

Vertical migration by *Cerithidea decollata* (Mollusca, Potamididae): addition but not subtraction

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The mangrove snail *Cerithidea decollata* feeds on the ground at low water, and about two hours before high water climbs *Avicennia marina* trunks settling 20–40 cm above the level that the incoming tide will reach. The moment that *C. decollata* must start to measure the vertical distance it has to creep up the trunk to avoid submersion corresponds to the point at which creeping switches from a horizontal to vertical movement (the “0” point). Two vertical movements interrupted by a short horizontal movement were added together; however, if the horizontal interruption was wider than 10 cm a new “0” point was set, and snails climbed higher than control snails, according to the level of the horizontal interruption, without adding the two vertical segments. Through forcing snails to both climb and descend, we observed that they do not appear to be capable of subtraction.

Keywords: mangrove snail; *Cerithidea decollata*; vertical migration; distance evaluation; intertidal adaptation

Introduction

The gastropod *Cerithidea decollata* (L.) (Gastropoda, Prosobranchia, Potamididae) is commonly found in Indo-pacific mangroves and within the *Avicennia marina* belt, i.e. between the average level of High water (HW) at Spring Tide (ST) and Neap Tide (NT) (Macnae 1963, Cockcroft and Forbes 1981, Vannini et al. 2006). *C. decollata* feeds on the ground at low water and rests for the duration of the high tide on trees or other vertical substrata, high above the water level, thus avoiding submersion (Cockcroft and Forbes 1981, Hodgson and Dickens 2012). Snails have been observed climbing trees about two hours before the arrival of water, settling 20–40 cm above the level that the water will eventually reach, being ready to disperse again on the muddy ground as the water disappears (Vannini, Mrabu et al. 2008; Vannini, Lori et al. 2008).

Due to the difference between NT and ST in the study area (Kenya), at HW the water level can vary from 0 cm, in which case snails may spend a few days permanently on the floor (Vannini, Mrabu et al. 2008), up to 60 cm, in which case most of the snails will climb and settle (often forming clusters of tens of individuals) 80–120 cm above the soil level. A biological clock is thought to control *C. decollata*

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migratory periodicity (Vannini, Mrabu et al. 2008); however, the capability of this species to predict not only “when” but also “how high” the incoming tide will remain unexplained (Vannini, Lori et al. 2008). Additionally, after *C. decollata* have “decided” which distance they must creep to avoid submersion they must also measure this distance.

Vertical periodical migration in intertidal animals has been studied in the field in molluscs (Vannini and Chelazzi 1978) and decapods (Gherardi and Vannini 1992, Vannini and Ruwa 1994). However, in these cases the migratory path had a definite “home”, a start or end point, unlike *C. decollata* which must simply avoid submersion by adjusting its position twice a day (diurnal disparity) and throughout the synodic month (from ST to NT).

The existence of a “step counting” mechanism (*C. decollata* creeps in a discontinuous manner, due to distinct rhythmic foot contractions) has been excluded (Vannini, Lori et al. 2008). However, a possible relationship between the energetic cost of creeping and distance was discovered by Vannini, Lori et al. (2008).

At the end of the feeding period on the ground, snails have to creep for a certain distance (1–2 m) to approach the trunk, where they may meet an irregular root and finally start climbing approximately vertically. How and when do snails determine the “0” point from which they should start to calculate the cost of their journey, and decide at which height on the trunk to settle? At the base of the trunk or at the moment they stop feeding and return to the tree?

We hypothesized that the abrupt change between horizontal and vertical creeping would correspond to the “0” point at which the calculation of height to be reached commenced. Thus, we designed a technique of manipulating the “0” point to test this hypothesis. We interrupted the vertical migration by inserting a horizontal path at a certain distance from the ground. Therefore, if experimental snails climbed higher than control snails, we could assume that a new “0” had been set. Conversely, if no difference in height attained between the two groups of snails was observed, we could assume that snails calculate the energy cost of the entire backward migratory trip, independent of their body inclination.

Material and methods

The study site was Bandarini in Mida Creek, a 3–4 km wide lagoon 80 km north of Mombasa (Kenya) and 25 km south of Malindi. It is a wide mangrove swamp dominated by *Rhizophora mucronata* and *Ceriops tagal* on the mid-lower levels, and by *A. marina* on the upper levels.

PVC pipes (2 m long and 20 cm diameter), simulating *Avicennia* trees, were “planted” in the muddy floor of the mangrove, and animals were allowed to climb on the pipes (Vannini, Lori et al. 2008).

Snails climb trees, or pipes, following a reasonably straight path until they settle somewhere on the surface. “Settling” means producing thick highly adhesive mucus, and withdrawing the foot within the shell until the entire mollusc remains in contact with the tree (or pipe) due to the mucus filament only. Once snails had experienced one or two tides, approximately 24 h after their release, three types of ring were created at the base of the pipes using concrete bricks. Rings were then covered with mud, and snails henceforth had to climb the artificial rings in order to ascend the pipes.

The first set of rings were 10 cm high and of varying width. The second set were 35 cm wide, while the height varied from 10 to 30 cm (Table 1). The third set were

Table 1. Different sizes of experimental rings.

Width (cm)	Height (cm)	Replicates
Rings of varying width (see Figure 1)		
10	10	2
15	10	2
20	10	1
25	10	1
30	10	2
60	10	1
Rings of varying height (see Figure 2)		
25	10	2
25	20	3
25	30	1

toroidal rings, created so that snails were forced to climb upwards for 30 cm, then travel horizontally for 10 cm, descend for 13 cm and travel horizontally for a further 10 cm; thus meeting the vertical pipe 17 cm above the ground.

Four pictures (from four different positions) were taken of each pipe at HW when all animals had settled. Vertical and horizontal marks on the surface of the pipes allowed us to measure the exact position of each snail.

For each test, control snails, which were released and treated similarly to experimental snails, were observed on pipes with no rings. For each test, 70 snails were released close to the pipes; since a fraction of the snails were attracted by some of the surrounding trees, the number of snails actually climbing the pipes varied between 50 and 70. Different individuals were used in each test. Single individual measures could not be treated as independent data due to possible inter-individual interactions. However, the average position of snails recorded in the four pictures, i.e. on the four sides of each pipe (16 × 200 cm strips), were considered to be independent. Thus, each test, independent of the actual number of snails, produced four independent output values (i.e. the average height of all snails on each quarter of the pipe circumference).

Due to the normal distribution of the snails along the pipe (Vannini, Mrabu et al. 2008), data from experimental and control pipes were compared by applying parametric tests: *r* Pearson, for regression analysis, and one-way ANOVA to compare the average height of snails on four sides of the pipe. Two-way ANOVA tests were applied when the results of three identical tests were pooled.

Tests were conducted in February 2009 and February 2012, during the dry season.

Results

In experiments using a 10 cm high ring (width varied from 10–60 cm), the average distance reached by the experimental and control snails did not differ with a ring width of 10 cm (Figure 1). On the contrary, experimental animals that crossed rings wider than 10 cm consistently settled about 10 cm higher than control animals, although this distance was not always statistically significant (Figure 1, square symbols). The intercept crossing of the 15–60 abscissas was virtually horizontal and about 10 cm above the ground (Figure 1, dotted line).

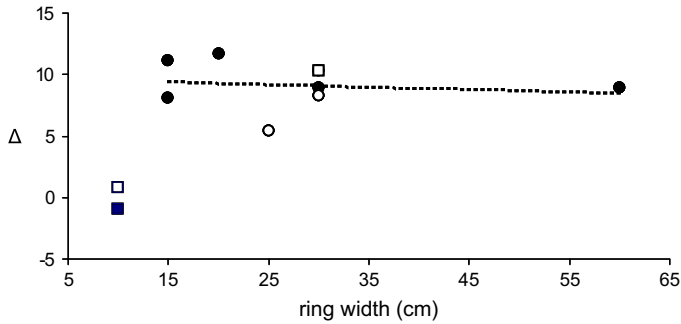


Figure 1. Results of test with a 10 cm high brick ring of various widths. Δ =average difference (cm) between experimental and control pipes. Open symbols=2009, solid symbols=2012 tests. Circles and squares represent significant and non-significant at one-way ANOVA (df 1, 6; $p < 0.05$), respectively. Dotted line is a regression line through the points corresponding with ring width > 10 cm.

In tests with a ring width of 25 cm, and varying heights (10–35 cm), snails regularly climbed higher (distance corresponding with the height of the brick ring) than control snails (Figure 2, $r = n = 0.933$, $df = 4$; $p < 0.05$).

In tests with toroidal rings, where snails had to first climb and then descend before meeting the pipe, the average difference in height of settlement between experimental and control snails was 12.7 cm (two-way ANOVA, $F = 78.59$; $df = 1, 18$; $p < 0.01$). This difference was quite close to 17 cm, the height above the ground that snails reached on the pipes after crossing the ring, allowing us to presume that subtraction had not been performed and a new “0” had been set.

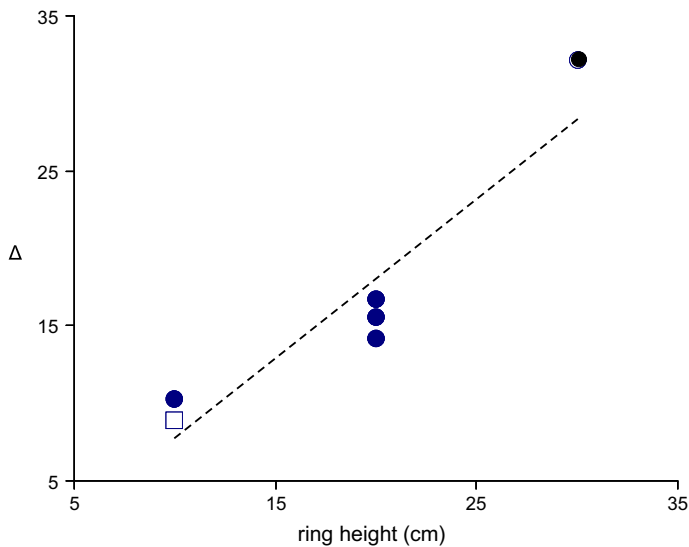


Figure 2. Results of test with a brick ring 25 cm wide, of various heights. Δ =height difference (cm) in the average settling of snails on experimental and control pipes. Symbols as in Figure 1. Dotted line, regression line.

Discussion and conclusions

The mechanism which enables *C. decollata* to determine, 2 h in advance of the tide, how high to creep to avoid submersion is still unknown (Vannini, Lori et al. 2008). In this study, we focused only on the mechanism which enables *C. decollata* to measure distance once the target height has been “decided” (Vannini, Lori et al. 2008). Thus, snails should set a “0” point from which to start calculating the distance they must creep in order to avoid submersion.

Manipulation of the snails’ upward migrations, using concrete rings, revealed that if the horizontal ring surface was 10 cm or less, the two vertical paths (the first part on the ring and the second part on the pipe) were added and the snails settled at the same level as control snails. With rings wider than 10 cm, a new “0” point was set and snails climbed higher than control snails (Figure 2). This height difference accorded with the height at which resetting occurred.

The results of this study suggest that this “0” point does indeed exist and, furthermore, it corresponds to the moment when creeping movement switches from the horizontal to vertical rather than the beginning of backward migration, 1–2 m away from the tree or the pipe base. Interrupting the vertical path with a horizontal platform of 10 cm did not disturb computation of vertical distance. However, the “0” point was reset when the migration was interrupted by a horizontal platform wider than 10 cm.

If snails had to first climb and then descend, a new “0” point was reset and snails climbed higher than controls. It is impossible to ascertain whether this reset was due to the double 10 cm horizontal traits or to descent; however, it appears that height subtraction cannot be performed.

Distance estimation, in terms of the cost of travelling, was previously thought to be a feature of honeybees’ behaviour (Otto 1959; Von Frisch 1967). Loading foragers caused them to signal larger feeder distances (von Frisch 1967), as loading *C. decollata* caused them to climb lower than control snails (Vannini, Lori et al. 2008). However, this hypothesis has since been criticized; Esch and Burns (1986) found honeybees to rely on the speed of images in their visual field when flying back to their hive, and not on the energetic cost of such a flight.

Since the first experiments on bees, the problem of measuring excursion distance in arthropods, predominantly insects, has been repeatedly encountered (Wolf 2011). However, *C. decollata* behaviour appears unique since in the case of this animal distance must be “foreseen”, i.e. estimated in advance (Vannini, Lori et al. 2008). We hypothesized that estimation would be based on the amount of energy to be invested starting from the “0” point (Vannini, Lori et al. 2008). This postulates that snails may be able to allocate metabolic resources in proportion to the amplitude of the incoming tide. This would enable them to achieve a level just above the level the sea water will reach.

We suggest that distance evaluation in *C. decollata* may be a unique phenomenon, and further physiological investigation should be carried out to determine the relationship between distance evaluation and metabolic investment.

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