# Substrate Attributes Determine Gait in a Terrestrial Gastropod

AMBERLE MCKEE[1], JANICE VOLTZOW[2], AND BRUNO PERNET[1,*]

[1]*Department of Biological Sciences, California State University Long Beach, Long Beach, California 90840; and* [2]*Department of Biology, University of Scranton, Scranton, Pennsylvania 18510*

**Abstract.** Some terrestrial gastropods are able to move using two gaits: adhesive crawling, where the entire foot is separated from the substrate only by a thin layer of mucus and the snail leaves a continuous mucus trail; and loping, where regions of the foot arch above the substrate and the snail leaves a discontinuous mucus trail. Loping has been interpreted as a means of rapidly escaping predators. We found that the pulmonate *Cornu aspersum* moved using adhesive crawling on dry acrylic or glass substrates, but loped on dry concrete or wood. Loping snails did not move more rapidly than snails using adhesive crawling. Snails moving on concrete secreted a greater volume of pedal mucus per area of trail than those moving on acrylic; locomotion on concrete thus requires greater expenditure of mucus than does locomotion on acrylic. Because loping snails deposit a smaller area of mucus per distance traveled than do snails using adhesive crawling, loping may conserve mucus when moving on porous, absorbent substrates. Members of several other terrestrial pulmonate taxa can also lope on concrete, suggesting that this plasticity in gait is widespread among terrestrial snails.

## Introduction

Terrestrial gastropods typically crawl over smooth surfaces using adhesive crawling, a mode of locomotion in which most of the foot is separated from the surface over which it is moving by only a thin ($\sim$10–70 $\mu$m) layer of mucus (Fig. 1A; Supplementary Online Video S1: http://www.biolbull.org/content/supplemental; Denny, 1980a; Lai *et al.,* 2010). The mucus, which is composed primarily (91%–99%) of water and dissolved salts, with 1%–9% high-

molecular-weight glycoprotein (Denny, 1984), is secreted by the pedal mucous gland and by secretory cells on the sole of the foot (*e.g.,* Cook and Shirbhate, 1983). Locomotory power is provided by a series of rapidly moving pedal muscular waves. When passing over the sheet of mucus, these waves reduce its viscosity locally ("shear-thinning"), allowing for forward motion (Denny, 1980b). When using adhesive crawling, snails leave a continuous trail of mucus behind them (Buyssens, 2004). Denny (1980a) showed that this mode of locomotion was extremely costly relative to the locomotion of vertebrates of similar size (in particular, adhesive crawling by a slug was about 12 times as costly as running by a mouse), and that most of the energetic cost of adhesive crawling was attributable to the cost of producing the glycoprotein component of pedal mucus. He speculated that the high energetic cost of movement in terrestrial gastropods might have important effects on their behavior and ecology.

Though terrestrial gastropods do not move rapidly by adhesive crawling, they are able to move over many kinds of surfaces in topographically diverse habitats, using only a single muscular foot. Their unusual locomotory mode has inspired the design of biomimetic robots that move by an adhesive-crawling-like process (*e.g.,* Chan *et al.,* 2005, 2007; Ewoldt *et al.,* 2009). Initial versions of these robots have been tested moving over surfaces covered with rheologically appropriate fluids that serve as analogs of pedal mucus (*e.g.,* Chan *et al.,* 2005). For such robots to be useful in more natural habitats, however, they will need to carry a supply of these fluids. Travel distances may be limited by the quantity of fluid that they can carry. Thus, like the pedal mucus of snails, "mucus" for robots using adhesive crawling will be costly, although for different reasons.

Snails (and biomimetic robots) might be able to mitigate the high cost of adhesive crawling by using alternative gaits, as have been observed in some terrestrial gastropods.
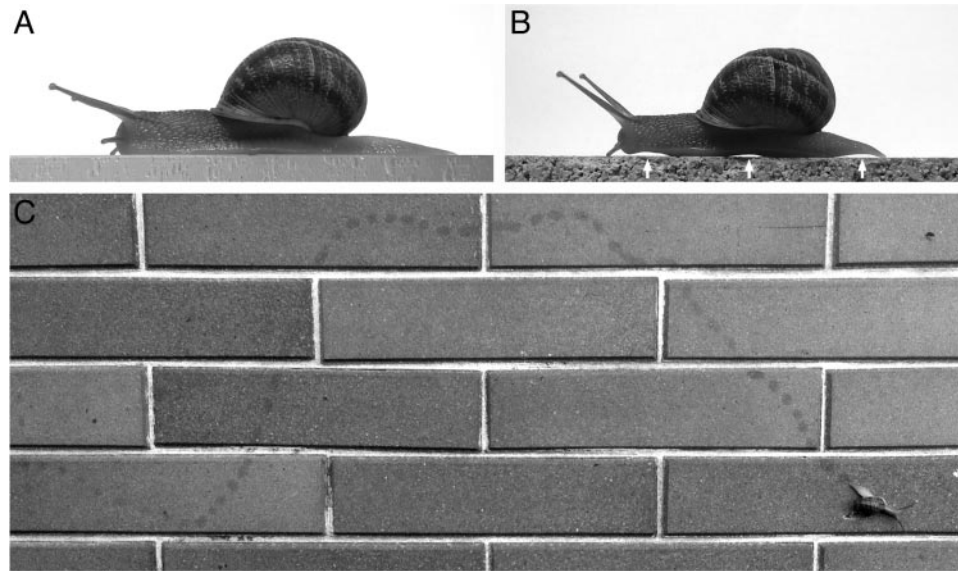
**Figure 1.** Adhesive crawling and loping in *Cornu aspersum*. (A) An individual of *C. aspersum* (shell length 23.5 mm) moving by adhesive crawling on an acrylic plate. A snail moving in this fashion leaves a continuous mucus trail. (B) The same snail as shown in (A), loping on a concrete plate. White arrows indicate the locations of the three arches present. A loping snail leaves a discontinuous mucus trail, like that shown in (C). (C) The discontinuous mucus trail of a loping adult of *C. aspersum*, observed on a brick wall in Long Beach, California, in May 2012. Note that the snail has loped while crawling up, down, and sideways on this vertical surface. Each brick is 29.3 cm in width; the snail is about 20 mm in shell length.

Specifically, members of numerous species are capable of "loping" locomotion, a modification of adhesive crawling in which the head is periodically lifted well off the substrate, extended forward, and then returned to the substrate. This creates an arch in the foot over the substrate. Head extension is repeated periodically, leading to the presence of several arches along the foot of an actively loping snail (Fig. 1B; Supplementary Online Video S2: http://www.biolbull.org/content/supplemental). In regions of contact with the substrate, the foot is propelled by typical pedal waves. The positions of the arches do not move relative to the substrate. An obvious consequence of this mode of locomotion is the deposition of a discontinuous mucus trail on the substrate, as the foot never contacts the substrate beneath each arch (Fig. 1C). The resulting potential conservation of costly pedal mucus could provide an energetic advantage to snails. This fluid-conserving gait might also allow snail-inspired robots to carry less fluid, or to achieve much greater travel distances per mission.

Loping locomotion was first described by Carlson (1905) in the terrestrial gastropod *Helminthoglypta* (as *Helix*) *dupetithouarsi* (DeShayes, 1840) (Carlson called it "galloping," but most recent authors now call it loping, the term we use here). Parker (1937) then described it in members of *Cornu aspersum* (Müller, 1774) (as *Helix aspersa*), further noting that individual snails could alternate between adhesive crawling and loping, and that snails began to lope only after pedal waves characteristic of adhesive crawling had

commenced. Both of these authors argued that loping allowed snails to move more rapidly than adhesive crawling, and that it was used to escape predators. Subsequent to Parker's (1937) work, the topic of loping was mentioned only rarely in the literature (usually in reports that simply restate earlier results and note that loping is a rare or unusual mode of locomotion—for example, Pilsbry, 1939; Jones, 1975; Trueman, 1983) until Pearce's (1989) review of the phenomenon. Pearce found that loping had been reported to occur in a diversity of pulmonates (nine species in three families), tentatively rejected the hypothesis that loping allows for more rapid locomotion than adhesive crawling, and suggested several alternative hypotheses on its functional and adaptive signficance (specifically, that loping might confound trail-following predators, that it might reduce contact of the foot with irritating substrates, and that it might reduce expenditure of mucus on dry substrates).

Our interest in these alternative locomotory gaits was sparked by numerous observations of loping in members of *C. aspersum* in southern California. Members of this species are common garden and landscaping pests in this area. When moving on dry concrete sidewalks or brick walls, they often lope, leaving behind obviously discontinuous mucus trails (Fig. 1C). In this study, we compare the behavior of members of *C. aspersum* on several different substrates, demonstrating that individual snails typically use adhesive crawling on smooth, nonporous materials like

glass and acrylic, but typically lope on porous, absorbent substrates like concrete and wood. The dependence of gait on substrate allowed us to manipulate gait in the laboratory, which permitted us to test several hypotheses on the functional significance of gait choice in members of this species. We also observed locomotion in members of several other pulmonate taxa in an attempt to broaden knowledge on the taxonomic distribution of alternative locomotory gaits in terrestrial gastropods.

## Materials and Methods

### Collections

Individuals of *Cornu aspersum*, which were used for most experiments, were collected from the leaves of plants (*Agapanthus* sp.) in a suburban neighborhood of Long Beach, California (33°46′14″N, 118°09′52″W). They were transported to the laboratory in a plastic container containing fresh leaves of *Agapanthus* sp., and left in that container until they were used in experiments within a few hours of collection. Other gastropods were collected from the campus of California State University, Long Beach (*Deroceras* sp. and *Lehmannia valentiana* [Férussac, 1823]); purchased from local garden supply shops (*Rumina decollata* [Linnaeus, 1758]); or observed on San Juan Island, Washington (*Arion ater* [Linnaeus, 1758]), or Oahu, Hawaii (*Achatina fulica* [Férussac, 1821]).

### Substrate dependence of gait, speed, and mucus deposition

We carried out three experiments to examine the effects of substrate type and orientation on locomotory gait, speed, and mucus deposition in *C. aspersum*. All experiments were done in the laboratory between about 0700 and 1100, when snails were generally active, using snails that had been collected earlier the same morning. During experiments, laboratory temperatures ranged from 18 to 22°C.

*Locomotion on horizontal acrylic, glass, and concrete surfaces.* To examine snail gait, speed, and mucus deposition on different horizontal surfaces, 25 snails were observed moving on dry acrylic, glass, and concrete plates. Concrete plates were pavers purchased from a local building supply company, and their surfaces were slightly rougher in texture than those of a typical sidewalk. The concrete plates were dramatically more absorbent than glass or acrylic, as determined by the time it took for 500 $\mu$l of distilled water to disappear when placed on the surface: on concrete, the water disappeared in about 7 s, but on glass and acrylic the water had not disappeared after 10 min, after which the trial was ended.

Each snail was assigned an identification number that was inscribed on its shell using an ink marker. Their masses were estimated to the nearest 0.1 mg using an electronic balance, and their shell lengths were measured to the nearest 0.1 mm using calipers.

Each snail was presented with all three substrates in randomized order. A Panasonic PV-GS150 video camera mounted on a tripod was positioned over the substrate. The acrylic plate used was 44 × 44 cm, the glass 43 × 34 cm, and the concrete plate 30 × 30 cm. A ruler was placed in the field of view of the camera to provide a scale. The snail was placed in the center of the first plate and its movements were recorded. As the snail moved, its mucus trail was immediately (while it was wet and easily seen) traced using an ink marker (on acrylic and glass) or a pencil (on concrete). The snail was also observed from the side as it moved, to determine whether arches in the foot were visible. The snail was then transferred to the second plate and observed as above, and then to the third plate and observed as above. Between trials, acrylic and glass plates were thoroughly scrubbed using ethanol, then rinsed in water and dried using paper towels. Concrete plates were scrubbed in water and allowed to air-dry. Because of the topographical complexity of the concrete plates, it is possible that some old mucus remained on them after cleaning. Such possible remnant mucus apparently did not affect gait choice: gaits of snails were extremely consistent on concrete surfaces (see Results, below), whether they were being used for the first time (18 surfaces) or being re-used.

Videos were then imported into iMovie HD 6.0.3 and analyzed to estimate the gait, speed, and amount (as surface area) of mucus deposited by each snail. The start point for all snails was the point at which they were put on the plate, except for lopers; there, the start point was when they started loping (which was always <10 cm from the point at which they were put on the plate). For each trial, analyses were ended just before the snail reached the edge of the plate. Loping was identified by observation of obvious arches in the foot, as well as by a discontinuous mucus trail; the absence of arches and a continuous mucus trail indicated adhesive crawling. Snails were recorded as loping if they did so at all during the trial. The initial and final frames of each video sequence were exported from iMovie and superimposed using Adobe Photoshop CS3 10.0.1. The composite image was opened in ImageJ 1.46, where the length of the traced mucus trail between the positions of the snail at the initial and final times was measured using the segmented line tool. The speed of each snail was determined by dividing the distance moved by the time the snail was moving. To estimate the area of mucus deposited, the area of the traced outline of each mucus trail was estimated using ImageJ.

*Locomotion on vertical acrylic, glass, and concrete surfaces.* To examine snail gait on different vertical surfaces, an experiment similar to the first was carried out, except that moving snails were not videotaped, and snail speed and

mucus deposition were not quantified. Twenty-four snails were allowed to commence movement on horizontal plates, but after the snails moved 5 cm, the plates were slowly tilted until they were oriented vertically, with the snail crawling upward. The snail was then allowed to move along the surface until it reached the edge. As it moved, the trail it left behind was outlined with an ink marker or pencil. As it moved, its gait was scored as adhesive crawling (no foot arches, continuous mucus trail) or loping (obvious arches, discontinous mucus trail). Snails were scored as loping if they loped at all during the vertical portion of the trial. Each individual snail was presented with all three substrates in randomized order.

*Locomotion on horizontal acrylic and wood surfaces.* To assess gait on another porous, absorbent substrate (wood), we compared snails moving on acrylic *versus* wood. Acrylic was chosen because it was easier to handle than glass and results from acrylic and glass in the prior two experiments were very similar in all respects. Each of 12 snails was placed on an acrylic plate or on the bark of a washed and air-dried white birch log about 12 cm in diameter and about 40 cm long (presentation order was determined randomly). Its gait was immediately recorded, using the same criteria as above. Each snail was then exposed to the other substrate and its gait recorded.

### Effects of substrate type on mucus expenditure during locomotion

To assess the effects of a smooth, nonabsorbent substrate (acrylic) and a rough, absorbent substrate (concrete) on mucus expenditure during locomotion, we compared initial and final masses of snails after they had moved on each of the two surfaces. Snails of approximately the same length and weight were collected and haphazardly divided into "acrylic" ($n = 18$ individuals) and "concrete" ($n = 15$) groups. Each snail was weighed to the nearest 0.1 mg, then immediately placed on a plate of the relevant material. The mucus trail left by the snail was traced with an ink marker or pencil as it crawled, and the presence or absence of foot arches during locomotion was also noted. As the snail approached the edge of the plate, it was removed and immediately weighed again. A photograph of the plate (including a ruler for scale) was then taken and imported into ImageJ, and total trail length was determined using the segmented line tool. In addition, the area of deposited mucus was also determined, again in ImageJ, from the area of the continuous mucus trail (for adhesive crawlers) or the area of the discontinuous mucus trail (for lopers). Both absolute mass loss and the percentage of initial weight lost were examined as functions of trail length and of the area of deposited mucus. Mass loss might have been a result of defecation, evaporation, or mucus expenditure. None of the

snails examined defecated during experiments, and experiments on the two substrates were carried out within a few hours in a laboratory with stable temperature and humidity, so all differential mass loss between the two treatments was assumed to result from differential expenditure of mucus.

### Distribution of loping among terrestrial gastropods

In addition to studying individuals of *C. aspersum*, we observed locomotion on concrete by members of several other species of terrestrial pulmonates to determine if other species were also capable of loping. Specimens of the shelled snail *Ac. fulica* and the slug *Ar. ater* were observed on concrete sidewalks on Oahu, Hawaii, and San Juan Island, Washington, respectively; the other species (the shelled snail *R. decollata* and the slugs *Deroceras* sp. and *L. valentiana*) were observed in the laboratory in Long Beach on the same concrete plates used for earlier experiments. Gait was determined by observation of the presence or absence of foot arches and by the form of the mucus trail (discontinuous *versus* continuous).

### Statistical analyses

All statistical analyses were carried out using GraphPad Prism 4.0c.

## Results

### Substrate-dependence of gait, speed, and mucus deposition

*Locomotion on horizontal acrylic, glass, and concrete surfaces.* All individuals of *Cornu asperum* moved on all substrates. Scoring locomotory mode as adhesive crawling or loping was unambiguous, except for one snail that alternated between the two gaits while on concrete. This individual was removed from further analyses, leaving a sample size of 24 snails, each tested on all three substrates. These ranged in length from 11.75 to 29.35 mm (mean 19.61 mm, standard deviation [SD] 5.439 mm), and in mass from 0.4058 to 6.895 g (mean 2.906, SD 1.926). On concrete, all snails started moving using adhesive crawling, but most of these (23/24, 96%) transitioned to loping after adhesive crawling between 2 and 9 cm. These 23 snails each loped continuously for at least 6 cm (mean 14.6 cm, range 6.2–24.9 cm). None of the 24 snails loped on acrylic or glass; on these substrates, all snails used adhesive crawling. There was a clear and statistically significant difference in gait as a function of substrate, with snails loping more frequently on concrete than on acrylic or glass (Chi-square, $P > 0.0001$).

Snail speed was estimated over the length of the mucus trail between start and end points as defined above; thus, speeds on acrylic and glass were determined for the entire distance moved (acrylic: mean 24.5 cm, range 15.1–66.7 cm; glass: mean 21.8 cm, range 10.5–54.3), but speeds on concrete were determined only over the distance during

which snails loped (as noted above, mean 14.6 cm, range 6.2–24.9 cm). Because individual snails were tested on each of the three substrates, we had planned on analyzing these data by repeated measures ANOVA. Though speeds on acrylic and concrete were not normally distributed (Shapiro-Wilk test) and transformations of the data did not solve this problem, we did use repeated measures ANOVA, relying on the test being robust to deviations from normality. Only the 23 snails that had loped on concrete and used adhesive crawling on acrylic and glass were included in this analysis. The repeated measures ANOVA showed a significant effect of gait on speed ($P = 0.043$). Tukey's *post hoc* multiple comparisons revealed that this effect was due to a difference in speeds on glass and concrete: snails moved more rapidly when using adhesive crawling on glass than when loping on concrete ($P > 0.05$). The mean speed of the snails using adhesive crawling on glass was 0.20 cm/s (SD 0.08), while the mean loping speed on concrete was 0.16 cm/s (0.09). Mean adhesive crawling speed on acrylic was 0.19 cm/s (0.07). There were no clear effects of snail size (as shell length) on speed on any of the three tested substrates (Fig. 2A).

These comparisons of speed as a function of gait are confounded by substrate type. However, because snails on concrete started moving using adhesive crawling and only then transitioned to loping, we were able to compare their speeds using the two gaits on the same substrate. Of the 23 snails that loped on concrete, 10 first moved using adhesive crawling for at least 5 cm. These data were normally distributed (Shapiro-Wilk test), so we used a paired Student's *t*-test to compare the speeds of these 10 snails while they were using adhesive crawling (mean 0.14 cm/s, SD 0.03) to their speeds while loping (0.15 cm/s, SD 0.05). Speeds using the two gaits on concrete were not significantly different ($P = 0.723$).

The area of mucus deposited per length of trail moved was determined for each snail on each substrate. These data met the assumptions of normality (Shapiro-Wilk test) and equality of variances (Bartlett's test). Because individual snails were tested on each substrate, we analyzed these data using repeated measures ANOVA. Gait significantly affected the area of pedal mucus deposited ($P > 0.0001$; Fig. 2B). Tukey's *post hoc* multiple comparisons showed that the area of mucus deposited by snails using adhesive crawling on acrylic and glass did not differ ($P < 0.05$), but that snails loping on concrete deposited significantly less mucus than those using adhesive crawling on either acrylic ($P > 0.001$) or glass ($P > 0.001$). Snails using adhesive crawling on acrylic deposited a mean of 0.85 cm$^2$ of mucus/cm of trail (SD 0.21) and those on glass deposited a mean of 0.87 cm$^2$ mucus/cm of trail (SD 0.21); snails loping on concrete deposited only 0.57 cm$^2$ mucus/cm of trail (SD 0.15).

*Locomotion on vertical acrylic, glass, and concrete surfaces.* Twenty-four snails were tested on all three substrates,
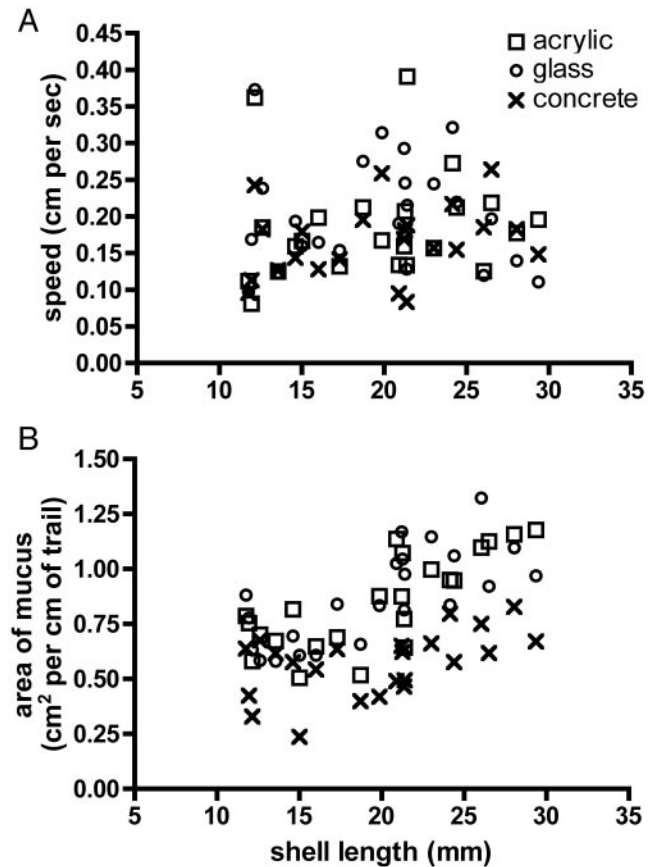


**Figure 2.** Speed and mucus deposition of snails moving on horizontal surfaces via adhesive crawling (on acrylic or glass) and loping (on concrete). (A) Speed as a function of snail size on the three surfaces. (B) Area of mucus deposited on the trail, per unit trail length, as a function of snail size on the three surfaces.

but one individual did not move and was omitted from analyses, leaving a final sample of 23 snails. No snails loped on acrylic or glass; on these surfaces, all snails used adhesive crawling. Fourteen of 23 snails loped while moving upward on the vertically oriented concrete substrate. Of the nine snails that did not lope while the concrete was vertical, three had started loping while the substrate was horizontal, but stopped moving as it was tilted to the vertical; the remaining six snails did not lope at all. Gait varied significantly among substrates, with snails loping significantly more frequently on concrete than on acrylic or glass (Chi-square, $P > 0.0001$).

*Locomotion on horizontal acrylic and wood surfaces.*

Twelve snails were tested on both substrates, but one individual did not move and was omitted from analyses. None of the 11 snails loped on the acrylic; all used adhesive crawling. All 11 snails loped on the wood. This difference was significant (Chi-square, $P > 0.0001$).

*Effects of substrate type on mucus expenditure during locomotion*

In this experiment, loss of mass during locomotion (a proxy for mucus expenditure) was estimated for a group of snails moving using adhesive crawling on acrylic and a group of snails loping on concrete. Two snails in the acrylic group did not move at all (leaving 16 in that group), and one snail on concrete did not lope continuously (leaving 14). Of the 16 snails in the acrylic group, all moved using only adhesive crawling, and on average, snails in this group moved 32.4 cm (range 13.0–80.3 cm) during observations. Mean initial body mass in this group was 3.1301 g (SD 1.3149). The 14 snails in the concrete group all moved using only loping, and moved on average 17.8 cm (range 13.9–25.5 cm). Mean initial body mass in this group was 3.2142 g (SD 1.2089).

One individual loping on concrete lost much more mass (55.5 mg/cm of trail, 75.9 mg/cm$^2$ of mucus deposited) than did other snails in this treatment. As this amount of mass loss was an order of magnitude higher than other snails in this treatment, this individual was treated as an outlier and omitted from analyses.

Overall, the 16 snails in the acrylic group lost a mean of 1.3 mg/cm of trail (SD 1.2 mg) and 1.2 mg per cm$^2$ of mucus deposited (SD 1.0 mg; Fig. 3A). Excluding the outlier, the 13 snails in the concrete group lost on average 1.9 mg/cm of trail (SD 0.9 mg) and 4.4 mg/cm$^2$ of mucus deposited (SD 1.2 mg; Fig. 3A). Mass loss data in the acrylic group were not normally distributed (Shapiro-Wilk test), so the effects of substrate and gait on mass loss were examined using nonparametric Mann-Whitney *U* tests. Snail mass loss per centimeter of trail was significantly higher in the concrete group than in the acrylic group ($P = 0.009$); similarly, when mass loss was scaled to the area of mucus deposited, members of the concrete group lost significantly more mass per square centimeter of mucus deposited than did members of the acrylic group ($P > 0.0001$).

To correct for variation in the sizes of test snails, we repeated this analysis using mass loss normalized by initial mass as the response variable. The 16 snails in the acrylic group lost a mean of 0.04% initial body mass/cm of trail (SD 0.03%) and 0.04% initial body mass/cm$^2$ of mucus deposited (SD 0.03%; Fig. 3B). Excluding the outlier, the 13 snails in the concrete group lost an average of 0.06% initial body mass/cm of trail (SD 0.02%) and 0.15% initial body mass/cm$^2$ of mucus deposited (SD 0.06; Fig. 3B). Because data were not normally distributed in the acrylic group (Shapiro-Wilk test), the effects of substrate on normalized mass loss were examined using nonparametric Mann-Whitney *U* tests. Normalized mass loss per centimeter of trail was significantly higher in the concrete group than in the acrylic group ($P = 0.002$); when normalized mass loss was scaled to the area of mucus deposited, mem-
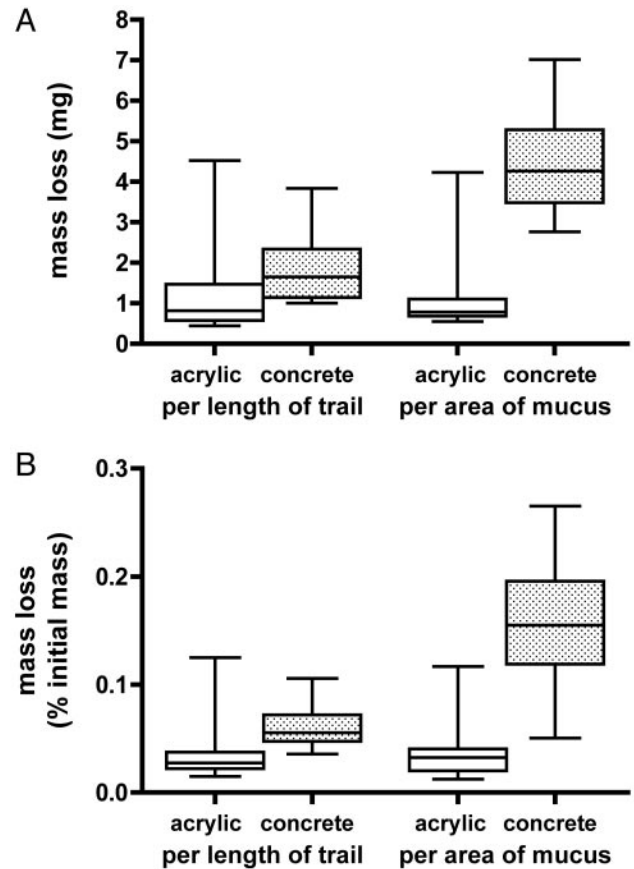


**Figure 3.** Loss of snail mass during locomotion on acrylic (adhesive crawling) *versus* concrete (loping). (A) Mass loss as a function of total distance traveled (milligrams lost per centimeter of trail) or of the area of mucus deposited in the trail (milligrams lost per square centimeter of mucus deposited). (B) Mass loss normalized to initial body weight as a function of total distance traveled (milligrams lost per centimeter of trail) or to the area of mucus deposited in the trail (milligrams lost per square centimeter of mucus deposited). In both panels, sample sizes are $n = 16$ snails (acrylic) and $n = 13$ snails (concrete). The central horizontal line in each box-and-whisker plot indicates the median, the box encompasses the 25th and 75th percentiles, and the whiskers indicate minimum and maximum values.

bers of the concrete group lost significantly more mass per square centimeter of mucus deposited than did members of the acrylic group ($P > 0.0001$).

*Distribution of loping among terrestrial gastropods*

In addition to carrying out experiments with *Cornu aspersum* (F. Helicidae), we observed loping in members of five additional species of terrestrial pulmonates on concrete surfaces in the laboratory or in the field. All nine individuals of *Rumina decollata* (Subulinidae) examined loped in the laboratory. Four individuals of *Achatina fulica* (Achatinidae) were observed loping on a sidewalk on Oahu, Hawaii. Numerous individuals of the shell-less pulmonates *Arion ater* (Arionidae), *Deroceras* sp. (Agriolimacidae), and

*Lehmannia valentiana* (Limacidae) were observed loping in both the field and the laboratory (all in Long Beach, California, except for *Ar. ater*, which was observed on San Juan Island, Washington).

## Discussion

The gait used by individuals of *Cornu aspersum* clearly depends on substrate attributes; in our experiments, snails typically moved by adhesive crawling on glass or acrylic, but loped when transferred to concrete or wood. They exhibited plasticity in gait both on horizontal and vertical substrates. Loping had not, to our knowledge, previously been documented on vertical substrates (Pearce, 1989). Loping was observed not only in the laboratory, but also in suburban populations of *C. aspersum*, where individuals moved on concrete sidewalks, brick walls, and natural wood substrates (Pernet, pers. obs.). Like Pearce (1989), we also observed members of several other species of terrestrial pulmonates loping on concrete or brick in the laboratory or the field. Together with the observations of previous workers, our results suggest that loping may be a taxonomically widespread alternative gait among both shelled and shell-less terrestrial gastropods.

In most accounts of the locomotion of terrestrial gastropods, adhesive crawling is described as the normal locomotory mode, and loping is briefly mentioned as an unusual gait observed in just a few species, if it is mentioned at all (*e.g.,* Jones, 1975; Trueman, 1983; Chan *et al.,* 2005). We suspect that the view of adhesive crawling as typical is a consequence of the fact that almost all studies of gastropod locomotion have been done in the laboratory on substrates chosen for their transparency (*e.g.,* glass or acrylic) so that the investigator was able to clearly visualize pedal muscular waves; these substrates, according to our results, also happen to induce adhesive crawling. We know of no reports of gait choice in terrestrial gastropods moving in natural habitats. In nature, one might expect that snails come in contact with substrates of many different surface properties—from relatively smooth, nonporous, and nonabsorbent (*e.g.,* living plant leaves) to more rough, porous, and absorbent (soil, rock, wood, and dead leaves). Given the clear substrate-dependence of gait we observed, loping may be as common as adhesive crawling, or more so, in heterogeneous terrestrial habitats. Field behavioral studies are clearly needed to assess the gaits used by pulmonates in nature.

### Plasticity in gait choice in terrestrial pulmonates

Pearce (1989) summarized earlier ideas on the adaptive significance of loping in terrestrial pulmonates and suggested additional hypotheses of his own. Our data permit evaluation of several of these hypotheses.

*Loping snails move more rapidly than those using adhesive crawling, and loping is used only to escape enemies.* Until Pearce's (1989) review of loping, these two related ideas were the most common hypotheses in the literature to explain loping. Both were first suggested by Carlson (1905) and repeated by other authors (*e.g.,* Parker, 1937; Jones, 1975; Trueman, 1983). As a one-sentence aside in his review, Pearce (1989) presented the first data comparing the speeds of members of *Cepaea nemoralis* (Linnaeus, 1758) moving using the two gaits; he found no gait-related differences in speed (but presented no details on experimental or analytical methods). Our results are also inconsistent with the hypothesis that loping is more rapid than adhesive crawling; indeed, we found that snails moved more rapidly using adhesive crawling on glass than they did using loping on concrete (Fig. 2A). It is, of course, possible that the maximum speeds attainable by snails are higher using loping than adhesive crawling; however, routine loping does not appear to be any faster than routine adhesive crawling. The speeds we measured for members of *C. aspersum* are very similar to those measured for similarly sized individuals of the same species by Buyssens (2004).

The second idea, that the primary function of loping is to flee enemies, suffers from an inherent weakness—loping of terrestrial gastropods has never been observed in the presence of a potential predator or other enemy (unless one considers the observer an enemy), but has been observed many times in the absence of enemies. Though it is possible that snails use loping to escape predators, most loping that has been observed by scientists was likely induced by some other factor.

*Loping confounds trail-following predators.* Some predators of snails (largely other snails) track their prey by following the prey's mucus trails (*e.g.,* Davis-Berg, 2012); for such predators, discontinuous mucus trails like those left by loping snails might be more difficult to follow than continuous trails. If this were the case, one might expect loping to be stimulated when the snail is in a habitat in which predators are frequently present, or when the snail detects a predator (Pearce, 1989). Although loping has not been observed in the presence of any such potential predators, it has been observed many times in their absence. These observations do not rule out this hypothesis, but suggest that predator evasion, if a benefit at all, is not the only benefit associated with loping.

*Loping decreases contact of the foot with "irritating" substances in certain substrates.* Pearce (1989) suggested that snails might lope to minimize contact of the foot with caustic or other irritating substances in the substrate, but did not provide any evidence in support of this hypothesis. Two observations suggest that this is unlikely. First, we routinely observed loping on concrete and brick substrates (specifi-

cally, sidewalks and walls) that had been made decades before and exposed to natural wetting and drying for that entire period. We expect that any caustic, soluble materials in these substrates would long since have been washed away. Second, loping was also observed in snails crawling on dry wood and bark in both the laboratory and field (Pernet, pers. obs.). It seems unlikely that these diverse materials all contain irritants that would stimulate loping.

*Loping decreases expenditure of mucus.* To our knowledge, this idea was first suggested by Pilsbry (1939), who noted that Carlson's (1905) original observation of loping might have been caused by the dry surface on which Carlson observed snail locomotion, thus implying that loping snails were conserving water. Pantin (1950), studying locomotion in the terrestrial flatworm *Geodesmus* (as *Rhynchodemus*) *bilineatus* Metschnikoff, 1865, noted that its "lope-like" gait was "much more economical of mucus" than that of other flatworms that move in a fashion more like adhesive crawling, with the entire ventral surface in contact with the substrate. Jones (1978) made additional observations of this phenomenon in flatworms, and noted that in the case of *Microplana terrestris* (Müller, 1774) switches in gait might be caused by changes in atmospheric humidity. Denny (1980a) argued that the glycoprotein components of gastropod pedal mucus are extremely costly. Conservation of water is also clearly important for terrestrial gastropods, which often live in relatively dry terrestrial habitats (*e.g., C. aspersum* is native to north African countries such as Morocco, Algeria, and Tunisia: Guiller and Madec, 2010). Thus it seems possible that terrestrial snails lope to conserve water, glycoproteins, or both.

No clear test of this hypothesis has previously been made in terrestrial snails (or in terrestrial flatworms). Our data on locomotory gait on dry substrates of various types show a clear effect of substrate type on gait. One major difference between the substrates that led to adhesive crawling *versus* those that induced loping is that the former are smooth and nonabsorbent, while the latter are rough, porous, and absorbent. Our data are thus consistent with the hypothesis that conservation of mucus is an important driver of gait choice in *C. aspersum*, and probably in other terrestrial snails. However, several older observations of locomotion on smooth, nonabsorbent surfaces are inconsistent with this hypothesis. Parker (1937) observed snails loping on glass, and Pearce (1989) observed snails loping on dry formica and vinyl. Neither of these authors provided estimates of the frequencies of adhesive crawling *versus* loping on these substrates. In contrast with Parker's (1937) observations, but like ours, Pearce (1989) was unable to induce snails to lope on glass.

Our data allow us to quantify the potential benefit, in terms of conservation of mucus, of loping *versus* adhesive crawling on absorbent substrates like concrete. Individuals of *C. aspersum* using adhesive crawling on acrylic or glass deposited mucus trails about 1.5 times the area per centimeter traveled as those of *C. aspersum* loping on concrete (0.87 and 0.57 cm² mucus/cm traveled, respectively). Area is not the best proxy for volume of mucus deposited, as it ignores the thickness of the mucus layer. We have not been able to measure trail thickness on the substrates of interest; a method for estimating thickness of mucus trails on smooth, nonabsorbent surfaces has been developed (Davies and Blackwell, 2007) but would be difficult to apply to the structurally complex, absorbent surfaces of interest.

A better proxy of the amount of mucus expended is the amount of mass snails lose when crawling. We found that snails loping on concrete lost significantly more mass per area of mucus deposited than snails using adhesive crawling on acrylic. Assuming that all of these losses are due to deposition of mucus, and that the density of mucus is that of fresh water, then a snail of about 3.15 g loping on concrete lost on average 4.4 $\mu$l of mucus/cm² of mucus deposited; a snail of similar size using adhesive crawling on acrylic lost 1.2 $\mu$l of mucus/cm² of mucus deposited (Fig. 3A). This suggests that snails moving on acrylic deposit a much thinner layer of mucus than those moving on concrete.

To predict the amount of mucus that a snail of about 3.15 g would expend using adhesive crawling on concrete, one can simply assume that such a snail would deposit the same area of mucus as a snail using adhesive crawling on acrylic, 0.87 cm²/cm traveled. Then a snail using adhesive crawling on concrete should expend about 3.8 $\mu$l of mucus/cm traveled (4.4 $\mu$l mucus/cm² × 0.87 cm² mucus deposited/cm traveled). Actual snails loping on concrete lost only 1.9 $\mu$l of mucus/cm traveled, slightly less than the predicted 2.5 $\mu$l (4.4 $\mu$l mucus/cm² × 0.57 cm² mucus deposited/cm traveled.) On dry concrete, then, loping represents a much more efficient (in terms of mucus conservation) gait than does adhesive crawling. Further, our comparisons suggest that adhesive crawling on the nonabsorbent substrates we tested is significantly less costly in terms of mucus than locomotion by either gait on the absorbent substrates we tested: snails using adhesive crawling on acrylic expended only 1.3 $\mu$l of mucus/cm traveled, on average. These differences might affect both gait choice and habitat use by gastropods in nature. For example, a 3.15 g snail moving 100 cm (a reasonable estimate of daily movement in *C. aspersum*: Bailey, 1989) on an absorbent substrate such as concrete might expend about 380 $\mu$l of mucus (~12% body weight) if using adhesive crawling, but only about 190 $\mu$l of mucus (~6% body weight) if loping.

Additional tests of the hypothesis that loping is a mode of locomotion adopted when conservation of mucus is important would be useful. Pearce (1989) suggested one such test: if conservation of the water component of mucus is important, water-stressed snails should lope more frequently on any given substrate than fully hydrated snails. In prelimi-

nary experiments aimed at testing this prediction, we found no differences between water-stressed and fully hydrated adults of *C. aspersum*; in all cases, snails on acrylic used adhesive crawling, and snails on concrete loped. Pearce (1989) also noted that if the hypothesis is correct, snails should be less likely to lope on wet concrete than they are on dry concrete. In preliminary observations, we found that all individuals of *C. aspersum* observed on dry concrete loped, but that on wet concrete, they did not move at all, instead adopting a posture that maximized the amount of pedal surface area in contact with the substrate. Such postures have previously been observed in terrestrial snails that are rapidly absorbing water across the pedal epithelium (Prior and Uglem, 1984; Uglem *et al.,* 1985). Pearce (1989) was able to observe loping by members of *C. nemoralis* on wet concrete. This difference might be related to differences in the species observed, or to differences in their initial hydration states, humidity, or the degree of wetting of the substrate.

Our results are generally consistent with the hypothesis that loping is used to conserve the water or glycoprotein components of pedal mucus when snails move over an absorbent substrate. However, given the value of both components of mucus, why don't terrestrial snails lope on all surfaces? In his review, Pearce (1989) identified two potential costs of loping. First, it is possible that the additional muscular movements involved in loping add significant energetic costs to locomotion (compared to adhesive crawling). This hypothesis might be addressed by measurements of oxygen consumption in snails using each gait, as has previously been done for adhesive crawling in the slug *Ariolimax columbianus* Gould, 1851 (Denny, 1980a). Second, tenacity, the ability of a snail to adhere to a substrate, is typically positively correlated with the amount of pedal surface area in contact with the substrate (Miller, 1974). Since much less of the foot is in contact with the substrate in loping snails relative to snails moving using adhesive crawling, loping snails may have lower tenacities. This might limit the abilities of loping snails to move vertically or while upside down, or to resist removal from the substrate by predators. To our knowledge, comparisons of the tenacities of snails moving using adhesive crawling *versus* loping have not yet been made.

As noted above, almost all observations of loping have been carried out on snails moving on artificial substrates. Field studies of snail locomotion are essential to address questions about gait choice in nature, the relative costs and benefits of the alternative gaits, and the possible effects of factors such as initial body hydration and atmospheric humidity on locomotory behavior.

## Acknowledgments

## Literature Cited

Bailey, S. E. R. 1989. Foraging behaviour of terrestrial gastropods: integrating field and laboratory studies. *J. Molluscan Stud.* **55:** 263–272.

Buyssens, N. 2004. Locomotion in *Helix aspersa*. *Malacologia* **46:** 211–216.

Carlson, A. J. 1905. The physiology of locomotion in gasteropods. *Biol. Bull.* **8:** 85–92.

Chan, B., N. J. Balmforth, and A. E. Hosoi. 2005. Building a better snail: lubrication and adhesive locomotion. *Phys. Fluids A.* doi: 10.1063/1.2102927

Chan, B., S. Ji, C. Koveal, and A. E. Hosoi. 2007. Mechanical devices for snail-like locomotion. *J. Intell. Mater. Syst. Struct.* **18:** 111–116.

Cook, A., and R. Shirbhate. 1983. The mucus producing glands and the distribution of the cilia of the pulmonate slug *Limax pseudoflavus*. *J. Zool.* **201:** 97–116.

Davies, M. S., and J. Blackwell. 2007. Energy saving through trail following in a marine snail. *Proc. R. Soc. B* **274:** 1233–1236.

Davis-Berg, E. C. 2012. The predatory snail *Euglandina rosea* successfully follows mucus trails of both native and non-native prey snails. *Invertebr. Biol.* **131:** 1–10.

Denny, M. 1980a. Locomotion: the cost of gastropod crawling. *Science* **208:** 1288–1290.

Denny, M. 1980b. The role of gastropod pedal mucus in locomotion. *Nature* **285:** 160–161.

Denny, M. 1984. Mechanical properties of pedal mucus and their consequences for gastropod structure and performance. *Am. Zool.* **24:** 23–36.

Ewoldt, R. H., A. E. Hosoi, and G. H. McKinley. 2009. Nonlinear viscoelastic biomaterials: meaningful characterization and engineering inspiration. *Integr. Comp. Biol.* **49:** 40–50.

Guiller, A., and L. Madec. 2010. Historical biogeography of the land snail *Cornu aspersum*: a new scenario inferred from haplotype distribution in the Western Mediterranean basin. *BMC Evol. Biol.* **10:** 18.

Jones, H. D. 1975. Locomotion. Pp. 1–32 in *Pulmonates,* Vol. 1., V. Fretter and J. Peake, eds. Academic Press, London.

Jones, H. D. 1978. Observations on the locomotion of two British terrestrial planarians (Platyhelminthes, Tricladida). *J. Zool.* **186:** 407–416.

Lai, J. H., J. C. del Alamo, J. Rodriguez-Rodriguez, and J. C. Lasheras. 2010. The mechanics of the adhesive locomotion of terrestrial gastropods. *J. Exp. Biol.* **213:** 3920–3933.

Miller, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *J. Exp. Mar. Biol. Ecol.* **14:** 99–156.

Pantin, C. F. A. 1950. Locomotion in British terrestrial nemertines and planarians: with a discussion on the identity of *Rhynchodemus bilineatus* (Mecznikow) in Britain, and on the name *Fasciola terrestris* O.F. Müller. *Proc. Linn. Soc. Lond.* **162:** 23–37.

Parker, G. H. 1937. The loping of land snails. *Biol. Bull.* **72:** 287–289.

Pearce, T. A. 1989. Loping locomotion in terrestrial gastropods. *Walkerana* **3:** 229–237.

Pilsbry, H. A. 1939. *Land Mollusca of North America (North of Mexico).* Academy of Natural Sciences of Philadelphia Monographs, no. 3. Philadelphia.

Prior, D. J., and G. L. Uglem. 1984. Analysis of contact-rehydration in terrestrial gastropods: absorption of $^{14}$C-inulin through the epithelium of the foot. *J. Exp. Biol.* **111:** 75–80.

Trueman, E. R. 1983. Locomotion in molluscs. Pp. 155–198 in *The Mollusca,* Vol. 4, *Physiology,* Part 1, A. S. M. Saleuddin and K. M. Wilbur, eds. Academic Press, New York.

Uglem, G. L., D. J. Prior, and S. D. Hess. 1985. Paracellular water uptake and molecular sieving by the foot epithelium of terrestrial slugs. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **156:** 285–289.