# Snail arboreality: the microdistribution of *Sitala jenynsi* (Gastropoda: Ariophantidae)

Peter F. Kasigwa
Department of Zoology and Marine Biology, University of Dar es Salaam, P.O Box 35064, Dar es Salaam, Tanzania
zoology@udsm.ac.tz

*Received 10 January 1999; accepted after revision 2 July 1999*

The habitats and patterns of vertical migration of the shell banding morphs of the snail *Sitala jenynsi* (Pfeiffer) were studied in Dar es Salaam and Wazo regions of central coastal Tanzania. Both dimorphic and trimorphic populations were arboreal throughout the year. The snails occurred randomly within mid-heights 180 to 360 cm. without apparent morph differences in micro-distribution. The pattern of circadial vertical distribution consisted of upward migrations during mornings and downward shifts during late evenings. These oscillations regressed negatively on relative humidity (RH), a unit advance in RH representing an eight-fold descent of snails on day-time height. Variations in RH accounted for much of the total variance in the mean vertical distance. During high RH, however, temperature and mating behaviour probably exerted major influences on snail micro-distribution. The effects of arboreality on snail survival and initiation of differentiating subpopulations are proposed.

## Introduction

Arboreal habitation among gastropods is neither unusual nor always absolute: locally, the slugs *Atoxon hildebrandti* (Simroth) and *Bukobia picta* Simroth (Urocyclidae) climb only occasionally, whereas the snails *Achatina fulica* (Bowdich) and *Limicolaria martensiana* (Smith) (Achatinidae) are relatively commoner climbers. The land prosobranch *Tropidophora letourneuxi* (Boettger) (Pomatiasidae), and the molluscivorous snail *Edentulina obesa* Taylor (Streptaxidae) are arboreal at all post-juvenile stages except during the droughts when they become fossorial. In the extreme, *Rhachidina mozambicensis* (Von Martens) and *R. braunsi* (Von Martens) (Enidae) seem to be permanently arboreal (P.F. Kasigwa personal observations; see also *Partula*, Murray, Johnson & Clarke 1982), as are *Caracolus* and *Polydontes* (Heatwole & Heatwole 1978).

Gastropod arboreality may, therefore, relate to the life modes and functional adaptations of the species under consideration. Arboreality may have a spatial perspective which encompasses the horizontal parameters of shrub forest distribution and floristic composition on the one hand, and the vertical parameters of tree branching, foliation and stratification of abiotic factors on the other. Temporal aspects of arboreality which relate to the animal's growth, reproductive behaviour and seasonal factors could also exist.

It is not very informative, therefore, to invoke animal arboreality without explaining the means by which this is practised, the factors which affect its definition and the animal's growth and behavioural correlates. The land snail *Sitala jenynsi* (Pfeiffer) is uniquely suitable for ecogenetical investigations because of its (i) reproductive semelparity, (ii) generation discreteness, (iii) simple shell banding variation and (iv) arboreal habitation, besides the other molluscan advantages (Kasigwa & Allen 1987). This report presents the ecological factors and parameters relating to the fine distribution of *S. jenynsi*

## Methods

### Abundance in shrub *vs* grassy habitats

Two experimental plots each 6 m in diameter were established in each of the five mixed forest localities near Dar es Salaam, Tanzania (for map, see Figure 1 in Kasigwa 1999). One plot in every locality was situated in a grassy patch whereas the second plot was situated among the neighbouring shrubs. The dominant flora of the grassy patches were *Andropogon sp.*, *Cymbopogon excavatus* (Hotsch) Stapf, *Dactyloctenium geminatum* Hack and *Eragrostis aethiopica* Chiov; the herbs *Blumea aurita* (L.f.) DC.; *Launaea cornuta* (Oliv. & Hiern) C. Jeffrey (Compositae) and *Tephrosia noctiflora* Baker (Papilionaceae) occurred only occasionally. The main flora in the shrub plots consisted of *Pluchea dioscoridis* D.C. (Compositae), *Phyllanthus recticulatus* Poir (Euphorbiaceae) and *Harrisonia abyssinica* Olive (Simaroubaceae); the climbers *Dalbergia vacciniifolia* Vatke (Papilionaceae), *Landolphia kirkii* Dyer (Apocynaceae) and *Opilia celtidifolia* Walp (Opiliaceae) were represented occasionally.

Movement of *Sitala jenynsi* was usually minimal at noon. the snails were retracted into shells or, in addition, their shells were mucus-attached onto leaf surfaces. At this time, therefore, a systematic search for snails was carried out through litter at the ground surface, and on stems, twigs and leaves; this search sequence was reversed on alternate sampling occasions. Snails were counted and scored for morph (narrow banded, medium banded, wide banded) in accordance with the morph classification of Kasigwa & Allen (1987). These investigations were conducted during the four seasons of contrasting weather, namely, July and November 1994 and March and July, 1995.

### Vertical distribution

Vertical distribution was studied in the homogeneous stands of *Pluchea dioscoridis* shrubs (40 m long × 40 m wide) behind the Department of Zoology, University of Dar es Salaam. Average shrub height (July 1995) was 2.3 m, the tallest vegetation reaching 4.8 m. A year-round growth increment of the tallest shrubs was 0.27 m, periods of rainfall exerting minimal observable effects on canopy height. The shrubs were green and dense with foliage from ground level to their apices, even during the dry months of January and February.

*Sitala jenynsi* snails were usually stationary in shrub heights at about noon. A cylindrical plot of 6 m radius was marked at the ground surface. Each snail enclosed in the plot between 14.00 and 16.00 hours was scored for morph and had its climbing height measured as the perpendicular distance from the ground surface direct to the point of snail attachment. The data provided basis for evaluating the vertical distribution of *S. jenynsi* in vegetation height at a point in time.

### Temporal patterns of vertical migration

Circadian patterns of vertical distribution were investigated by monitoring bi-hourly the vertical distance moved by snails from a horizontal plane drawn through their respective positions of 12.00 hours noon. The material for these investigations were batches of 15 *S. jenynsi* snails found located at 2.5 ± 0.2 m heights within a plot 6 m in radius in the *Pluchea* forest behind the Zoology Department. A pen-mark was made on the shell of each snail using Indian ink. An identical mark was inscribed on a leaf or twig site where the snail was originally found, to enable recognition of each snail's initial position. The vertical shifts of each snail from a horizontal plane passing through the snail's initial position were then measured bi-hourly for 24 hours. In addition, note was taken of the temperature and relative humidity at 1.5 m height within the shrub plot, by using a wet-bulb whirling psychrometer. At night, the snails were sighted using a torch equipped with a dark-blue filter (Eel 621).

The above procedure was repeated on alternate days within a week, each time using 15 fresh snails and a fresh plot. In this way four records each showing a bi-hourly pattern of vertical migration were obtained per week of sampling. The sampling weeks extended over peaks of seasonal diversity, namely, the seven days ending the months of July, (1994: warm and dry), November (1994: warm and humid), March (1995: hot and wet) and July (1995: warm and dry).

### Testing the direct effect of temperature

Experiments were conducted at a constant Relative Humidity (RH) of about 98% (for the test snails) and about 75% (for the control snails). Two potted *Hibiscus rosa-sinensis* plants, each measuring 1.8 m high (inclusive of pot) and 1.3 m maximum diameter of crown, were placed in separate transparent perspex chambers. Each perspex chamber (1 m length × 1 m width × 2 m high) was filled with cold de-humidified air and the vents adjusted to atmospheric pressure at ambient temperature. The RH of the first chamber was raised and maintained at 98 + 2% (wet bulb depression) by periodic steaming. The second perspex chamber contained the control experiment and was not steamed. After 15 minutes, 36 and 24 adult *S. jenynsi* snails were attached onto the potted plants through a lateral hood in the respective high humidity and low humidity chambers. The snails equilibrated for 15 minutes and were individually observed for retraction or protraction of the head, foot and/or tail; in addition, the speed and direction of motion of the body and the tail were noted. The observations were carried out during daytime in an air-conditioned room at 18°C, 24°C, 30°C and, using a shaded 60 watt bulb for warming, at 34°C. A rest period of 30 minutes was interposed between observations at different temperatures; conditions in the chamber tended to revert to room temperature (28°C) and RH (80%) during the rest period.

## Results

Table 1 shows the occurrence of the morphs of *Sitala jenynsi* in different localities among the grass and the forest plants. The narrow-banded and wide-banded snails were the two morphs found in the University localities; both morphs, plus the medium-banded snails, occurred in Wazo region. At each period, snails were significantly unequal in morph frequencies ($\chi^2 > 16.281^{***}$). The narrow-banded morph predominated in Hall Six and Zoology forests. The same morph,

**Table 1** The morph occurrence of *Sitala jenynsi* snails among shrubs *versus* among grasses at the different seasons in Wazo and University of Dar es Salaam regions

| Locality | | July | | 1994 | Nov. | | 1994 | March | | 1995 | July | | 1995 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | N | M | W | N | M | W | N | M | W | N | M | W |
| Kilima Hewa | S | 68 | – | 37 | 68 | – | 48 | 80 | – | 45 | 65 | – | 47 |
| UDSM | G | 0 | – | 0 | 0 | – | 0 | 5 | – | 2 | 0 | – | 0 |
| Weather Station | S | 40 | – | 32 | 32 | – | 26 | 51 | – | 30 | 60 | – | 4 |
| UDSM | G | 6 | – | 2 | 4 | – | 0 | 4 | – | 4 | 4 | – | 6 |
| Hall 6 | S | 78 | – | 28 | 70 | – | 25 | 87 | – | 26 | 92 | – | 25 |
| UDSM | G | 3 | – | 0 | 0 | – | 0 | 0 | – | 0 | 2 | – | 0 |
| Zoology | S | 98 | – | 24 | 67 | – | 16 | 84 | – | 15 | 94 | – | 209 |
| Forest UDSM | G | 6 | – | 0 | 4 | – | 0 | 0 | – | 0 | 2 | – | 2 |
| Wazo | S | 43 | 18 | 46 | 30 | 22 | 37 | 36 | 18 | 63 | 58 | 34 | 63 |
| Mid-Central Forest | G | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

For each locality

S = number of snails in shrub habitats, G = the number of snails in grasses, % = percentage proportion of shrub snails to the total number of snails in both habitats, N = Narrow-banded morph, M = Medium-banded morph and W = Wide-banded morph.

along with the wide-banded snails alternated in predominance in Wazo's Mid-Central locality. Kasigwa (1975) had found that specific morph frequencies, with slight temporal fluctuations, were characteristic of a given locality, and findings of recent years (Muruke & Nasuwa 1986; Kawasange & Luena 1994; James & Kyomo 1997) attest to the stability of this situation.

The three morphs inhabited shrub habitats in consistently high proportions throughout the year (i.e. entire life span of the snail), irrespective of season (Table 1). The grasses, on the other hand, harboured very few snails, *S. jenynsi* being encountered only in the margins and interiors of shrub forests. In Table 2 the sampling occasions when snails were found on both grasses and shrubs are pooled and examined for morph differences in habitation on either plant habitat. As the wide-banded morph did not occur on grass samples of Hall Six, the data of this locality are excluded from the contingency tests. No morph-biased occurrence was detected (Table 2): snail variants inhabited shrubs or grasses in direct proportion to morph abundance.

**Table 2** Testing for morph-dependent preference for shrubs or grass vegetation types by the shell banding morphs of *S. jenynsi*

| Locality | Narrow-banded morph | Wide-banded morph | $\chi^2_{(1)}\hat{c}$ with Yate's Correction NS = not significant |
|---|---|---|---|
| **Kilima Hewa** | | | |
| Shrubs | 85 | 45 | |
| Grasses | 5 | 2 | |
| | | | 0 339, NS |
| **Weather Station** | | | |
| Shrubs | 183 | 132 | |
| | | | 0 001, NS |
| **Zoology** | | | |
| Shrubs | 259 | 60 | |
| Grasses | 12 | 2 | |
| | | | 0 006, NS |

A comparison of snail proportions in shrubs at the University shows significant disparity between the different localities ($\chi^2 = 42.068$***; Table 3). Shrubs of the Weather Station harboured the smallest proportion of snails (91%) whereas elsewhere the shrubs exceeded 96%. The disparity could be a result of differences in floristic composition, abundance and coverage in the localities.

Results of the vertical distribution of snails at set points are presented in Figure 1. Very few individuals were found at heights below one metre, an indication of preferential climbing; snails were sighted near the ground only during humid weather. It is more probable for snails to occur within the mid-heights 125 to 395 cm than outside this range ($P > 0.75$, Chebychev's theorem [#1]: Mösteller, Rourker & Thomas 1970). The two morphs attained similar mean heights [261.4 + SD 60.6 cm for the narrow-banded snails (n = 237)] and 260.8 + S.D. 62.1 cm for the wide-banded snails (n = 53)], and did not differ in parameters of their vertical distribution ($z \geq -0.377$, $P = 0.3$; Mann-Whitney U-test). The overall vertical distribution was platykurtic at 180 to 360 cm (Figure 1 b: $\chi^2_{(8)} = 12.184$, NS), a height range which encompasses the mean shrub height. It is likely that the vertical distribution was affected by the branching and foliation patterns, vegetation parameters which result into a vertically heterogeneous leaf cover.

The relationship between mean shrub height and snail aggregations might occur by coincidence: in a tree forest community dominated by *Pteleopsis myrtifolia* (L.) Engl. & Diels (Combretaceae) and *Teramnus repens* (Taub.) Bak.f (Papilionaceae), no *S. jenynsi* were found as high as the 3.8 m mean tree height, though 145 snails rested at lower levels. Even in the case of the *Pluchea dioscoridis* shrubs studied above, the observed variation in snail climbing height (S.D$_{\bar{x}}$ ≥ 60 cm) suggests loose (or absence of) association of snails with mean vegetation height.

The following results were obtained concerning the pattern of vertical activity. In total 15 snails were marked on each of the four sampling days in a week and were monitored on 14 bi-hourly occasions each 'day' (i.e. 12.00 hours noon through 12.00 hours the following noon to 02.00 pm). This weekly procedure was conducted in four seasons and produced 2466 (i.e. 73.4%) of the maximum possible data. The outcome is held to be a reasonably high recapture rate, considering that half of the monitoring occasions took place at night.

The solid trace in Figure 2 shows the mean vertical distance (VM) to which the snails migrated. Snails climbed to high levels on shrubs (2.5 ± 0.5 m) and rested there from 10.00 am to 08.00 pm during the dry months (July). At night the individuals descended below 1.0 m shrub height and remained

**Table 3** Habitation of *Sitala jenynsi* in shrubs *versus* grassy habitats at the main campus, University of Dar es Salaam. For each locality, the monthly counts in one year are pooled

| Locality | Shrubs | | | Grasses | | |
|---|---|---|---|---|---|---|
| | No. of snails scored | % of the total in locality | $\chi^2$ | No of snails scored | Number expected | $\chi^2$ |
| Kilima Hewa | 458 | 98 5 | 0 161 | 7 | 15 5 | 4.676 |
| Weather Station | 315 | 91 3 | 1 062 | 30 | 11.5 | 26 670 |
| Hall 6 | 431 | 98.9 | 0.216 | 3 | 14.6 | 6 272 |
| Zoology Forest | 418 | 96.6 | 0 001 | 14 | 14.4 | 0 012 |
| | | | | $\Sigma \chi^2_{(3)} = 42.068$*** | | |

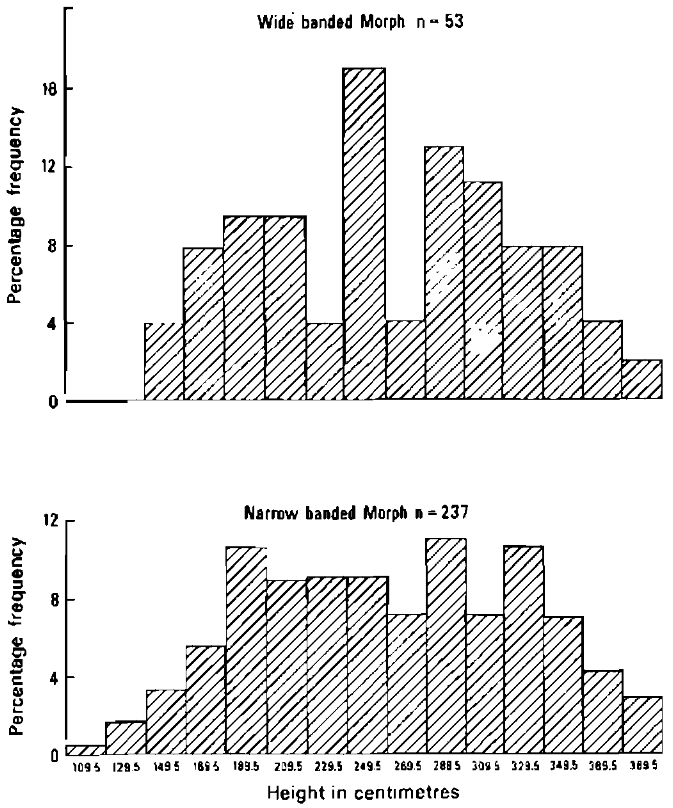

**Figure 1** The vertical distribution of *Sitala jenynsi* at a point in time

active here until about 8.00 am the next morning when they re-climbed. Similar shifts upward in daytime and downward at night were observed during the wet seasons (November and March). During the latter seasons, however, snails remained mobile for longer periods than during the dry months (20 *versus* 13 hours); correspondingly, the day time duration of quiescence (spent at 2.5 ± 0.5 m heights) were briefer in the wet than in the dry months (2.5 *versus* 10 hours). Thus the upward migrations of *S. jenynsi* were closely followed by snail withdrawal into shells whereas downward migrations were followed by continued mobility and/or activity.

The duration of each phase in the oscillations was probably influenced by time-dependent factors in the snail's microclimate. The most likely, because of their periodicity and reported ecophysiological effects on gastropods, were temperature and relative humidity (Dainton 1954; Cameron 1970a,b; Lyth 1983; Riddle 1983). The data of these factors during the study period and the corresponding mean vertical migrations (VM) of snails are presented in Table 4.

VM regressed positively linearly on temperature each season. The regression of VM on RH was negatively linear in November 1994, March and July 1995. In July 1994 similarly untransformed data of VM and RH fitted best the negative sigmoid regression curve ($r^2$ = 0.820), as compared to the exponential (0.734) and the linear relations (0.677). The values of the three relations do not differ significantly from each other. One could, therefore, conduct a linear multiple regression analysis of VM on both temperature and RH. However, at constant air moisture content and pressure, the relative humidity of a given volume of air is a negative function of temperature (Rosenberg 1974; Unwin 1980). That is, the variations in temperature and RH are not mutually independent to permit the application of multiple regression analyses. In the following account, therefore, the effects of temperature on VM are assumed to be expressed, at least indirectly, in the regression of VM on RH.

During the dry seasons (July and November 1994 and July 1995) VM decreased arithmetically by the factor $b_{y\,x}$ = 8 to 10 (S.E ≤ 2.6) per unit advance in RH (Table 5 rows 2 & 3). The three regression coefficients were significantly negative (P ≥ 0.001; Table 5 row 4) but they did not differ from one another at the 95% confidence level (Table 5 row 5). This suggests that RH exerted effects of more or less equivalent magnitudes from one dry season to the other. The standard error of the regression was highest during the rains (March; S.E = 23.57;

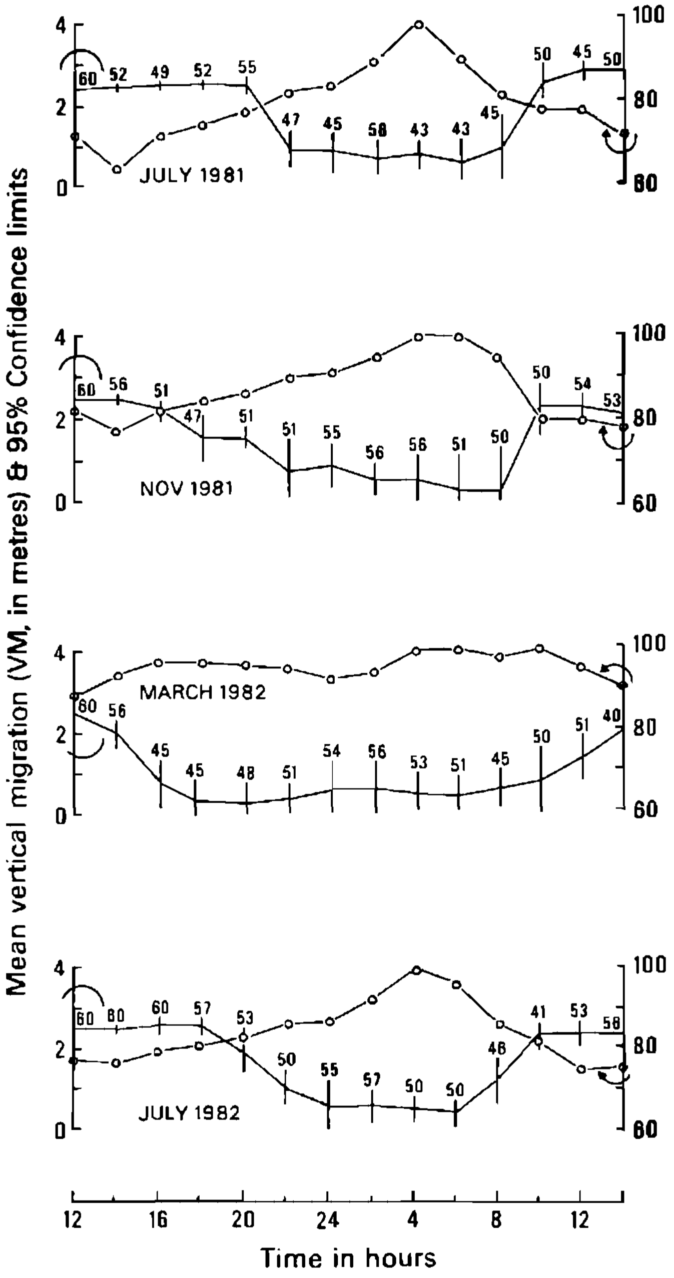

**Figure 2** *Sitala jenynsi*: bi-hourly mean Vertical Migration (VM) measured over 24 hours

**Table 4** Daily pattern of vertical migration of *Sitala jenynsi*. Mean snail vertical migration (MV in cm), corresponding temperature (t°C) and relative humidity (RH) at the indicated time

| Time in hours | July 1994 | | | November 1994 | | | March 1995 | | | July 1995 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | t° | RH | MV | t° | RH | MV | t° | RH | MV | t° | RH | MV |
| 12 00 | 29 | 73 | 250 | 30 | 82 | 250 | 31 | 89 | 250 | 28 | 77 | 250 |
| 14.00 | 29 | 64 | 250 | 32 | 77 | 250 | 32 | 94 | 200 | 29 | 76 | 250 |
| 16.00 | 26 | 72 | 250 | 30 | 80 | 220 | 29 | 97 | 88 | 27 | 79 | 260 |
| 18.00 | 27 | 75 | 250 | 27 | 84 | 160 | 28 | 97 | 32 | 26 | 81 | 258 |
| 20.00 | 26 | 89 | 246 | 26 | 86 | 156 | 29 | 96 | 25 | 25 | 83 | 190 |
| 22.00 | 26 | 83 | 83 | 26 | 90 | 80 | 29 | 95 | 50 | 24 | 86 | 100 |
| 24.00 | 25 | 84 | 80 | 25 | 91 | 93 | 28 | 93 | 60 | 23 | 87 | 60 |
| 02 00 | 25 | 90 | 60 | 25 | 95 | 67 | 27 | 94 | 60 | 22 | 92 | 60 |
| 04.00 | 25 | 100 | 65 | 23 | 100 | 55 | 26 | 100 | 43 | 23 | 100 | 55 |
| 0.600 | 23 | 90 | 50 | 24 | 100 | 30 | 28 | 100 | 40 | 25 | 96 | 43 |
| 08 00 | 24 | 81 | 84 | 27 | 94 | 28 | 30 | 98 | 60 | 28 | 86 | 129 |
| 10.00 | 28 | 89 | 240 | 28 | 80 | 235 | 31 | 100 | 75 | 27 | 82 | 217 |
| 12.00 | 29 | 78 | 275 | 31 | 80 | 235 | 34 | 85 | 130 | 29 | 75 | 220 |
| 14.00 | 30 | 70 | 270 | 30 | 78 | 218 | 33 | 90 | 200 | 30 | 76 | 220 |

**Table 5** Linear regression statistics of vertical migration of *Sitala jenynsi* on relative humidity

| | Term | | July 1994 | November 1994 | March 1995 | July 1995 |
|---|---|---|---|---|---|---|
| 1 | Intercept | | 830.44 | 1088 35 | 1460 3 | 1021 12 |
| 2. | Regression coef., $b_{x.y}$ | | -8 234 | -10 780 | -14 328 | -10 174 |
| 3. | S.E. of $b_{x.y}$ | | 1.833 | 1 178 | 23 574 | 2 174 |
| 4 | Significance of $b_{x.y}$ | | -4 493** | -9 151*** | 0.608 | -3.953** |
| 5. | 95% C L. of $b_{x.y}$ | upper | -12.266 | -13 371 | -66 191 | -15.836 |
| | | lower | -4 202 | -8 188 | +37 535 | -4 511 |
| 6. | 95% C.L. | upper | 203 796 | 160.076 | 117.573 | 186.298 |
| | of $\mu_y$ | $\bar{x}$ | 167.923 | 142 230 | 84 850 | 160.230 |
| | at x | lower | 132 050 | 124.384 | 52.127 | 134 162 |

Table 5 row 3); the negative sign of the coefficient was immaterial: the 95% confidence interval of the slope ranged from -66 to +34 (Table 5, row 5).

At mean RH the 95% confidence intervals of VM overlapped at mid-heights 120 to 210 cm during the dry seasons (see Table 5 row 6). The VM of rainy March, on the other hand, was significantly lowest, suggesting it was drawn from a universe of means which differed from that of the dry periods. The low mean vertical migrations during March were in part due to persistently high relative humidity during the rainy season and to certain unidentified factor(s). The latter's contribution to the total variance was also highest in March (61%, Table 6), though the regression value also remained significant ($F_{s(1,11)} = 8.708^{**}$). In the non-rainy seasons, on the other hand, similar unidentified factors accounted for less than 40% of the total variation in VM, thereby achieving greater regression values ($F_{s(1,11)} \geq 20.197^{***}$). Thus, whereas y values seem reliable at most seasons (Figure 2), use of the regression equation to estimate VM during the rainy season is not recommended.

Results from the manipulation of temperature under constant relative humidity are given in Table 7. At conditions of moisture saturation (H), the snails switched from retraction (18°C) to protraction of their heads, feet and tails outside the shells (24°, 30° and 34°C). In addition, the individuals changed from static positions to linear movements which later became omni-directional as the temperatures increased. Tail wagging was circular at lower temperatures but described horizontal strokes at higher temperatures. By contrast, the control snails (observed at low relative humidity, L in Table 7) progressively retracted the heads, feet and tails into their shells with an increase in temperature; where these parts remained protracted the snails were mostly immobile. The results suggest existence of some special effect of temperature which acts directly (not via RH) on the migration of snails.

**Table 6** Analysis of Variance of snail's mean vertical migration as affected by relative humidity and other factors

| Date | Source of variation | df | SS | MS | $F_s$ (1,11) ***p< .001 **p< .025 | Contribution by other factors |
|---|---|---|---|---|---|---|
| July '94 | Regression | 1 | 69812.5 | 69812.5 | 20.197*** | – |
| | Residual | 11 | 38022.4 | 3456.6 | – | 0.385 |
| | Total | 12 | 107834.9 | 8986.6 | – | – |
| Nov '94 | Regression | 1 | 84396.8 | 84386.8 | 98.645*** | – |
| | Residual | 11 | 9411.2 | 855.6 | – | 0.109 |
| | Total | 12 | 93808.0 | 7817.3 | – | – |
| March '94 | Regression | 1 | 25045.1 | 25045.1 | 8.708** | – |
| | Residual | 11 | 31636.6 | 2876.1 | – | 0.609 |
| | Total | 12 | 56681.7 | 4723.5 | – | – |
| Nov '94 | Regression | 1 | 73390.7 | 73390.7 | 40.213*** | – |
| | Residual | 11 | 20075.7 | 1825.1 | | 0.234 |
| | Total | 12 | 93466.4 | 7788.9 | – | - |

**Table 7** Effect of increasing temperature on behaviour of *Sitala jenynsi* snails at near 100% relative humidity

| Activity | Percentage of snails displaying the activity at the staed temperature at high relative humidity (H = 98 + 2%, N = 36 snails) and at low relative humidity (L – 75 ± 2%, N = 24 snails) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 18°C | | 24°C | | 30°C | | 34°C | |
| | H | L | H | L | H | L | H | L |
| **Retraction** | | | | | | | | |
| Head | 25 | 46 | 0 | 76 | 0 | 83 | 0 | 85 |
| Foot | 20 | 35 | 0 | 30 | 0 | 50 | 0 | 95 |
| Tail | 100 | 46 | 0 | 83 | 0 | 100 | 0 | 100 |
| **Locomotion** | | | | | | | | |
| Stationary | 100 | 100 | 28 | 55 | 8 | 76 | 0 | 100 |
| Linear | 0 | 0 | 63 | 43 | 78 | 21 | 21 | 0 |
| Haphazard | 0 | 0 | 9 | 0 | 14 | 3 | 79 | 0 |
| **Tail* motion** | | | | | | | | |
| Stationary | – | 48 | 19 | 100 | – | – | – | – |
| Circular | - | 54 | 82 | 0 | 92 | 0 | 32 | 0 |
| Strokes | – | - | – | 9 | 0 | 0 | 68 | – |

* for the protracted tails

## Discussion

### Climbing behaviour and arboreal *versus* graminaceous habitats

It could be argued that *Sitala jenynsi* is simply an opportunistic climber as the snail will climb onto dry liana stems and the wire-mesh roof of breeding cages. The local snail *Achatina fulica* will also climb onto poles and metal fencing (Mead 1961; Raut 1977), and the land prosobranch *Tropidophora letourneuxi* as well as the slug *Bukobia picta* climb over 4 m heights on brick and concrete walls, rocks and electricity transmission pylons (P.F. Kasigwa personal observations). The classification of *S. jenynsi* as an obligate climber, however, is its absence from the ground and subsurface levels throughout the year. Furthermore, *S. jenynsi* oscillates dynamically within a specific height range, whereas the 'occasional or seasonal climbing' pulmonates tend to occupy static height(s), displaying no rhythmic patterns of vertical activity.

Among heights, *S. jenynsi* was abundant on shrubs whereas it was rare on grasses. It is tempting to explain the disparity on the differences in the mean vertical range of the shrubs (1.9 m) when compared to that of the grasses (0.9 m). If the vertical distribution of *S. jenynsi* depended on availability of vertical anchorage only, then, assuming equal coverage of the ground surface by the grasses and the shrubs, about 32% of the snails would be expected to occur on grasses! The highest number of snails observed on the grasses, however, was only 10, a significant departure from the expected 36.6 snails ($\chi^2_{(1)}$= 19.372***, Weather Station, N = 114; Table 1). This indicates that *S. jenynsi* were fewer on grasses for reasons other than the mere shortness of the grasses. Grasses, for instance, are not common components of the snail's diet. During daytime, *S. jenynsi* snails observably remain close to their foraging sites of the previous night (Kasigwa 1991). It may, therefore, be expected that a vegetation community will harbour snails in direct proportion to the edible (i.e. shrub) component.

### Micro-temporal patterns of vertical activity

Fish and many plankters practise diel vertical migrations, ascending into the warm shallow layers of lakes and oceans nocturnally and descending into the cool deeper strata for the day (Clark & Levy 1988). The migrations were at one time postulated to serve demographic functions, especially group migration, epideictic displays and obviation of inbreeding (McLaren 1963). Lately the migrations have been ascribed to metabolic and growth-related advantages (McLaren 1963; Würtsbaugh & Neverman 1988), environmental cues (Vannini, Cannicci & Ruwa 1996), food resource exploitation strategies (Lampert 1989) and predation avoidance (Gliwicz 1986; Gliwicz & Pijanowska 1988; Stich & Lampert 1981, 1984; Clark & Levy 1988; Lampert 1993; Young & Watt 1996). Among non-plankters, Takada (1996) explained the reasons for vertical migration of trochid gastropods in the intertidal zone, while Cannicci, Ritossa, Ruwa & Vannini (1996) reported similar behaviour in grapsid crabs inhabiting mangrove shrubs. Comparable cases of rhythmic vertical migrations in non-aquatic ecosystems (e.g. along hill sides and tree heights) are rare. The vertical micro-distribution of *S jenynsi* is one purely terrestrial example. Suggestions about the evolutionary course and adaptiveness of land snail oscillatory arboreality may have to be derived from a special test design.

The vertical distribution of snails at a point in time (Figure 1) is just a single observation from a temporal distribution pattern of a population. The pattern is a sinusoidal oscillation up and down vegetation heights and is repeated approximately every 24 hours. It is therefore possible to conceive a distribution comparable to Figure 1 occurring at each point on the plot in Figure 2. The measurements of central tendency are also liable to a temporal oscillation: for instance, at 15.00 hrs the mean height was 261 ± S.D. 60 cm, whereas at 4.00 hours the mean height fell below 80 cm and showed reduction in sample variance (Figure 2).

A note of caution on the snails selected for studying the mean vertical migration patterns: any 15 snails found at 1.5 ± 0.2 m vegetation height on alternate days of the week were utilised in the study. It was assumed that the members of a population were randomly distributed vertically and, therefore, a reasonably large sample would represent population behaviour. However, would snails obtained from other plant heights produce results similar to those presented here? If, like some other pulmonates (Edelstam & Palmer 1950; Rollo & Wellington 1981; Chellazzi 1990; Papi 1990), *S. jenynsi* practises homing, the snails selected for the present observations might have been associated with a home height to which they habitually returned. The resulting patterns of vertical migration would then apply to the sample and not to the population. Table 4 shows that *S jenynsi* released only 24 hours previously missed their former heights by as much as -120 to −20 cm, suggesting a homing cycle lasting beyond 24 hours, a presence of a broad home range which is shared by a majority of the population, or a total absence of homing. It would be instructive to monitor over 24 hours the migration patterns of individuals in the top and bottom layers of a vertical distribution.

The second caution is on the validity of the temperature and RH measurements. Did these measurements truly represent conditions in which the snails were situated, or were they measurements of conditions from which the snails may have been escaping? By way of recollection, the tallest shrubs stood at 4.8 m, and snails marked for temporal patterns of vertical migration had been obtained at 2.5 ± 0.2 m. The mean height of shrubs was 2.3 m and the height at which temperature and RH were measured was 1.5 m. Recorded snail movements were notably oscillatory and their amplitude broadly encompassed the height at which temperature and RH were measured. This suggests that, firstly, RH may be the cue for a particular pattern of behaviour (including a favoured vertical height) and, secondly, vertical movement may simply be a way of remaining close to optimal RH by selecting the most humid part of the habitat when humidity is low.

### Micro-distribution: factors and consequences

The vertical migration of *S. jenynsi* was found to be a negative function of ambient relative humidity. This factor alone contributed 60 to 85% of the total variation in VM, the remaining variation being attributed to some unspecified factors. Temperature has been assumed to affect VM indirectly, namely, via relative humidity. Experimental manipulation of temperature while maintaining a moisture-saturated environment, however, suggests that temperature exerts some direct action on VM, independent of relative humidity (see also Abdel-Rehim 1983). The vertical migration during the rainy season (March) when RH approached saturation and daytime temperatures were high (28 ± 2°C) may have come under such direct effect of temperature: snail migration then seemed to lose the directionality which, during drier conditions, regresses negatively on RH. A similar loss of directional migration under temperature elevation was achieved experimentally by stabilising RH (Table 7). March, therefore, represents the season when correlation of VM and RH is absent (rows 3, 4 & 5 in Table 5).

Another factor which probably affects the micro-distribution of *S jenynsi* is mating behaviour. Courtship repertoire, copulation and its aftermath involve the pairing of organisms which otherwise respond as individuals to ecological factors. The duration of copulation was observed to be 3 5 hours (Kasigwa 1975) whereas those of courtship and the post-copulatory phase are unrecorded; the total duration of mating behaviour could be a period when the fine distribution of snails might seem discrepant with general VM. It is also likely that snails' photoperiodic and clock-compensated activities (Brown 1976; Palmer 1976) affect its micro-distribution: the achatinid snail *Limicolaria festiva* (Martens), for instance, employs circadian rhythms of locomotory activity in adaptive response to the desiccative Sahel conditions (El Rayah, Constantinou & Cloudsley Thompson 1984).

Finally, it is unlikely that predation exerted significant effects on VM, for instance, by causing localised depletion of the prey numbers; no evidence for predation (Kasigwa, Mrema & Allen 1983) was seen during the intervals between observations. Nor could *S. jenynsi* within the bi-hourly intervals between observations possibly re-distribute itself among the vegetation in response to the presence of predators. This species can barely recognise its principal sympatric predator *Edentulina obesa*, the green arboreal snail onto whose shell *S. jenynsi* occasionally perches despite the risk! It appears that relative humidity and the characteristics of the supportive vegetation are the most decisive factors in the microspatial distribution of *S. jenynsi*. Under a moisture-saturated environment micro-distribution is directly affected by temperature; other factors such as aggregation and clock-dependent behaviour could also play some role.

A consequence of permanent arboreality is that *S. jenynsi* is available throughout the year, a requisite for monitoring continuously the operation of micro-evolutionary processes (Muruke & Nasuwa 1986; Kasigwa & Allen 1987; Kawasange & Luena 1994; James & Kyomo 1997). In addition, arboreality could initiate differentiation within a population, as noted where evergreen shrubs resist destruction by fire and thereby harbour survivor snails: the intervening grassy areas are burned down, an event of nearly annual recurrence (Eltringham 1976; Vessey-Fitzgerald 1972). In view of the low dispersion rates of pulmonates generally (Goodhart 1962; Hickson 1972; Cameron & Williamson 1974; Murray & Clarke 1984; Kasigwa 1999a), such population fragmentation effectively reduces a previously continuous population into shrub-based inter-isolated sub-populations between which snail interchange and gene flow might be very limited.

## Acknowledgements

This article is dedicated to the late Professor Firmat Kagolo Kasule, a teacher and friend, whose scholarly fascination in ecology and invertebrate zoology raised the erudition of many students and colleagues in these fields in Eastern, Central and Southern Africa. I am grateful to him for his very useful comments.

## Note

1. $P[x \pm k\delta] \geq (1 - 1/k^2)$ where P refers to the probability of snail location within a given interval of height, x is the mean number of snails in the interval, δ the standard deviation and k is any positive integer.

## References

ABDEL-REHIM, A.H. 1983. The effects of temperature and relative humidity on the nocturnal activity of different shell colour morphs of the land snail *Arianta arbustorum*. *Biol. J. Linn. Soc.* 20. 385–395

BROWN, F.A. Jr 1976. Evidence for external timing of biological clocks. In: An introduction to biological rhythms, (ed.) J.D. Palmer. Academic Press, New York.

CAMERON, R.A.D. 1970a. The effect of temperature on the activity of three species of land snails (Mollusca: Grastropoda). *J. Zool.* Lond. 162: 303–315.

CAMERON, R.A.D. 1970b. The survival, weight loss and behaviour of three species of land snails in conditions of low humidity. *J. Zool. Lond.* 160: 143–157

CAMERON, R.A.D. & WILLIAMSON, P. 1977. Estimating migration and the effects of disturbance in mark recapture studies on the snail *Cepaea nemoralis*. *J. Anim. Ecol.* 46: 173–179.

CANNICCI, S., RITOSSA, S., RUWA, R.K. & VANNINI, M. 1996. Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma* (Decapoda: Grapsidae). *J. Exp. Mar. Biol. Ecol.* 196: 299–311

CHELLAZZI, G. 1990. Eco-ethological aspects of homing behaviour in molluscs. *Ethol. Ecol. Evol.* 2. 11–26.

CHOU, Y. 1975. Statistical analysis. 2nd edn. Holt, Rinehart & Winston, New York

CLARK, C.W. & LEVY, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Amer. Nat.* 131: 271–289.

DAINTON, B.H. 1954. The activity of slugs: induction of activity by changing temperatures. *J. Exp. Biol.* 31: 165–187.

EDELSTAM, C. & PALMER, C. 1950. Homing behaviour in gastropods. *Oikos* 2: 259–270

EL RAYAN, CONSTANTINOU, C. & CLOUDSLEY THOMPSON, J.L. 1984. Environmental adaptations of the African snail *Limicolaria festiva*. *Int. J. Biomet.* 28: 327–331.

ELTRINGHAM, S.K. 1976. The frequency and extent of uncontrolled grass fires in the Ruwenzori National Park, Uganda. *East Afr. Wildlife J.* 14: 215–222.

GLIWICZ, J.Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature, Lond.* 320: 746–748.

GLIWICZ, M.Z. & PIJANOWSKA, J. 1988. Effect of predation and resource depth on vertical migration of zooplankton. *Bull. Mar. Sci.* 43: 695–709.

GOODHART, C.B. 1962. Variation in a colony of the snail *Cepaea* nemoralis. *J. Anim. Ecol.* 31: 207–237.

HEATWOLE, H. & HEATWOLE, A. 1978. Ecology of Puerto Rican camaenid tree snail. *Malacologia* 17: 241–315.

HICKSON, T.G.L. 1972. A possible case for genetic drift in colonies of the land snail *Theba pisana*. *Heredity* 29: 177–190.

JAMES, M. & KYOMO, J. 1997. Spatial variation in the distribution of the morph frequencies of *Sitala jenynsi* (Pulmonata: Ariophantidae) on the Main Campus: the 1996–97 generation. Project Report, Department of Zoology and Marine Biology, University of Dar es Salaam.

KASIGWA, P.F. 1975. Studies on the ecological genetics of the land snail *Sitala jenynsi*. M.Sc thesis, University of Dar es Salaam.

KASIGWA, P.F. 1991. Diet and its ecological implications in the arboreal snail *Sitala jenynsi*. *J. Afr. Zool.* 105. 81–95.

KASIGWA, P.F. 1999. Dispersion factors in the arboreal snail *Sitala jenynsi* (Pfr.) (Pulmonata, Ariophantidae). *S. Afr. J. Zool.* 34(4) 145–153.

KASIGWA, P.F. & ALLEN, J.A. 1987. The shell band-width polymorphism of the arboreal snail *Sitala jenynsi*: a candidate for microevolutionary studies. *Rev. Zool. Afr.* 101: 379–396.

KASIGWA, P.F., MREMA, A.J. & ALLEN, J.A. 1983. Predation by mongooses, rodents and snails on *Sitala jenynsi*, *Achatina fulica* and other land snails in Coastal Tanzania. *J. East Afr. Nat. Hist. Soc. Nat. Mus.* 179. 1–10.

KAWASANGE, B.O.P. & LUENA, C.G. 1994. A Study of spatio-temporal variation in morph frequencies of *Sitala jenynsi* (Pfr) (Pulmonata: Ariophantidae) on the Main Campus, University of Dar es Salaam: 1993–94. Project Report, Department of Zoology and Marine Biology, University of Dar es Salaam.

LAMPERT, W. 1989. The adaptive significance of diel vertical migration in zooplankton. *Funct. Ecol.* 3: 21–27.

LAMPERT, W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator avoidanc hypothesis. *Adv. Limnol.* 39: 79–88.

LYTH, M. 1983. Water contents of slugs in natural habitats and the influence of culture conditions on water content stability in *Arion ater*. *J. Moll. Stud.* 49: 179–184.

MCLAREN, I A. 1963. Effects of temperature on growth of zooplankton and the adaptive significance of vertical migration. *J. Fish. Res. Bd Can.* 20: 685–727.

MEAD, A.R. 1961. The giant african snail: a problem in economic malacology. Chicago University Press, Chicago.

MÜSTELLER, F., ROURKER, R.E.K. & THOMAS, G B. Jr. 1970. Probability with statistical applications. 2nd edn. Addison-Wesley, London.

MURRAY, J. & CLARKE, B. 1984. Movement and gene flow in *Partula taeniata*. *Malacologia* 25: 343–348.

MURRAY, J.M, JOHNSON, M.S. & CLARKE, B. 1982. Microhabitat differences among genetically similar species of *Partula*. *Evolution* 36: 316–325

MURUKE, M.H.S. & NASUWA, E.J.G 1986. Spatio-temporal variation in morph frequencies of *Sitala jenynsi* (Pfr.) (Pulmonata: Urocyclidae) on Dar es Salaam University Campus, 1985–86. Project Report, Department of Zoology and Marine Biology, University of Dar es Salaam.

PALMER, J.D. 1976. An introduction to biological rhythms. Academic Press, New York.

PAPI, F 1990. Homing phenomena: mechanisms and classifications. *Ethol. Ecol. Evol.* 2. 3–10.

RAUT, S.K. 1977. Ecology and ethology of *Achatina fulica* and *Marochlamys indica*. Ph D thesis, University of Calcutta.

RIDDLE, W.A. 1983. Physiological ecology of land snails and slugs. In: The Mollusca. Ecology, (ed.) W.D. Russel-Hunter. Vol. 6. Academic Press, London.

ROLLO, C.D. & WELLINGTON, W G. 1981. Environmental orientation by terrestrial mollusca with particular reference to homing behaviour. *Can. J. Zool.* 59. 225–239.

ROSENBERG, N.J 1974. Microclimate, the biological environment. Wiley Interscience

SOKAL, R.R. & ROHLF, J F. 1981 Biometry 2nd edn W H Freeman

STICH, H.B. & LAMPERT, W 1981 Predator evasion as an explanation of diurnal vertical migration by zooplankton *Nature, Lond.* 293: 396 398

STICH, H.B. & LAMPERT, W 1984 Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated conditions of diurnal vertical migration *Oecologia* 61: 192–196

TAKADA, Y. 1996. Vertical migration during the life history of the intertidal gastropod *Monodonta labio* on a boulder shore. *Mar Ecol Progr Ser.* 130: 117–123.

UNWIN, D.M. 1980. Microclimate measurement for ecologists. Academic Press, London

VANNINI, M., CANNICCI, S. & RUWA, K. 1996. Effect of light intensity on vertical migrations of the tree crab, *Sesarma leptosoma* (Decapoda, Grapsidae). *J Exp Mar Biol. Ecol* 185 181–189.

VESSEY-FITZGERALD, D.F. 1972 Fire and animal impact on vegetation in Tanzania national parks. *Proc Tall Timb Centre Fire Ecol Conf* 11, 297–317.

WÜRTSBAUGH, W.A. & NEVERMAN, D. 1988. Postfeeding thermotaxis and daily vertical migration in a larval fish *Nature Lond.* 333: 846–848.

YOUNG, S. & WATT, P.J. 1996 Daily and seasonal vertical migration rhythms in *Daphnia*. *Fresh Biol* 36: 17–22.