How fast is a snail's pace? The influences of size and substrate on gastropod speed of locomotion

Running Title: How size and substrate affect gastropod speed

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ABSTRACT

Terrestrial gastropods display monotaxic direct crawling. During locomotion smooth muscle contraction stimulates a series of pedal waves that move along the ventral surface of the foot. These waves interact with a thin layer of mucus produced by the foot, propelling the animal forward. Although the mechanism by which this process occurs has been well studied, less is known about how morphological or environmental factors affect this process, and ultimately how they may alter the speed of propulsion. In this study we tested the influences of body size, substrate type, and substrate orientation on crawling speed in the terrestrial snail *Cornu aspersum*. We found that substrate texture and orientation had a strong effect on speed, whereas snail body size and the presence of a conspecific trail did not. Crawling speed across rough sandpaper was the most striking, showing a clear inversely proportional relationship between the size of abrasive particle and speed. We suggest that this may be the result of substrate attributes interfering with mucus adhesion or mucus production, subsequently affecting locomotion, although gait choice or the frequency and length of wave contraction may also play a role.

KEYWORDS: *Gastropod, propulsion, adhesive locomotion, substrate, size*

INTRODUCTION

When investigating the diversity of locomotion within the animal kingdom, gastropods have fascinated biologists and biophysicists for centuries (Iwamoto, Ueyama & Kobayashi, 2014). Gastropods lack extremities, making movement highly variable and unusual (Miller, 1974; Hemmert & Baltzley, 2016). Terrestrial snails display monotaxic propulsion as they crawl using “monotaxic direct” waves. Within the foot, smooth muscle periodically contracts and relaxes, producing a series of pedal waves, separated by interwaves (Denny, 1980a; Lai *et al.*, 2010), surrounded by a rim. The interwaves are stationary with respect to the ground whereas the waves have a faster velocity than the rim, the speed of which equates to the animal’s speed across the substrate (Denny, 1981). During movement, mucus is secreted from a ventral pedal gland, cells on the foot’s surface and the mantle collar (Campion, 1961; Buyssens, 2004). Pedal mucus is a non-Newtonian substance and has a finite yield stress (Chan *et al.*, 2005; Lai *et al.*, 2010; Lee *et al.*, 2018). Under small stress it remains highly viscous as an adhesive solid, allowing the snail to remain attached to a substrate. Under periods of high stress (above its yield point), it has a low viscosity and flows like a liquid (Denny, 1980b; Lauga & Hosoi, 2006). When smooth muscle contracts at the beginning of a wave, the mucus layer under this area of the foot is stressed to yielding. Subsequently, most of the wave area moves over mucus in its liquid form, allowing this portion of the foot to move forward (Denny 1980a; Denny, 1980b; Denny, 1984). As sections of the foot relax, yield stress decreases. This means that mucus beneath the interwave quickly solidifies, allowing this part of the foot to remain stationary on the mucus layer in its solid form (Denny & Gosline, 1980). This prevents the snail from slipping backwards (Iwamoto *et al.*, 2014). Each pedal wave will propagate from the tail and travel across the central portion of the foot's surface, extending across the width to the head (Lai *et al.*, 2010; Kuroda *et al.*, 2014). Although propulsion is slow, gastropod movement has interested engineers for a number of years, leading to the production of many biomimetic robots which can move across layers of fluid via this method of locomotion (e.g., Chan *et al.*, 2005, 2007; Lauga & Hosoi, 2006; Ewoldt *et al.*, 2007), as it provides information on the feasibility of applying natural mechanisms to manmade applications (Chan *et al.*, 2007).

Monotaxic propulsion is observed in the common terrestrial snail, *Cornu aspersum*. There are many aspects of snail physiology that have been shown to affect crawling speed, such as wave length (Lai *et al.*, 2010), wave frequency (Crozier & Pilz, 1924; Crozier & Federighi, 1925; Donovan & Carefoot, 1997; Pavlova, 2001; Lai *et al.*, 2010) and body size (Pavlova, 2001, 2013). Recent work by Hemmert & Baltzley (2016) investigating the relationship between body size and speed across individuals within a species found that this relationship was orientation dependent. Consistent with findings by McKee *et al.* (2013) they found no correlation between speed and body size when individuals moved horizontally but a negative correlation when individuals moved vertically. This is particularly relevant when observing locomotion in *C. aspersum* as this species feeds in trees as well as on the ground (Iglesias & Castillejo, 1999; Alvarez *et al.*, 2009).

As well as adhesive crawling facilitating both horizontal and vertical movement, the garden snail *C. aspersum* is a synanthropic species, which are geographically widespread, residing in a diverse range of habitats (Balbi *et al.*, 2018). This makes the ability to move over many kinds of surfaces which vary in texture, angle and moisture essential for survival. Although it is accepted that *C. aspersum* is sensitive to the type of substrate they are moving across (Baur & Baur, 1990; Arnaud, 2003; Balbi *et al.*, 2018) no study has directly investigated the effect of substrate on crawling speed, with most existing research producing contradictory results and observing trends indirectly when investigating gait choice (McKee *et al.*, 2013; Munn & Treloar, 2016). For example, McKee *et al.* (2013) when investigating substrate driven gait choice found that routine speed did not appear to differ based on gait, but overall speed was quicker when individuals were adhesive crawling on glass than when loping (See McKee *et al.*, 2013 for more information and a video outlining this behaviour) on concrete. In contrast, Munn & Treloar (2016) found that snails also adopted a loping gait and produced less mucus when moving across a rough surface (sandpaper), as opposed to PVC plastic (on which adhesive crawling was adopted), but average speed did not significantly vary across the two surfaces. Although both mucus conservation (McKee *et al.*, 2013) and foot "irritation" (Pearce, 1989) have been considered as factors which likely affect gait choice and speed, neither have been directly tested.

Although the benefits of mucus trail-following have been extensively investigated, facilitating prey (Pearce & Gaertner, 1996; Shaheen *et al.*, 2005; Clifford *et al.*, 2003; Davis-Berg, 2012; Holland *et al.*, 2012) and mate (Reise, 2007; Ng *et al.*, 2011) location, homing (Cool, 1992) and energy conservation (Davies & Blackwell, 2007), little research has been conducted on this behaviour in *C. aspersum* specifically, and how it may affect crawling speed. Recent research on *C. aspersum* has found that individuals which tend to disperse from a given habitat are more likely to follow a mucus trail than expected by chance and this trail-following behaviour is not observed in non-dispersers (Vong, Ansart & Sahirel, 2019). Vong *et al.* (2019) suggest that trail-following may minimise movement and mucus production costs and could facilitate habitat or resource location. As *C. aspersum* exist predominantly in aggregated colonies, they are likely to encounter conspecific trails regularly. This would make the presence of a trail a common component of the substrate that they move across. Subsequently, the presence or absence of a trail may alter speed by lowering energetic costs or as a result of its association with a potential mate or habitat, however, this is yet to be investigated.

Our study has two aims. First, to re-examine the relationship between foot length, shell size and speed in snails moving across both horizontal and vertical surfaces. Despite their interesting results, Hemmert & Baltzley (2016) measured vertical and horizontal speed at different times of year. As seasonal differences could affect foot physiology and mucus production, it seems sensible to replicate this work across a shorter time scale. Second, to determine how speed is affected by surface type and texture. The lack of conclusive information on substrate-driven speed and locomotion is likely due to the types of materials used in previous studies not being consistent or as diverse as those experienced by *C. aspersum* under natural conditions. We analysed the speed of each individual across five different substrates: smooth nonporous PVC, wet PVC, sandpaper with a "P120" Grit designation and PVC in the presence of conspecific trail, using a repeated measures design. We also measured the relationship between speed and the size of abrasive particles (µm) and conducted a choice trial between two types of sandpaper which contrasted in average particle diameter (Apd) to identify if surface driven substrate preference is selected for in this species. Although we acknowledge that the substrates used in our experiment study may not be encountered regularly by *C. aspersum* in their natural habitat, as this species has a large geographical range, residing in many rural and urban environments, by selecting a wide range of substrates we hope to mirror the diversity experienced by this species.

MATERIALS and METHODS

Experimental Procedure

The experiment was conducted between 11/05/2020 and 15/06/2020 using the common land snail *Cornu aspersum.* Individuals were collected from local gardens in London, United Kingdom, within 48 hours of conducting the experiment, and released immediately afterwards. Individuals varied in size, ranging from 12mm to 58mm in foot length, 10mm to 65.5mm in shell length, 7mm to 56mm in shell width and 20mm to 84mm in shell circumference. Shell circumference was measured around the entire based of the shell, length was measured as total shell length from the apex to the lower apertural lip and width was measured as the maximum width. All shell measurements were taken when the foot of the snail was not protruding out of the shell using a thin wire. The length of each wire was then measured using a ruler. Foot length measurements were taken using a using a Canon 600D (18-megapixel CMOS sensor, 18mm lens, f/5.6). Each individual was placed on a section of clear PVC next to a ruler and a series of digital photographs were taken of the ventral side of the foot as the individual moved. The photograph which showed maximum foot length was identified and the measurement taken.

To measure speed, a ruler was placed beside the crawling snail for scale. Snails were recorded for 1–10 minutes in order to collect 30 seconds of video showing snails crawling at what subjectively (with reference to the ruler) appeared a steady rate (following to protocol of Pavlova, 2001). All video footage was recorded using the camera described above. The videos produced had a recording rate of 25 frames per second (FPS) and a recording size of 640:25. The camera was positioned 30 cm away from the ruler which was positioned parallel to the snail. The video footage recorded was then reviewed on a computer monitor to identify distance travelled during the 30-second segment. To determine distance, we recorded the position of the anterior margin of the foot (following methodology by Hemmert & Baltzley, 2016) the position of the snail at the beginning and the end of the measurement period was noted and the total distance was derived from the ruler in the video.

We collected data on 87 snails. For each snail, speed was measured (in a random order) on five different surfaces: a horizontally-orientated PVC sheet, a vertically-orientated PVC sheet, a horizontally-orientated wet PVC sheet, horizontally-orientated sandpaper with a P120 FEPA (Federation of European Producers of Abrasives) "P grade" grit designation (125 μm Apd), and a horizontally-orientated PVC sheet with the presence of a trail left by another snail. When testing snail speed in the presence of another snail trail, the same trail-leaving snail was used for each experiment. To produce a wet surface, 18 mL of water was placed onto a horizontal PVC sheet and spread over the surface with a cloth to evenly distribute the water. The PVC sheet was cleaned after each experiment.

We also conducted a further two experiments to investigate the relationship between snail behaviour and surface roughness. First, we measured snail speed at different sandpaper grit sizes to identify if speed changes depending on the average particle diameter (μm). For this experiment we recorded data for 44 snails. Snail speed was obtained using the same method above across horizontally orientated dry sandpaper with 4 different FEPA Grit designations (in random order): P40 (coarse: 425 µm Apd), P60 (medium: 269 µm Apd), P80 (medium: 201 µm Apd) and P120 (fine: 125 µm Apd). As the FEPA Grit designation increases, the average particle dimeter decreases. Like the former experiment, a foot length measurement data was also taken. A piece of sandpaper was used only once.

Second, we conducted a series of choice trials in order to identify if there was preference for surface texture. Individual snails were introduced into the centre of a test arena which was divided into two types of sandpaper with different FEPA Grit designations: P40 (425 µm Apd) and P120 (125 µm Apd). Both sections of sandpaper were 90x90mm squares, making the total arena floor 180x180mm. A plastic circular tube (height 52mm, diameter 165mm) was placed on top of this surface to construct the arena. The circular tube was uniform in colour and texture so that only the floor surface varied within the arena itself. Introduction in the middle of the arena so that the foot was in contact with both types of sandpaper eliminated preference derived from the individuals initial position. Both types of sandpaper were the same colour to further eliminate colour preference. Once in the arena, surface preference was identified for each snail by recording the initial positive movement direction. This was defined as the surface which was in contact with over 50% of the snail's foot after 30 seconds. To avoid bias linked to compass direction, the arena was rotated by a random number (uniformly drawn from [0-360] degrees before every trial). All test arenas were equal distance away from an artificial light source. Individuals were used only once. All background options had the same area in each experiment and all individuals had a new test arena in order to avoid potential bias from the previous presence of a snail trail.

During all experiments, temperature was monitored and predominantly maintained at 22 °C but ranged from 20 to 24°C.

Statistical Analysis

All data analysis was performed using R (VERSION 3.4.1; R Core Team, 2018).

We performed a series of regression analyses in order to identify if there was a consistent relationship between our morphometric measurements: foot length, shell length, shell circumference and shell width. To determine whether the morphometric measurements affected crawling speed, and whether the relationship between each pair of variables was significantly different for snails crawling on a horizontal or a vertical surface, we performed a series of ANCOVAs. All ANCOVA models contained "individual" as a random effect and were performed using the package *lme4* (Bates *et al.*, 2015) via the *lmer()* function. For each ANCOVA, we determined whether the relationship between speed and the morphometric variable was dependent on snail orientation. This was identified based on the *P* value of the interaction term (morphometric variable x orientation) in the model. If the slopes were not significantly different the interaction term was removed to derive the slope and intercept of the regression. All regression analyses were performed on log10 transformed data.

We also performed a linear mixed effects model via the *lmer()* function to determine if there was a significant difference between snail speed when moving on a horizontal surface in comparison to the other surface mediums. Speed was treated as a continuous dependent response variable and medium (horizontal PVC, vertical PVC, wet PVC, P120 sandpaper and PVC in the presence of a conspecific trail) was treated as a fixed categorical effect. Individual was treated as a random effect to avoid pseudoreplication. As each snail was measured on each substrate, the substrate measured first (to ensure that substrate order would not affect the results), foot length and the interaction between medium and foot length were included as fixed effects in the original model, however these were not present in the final model, likely because of the inclusion of individual in the model. Horizontal PVC was treated as the baseline of the model.

To identify if there was a significant preference for abrasive particle size between P40 sandpaper and P120 sandpaper we conducted Pearson's chi-Squared test (*chisq.test*) on frequency data obtained from 50 choice trials using the null hypothesis that snails would not chose one surface over the other more or less often than expected by chance.

Another linear mixed effects model was conducted to determine if there was a significant difference in speed between the four sizes of abrasive particle. In this model, speed was treated as a continuous dependent response variable and FEPA Grit designation (P40, P60, P80, P120) was treated as a fixed categorical effect. Individual was treated as a random effect. As each snail was measured on each type of sandpaper, the sandpaper Grit designation measured first, foot length and the interaction between Grit designation and foot length were included as fixed effects in the original model, however these were not present in the final model, again likely because of the inclusion of individual in the model.

For the linear mixed effect analyses, models were ranked by their Akaike's information criterion with sample size adjustment (AICc; Burnham and Anderson 2002). P values were subsequently derived from the minimum adequate models (Supplementary File Table S1).

RESULTS

When investigating snail speed across different surface mediums we found that there was a significant difference in crawling speed and substrate medium (Table 1). Mean crawling speed was significantly faster when snails were travelling across a horizontal PVC in comparison to vertical PVC, sandpaper (P120), or wet PVC (Fig. 1; Table 1). There was no significant difference in speed across either clean horizontal PVC or horizontal PVC in the presence of a conspecific trail (Fig. 1; Table 1).

When investigating snail speed across different grit sizes we found that there was a significant difference in speed between the four sizes of abrasive particle (Table 2). Snails were significantly slower when travelling across sandpaper with a grit designation of P40 in comparison to P80 and P120 (Fig. 2; Table 2). Despite grit size significantly altering speed, the results from the chi-squared analysis showed no significant preference for abrasive particle size between P40 and P120 sandpaper ($\boldsymbol{X}^2 = 1.28$, $P = 0.258$).

Similar to previous results, there was a significant positive correlation between foot length and shell circumference, shell length and shell width (Supplementary File Table S2). Surprisingly, we found no relationship between foot length or shell length and snail speed, and this did not significantly differ when snails were crawling horizontally or vertically (Supplementary File Table S3).

DISCUSSION

We examined the relationship between size, substrate texture and speed in the common land snail *C. aspersum*. Analogous with previously reported results, snails were significantly slower when moving over a vertical surface, in comparison to a horizontal surface. In all of our vertical speed tests the snail moved upwards. It has been proposed by Denny (1981) and later by Hemmert & Baltzley (2016) that the weight of the snail, along with gravity, acts over the interwaves during upward vertical movement, increasing the amount of stress put on the moving gastropod, meaning that each muscular wave translates to less forward movement (See "V_s" in Fig. 3) . Denny (1981) also proposed that gastropods decrease the thickness of the mucus layer when crawling on a vertical surface. In fact, Zhong *et al.* (2018) found that nanoparticle assembly during mucus production was altered to improve viscosity when moving across an inclined plate in order to overcome the influence of gravity. Although this does reduce slippage, it increases the force needed to move the individual forward, likely reducing speed.

Although both wet and rough surface textures significantly slowed crawling speed, the latter result was the most striking as this decrease in speed was considerably greater than the other surfaces tested. Course substrates may interfere with stationary interwave adhesion. In order to move forward, the force beneath the interwave must be greater than the frictional force (shear force) produced by the waves and the rim (Chan *et al.*, 2010) (Fig. 3). If certain substrates reduce mucus-foot adhesion at each interwave, this could reduce speed. Similarly, if certain substrates alter the stress required to yield the mucus into a liquid state during muscle contraction (Fig. 3), this could also affect propulsion. This interference could occur in two ways: by minimising the surface area available for adhesion or by increasing mucus production. Data produced by Kim, Kim & Kim (2010) support the former hypothesis as they calculated that the total area that could adhere to a rough surface was less than half of what could adhere to a smooth surface meaning that as the size of abrasive particles increases, the available surface to adhere to decreases. Previous literature also supports the latter hypothesis as effective movement over rough substrates has been shown to stimulate the production of a larger volume of mucus to minimise the effect of friction (Kobayashi, Yamamoto & Aoyama, 2003; Shirtcliffe, McHale & Newton, 2012). As indicated previously, increasing mucus production reduces viscosity, which is likely to weaken adhesion at each interwave, making overall net movement lower in comparison to movement over a smooth substrate. This is supported by Kobayashi *et al.* (2003) who recorded a negative correlation between mucus thickness and shear strength (the pulling adhesive force of the snail). In a similar vein, a wet surface may slow crawling speed as the mucus produced by the snail and the surface liquid likely interact at the interwave-mucus layer, reducing the ability of a snail to adhere to a substrate (Kim *et al.*, 2010), affecting speed.

Substrate texture may also affect speed by altering gait. Data by McKee *et al.* (2013) showed that substrate attributes determine crawling gait in *C. aspersum*. Rough substrates initiate loping as a means to conserve mucus production across rough surfaces (which require a higher volume of mucus to minimise friction). Although we did not make note of gait choice in our experiment, gait variation across rough and smooth substrates may have affected speed. This idea is supported by the fact that McKee *et al.* (2013) did not find a significant difference in speed when crawling was adopted across both smooth and rough surfaces, but speed decreased when a loping gait was adopted across the latter. The higher levels of mucus required to move across a rough surface may also affect speed by increasing energy expenditure as mucus production is metabolically expensive (Denny, 1980a). Whether we would observe this affect during the short time scale over which the experiment was conducted seems unlikely, however, the effect of costly mucus production on snails which move over rough substrates for extended periods of time warrants further investigation.

The time it takes for the mucus at each interwave to re-solidify should also be considered. After wave contraction has propelled a portion of the foot forward, the individual will have to wait for the mucus under that portion of the foot to yield before the next portion of the foot can move forward. As such, restructuring time and post-yield viscosity have been shown to be inversely proportional to speed, limiting the maximum crawling velocity which can be achieved by an individual (Ewoldt *et al.*, 2007). Substrate-driven variation in mucus production may alter properties of the mucus itself, increasing or decreasing restricting time and/or post-yield viscosity.

Despite observing a significant negative correlation between speed and the size of abrasive particles on a rough surface, our snails did not display a significant tendency to select substrates based on grit size.

This does not support the theory that abrasive surfaces cause foot "irritation" and suggests that speed reduction is either not important or the effect of abrasive particle size experienced by the snails in this study is negligible. Although reduced speed has been shown to increase predation risk in a variety of taxa (Webb, 1984; Lima & Dill, 1990), its effect on this species may be minimised as they already have low mobility.

Interestingly, we found no significant difference in crawling speed in the presence or absence of a trail. Trail following has previously been shown to act as an energy-conserving mechanism, as it minimises the volume of mucus required to produce an individual's own trail (Tankersley, 1989; Davis & Blackwell, 2007). Conspecific trail following is also adopted to locate potential mates. It subsequently appears logical to theorise that movement in the presence of a trail might increase snail speed. However, previous investigations have shown that trail-following behaviour is plastic, only being observed when individuals were seeking to disperse (Vong *et al.*, 2019). Our experimental apparatus did not allow snails to perform sustained movement on a scale of metres, so may have hindered snail's plastic expression of dispersal-related behaviours. Further, even if the presence of a trail conserves energy, or provides a mating advantage, this need not equate to a change in speed over the short period of time that we carried out the investigation.

Interestingly, unlikely previous studies (Hemmert & Baltzley, 2016), we did not observe a significant difference between speed and foot length or speed and shell length when moving across a horizontal or vertical surface. One possible explanation is that, as the foot length measurements taken in our experiment were predominantly larger than those studied previously, the relationship between foot length and speed is stronger at smaller sizes. Indeed, smaller organisms with relatively larger foot sizes are likely to produce a stronger propulsive force in relation to their body size due to their body-mass to body-surface relationship (Shvydka, Kovalev & Gorb, 2020).

In conclusion, there is little doubt that substrate attributes affect snail locomotion, altering the speed at which an individual moves. The consistent reduction in speed shown by *C. aspersum* across tested substrate types indicates that surface texture and angle clearly impact the process of adhesive crawling in this species. Although the size of abrasive particle had the strongest negative effect on crawling speed, we found no evidence that snails select surfaces to minimise this effect, weakening theories proposed by a number of studies which suggest that snails avoid certain substrates to minimise foot irritation. Similarly, although trail-following has been documented countlessly across gastropod research, we found no evidence to suggest that this affects speed. This does not mean that the presence of a conspecific trail is not important in this species, rather that the benefits of trail following under these conditions were not significant or that any benefits which trail following provide do not warrant an increase in speed. Finally, we accept that there are a number of factors which affect speed which interact under natural conditions. The importance of pedal waves and interwave frequency and length (Crozier & Pilz, 1924; Denny, 1981; Donovan & Carefoot, 1997; Pavlova, 2001; Lai *et al.*, 2010), the physiological state of the snail (Pavlova, 2001, 2019), or the presence of absence of a predator warrant further investigation in order to get an even better understanding on what affects the process of locomotion in terrestrial gastropods under natural conditions.

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BIBLIOGRAPHY

Alvarez, L.A., Gramaje, D., Abad-Campos, P. & García-Jiménez, J. (2009). Role of the Helix aspersa snail as a vector of Phytophthora citrophthora causing branch cankers on clementine trees in Spain. *Plant Pathol.* **58**, 956–963.

Arnaud, J-F. (2003). Metapopulation genetic structure and migration pathways in the land snail Helix aspersa: influence of landscape heterogeneity. *Landscape Ecol*. **18**, 333–346.

Balbi, M., Ernoult, A., Poli, P., Madec, L., Guiller, A., Martin, M-C., Nabucet, J., Beaujouan, V., Petit, E. (2018). Functional connectivity in replicated urban landscapes in the land snail (Cornu aspersum). *Mol. Ecol*. **27**, 1357–1370.

Baur, B., Baur, A. (1990). Are roads barriers to dispersal in the land snail Arianta arbustorum? *J. Zool.* **68**, 613–617.

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

Campion, M. (1961). The structure and function of the cutaneous glands in Helix aspersa. *Q. J. Microsc. Sci*. **102**, 195–216.

Chan, B., Balmforth, N.J. & Hosoi, A.E. (2005). Building a better snail: lubrication and adhesive locomotion. *Phys. Fluids A.* **17**, 113101.

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

Cook, A. (1992). The function of trail following in the pulmonate slug, *Limax pseudoflavus*. *Anim. Behav.* **43**, 813–821.

Crozier, W.J. & Pilz, G.F. (1924). The locomotion of *Limax. I.* Temperature coefficient of pedal activity. *J. Gen. Physiol.* **6**, 711–721.

Crozier, W.J. & Federighi, H. (1925). The locomotion of *Limax*. II. Vertical ascension with added loads. *J. Gen. Physiol.* **7**, 415–419.

Davies, M.S. & Blackwell, J. (2007). Energy saving through trail following in a marine snail. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 1233–1236.

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

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

Denny, M.W. (1981). A quantitative model for the adhesive locomotion of the terrestrial slug, *Ariolimax columbianus*. *J. Exp. Biol.* **91**, 195–217.

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

Denny, M.W. & Gosline, J.M. (1980). The physical properties of the pedal mucus of the terrestrial slug, *Ariolimax colurnbinus*. *J. Exp. Biol.* **88**, 375–393.

Donovan, D.A. & Carefoot, T.H. (1997). Locomotion in the abalone *Haliotis kamtschatkana*: pedal morphology and cost of transport. *J. Exp. Biol.* **200**, 1145–1153.

Ewoldt, R.H., Clasen, C., Hosoi, A.E. & McKinley, G.H. (2007). Rheological fingerprinting of gastropod pedal mucus and synthetic complex fluids for biomimicking adhesive locomotion. *Soft Matter*. **3**, 634–643.

Hemmert, H.M. & Baltzley, M.J. (2016). Intraspecific Scaling Relationships Between Crawling Speed and Body Size in a Gastropod. *Biol. Bull.* **230**, 78–84.

Holland, B.S., Chock, T., Lee, A. & Sugiura, S. (2012). Tracking behavior in the snail *Euglandina rosea*: first evidence of preference for endemic vs. biocontrol target pest species in Hawaii. *Am. Malacol. Bull.* **30**, 153–157.

Iglesias, J. & Castillejo, J. (1999). Field observations on feeding of the land snail Helix aspersa Müller. *J. Molluscan Stud.* **65**, 411–423.

Iwamoto, M., Ueyama, D. & Kobayaski, R. (2014). The advantage of mucus for adhesive locomotion in gastropods. *J. Theor. Biol.* **353**, 133–141.

Kim, K.L., Kim, Y.T. & Kim, D.E. (2010). Adhesion characteristics of the snail foot under various surface conditions. *Int. J. Precis. Eng. Manuf.* **11**, 623–628.

Kobayashi, A., Yamamoto, I. & Aoyama, T. (2003). Tribology of a snail (terrestrial gastropod). *Tribol. Res. Des. Eng. Syst.* **41**, 429–436.

Kuroda, S., Kunita, I., Tanaka, Y., Ishiguro, A., Kobayashi, R. & Nakagaki, T. (2014). Common mechanics of mode switching in locomotion of limbless and legged animals. *J. R. Soc. Interface.* **11**, 20140205.

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

Lauga E. & Hosoi A.E. (2006). Tuning gastropod locomotion: modeling the influence of mucus rheology on the cost of crawling. *Phys. Fluids.* **18**, 113102.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation – a review and prospectus. *Can. J. Zool.* **68**, 619–640.

McKee, A., Voltzow, J. & Pernet, B. (2013). Substrate attributes determine gait in a terrestrial gastropod. *Biol. Bull.* **224**, 53–61.

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

Munn, A.J. & Treloar, M. (2016). Phenotypic plasticity in the common garden snail: big guts and heavier mucus glands compete in snail faces with the dual challenge of poor diet and coarse substrate. *J. Comp. Physiol. B.* **187**, 545–561.

Ng, T.P., Saltin, S.H., Davies, M.S., Johannesson, K., Stafford, R. & Williams, G.A. (2013). Snails and their trails: the multiple functions of trail-following in gastropods. *Biol. Rev. Camb. Philos. Soc.* **88**, 683–700.

Ng, T.P., Davies, M.S., Stafford, R. & Williams, G.A. (2011). Mucus trail following as a mate-searching strategy in mangrove littorinid snails. *Anim. Behav.* **82**, 459–465.

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

Pavlova, G.A. (2001). Effects of serotonin, dopamine and ergometrine on locomotion in the pulmonate mollusc *Helix lucorum*. *J. Exp. Biol.* **204**, 1625–1633.

Pavlova, G.A. (2013). Sole smooth muscle states determine gliding rate in the freshwater snail Lymnaea stagnalis. *Biol. Bull.* **225**, 184–193.

Pavlova, G.A. (2019). The similarity of crawling mechanisms in aquatic and terrestrial gastropods. *J. Comp. Physiol. A.* **205**, 1–11.

Pearce, T.A. & Gaertner, A. (1996). Optimal foraging and mucus trail following in the carnivorous land snail *Haplotrema concavum*. *Malacol. Rev.* **29**, 85–99.

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

R Core Team. (2018). R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Reise, H. (2007). A review of mating behaviour in slugs of the genus Deroceras (Pulmonata: Agriolimacidae). *Am. Malacol. Bull.* **23**, 137–156.

Shaheen, N., Patel, K., Patel, P., Moore, M. & Harrington, M.A. (2005). A predatory snail distinguishes between conspecific and heterospecific snails and trails based on chemical cues in slime. *Anim. Behav.* **70**, 1067–1077.

Shirtcliffe, N.J., McHale, G. & Newton, M.I. (2012). Wet adhesion and adhesive locomotion of snails on adhesive non-wetting surfaces. *PLoS ONE.* **7**, e36983.

Shvydka, Z., Kovalev, A. & Gorb, S.N. (2020). The frictional and adhesive properties of the shells of terrestrial hairy snails. *J. Zool.* **310**, 180–190.

Smith, A.M. (2002). The structure and function of adhesive gels from invertebrates. *Integr. Comp. Biol.* **42**, 1164–1171.

Tankersley, R.A. (1989). The effect of trail-following on the locomotion of the marsh periwinkle *Littorina irrorata* (Mesogastropoda: Littorinidae). *Mar. Behav. Phy.* **15**, 89–100.

Vong, A., Ansart, A. & Dahirel, M. (2019). Dispersers are more likely to follow mucus trails in the land snail *Cornu aspersum*. *Sci. Nat.* **106**, 43.

Webb, P.W. (1984). Form and function in fish swimming. *Sci. Am.* **251**, 72–82.

Zhong, T., Min, L., Wang, Z., Zhang, F. & Zuo, B. (2018). Controlled self-assembly of glycoprotein complex in snail mucus from lubricating liquid to elastic fiber. *RSC Adv.* **8**, 13806–13812.

FIGURE AND TABLE LEGENDS

Figure 1.

The difference in mean snail speed (cm/30s) across horizontal PVC ("Horizontal") compared to different surface mediums: P120 sandpaper, horizontal PVC in the presence of a trail ("Trail"), vertical PVC and horizontal wet PVC ("Wet"). Snails were significantly slower when travelling across a rough surface ($P < 0.001$), a wet surface ($P < 0.001$), and a vertical surface ($P = 0.016$) in comparison to a horizontal surface. The dots indicate individual data points.

Figure 2.

The difference in mean snail speed across P40 sandpaper in comparison to other sandpaper designations which decrease in average particle size. Snails were significantly slower when travelling across sandpaper with a grit designation of P40 in comparison to P80 ($P = 0.037$) and P120 ($P = 0.001$), suggesting that as grit diameter increased snail crawling speed decreased. The dots indicate individual data points.

Figure 3.

Sketch of the ventral foot (left) and side view (right) of a terrestrial gastropod. The ventral foot displays a series of waves and interwaves surrounded by a rim. The velocity of the gastropod (V_s) is determined by the velocity of the waves (V) in relation to the stationary interwaves. The side view of the gastropod illustrates the effect of each wave on the non-Newtonian mucus layer which separates the foot from the substrate. Waves exert high stress, causing the mucus to become a liquid. The mucus under each interwave experiences low stress and remains in a more solid state (highly viscous), allowing the snail to adhere to the substrate. The gastropod is moving left to right.

Table 1.

Results of the linear mixed effects model showing the difference in speed across a horizontal plastic surface and an alternative medium. The top line outlines the results from an ANOVA. Estimate ± SE presents the difference in the mean speed when moving across the medium tested in comparison to horizontal PVC. Proportion of variance explained by the individual was 39%. SE is the standard error of the mean value. Bold type face indicates a significant result.

Table 2.

Results of the linear mixed effects model showing mean crawling speed difference across sandpaper FEPA grit designations: P40, P60, P80 and P120. The top line outlines the results from an ANOVA. Estimate ± SE presents the difference in mean speed when moving across sandpaper with a P40 designation in comparison to P60, P80 and P120. Proportion of variance explained by the individual was 53%. SE is the standard error of the mean value. Bold type face indicates a significant result.

TABLES

Table 1

	Estimate ± SE	*df*	*F/t value*	*p*
Medium		4	82.262	**<0.001**
Horizontal PVC (Intercept)	4.47±0.12	267.527	36.207	**<0.001**
Vertical PVC	-0.41±0.13	344	-3.084	**0.002**
Sandpaper "P120"	-2.01±0.13	344	-15.131	**<0.001**
Wet PVC	-0.65±0.13	344	-4.930	**<0.001**
PVC in presence of a trail	0.12±0.13	344	0.892	0.373

Table 2

	Estimate ± SE	*df*	*F/t value*	*p*
Grade		3	3.845	**0.011**
P40 (Intercept)	2.240 ± 0.112	114.943	19.961	**<0.001**
P60	0.140 ± 0.109	159	1.286	0.200
P80	0.229 ± 0.109	159	2.103	**0.037**
P120	0.358 ± 0.109	159	3.296	**0.001**