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Intraspecific Scaling Relationships Between Crawling Speed and Body Size in a Gastropod

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Abstract. Across various modes of locomotion, body size and speed are often correlated both between and within species. Among the gastropods, however, current data are minimal for interspecific and intraspecific scaling relationships. In this study, we tested the relationships between various measurements of body size and crawling speed in the terrestrial snail *Cornu aspersum*. We also investigated the relationships between crawling speed, muscular wave frequency, and muscular wavelength, because—while these relationships within individuals are well studied—the relationships among individuals are unknown. We recorded snails crawling on both a horizontal and a vertical surface. We found that when they crawled on a horizontal surface, foot length was positively correlated with pedal wavelength and crawling speed, but was not correlated with wave frequency. In comparison, when they crawled on a vertical surface, foot length was positively correlated with wavelength, negatively correlated with wave frequency, and not correlated with crawling speed. Body mass had no correlation with crawling speed when snails were crawling on a horizontal surface, but was negatively correlated with speed when snails crawled on a vertical surface.

Introduction

Across a wide range of phyla and diverse modes of locomotion, the speed of locomotion generally increases with increasing body size (Schmidt-Nielsen, 1975). This relationship has been found interspecifically for running mammals, running birds, flying birds, swimming ciliates and flagellates, and swimming vertebrates (Garland, 1983; Gatesy and Biewener, 1991; Alerstam *et al.*, 2007; Vogel, 2008). Intraspecifically, however, the correlation between size and speed is more variable. Speed increases with size in a chipmunk (Schulte-Hostedde and Millar, 2002), a jellyfish (McHenry and Jed, 2003), a sea urchin (Domenici *et al.*, 2003), and a sea star (Mueller *et al.*, 2011). In contrast, speed does not appear to be correlated with body size in a lizard (Garland *et al.*, 1990), or in four species of sea stars (Mueller *et al.*, 2011; Montgomery and Palmer, 2012).

Among gastropods, the basic scaling relationships between size and speed, both interspecifically and intraspecifically, are unclear. One of the reasons the relationships between size and speed have not been fully explored is that the mechanism of propulsion in crawling gastropods is variable (Miller, 1974a). Gastropods crawl using 1) compression (“direct”) waves, which move from the posterior to the anterior of the foot; 2) elongation (“retrograde”) waves, which move from the anterior to the posterior of the foot; 3) muscular waves that extend the width of the foot (“monotaxic”); 4) muscular waves that move out of phase on the left and right sides of the foot (“ditaxic”); 5) lateral or diagonal waves (“composite”); and 6) arrhythmic muscular locomotion, with an absence of distinct muscular waves (Jones and Trueman, 1970; Miller, 1974b). In this study, we examined the scaling relationships between size and speed in *Cornu aspersum* Müller, 1774 (formerly known as *Helix aspersa*), a terrestrial snail that crawls using direct monotaxic muscular waves.

In gastropods that crawl using muscular waves, speed is determined by the combination of pedal wavelength and frequency (Miller 1974a). Within individual animals, the frequency of pedal waves is positively correlated with crawling speed (Crozier and Pilz, 1924; Denny, 1981; Donovan and Carefoot, 1997; Pavlova, 2001; Lai *et al.*, 2010). In addition, individual snails increase both wavelength and foot length when crawling speed increases

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(Donovan and Carefoot, 1997; Pavlova, 2001, 2013). Because snails with a larger shell tend to have a longer foot, then both shell size and foot length should be positively correlated with speed—if there is an intraspecific positive correlation between foot length and wavelength. However, in *C. aspersum*, shell size is not correlated with crawling speed (McKee *et al.*, 2013). Therefore, in addition to examining the intraspecific relationship between foot length and speed, we also tested whether an intraspecific positive correlation exists between foot length and wavelength.

Another factor that may influence the scaling relationships between size and speed in gastropods is whether the animals are crawling on a vertical or a horizontal surface. Foot shape affects the ability of a snail to adhere to the substratum (Miller, 1974a). A snail crawling on a vertical surface may experience constraints on foot shape that affect locomotion, and thereby affect scaling relationships between size and speed. As *C. aspersum* feed in trees as well as on the ground (Iglesias and Castillejo, 1999; Alvarez *et al.,* 2009), the relationships between size and speed on vertical surfaces are relevant to the natural behavior of the animal. Therefore, we compared the scaling relationships between size and speed for snails on both horizontal and vertical surfaces.

Materials and Methods

Cornu aspersum were collected from local gardens in Monmouth, Oregon, within 24 hours of conducting the experiments. Snails ranged from 0.2 to 7.2 g in body mass, and from 15.2 to 58.5 mm in foot length. Data for snails crawling on a vertical surface were collected between September and November, 2014; data for snails crawling on a horizontal surface were collected between March and May, 2015. For the vertical surface measurements, foot length, wavelength, wave frequency, and crawling speed of each snail were measured by two independent observers at different times of the day so as to obtain an estimate of repeatability. One of the observers who collected data for snails crawling on a vertical surface, also collected data for snails crawling on a horizontal surface.

We used a digital video camera to record the ventral side of the foot while snails crawled in a glass aquarium for the vertical surface measurements, and while they crawled along a Plexiglas platform for the horizontal surface measurements. Crawling speed and mucus production by *C. aspersum* are not different on glass compared to acrylic (McKee *et al.*, 2013). A ruler was placed beside the crawling snail for scale. Snails were recorded for 1–15 min in order to collect 30 seconds of video showing snails crawling at a steady rate (Pavlova, 2001). Video footage was played back on a computer monitor with a transparent plastic sheet placed over the screen. We made initial markings on the plastic sheet, then created a digital version of the data using Adobe Illustrator CS5.1 (Adobe Systems Inc., San Jose, CA), by tracing the markings. We recorded foot width at the middle of the foot. We recorded the distance from the middle of one pedal wave to the middle of the next pedal wave (wavelength) from the two waves closest to the middle of the foot. Wave frequency was calculated based on the length of time it took 10 waves to reach the anterior margin of the foot. To determine crawling speed, we recorded the position of the anterior margin of the foot every second for 30 s. We then created a path using Adobe Illustrator CS5.1, measured the length of the entire path, and divided the path length by 30 s.

We recorded data for 30 snails crawling on a horizontal surface and 35 snails crawling on a vertical surface. During the data analysis, we had to discard horizontal crawling data for wavelength from two snails, and wave frequency from one snail, because clarity of the video precluded accurate measurements.

We performed regression analyses on $\log_{10}$ transformed data. For all regression analyses, we used studentized residual values to identify statistically significant outliers (Stevens, 1984). Scaling coefficients were calculated using ordinary least squares (OLS) regression for all pairs of variables except shell length *versus* body mass, foot length *versus* shell length, foot length *versus* body mass, and foot length *versus* foot width. For these comparisons, we calculated scaling coefficients using the reduced major axis (RMA). We chose whether to use OLS or RMA based on the criteria described in Smith (2009).

To determine whether wavelength affected crawling speed independent of foot length, we used the regression for wavelength *versus* foot length to calculate an expected wavelength for each snail, then calculated the residual wavelength to determine how much the measured wavelength differed from the expected wavelength. We then performed a regression analysis of crawling speed *versus* wavelength residuals. We performed a similar analysis to determine whether wave frequency affected crawling speed independent of foot length.

We performed ANCOVAs to determine whether regression analyses between each pair of variables were significantly different for snails crawling on a vertical surface compared to snails crawling on a horizontal surface. For comparisons of vertical crawling and horizontal crawling, we used data collected by the same observer for all snails. For snails crawling on a vertical surface, we also performed ANCOVAs to determine whether regression analyses between each pair of variables were significantly different based on which observer collected the data. For all ANCOVAs, we first determined whether the slopes of the regressions were significantly different. If the slopes were not different, we then determined whether the intercepts were significantly different (Zar, 1999). All statistical analyses were performed using IBM SPSS Statistics 21 (IBM Corp., Armonk, NY).

Table 1

Summary of regression analyses for crawling Cornu aspersum

	Horizontal surface crawling				Vertical surface crawling				ANCOVA (*P*-value)		
	P-value	r^2	a	k	*P*-value	r^2	a	k	Slope	Intercept	Figure
Shell length *vs.* body mass	**<0.001**	**0.95**	**0.39**	**15.27**	**<0.001**	**0.88**	**0.35**	**15.09**	0.08	0.06	1A
Foot length *vs.* shell length	**<0.001**	**0.71**	**0.98**	**1.72**	**<0.001**	**0.71**	**0.86**	**2.77**	0.42	**0.004**	1B
Foot length *vs.* body mass	**<0.001**	**0.80**	**0.38**	**25.13**	**<0.001**	**0.76**	**0.30**	**28.74**	0.06	**0.03**	1C
Foot length *vs.* foot width	**<0.001**	**0.63**	**0.67**	**9.33**	**<0.001**	**0.74**	**0.58**	**10.37**	0.76	0.40	1D
Crawling speed *vs.* foot length	**0.02**	**0.18**	**0.41**	**0.38**	0.49	0.02	−0.15	2.33	0.34	**0.03**	2A
Crawling speed *vs.* shell length	0.34	0.03	0.17	0.96	0.05	0.11	−0.40	4.67	**0.04**	–	N/A
Crawling speed *vs.* body mass	0.19	0.06	0.09	1.51	**0.03**	**0.14**	**−0.16**	**1.59**	**0.01**	–	2B
Wavelength *vs.* foot length	**0.007**	**0.25**	**0.43**	**1.00**	**0.007**	**0.20**	**0.36**	**1.48**	0.72	**0.01**	3A
Crawling speed *vs.* wavelength residuals	0.21	0.06	0.38	1.66	**0.04**	**0.13**	**0.52**	**1.41**	0.73	**0.02**	3B
Frequency *vs.* foot length	0.38	0.03	−0.08	1.11	**<0.001**	**0.38**	**−0.42**	**3.72**	**0.02**	–	4A
Crawling speed *vs.* frequency residuals	**0.005**	**0.26**	**1.09**	**1.63**	**<0.001**	**0.73**	**1.83**	**1.38**	0.06	**0.002**	4B
Crawling speed *vs.* wave speed	**0.005**	**0.26**	**0.64**	**0.70**	**<0.001**	**0.43**	**0.74**	**0.46**	0.71	**<0.001**	5

Regression statistics are for the equation log y = a log x + log k, or $y = kx^a$ for the untransformed variables. In the Horizontal surface crawling and Vertical surface crawling columns, boldface type indicates statistical significance for the regression analyses. For ANCOVA (*P*), boldface type indicates significant difference between the Horizontal and Vertical regressions. Scaling coefficients are reduced major axis (RMA) for shell length *versus* body mass, foot length *versus* shell length, foot length *versus* body mass, and foot length *versus* foot width. For all other comparisons, coefficients are ordinary least squares (OLS). N/A, no corresponding figure.

Results

Because the experiments were performed at different times of the year, we compared the overall size of snails crawling on a vertical surface with those that crawled on a horizontal surface. Snails collected in the fall, which were measured while crawling vertically, had a mean shell length of 21.9 ± 1.0 mm (± SEM) and a mean body mass of 3.4 ± 0.3 g. Snails collected in the spring, which were measured while crawling horizontally, had a mean shell length of 21.3 ± 1.0 mm and a mean body mass of 2.7 ± 0.3 g. Neither shell length nor body mass was significantly different between the two groups (*t*-tests: shell length: $P = 0.64$; body mass: $P = 0.10$). Additionally, shell length was positively correlated with body mass for both populations, and the regressions for the two populations were not significantly different (Table 1; Fig. 1A).

Foot length *versus* shell length, foot length *versus* body mass, and foot length *versus* foot width all showed positive correlations (Fig. 1). For foot length *versus* shell length and foot length *versus* body mass, the elevations of the regressions were greater for snails crawling on a vertical surface than for snails crawling on a horizontal surface. When snails were crawling on a horizontal surface, crawling speed was positively correlated with foot length, but not with shell length or body mass (Table 1; Fig. 2). In comparison, when snails crawled vertically, speed was not correlated with foot length or shell length, but was negatively correlated with body mass.

Wavelength was positively correlated with foot length for snails that crawled on both a horizontal and a vertical surface (Fig. 3A). We found no correlation between crawling speed and wavelength residuals for snails crawling on a horizontal surface, but crawling speed and wavelength residuals were positively correlated for snails crawling on a vertical surface (Fig. 3B). Wave frequency was negatively correlated with foot length for snails crawling on a vertical surface, but not for snails crawling on a horizontal surface (Fig. 4A). We found a significant positive correlation between crawling speed and wave frequency residuals for snails that crawled on both a horizontal and a vertical surface (Fig. 4B).

For each snail, we calculated the wave speed by multiplying wavelength by wave frequency. *Cornu aspersum* had a mean wave speed to crawling speed ratio of 2.2 ± 0.1 when crawling on a horizontal surface, and a mean wave speed to crawling speed ratio of 3.2 ± 0.2 on a vertical surface. Crawling speed was positively correlated with wave speed on both horizontal and vertical surfaces, and the scaling relationships on the two surfaces were significantly different (Fig. 5).

Two different observers measured the foot length and crawling speed of the same snails on the same vertical surface at different times to determine how much variability there was in foot length and crawling speed, as well as to test the repeatability of the correlation analyses between speed and foot length, wavelength, and wave frequency. The measurements of foot length (ANOVA: $P = 0.96$; average error in measurements = 10%), crawling speed (ANOVA: $P = 0.96$; average error = 7%), and wave frequency (ANOVA: $P = 0.57$; average error = 14%) by

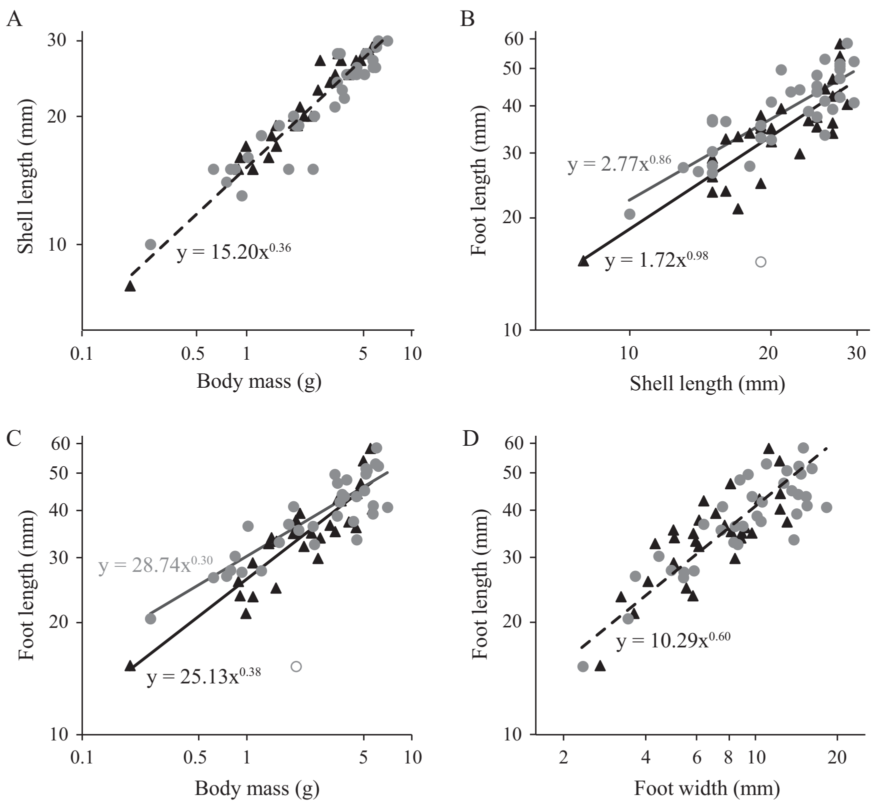

Figure 1. Relationships between morphological characteristics of *Cornu aspersum* while crawling on a horizontal surface (black) and on a vertical surface (gray). Open circles represent outliers for snails crawling on a vertical surface. Outliers were not included in the regression analyses. (A) Shell length *versus* body mass. (B) Foot length *versus* shell length. (C) Foot length *versus* body mass. (D) Foot length *versus* foot width. Regressions for pooled data are shown for panels (A) ($P < 0.001$, $r^2 = 0.90$) and (D) ($P < 0.001$, $r^2 = 0.69$), because, for each pair of variables, the regression for snails on a horizontal surface was not significantly different from the regression for snails on a vertical surface. See Table 1 for regression statistics.

different observers were not significantly different. The measurements of wavelength by different observers were significantly different (ANOVA: $P < 0.001$; average error = 78%), although the measurements of wavelength were significantly correlated ($P < 0.001$; $r^2 = 0.36$). Importantly, despite the different measurements in wavelength, neither

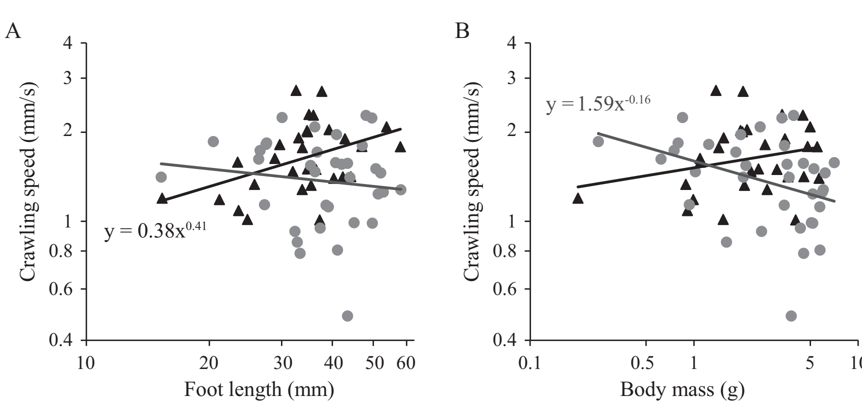

Figure 2. Relationship between crawling speed and morphological characteristics of *Cornu aspersum* while crawling on a horizontal surface (black) and on a vertical surface (gray). Regression equations are shown only if the regression was statistically significant. (A) Crawling speed *versus* foot length. (B) Crawling speed *versus* body mass. See Table 1 for regression statistics.

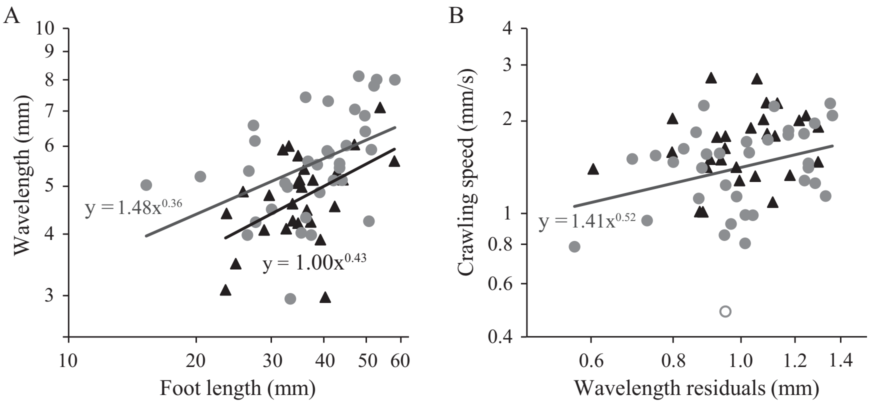

Figure 3. Relationships between wavelength, foot length, and crawling speed of *Cornu aspersum* while crawling on a horizontal surface (black) and on a vertical surface (gray). Open circles represent outliers for snails crawling on a vertical surface. Outliers were not included in the regression analyses. Regression equations are shown only if the regression was statistically significant. (A) Wavelength *versus* foot length. (B) Crawling speed *versus* wavelength residuals. See Table 1 for regression statistics.

observer found a correlation between speed and wavelength (Observer #1: $P = 0.16$, $r^2 = 0.06$; Observer #2: $P = 0.49$, $r^2 = 0.02$; ANCOVA: slope $P = 0.56$, intercept $P = 0.80$). Similarly, neither observer found a correlation between speed and foot length (Observer #1: $P = 0.49$, $r^2 = 0.02$; Observer #2: $P = 0.10$, $r^2 = 0.08$; ANCOVA: slope $P = 0.43$, intercept $P = 0.78$). Both observers found a negative correlation between speed and wave frequency (Observer #1: $P < 0.001$, $r^2 = 0.55$; Observer #2: $P < 0.001$, $r^2 = 0.59$; ANCOVA: slope $P = 0.72$, intercept $P = 0.87$).

Discussion

We found that foot length and crawling speed were significantly correlated when *Cornu aspersum* were crawling on a horizontal surface, but not when they crawled on a vertical surface (Fig. 2A). In comparison, even though body mass and foot length showed a strong positive correlation (Fig. 1C), crawling speed was not correlated with body mass when snails were crawling on a horizontal surface; crawling speed and body mass were negatively correlated when snails were crawling on a vertical surface (Fig. 2B). Additionally, wavelength was positively correlated with foot length for snails crawling on both a horizontal and vertical surface (Fig. 3A). Wave frequency was negatively correlated with foot length for snails crawling on a vertical surface, but not for those crawling on a horizontal surface (Fig. 4A).

A number of studies in snails and slugs have demonstrated positive correlations between crawling speed and wave frequency (Crozier and Pilz, 1924; Crozier and Federighi, 1925; Pavlova, 2001; Lai *et al.*, 2010); between crawling speed and wavelength (Lai *et al.*, 2010); and

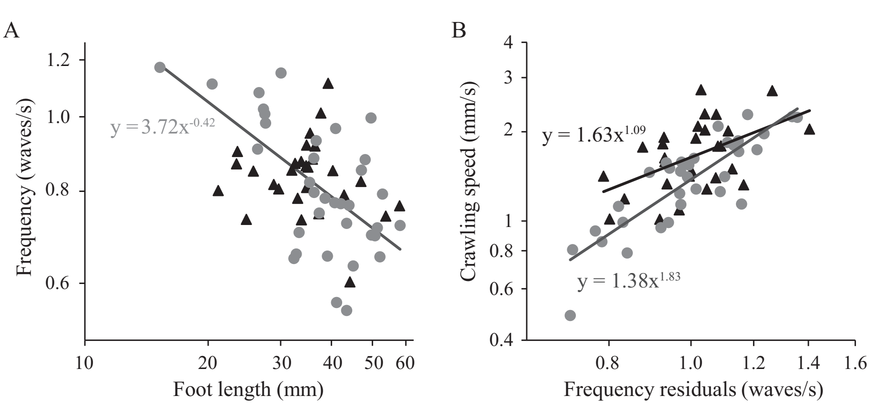

Figure 4. Relationships between frequency, foot length, and crawling speed of *Cornu aspersum* while crawling on a horizontal surface (black) and on a vertical surface (gray). Regression equations are shown only if the regression was statistically significant. (A) Frequency *versus* foot length. (B) Crawling speed *versus* frequency residuals. See Table 1 for regression statistics.

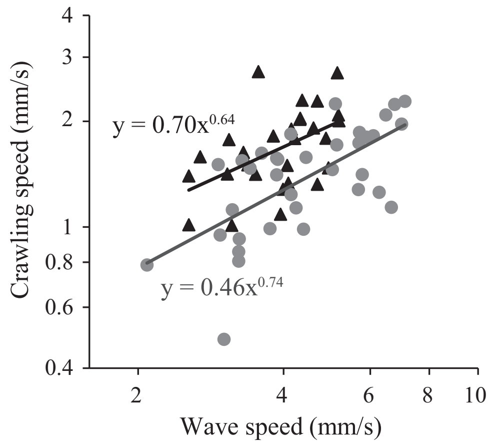

Figure 5. Relationship between crawling speed and wave speed of *Cornu aspersum* while crawling on a horizontal surface (black) and on a vertical surface (gray). See Table 1 for regression statistics.

between crawling speed and foot length (Pavlova, 2001, 2013). However, each of these studies examined how the frequency, wavelength, and/or foot length of an individual animal change as crawling speed changes. The distinction between our data and the data previously reported is not trivial. When collecting data from the same individual at different speeds, the earlier researchers asked how wavelength and wave frequency change as an individual changes speed. By comparing across animals, we are asking whether larger individuals tend to move faster, and, if so, what is responsible for producing faster crawling speeds?

When snails crawled on a horizontal surface, crawling speed and foot length were correlated, as were wavelength and foot length. However, wavelength residuals were not correlated with crawling speed (Fig. 3B). In contrast, frequency and foot length were not correlated, but frequency residuals were positively correlated with crawling speed (Fig. 4B). Taken together, these results indicate that larger snails produce larger muscular waves; and, for a given foot length, increases in speed are due to increases in wave frequency, not increases in wavelength.

Even though foot length was strongly correlated with both shell length and body mass, crawling speed on a horizontal surface was not correlated with shell length or body mass. This is consistent with previous findings in *C. aspersum,* which showed that shell size was not correlated with crawling speed (McKee *et al*., 2013). On a vertical surface, crawling speed was negatively correlated with body mass, but was not correlated with shell length, although the negative correlation between crawling speed and shell length did approach significance ($P = 0.054$). Just as on a horizontal surface, wavelength was positively correlated with foot length, but—unlike on a horizontal surface—the wavelength residuals were correlated with crawling speed. Similar to crawling on a horizontal surface, the wave frequency residuals were correlated with crawling speed; however, unlike crawling on a horizontal surface, there was a negative correlation between foot length and frequency. Therefore, we conclude that when crawling on a vertical surface, snails with a longer foot produce longer muscular waves, but they produce those waves at a lower frequency. On a vertical surface, differences in speed for snails of a given foot length were due to differences in both wave frequency and wavelength.

Crawling on a vertical surface appears to change the relationship between the speed of muscular waves along the foot and the speed of locomotion. For a given speed of muscular waves, snails on a horizontal surface crawled faster than snails on a vertical surface; that is, each muscular wave translated into less forward movement on a vertical surface than on a horizontal surface (Fig. 5). Terrestrial slugs experience more stress on their foot when crawling on vertical surfaces than on horizontal surfaces (Denny, 1981). Denny (1981) proposed that slugs decrease the thickness of the mucus layer on their foot when crawling on a vertical surface, which would cause an increase in the force needed to move the slug forward. If more force is required to move the animal forward, then any given muscular wave will not produce as much forward propulsion.

An alternative explanation for the differences that we found between snails crawling on a vertical *versus* a horizontal surface is that the experiments were performed at different times of the year; our results may be due to seasonal variations in foot muscle physiology, foot morphology, or the composition of mucus. Over the course of the year, protein concentration, glycogen concentration, and lactate dehydrogenase activity all vary in *Cornu aspersum* (Kotsakiozi *et al.*, 2012), each of which could affect foot muscle physiology. In regard to foot morphology, while seasonal variation in foot size has not been documented in snails, foot size in at least one species of marine snail has been shown to be plastic, and varies based on environmental conditions (Trussell, 1997). In addition, seasonal differences in the composition of pedal mucus have been observed in a limpet (Davies *et al*., 1990). Our conclusions concerning the differences between crawling on vertical and horizontal surfaces are thus tentative. In future studies, we will compare horizontal and vertical crawling in individual snails over time so as to isolate the effects of orientation and season on locomotion.

Another obvious question to address is whether there is an interspecific correlation between gastropod crawling speed and size. Based on other forms of locomotion (Schmidt-Nielsen, 1975; Garland, 1983; Alerstam *et al*., 2007; Vogel, 2008), we predict that size and speed are likely correlated. However, data presented in Miller (1974a) suggest that the relationship between body size and speed may vary depending on the type of locomotion being used. For example, size and speed might be correlated in species that crawl using retrograde waves, but not in species using arrhythmic waves. Just as we found that the rules governing locomotion in *C. aspersum* differ on horizontal and vertical surfaces, the rules governing locomotion across species may differ on horizontal and vertical surfaces, and also between marine and terrestrial gastropods.

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