Dispersion factors in the arboreal snail *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

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Sitala jenynsi snails from the University and Wazo populations of Dar es Salaam, Tanzania, were released on grass, and on forest terrain, in both regions during the dry (February, March) and the rainy seasons (April). Snail dispersion was assessed as weekly quadratic means and as the overall Diffusion Coefficient 0.423 m^2/week. The coefficient was enhanced by grassy habitats, continuous vegetation cover, absence of edible plants and rainy weather; conversely, dispersion was retarded by shrubs, vegetation discontinuities, presence of edible plants and dry weather. There were differences in the rate of dispersion between populations, snails from the University Campus being faster. In each release a broadly unidirectional dispersion was recorded. The populations in question, seasons and the direction of origin of the snails seemed immaterial to directionality of dispersion. The dispersion rates of *Sitala jenynsi* exceeded those of the helicids *Cepaea nemoralis* and *Theba pisana* and of the partulid *Partula taeniata*. While observed dispersion rates of *S. jenynsi* may warrant the mixing of individuals in a population, they seem insufficient to facilitate appreciable migration of snails between neighboring populations.

Introduction

Drastic spatial changes in the morph-frequencies of adjacent populations have been reported in several species of land snails (Lamotte 1959; Owen 1965; Clarke 1968; Jones 1973; Cowie 1984a) Explanations of these distributions invoked genetic sampling drift (Goodhart 1963; Hickson 1972), the founder process (Mayr 1963) and natural selection either by the external environment (Cain & Sheppard 1954; Cain & Currey 1968) or by the internal environment (Clarke 1968; for a review, see Jones, Leith & Rawlings 1977).

Due to prolonged periods of drought in some years and the land-clearing activities by humans, populations of the arboreal snail *Sitala jenynsi* (Pfr.) undergo considerable reductions in numbers (Kasigwa 1975), ideal situations for the occurrence of genetic drift. There is also evidence to suggest that the snail, through the agency of the annual fires, is being reduced into founder stocks centred on the 'island' thickets which survive the fires; an island thicket is equivalent to a *deme* – an effectively panmictic aggregation of organisms which is spatially discrete and lasts for at least one breeding season. Assuming the population was originally genetically homogeneous, subsequent heritable differences between the progeny of different demes will depend mostly on random genetic drift, genic and gametic combination events intrinsic in each deme, the selective environment and the duration of inter-isolation preceding deme conjunction.

This article documents the dispersion of *Sitala jenynsi* at presumed maximum dispersion rates, and the extrinsic factors influencing the dispersion. Then it asks whether, given maximum dispersion rates, founder populations inter-isolated by small distances, could remain isolated long enough to undergo genetic divergence before dispersion-facilitated gene-flow sets in. In this account dispersion is used in the sense of Platnick (1976), namely, the regular movement of individuals, usually over short distances, in active response to intrinsic and/or extrinsic factors (Williamson, Cameron & Carter 1977; Peake 1981; Wipfli, Peterson, Hogg & Wedberg 1992). The term 'dispersal' (*sensu* Baker 1978), the passive and usually accidental migration of an animal as initiated and maintained by environmental agents (see Rees 1965; Athias-Binche 1993), may not accurately apply to the present study.

Methods

Adult *Sitala jenynsi* snails of the same generation (7.5–10.0 mm in shell diameter) were collected from the Mosque forest within the University of Dar es Salaam's main campus and from the airfield at Wazo Cement Factory (Figure 1). The two regions are almost central in the latitudinal range of the species; they are about 14 km apart in central Coastal Tanzania (6^{0} 28' - 32' South by 39^{0} 13' - 38' East). After collection, snail shells were marked at a sutural point using enamel ink Scraping the periostracum before marking was avoided as shells of the snails from the university campus are very thin and liable to fracture. The enamel mark lasted over three months, well beyond the duration of the experiment, even without paint reinforcement. Snail handling and marking were carried out between 10.00 and 15.00 hours, the period when *S. jenynsi* is most quiescent (Kasigwa 1999). The snails were released in the evening (18.00 19.00 hrs) before their nocturnal periods of activity. Release consisted of placing individual snails withdrawn into their shells onto 2 × 2 cm grids marked on a 1 × 1 m green card-board quadrat. The quadrat, with its snails equidistant from one another was then either attached to shrubs at 1.5 m height from ground surface or located on a lawn of 15–20 cm grass height; the snails thus became free to disperse from a central aggregation. The minimum distance from the centre of release to the shrub boundary was 36 m while that to the lawn margins was 25 m. After a minimum of 24 hrs the new position of each snail was

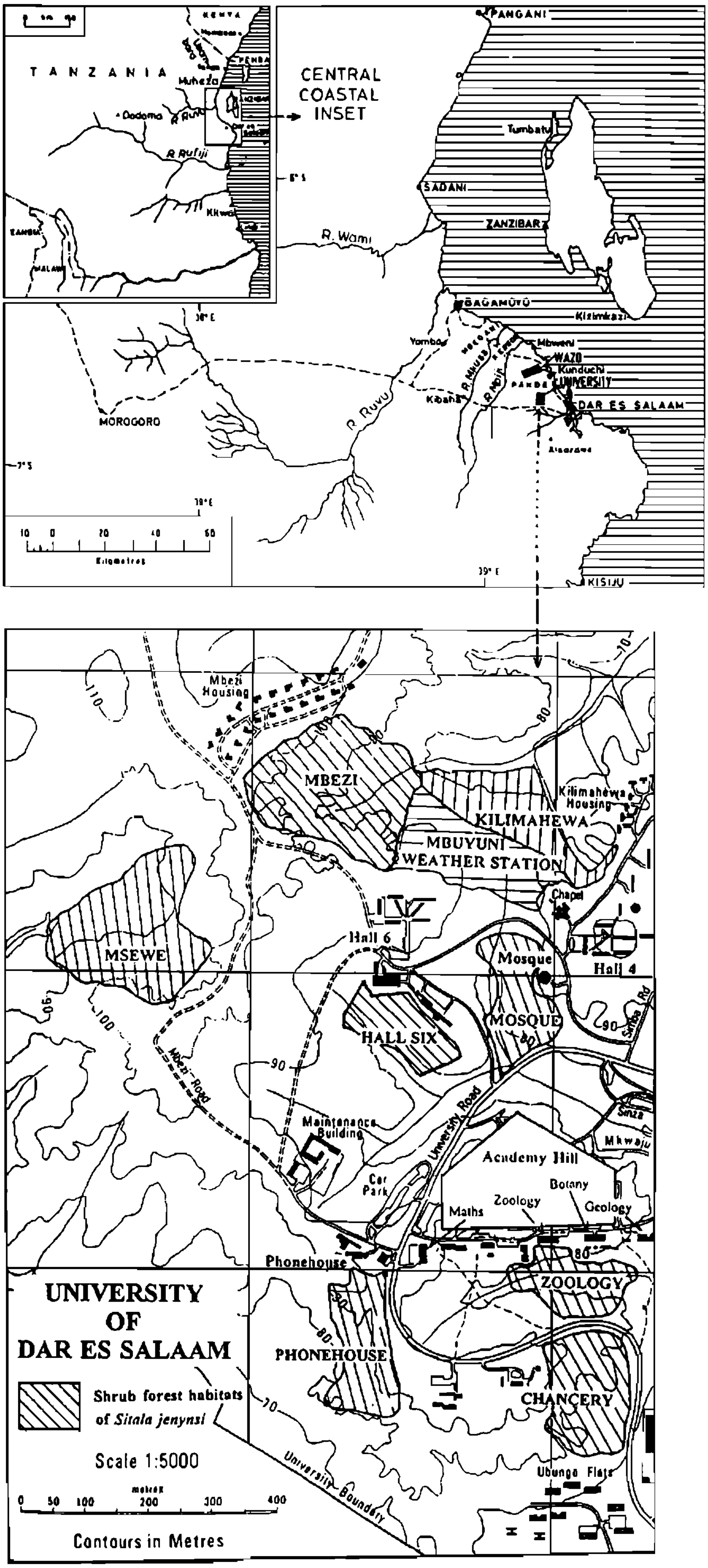

Figure 1 Central Coastal Tanzania and the University of Dar es Salaam, showing the localities mentioned in the text

Table 1 Details of *Sitala jenynsi* released during studies on snail dispersion

Release reference	No. and source locality of snails	Release site and dominant flora	Season, release duration in days and (no of sampling occasion)	Least no of snails recovered
1R	75 University Mosque	University lawn *Eragrostis aethiopica*	Rainy April 8 (7)	48
2R	60 University Mosque	University shrubs *Pluchea dioscoridis*	Rainy April 14 (7)	43
3R	90 Wazo Airfield	Wazo lawn *Cymbopogon* spp	Rainy April 15 (14)	50
4R	75 Wazo Airfield	Wazo shrubs *Markhamia zanzibarica*	Rainy April 18 (8)	38
1D	50 University Mosque	University lawn *Eragrostis aethiopica*	Dry February 13 (10)	26
2D	106 University Mosque	University shrubs *Pluchea dioscoridis*	Dry February 21 (3)	41
3D	143 Wazo Airfield	University lawn *Eragrostis aethiopica*	Dry March 14 (13)	15

measured as the straight-line distance from the common point of release. Information regarding release reference code, snail number and origin, release site, vegetation, season, duration of release and the re-capture occasions are summarised in Table 1.

The Quadratic mean and the Diffusion Coefficient were applied to express the dispersion data. In the quadratic mean (or root mean square) dispersion (D) equals $^2\sqrt{[(\Sigma d^2)/N]}$, where d is the linear distance between the release point and the recapture point of an animal and N is the number of animals recaptured (Clark 1962). Generally, the chance of encountering a dispersing animal decreases the farther one searches from the point of release. For animals in the same release, those which disperse in the vicinity of the release point have a higher probability of being discovered in comparison with their faster moving counterparts. Should dispersion tend towards a normal distribution (see Figure 2) the arithmetic mean ($\bar{x}$) would fall left of the actual mean because the former statistic ignores the disparate chances of snail discovery in the dispersion range. A correction for the undiscovered animals, most of which occur in the periphery of the dispersion range, is contained in the quadratic mean (D). This measure of central tendency usually exceeds the arithmetic mean and is an efficient estimator of dispersion rates.

The Diffusion Coefficient $\sigma^2/(2t)$ is the variance of dispersion distances divided by twice the dispersion time. The time variable in the divisor reduces the dispersion variance and produces near constant results regardless of occasional spuriousness and duration of release.

Results

It was logistically impossible to measure the performance of all the releases on the same days. The D-values obtained are presented in Figures 3 and 4 and the Diffusion Coefficients in Table 2.

Effects of plant habit, floristic composition and weather on snail dispersion

The snails of 1R and 2R originated from the same Mosque population and were released during the April rainy month at

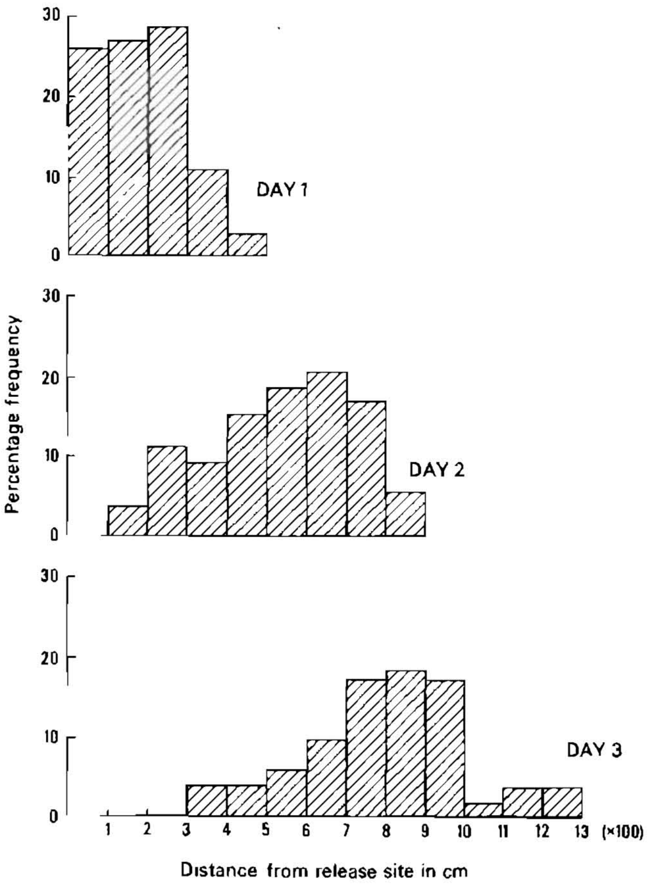

Figure 2 An instance of the horizontal distribution of *Sitala jenynsi* dispersion of 1R, release 1 on a lawn in the rainy season during the initial three days

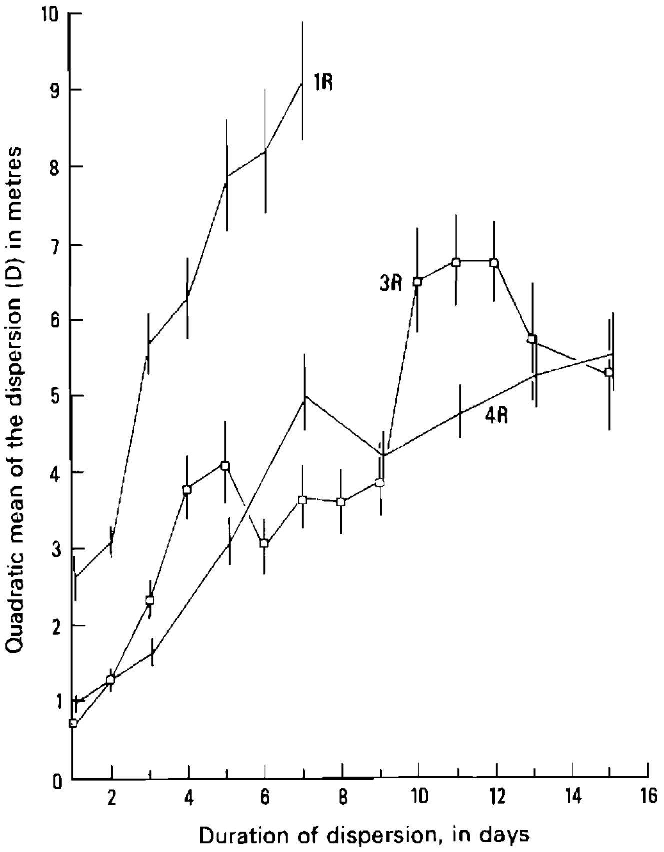

Figure 3 Dispersions of *Sitala jenynsi* on University lawns and shrubs during dry weather and rainy weather. Vertical bars indicate the 95% confidence intervals of quadratic means (D). 1R, 3R and 4R are release references, details of which are given in Table 1

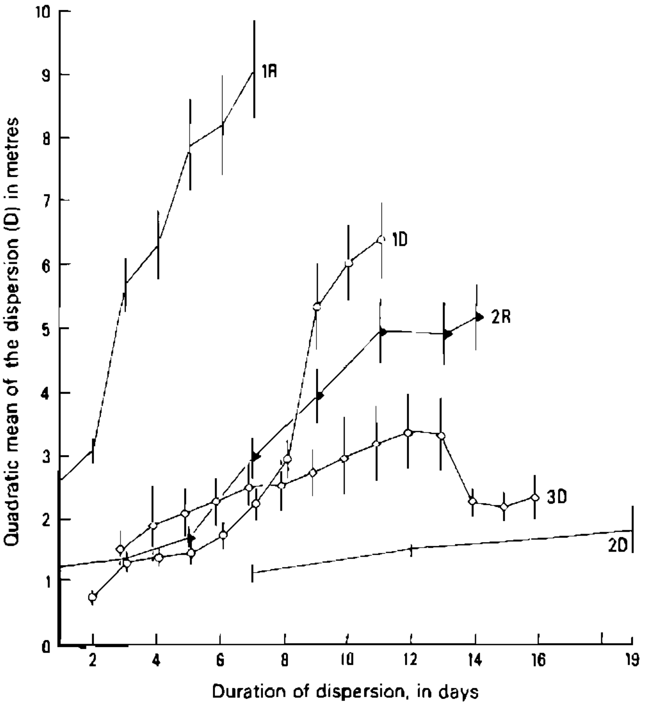

Figure 4 The dispersion of *Sitala jenynsi* on Wazo lawns and shrubs during rainy weather. Vertical bars indicate the 95% confidence intervals of quadratic means (D). 1R, 2R, 1D, 2D and 3D are release references, details of which are given in Table 1

the University (Table 1). Whereas the release on a lawn (1R) attained a D-value of 9.0 m within a week, the release on shrubs (2R) managed some 3 m in the first week and just 5 m by day 14 (Figures 3 & 4); the two dispersion rates differ significantly at $p \leq 0.05$. The corresponding Dif. Coefs. were 3.02 m^2 per week (i.e. potentially 157.28 m^2 per year) for the release on grasses and 0.77 m^2 per week (or 39.63 m^2 per year) for the release on shrubs (Table 2). As for the release during the dry season on lawn (1D) compared with the release on shrubs (2D, Table 1), again the latter snails showed significantly slower dispersions, lagging some 4 m behind by the second week (Figure 4).

The release of Wazo originated snails during the rainy season on Wazo shrubs (4R, Table 1) produced spectacular results, their initial weekly dispersion rate (Dif. Coef. 1.0 m^2) being remarkably high for a release on shrubs. However, when the snails moved beyond *Markhamia zanzibarica* (DC.) Engl. shrubs and their climber *Bonamia poranoides* Hall f. and on to *Hoslundia opposita* Vahl., *Suregada zanzibariensis* Muel. Arg. and *Premna chrysoclada* Boj. Guerke, their dispersion rate declined (Dif. Coef. 0.516 m^2/week, see Table 2). Both *Markhamia zanzibarica* and *Bonamia poranoides* are not edible to *S. jenynsi*; the snails actively move away from inedible plant species (Kasigwa 1991).

As for the effects of the weather, the relevant releases are snails from the University Mosque population released on the same site of a lawn during the rainy weather (1R) and the dry weather (1D, in Table 1). 1R attained 9 m in a week as compared either to 1D's 2.2 m during the same interval of time or to 6.4 m on the eleventh day (Figure 4). Steady showers on days 3, 5 and 7 of 1R were associated with maximal increments in D-values relative to the dispersions on showerless days 2, 4 and 6 (Figure 3). In addition, a rare shower on day 9 during the dispersion of 1D promoted the daily mean D-value from 0.36 m to 1.35 m. Snail dispersions on shrubs were also enhanced by rainy weather: the greatest D-value of 2R was 5.19 m (Dif. Coef. 0.77 m^2 per week), a significant contrast to 1.75 m (Dif. Coef. 0.08 m^2 per week) for 2D during the same duration of dispersion (Figure 4 and Table 2).

Population characteristics and snail dispersion

A comparison of 1R (the rainy season release on University lawn) with 3R (the rainy season release on Wazo lawn) reveals constantly higher dispersion rates by 1R (Figure 3). The vegetation in the dispersion ranges were mainly *Eragrostis aethiopica* Chiov. at the University lawn and *Bothriochloa* sp., *Cymbopogon* spp. and *Dactyloctenium* sp. in the Wazo Airfield; these grasses are only moderately edible (Kasigwa 1991). The D-values of 9.0 m for 1R and under 4.0 m per week for 3R differ sufficiently to merit explanations beyond the floristic differences at the release sites.

1D (University *S. jenynsi*) and 3D (Wazo *S. jenynsi*) both released during the dry season at the University lawn also suggest population differences in snail dispersion: after an initial Dif. Coef. of 0.471 m^2, a probable effect of the transfer, 3D settled to an overall Dif. Coef. of 0.333 m^2/week. 1D, on the other hand, had a slow start (0.241 m^2/week) but

Table 2 The daily Diffusion Coefficients {[$\sigma^2/(2t)$] cm^2} of released *Sitala jenynsi* and (in brackets) the numbers of snails recorded

	Diffusion coefficient						
Days following date of release	1R	2R	3R	4R	1D	2D	3D
1	2993(60)	1363(50)	869(92)	1135(74)	–	-	–
2	1159(59)		1118(73)	–	241(42)	–	–
3	4359(53)	737(52)	968(74)	818(60)	506(41)	-	875(21)
4	3964(52)	–	3853(63)	–	384(37)	–	1242(11)
5	5578(49)	747(48)	4684(59)	1729(61)	300(37)		469(12)
6	6711(51)	–	1400(53)	–	294(35)	–	411(14)
7	5483(51)	104(50)	1976(63)	1973(51)	339(34)	149(41)	366(15)
8	–	–	1737(57)		444(32)	-	347(14)
9	–	1345(51)	1364(42)	665(53)	1566(26)		293(15)
10	–		3649(59)	-	1291(28)	-	725(15)
11		1380(48)	2674(64)	614(46)	1212(28)	–	645(15)
12	-	–	1872(64)	–	–	99(64)	521(14)
13	–	1042(46)	3313(56)	798(46)	-		447(15)
14		1097(46)	–	–			65(15)
15		–	2688(58)	870(38)	–	–	74(17)
16	–	–	–				72(17)
19	–	-		–	–	90(19)	–
95% Confidence Limits							
L_1	3052.02	924.21	1791.94	746.31	366.02	83.51	313.63
X	4320.79	1094.1	2366.18	1075.30	657.60	112.85	475.05
L_2	5589.57	1262.0	2940.43	1404.29	949.18	142.18	636.45
Weekly Diffusion Coefficient, in m^2							
	3.025	0.766	1.656	0.753	0.460	0.079	0.333

adopted a higher overall Dif. Coef. (0.460 m^2 per week), thus dispersing faster than the snails from the Wazo population (Table 2). The latter snails have a larger body and shell mass (Kasigwa 1975) although these parameters may have little bearing on relative speeds. It would be useful to determine dispersion rates as related to the age (= size) of snails, as in some cases of *Helix pomatia* (Hansson 1991).

The onset of movements which are of no consequence to snail dispersion is also relevant to the population differences. Consider dispersion, expressed here by quadratic means, as the mean linear distance between the release point and the recapture points of a large sample of animals. Suppose the sample has already achieved r, a certain dispersion distance. As long as the animals move along the circumference and maintain the same distance from their release point, their dispersion would register as r, the radius denoting the circumference. Nor can changes in dispersion occur if the animals oscillate on either side of the circumference. I refer to such movements as 'ineffective migration' in the sense that they are of no consequence to dispersion. Snails from the Wazo population attained dispersion plateaux during the period of observation (see 3R and 3D in Figures 3 and 4); they reached about 4 m on average, after which distance they engaged in ineffective migration. Snails from the University population on the other hand did not show ineffective migration (see 1R and 1D in Figure 4). Their D-values exceeded 6 m and were dispersing effectively throughout the period of observation.

Direction of dispersion

Snails adopted directional migration, occurring more abundantly in some quadrants from about day four following their release. In the releases on grasses the quadrants eventually narrowed into small sectors whereas the releases on shrubs described bigger sectors of the compass. Table 3 is a record of the development of unidirectionality for 1R and 3R, the compass quadrants named clockwise; snails found in each quadrant are indicated as a percentage of the total number of snails recorded on a particular day. In 1R the snails dispersed progressively into quadrant 3 (sector radials 185°–235°) whereas in 3R the snails selected quadrants 1 and 2 (sector radials 76° –126°). The overall direction of dispersion on the last day of the experiment is represented diagrammatically in Figure 5, the radii encompassing the dispersing snails within the subtended angle.

Discussion

Snail dispersion as influenced by plant habit and flora

Reference to 1R *versus* 1D (Figure 4 and Table 2) justifies the conclusion that plant habitat exerts considerable effect on the

Table 3 Directional dispersion of *Sitala jenynsi* indicated as the proportion of snails in a compass quadrant on each day of sampling

	Dispersion day	No of snails recorded	Percentage of snails in Quadrant			
			1	2	3	4
1R	1	73	9	32	52	8
	2	60	4	25	70	1
	3	58	2	21	78	–
	4	54	–	10	89	–
	5	52	–	4	97	–
	6	48	–	–	100	–
	7	52	–	–	100	–
Mean daily rank of Quadrant			3	2	1	4
SD			0	0	0	0
3R	1	93	27	20	22	30
	2	76	24	29	25	22
	3	77	25	32	17	26
	4	70	31	48	14	8
	5	64	33	48	10	8
	6	59	28	53	11	7
	7	64	23	60	9	7
	8	59	18	68	8	8
	9	50	12	75	10	4
	10	62	12	75	8	3
	11	64	10	76	9	6
	12	50	14	73	6	6
	13	58	12	77	6	3
	15	58	14	78	5	5
Mean daily rank of Quadrant			2.07	1.21	3.11	3.61
SD			0.267	0.802	0.446	0.813

dispersion of *S. jenynsi*. Shrub habitats reduce the rates of dispersion because in such vegetation the snails cover long distances three-dimensionally while achieving dispersion, the linear distance between the animal's release and recapture points. Short grasses and herbs, on the other hand, enhance snail dispersion.

The effect of flora on snail dispersion is positively related to the edibility of the plant. The snail seeks suitable plant species for nocturnal browsing and then rests on the browsed plant (Kasigwa 1991). Inedible plants tend to be avoided, the snail then proceeding to species stands of dietary appeal. It is considered that the fast rates of dispersion elicited on *Markhamia zanzibarica* and *Bonamia poranoides* were manifestations of avoidance behaviour rather than spontaneous migration from a central aggregation. In addition to affecting the rates of dispersion, avoidable flora could alter the direction of dispersion by obstructing a dispersing trend. A corresponding case of positive correlation between vegetation (? food and shelter) and the microhabitat distribution of *Cepaea nemoralis* was reported by Chang & Emlen (1993).

The dispersion rates of *S. jenynsi*, a nearly permanently arboreal snail, are probably nearer to 2R and 2D than to 1R and 1D. The mean dispersion rate in the shrubs during both seasons; $\{[\sigma^2/(2t)]_{2R} + [\sigma^2/(2t)]_{2D}\}/2$, therefore estimates the dispersion of *S. jenynsi* as 0.423 m^2 per week i.e. 4225 cm^2/wk or 21.97 m^2 per year. However, on an ideal low mown lawn, the snail could cover, $\{[\sigma^2/(2t)]_{1R} + [\sigma^2/(2t)]_{1D}\}/2$, i.e. 1.743 m^2/wk or 90.6 m^2/year. This is possibly the maximum dispersion rate attainable.

Population and weather factors and the direction of dispersion

Populations differed in the rates of dispersion and in the ultimate distances attained, snails from the University being the faster. The relative slowness of Wazo snails (suggesting reduced intermixture of individuals) might relate to the greater spatial variation in the distribution of morph frequencies which Kasigwa (1975) reported in that region. It would be desirable to release Wazo snails at Wazo itself during the dry season and at the University during the rainy season, in addition to releasing the snails from the University campus at Wazo during both seasons. The four reciprocal transfers would make comparisons between populations more comprehensive. The transfers were deliberately omitted in this study to avoid the risks of post-transfer mortality and of artificially contaminating the natural populations at either region.

The positive effects of the humid weather on snail dispersion rates possibly arose from correspondingly high relative humidity, during which weather the snails remained active and mobile longer. A related study has demonstrated that the vertical migration of snails regresses negatively on relative humidity (Kasigwa 1999). As an arboreal animal descends from plant heights it tends (from multiplanar) towards uniplanar movement, thereby acquiring faster dispersion rates. On the other hand, it should be noted that heavy showers, through physically pattering on snail bodies and facilitation of surface pools, could block directional dispersion and lead to ineffective migration: release 3R during the heavy rains on days 5–9 may have thus been affected (see Figure 3). A moderately heavy rain could effect the greatest dispersion rates. Dry weather, through its generally high evaporative potentials, causes the snail to withdraw into stationary quiescence rather than remain active for dispersion (Cameron 1970).

The direction of dispersion was generally locality specific. The source from which the released sample had been collected appeared to have no bearing on the direction of dispersion. Snails of 3R, for instance, did not disperse into all directions though they had been collected from all over the airfield and released at a central point: instead, they moved into a particular direction irrespective of their sites of origin. It is possible that *S. jenynsi* does not exhibit homing behaviour as do *Achatina*, *Ariolimax*, *Helicella* and some other pulmonates (Edelstam & Palmer 1950; Pollard 1975; Cook 1979; Rollo & Wellington 1981; Chelazzi, Le-Voci & Parpagnoli 1988; Tomiyama 1992).

Falling rain and prevailing wind are presumably the two major seasonal factors which have localised direction. That the cause of directional dispersion was not related to the seasonal factors is suggested by the directional similarity of the dry (1D) and of the rainy (1R) season releases of snails from the University Campus (Figure 5b). The snails originating from Wazo (3D) also orientated southwardly, overlapping the

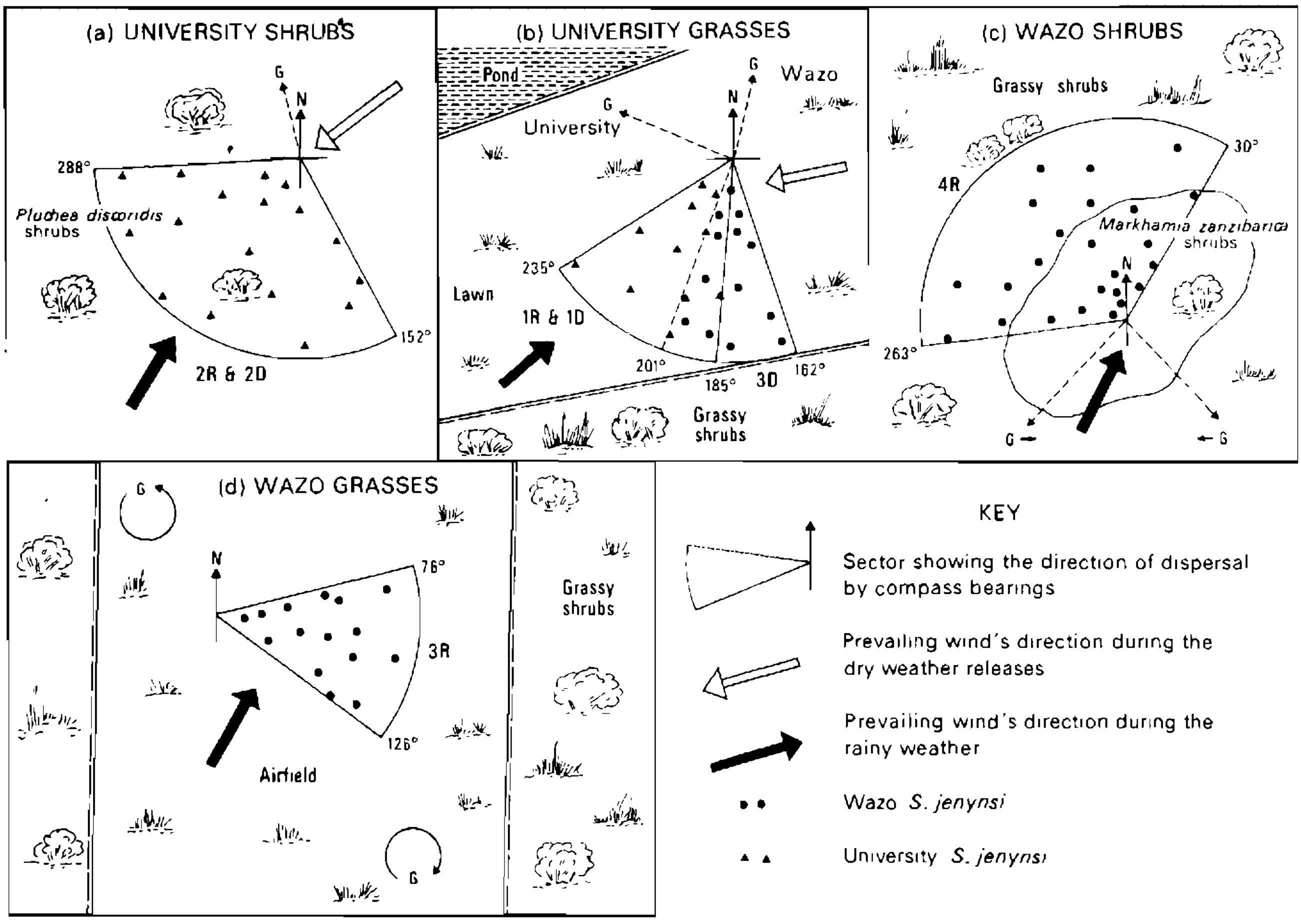

Figure 5 Directional dispersion of *Sitala jenynsi*

other two sectors (Figure 5b). Moreover, the directions of the releases during the rainy season (1R and 2R) and the South-West Monsoon winds were incongruous, snails generally adopting the compass sectors of 1D and 2D, the earlier releases of the dry season. Nor did the dispersions on Wazo shrubs and Wazo grasses suggest directional concordance either with falling rain or with the prevailing wind (see Figures 5c and 5d). The causes, factors and process of directional dispersion are subjects of a separate investigation (Kasigwa 1999). Some directionality of dispersion is known also for released *Cepaea nemoralis* (Goodhart 1962).

Dispersion rates of *S. jenynsi* and of other snails

The mean dispersion rates of *S. jenynsi* (= 0.423 m^2/week) can be compared with the reported rates of other externally polymorphic snails. Several species of the genera *Cepaea*, *Partula* and *Theba* are also polymorphic for shell colour and patterning. In addition, each species shows spatio-temporal patterns in the distribution of its shell morph frequencies usually in form of dynamic equilibria, genetic clines and area effects. Species under these genera have therefore been invaluable for micro-evolutionary studies (Cain & Currey 1968; Cook 1971; Murray & Clarke 1980; Cowie 1984b; Muruke & Nasuwa 1986; Kawasange & Luena 1994; James & Kyomo 1997). The diffusion rates of *Cepaea nemoralis* L. were determined by Goodhart (1962; see also Cameron & Williamson 1977). Hickson (1972) calculated the rates for *Theba pisana* Muller, and those of *Partula tueniata* are derived from Murray & Clarke (1984). The latter three snails have fairly low dispersion rates (Table 4). Their life cycles are longer than that of *S. jenynsi*, namely about four years for *C. nemoralis* and *P. taeniata* and two years for *Theba pisana* (Lamotte 1959; Murray & Clarke 1984; Cowie 1984b). Relative to *S. jenynsi*, *C. nemoralis* and *T. pisana* have larger shell sizes, assuming that size may have an inverse bearing on dispersion rate. They measure 20–30 mm in diameter (*C. nemoralis* Cook & O'Donald 1971; Lamotte 1959; Cook & Peake 1962) and 17-20 mm (*T. pisana*: Hickson 1972, Cowie 1984b). *P. taeniata* is more conical than helicoid, and measures 20 mm high by 15 mm wide (Crampton 1932). *C. nemoralis* is found in mixed habitats including the grasses, hedgerows and forests of the temperate regions (Cain & Sheppard 1954; Lamotte 1959) whereas *T. pisana* inhabits the grasses and herbs of coastal subtropical sand (Bishara, Hassan & Kaliny 1968; Cowie 1984a, 1984b). Relatively smaller sized *S. jenynsi* (11.0 + 1.5 mm shell diameter) have only a year-long life span and this is not subject to the harshness of winter; the snail is active for longer periods, undertaking neither aestivation nor prolonged quiescence. It would take *C. nemoralis* about two years and *T. pisana* 2.4 years to cover the optimum area (i.e. 22 m^2) which *S. jenynsi* presumably covers in its twelve months of life.

Although the rates of dispersal of *S. jenynsi* exceed those of the other snails by a factor of two, they are nevertheless too

Table 4 A comparison of the dispersion rates of *Sitala jenynsi*, *Cepaea nemoralis*, *Partula suturalis* and *Theba pisana*

Snail	Time in weeks	$\sigma^2/(2t)$ m^2/wk	Variance	Mean
S. jenynsi	0–1	393	904	.426
	1–2	461	865	–
C. nemoralis[1]	0–4	.501	4.01	–
	4–14	104	2.09	.221
	14–51	058	4.27	–
P. taeniata[2]	1–2	027	–	–
	3–4	.032	192	.195
	5–6	.389	–	–
	7–8	331		–
T. pisana[3]	0–1	079	159	–
	1–2	.035	071	175
	2–3	410	821	–

Sources

1 Goodhart (1962), Cameron & Williamson (1977)

2 Murray & Clarke (1984)

3 Hickson (1972)

low to facilitate rapid intermixture of adjacent populations. For instance, it would take nearly five years (that is five generations) for two colonies of *S. jenynsi* located 200 m apart in a forest to merge. This time interval is arrived at through two simplifications, firstly, that a spatially continuous vegetation cover persists through the period of mutual isolation and, secondly, that the different age groups of a generation adopt dispersion rates similar to those of adult *S. jenynsi* studied here. Whether the eventual conjunction and admixture of neighbouring populations would lead to population de-differentiation remains a puzzle. Some populations can diverge parapatrically even in the face of considerable gene flow as, for instance, under (i) large selection differentials between neighbouring environments (Jain & Bradshaw 1966; Cook 1971; Adams 1975), (ii) geographically uniform selection gradients (Murray 1972; Endler 1973, 1977), (iii) disruptive selection in a heterogeneous environment (Maynard Smith 1966, Dickinson & Antonovics 1973; Halkka 1978) and/or (iv) stasipatric chromosomal arrangements (White 1978; Hammond 1981). On the other hand, the genetic differentiation of other populations seems retarded and/or nullified by gene flow as, for instance, under a high immigrant to native ratio (Mayr 1979) and low selection coefficients (Wright 1969; Rohlf & Schnell 1971). The case with *S. jenynsi* is one where the territories of (and distances between) different populations are small; the environmental heterogeneity and selection differentials entailed are probably also minimal, within the coefficients which foster effective (de-differentiating) gene flow.

Some limitations of using dispersion studies in the estimation of gene flow (see Mallet 1986) may be inapplicable to the present case of *S. jenynsi*; this is largely because the degree of snail recapture was fairly high, rendering greater accuracy to the dispersion variances. Secondly, simultaneously hermaphroditic *S. jenynsi* has no demographic complications that are posed by gonochorism, the separateness of the sexes. It may owe, at least in part, to low magnitudes of snail exchange and gene flow that some neighbouring localities interspaced by just 100 m of shrub discontinuity show heterogeneity in the frequencies of their genetic morphs (Muruke & Nasuwa 1986; Kawasange & Lucena 1994, James & Kyomo 1997; Baur & Baur 1990).

A behaviour which may hamper dispersion is that *S. jenynsi* snails are not aggregative (compare *Theba pisana* and *Helicella virgata*. Hickson 1972; Pomeroy 1968; Cowie 1984b). In the Zoology forest (Figure 1), a densely inhabited locality, the mean direct distance to the nearest neighbour was 64 cm among juveniles and 70 cm in the adults outside the breeding season (Kasigwa 1975). The dispersion of individuals who are already interspersed is likely to be lower than that of aggregated individuals, simply because the former engage more into ineffective migrations (analogous to random molecular diffusion). In terms of dispersion (from a release point) such behaviour, however intensive, registers nil dispersion. The aggregated individuals, on the other hand, tend to disperse outwardly either omnidirectionally (as in response to high density) or uni-directionally (such as towards a localized resource). In contrast to aggregative behaviour, therefore, interspersive behaviour may prove to be a factor retarding snail dispersion.

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