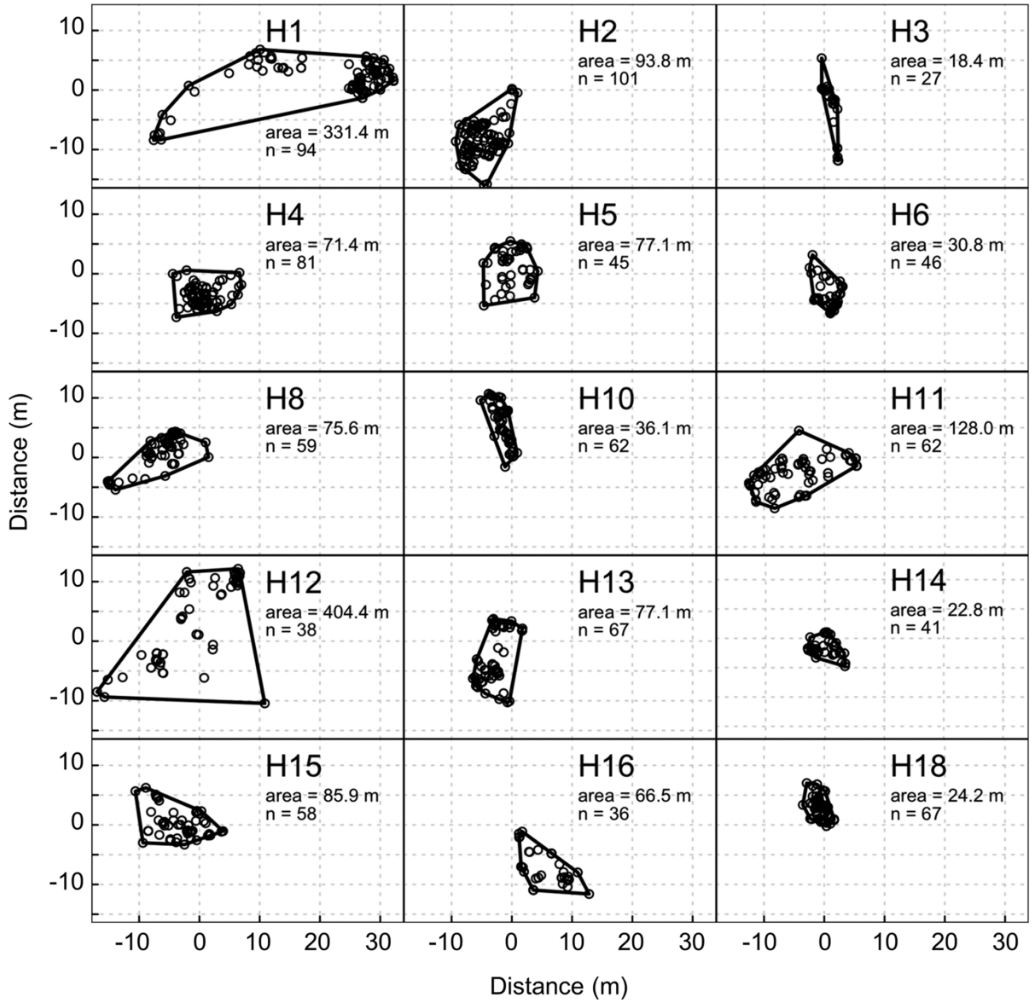
Fig. 2. Distance from initial location across time for 21 Oregon forestsnails (*Allogona townsendiana*) in Langley, British Columbia, Canada. Time is measured from the day that we tagged the first group of snails, which is 4 May 2005. Level sections of the plots are times when the snails were hibernating or aestivating.



habitats with high availability of stinging nettle, which may be in an indicator of high-quality habitat (Fig. 4). There was also a trend of decreasing home-range size with greater availability of coarse woody debris; however, it was not statistically significant (Fig. 4). Snail distance to coarse woody debris averaged 1.05 m (SD = 0.88 m) and distance to stinging nettle averaged 0.52 m (SD = 0.40 m) (Table 1). We hypothesized that coarse woody debris might only be important during mating season and tested for a difference in snail proximity to coarse woody debris during peak mating season (Mar.–Apr.) versus the rest of the year, but we did not detect a difference (mean effect size = 0.12 m, SD = 0.77 m; paired-sample t test, t = –64, p = 0.53). We found snails in both forest habitat and in disturbed meadow habitat, and despite apparent differences in quality, home-range sizes were similar in these habitats (Student's t test, t = –0.013, p = 0.99).

Nine snails used forest habitat exclusively, 12 used both forest and meadow habitat, and none of the snails used meadow habitat exclusively (Table 1). Stinging nettle was the plant species with the highest frequency of presence at snail locations (0.63 ± 0.21, mean ± SD), followed by reed canarygrass (0.41 ± 0.38) and creeping buttercup (0.25 ± 0.31) (Table 3). Across habitat types, stinging nettle was the most frequent plant present in both forest and meadow habitats (0.56 ± 0.05 and 0.75 ± 0.07, respectively; Table 3). Snails were sighted on native vegetation, on average, 9% of the time, and one-third of these sightings were on stinging nettle (3.5% of the total; 35 sightings). Stinging nettle was also the only plant species detected as a dominant species in the occupied home range of every snail (range in frequency across individual snails = 0.18–0.95). In forest habitat, common plant species (present in >15% of plots) included stinging nettle, creeping buttercup, reed canarygrass, western swordfern (*Polystichum munitum* (Kaulfuss) K. Presl), Indian plum (*Oemleria cerasiformis* (Torr. & A. Gray ex Hook. & Arn.) Landon), piggy-back plant (*Tolmiea menziesii* (Pursh) Torr. & A. Gray), salmonberry (*Rubus spectabilis* Pursh), and lady fern (*Athrium filix-femina* (L.) Roth), while in meadow habitat, common plants included stinging nettle, reed canarygrass, trailing blackberry (*Rubus ursinus* Cham. & Schltdl.), and creeping buttercup. Of these common species,

Fig. 3. Relocation points and minimum convex polygons for 15 Oregon forestsnails (*Allogona townsendiana*) in Langley, British Columbia, Canada. Snail IDs, home-range areas (m^2), and number of relocations are reported in each plot. The grid origin represents each snail's initial location.



stinging nettle and reed canarygrass were present more frequently in meadow habitat than in forest habitat, while western sword fern was present more frequently in forest habitat (Table 3). There was a trend that most of these plant species were more common in forest habitat than in meadow habitat (21 of 29 species), but few of the differences were statistically significant (Table 3). Cooley's hedgenettle (*Stachys chamissonis* Benth. var. *cooleyae* (A. Heller) G.A. Mulligan & D.B. Munro) was more frequently used in meadow habitat, but it was rarely used in both habitats and there is no prior evidence to suggest that Oregon forestsnail is associated with it.

Discussion

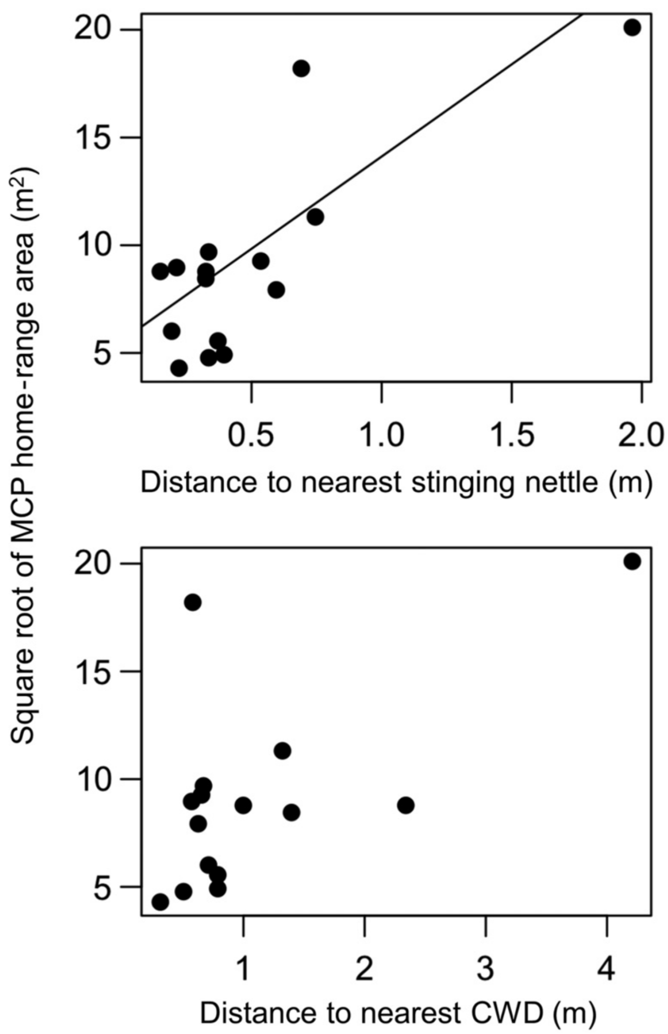
Dispersal distances

Although limited dispersal prevents colonization of suitable habitat patches, it also reduces the risk of moving into unsuitable habitat. In southwestern British Columbia, where forest fragments are surrounded by rural and urban development and intersected by roads, dispersal is a risky behaviour. We found that Oregon forestsnails were relatively sedentary. Their dispersal distances were limited (mean = 2.6 m per month) and they remained within a core area, rather than increasing distance from their initial location. The terrestrial snail *Arianta arbustorum* L., 1758 from central Sweden had comparable dispersal distances of 1.5–4.9 m net displacement during 3 months, depending on habitat type (Baur and Baur 1990). The maximum observed displacement of *A. arbustorum* was 14 m (Baur and Baur 1990). In contrast, the Australian land snail *Hedleyella falconeri* (Gray, 1834) had impressive dispersal distances of up to 21.7 m per night (Murphy 2002). However, the net displacement after 3 months of tracking was only 31.6 m. The giant African land snail (*Achatina fulicai* (Férussac, 1821)) also had greater dispersal distances, especially in juveniles, which travelled 12.1 m per night and moved away from their original locations in nearly straight lines (Tomiyama and Nakane 1993). Young adults and old adults of giant African land snails travelled less distance per night (3.65 and 1.45 m, respectively) and circled back near their original locations. It is possible that Oregon forestsnails also disperse as juveniles, rather than as adults.

Broad-scale habitat use and home-range sizes

The few previous studies of the Oregon forestsnail describe its habitat as primarily intact, mixed-wood forests

Fig. 4. Relationships of home-range area (square-root-transformed minimum convex polygons (MCP)) with proximity to stinging nettle (*Urtica dioica*) and coarse woody debris (CWD) for 15 Oregon forestsnails (*Allogona townsendiana*) in Langley, British Columbia, Canada. The solid line represents a statistically significant relationship between home-range area and snail proximity to stinging nettle (slope = 8.56, SE = 2.26, $F_{[1,13]}$ = 13.46, p = 0.002). The relationship between home-range area and snail proximity to coarse woody debris was not significant (slope = 2.15, SE = 1.32, $F_{[1,13]}$ = 2.64, p = 0.13).



(Ovaska et al. 2001), though at least one population has been discovered in disturbed habitat dominated by cottonwood (genus *Populus* L.) and willow (genus *Salix* L.) trees (Cameron 1986). Our study shows that there can be high value in mosaic habitats that include both forest and meadow patches, but no home ranges were exclusively in open meadow. Thirteen of the 21 snails that we tracked used both forest and meadow habitat (62%), while the remaining eight used forest habitat exclusively. Because much of the habitat remaining in southwestern British Columbia is fragmented with a high proportion of forest–meadow edges, it is important to realize that these mixed habitats, in addition to intact continuous forest, are potentially suitable habitat for the Oregon forestsnail.

Despite large differences in habitat characteristics, we did not detect a difference in home-range size between snails that used primarily forest habitat and those that used primarily edge or meadow habitat. We predicted that snails sighted in edge or meadow habitat >50% of the time might have larger home ranges because of their apparently poor-quality habitat; meadows lack cover from coarse woody debris, understory vegetation, and the forest canopy, possibly increasing risk of predation and desiccation. However, the thickly matted reed canarygrass, which dominated meadows, may provide some shelter from both sunlight and predators. Interestingly, stinging nettle was frequently encountered in both forest and meadow habitat. Snails that either selected or randomly dispersed to edge or meadow habitat may have benefited from the high abundance of stinging nettle. If stinging nettle is an important plant for the Oregon forestsnail, then lower quality habitats within forest edges and meadow that lack stinging nettle might be improved by encouraging its growth. An investigation of reproductive rates and survival in the various habitat types is necessary to determine whether meadows along forest edges are truly suitable habitats for the Oregon forestsnail, or are ecological sinks.

Stinging nettle and coarse woody debris

Home-range area was positively related to distance to stinging nettle, with snails persisting on smaller home ranges where stinging nettle was in close proximity (indicating high availability of stinging nettle). If small home-range size is an indicator of habitat quality, stinging nettle contributes to high-quality habitat for the Oregon forestsnail. Alternatively, snails may be seeking out wet or moist habitat, which is also important for stinging nettle (Pojar and MacKinnon 1994). Like other snails, the Oregon forestsnail is sensitive to desiccation and experiences periods of inactivity during summer months, aestivating with an epiphragm during the hottest days (Prior 1985; Steensma et al. 2009). However, stem density of stinging nettle was approximately 2 stems per 50 m^2 across the study site (K.M.M. Steensma, unpublished data), thus a distance to stinging nettle of 0.52 ± 0.40 m (mean ± SD) suggests that snails were selecting for habitat near stinging nettle. Both adult and juvenile Oregon forestsnails have been observed eating live stinging nettle and it may form a large proportion of the diet of juvenile Oregon forestsnails, as well as providing cover habitat for juveniles that climb nettle stalks during early dispersal (Steensma et al. 2009). An experimental feeding trial in Europe identified stinging nettle as a preferred and palatable food source for another terrestrial snail, *Arianta arbustorum* (Grime and Blythe 1969). This combination of evidence supports past suggestions that stinging nettle is important to the ecology of the Oregon forestsnail (COSEWIC 2002; Steensma et al. 2009).

Coarse woody debris is thought to provide a moderate microclimate, trap moisture, and harbour potential food items such as fungi, bacteria, and algae (Kappes et al. 2006; Sólymos et al. 2009). Distance to coarse woody debris was positively, but not significantly, related to home-range area. However, our analysis was limited by the narrow range of coarse woody debris availability at our study site. Most snails maintained mean distances of <1.5 m from coarse woody debris, and it is possible that in very poor quality habitats, they would be forced to travel farther for these resources. The most striking use of coarse woody debris by the Oregon forestsnail occurs during mating; in our study population, >50%

Table 3. Plant use as a frequency (mean ± SD) of presence in vegetation plots (1 m radius around sighting location) for 21 Oregon forestsnails (*Allogona townsendiana*) in both forest habitat (n = 12) and meadow habitat (n = 9) in Langley, British Columbia, Canada.

Plant species	Forest	Meadow	t	p
Stinging nettle (*Urtica dioica*)	0.56±0.05	0.75±0.07	–2.24	**0.04**
Creeping buttercup (*Ranunculus repens*)	0.29±0.09	0.19±0.11	0.67	0.51
Reed canarygrass (*Phalaris arundinacea*)	0.24±0.09	0.69±0.11	–3.18	**0.01**
Sword fern (*Polystichum munitum*)	0.21±0.05	0.00±0.07	2.38	**0.03**
Indian plum (*Oemleria cerasiformis*)	0.21±0.04	0.11±0.05	1.54	0.14
Piggy-back plant (*Tolmiea menziesii*)	0.20±0.07	0.12±0.09	0.70	0.49
Salmonberry (*Rubus spectabilis*)	0.17±0.05	0.14±0.06	0.28	0.71
Lady fern (*Athrium filix-femina*)	0.16±0.05	0.01±0.07	1.68	0.11
Trailing blackberry (*Rubus ursinus*)	0.13±0.06	0.25±0.08	–1.17	0.26
Red elderberry (*Sambucus racemosa* L.)	0.05±0.01	0.01±0.02	1.86	0.08
Thimbleberry (*Rubus parviflorus* Nutt.)	0.04±0.03	0.03±0.03	0.05	0.96
Western brackenfern (*Pteridium aquilinum* (L.) Kuhn)	0.04±0.02	0.01±0.02	1.16	0.26
Herb-Robert (*Geranium robertianum* L.)	0.04±0.02	0.00±0.02	1.34	0.20
Himalayan blackberry (*Rubus discolor* Focke)	0.04±0.02	0.00±0.03	0.91	0.38
Other*	0.04±0.02	0.03±0.02	0.16	0.87
Common snowberry (*Symphoricarpos albus* (L.) S.F. Blake)	0.03±0.02	0.02±0.02	0.52	0.61
Pacific bleeding heart (*Dicentra formosa* (Haw.) Walp.)	0.03±0.02	0.00±0.02	1.18	0.25
Enchanter's nightshade (*Circaea alpina* L.)	0.03±0.02	0.00±0.03	0.82	0.42
Cleavers (*Galium aparine* L.)	0.03±0.01	0.02±0.01	0.55	0.59
Fringecup (*Tellima grandiflora* (Pursh) Douglas ex Lindl.)	0.03±0.01	0.00±0.01	1.70	0.11
Vine maple (*Acer circinatum* Pursh)	0.03±0.01	0.01±0.02	0.94	0.36
Small balsam (*Impatiens parviflora* DC.)	0.02±0.02	0.05±0.02	–1.00	0.33
Hooker's fairybells (*Prosartes hookeri* Torr.)	0.02±0.01	0.00±0.01	1.06	0.30
Beaked hazelnut (*Corylus cornuta* ssp. *californica* (A. DC.) A.E. Murray)	0.02±0.01	0.02±0.02	1.18	0.25
Shield fern (*Dryopteris expansa* (K. Presl) Fraser-Jenkins & Jerry)	0.02±0.01	0.00±0.01	1.67	0.11
Red alder (*Alnus rubra* Bong.)	0.02±0.01	0.00±0.01	0.97	0.35
Moss spp.	0.01±0.01	0.02±0.01	–0.17	0.86
Cooley's hedge nettle (*Stachys cooleyae*)	0.00±0.02	0.06±0.02	–2.12	**0.05**
Common horsetail (*Equisetum arvense* L.)	0.00±0.02	0.05±0.02	–1.72	0.10
Himalayan balsam (*Impatiens glandulifera* Royle)	0.00±0.02	0.04±0.02	–1.45	0.16

Note: The t and p values given are for Student's t tests for differences in plant presence between forest and meadow habitats. Values in boldface type indicate plant species that differ significantly in frequency of use by the snails between habitat types ($p < 0.05$).

*Includes black twinberry (*Lonicera involucrata* (Richardson) Banks ex Spreng.), grass species, mountain sweet cicely (*Osmorhiza chilensis* Hook. & Arn. = *Osmorhiza berteroi* DC.), false Solomon's seal (*Smilacina racemosa*), hardhack (*Spiraea douglasii* Hook.), black gooseberry (*Ribes lacustre* (Pers.) Poir.), baldhip rose (*Rosa gymnocarpa* Nutt.), cardamine species (genus *Cardamine* L.), western oakfern (*Gymnocarpium dryopteris* (L.) Newman), sitka spruce (*Picea sitchensis* (Bong.) Carrière), and trailing yellow violet (*Viola sempervirens* Greene).

of observed copulations took place on coarse woody debris (Steensma et al. 2009). However, mating is restricted to a brief period during the spring (Steensma et al. 2009), and when the use of coarse woody debris as a substrate was averaged across the year, it was rare (proportion of detections = 0.018 ± 0.030, mean ± SD). Thus, the effect of coarse woody debris may appear weak across the year because mating is a brief event in a snail's life. We did not detect a preference for coarse wood debris even when we compared peak mating months (Mar.–Apr.) with the rest of the year. Similarly, Murphy (2002) studied the use of coarse woody debris as daytime shelter by the Australian land snail *H. falconeri* and found that snails simply sheltered where they found themselves at the end of the night, often in the open on the forest floor; there was no selection for coarse woody debris.

Management implications

The Oregon forestsnail has poor dispersal in its adult stage and it is likely that urban and rural environments present many impassable barriers, including roads, yards, and agricultural fields. However, limited dispersal may also be an advantage. Because Oregon forestsnails stay in a core area, typically with a radius of <15 m, they are not at risk of migrating out of suitable habitat patches unless their core area is within 15 m of an edge. Additionally, they may be able to persist in small habitat patches given their small home-range areas, though the long-term genetic effects of small isolated populations are unknown for the Oregon forestsnail.

Conservation of habitat of Oregon forestsnails should focus on mixed-wood forest, but should also include disturbed meadow and edge habitats immediately adjacent to wooded areas, especially because these are the most common habitat types remaining throughout the snail's Canadian range. Although 62% of our tagged snails used some edge or meadow habitat, 100% of the snails made use of the intact mixed-wood forest at our site, which contained >30 native plant species. The forest undergrowth may provide favoured food sources, as well as protection from desiccation and predators. Stinging nettle was a consistent feature across habitats where we found Oregon forestsnails and coincides with high-quality home ranges. Thus, it may be a valuable indicator of habitat for previously undiscovered populations of Oregon forestsnails, or suitable habitat for potential snail relocation.

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