Morphology, distribution and desiccation in the brown garden snail (*Cantareus aspersus*) in northern New Zealand

John K. Perrott[1]*; Iris I. Levin[1,2] and Elizabeth A. Hyde[1,3]
[1] EcoQuest Education Foundation, Ecological Field Centre, East Coast Road, RD 3, Pokeno, New Zealand
[2] Department of Biology, Bowdoin College, Brunswick, Maine 04011, USA
[3] Department of Natural Resources, University of New Hampshire, Durham, New Hampshire 03824, USA
* Author for correspondence (E-mail jkperrott@xtra.co.nz)

Published on-line: 21 May 2007

Abstract: Size, density and distribution of the brown garden snail (*Cantareus aspersus*) were observed relative to cover at a coastal reserve on the North Island, New Zealand. Cover variables depended on vegetation height and available debris (rubbish, wood, cow dung). Air temperature, ground temperature, and relative humidity were recorded continuously during the field survey for the various cover types. Live snails used debris disproportionately as resting habitat, where relative humidity and temperature were the least variable. Desiccation rates were obtained by dehydrating snails of three size-classes and calculating desiccation rates as a function of water loss over time under controlled conditions in the laboratory. Results suggest that the shell aperture:size ratio is an important factor regarding desiccation stress in *C. aspersus*, especially in young and small-sized snails.

Keywords: *Cantareus aspersus*; coastal reserve; density; distribution; desiccation; shell size; shell aperture: size ratio

Introduction

The brown garden snail *Cantareus aspersus*, formerly *Helix aspersa* (Barker 1999), is a cosmopolitan pest species the biology of which is well understood, but its invasion of New Zealand indigenous ecosystems is not well documented. The species occurs widely in New Zealand and there is growing concern about its potential adverse effects on indigenous ecosystems (Barker & Watts 2002). Concerns about negative impacts include herbivore pressure, resource competition, habitat fouling, and parasite and disease transmission. The snail is calciphile and most prevalent in coastal environments, especially the scrubland and dune systems of the upper North Island. The New Zealand Department of Conservation is currently considering strategic options and methodologies for the control of *C. aspersus* on conservation lands. This study was conducted at a coastal reserve and provides information on the effects of desiccation stress on the density and size distribution of *C. aspersus* at the Robert Findlay Wildlife Reserve, Miranda, Firth of Thames.

Cantareus aspersus was introduced into New Zealand during the 1860s and is now the most abundant and widespread terrestrial snail species. It is a potential pest due to its high fecundity and dispersal ability. Because it is hermaphroditic, populations are able to establish from a single individual. In addition, under optimal conditions, *C. aspersus* can lay up to 2500 eggs in a season (Runham 1989). However, under dry conditions, juvenile survival and recruitment can be significantly reduced (Heatwole & Heatwole 1978). Water loss in land snails occurs mainly from the mantle cavity via respiration, through the shell aperture, and through the shell itself depending on age and thickness (Goodfriend 1986). Pulmonates minimise water loss via three primary means: structure, behaviour and physiology (Asami 1993). A snail's shell and the secretion of a mucus epiphragm over the shell aperture are its primary structural means of protection from water loss (Machin 1967). Retraction of the entire body inside the shell or avoiding daytime heat and dryness are behavioural means to reduce water loss (Machin 1967; Cameron 1978). Physiological means include aestivation and the retention of pallial fluid within the mantle cavity (Blinn 1964; Riddle 1981; Smith 1981).

Temporal variation in population density, growth, and reproductive activity in land snails is largely controlled by environmental conditions (Albuquerque de Matos 1989, 1990; Elmslie 1989). Shell size and shape can be highly variable, often reflecting age or adaptations to particular habitats. Reproductive output is often positively correlated with shell size (Goodfriend

1986). Because surface area to volume ratios decrease with increasing size, one would predict that conditions of greater desiccation stress would favour larger snails (Nevo et al. 1983; Goodfriend 1986). This is not found at the faunal level as both large and small snails occur in dry and wet conditions (Goodfriend 1986) even though within species, larger snails have greater survivorship compared with smaller snails in low-humidity environments (Heatwole & Heatwole 1978; Knights 1979).

Variation in shell aperture area relative to shell size has usually been interpreted in the context either of regulation of water loss or of reduction in predation pressure (Goodfriend 1986). Machin (1967) compared three sympatric land snail species and found that, when inactive, the mean water loss through the shell aperture increased with mean aperture size, regardless of the presence of an epiphragm. Water loss through the shell aperture is proportional to aperture area (Goodfriend 1986). *C. aspersus* is typically active in wet conditions and at night, when moisture loss is supposedly less than during daytime. Activity and population dynamics of *C. aspersus* are often dictated by climate, as well as by availability of cover sites (tall vegetation and debris).

The functional significance of cover availability is key to understanding population dynamics of *C. aspersus*. The density and distribution of suitable cover sites may regulate population structure in several ways. High-density cover sites can contribute to high snail densities by providing greater spatial and temporal opportunities for egg-laying, less clumping and greater potential to avoid avian predators, greater opportunity to escape adverse weather conditions, increased activity due to greater likelihood of finding cover, and increased fecundity due to increased activity. Aestivation, grouping and homing behaviours in *C. aspersus* may compensate to some degree in low-density cover sites. Considering that exotic weedy species often compete best with native species in disturbed environments, the unpredictability of cover in coastal environments may benefit *C. aspersus* via reduced competition for space. Therefore, while it should not be surprising to find calciphiles like *C. aspersus* predominately in coastal environments, their success in these habitats may be primarily due to their broad environmental tolerances, high fecundity, and adaptability to stochastic environments.

In low-density cover sites, snails can manage water loss by grouping together and by forming an epiphragm. Formation of an epiphragm (at which time the snail is said to be in aestivation) creates an effective barrier to moisture loss over the aperture (Asami 1993). Aestivation generally occurs in the dry, hot seasons, and can last months at a time. There are records of snails in aestivation for several years (Boss 1974; Barnes 1986). In aestivation, *C. aspersus* can survive water loss equal to 50% of its body weight (Barnes 1986). Understanding the occurrence and frequency of aestivation in relation to desiccation stress may allow wildlife managers to design more effective control measures.

In general, moisture conditions appear to be the best-documented environmental correlate of shell size across a wide range of terrestrial land snail species (Goodfriend 1986). Higher levels of moisture tend to correlate with increased snail densities, growth rates, and larger adult sizes (Brown 1913; Sacchi 1965; Gould 1984). High snail densities probably correlate with both increased snail fecundity and more efficient snail matings. These will be due in part to more frequent or extended periods of activity and higher food intake rates. However, there are many possible confounding variables such as calcium levels, population density, and food availability. *C. aspersus* represents an abundant, non-toxic, easily captured prey, and therefore they are consumed by a wide range of predators. Avian and mammal predators have little difficulty extracting the snail from its shell. The function of the shell, multipurpose or not, appears to be primarily related to protection from insect predators and water conservation. In this paper we investigate *C. aspersus* densities, distributions, and morphology in relation to cover type and desiccation stress. We test the following predictions: (1) snail densities and size distributions vary according to cover type, (2) smaller *C. aspersus* have elevated desiccation rates, and (3) *C. aspersus* with reduced shell aperture:size ratios have reduced desiccation rates.

Methods

Study site

The Robert Findlay Wildlife Reserve, about 25 ha, is situated at Miranda (37º13'S and 175º23'E; Fig. 1), on the south-western coast of the Firth of Thames in northern New Zealand. The reserve is an internationally important habitat for shorebirds, providing a stopover and feeding site for up to 25 000 birds at a time, most of which are migratory wading species. The reserve is open to the public and largely comprised of pasture grass. Up to 90 head of domestic cattle are grazed periodically throughout the year on 15 of the 25 ha, but were not present during this study. Cattle grazing is used to keep vegetation low, which may benefit the shorebirds by making predators more visible. The short vegetation may decrease ground humidity levels, thus affecting snail distributions. Low vegetation exposes the soil to sun, elevating soil temperatures and lowering surface moisture levels. The study site is on a Chenier plain, and crushed shells are found in the substratum

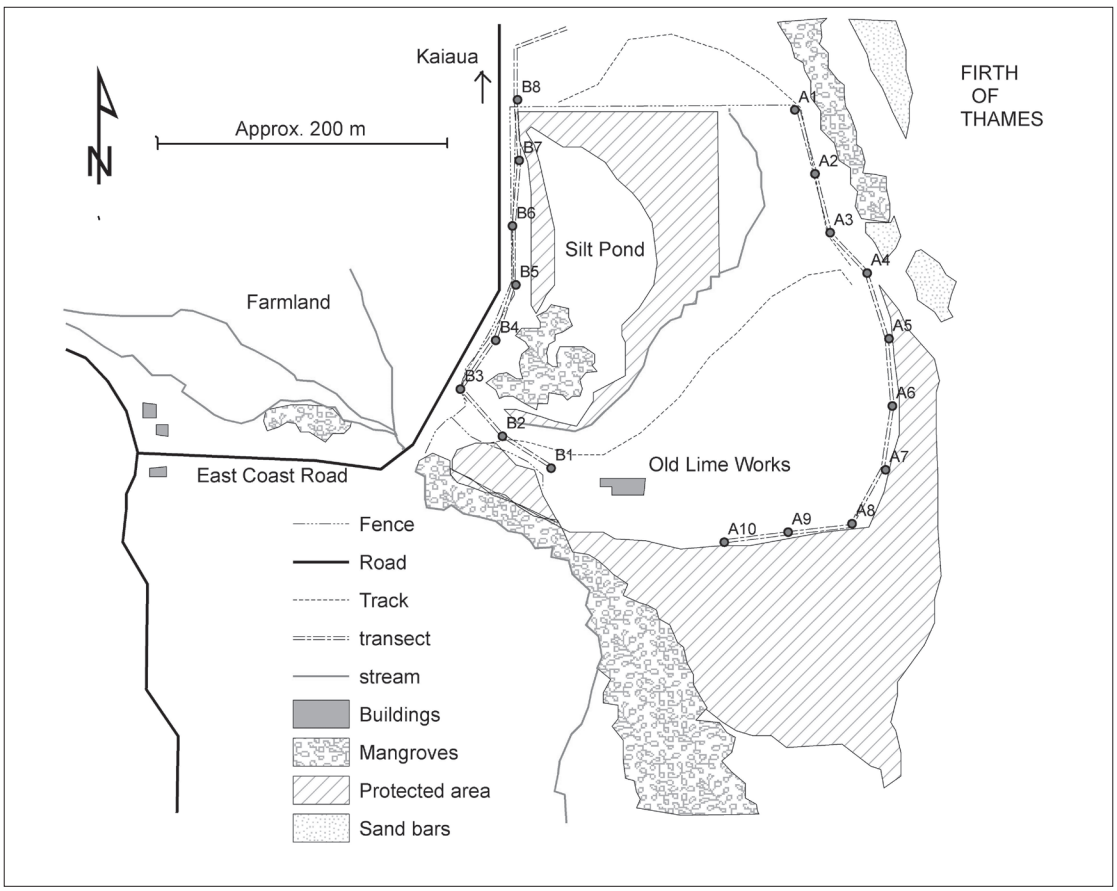

Figure 1. Map of the Robert Findlay Wildlife Reserve, northern New Zealand, and surrounding areas showing locations of transect lines and *Cantareus aspersus* sample areas.

throughout the study site. Within the study site there are various microhabitats, including areas of tall fennel plants (*Foeniculum vulgare*), moderately tall grasses, and short grass and glasswort (*Sarcocornia quinqueflora*). The shoreline has both shell banks and mangroves (*Avicennia marina*). Debris, mostly comprising driftwood, litters the ground both near and far from the shore, and can serve as an ideal cover and habitat for snails.

Field methods

Fieldwork was conducted from 19 to 28 April 2004. Snail densities in different heights of vegetation were estimated using 1-m^2 quadrats, along two parallel transect lines (Fig. 1). Transect A ran along the coast about 10 m from the high tide mark and Transect B, 200 m from the high tide mark, ran along the inside of a permanent stock fence adjacent to the East Coast Road. Both transect lines were 500 m long and sampling was conducted every 50 m. Six Hobo™ data loggers (RH Temp 2x external) were used to measure climatic conditions including ground temperature, air temperature and relative humidity in short, medium, and tall vegetation. Two data loggers measuring temperature and relative humidity were also placed under separate pieces of debris (driftwood). Air temperature was recorded at two separate locations along the shoreline.

At each sample point, (every 50 m along transect), a randomised stratified sampling method was used for three vegetation height categories: short (0–5 cm), medium (5–25 cm), and tall (>25 cm). The quadrat was placed in vegetation of appropriate height closest to the sample point. All living and dead snails were

counted and great care taken to account for 100% of snails within each 1-m^2 quadrat, and their shell and apertures sizes measured across the widest part using 150-mm digital callipers. The closest piece of debris, classified either as driftwood, rubbish or cow dung, was located and cover area measured. Snails on or under debris were then counted and measured as above. Data from each quadrat were analysed independently with several parameters recorded: (1) number of snails per square metre of vegetation; (2) number of snails relative to vegetation height; (3) number of snails per square metre of cover (e.g. driftwood, rubbish); (4) snail sizes relative to vegetation height; (5) mean snail size per square metre of cover; (6) shell aperture:size ratios relative to vegetation height and cover type.

Laboratory methods

Snails used in this study were collected from the study site on 14 April 2004 and initially stored in a refrigerator at 10ºC. Ample food (fennel and grass) and water was provided and health and activity were monitored daily for 4 days. On 18 April 2004, 60 individuals representing three shell-size categories measured across the widest part (small, <10 mm; medium, 10–20 mm; large, >20 mm; $n = 20$ each) were sorted and placed in an aquarium (40 × 26 × 23 cm) under moist conditions (70–100% humidity) at approximately 17ºC. Food was withheld from this point to clear digestive tracts and minimise error in body mass measurements (see Asami 1993). Individuals were numbered for identification using a permanent marker on a small area on the shell. Two days later, they were weighed using an Ohaus Scout II™ digital scale (precision: 0.1 g) and shell and aperture measurements were made (across the widest part, precision: 0.1 mm). Subsequently, humidity was lowered using Damp Rid™ (calcium chloride) as a desiccant, placed within the aquarium, taking care that snails were not in contact with it. Relative humidity and temperature inside and outside the aquarium were monitored using a Hobo™ data logger. On days 2, 4, 6, and 8, all snails were reweighed and their survivorship was recorded. Dead snails were removed from the aquarium. Twenty-four (eight each of small, medium, and large) snails were kept as a control group in a similar container (16 ×16 × 8 cm) at approximately 17ºC, but without the desiccant. All individuals within the control group were marked, weighed and measured as above and reweighed on days 2, 4, 6 and 8. Desiccation rate (r) was calculated (day 0–8) for each individual and for group size (small, medium, large) (see Asami 1993): $r = (M_0 - M_t)/M_0$, where M_0 is initial body mass and M_t the mass at day 8. Daily rate (dr) was calculated as: $dr = (M_0 - M_t)/t$, where $t = 8$. Proportional body mass loss (pbml) was calculated as: pbml = $100 - 100(M_0 - M_t)$.

Statistical analysis

Regression analysis was used to determine whether number or size was correlated with height of vegetation and to test whether shell aperture:size ratios are correlated with vegetation height and cover area. All analyses were performed using StatView for Windows, version 5.1.0, and Excel for Windows 2000. Regression analysis is used to compare shell size and desiccation rate, size and daily rate, shell aperture:size ratio and proportional weight loss, and shell aperture:size ratio and desiccation rate. One-way ANOVA was used to test whether variables (shell size, snail density, and number of individuals) varied significantly between four dependent cover-type parameters (short, medium and tall vegetation and debris).

Results

Density and size distribution of *C. aspersus*

In total, 729 live and dead snails were counted from 60 vegetation quadrats and 14 debris samples. Of these, 631 were alive (active or in aestivation) and 98 were empty shells of dead snails. Of the live snails, 523 were recorded from the vegetation quadrats, and 108 under debris. There were 8.7 ± 2.4 (mean ± SE; range 0–139) live snails m^{-2} on vegetation. The highest density of live snails (82.4 ± 3.4 snails m^{-2}) was recorded under debris (total area = 1.31 m^2). Higher live snail densities were recorded in tall vegetation (22.4 ± 7.1 live snails m^{-2}) than in medium (3.7 ± 2.2 snails m^{-2}) and short vegetation (0.05 ± 0.05 snails m^{-2}; Fig. 2). Only two snails were found in short vegetation (one alive and one empty shell). Snail densities in short, medium and tall vegetation and under debris did not depend on the sampling point along the transect ($F_{19,696} = 0.953$; $P = 0.526$), but did depend on cover type (short, medium, tall vegetation or debris; $F_{3,696} = 7.931$; $P = 0.0001$) with greater numbers of snails being located in tall vegetation ($F_{3,696} = 6.195$; $P = 0.0008$).

Maximum shell and aperture size was measured on 696 live and dead snails from the vegetation and debris survey. Snail-shell aperture sizes ranged from 5.2 to 35.5 mm (Fig. 3), with a mean shell size of 15.5 ± 0.3 mm across all status categories (alive, aestivating, dead, dead predated; Fig. 4). Mean snail shell sizes (mm) per status category in the vegetation quadrat samples were: alive (13.9 ± 0.3 mm, $n = 460$), aestivating (20.1 ± 1.1 mm, $n = 37$), dead (19.1 ± 1.0 mm, $n = 74$), and predated (based on mouse (*Mus musculus*) teeth marks or thrush (*Turdus* spp.) anvil sites; 23.9 ± 0.9 mm, $n = 7$). Snail status was dependent on vegetation/cover type ($\chi^2_9 = 34.51$, $P \leq 0.0001$; Table 1). Mean snail shell sizes (mm) from debris were: alive (15.8 ± 0.6, $n = 93$), aestivating (18.9 ± 2.4, $n = 14$), dead (23.2 ± 1.8, $n =$

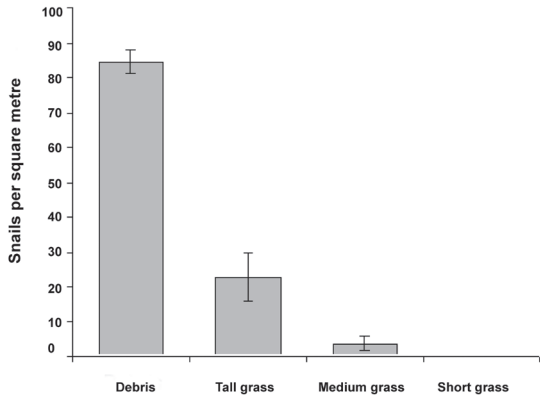

Figure 2. Mean live snail densities per cover type (debris, tall grass, medium grass, short grass) for *Cantareus aspersus* (n = 631) at the Robert Findlay Wildlife Reserve, northern New Zealand. Bars indicate SE.

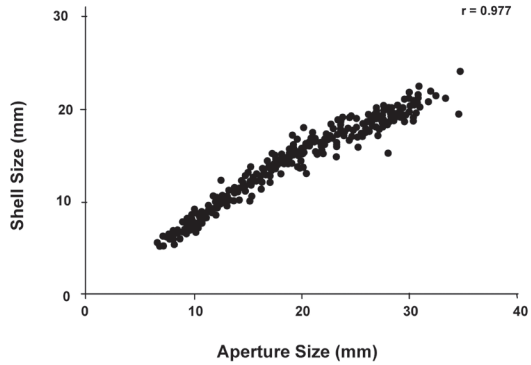

Figure 3. Correlations of shell size and shell aperture size for *Cantareus aspersus* (n = 696) at the Robert Findlay Wildlife Reserve, northern New Zealand (April 2004).

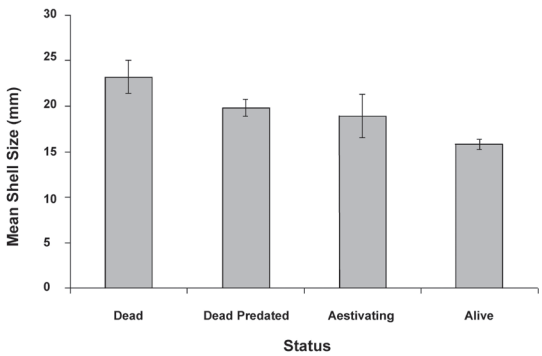

Figure 4. Mean shell size per status category (dead, dead predated, aestivating, alive) of *Cantareus aspersus* (n = 696) at the Robert Findlay Wildlife Reserve, northern New Zealand. Bars indicate SE.

19), dead predated (19.8 ± 0.9, n = 10). Shell size was partially dependent on cover type, with larger snails under debris than in tall, medium or short vegetation ($F_{3,696}$ = 6.614; P = 0.0002). Mean shell size (per sample site) varied little between transects lines ($F_{3,696}$ = 0.811; P = 0.37). There was a very strong correlation between shell size and aperture size (r_{696} = 0.977; $P \leq 0.0001$; Fig. 3).

Shell aperture:size ratio in relation to snail status and cover type

Shell aperture:size ratio was 0.75 ± 0.003 (range = 0.51–0.91; n = 696). The mean shell aperture:size ratio was significantly higher in active than dead snails ($F_{3,3}$ = 2.74, P = 0.04) (mean shell aperture:size ratio for active snails = 0.751, ± 0.002, n = 460; mean shell aperture: size ratio for dead snails = 0.734, ± 0.010, n = 74).

Table 1. Observed and expected frequencies for status versus cover type generated by a chisquare test (n = 696, P ≤ 0.0001) for *Cantareus aspersus* at the Robert Findlay Wildlife Reserve (April 2004), northern New Zealand.

	Short vegetation	Medium vegetation	Tall vegetation	Debris	Total
Observed values:					
Aestivating	0	4	33	14	51
Dead	1	9	46	19	75
Predated	0	3	4	10	17
Alive	0	67	393	93	553
Total	1	83	476	136	696
Expected values:					
Aestivating	0.073	6.082	34.88	9.97	51
Dead	0.22	8.94	51.293	14.66	75

Additional patterns are revealed when shell aperture: size ratio is tested as a factor of status within the three size categories (small, medium, and large snails). Live small snails had smaller ratios than aestivating and dead snails respectively ($F_{2,180} = 6.912$; $P = 0.0013$). In medium-sized snails, status did not depend on the shell aperture:size ratio ($F_{3,363} = 1.660$, $P = 0.18$). Among large snails, dead snails had larger ratios than live and aestivating snails ($F_{3,153} = 2.908$: $P = 0.037$).

Temperature and humidity

The mean temperature in the field during the study was 15.7ºC (calculated from daily high and low temperatures). Relative humidity under debris was 73.2% and 67.6% on transects A and B, respectively. Relative humidity was 65.5% in tall grass, with an average temperature of 19.5ºC. Ground temperature in tall grass on transect B (19.5ºC) was significantly higher than that under debris along transect B (17.2ºC) (Student's paired *t*-test, $P = 0.0035$, d.f. = 18).

Desiccation laboratory experiments

Relative humidity in the tank with desiccant was 81.0% (range: 73–85%) and in the control tank was 97.2% (range: 77–100%). Temperature in the tank with desiccant, was 17.2ºC (range: 16.5–18.5ºC) and in the control tank was 17.1ºC (range 15.7–18.5ºC). The mean snail size for laboratory experiments was 21.8 ± 0.84 mm and the mean shell aperture:size ratio was 0.73 ($n = 60$). All snails in the experimental tank went into aestivation within 12 h, and came out only when handled (for weighing), then went back into aestivation. The desiccation rate varied negatively with shell size (mm); smaller snails had higher desiccation rates than larger snails ($r^2_{60} = -0.461$; $P = 0.0002$). Large snails lost more water per day than the smaller snails ($r^2_{60} = 0.432$; $P \leq 0.0001$). Mean proportional water loss was 12.24% (range: 0–33.3%). Snails with larger shell aperture:size ratios lost proportionally more mass due to desiccation stress ($r^2_{60} = 0.15$; $P = 0.0023$; Fig. 5).

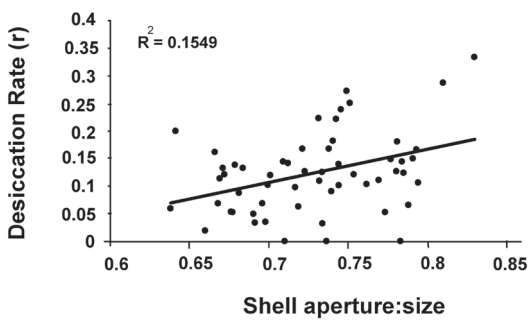

Figure 5. Regression of desiccation rate and *Cantareus aspersus* ($n = 60$) shell aperture:size ratio. Desiccation rate increases with increasing shell aperture:size ratios in laboratory experiments.

Discussion

Size distribution and density

The size distribution of living *C. aspersus* was broad and indicates more than one size/age cohort. Results indicate a relatively low number of large mature snails and a high proportion of small-sized juveniles. *C. aspersus* can lay eggs several times in one breeding season, producing many young at frequent intervals (Barker & Watts 2002). The strong relationship between shell size and aperture size is further evidence of at least two size/age cohorts, assuming growth is isometric. Disproportionately high numbers of live snails were found under debris or in tall vegetation, probably because of higher humidity and lower temperature levels. Based on the inverse relationship between temperature and relative humidity, relative humidity is likely to be lower in short vegetation. In addition, offshore winds may also increase desiccation stress in short vegetation in this reserve, where topography is flat.

Size, density and survival relative to cover

Tall vegetation or debris may also provide protection against predation. Most snails were found in tall vegetation or under debris – cover-types that could make them less conspicuous to thrushes or mice, which seem to be the main snail predators at this site. Predation by invertebrates and cannibalism of hatchlings may also be important, and probably occurs more commonly in covered areas but were not quantified in this study.

Shell size was strongly dependent on cover type, although locations of smaller snails could be more arbitrary, as location could be a result of where eggs were laid. Size dependency on cover type, with larger snails under debris or in tall vegetation, may also be an example of anti-predator behaviour. However, more snails showing evidence of predation were found under debris and in tall grass than in short or medium grass (Table 1). It is possible that fewer of these snails were found in the short grass because predators had removed them. For example, song thrushes (*Turdus philomelos*) and blackbirds (*Turdus merula*) tend to take their prey to a nearby rock and break open the shell using the rock as an anvil. From observing the shell caches left around anvil sites, one can demonstrate that birds are selective predators, choosing larger snails that provide more calories per unit of energy expended. In a mixed population of *Cepaea nemoralis* and the smaller *Cepaea*

hortensis, *C. nemoralis* was preferentially preyed upon by song thrushes (Bantock & Bayley 1973). Mice appear to be more opportunistic predators, preying upon both small and large snails.

Shell aperture:size ratio and survival in the field

We predicted a small aperture:size ratio (proportional size of aperture relative to shell size) would decrease desiccation stress. The ratio was smallest in adults (the aperture size was smallest relative to body size), and largest in the medium- and small-sized snails. A small snail must have an aperture large enough to move and feed effectively. In addition, there may be a period of rapid growth in young snails, when shell size increases disproportionately relative to aperture size. The small shell aperture:size ratio in large snails seems due to the growth of a shell-lip around the aperture, formed when the snail reaches maturity (Barker & Watts 2002).

Ratio and density data for large and medium-sized dead snails have the potential for bias due to selective foraging by birds. Shell thickness must also be taken into consideration; small snails had thinner shells, although this was not quantified in this study. Results suggest the shell aperture:size ratio is an important factor influencing desiccation stress in terrestrial snails, especially in young and small-sized snails.

Desiccation laboratory experiments

Results from the laboratory experiments support the hypothesis that reduced shell aperture:size ratios decrease the desiccation stress and proportional water loss. A consistent trend was identified in all size categories, where snails with relatively small shell aperture:size ratios experienced less desiccation stress. The snails were very susceptible to moisture loss; a difference of approximately 16% humidity was enough to cause a loss of up to 33% body mass. Variability in moisture loss could mostly be attributed to difference in the shell aperture:size ratio, although shell thickness could also be a contributor; unlike Machin (1967), who found that water loss through the aperture increased in a non-linear fashion with aperture size. Other relationships between aperture size, shell aperture:size ratio, size, and water loss were linear. This suggests that the shell aperture:size ratio affects moisture loss of different sized snails in a similar way. Jokinen (1978) found in *Lymnaea elodes* that aestivation occurred primarily in juvenile snails, which she attributed to thin shells and less favourable surface: volume ratios. In that study snails of all sizes were found in aestivation, and in our laboratory experiment there was no observed difference in state (aestivating or not) between size categories during the 8 days of desiccation. Nevertheless, aestivation can be linked to desiccation prevention in this study, as the controls did not aestivate. Morphology, and especially the shell aperture:size ratio, does impact on desiccation rates and proportional water loss, which could be a critical factor in differential mortality in the field.

Acknowledgements

We thank Bill Douglas and Steven Lane (landowners), Keith Woodley and the Miranda Wildlife Trust for their contributions and support. We also thank the entire EcoQuest staff, particularly John Longdon, Ria Brejaart, Peter Maddison, Jono Clark, and Stephanie Todd, for the time and effort they put into this study. We are grateful to Lauren Sherwonit and Carl Gasowski for their fieldwork during a pilot study.

References

Albuquerque de Matos RM 1989. Contributions of genetics to snail farming and conservation. In: Henderson IF ed. Slugs and snails in world agriculture. British Crop Protection Council Monograph 41. Thornton Heath, Surrey, UK. Pp. 11–18.

Albuquerque de Matos RM 1990. Genetic and adaptive characteristics in *Helix aspersa* of direct interest in snail farming. Snail Farming Research 3: 33–43.

Asami T 1993. Interspecific differences in desiccation tolerance of juvenile land snails. Functional Ecology 7: 571–577.

Bantock CR, Bayley JA 1973. Visual selection for shell size in *Cepaea* (Held.). Journal of Animal Ecology 42: 247–261.

Barker GM 1999. Naturalised terrestrial *Stylommatophora* (Mollusca: Gastropoda). In: Fauna of New Zealand 38. Lincoln, Manaaki Whenua Press. Pp. 62–68.

Barker GM, Watts C 2002. Management of the invasive alien snail *Cantareus aspersus* on conservation land. DOC Science Internal Series 31. Wellington, Department of Conservation. 30 p.

Barnes RD 1986. Invertebrate zoology. 5th edn. New York, Saunders College Publishing. Pp. 347–391.

Blinn WC 1964. Water in the mantle cavity of land snails. Physiological Zoology 37: 329–337.

Boss KJ 1974. Oblomovism in the mollusca. Transactions of the American Microscopical Society 93: 460–481.

Brown AP 1913. Variation in two species of *Lucidella* from Jamaica. Proceedings of the Academy of Natural Science Philadelphia 63: 3–21.

Cameron RAD 1978. Differences in the sites of activity of coexisting species of land mollusc. Journal of

Conchology 29: 273–278.
Elmslie LJ 1989. Snail farming in field pens in Italy. In: Henderson IF ed. Slugs and snails in world agriculture. British Crop Protection Council Monograph 41. Thornton Heath, Surrey, UK. Pp. 19–25.
Goodfriend GA 1986. Variation in land-snail shell form and size and its causes: a review. Systematic Zoology 35: 204–223.
Gould SJ 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: a way of studying nonadaptation. Systematic Zoology 33: 217–237.
Heatwole H, Heatwole A 1978. Ecology of the Puerto Rican comaenid tree snails. Malacologia 17: 241–315.
Jokinen EH 1978. The aestivation pattern of a population of *Lymnaea elodes* (Say) (Gastropoda: Lymnaeidae). The American Midland Naturalist 100: 43–53.
Knights RW 1979. Experimental evidence for selection on shell size in *Cepaea hortensis* (Mull). Genetica 50: 51–60.
Machin J 1967. Structural adaptation for reducing water-loss in three species of terrestrial snail. Journal of Zoology, London 152: 55–65.
Nevo E, Bar-El C, Bar Z 1983. Genetic diversity, climatic selection and speciation of *Sphincterochila* landsnails in Israel. Biological Journal of the Linnean Society19: 339–373.
Riddle WA 1981. Cold hardiness in the wood snail, *Anguispira alternate* (Say) (Endodontidae). Journal of Thermal Biology 6: 117–120.
Runham NW 1989. Snail farming in the United Kingdom. In: Henderson IF ed. Slugs and snails in world agriculture. British Crop Protection Council Monograph 41. Thornton Heath, Surrey, UK. Pp. 49–55.
Sacchi CF 1965. Ecological and historical bases for a study of the Iberian terrestrial Mollusca. Proceedings of the First European Malacologists Congress (1962). Pp. 243–257.
Smith G 1981. Copulation and oviposition in *Lymnaea truncatula* (Muller). Journal of Molluscan Studies 47: 108–111.

Editorial Board member: Gábor Lövei