



# Food choice behaviour may promote habitat specificity in mixed populations of clonal and sexual *Potamopyrgus antipodarum*

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Genetic polymorphism along an environmental gradient may be maintained if disruptive selection on habitat-specific traits leads to a correlated response in traits that reduce gene flow between habitats. We studied a short-distance cline in a population of freshwater snails *Potamopyrgus antipodarum* in which sexual and clonal snails coexist. Sexuals and clones show a life history cline by depth: snails reproduce at a smaller size in shallower habitats. Clones are also structured genetically across habitats and seem not to mix, even though habitats are within the dispersal distance of the snails and the opportunity for gene flow via migration must be considerable. Because habitat preference may promote divergence in both clones and sexuals along the depth gradient, we investigated whether snails show habitat-specific food choice behaviour that could reduce migration. We tested the food choice behaviour of the snails by exposing them simultaneously to food from their home and adjacent habitats. Both juvenile and adult snails from the shallow shore bank and a mid-water macrophyte habitat preferentially grazed on the vegetation of their original habitats. We suggest that the observed genetic and life history cline may be maintained by food choice behaviour that may promote a partial barrier to gene flow between the habitats.

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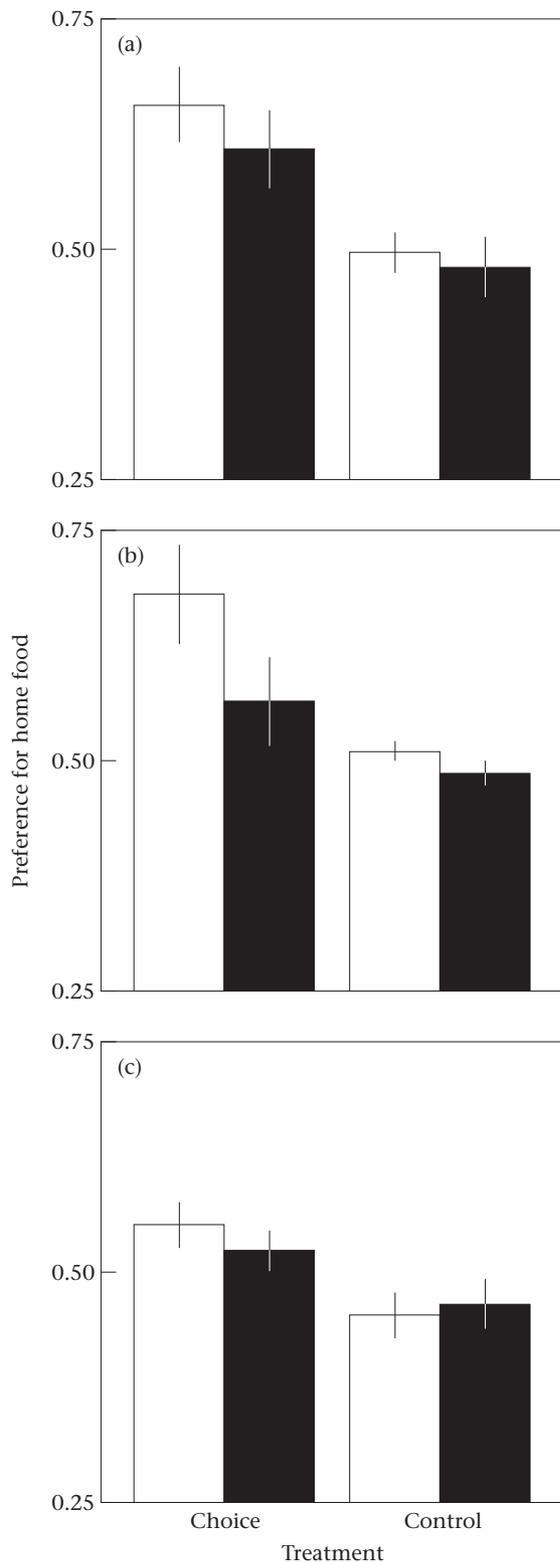
In the freshwater snail *Potamopyrgus antipodarum*, mixed populations of diploid sexual and triploid clonal individuals are frequently found in their native New Zealand. Allozyme data from two lakes on South Island (Lake Alexandrina and Lake Tennyson) revealed a short-distance cline by depth in the genetic structure of the clonal population, with habitat-specific clonal assemblages occupying different habitat zones of the lakes (Fox et al. 1996; Jokela et al. 1999). Additionally, in Lake Alexandrina, snails with broods are smaller in shallow than in deep habitats and the proportion of sexual snails and risk of infection by trematode parasites decrease with depth (Jokela & Lively 1995; Lively & Jokela 1996; Jokela et al. 1997). Sympatric clones and sexuals have similar phenotypes and share many alleles (Dybdahl & Lively 1995; Jokela et al. 1997). At Lake Tennyson, where the population is all clonal, parasite and life history clines are absent, but habitats still have a specific clonal structure (Jokela et al. 1999). However, in both lakes the opportunity for gene flow through migration must be considerable and it is surprising that so little mixing of the clonal populations has taken place, as the distance between the habitats is measured in metres and lies well within the dispersal distance of the snails. We investigated whether

habitat-specific food choice behaviour of individual snails, which may reduce migration between habitats, could help maintain the short-distance cline and we argue that the conditions under which genetic polymorphism may be maintained should also apply to clonal organisms.

The maintenance of a genetic and phenotypic cline requires a balance between habitat-specific selection and migration/recombination. Selection promotes the formation of coadapted gene complexes in linkage disequilibrium and increases the association between isolating mechanisms, while recombination breaks up the combinations and acts together with migration to homogenize subpopulations living in different environments. This selection–recombination antagonism (Felsenstein 1981) is considered the principal genetic constraint on population divergence via disruptive selection, but it may be overcome if there are positive pleiotropic interactions between genes enhancing habitat preference and genes promoting reproductive isolation (Slatkin 1982; Rice 1984). When selection is strong and discontinuous (Rice & Hostert 1993), it may lead to a habitat-specific distribution of phenotypes, thus producing a barrier to gene flow and enhancing habitat specialization (Rice 1987).

In general, empirical studies supporting this model (e.g. Johannesson et al. 1993, 1995; Rice & Hostert 1993; Stanhope 1993; Duffy 1996; Hellberg 1998) indicate that

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**Figure 1.** Preference ( $\bar{X} \pm \text{SE}$ ) for home food. (a) Food-deprived juveniles, (b) food-deprived adults and (c) satiated adults. Preference is defined as the proportion of snails choosing food from their home habitat over the total number of snails feeding on food from the home and other habitat. In the control treatment, snails were given only home food. Snails showed no preference when preference=0.5. Origin of snails: □: willow (shore bank) habitat; ■: *Isoetes* habitat.

within-population variability for resource use may be widespread. Such variation is often associated with behavioural, physiological or morphological variation, for example in salivary and digestion enzymes, assimilation efficiency or radular tooth morphology in gastropods (Bleakney 1990; Trowbridge 1991). However, whether differential resource use is sufficient to reduce gene flow between subpopulations, to maintain genetic and phenotypic diversity, and ultimately lead to divergence, remains unresolved (Duffy 1996).

Furthermore, these studies have all considered sexual species, but in our view, the above theory is also applicable to the maintenance of polymorphism in parthenogens, where divergence is constrained by gene flow through migration. If habitat preference and performance in a habitat are genetically correlated, maintenance of such an association, once established, should be more likely in parthenogens than in sexuals, as the whole genome is linked and no recombination takes place (Mitter & Futuyma 1983). Thus, the processes that maintain clonal diversity may be similar to those that maintain polymorphism in a sexual cline. Striking spatial segregation, even on very local scales, has been observed in various taxa of cooccurring clones. Habitat-specific clones may differ in numerous traits, indicating that clonal diversity is correlated with variation in habitat preference and different ecological requirements (e.g. Harshman & Futuyma 1985; Schenk & Vrijenhoek 1986; Ellstrand & Roose 1987; Weider 1989; Case 1990; Bolger & Case 1994). Thus, in both clonal and sexual organisms, habitat selection may help maintain a genotypic and phenotypic polymorphism along an environmental gradient.

We focused on habitat preference, and asked whether food choice behaviour exists in *P. antipodarum*. Strong food preferences, irrespective of whether these have an environmental or genetic basis, may help to decrease dispersal between adjacent habitats over the observed short-distance cline. We tested juvenile and adult *P. antipodarum* snails from two habitats and found that they indeed showed a strong preference for their local food. Snails rear their young in a brood pouch until the latter can crawl away; juvenile snails are thus likely to experience the same environment as their parent. Hence, our results indicate that despite the close geographical distance between the habitat zones, behavioural traits may reinforce genetic separation of the populations.

## METHODS

We conducted two food choice experiments by exposing snails from two habitats to food from their own and the adjacent habitat, to determine whether preference for 'home' food could help maintain the genetic structure across the habitat gradient. We collected the snails at a site in Lake Alexandrina, New Zealand ('Camp site' in Jokela & Lively 1995) by dragging a dip net through the vegetation. We used snails from both the shallow shore bank habitat ('willow' habitat: 0.0–0.5 m deep; dominated by willow roots) and the deeper macrophyte habitat ('*Isoetes*' habitat: 1.5–3 m deep; dominated by

**Table 1.** ANOVA (mixed model) table for the effect of treatment (choice, control), origin (willow, *Isoetes*) and block (days 1 and 2) on preference and activity of juvenile *P. antipodarum* snails

Effect	Mean square	df	F	P
<b>Preference</b>				
Treatment (TR)	0.168	1	19.55	<0.001
Origin (OR)	0.008	1	0.96	0.337
Block	0.005	1	0.64	0.432
TR×OR	0.002	1	0.22	0.644
Error	0.009	24		
<b>Activity</b>				
Treatment (TR)	0.001	1	0.03	0.867
Origin (OR)	0.333	1	30.72	<0.001
Block	0.013	1	1.15	0.293
TR×OR	0.005	1	0.63	0.436
Error	0.012	24		

*Isoetes kirkii*). We transported the snails to the Edward Percival Field Station (Kaikoura, New Zealand). We kept them outdoors in large, uncovered tubs (20 litres) until used and reared them for 2 weeks on a diet of powdered commercial *Spirulina* pellets, not used in the feeding trials. Food choice in gastropods is often influenced by the diet eaten prior to the test, and such ingestive conditioning may last up to 2 weeks (e.g. Hall et al. 1982; Desbuquois & Daguzan 1995). However, if they have a food preference, snails should retain and not switch their behaviour within a few days. At the end of the experiment, the snails were used to set up laboratory cultures.

After 2 weeks, we collected fresh willow roots and *I. kirkii* to use as food in the choice experiments. The trials were run in plastic trays (35 × 25 cm) filled with 3 litres of aged tap water. Each tray was subdivided into three equal sectors: the outer two sectors were provided with the food plants and the central sector was used as a starting place for the snails. In the choice treatment we exposed snails to approximately equal amounts of plant material from their own habitat ('home food', HF) on one side of the tray, and plant material from the other habitat ('novel food', NF) on the other side of the tray. In the control treatment we provided snails with home food on both sides of the tray. We covered the trays with lids to exclude any orientation to light gradients and rotated replicate trials on laboratory benches.

We calculated two measures of feeding behaviour. First, we defined 'food preference' as the proportion of snails found in their home food relative to the total number of snails feeding on either food

$$\text{Preference} = N_{\text{HF}} / (N_{\text{HF}} + N_{\text{NF}})$$

where *N* refers to the number of snails in the respective compartments. Snails found in the middle compartment were excluded from the calculations. If preference=1, all active snails were found among the home plants; if preference=0, all active snails were found among the plants of the neighbouring habitat; and if preference=0.5, then snails showed no preference. In the control

treatment, we randomly assigned the two outer sectors as *N<sub>HF</sub>* or *N<sub>NF</sub>* for the calculations. Therefore, preference in the control treatment was expected to equal 0.5. We also recorded overall snail activity, defined as the proportion of all active snails found in the two food compartments

$$\text{Activity} = (N_{\text{HF}} + N_{\text{NF}}) / 60.$$

In the first experiment, we used juvenile snails (1.6–2.4 mm) that were not fed for 2 days preceding a trial, and replicated the treatments eight times on 2 consecutive days with different snails. Each replicate contained 60 snails and lasted for 2.5 h. At the end of the trials (2.5 h) we recorded the location of the snails. Preference and activity were both analysed with a 2 × 2 fixed-factor ANOVA with two blocks (days 1 and 2). The factors were treatment (choice, control) and origin of snails (willow, *Isoetes*). The main effect of block was included in the analysis, and was treated as a random effect.

In the second experiment, we used adult snails (≥2.5 mm) that were either not fed for 2 days preceding a trial, or fed ad libitum with commercial *Spirulina*. The purpose of this treatment was to determine whether foraging or seeking shelter motivated the potential preference for home plant material. Each treatment was replicated eight times with different snails, with 60 snails per replicate. The location of all snails was recorded at 0.5, 1, 1.5 and 2 h after the start of the experiment. All trials were carried out in a fully randomized series between 24 and 31 January. We analysed preference and activity with a 2 × 2 × 2 fixed-factor repeated measures ANOVA with five blocks (days 1–5). The within-tray repeated measures factor (Time) corresponded to the four counts taken during a trial. The three between-tray factors were treatment (choice, control), origin of snails (willow, *Isoetes*) and state of the snails (not fed, fed). The main effect of block was included as a random effect in the analysis. In all these analyses, the assumptions of homogeneity of variance and normality of residuals were checked. All statistical analyses were conducted with SPSS statistical software. All tests are two tailed.

**Table 2.** ANOVA (repeated measures, mixed model) table for the within- and between-subject effects of treatment (choice, control), origin (willow, *Isoetes*) and state (food deprived, fed) on preference and activity of adult *P. antipodarum* snails

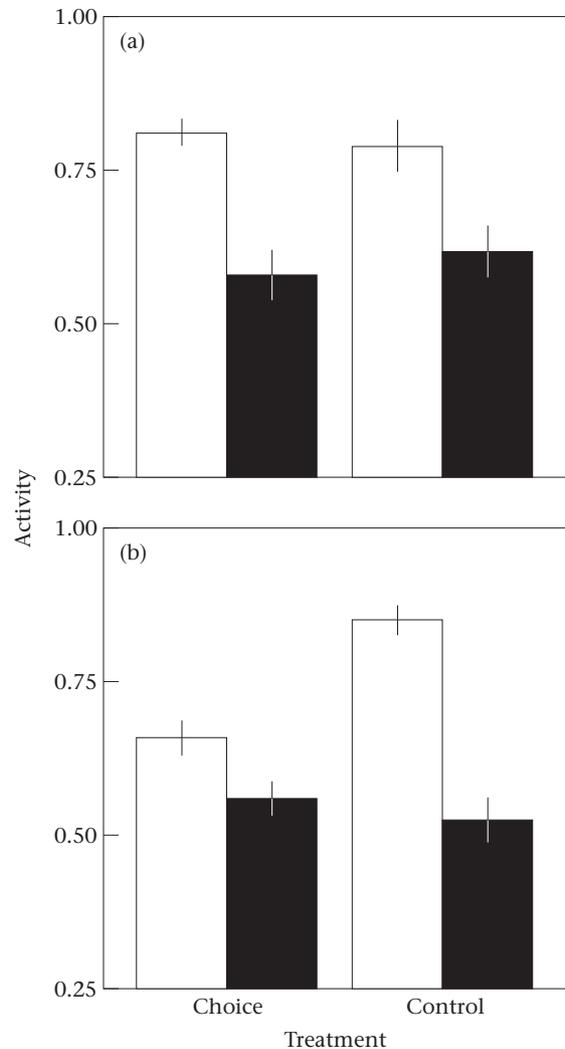
Effect	Mean square	df	F	P
<b>Preference</b>				
Between-subjects				
Treatment (TR)	0.662	1	22.09	<0.001
Origin (OR)	0.095	1	3.17	0.081
State (ST)	0.259	1	8.36	0.005
Block (BL)	0.020	4	0.68	0.610
TR×OR	0.073	1	2.43	0.125
TR×ST	0.035	1	1.15	0.288
OR×ST	0.060	1	2.00	0.163
TR×OR×ST	0.011	1	0.36	0.550
Error	0.030	52		
Within-subjects				
Time (TI)	0.007	3	1.83	0.182
TR×TI	0.002	3	0.47	0.496
OR×TI	0.001	3	0.36	0.553
ST×TI	0.003	3	0.86	0.358
BL×TI	0.003	12	0.67	0.615
TR×OR×TI	0.011	3	2.70	0.106
TR×ST×TI	0.003	3	0.89	0.351
OR×ST×TI	0.005	3	1.23	0.272
TR×OR×ST×TI	0.005	3	1.29	0.262
Error	0.004	156		
<b>Activity</b>				
Between-subjects				
Treatment (TR)	0.243	1	7.29	0.009
Origin (OR)	0.001	1	0.03	0.860
State (ST)	3.396	1	101.98	<0.001
Block (BL)	0.213	4	6.38	<0.001
TR×OR	0.081	1	2.43	0.125
TR×ST	0.596	1	17.89	<0.001
OR×ST	0.161	1	4.83	0.032
TR×OR×ST	0.012	1	0.37	0.544
Error	0.033	52		
Within-subjects				
Time (TI)	0.761	3	139.55	<0.001
TR×TI	0.026	3	4.73	0.003
OR×TI	0.002	3	0.37	0.775
ST×TI	0.078	3	14.28	<0.001
BL×TI	0.016	12	2.96	0.001
TR×OR×TI	0.001	3	0.16	0.925
TR×ST×TI	0.009	3	1.64	0.182
OR×ST×TI	0.002	3	0.46	0.713
TR×OR×ST×TI	0.005	3	0.86	0.466
Error	0.005	156		

Block (days 1–5) was included in the analysis as a random effect.

## RESULTS

### Preference

Juvenile snails chose plants from their own habitat over plants of the neighbouring habitat (Fig. 1a, Table 1). We found 32 of 49 active juvenile willow snails and 21 of 35 *Isoetes* snails in their home food. The strength of preference for home food did not differ significantly between the snails from the two habitats (Table 1). Food-deprived adult snails also preferred plants of their own habitat (Fig. 1b, Table 2). Preference was much weaker when snails were fed prior to the trials, indicating that they were foraging and not just choosing a specific habitat, for example for shelter (Fig. 1c). Of 42 active, food-deprived

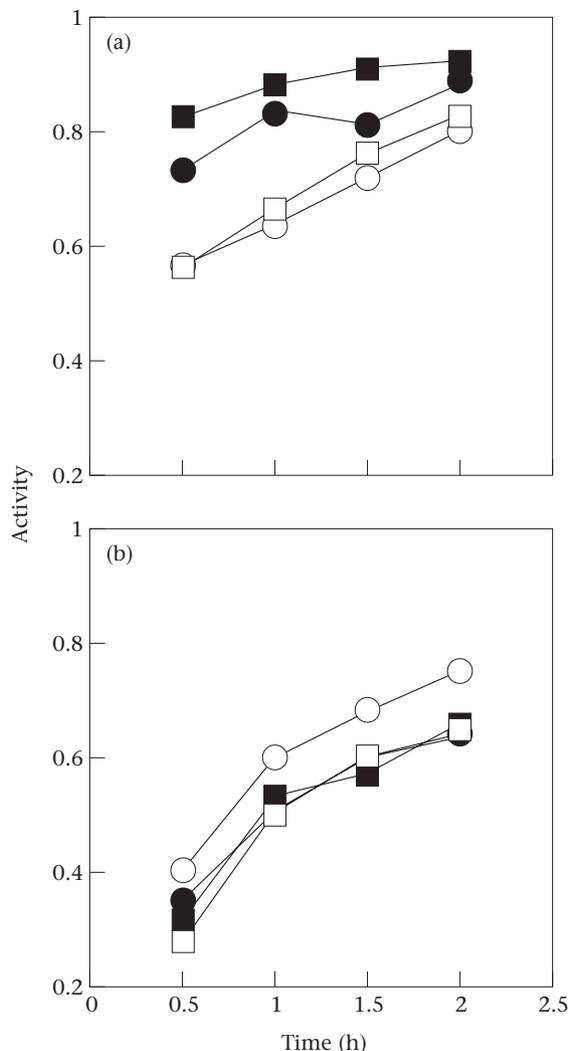


**Figure 2.** Activity ( $\bar{X} \pm \text{SE}$ ; proportion of active snails in the trial). (a) Juvenile snails from willow ( $\square$ ) and *Isoetes* ( $\blacksquare$ ) habitats. (b) Food-deprived ( $\square$ ) and satiated ( $\blacksquare$ ) adult snails. In the control treatment snails were given only home food.

willow adults 29 showed a significant preference for their home food, as did 24 of 41 *Isoetes* adults. The difference between snails from the two habitats was not statistically significant.

### Activity

Juvenile willow snails were significantly more active than juvenile *Isoetes* snails, but activity was independent of the food choice treatment (Fig. 2a, Table 1). Adult willow snails were in general not more active than adult *Isoetes* snails, but snails were more active in the control than in the choice treatment, and also more active when food deprived than when fed (Fig. 2b, Table 2). Whereas both willow and *Isoetes* snails were more active in the control treatment than in the choice treatment (origin  $\times$  treatment, Table 2), they responded differently to food deprivation (origin  $\times$  state, Table 2). *Isoetes* snails



**Figure 3.** Activity (proportion of active snails in the trial) of (a) food-deprived and (b) satiated adult snails. The location of snails was recorded every 30 min after the start of the experiment (Time). □: Willow; ○: *Isoetes*; ■: willow control; ●: *Isoetes* control.

were more active than willow snails when fed, but slightly less active when food deprived (Fig. 3). The interaction of treatment by state was also significant (Table 2), indicating that the difference in activity between the choice and the control treatment was especially pronounced in food-deprived snails (Fig. 2b, Table 2). Food-deprived snails were more active than fed snails, and much more so in the control than in the choice treatment. This result could be due to unequivocal cues in the water in the control treatment, as opposed to the choice treatment, where cues from different plants were mixed. Activity was lowest at the beginning of the experiment and increased steadily with time, and was generally higher when snails were food deprived (Fig. 3, Table 2). Overall, activity on days 1 and 2 was lower than on days 3, 4 and 5. Between 26 and 28 January air temperature dropped from 24 to 21°C, which could account for the increase in activity and the significant block effect (Table 2).

## DISCUSSION

We found significant differences in the food choice behaviour of *P. antipodarum* from two littoral habitat zones. Snails of both habitats preferred their home food to food from the adjacent habitat. Preference for home food was weaker when adult snails were fed prior to the trials, indicating that the behaviour was motivated by foraging and not by seeking shelter (e.g. from predators).

These results suggest that the feeding behaviour of the snails may reduce migration between the habitats, and help to maintain the short-distance cline found in Lake Alexandrina. The mechanisms that constrain the diet specificity of *P. antipodarum* could depend either on physiological or behavioural differences between genotypes. Dietary preference may be related to physiological differences between snail genotypes, such as enzyme activity and assimilation efficiency (Calow & Calow 1975). Alternatively, changes triggered during development may affect subsequent food choice, for example broods may be labelled by maternal diet (Trowbridge 1991). This species has been described as having a broad diet, and feeding preferences range widely (plant and animal detritus, green algae, bacteria on decaying plant material, decaying macrophytes, periphyton and diatoms (Frenzel 1979; Hanlon 1981; Haynes & Taylor 1984; Roth 1987)). However, no study has dealt with the ecological implications of these feeding preferences or variation in preference. Such variation in preference may lead to divergence, if it has a genetic basis.

From our results it is difficult to determine whether food preference has a genetic or environmental basis. It may either be directly disruptively selected or positively correlated with performance or other habitat preference traits that interact positively with performance; choice experiments that use snails reared on laboratory food are needed to resolve the question. Alternatively, these behaviours may have no genetic basis. For example, conditioning, learning or imprinting could cause individuals to prefer a habitat that they have used previously. However, with respect to divergence, this would have the same effect as an extrinsic barrier between parapatrically distributed habitats and might thus increase the likelihood of divergence (see Jaenike 1988). Conditioning to the host plant may initiate and maintain fidelity to the new host during genetic diversification and the evolution of other, genetically based, reproductive isolating mechanisms. If larval experience influences adult preference, as in our case, diversification may be further enhanced. The evolution of habitat preferences is widely thought to set the stage for the later evolution of other adaptations to the habitat or resource (Futuyma 1989). We have shown that even if preference were reversible through ingestive conditioning, it would take at least several weeks to be complete, and would not be strong enough to level out the genetic differences between ecotypes.

We presume that if snails are conservative in their food habits and simply continue eating their respective diets, such behaviour may reduce migration and reinforce the mechanisms maintaining the cline. Thus, behaviour may be the key to initiate evolutionary transitions, and both

genetic control of host or habitat selection and simple conditioning to the host or habitat may facilitate the process. Results from other studies indicate that food choice behaviour, if not genetically fixed, should, however, be correlated with some other, in our case less obvious but genetically fixed, preference trait that is disruptively selected. Allozyme studies (Fox et al. 1996; Jokela et al. 1999) have shown that clonal composition is correlated with habitat segregation. Variation in prevalence of parasite infection and life history traits among the subpopulations (Jokela & Lively 1995; Lively & Jokela 1996; Jokela et al. 1997, 1999) further confirm that the habitats present substantially different environments for the snails, and suggest that different habitats support specialized snail populations. A positive correlation between habitat preference and fitness traits may be sufficient to enhance local adaptation and population divergence (Rice 1987; Diehl & Bush 1989). Local adaptation could also be enhanced if intermediate phenotypes (generalists) experience reduced fitness in competition with habitat specialists. Hence, local adaptation may contribute to the maintenance of genetic variation, especially because the relative fitness of genotypes seems to vary between environments (Negovetic 1999). However, selection on habitat-specific fitness traits would have to be very strong to maintain the genetic polymorphism over a short distance unless associated behavioural traits, such as food choice behaviour, lead to reduced gene flow.

The process of local adaptation and genetic differentiation will differ for clonal and sexual snails, but may be reinforced by competition. Because there is no recombination in clones, the mean fitness of the clonal population after selection cannot exceed the fitness of the fittest clone present before selection (Bell 1997), and therefore selection will be more efficient in sorting the clonal subpopulations than the sexuals. Those clones that are better adapted will increase in frequency, and inferior clones will be eliminated. Sexuals may respond to selection more slowly than clones, because local adaptation will be opposed by recombination, which breaks beneficial gene combinations. Thus, in clones, selection sorts genotypes, but in sexuals, it mainly sorts the independent effects of genes (Bell 1997). Initially, selection will operate faster in clones, but the same mechanisms that sort the different clones may affect the sexual population as well, eventually resulting in a phenotypic cline with increasingly specialized subpopulations along the habitat gradient.

In summary, our results suggest that the known distribution of clones and the life history cline in the sexual subpopulation may be reinforced by food choice behaviour. They show that short-distance clines may be maintained by behavioural traits that effectively reduce gene flow, and are likely to have evolved together with other traits associated with habitat specialization.

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