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RESEARCH NOTES

Spatial differentiation of allozyme frequencies in a subdivided population of the land snail *Helix aspersa*

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Many evolutionary forces like selection, genetic drift or migration can be taken into account to explain the genetic variability among subdivided populations. Because of their limited ability for dispersal, land snails live in colonies which are often subjected to a strong local differentiation. For fragmented agricultural habitats, in which frequent and severe bottlenecks occur, the successful colonization by *Helix aspersa* suggests an organization of colonies in semi-isolated demes (metapopulation).[1] In order to investigate the structure of the genetic variability among natural populations of *H. aspersa* located in an anthropic environment, autocorrelation statistics were used to analyze the spatial isozyme differentiation in 14 sampled populations along a transect in the polders of the bay of Mont-Saint-Michel, Western Brittany (Fig. 1).

From an initial survey based on 12 enzymatic systems, the most polymorphic loci (Lap-2, Aat-1 and Est-3) were retained to be tested for autocorrelation. Electrophoresis techniques used are described in detail in Guiller *et al.*[2] Spatial heterogeneity was firstly tested for all loci among populations with an exact test of differentiation provided by the GENEPOP program.[3] In order to detect an eventual structure in heterogeneity of allozyme frequencies, a correlogram was generated for each allele considered by computing Moran's I for all pairs of sampling locations falling within one of each geographic distance ($=dm$) class created.[4] A value of 500 m was chosen and ten distance classes were considered: 500 m (0–500 m) to 5000 m (4500–5000 m). A test for a significant autocorrelation was obtained by comparing the observed value of I with the expected value $E(I) = -(n-1)^{-1}$ under the null hypothesis of no spatial structure.[4] Significance of each correlogram was tested with a Bonferroni procedure.[5] Moreover, rare alleles at loci Lap-2 and Aat-1 (respectively Lap-2^{92} and Aat-1^{110}) were excluded from analyses in order to maintain statistical independence of tests.[6] For loci with two alleles (Aat-1), one gene frequency needs to be analyzed.

Populations were also connected according to the following criteria:

– *cg*: Gabriel-connected graph[7] which leads to a global Moran's I;
– *dcg*: minimal distance between two locations, considered as the least number of edges sufficient to connect these locations according to the Gabriel network.[4] Such a connection criterion has the advantage to be a real distance which avoids problems related to an irregular sampling grid.

The Mantel multivariate approach was also used to estimate linear relations[8] between genetic distances and *dm*, *cg* (test for low order spatial autocorrela-

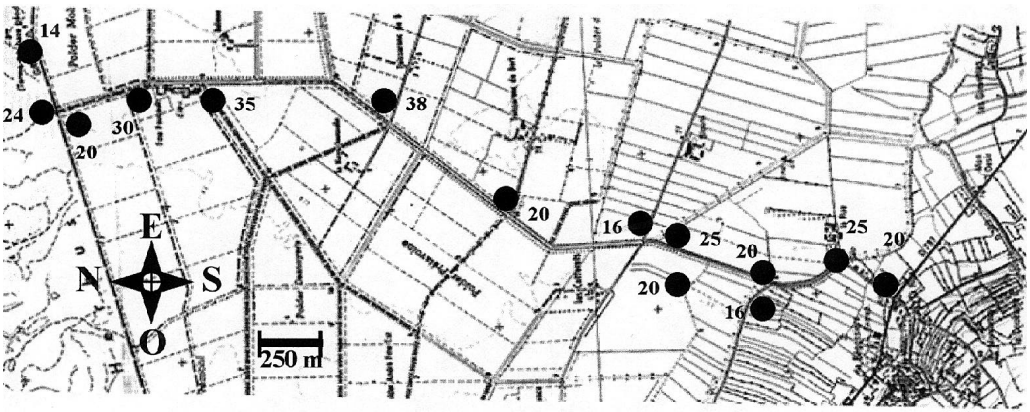

Figure 1. Population locations and sample size.

tion) and *dcg*. For each comparison, a normalized Z was calculated and its significance was tested by randomly permuting (10000 permutations) the rows and columns of one of the matrices considered.[9] This procedure was carried out by a program of the NTSYS-pc package.[10]. In the case of *dm*, all normalized Z obtained were plotted against geographic distance in order to obtain a Mantel correlogram which can be used to test for isolation by distance.[11] Nei's[12] genetic distances were computed for each pair of populations and used for the construction of a matrix of genetic distance. Two metric distances were also employed as genetic measurements of population differentiation: the Cavalli-Sforza & Edwards'[13] chord distance and Rogers'[14] distance. As complementary information, inbreeding and subdivision were tested using estimators of F-statistics according to the Weir & Cockerham[15] procedure.

A significant heterogeneity was shown for all loci among populations ($P<0.001$), indicating a differentiation at the scale of the studied area. In addition, maps of allele frequency surfaces (not shown), and the average inter-deme fixation index confirmed the differentiation between colonies (Table 1). Average genetic differentiation reflected a significant relationship to geographic distance (Table 2). However, tests of association between geographic connections and F_{st}, which would be a better indicator of genetic distance at a microgeographic scale, yielded only one significant correlation with the Gabriel network (*cg*) (Table 2). It would indicate an overall spatial autocorrelation according to a 'step-by-step' communication between colonies. Mantel correlograms showed the same profiles for all genetic distances considered, with very closed values of *rz* when Nei's genetic distances and inter-deme fixation indices were compared (Fig. 2). Nevertheless, the shape of these Mantel correlograms illustrated random fluctuations of *rz* and failed to reveal a decline of genetic similarity with increasing geographic distance. This lack of relationship between geographical and genetic distance, as illustrated in Fig. 2, could reflect the fact that populations are not at equilibrium,[16] because of the recent colonization of the polders, the last of which was created only fifty years ago. An alternative hypothesis could be that this is due to the sampling scale which was inappropriate to detect a decline of genetic similarity according to an isolation by distance model.

Moran's I calculated with the Gabriel-connected graph revealed only one highly significant value for allele Est-3^{105} (Table 3). All correlograms based on Moran's I indicated a spatial structure at an overall significance level of $P<0.05$ (Bonferroni technique[5]), except for allele Lap-1^{100}. Some trends were apparent from examination of all the correlograms but exhibit non-parallel spatial structures (Fig. 3). Correlograms relative to alleles Est-3^{100} and Est-3^{105} showed a consistent pattern of high positive indices at short distance and next, a decrease with significant negative autocorrelations at far distances. It would indicate a progressive isolation of colonies with geographic dis-

Table 1. F-Statistics estimated over all the fourteen populations: means values per locus and standard deviate calculated by jackknifing among the samples; average index (standard deviate) calculated by jackknifing over all loci; 99% confidence interval (bootstrap). Bonferroni correction: *P < 0.05; ** P < 0.01; NS: non significant.

Locus	F_{is}	F_{it}	F_{st}
Lap-2	0.073 (0.042) NS	0.109 (0.037) *	0.038 (0.016) **
Aat-1	0.019 (0.073) NS	0.065 (0.073) NS	0.047 (0.030) **
Est-3	−0.090 (0.053) NS	− 0.026 (0.050) NS	0.059 (0.017) **
Mean (st.dev.)	0.003 (0.051) NS	0.050 (0.041) NS	0.047 (0.007) **
C.I. (99%)	(−0.089 ; 0.075)	(−0.023 ; 0.108)	(0.036 ; 0.060)

Table 2. Mantel's test based on all pairs of populations. Geographic connections: geographic distance (*dm*), Gabriel-connected graph (*cg*) and minimal distance between two locations according to the Gabriel network (*dcg*). CAV, ROG and NEI are respectively the matrices of Cavalli-Sforza & Edwards' chord distance, Rogers' and Nei's genetic distances; FST is the matrix of inter-deme fixation indice (*rz*: normalized Z; * P < 0.05; ** P < 0.01; NS: non significant).

	ROG	CAV	NEI	FST
		rz		
Geographic connection				
dm	0.233 *	0.347 **	0.185 *	0.164 NS
dg	−0.165 *	−0.177 *	−0.169 *	−0.161 *
dcg	0.269 *	0.243 *	0.233 *	0.204 NS

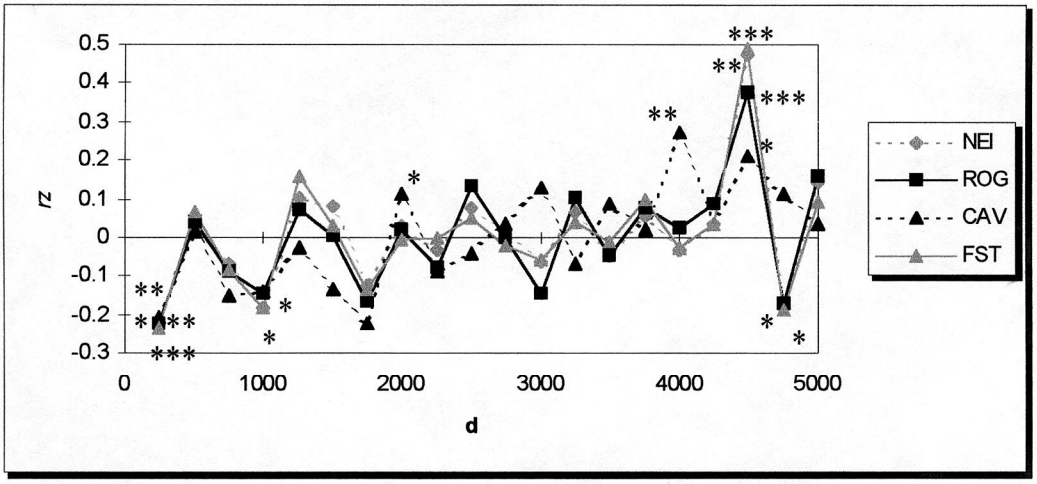

Figure 2. Mantel correlograms. Populations were connected within geographic distance classes of 250 meters. For each distance class, a normalized Z was calculated with the matrices of Cavalli-Sforza & Edwards' (CAL) chord distance, Nei's (NEI) and Rogers' (ROG) genetic distances, and the matrix of inter-deme fixation (FST) indice (*rz*: normalized Z; d: geographic distance (meter); *:P $<$ 0.05; **:P $<$ 0.01; ***:P $<$ 0.001).

Table 3. Moran's I computed on the basis of the Gabriel network (*cg*) (** P $<$ 0.01; NS: non significant).

Locus	I
Lap-2^{100}	−0.020 NS
Lap-2^{94}	−0.043 NS
Lap-2^{96}	−0.130 NS
Aat-1^{100}	0.028 NS
Est-3^{100}	0.335 NS
Est-3^{95}	−0.045 NS
Est-3^{105}	0.745 **

tance.[4,17,18,19] Considering the lack of independence between allele frequencies, one would expect a similar pattern of autocorrelation for Est-3^{95}. However, this allele seemed to exhibit random variations of Moran's I which were not congruent with those of Est-3^{100} and Est-3^{105}. In fact, these three alleles had approximately the same relative frequencies but when we considered the allele frequency surfaces, Est-3^{95} appeared to be randomly distributed in the studied area, whereas Est-3^{105} showed a consistent gradient from North to South. Such a decrease of Moran's I with increasing geographic distance was not observed for other alleles which exhibit a higher stochastic variation leading to a lack of similarity in correlograms. Furthermore, correlograms for alleles Est-3^{95} and Lap-2^{96} showed negative indices at the shortest geographic distances, that theoretically reflect spatially heterogeneous small patches in the environment.[17] The patchy and unstructured genetic variation observed at the loci Lap-2 and Aat-1 may also be related either to genetic drift or to an unpatterned heterogeneous selection,[17] which seems not to be a serious hypothesis in the context of this work. Indeed, there was no consistent observable microhabitat heterogeneity to suggest such small-scale selection. A stochastic interpretation involving several immigration events followed by founder effects could also explain clinal patterns reflected by alleles Est-3^{100} and Est-3^{105}, which might not be produced by clinal variation in selection. It would be more appropriate to consider a directional migration from an other population differing in such allelic frequencies.[18,19] However, the spatial scale of our studied area should be refined. Indeed, Moran's I statistics have high statistical power, and low stochastic and statistical variation, in cases where the spatial scale of sampling is within the area of a larger spatial pattern, i.e. as long as the spatial scale of sampling is smaller than the scale of spatial autocorrelation.[20,21] Within this context, Selander & Kaufman[22] and Sokal & Oden[4] showed a weak but significant spatial arrangement among subpopulations of *H. aspersa* over distance of less than 100 m and suspected an isolation by distance model involving random genetic drift and migratory events followed by diffusion. Otherwise, the number of loci considered in our study was too small to make precise inferences about the various evolutionary processes that could potentially generate the observed patterns and to make discrimination between these different forces. Moreover, it has been suggested that the statistical power and utility of spatial autocorrelation statistics for inferring biological processes are subject to caution, and that F-statistics should be more relevant and used instead.[23,24] However, this latter method requires averaging or lumping together subpopulations at one or more hierarchical levels, and values of F_{st} only measure the

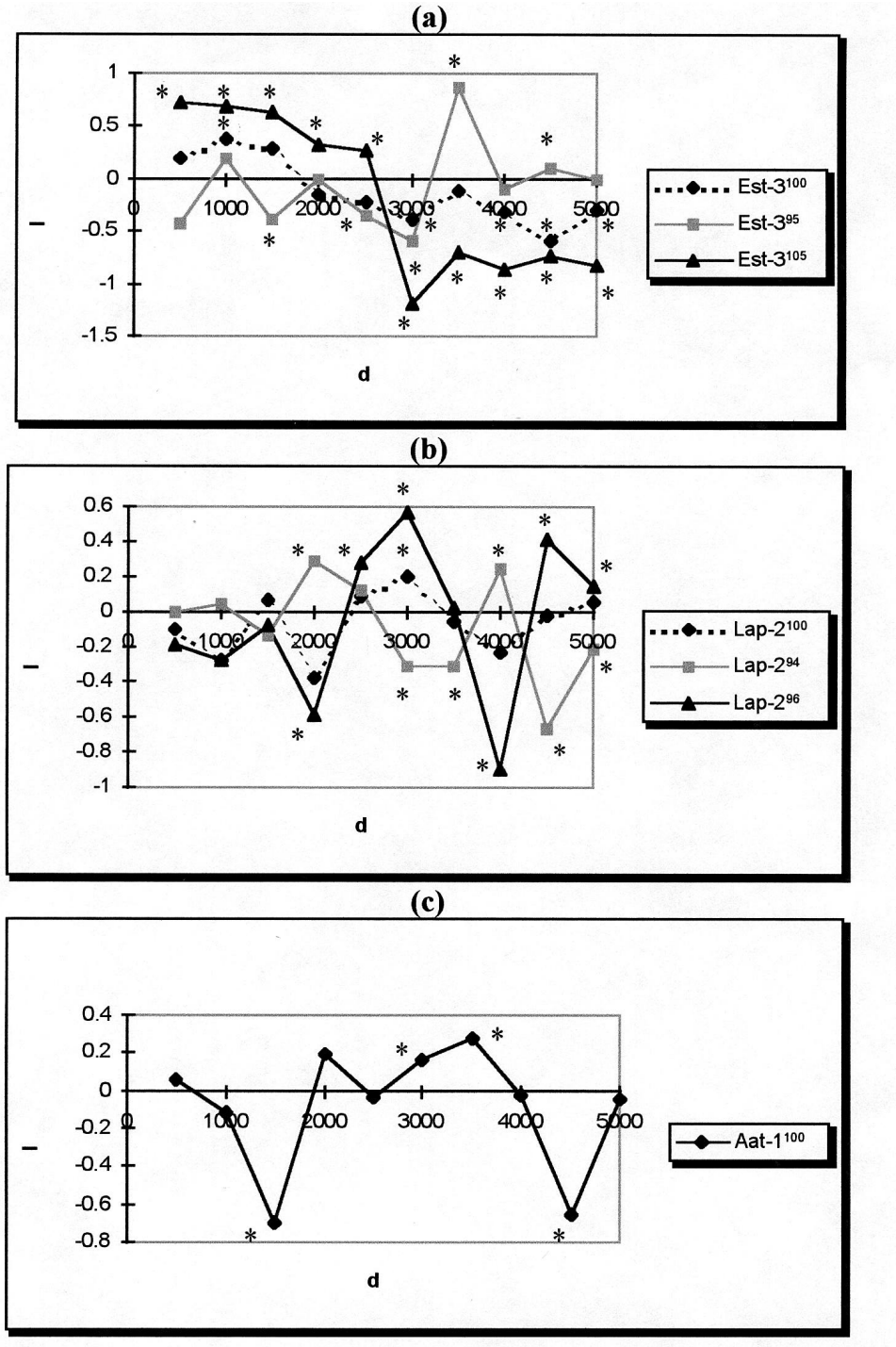

Figure 3. Correlograms for local variation patterns of allozyme frequencies in the 14 populations; (a), (b), (c) for loci Est-3, Lap-2 and Aat-1 respectively. I is the Moran's index and d the geographic distance (meter); significant autocorrelation coefficients ($P < 0.05$) are indicated by an asterisk.

spatial variance in gene frequencies. On the contrary, spatial statistics use the genetic information from all pairs of locations and measure aspects of spatial patterns. Moreover, simulations of Epperson & Li[21] have shown that spatial autocorrelation statistics are often more efficient and powerful than F_{st} in studies of within-population structure. More recently, Sokal *et al*.[25] demonstrated that spatial autocorrelation methods lead in many cases to useful microevolutionary inferences.

Finally, this preliminary study shows a significant genetic differentiation among colonies of *Helix aspersa* at a microgeographic scale. A spatial structure was also detected by means of autocorrelation methods and interpretable as a pseudo-clinal variation for somes alleles, whereas others exhibited no significant spatial pattern above the transect. Low dispersal ability combined with extinction/recolonisation processes, which occur frequently in such man-disturbed environments, were involved to explain the patchy genetic structure observed along the studied site. However that may be, results of this paper suggest that autocorrelation methods will provide useful information about local spatial genetic arrangement in land snail populations.

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Removal of calcium by *Natalina cafra* (Pulmonata: Rhytidae) from the shells of its prey.

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The carnivorous land snail *Natalina cafra* (Férussac, 1821) is found along the coastal belt of south-eastern Africa from Cape Agulhas, South Africa, in the west to Vila Luiza, Mocambique, in the east.[1,2,3] In Africa the family Rhytidae is endemic to southern Africa but has a Gondwanaland distribution pattern, occurring also in Australasia.[4]

Natalina cafra is known to feed on terrestrial gastropods and oligochaetes.[5] While malacophagy is frequently observed, it is less often recorded that these predators may attach the empty shells of their victims to the posterior end of the foot and carry them for up to four days. At the end of this period the victim's shell has been reduced to the consistency of tissue

paper; most of the calcium-rich matrix has been removed and the residue plus the periostracum is discarded. Since not every victim's shell is decalcified, the removal of calcium by *N. cafra* from some may be due to a calcium demand for building or repairing its own shell, egg laying or preparatory to aestivation. The calciferous glands of oligochaetes may represent an additional source of calcium. This is a preliminary investigation into the removal of calcium from the shells of its gastropod prey by *N. cafra*.

Adult *N. cafra* (>60 mm shell diameter) from Pietermaritzburg, South Africa (29° 37′S, 30° 26′E), were kept in the laboratory and fed live *Helix aspersa* Müller, 1774. Pieces cut from the basal whorls (top, middle) of shells of eaten snails were subjected to EDAX analysis and the relative mass % obtained for six elements including calcium in each. The shell of an uneaten snail served as a control (A). Prey shells were examined as follows: (B) immediately after the soft parts had been eaten (0h), (C) 24 h after attachment to the predator's tail, (D) after the remains of the shell were discarded at approximately 72 h.

Pieces of these same whorls were fractured in liquid N_2 and examined under the SEM.[6] Normal (not regenerated) *Helix aspersa* shell comprised the same five layers recognized in *H. pomatia* Linné 1758.[7] In sample A the periostracum and four calcium-rich layers (prismatic, cross lamellar 1 and 2, nacreous) were present. The inner surface was finely ridged with a mean ±SD of 6.0 ± 0.6 ridges. 10 μm^{-1} (n = 10). Sample B lacked the nacreous layer and showed slightly coarser ridging on its inner surface (5.2 ± 0.6 ridges. 10 μm^{-1}, n = 10). After being carried on the predator's foot for 24 h (sample C), only the periostracum and prismatic layer remained. The ridges on the inner surface were much broader (1.0 ± 0.3. 10 μm^{-1}, n = 10). When discarded at ±72 h (sample D), little more than the periostracum was left. The ridges on the inner surface were broader than at 24 h, 0.8 ± 0.3. 10 μm^{-1} (n = 10).

Accumulations of empty *H. aspersa* shells were found close to living *N. cafra* under vegetation in gardens in Pietermaritzburg. These may be larders to which *N. cafra* carries its prey's shells either to satisfy a calcium demand or as a store of calcium-rich shell for later use. Snails with empty shells attached to their tails would be vulnerable to predation and such larders would offer them a refuge in which to rebuild their calcium stores. The inner surfaces of six of the seven shells (26–33 mm diameter) from one larder showed coarse parallel ridging comparable to sample B (i.e. 4–5½ ridges. 10 μm^{-1}) while the 7th showed broader ridging similar to samples C and D (i.e. ½–1 ridge. 10 μm^{-1}), suggesting that it had been attached to the foot of *N. cafra* for 24 h or longer. Similar larders have been observed in species of the New Zealand rhytid genus *Rhytia* (Dr M.G. Efford, in litt., 7.4.92).

Three assumptions were made when interpreting the data in Table 1. (1) Sulphur, as a constituent element of the amino acids cystine and methionine, is part of the organic matrix and periostracum of the *Helix* shell.[8] Its increase in the prey shell samples during attachment to the foot of *Natalina cafra* would represent the progressive exposure of the matrix, and ultimately the surface of the periostracum itself, as $CaCO_3$ is removed from the calcified layers. (2) Chlorine can only be balanced by Ca, as there are no other cations present, and therefore occurs as $CaCl_2$, the form in which it is likely to be absorbed. Such Ca will have had to be derived from the $CaCO_3$ of the prey shell, implying that Cl is secreted by *N. cafra*. (3) Aluminium, silicon and potassium, all common soil constituents, are exogenous, being neither secreted nor absorbed but randomly distributed in the shell. As such, this fraction (Al + Si + K) forms a useful constant against which to measure changes in surface composition of the prey shell. (4) As the differences between shells A and B are minimal, feeding by *N. cafra* foes not appear to affect shell surface composition. Their mean values are therefore regarded as representative of the *H. aspersa* shell prior to Ca removal by *N. cafra*.

Accepting the above points, the change in the ratios of individual accountable components of the *H. aspersa* shell (Ca, S, Cl) to the exogenous inor-

Table 1. The relative mass % of six elements in *H. aspersa* shell samples A–D.

Shell	Ca	S	Cl	Al	Si	K
A	97.07	0.00	0.31	0.97	1.65	0.00
B	93.91	0.57	0.52	4.05	0.53	0.41
C	62.63	7.78	5.21	14.78	9.60	0.00
D	27.93	24.98	20.93	7.14	16.49	2.53

Table 2. Changes in the proportions of calcium, chlorine and sulphur to the exogenous fraction in samples C (after 24 h) and D (after rejection by *N. cafra* at about 72 h).

	$CaCO_3$	$CaCl_2$	S	Exogenous fraction
After 24 h	−90%	+66%	+358%	+676%
After rejection	−98%	+571%	+1263%	+1012%

ganic fraction (Al, Si, K), enable an approximation to be made of the percentage change in shell composition brought about by prolonged contact with the foot of *N. cafra* (Table 2).

The width of ridges on the inner surface of the *H. aspersa* shells increased dramatically after attachment to the foot of *N. cafra*, presumably as a consequence of the crystalline structure of the cross-lamellar layers. This feature could provide a useful marker for studies on the role of *N. cafra* in the control of *H. aspersa*, a common garden pest in built-up areas of South Africa.

Shell-carrying by *N. cafra* results in a rapid and almost complete decalcification of its prey's shells, the calcium presumably being absorbed via the epidermis of the dorsal surface of the foot. The rapidity of this calcium removal suggests the secretion of a strong acid. The progressive increase in chlorine in shell samples A to D suggests that dilute hydrochloric acid may be secreted by the foot to solubilize $CaCo_3$ as $CaCl_2$ prior to absorption. The finding of what appear to be larders of empty calcium-rich shells associated with *N. cafra* parallels observations made on a related species in New Zealand and may point to an unusual behaviour pattern by rhytid snails.

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Island land snail relocated

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At a time when many insular molluscan faunas are seriously threatened[1,2,3] or destroyed by human activity[4,5] it is a pleasure to record a rediscovery. *Discus guerinianus* (Lowe) (Endodontidae. Synonym: *D. semiplicatus* (L. Pfeiffer)[6,7]), is currently recorded as extinct.[8] It is similar in shape to the European *D. rotundatus* (Müller) but larger, with an even more open umbilicus, and a polished shell with reddish brown transverse bands. It was rare when it was described by Wollaston[9] as one of the most elegant Madeiran land shells. In the 19th century it was found sparingly in damp forested inland localities, living under stones and in decaying vegetation.[7] *D. calathoides* (Lowe), which may be a subspecies,[6] is a similar taxon from the neighbouring island of Deserta Grande and fossil from the southern Desertan island of Bugio. The habitat or these small oceanic outcrops is stony and eroded, with sparse grasses and drought-resistant shrubs. Although the vegetation was probably once richer,[10,11] it never resembled the wooded central part of Madeira.

In July 1997, as part of an ongoing survey of the islands, we obtained fresh shells of *D. guerinianus* from two sites on precipitous hillsides facing the ocean at the western end of Madeira. Although containing some endemic vegetation, these locations are highly disturbed. In general ecology they are more like the Desertas before they became heavily grazed by feral goats and rabbits, than the forested hinterland of Madeira. Both, however, have rich faunas for that part of the island, including some species found in damp habitats. One is close to the valley of the Ribeira da Cruz, which still retains sufficient endemic forest flora for it to be a site of special interest to the authorities of the Parque Natural da Madeira.[12]

Many endemic species on the Madeiras have limited distributions but are abundant within them. This is partly because they require specific habitats of small extent, where they can do well. For example, several species of semi-slug *Phenacolimax* (Vitrinidae) thrive in the damp laurel forest on Madeira, but would be vulnerable to changes which degraded it. In addition, some species have arisen as a result of past isolation and are now successful within very restricted ranges. They include distinctive species such as *Actinella laciniosa* (Lowe) on the northern Deserta, *Discula turricula* (Lowe) on an islet off Porto Santo and some of the *Discula* species with

limited ranges on one or other of the Porto Santo mountains.[13,14] In these cases the limited range presents a conservation problem.[15] Even small industrial or leisure developments could have a drastic effect (analogous to the effect of the large foot which used to appear in the Monty Python programmes).

There are other endemic species, however, which seem to be rare wherever they are found. Thus, several members of the genus *Leiostyla* (Pupillidae) are present in the laurel forest but are always sporadic. It has not been possible to establish their ranges, minimum habitat requirements or degree of separation,[16] and new species continue to be described.[17] Although the genus is best represented in the moist subtropical rainforest, at least one species (*L. millegrana* (Lowe)) occurs in dry habitats including the Desertas, so that alternative habitats are sometimes occupied. *Discus guerinianus/calathoides* appears to be a case where the range of niches is wide. Why are some species both ecologically tolerant and rare? In theory there could be a negative relation between competitive and dispersive ability, which would tend to maintain diversity in a mosaic environment.[18] Such a model works well for plant communities, where the trade-off may occur via seed size. Large seeds may mean better nutrient store, greater competitive ability but lower dispersal. Very small land snail species may be transported by wind[19] but none has evolved effective means of active dispersal, so that a balancing model for snails cannot work in such a simplistic way. Although competition has been noted between some similar snail species,[20] evidence that it is an important agency explaining the Madeiran faunas is not strong.[15,21] If passive dispersal is widespread, then more tolerant species may sometimes be encountered in suboptimal conditions where less tolerant ones are missing, but at present it is not clear what dispersal agencies would operate to aid this process. There is much more to be learnt about the evolutionary patterns of insular endemic land snail species.

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