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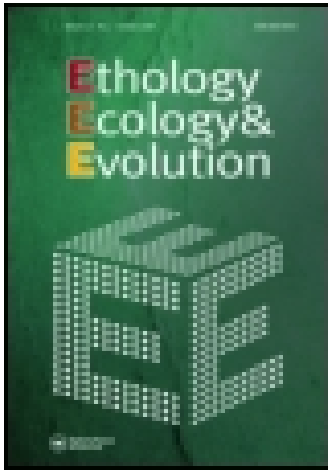


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Lack of inter-individual information exchange among migrating *Cerithidea decollata* (Mollusca Potamididae)

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The gastropod *Cerithidea decollata* typically feeds on mud at the mangrove soil surface at low tide and rests on *Avicennia marina* trunks throughout high tide. Tens of individuals can be observed climbing the trunks and clustering, 2–3 hr before the incoming high tide, approximately 40 cm higher than the level that the tide will reach. As soon as the water disappears, snails descend and disperse on the ground again. Signals able to tell the snails the height of the incoming tide are still unknown but we wanted to investigate whether or not some information may be transferred from resident snails to snails translocated from areas undergoing a different tidal regime. Snails from sites where tides never exceed 5 cm above ground level (translocated) were transported to sites flooded by higher tides (up to 80 cm above the ground), and their behaviour was compared with local snails (residents). At the beginning of the experiment, sea water occasionally made contact with translocated snails as they ascended the trunks later than resident snails and clustered closer to the water. After several tides, translocated snails started to behave similarly to resident snails and, by the 10th tide, the behaviour of the two groups was indistinguishable. However, the behaviour of translocated *C. decollata* was not affected by being in contact or not with resident snails; thus, it appears that no information was transferred from resident to translocated snails.

KEY WORDS: *Cerithidea decollata*, mangrove fauna, inter-individual information exchange, mollusc intertidal adaptation, vertical migration.

INTRODUCTION

The gastropod *Cerithidea decollata* is commonly found in Indo-Pacific mangroves, feeding on the ground at low tide and resting throughout the high tide on trees or any vertical substrata above the water level (COCKCROFT & FORBES 1981), thus avoiding submersion. During neap tide (NT), migration is suspended and many snails (all of them, in a related Australian species, *C. antcipata*; MCGUINNESS 1994) remain on the trunk, far

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from the hot and dry ground. Snails have been observed to climb trees about 2 hr before the arrival of water, settling between 20 and 60 cm above the level that the water will reach; as the water retreats, they descend to the ground to feed (VANNINI et al. 2008b).

A biological clock is thought to control *C. decollata* migratory periodicity (VANNINI et al. 2008c), but the capability of this species to predict not only when the tide will arrive, but also how high the incoming tide will be remains unexplained (VANNINI et al. 2008b).

In Kenya, the location of this study, *C. decollata* are restricted to the upper mangrove forest, dominated by *Avicennia marina*, and are only found within areas where the *A. marina* belt is protected by a wide belt of *Rhizophora mucronata*, the mangrove species that usually dominates the lower intertidal zone (LORI 2008). Thus, *C. decollata* inhabits areas where, even at spring tide (ST) high water (HW), occasional breezes are unable to create much water movement or spray.

In the study area at HW, as a result of the difference between NT and ST, the water level may vary from 0 cm, in which case many snails can even spend a few days permanently on the ground (VANNINI et al. 2008a), up to 80 cm, in which case all the snails will climb tree trunks. They settle, often in clusters of tens of individuals, 20–60 cm above the level that the incoming tide will reach.

Since East African tidal patterns are complicated due to both diurnal disparity and semi-monthly variation (from NT to ST), and as snails do not appear to make contact with the water, it is difficult to understand how they are able to keep their clock in phase with the tides (i.e. to understand the nature of their tidal Zeitgeber) and, particularly, how they are able to predict the level that the tide will reach.

While other aspects of the behaviour of *C. decollata* and the behaviour of similar species have been investigated (COCKCROFT & FORBES 1981; MCGUINNESS 1994; HARUMI et al. 2002; HODGSON & DICKENS 2012), studies have rarely focused on understanding how the snails may foresee the timing of the tides and the tide level (VANNINI et al. 2008b). Other intertidal molluscs, gastropods (*Nerita textilis*, VANNINI & CHELAZZI 1978) and chitons (*Acanthopeura* spp., CHELAZZI et al. 1983), living on exposed rocky shores are known to vertically migrate twice a day, preceding the HW, being regularly submerged or at least contacted by the waves (at ST) or water spray (at NT). In all of these cases, animals retreat to a definite “home” (usually a hollow in the rock) irrespective of the level of the incoming tide.

Evidence indicates that *C. decollata* from the upper areas of mangrove forests (where they are reached by 5–10 cm of water a few days a month only) do not usually climb tree trunks (LORI 2008). If those snails are translocated to lower areas of the mangrove (regularly flooded twice a day, nearly every day), they soon modify their behaviour and start to exhibit vertical migration on tree trunks twice a day, similar to the resident snails (VANNINI et al. 2008c).

The aim of our study was to confirm and evaluate this learning process by focusing on a single question. Is there an information exchange between translocated and resident snails?

MATERIAL AND METHODS

Locality

The study area, which we visited during February 2012, was the Mida Creek (03°21'S; 39°59'E), a 3–4-km-wide lagoon 80 km north of Mombasa (Kenya) and 25 km south of Malindi.

At the study site, Bandarini, the mangrove forest is dominated by *Rhizophora mucronata* and *Ceriops tagal* on the mid-lower levels, and by *Avicennia marina* on the high levels. The upper levels of the mangrove are bordered by scattered bushes of *Lumnitzera racemosa*.

Species

Cerithidea decollata (L.) (Gastropoda Potamididae) is a widespread Indo-pacific caenogastropod characterized by a shell approximately 15–25 mm long with a truncated apex. In East Africa, it is commonly found within the *A. marina* belt (MACNAE 1963; COCKCROFT & FORBES 1981; VANNINI et al. 2006), i.e. in the landward mangrove areas, between the average levels of HW during ST and NT.

Animal observation

Polyvinyl chloride (PVC) pipes (length 2 m, diameter 20 cm), simulating *Avicennia* trees, were planted vertically in the muddy ground of the mangrove, at least 1 day before testing, and animals were released within few centimetres of the pipe base (VANNINI et al. 2008b). A fence (a vertical plastic net) was set up to keep the different pipes with different experimental groups separated. Three pipes were used which were carefully washed after each test.

Snails climb tree trunks (or the pipes) following a relatively straight path until they settle. “Settling” involves the production of thick, highly adhesive mucus and retreat of the foot into the shell. Thus, the entire body of the mollusc is hidden but remains in contact with the tree (or the pipe) due to the dried mucus filament. At the right moment, snails extend their head and foot from their shell and start a downward migration. For unknown reasons, rarely do all snails exhibit downward migration and a fraction may remain immobile on the trunk (or pipe), sometimes for more than one tide.

Snails were marked with a white spot on the shell using innocuous Tippex, which was renewed after each test. Observations (starting 24–36 hr after release of snails) were performed using two methods: (1) time-lapse cameras (1 shot/5 min for 3–5 days, with flash when necessary) and (2) single photographs taken from four different positions at high tide when snails had settled. Vertical and horizontal marks were drawn on the pipe surface to allow measurements to be taken.

PVC pipes have been shown to be efficient substitutes for tree trunks, and they allow procedure standardization, facilitating the identification of exact position, and image capture (VANNINI et al. 2008b).

We used resident snails (R, snails living in the vicinity of the experimental site, i.e. lower snails) and translocated snails (T, snails living in the landward mangrove fringe, i.e. upper snails); these two groups of snails inhabited areas of the mangrove forest 150 m apart with a height difference of 80 cm (VANNINI et al. 2006).

Snails were categorized into groups and released on three different pipes: group R (40 resident snails), group RT (20 residents and 20 translocated) and group T (40 translocated). In addition, we created a control group of snails (C, resident snails released at least 5 days earlier). Group C could be considered an untreated one since, during previous experiences, we could observe that after about 3 days, the behaviour of manipulated and untouched snails was undistinguishable). Subsequently, time-lapse photographs (one shot/5 min for 3–4 days) of pipes R, RT and T were taken and analyzed. We measured when snails climbed, at which level they settled and clustered, and whether or not they made contact with the water. On pipe C, only single photographs at high tide were taken.

To calculate the exact moment at which migration took place, we counted the number of snails settled or crawling on the pipe every 5 min (using time-lapse photography) and defined the moment of pipe semi-saturation as F_{50} , i.e. the moment at which half of the total number of snails that finally settled on the pipe were on the pipe (VANNINI et al. 2008b).

Experiments were repeated 5 times, never using the same animals, on 8, 12, 14, 20 and 25 February; however, in certain cases, data from only three tests were available due to low numbers of migrating animals during NT, or technical problems with the camera. Unless otherwise indicated, the number of snails on each pipe varied between 25–50 individuals.

Two-ways parametric analysis of variance (ANOVA) tests with Tukey-test and Pearson correlation tests (two-tailed) were applied to analyze the data.

RESULTS

The results of the three experiments conducted on 5 different days are displayed in Fig. 1. Observations revealed that *C. decollata* translocated from levels where tidal excursion is minimal (T group) settled at lower levels on pipes, displaying a different migratory pattern to resident snails (R) and non-manipulated control snails (C). T snails clustered approximately 15 cm above the level reached by the sea water, while residents (manipulated, R and non-manipulated) as well as C snails clustered approximately 35 cm above water level. RT pipes are pipes where R (resident) and T (translocated snails) coexist.

A two-way ANOVA and Tukey test performed on mean data for each day revealed that both translocated groups (T and T with R) were different from all resident groups (R, R with T and C), while no differences were detectable, within each day, within T and R groups ($F_{\text{treatments}} = 35.26$, $df = 4,16$, $P < 0.01$; $F_{\text{days}} = 18.3$, $df = 4,16$; $P < 0.01$; Tukey test, $P < 0.05$).

Over time, the differences between T and R snails decreased (Fig. 2) and, after eight tides, the two groups were almost indistinguishable (log correlation, $r = 0.715$, $df = 13$, $P < 0.01$).

In Fig. 2, T and R results from different pipes have been clustered and their relative difference in height represented on the y axis, in order to obtain results independent of the different tide level on different days.

We then considered the time of upward migration, independent of the level reached by the snails. T snails displayed a distinct delay in their migration compared to R snails. For example, F_{50} occurred at 16:18 and 16:36 for the two R groups and later

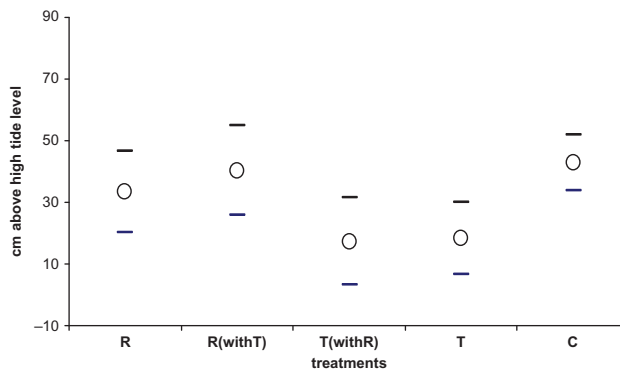


Fig. 1. — Level above the water level reached at high tide by different snail groups on different pipes. R, resident snails alone; R (with T), resident on RT pipe; T (with R), translocated on RT pipe; T, translocated alone; C, control. Bars, 95% confidence limits. RT pipes are pipes where R (resident) and T (translocated snails) coexist.

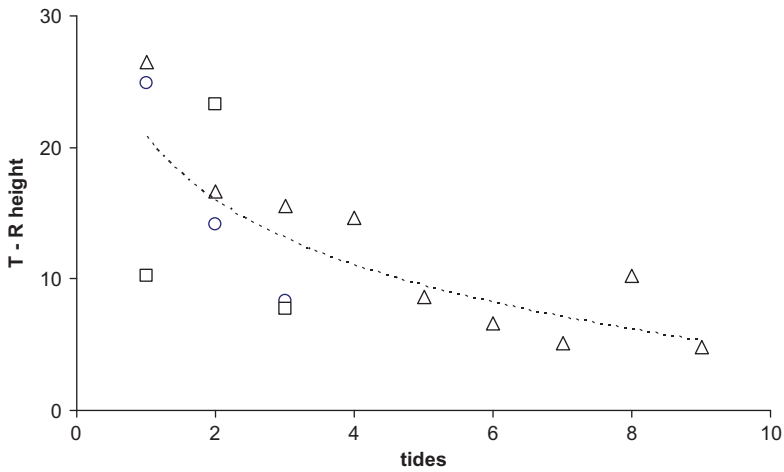


Fig. 2. — Average differences of level (cm) between translocated (T) and resident (R) snails during the tides following release (experiments of 8, 20 and 25 February). Data from time-lapse images.

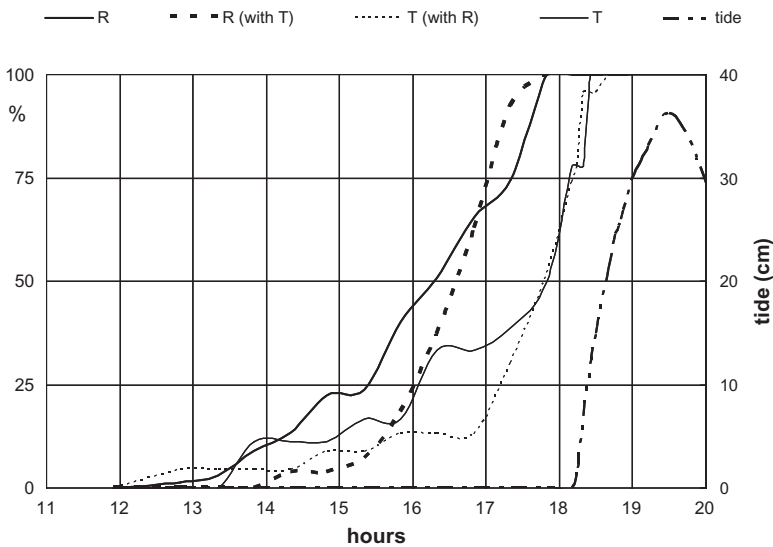


Fig. 3. — An example of the upward migration of different snail groups 24 hr after release; data obtained from time-lapse images (25 February 2012). The maximum number of snails recorded on each pipe is shown on ordinates. The ordinate 50% corresponds to pipe semi-saturation (F_{50}).

at 17:47 and 17:49 for the two T groups (Fig. 3). When water arrived (at 18:15), 100% of R snails were already settled, and had been for at least 30 min, while about 25% of T snails had not started to ascend the pipes.

In 13 cases, we could determine the difference in F_{50} between T and R snails (based on cumulative data from all pipes, Fig. 4). A significant negative correlation was

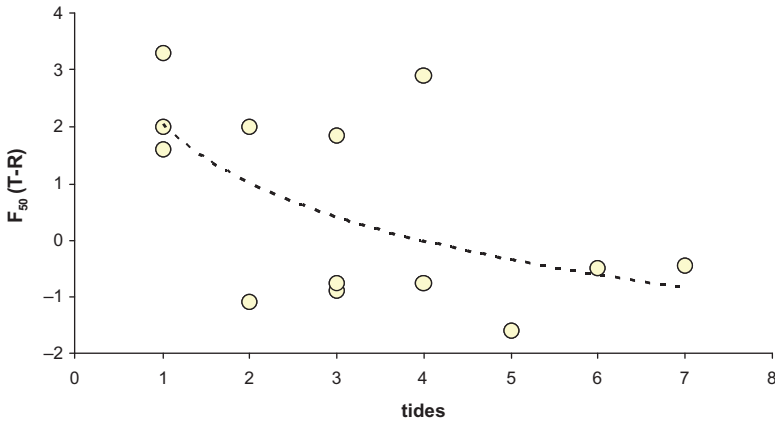


Fig. 4. — Difference in the timing of upward migration between translocated (T) and resident (R) snails through successive tides. $F_{50}(T-R) = F_{50} \text{ translocated} - F_{50} \text{ resident}$.

found between time (tides) and the migratory lag of T groups (log correlation, $r = 0.577$, $df = 11$; $P < 0.05$).

In many cases, sea water made contact with snails from group T, which subsequently climbed higher, or even occasionally remained submerged for all or part of the high tide (based on observation of time-lapse images). Since snails were not individually marked, we could not distinguish between single individuals submerged more than once and many snails submerged a single time. Aggregating all the data concerning total contact with water in the course of 17 high tides and relating them to the total number of snails on each pipe, we found a significant negative correlation (log correlation, $r = 0.704$, $df = 13$, $P < 0.01$; Fig. 5); the pattern was similar to Fig. 2.

In the course of the same 17 high tides, images captured of 60 resident *C. decollata* showed only a single snail being reached once by the tide and subsequently climbing upwards immediately.

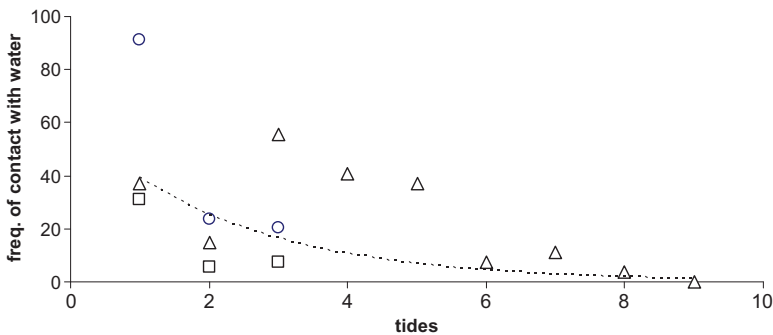


Fig. 5. — Frequency of total number of snail contacts with sea water related to the total number of translocated (T) snails on each pipe during each high tide (circles, 8–10 February; triangles, 20–24 February; squares, 25–27 February).

DISCUSSION AND CONCLUSIONS

During the early stages of the experiment, *C. decollata* from the upper shore translocated downshore on experimental pipes appeared to climb to lower heights compared to residents (–20 cm; Fig. 1), with a relative delay (30–90 min; Figs 3 and 4). Frequently, they were reached by the incoming tide, and thus were washed or even submerged (Fig. 5). Within 8–10 tides, the translocated snails appeared to gradually modify their behaviour which, ultimately, was indistinguishable from the behaviour of local *C. decollata* (Figs 2, 4 and 5), confirming previous observations on trunks (VANNINI et al. 2008b) and, furthermore, the validity of the pipes as tree substitutes.

It is possible that if snails had been followed individually, some difference may have been detected between T and R groups but, with the present data, we can only conclude that behavioural modifications of translocated *C. decollata* do not appear, on average, to be affected by proximity to the resident snails. More specifically, no matter how the snails are adapting their behaviour to the new environment, it does not appear that they have been influenced by their conspecifics (Figs 1 and 3).

External cues are probably involved but the most obvious ones can be easily excluded, such as hydrostatic pressure, wave action, temperature and salinity (VANNINI et al. 1995; NAYLOR 2001). In addition, a direct view, or smell, of the sea (VANNINI et al. 2008b) can also be excluded, considering that when upward migration commences the sea edge is still hundreds of metres away, beyond a 150-m wide *Rhizophora mucronata* forest (VANNINI et al. 2006).

Gastropods and other intertidal molluscs have long been known to rely on chemical cues, both on substrata and airborne, to detect trails (EDELSTAM & PALMER 1950; KOHN 1961; CHELAZZI et al. 1988; CHELAZZI 1992; NG et al. 2013). The role of mucus trail-following has been recently studied on intertidal mangrove periwinkle (*Littorina scabra*; ALFARO 2007) where vertical migration seem also to occur; in *L. scabra*, chemical cues play a role in aggregating the snails at the end of each migration (ALFARO 2007). It is likely that *C. decollata* may also be able to trace conspecific mucus trails or even an individual's own trail when migrating upwards (S. FRATINI pers. obs.). However, even if inter-individual chemical communication does exist, it does not seem to play a role in the slow process of adaptation of *C. decollata* to different tidal levels.

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