RESEARCH ARTICLE

Rhythmic vertical migration of the gastropod *Cerithidea decollata* in a Kenyan mangrove forest

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Abstract In Mida Creek, Kenya (3°20′S, 40°5′E), at high water, the snail *Cerithidea decollata* dwells on the trunks of mangrove trees (*Avicennia marina*), while during low water it migrates to the ground, foraging at various distances from the trunk, where it aggregates again well before the incoming tide. Snails from the upper shore level are 150–200 m distant from those living at the lower shore level and they cluster at lower heights on trunks. In any case, sufficient height is usually attained to avoid being submersed. An experiment was designed (February and October 2005), exchanging individuals from different shore levels subject to different tide regimes, in order to test whether snails rely on internal information or on external, direct cues, to adapt their behaviour to local conditions. Results show that *C. decollata* mostly rely on internal information, presumably based on an internal clock. When individuals from upper and lower shore levels were exchanged, their internal clocks continued to govern when to ascend the home trunk and how high to climb for five to six successive tides, after which the behaviour was reset to the new local conditions.

Introduction

In coastal regions where the ocean tides are relevant, many intertidal animals go through regular vertical migrations to

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avoid the tidal phase less suitable for their survival (Underwood 1979; Levings and Garrity 1983). Gibson (2003) recently reviewed the case of strictly marine animals but examples exist dealing with semi-terrestrial species, typically inhabiting cliffs and mangrove forests, that periodically migrate downwards, at low tide, for foraging excursions and upwards, at high tide, to avoid submersion and/or predation (the gastropod *Nerita textilis*, Vannini and Chelazzi 1978; the chiton *Acanthopleura* spp., Chelazzi et al. 1988, Chelazzi 1992; the brachyurans *Pachygrapsus marmoratus*, Cannicci et al. 1999; *Eriphia smithi*, Vannini and Gherardi 1988). A reverse situation is found with the anomuran *Clibanarius laevimanus* (Gherardi and Vannini 1992), foraging on the seafloor at high tide and climbing the mangrove aerial roots at low tide.

In view of the strong adaptive value of matching their activity with the tidal phases, it is not surprising that intertidal animals usually exhibit activity rhythms: these rhythms are correlated with daily tidal excursions and/or modulated over a semi-lunar periodicity in accordance with the tide amplitude variation occurring throughout the synodic month (the neap/spring cycle) (for a review see Morgan 2001; Naylor 2001). Moreover, for many species it has also been demonstrated that rhythmic locomotory patterns are expressed in constant conditions (for a review see Palmer 1995), revealing the presence of endogenous rhythms controlled by biological clocks.

Conversely, little is known about the control and maintenance of this migratory behaviour, since very few field studies have been conducted, due to the difficulties of following and manipulating single individuals for a long time.

Cerithidea decollata lives typically (even if not exclusively, Cockcroft and Forbes 1981) on mangrove trees usually situated between high water spring and low water neap tide levels (Cockcroft and Forbes 1981; McGuinness 1994),

a quite typical habitat for many members of the same genus (Balaparameswara and Sukumar 1982; Houbrick 1984; Harumi et al. 2002). *C. decollata* usually forages on the sediment at low water and clusters on the trunk, at various heights, during high water. Snails from the upper shore are quite indifferent to the tidal excursion and, when on the trunks, they cluster few centimetres above the ground. In contrast, snails inhabiting lower shore level trees descend in unison a few minutes after the tide retreats and return to aggregate again on the trunks well before the incoming tide (about 1–2 h before), clustering at the proper height to avoid submersion, hence higher at spring than at neap tide (Vannini et al. 2006).

Is the migratory strategy of *C. decollata*, i.e. the decision of when to move to the ground or back to the trunk and at which level to settle, mostly based on internal information (biological clock)? Or is it driven by direct information (visual, chemical, mechanical stimuli) from the environment?

In order to answer these questions, a double transloca-tion experiment was designed, switching individuals from upper level to lower trees and vice versa. If translocated individuals behave like those living at a specific shore level, it would be possible to assume that the migratory behaviour is primarily a response to local stimuli; on the contrary, if the snails, even after translocation, continue to behave like those living at their original shore level, it will be possible to assume that the migratory behaviour is based on internal information.

Methods

Study site

Mida Creek is a roughly circular mangrove creek 20 km south Malindi, Kenya (3°20′S, 40°5′E), bordered by a nearly continuous belt of mangroves, about 300 m wide, dominated by *Avicennia marina*, at the landward level, and by *Rhizophora mucronata* together with *Ceriops tagal*, at the seaward level (Fig. 1). Tides, typically semidiurnal, have a maximum range of 4 m along the continental coast, and about 1.9 m within the Creek.

The species

Cerithidea decollata (L.) is a gastropod (fam. Potamididae) characterised by a shell with a truncated apex, about 7–11 mm maximum diameter, 16–25 mm height. In the study site, smaller individuals are quite rare and animals less than 4 mm wide are never found on trunks but only on mud. It is a widespread inhabitant of East African man-
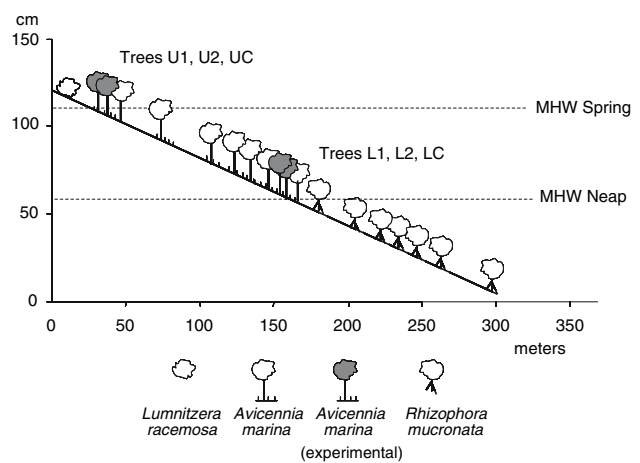

Fig. 1 Mida Creek, Kenya. Simplified cross section, within the upper mangrove belt, of the site where *Cerithidea decollata* was studied in February and October 2005. Upper experimental (U1, U2) and upper control (UC) trees; lower experimental (L1, L2) and lower control (LC) trees. From 300 m on, the shore forms a bare, muddy sand plat-form to the Low Water marks

groves, where it is commonly found within the *Avicennia marina* belt, i.e. within the landward mangrove level between the average level of High Water Spring Tides (HWST) and High Water Neap Tides (HWNT) (Macnae 1963; Brown 1971; Cockcroft and Forbes 1981; Machiwa and Hallberg 1995; Vannini et al. 2006).

Translocation experiments

All *C. decollata* present on two *A. marina* located at the HWST shore level (U1 and U2, Fig. 1) and on two man-grove trees at the HWNT shore level (L1 and L2) were marked. Trees were chosen at the two extremes of the *A. marina* belt (about 150 m apart). Lower level trees (L trees) were always partially submersed by the high tides, with the exception of 3–4 days around neap tide, while upper level trees (U trees) were reached by water only 3–4 times around spring tide, and about 1 h later with respect to the lower level trees (Vannini et al. 2006).

Snails were marked with white fluid corrector (Tippex) and with additional nail varnish of different colours on the dried corrector, utilizing a specific code for each tree.

Marking occurred just before the beginning of the down-ward migration. Snails were marked directly on trunks or removed from the trunk. In the latter case they were painted, kept for 10 min in a plastic tank until the varnish dried, and then all at once gently placed on the floor just around the trunk they had been picked up from, or around the trunk to which they had been translocated. To operate contemporaneously and reduce manipulation time, two teams of three persons each were employed at the two different shore levels.

The experiment consisted of observing groups U1 and L1 on their own trunks (home-trunks), while groups U2 and L2 were treated as follows: from each of the two groups, three sub-groups were created. The first groups (U2a, L2a) were left on their home-trunk, the second (U2b, L2b) were placed close to U1 and L1, respectively, i.e. on different trees at the same shore level, and the third (U2c, L2c) were moved close to different trees at a different shore level (Fig. 2, Table 1). After having released the snails, two teams of two observers each counted the marked individuals present on the trunks, every 30 min, till the incoming high tide had reached its maximum, i.e. for 3–9 h. To evaluate the presence of a manipulation effect, the behaviour of individuals from other trees (Fig. 1, UC, LC), which had been marked 2 weeks before the translocation experiment, was observed.

The translocation experiment was replicated in 2005, on 14 February and, on different trees, on 17 October. During this second field trial, snails were also followed for 4 days after translocation, and their heights on the trunks were recorded (within ∼ 10 cm).

In both the experiments, we thus followed the behaviour of snails from trees at upper and lower shore levels, which (a) did not change neither tree nor level, (b) changed tree but not level and (c) changed both tree and level. Group (a) was represented by marked individuals that had been (U2a, L2a) and not been (U1, L1) removed from their trunks.

Statistics

A two-way ANOVA was used to compare the frequency of snails on trunks, in relation to the different treatments. Since frequency values on upper and lower trees were expected to be very different, because the upward migration
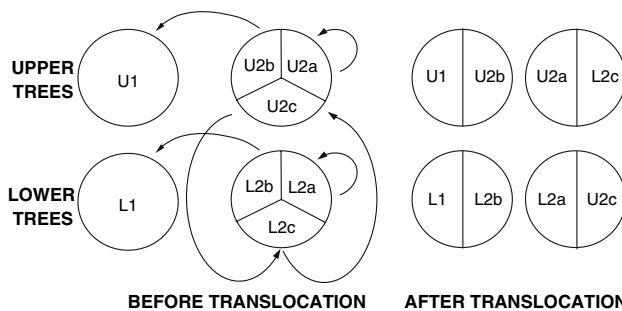
Table 1 Number of *C. decollata*, recorded during the two experiments, from different trees

Experimental trees	February 2005	October 2005
UC	–	83
LC	–	143
U1	108	105
L1	24	95
U2	316	280
U2a	105	93
U2b	105	93
U2c	106	94
L2	105	320
L2a	35	106
L2b	35	107
L2c	35	107

UC, *LC*, control trees, on upper and lower levels, respectively. *U1*, *L1*, snails from same tree, on upper and lower levels, respectively. Within *U2* and *L2* treatments: *U2a*, *L2a*, snails left on their home-tree; *U2b*, *L2b*, translocated on different trees at the same level; *U2c*, *L2c*, translocated on different trees at different level (see also Figs. 1, 2)

was much more intense among snails from the lower shore (Vannini et al. 2006), data needed a prior standardization. Given that the different values of R_i (i.e. for upper level: R_{U1}, R_{U2a}, R_{U2b}, R_{L2c}) represented the ratio of snails on trunks versus total, as recorded when water invaded the study area, we then calculated their average, $R_m = \Sigma R_i/4$ and the difference, in absolute value, between each R_i and R_m, $\Delta R_i = |\Delta(R_i - R_m)|$. Applying the ANOVA to ΔR_i instead of R_i allowed us to treat contemporaneously cases where frequency of translocated snails were both much smaller and much bigger than controls, having all being transformed in values much different than controls.

ANOVA was performed applying GMAV5 software (University of Sydney, Australia), considering treatments as fixed factors, time as random factors. SNK test was used to compare the relative effects of different treatments. Comparison of the level reached by snails on the trunks was performed by applying Spearman correlation test to the height of the snails above the water level during the tides following the translocation experiment. On trunks, many snails cluster together: an average distance from the water level was easily calculated but, due to a possible group effect, a measure of variability around such an average would have been meaningless.

Results

Results clearly indicate that individuals from the lower shore level trees translocated to upper level ones (Figs. 3A, 4A, L2c) tend to migrate upwards well before high tide,
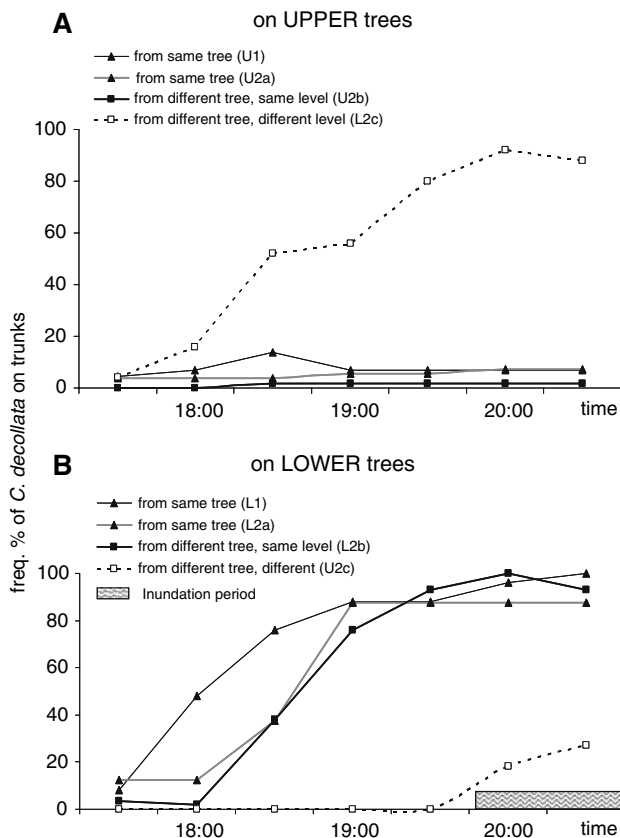
Fig. 2 Translocation experiment scheme. Before translocation: *C. decollata* U1 (see Fig. 1) were marked and left close to their home-tree while snails U2 were split into three sub-groups: U2a placed close to their home-tree, U2b close to U1 and U2c to be translocated close to the lower level tree, L2. A symmetrical procedure was applied for snails from two lower level trees (L1, L2). After translocation, on both shore levels, we thus had snails that changed neither tree nor level (U1, L1, U2a, L2a), snails that changed tree but not level (U2b, L2b) and snails that changed both tree and level (U2c, L2c)

Fig. 3 Translocation experiment, 14 February 2005. Frequency of *C. decollata* on trunks at different times after translocation. Striped area, water covering the trunk base. In both diagrams, *continuous lines* local snails and snails translocated from the same level; *dotted lines* snails translocated from different levels

behaving differently from the local snails (Figs. 3A, 4A, U1, U2a, U2b), but like those that were left on lower trees (Figs. 3B, 4B, L1, L2a, L2b). Similarly, on lower trees, individuals originally from upper trees (Figs. 3B, 4B, U2c) tend to migrate upwards very late, behaving differently from the local snails (Figs. 3B, 4B, L1, L2a, L2b) but just like those that remained on upper trees (Figs. 3A, 4A, U1, U2a, U2b).

During the first experiment, despite the quick climbing reaction of lower *C. decollata* translocated to the upper trees (Fig. 3A, L2c), those trees were never reached by the water. At the same time, in both experiments, upper snails translocated to lower trees (Fig. 3B, 4B, U2c), were flooded before they started climbing, and less universally (20–40% of all individuals) than the local snails (90–100%).

In all cases, snails remaining at their original shore level behave similarly, apparently not affected by the tree exchange and different manipulation (Figs. 3A, 4A, U1, U2a vs. U2b; Figs. 3B, 4B, L1 and L2a vs. L2b).

In October 2005, individuals marked 2 weeks before the experiment were followed from trees adjacent to L1 and U1 (Fig. 4, "untreated"). Previously marked individuals behaved
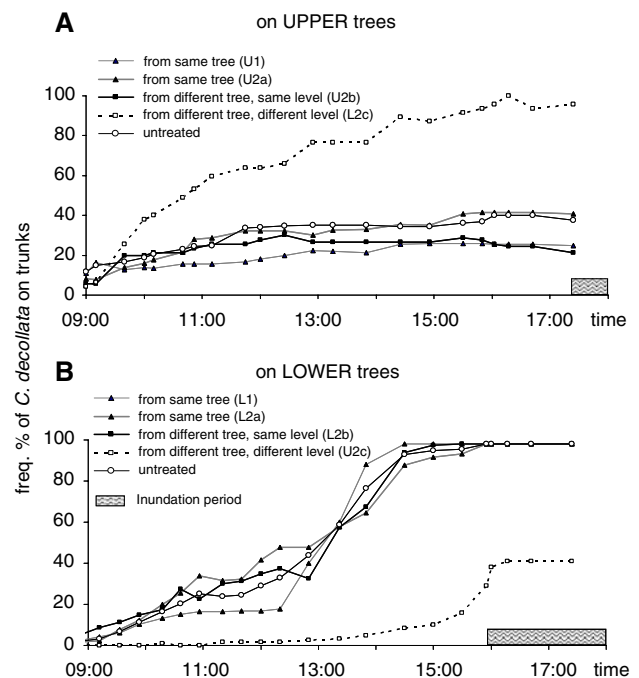

Fig. 4 Translocation experiment, 17 October 2005. See Fig. 3 for details

just like freshly marked ones, thus confirming that the marking process had not affected their behaviour.

The frequency of snails present on trunks when seawater invaded the study areas (at 19.45 and 15.45 h, for February and October, respectively) for each treatment was compared (ANOVA test, Table 2) showing that snails whose tree and level both had been changed, behaved differently from all the other treatments, while no difference was detectable among the latter (SNK test). A difference was also found between the two periods because in October high tides were much higher and invaded more of the upper shore and for a longer time than in February.

In October 2005, after translocation, snails were followed for 4 days. Results are presented in Fig. 5, where, for simplicity, U2a and U1, as well as L2a and L1 data were merged, since the distinction between recently or previously marked individual became less meaningful as time went on. It was evident that on lower trees, from the day after translocation individuals from sub-group U2c (from upper trees) behaved like the residents (L2a, L2b), showing the same migratory pattern. On the contrary, on upper trees, snails of sub-group L2c (from lower trees) continue to climb earlier than the residents (U2a, U2b) for at least two more days.

Finally, the average distance from the water of the various *C. decollata* groups, measured at HW, was recorded following the translocation (Fig. 6). A regression of the average distance with time (Fig. 6, Table 3) showed that both on upper and lower trees, the regression coefficient *b* was significantly different from zero; the opposite was true

Table 2 Frequency of *C. decollata* on trunk at 19:45 h (February) and at 15:45 h (October), i.e. when seawater invaded the lower study areas under different treatments (upper table)

Trees	Month	Different tree different level		Treatments				Same tree same level	
				Different tree same level		Same tree same level			
Upper	February 2005	60.8	L2c	23.3	U2b	18.3	U2a	19.3	U1
		48.0	L2c	17.0	U2b	4.0	U2a	19.0	U1
Lower	October 2005	62.3	U2c	24.8	L2b	16.8	L2a	20.8	L1
		57.8	U2c	15.2	L2b	13.2	L2a	15.2	L1

ANOVA test

Source	SS	*df*	MS	*F*	*P*
Treatment	4,904.68	3	1634.89	206.36	0.0006
Time	203.06	1	203.06	15.67	0.0042
Time × treatment	23.77	3	7.92	0.61	0.626
RES	103.68	8	12.96		
TOT	5,235.18	15			

Results of a two-factor mixed-model ANOVA (lower table). Data were not transformed (Cochran's test: $C = 0.4632$, $P = $ n.s.)
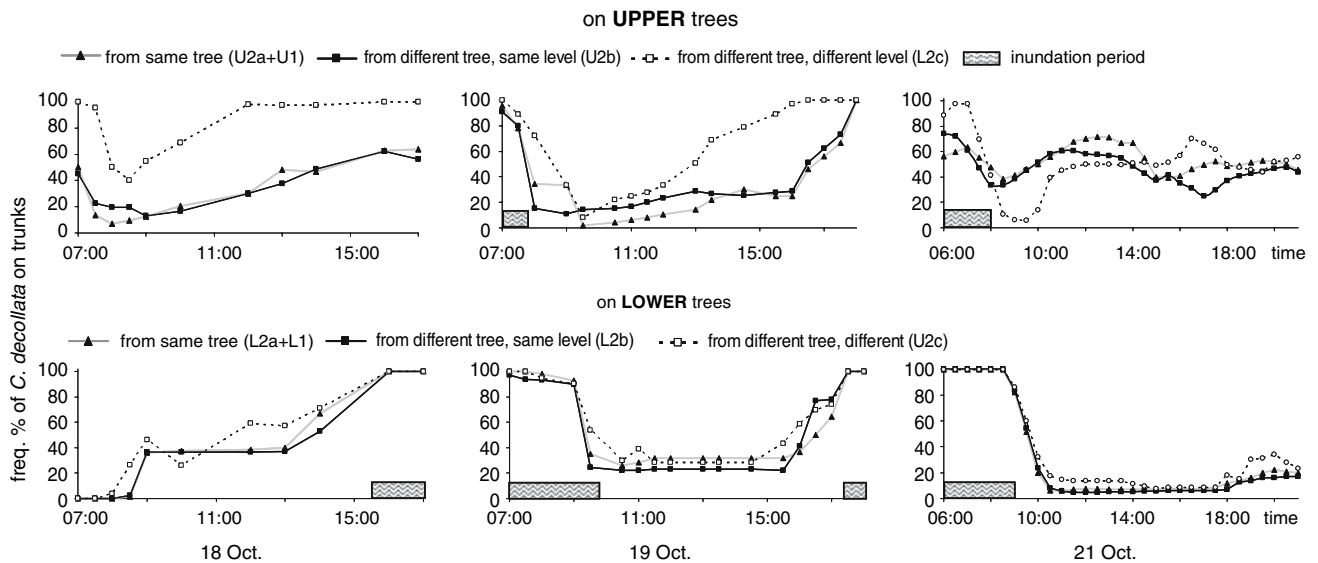

Fig. 5 Frequency of *C. decollata* on trunks at different times 1, 2 and 4 days after translocation (2005). See Fig. 3 for further details

for the residents, which constantly settled about 20 cm (on upper trees) and about 40 cm (on lower trees) above water. However, between tides 7 and 9 following translocation, snails started behaving like residents.

Discussion and conclusions

It had been observed (Vannini et al. 2006) that *C. decollata* foraging on the sediment surface seems to predict the incoming tide and, especially those living on lower shore levels, move back to the trunks of *A. marina* well in

advance of being submersed. We hypothesized that internal information direct the movement, since information from the environment is not available, the sea being about 70–100 m away when the migration begins.

Our field experiments were designed to answer the following questions: before the incoming tide, during the feeding excursion on the sediments, do individuals of *C. decollata* "decide" to move back to the trunk driven by internal information or by direct signals from the environment? Are snails able to "decide" at which height on the trunk to stop in order to avoid being submersed by the incoming tide?
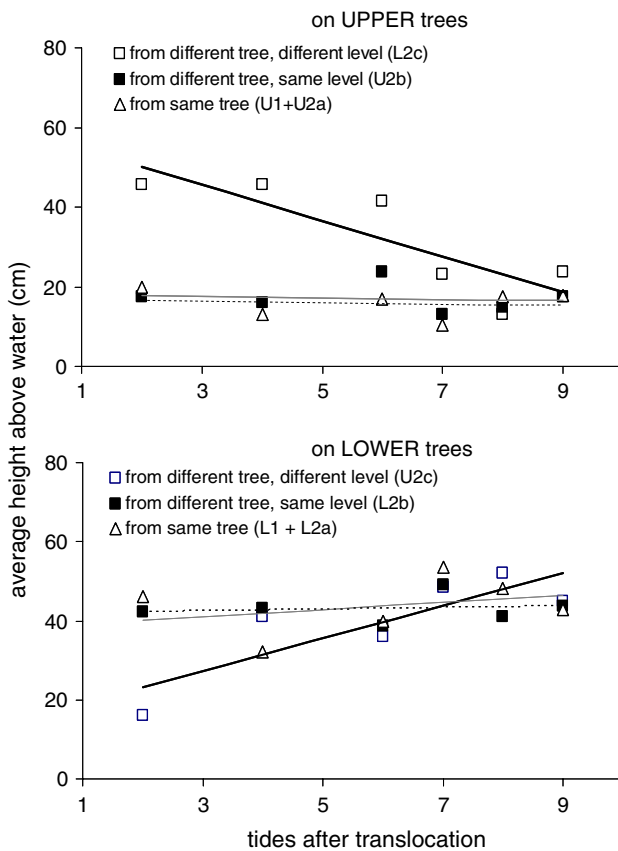
Fig. 6 Difference between average height (cm) of *C. decollata* on trunk and level reached by water during HWs following translocation (October 2005)

Translocation experiments answered both questions positively. Translocated snails apparently maintain the information system tuned to their home-tree until the tidal cycle resets the system: snails that did not "expect" water (upper

snails moved to lower trees) were flooded and immediately reset their timing mechanism to local conditions, in one or a few days. Snails "waiting for" water that never came continued to rely on their own time mechanism and were always the first to climb for several more days.

It was previously observed that the average clustering height on the trunk changed between spring tide (higher) and neap tide (lower) (Vannini et al. 2006). Our experiments suggest that a mechanism of space evaluation (or of the time necessary to cross it) must thus exist, lasting for several migrations after translocation, related to the home-tree conditions and not to the new position of the shore.

An internal clock regulating mechanism must thus exist, informing snails of when and how far to move. Exposing *C. decollata* to constant tidal conditions was beyond our scope, and further work may elucidate the mechanism of such an efficient regulation.

Other intertidal gastropods (Vannini and Chelazzi 1978) and chitons (Chelazzi 1992) behave somewhat similarly, regularly migrating downwards during low tide, and crawling upwards before high tide, reaching different levels during different periods of the month. However, those species are submersed—or at least reached by waves and sprays—by practically every tide, and can thus, twice a day, tune the length of their migration and the position on the cliff to precise environmental conditions.

Further investigations should thus focus on identifying the zeitgeber in *C. decollata* that ensures a suitable time response depending on the snail's position in the intertidal, and to find out how this snail evaluates and modulates the height to climb on the home-tree before high tide, since most of the individuals always leave the trunks after the water recedes and climb back when the water is still tens of meters away.

Table 3 *C. decollata:* regression of average distance from the water of resting snails, with time (upper table), and comparison of regression coefficient, *b* (lower table)

Data from Fig. 6

Trees	Code	Treatment	*b*	*r*	*df*	*P*
Lower	L2c	1—from different tree, different level	−4.511	−0.847	4	**0.037**
	U2b	2—from different tree, same level	−0.206	−0.144	4	0.771
	U1 + U2a	3—from same tree	−0.196	−0.146	4	0.546
Upper	U2c	1—from different tree, different level	4.150	0.840	4	**0.033**
	L2b	2—from different tree, same level	0.207	0.154	4	0.789
	L1 + L2a	3—from same tree	0.891	0.313	4	0.784
Trees	*cfr b*	*t*		*df*	*P*	
Lower	1 versus 2	2.72		8	**0.031**	
	1 versus 3	2.76		8	0.126	
	2 versus 3	0.01		8	0.663	
Upper	1 versus 2	2.63		8	**0.026**	
	1 versus 3	2.76		8	**0.025**	
	2 versus 3	0.45		8	0.995	

1053

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