

# A SNAIL'S SPACE SETS A SNAIL'S PACE: MOVEMENT RATES OF *LAVIGERIA* GASTROPODS IN LAKE TANGANYIKA, EAST AFRICA

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## ABSTRACT

Endemic *Lavigeria* gastropods are diverse and common in the benthos of Lake Tanganyika. We used *in situ* studies of marked individuals to quantify rates of daily movement by three species, and test the effects of size, sex, reproductive status and parasitism on movement. Average net travel distance was 50 cm day<sup>-1</sup>, which corresponds to about 20 times shell length. Male *L. coronata* moved significantly farther than *L. coronata* females or *L. grandis*, and *L. nassa* of either sex. There were also significant differences among individuals within each group; however, these differences were not predicted by size, reproductive status or parasitism. We interpret greater movement of *L. coronata* males as a reflection of mate searching; the ratio of males to non-brooding, non-parasitized females was three times as high in *L. coronata* (21:1) as in the other species (6:1). Our results indicate that these snails are capable of moving considerable distances, and that the highly localized distribution of *L. coronata* populations is not simply a reflection of limited movement by individual snails.

## INTRODUCTION

Movement rates dictate gastropods' ability to select habitats with desirable characteristics such as ample food, appropriate substrate, protection from parasites and predators, and access to mates. The majority of gastropod movement is likely to be related to foraging (Underwood, 1977; Chapman, 2000a). However, predator avoidance is another common motivation for snail movement. For example, directional movement in some subtidal/intertidal snails is predominantly upslope, away from areas of frequent crab presence (Rochette & Dill, 2000). Parasites also may affect the locomotory behavior of their gastropod hosts by stimulating movement into areas where exposure to the parasite's next host (often a snail predator) is enhanced (Levri & Lively, 1996; McCarthy, Fitzpatrick & Irwin, 2000; Miller & Poulin, 2001).

Optimal movement patterns are also influenced by sex and reproductive strategy. Males must travel to find females, and their movement rates depend on sex ratios and the intensity of sexual selection (Erlandsson & Johannesson, 1994; Cruz, Rolan-Alvarez & Garcia, 2001; Parmakelis *et al.*, 2005). The travel distance required to find a mate is expected to decrease in proportion to the ratio of females to males. Other characters such as sperm storage could also affect male movement strategies by shifting the frequency of encountering a receptive mate. Sex-associated differences in movement have also been interpreted as risk-aversion on the part of brooding females (Pardo & Johnson, 2004).

Despite the many ways in which they influence snail fitness, movement rates have been quantified in surprisingly few species. Previous work has emphasized the influence of environmental conditions and species identity on average snail movement in marine (Underwood, 1977; Underwood & Chapman, 1989; Chapman 1999, 2000a, b), freshwater (Brown, Alexander & Thorp, 1998) and terrestrial (Parmakelis & Mylonas, 2004) ecosystems. In contrast, few studies have examined individualistic variables such as sex and reproductive status (but see Pardo & Johnson, 2004).

The goal of this study was to evaluate the influences on movement rates of three closely related species of gastropods in Lake Tanganyika. In addition to potential interspecific differences, we were interested in how sex, size, reproductive status and parasitism affect movement. These comparisons can illuminate influences on the ecological space occupied by individual snails, and how different species interact with their shared environment.

Lake Tanganyika is one of the world's most species-rich freshwater ecosystems (Coulter, 1991). It is home to a gastropod species flock in the genus *Lavigeria* (Cerithioidea: Tanganyikan superflock, West & Michel, 2000) whose approximately 45 known species dominate the gastropod fauna in rocky habitats above 30 m depth (Michel, 1995, 2000; West *et al.*, 2003; Michel *et al.*, 2004). These large-bodied, thick-shelled snails are gonochoristic, ovoviviparous and continuously produce young that are brooded internally (Kingma & Michel, 2000; Michel, 2000). Their distributions range from very narrow to lake-wide (Michel *et al.*, 2004), and multiple species are found at most rocky littoral sites in the lake.

## MATERIAL AND METHODS

We quantified movement rates of three large *Lavigeria* species on the surfaces of large rocks and boulders: *L. coronata* Bourguignat, 1888, *L. grandis* (Smith, 1881) and *L. nassa* (Woodward, 1859). These species have contrasting large-scale distribution patterns; *L. nassa* is found lake-wide on most hard substrates (from cobbles to boulders), with a tolerance for some sedimentation and at depths from 2–30 m; *L. grandis* is found in most of the lake but only on large rock and boulder substrates in clear water, at depths from 0–8 m; *L. coronata* appears to be a relict, and currently point, endemic we found living at only two sites, on large rock and boulder substrates in pristine conditions at depths from 2–12 m. This project was conducted on the northeastern shore of Lake Tanganyika at Jakobsen's (Mwamahunga) Beach (4° 54.64' S 29° 35.92' E), located 5 km south of Kigoma, Tanzania. At this site, all three species occur in microsympatry.

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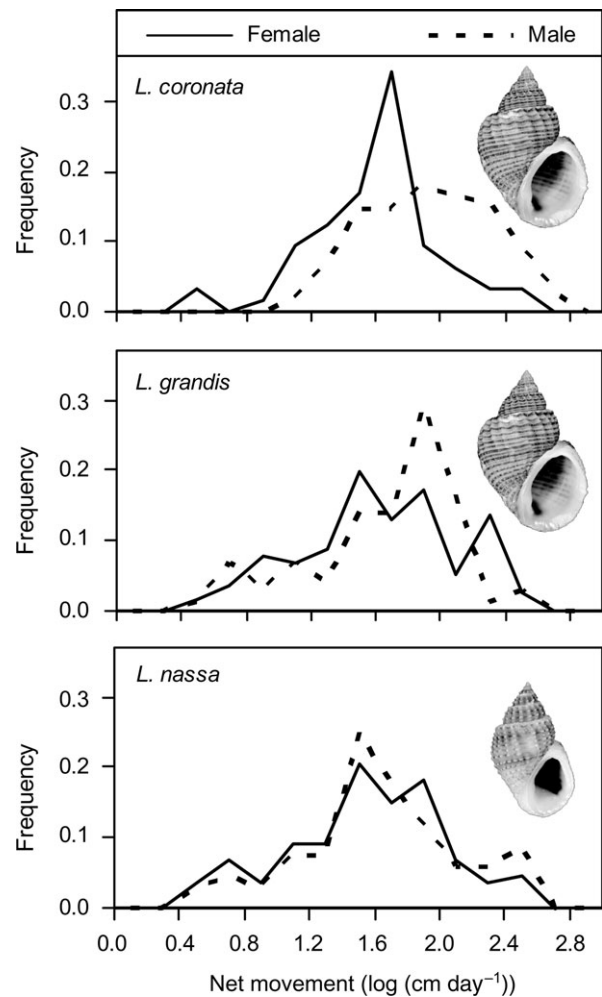
Snails were collected haphazardly at a depth of 3 m along a 215-m stretch of rocky shoreline, and represented the full adult size range of each species (*L. coronata* 20.7–38.6 mm, *L. grandis* 20.9–31.6 mm, *L. nassa* 19.0–26.3 mm). They were marked with nail varnish to facilitate tracking, and released along the same shoreline at a depth of 3 m and with a spacing of >5 m between conspecifics. They were allowed 24 h to recover after handling, then their locations were marked using numbered pebbles. Each morning during the subsequent four days, we measured net movement (rounded to nearest cm) over the previous 24-h period using a string placed flush against the substrate. This method did not encumber snail movement, and was better suited to the wavy conditions than alternative approaches. After four days of tracking, snails were brought to the laboratory for measurement of shell size and dissection to determine sex, reproductive status (brooding vs non-brooding in females) and parasitism.

We tracked movement of three replicate groups of snails between 12 July and 5 August 2002. Each group comprised 24 snails from each of the three focal species for a total of 72 individuals per species. Our analyses focused on individuals that could be tracked for all four days (39 *L. nassa*, 47 *L. grandis* and 52 *L. coronata*), for which we were able to evaluate differences among days, individuals and species.

We used repeated-measures, mixed model ANCOVA to test for differences in movement rates attributable to species (fixed), sexes (fixed), species-sex interactions (fixed), individuals (random) and size (covariate, fixed) using Proc Mixed in SAS. Tukey's HSD tests were used for pairwise comparisons of mean movement among all six species-sex groups. The significance of individual differences within groups was tested using a likelihood ratio test, and fixed factors were tested against their interaction with the random factor. To further evaluate differences in movement patterns, we compared frequency distributions of mean movement among species-sex groups using two-sample Kolmogorov-Smirnov tests ( $\alpha = 0.003$  following Bonferroni correction for multiple comparisons). Additional analyses of the effects of reproductive status and parasitism were conducted separately for each species. In each case, movement rates were compared between brooding and non-brooding (and non-parasitized) females using repeated-measures ANCOVA with size as a covariate. A similar ANCOVA was used to test the effects of parasitism, sex and size on movement of *L. nassa*, the only species parasitized by trematodes in our study. To meet statistical assumptions (i.e. normality, homoscedasticity), movement rates were log<sub>10</sub>-transformed. For all ANCOVA analyses, preliminary models indicated no significant interaction between the covariate and main effects, therefore the homogeneity-of-slopes assumption was satisfied.

## RESULTS

Individual daily movement ranged from 2 cm day<sup>-1</sup> to 267 cm day<sup>-1</sup>, with an approximate overall average of 50 cm day<sup>-1</sup> (Fig. 1). There were significant differences among species ( $F_{2,131} = 3.31$ ,  $P = 0.040$ ) and sexes ( $F_{1,131} = 6.33$ ,  $P = 0.013$ ); however, a significant interaction between species and sex ( $F_{2,131} = 3.83$ ,  $P = 0.024$ ) indicated that the difference between males and females varied among species. There was no significant effect of snail size ( $F_{1,131} = 1.17$ ,  $P = 0.2821$ ). Pairwise comparisons showed that *Lavigeria coronata* males travelled significantly farther than any other species-sex group ( $P < 0.002$ ; Table 1), and that all other groups were statistically equivalent ( $P > 0.144$ ). The same pattern was evident in the frequency distributions of movement rates. *Lavigeria coronata* males differed from all other groups ( $P = 0.005$  vs *L. grandis* males;  $P < 0.003$  in all other comparisons) both because their maximum distance moved was greatest and because few



**Figure 1.** Frequency distributions of daily movement by males and females of three *Lavigeria* species, illustrated to scale. Each species-sex combination was represented by 16–36 individuals, each of which was tracked for four days to yield 64–144 observations.

individuals moved short distances (Fig. 1). There were no significant differences among other groups.

After accounting for differences among groups, there remained significant differences among individuals in movement

**Table 1.** Summary of sample sizes and movement rates of *Lavigeria* snails observed in this study.

Species	Sex	Status	No. of individuals	Mean displacement ± SE (cm day <sup>-1</sup> )
<i>L. coronata</i>	Male	Non-parasitized	36	75.0 ± 7.5
	Female	Non-brooding	3	29.8 ± 8.1
		Brooding	13	37.5 ± 8.6
<i>L. grandis</i>	Male	Non-parasitized	18	43.5 ± 5.2
	Female	Non-brooding	7	63.6 ± 15.0
		Brooding	22	40.3 ± 6.3
<i>L. nassa</i>	Male	Parasitized	4	36.2 ± 9.0
		Non-parasitized	13	48.8 ± 8.7
	Female	Parasitized	2	20.3 ± 11.0
		Non-brooding	5	46.7 ± 26.5
	Brooding	15	36.8 ± 4.2	

rates ( $\chi^2 = 30.62$ ,  $df = 1$ ,  $P < 0.001$ ). In each case, a few individuals consistently moved quickly, while a majority moved more slowly (Fig. 1). However, these differences were not attributable to any of the other factors that we measured. Among females of each species, there were no significant differences in movement associated with brooding young (*L. coronata*:  $F_{1,12} = 1.49$ ,  $P = 0.246$ ; *L. grandis*:  $F_{1,25} = 0.29$ ,  $P = 0.596$ ; *L. nassa*:  $F_{1,18} = 0.59$ ,  $P = 0.454$ ) or individual size (*L. coronata*:  $F_{1,12} = 3.45$ ,  $P = 0.088$ ; *L. grandis*:  $F_{1,25} = 0.12$ ,  $P = 0.736$ ; *L. nassa*:  $F_{1,18} = 3.76$ ,  $P = 0.068$ ). In *L. nassa*, there were no significant effects of parasites ( $F_{1,34} = 0.08$ ,  $P = 0.773$ ), sex ( $F_{1,34} = 1.54$ ,  $P = 0.223$ ), size ( $F_{1,34} = 0.24$ ,  $P = 0.631$ ) or parasite-sex interactions ( $F_{1,34} = 1.46$ ,  $P = 0.236$ ) on average movement rates. There were also no significant differences among observation days for any species ( $P > 0.3$ ), suggesting that movement of individual snails was relatively consistent during our four-day observation period.

## DISCUSSION

Our measurements show that these large *Lavigeria* snails move regularly in Lake Tanganyika, covering an average distance of approximately 20-times shell length per day. This is a minimum distance because we recorded net linear displacement over 24 h; the actual distance travelled is likely to be considerably higher. However, when integrated over longer time intervals, net rates of movement may be less than we measured. For instance, Pardo & Johnson (2004 and personal communication) found that net displacement over six days was approximately 26% lower than the daily rate observed during two-day observations due to a lack of consistent directional movement in *Littorina saxatilis*. Our qualitative observations during this study indicated that some individuals consistently moved in one direction during the observation period, whereas others had little net movement over four days despite considerable daily movement. We have also recaptured marked *L. coronata* at our study site at locations <30 m from their point of release a year earlier. These anecdotes illustrate the value of repeating measurements of movement at different time scales (Chapman, 2000a, b; Pardo & Johnson, 2004), but daily measurements like ours are nonetheless appropriate for evaluating the factors influencing movement rates at small spatial and temporal scales.

Male-biased dispersal patterns are widespread among plants and animals with polygynous mating systems (Perrin & Mazalov, 2000), and previous work suggests that it may exist in gastropods, (e.g. Erlandsson & Johannesson, 1994; Erlandsson & Kostylev, 1995; Pardo & Johnson, 2004). In this study, male *L. coronata* moved farther than other groups, whereas movement of males of the other two species was similar to that of conspecific females (Fig. 1). We interpret these patterns as reflections of the probability of males encountering receptive females in each species. *Lavigeria coronata* exhibited male-biased sex ratios in both this study (70% male) and in another survey at the same site (65% male,  $n = 59$ , E. Michel & I. Kingma, unpubl.), and males moved significantly farther than most other groups. In contrast, sex ratios are female-biased in *L. nassa* (56% female in this study; 65%,  $n = 35$ , in Michel & Kingma, unpubl.; 50–65% over four sites,  $n = 16–159$  in Wagner, 2004) and *L. grandis* (62% female in this study; 65%,  $n = 45$ , Michel & Kingma, unpubl.).

Furthermore, males must find females that are both receptive and capable of reproduction (i.e. free from parasitism by castrating trematodes). In the absence of evidence of multiple matings, we interpret this to be females that are not currently brooding young. We do not yet know enough about the reproductive biology of these animals to comment on whether females currently brooding young still could be appropriate

mates, but anecdotal evidence suggests that they are not. Anatomical work has shown that female *Lavigeria* do store sperm (Michel, 1995, 2004), thus in principle do not require regular mating to achieve continuous production of young. We have rarely seen *Lavigeria* that appear to be mating (despite hundreds of hours of time underwater, and having observing apparent mating in other less-abundant genera of Lake Tanganyika gastropods), so it seems likely that mating is a rare event. However, this assumption should be tested with genetic data, as extensive work in recent years on sperm competition indicates that multiple matings may still be strategic for both potential mothers and fathers (Oppliger, Hosken & Ribí, 1998; Evanno, Madec & Arnaud, 2005). In our study population, the criteria of being receptive and reproductive were met by only 14% of *L. coronata* females, whereas 25% and 24% of *L. nassa* and *L. grandis* females, respectively, were potentially suitable mates. Given the combination of skewed sex ratios and scarcity of non-brooding females in *L. coronata*, males of this species may move farther than their congeners simply to increase their odds of encountering potentially receptive females.

We were surprised to find no evidence that size, brooding or parasitism influenced movement rates of *Lavigeria*, though our small sample size limits the strength of our conclusions regarding the potential effects of brooding and parasitism. Studies of other snail taxa have generally suggested that large animals move farther than smaller ones (Baur & Baur, 1995; Rochette & Dill, 2000; Miller & Poulin, 2001; but see Pardo & Johnson, 2004). Our work failed to support this pattern within or across species; for example, female *Lavigeria* are generally slightly larger than males, yet they moved no farther. Furthermore, in contrast to the findings for *Littorina saxatilis* (Pardo & Johnson, 2004), there was no difference in movement patterns between gravid and non-gravid female *Lavigeria*. Trematode parasites can also manipulate snail movement rates in order to maximize their probability of transmission (e.g. McCarthy *et al.*, 2000; Miller & Poulin, 2001), but parasitized *L. nassa* did not differ from non-parasitized counterparts in movement rate.

The observed differences in movement rates both among species-sex groups and among individuals within groups support previous inferences of the individualistic nature of snail movement (e.g. Chapman & Underwood, 1992; Chapman, 2000c; Pardo & Johnson, 2004). Though the specific characteristics that gave rise to individual differences in movement within *Lavigeria* species remain uncertain, we have suggested that high operational sex ratios may explain the relatively rapid movement of *L. coronata* males. Interestingly, this species has a very restricted distribution along the shoreline of Lake Tanganyika relative to *L. grandis* or *L. nassa* (Michel *et al.*, 2004). Our comparisons of daily net movement among species suggest that the limited distribution of *L. coronata* does not arise from low movement rates of individual snails, but rather reflects other historical or current constraints on dispersal.

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