

Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma*

Article (Unspecified)

Craze, P.G. and Lacey, L.A. (2000) Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma*. *Biological Journal of the Linnean Society*, 71 (4). pp. 665-676. ISSN 0024-4066

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/2166/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.



Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma*

PAUL G. CRAZE* AND LESLEY A. LACE

Behavioural and Environmental Biology Group, Department of Biological Sciences, Manchester Metropolitan University, Chester Street, Manchester M1 5GD

Received 30 November 1999; accepted for publication 22 May 2000

The Madeiran land snail genus *Heterostoma* expresses two forms of genital anatomy. One form (hemiphallic) lacks the distal male organs while the other (euphallic) has fully developed hermaphroditic genitalia. Recent evidence suggests this genital variation characterizes two sibling or incipient species. The spatial ecology and habitat associations of these taxa are described in the light of recent ideas on the role of ecology in speciation. Hemiphallic snails are found at a lower density and show a tendency to be more separated from each other compared to euphallic snails. Both taxa are more likely to be closer to other members of the same taxon. The genus as a whole is not found in the presence of sand or pale rock. However, when only areas actually containing snails are examined, hemiphallics show a positive association with sand and rock while euphallics continue to show a negative association. The differences in population density and spacing may suggest an adaptive explanation for reduction of male organs in hemiphallics since this taxon would be expected to have significantly fewer mating encounters. The observed differences in habitat association may suggest a mechanism for sympatric or parapatric divergence in keeping with current models of habitat-driven adaptive speciation. Both of these factors (selection on the mating system in a marginal environment and small scale separation based on habitat) may have been significant in the divergence of hemiphallic and euphallic taxa.

© 2000 The Linnean Society of London

ADDITIONAL KEY WORDS:—sympatric – parapatric – *Steenbergia* – Madeira – hemiphally – genital dimorphism.

CONTENTS

Introduction	666
Material and methods	667
Study organisms and sampling sites	667
Sampling	668
Results	669
Spatial analysis	669
Associations with habitat variables	672

* Corresponding author. E-mail: P.Craze@mmu.ac.uk

Discussion	672
Spatial ecology	672
Habitat	673
Speciation	673
Acknowledgements	674
References	674

INTRODUCTION

The role played by ecology in the speciation process has recently been re-examined (Schluter, 1996; Orr & Smith, 1998) with an emphasis on two main ideas. Firstly, it appears that intraspecific differences in spatial ecology and habitat choice may be able to drive speciation without the need for allopatric separation (Maynard Smith, 1966; Tauber & Tauber, 1977; Rice, 1984; Diehl & Bush, 1989; de Meeûs *et al.*, 1993; Bush, 1994; Bush & Smith, 1998). Secondly, where ecological separation exists within a population, the action of natural selection may be strong enough to cause evolutionarily significant divergence even in the presence of gene flow (Lande, 1982; Smith *et al.*, 1997). These findings suggest that further studies of spatial ecology, habitat and selection in sibling species and incipient species may prove useful in understanding the role of ecological divergence in speciation.

The Madeiran endemic land snail genus *Heterostoma* is a useful experimental system in this context. It has low mobility and a tendency towards local adaptation increasing the likelihood that ecological divergence has been a significant factor in its evolutionary history (Lace, 1992; Cook & Lace, 1993). Furthermore, the genus has an unresolved taxonomy and may be an example of incomplete speciation (Cook & Lace, 1993). There is considerable variation in *Heterostoma* shell morphology across the Madeiran Islands as a whole but perhaps the most interesting and problematic source of variation is in genital anatomy. Like all pulmonates, *Heterostoma* is hermaphroditic but unusually it expresses two forms of genitalia. One form (euphallic) has a fully developed set of male and female organs while the other (hemiphallic) lacks the flagellum and has a much reduced epiphallus. Both these lost or reduced organs are involved in male outcrossing (Tompa, 1984). These differences have been variously interpreted as evidence for two monospecific genera (*Heterostoma paupercula* and *Steenbergia duplex* [Mandahl-Barth, 1943]) or a single species (*Heterostoma paupercula*) showing genital dimorphism (Waldén, 1983; Lace, 1992; Cook & Lace, 1993) of a kind encountered in some other land and freshwater gastropods (Baur *et al.*, 1993; Schrag & Read, 1996; Doums, Viard & Jarne, 1998). The most recent evidence suggests that variation in *Heterostoma* genitalia characterizes a systematic division at the species level but without there being complete reproductive isolation between euphallics and hemiphallics (Craze, 1999; Craze *et al.*, submitted). Given that the taxonomic relationship between euphallics and hemiphallics remains unresolved, they will be referred to using the relatively neutral term 'taxa', with the generic name *Heterostoma* taken to include snails that might otherwise be classified as *Steenbergia*.

Although Lace (1992) and Cameron, Cook & Gao (1996) discuss the general environment of *Heterostoma* there has been little study of the ecology of the genus and, in particular, no specific study of differences in ecology between taxa. We have therefore compared the local population density, spacing and habitat associations of hemiphallic and euphallic taxa in the light of recent ideas concerning the role of ecology in speciation.

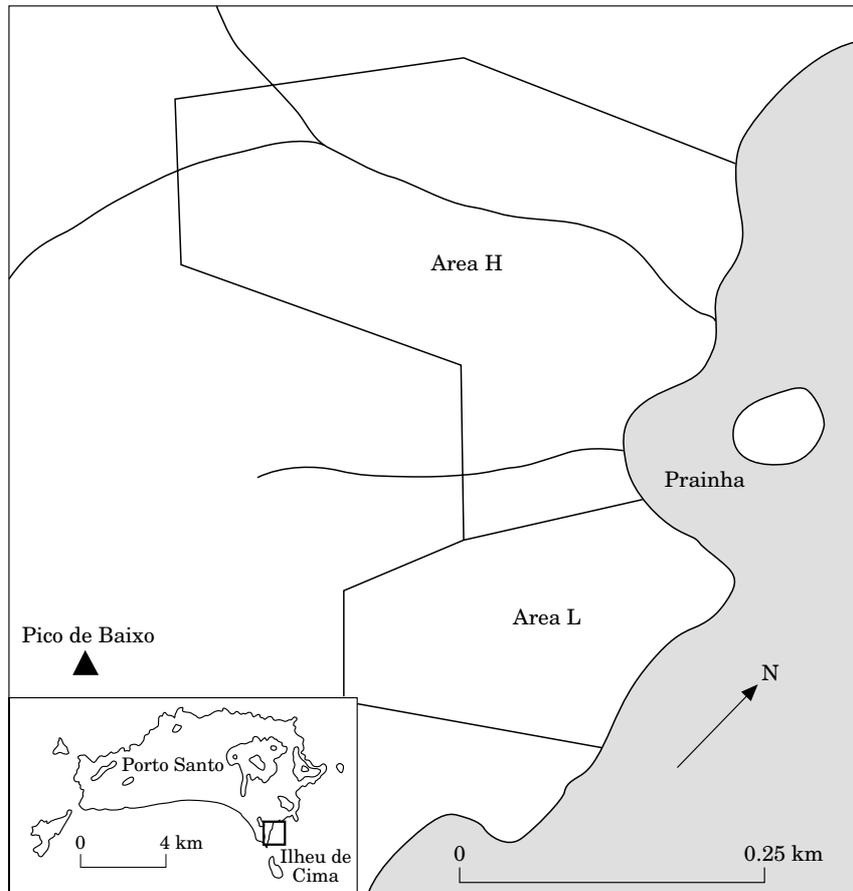


Figure 1. Location of sites used in sampling. Area H is the area of high snail density while area L contains few snails. The inset shows the location of the study area in relation to the island of Porto Santo. Stipple = sea. Also shown are the locations of eroded gullies.

MATERIAL AND METHODS

Study organisms and sampling sites

Snails of the genus *Heterostoma* occur on all islands of the Madeiran archipelago. They are associated with semi-arid, open habitats where they are found aestivating in large numbers, often in very densely packed groups and usually in the presence of a rocky substrate. They are most prevalent on Porto Santo, the second largest island of the group, and the smaller islands surrounding it. Hemiphallics are restricted to the eastern slopes of Pico de Baixo on Porto Santo and the nearby island of Cima while euphallics occur in almost all parts of the Porto Santan islands (Fig. 1). On Ilhéu de Cima the taxa are fully sympatric while at Pico de Baixo there are areas containing a single taxon as well as a broad band where the taxa are sympatric. In both areas the taxa can be clearly distinguished by features of shell morphology such that euphallics are smaller (mean width = 4.57 mm; $n = 32$), variable in colour and have a tooth in the aperture while hemiphallics are larger (mean width =

5.33 mm; $n=48$), pale and lack a tooth (Lace, 1992; Cameron *et al.*, 1996). All animals found so far at sites away from Pico de Baixo and Ilhéu de Cima have been euphallic although in some cases they may show individual features of shell morphology associated with hemiphallics (Lace, 1992).

Study was restricted to east-facing slopes of Pico de Baixo on Porto Santo. This is a dry, highly eroded basalt area covered with sand, dry soil, and stone. It is flat and sandy near the sea but steadily rises so that the upper slopes of Pico de Baixo are steep and rocky. Throughout most of the year there is only sparse vegetation dominated by *Nicotinella* and, in soil-covered areas, patchy grass. After winter rains most soil-covered areas have a loose covering of grass and short-lived, herbaceous plants.

Sampling

This was based on a system of 8 m² quadrats covering area H in Figure 1. Separation between quadrats was no less than 15 m. Quadrats were exhaustively searched between March and April 1994 and the number of each taxon was recorded. Taxa were defined using the presence (euphallic) or absence (hemiphallic) of a tooth in the aperture. In all animals examined to date there has been complete correspondence between genital anatomy and presence or absence of the tooth as long as samples are taken only from Pico de Baixo or Ilhéu de Cima (Lace, 1992; Craze *et al.*, submitted). Almost all snails had a fully developed lip to the aperture indicating that they were adult. The very few juveniles found were not recorded since they had not reached the stage where they would develop a tooth. Within a subset of quadrats the distance to the nearest neighbour was recorded either for all snails or, if the number of snails of a given taxon was too large, for a randomly chosen sample such that six nearest neighbour distances were recorded. To investigate the tendency of snails to aggregate, these same quadrats were each divided into 16 sub-quadrats of 0.5 m². Counts in sub-quadrats were used to calculate an index of dispersion for each taxon (Fisher, Thornton & Mackenzie, 1922). This method is unreliable where the population size (in this case, number of snails per large quadrat) is less than 20 (Fisher *et al.*, 1922). Where this was the case, the nearest neighbour method of Clark and Evans (1954) was used.

Habitat was scored as percentage cover of 11 categories in 15 quadrats containing hemiphallics only, 31 quadrats containing euphallics only and 31 quadrats with both taxa. Habitat categories were defined as follows:

Sand: continuous cover by sand. A very thin covering of sand with patches of substrate was not classed as sand.

Rock: total cover by rock of all types.

Light: light coloured rock, including alluvial deposits

Dark: dark coloured, mostly igneous rock

Vég: total cover by vegetation of all types.

Grass: all grass species

Nicotinella: plants of the *Nicotinella* genus

Other: all other vegetation

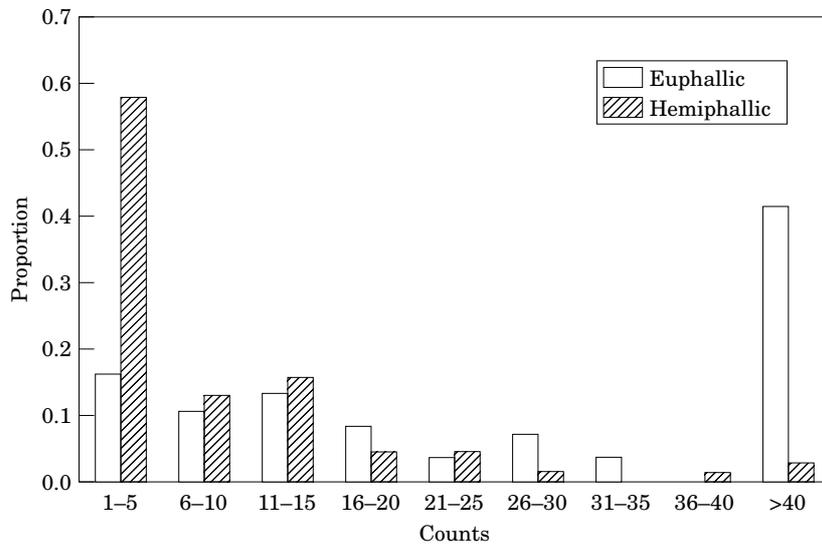


Figure 2. Frequency histogram for counts of snails in quadrats. Quadrats with more than 40 snails were pooled since almost all hemiphallic samples had counts smaller than this. The two exceptions were extreme outliers with counts of 70 and 146.

Lichen: epilithic lichen visible with a 10 × hand lens.

Stones: stones and rock fragments <20 cm in diameter.

Soil: ground covered by soil. This may be loose or compacted.

The aestivation position of each snail also was recorded as *rock*, *soil*, *stone* or *veg* using the definitions given above.

A second area was searched for *Heterostoma* (area L, Fig. 1). Here there was deep sand with occasional small patches of rock and no vegetation. Snail density was very much lower and so quadrats were not used. Instead, total number of each taxon was recorded for the whole area. When a snail was encountered, the distance to its nearest neighbour was determined by exhaustive searching in steadily widening circles with the focal snail at the centre. Data for areas H and L were treated separately.

RESULTS

Spatial analysis

Of the 148 quadrats from area H, 102 contained *Heterostoma* with 56 having both taxa, 31 with euphallics only and 15 with hemiphallics only. The median number of euphallics in a quadrat was 26 (min = 1, max = 1551) while for hemiphallics it was 4 (min = 1, max = 146). Total number of *Heterostoma* was 8665 with 7947 (92%) of these being euphallic and 718 (8%) hemiphallic. There was a clear difference between taxa in number of quadrats showing very low and very high density with hemiphallics more often at low density and euphallics more often at high density (Fig. 2). Only 3 (3%) quadrats contained a single euphallic snail compared to 11 (13%) for hemiphallics.

TABLE 1. Identity of nearest neighbour of focal snails. Results for all quadrats include those containing both taxa, euphallics only and hemiphallics only. Values for χ^2 result from testing observed frequencies against those expected if nearest neighbour distance is based on local density

	Focal snail	Same taxon	Diff. taxon	χ^2	Sig. prob.
All quadrats	Euphallic	184	12	3.63	NS
	Hemiphallic	42	21	32.07	$P < 0.01$
Both taxa present	Euphallic	61	6	1.98	NS
	Hemiphallic	19	18	51.81	$P < 0.01$
Site L	Euphallic	20	17	5.23	$P < 0.05$
	Hemiphallic	50	14	6.28	$P < 0.05$

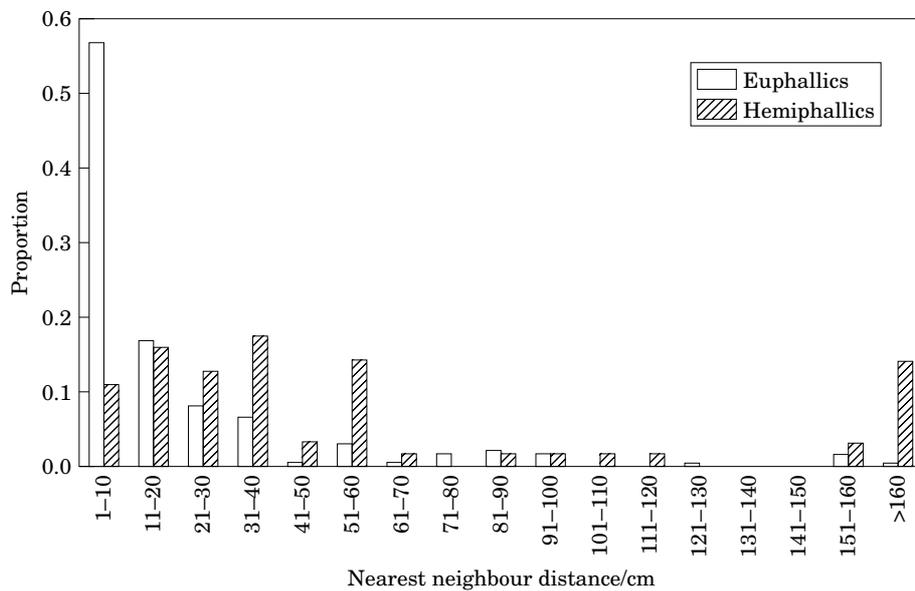


Figure 3. Frequency histogram for nearest neighbour distances of snails in area H. Separations greater than 160 cm were pooled since almost all euphallic separations were smaller than this. The exception was a single outlier with nearest neighbour distance of 406 cm.

Analysis of local spatial distribution was carried out on 49 quadrats containing euphallics and 25 containing hemiphallics. The identity of nearest neighbours is shown in Table 1. A hemiphallic individual had a nearest neighbour of the same taxon significantly more often than expected based on local density. For euphallics, nearest neighbour identity was not significantly different from that expected. The median separation of hemiphallics was 45 cm and for euphallics was 6 cm, although many euphallics showed zero separation. There was a difference between taxa in nearest neighbour distance with euphallics tending to be closer together than hemiphallics (Fig. 3). Spatial distribution in quadrats was scored as clumped or non-clumped (i.e. random or regular) (Table 2). Log-linear analysis shows a significant difference in distribution between taxa (deviance = 6.69; $df = 1$; $P < 0.01$) and a significant difference in distribution at different population densities (deviance = 17.26; $df = 3$; $P < 0.01$). This can be interpreted as a tendency for snails of both taxa

TABLE 2. Numbers of quadrats showing a clumped or non-clumped (random or regular) distribution of snails at a range of population densities. Results for quadrats with more than 30 snails were pooled because number of hemiphallics is almost always below this. The two exceptions are extreme outliers with counts of 70 and 146

Count per quadrat	Euphallic		Hemiphallic	
	Non-clumped	Clumped	Non-clumped	Clumped
2–10	4	9	9	4
11–20	6	10	6	2
21–30	3	0	2	0
>30	1	12	0	2

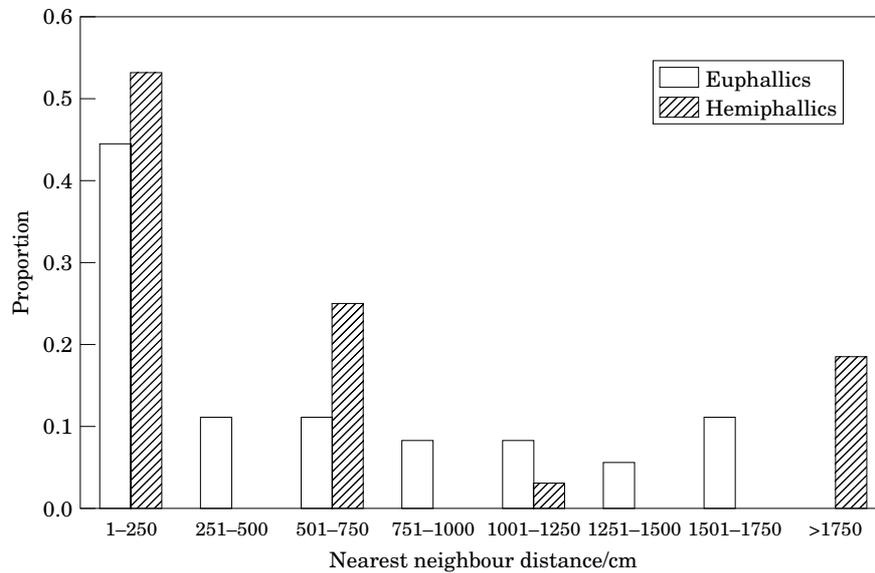


Figure 4. Frequency histogram for nearest neighbour distances of snails in area L. Separations greater than 1750 cm were pooled since no euphallic nearest neighbour distance was greater than this.

to aggregate at high density and for euphallics to aggregate more often than hemiphallics at low density. Although euphallics are at high density more often than hemiphallics overall (Fig. 2), the difference is not significant for this data set (deviance = 6.17; df = 3; $P = 0.10$) so this cannot account for any apparent difference between taxa in spacing behaviour.

In area L, although median separations were similar (253 cm for euphallics and 247 cm for hemiphallics; $\chi^2 = 0.493$; df = 1; $P = 0.48$) more hemiphallics were separated by a large distance (maximum euphallic separation = 1583 cm; median of hemiphallic separations greater than this = 3874 cm; Fig. 4). Both euphallics and hemiphallics had a nearest neighbour of the same taxon significantly more often than expected (Table 1).

Associations with habitat variables

Aestivation site of hemiphallics was usually on rock (526; 73%) with fewer on stones (156; 22%) and a small number on vegetation (36; 5%). This was clearly different from euphallics ($\chi^2=66.5$; $df=3$; $P<0.01$) where 4687 (59%) were found on rock, 2385 (30%) on stones, 644 (12%) on vegetation and a smaller number (231; 3%) in the soil.

Stepwise logistic regression of presence/absence of *Heterostoma* on habitat variables showed *light* and *sand* to be significant factors such that *Heterostoma* is negatively associated with both (deviance = 36.32; $df=2$; $P<0.01$; goodness of fit = 118.3). Quadrats without *Heterostoma* were then removed from the data set and the analysis repeated for each taxon separately. Hemiphallics were positively associated with *sand* and negatively associated with plants of the *Nicotinella* genus (deviance = 24.49; $df=2$; $P<0.01$; goodness of fit = 145.5). Euphallics were negatively associated with both *sand* and *rock* (deviance = 23.68; $df=2$; $P<0.01$; goodness of fit = 60.8). A negative association with *sand* is not unexpected but that with *rock* is surprising given the number of euphallics found aestivating on rock.

Stepwise linear regression of log-transformed number of euphallics (nulls removed) against habitat variables showed a negative association with both *sand* and *lichen* ($F=5.48$; $df=2$; $P<0.01$; adjusted $r^2=0.14$).

No transformation was able to convert numbers of hemiphallics per quadrat (again, with nulls removed) to a normal distribution. However, a negative binomial model produced a good fit to the data (deviance = 24.05; $df=3$; $P<0.01$) with no cases having large residuals. There is a positive association between number of hemiphallics and the variables *other*, *light* and *sand*.

Quadrats containing both taxa may be less revealing of habitat differences than those containing a single taxon. With these quadrats removed, discriminant function analysis was able to distinguish between the 15 quadrats containing hemiphallics only and the 31 quadrats containing euphallics only using the variables *sand* and *rock* (overall classification success of 84.5%). Hemiphallics were positively associated with these variables while euphallics were negatively associated with them.

DISCUSSION

Spatial ecology

There seem to be clear differences in the spatial ecology of *Heterostoma* taxa. The hemiphallic taxon is much rarer and is found at a lower local density. Both taxa tend to be near other individuals of the same taxon, which may indicate a spatial division of the available environment between them.

In spite of the finding that their nearest neighbours are of the same taxon more often than expected, hemiphallic individuals tend to be separated by larger distances than euphallic individuals and can become isolated. There is some evidence that this is due to a greater tendency towards aggregation in euphallics, perhaps because of a more patchy distribution of suitable aestivation sites. Whatever its cause, the greater separation of hemiphallics suggests that encounters between them are rarer than encounters between euphallics.

Habitat

Overall, snails of the *Heterostoma* genus tend not to occur where there is a great deal of sand or light-coloured rock. Euphallics aestivate on stone or rock (occasionally on vegetation) but not where there is sand or large amounts of rock. Hemiphallic aestivation position is usually on rock, often near sandy areas with a noticeable cover of rock (especially light-coloured rock) and vegetation other than grass and *Nicotinella*. The association with *rock*, *light* and *sand* suggests a distribution of hemiphallics on rock in more exposed areas but the inclusion of *other* is not expected. However, this variable contains a large number of nulls with the few positive occurrences coinciding with unusually large concentrations of hemiphallics. Other vegetation therefore seems associated with conditions that support large numbers of hemiphallics but it need not be present where this taxon is at low density.

Exactly what most of these habitat variables represent to aestivating snails is not clear. For example, the presence or absence of sand is an important factor but since *Heterostoma* was never found attached to sand the habitat relationship must be indirect or must operate under environmental conditions other than those encountered. This study took place when snails were aestivating. Sand is unlikely to be a good substrate for aestivation due to its mechanical instability. Whatever the nature of the relationship, this factor and *rock* seem best able to distinguish taxon distributions. It is possible that the presence of sand and rock indicate a more exposed environment.

Neither of the regression models for euphallics fit the observed data particularly well but this does not necessarily invalidate them. This same effect has been found in other studies of land snail ecology (e.g. Willig, Sandlin & Gannon, 1998) and is probably due to the coarseness of this method of describing habitat compared to the scale of microhabitats actually experienced by snails. Surface topography of individual rocks and stones, for example, may significantly influence local temperature and humidity. The fit between model and data is much better for hemiphallics. This may suggest that hemiphallics respond more to general features of the habitat. This would fit with the overall impression of hemiphallics as snails found exposed in open habitats and euphallics as snails of rock crevices and the underside of stones.

Speciation

Most models of habitat-driven speciation require a spatial element to mate choice (Maynard Smith, 1966; Tauber & Tauber, 1977; Rice, 1984; de Meeûs *et al.*, 1993; Bush, 1994). The results described here suggest that an individual snail becoming active from aestivation will tend to encounter other members of its own taxon first so this requirement is potentially met for *Heterostoma*. There are as yet no behavioural data on reproduction in *Heterostoma* but results of genetic analysis suggest local mating (Craze *et al.*, submitted). These same genetic results suggest that reproductive isolation between taxa is not complete (Craze, 1999; Craze *et al.*, submitted) making it less likely that this is a straightforward case of ecological divergence following secondary contact (Mayr, 1963; MacArthur & Levins, 1967). Habitat may therefore be involved in the maintenance of separation between *Heterostoma* taxa and may have been involved in the origin of this difference, although it remains to be shown that physical features of the snails themselves are not the sole factors used in mate choice (cf. Pickles & Grahame, 1999).

A second but related question concerns the interaction of selection with spatial ecology and habitat. Both sex-allocation theory (Charlesworth & Charlesworth, 1981; Charnov, 1982) and empirical studies (Charnov, 1980; Schoen, 1981; Sakal *et al.*, 1997) strongly suggest that limited mating encounters or selfing by hermaphrodites are conditions that favour a bias in resource allocation to the female function. The lower density and greater tendency towards isolation of hemiphallics may result in fewer mating encounters. There is also indirect, genetic evidence of more frequent selfing in hemiphallics although this remains to be confirmed (Cook & Lacey, 1993). The fact that hemiphallics lack a full set of male outcrossing genitalia may therefore be significant. In hermaphroditic plants, variation in anatomy of the reproductive organs is believed to have been involved in some speciation events either through direct, structural reproductive isolation or indirectly through variation in reproductive mode (Barrett, 1998). Such mechanisms could have interacted with ecological separation in *Heterostoma* to produce divergence. This suggests a potentially informative area of study.

The hemiphallic taxon often occurs in a habitat that is marginal for the genus as a whole and this may largely explain its low population density. Selection on peripheral populations is often much stronger compared to populations from the centre of a species' range (Lesica & Allendorf, 1995). Furthermore, self-fertilizing populations of plants can occur at the geographical periphery of outcrossing species or species complexes (Ornduff, 1966; Solbrig & Rollins, 1977). Peripheral populations have long been considered important in speciation (Carson, 1959; Mayr, 1963; Stebbins & Major, 1965; Levin, 1970, 1993) with this being largely a consequence of genetic drift combined with selection (Lesica & Allendorf, 1995). The habitat occupied by hemiphallics may therefore be significant in terms of the evolutionary divergence of taxa.

ACKNOWLEDGEMENTS

We would like to thank Paulo and Luisa Oliveira, Martin Jones, Emma Harrison and especially José de Sousa for assistance on Porto Santo and Martin Tyson for retrieving data. The manuscript was much improved by comments from Barry Stevens-Wood, Laurence Cook, Rory Putman and two anonymous referees.

REFERENCES

- Barrett SCH.** 1998. The reproductive biology and genetics of island plants. In: Grant PR, ed. *Evolution on Islands*. Oxford: Oxford University Press, 18–34.
- Baur B, Chen XF, Baur A.** 1993. Genital dimorphism in natural populations of the land snail *Chondrina avenacea* and the influence of the environment on its expression. *Journal of Zoology* **231**: 275–284.
- Bush GL.** 1994. Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution* **9**: 285–288.
- Bush GL, Smith JJ.** 1998. The genetics and ecology of sympatric speciation: A case study. *Researches on Population Ecology* **40**: 175–187.
- Cameron RAD, Cook LM, Gao G.** 1996. Variation in snail species widespread on Porto Santo. *Journal of Molluscan Studies* **62**: 143–150.

- Carson HL. 1959.** Genetic conditions which promote or retard the formation of species. *Cold Spring Harbour Symposium in Quantitative Biology* **24**: 87–105.
- Charlesworth B, Charlesworth D. 1981.** Allocation of resources to male and female functions in hermaphrodites. *Biological Journal of the Linnean Society* **15**: 57–74.
- Charnov EL. 1980.** Sex allocation and local mate competition in barnacles. *Marine Biology Letters* **1**: 269–272.
- Charnov EL. 1982.** *The Theory of Sex Allocation*. Princeton: Princeton University Press.
- Clark PJ, Evans FC. 1954.** Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* **35**: 445–453.
- Cook LM, Lacey LA. 1993.** Sex and genetic variation in a helicid snail. *Heredity* **70**: 376–384.
- Craze PG. 1999.** Molecular genetic analysis of taxa defined by genitalia in the Madeiran endemic land snail genus *Heterostoma*. *Bulletin of the Malacological Society of London* **32**: 2–3. <http://socrates.edsu.ulst.ac.uk/bull/Bull32/Craze.html>
- de Meeùs T, Michalakakis Y, Renaud F, Olivieri I. 1993.** Polymorphism in heterogeneous environments: evolution of habitat selection and sympatric speciation – soft and hard selection models. *Evolutionary Ecology* **7**: 175–198.
- Diehl SR, Bush GL. 1989.** The role of habitat preference in adaptation and speciation. In: Otte D, Endler JA, eds. *Speciation and its Consequences*. Sunderland, Massachusetts: Sinauer Associates Inc.
- Doums C, Viard F, Jarne P. 1998.** The evolution of phally polymorphism. *Biological Journal of the Linnean Society* **64**: 273–296.
- Fisher RA, Thornton HG, Mackenzie WA. 1922.** The accuracy of the plating method of estimating the density of bacterial populations. *Annals of Applied Biology* **9**: 325–359.
- Lacey LA. 1992.** Variation in the genitalia of the land snail *Heterostoma paupercula* (Lowe, 1831) (Helicidae) in Madeira. *Biological Journal of the Linnean Society* **46**: 115–129.
- Lande R. 1982.** Rapid origin of sexual isolation and character displacement in a cline. *Evolution* **36**: 213–223.
- Lesica P, Allendorf FD. 1995.** When are peripheral populations valuable for conservation? *Conservation Biology* **9**: 753–760.
- Levin DA. 1970.** Development instability and evolution in peripheral isolates. *American Naturalist* **104**: 343–353.
- Levin DA. 1993.** Local speciation in plants: the rule not the exception. *Systematic Botany* **18**: 197–208.
- MacArthur R, Levins R. 1967.** The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* **101**: 377–385.
- Mandahl-Barth G. 1943.** Systematische Untersuchungen über die heliceden-Fauna von Madeira. *Abh. Senckenbergische Naturforschende Gesellschaft* **469**: 1–193.
- Maynard Smith J. 1966.** Sympatric speciation. *American Naturalist* **100**: 637–650.
- Mayr E. 1963.** *Animal Species and Evolution*. Cambridge, Massachusetts: Belknap Press.
- Ornduff R. 1966.** A biosystematic survey of the goldfield genus *Lasthenia* (Compositae: Helenieae). *University of California Publications in Botany* **41**: 11–37.
- Orr MR, Smith TB. 1998.** Ecology and speciation. *Trends in Ecology and Evolution* **13**: 1–7.
- Pickles AR, Grahame J. 1999.** Mate choice in divergent morphs of the gastropod mollusc *Littorina saxatilis* (Oliv): speciation in action? *Animal Behaviour* **58**: 181–184.
- Rice WR. 1984.** Disruptive selection on habitat preference and the evolution of reproductive isolation. *Evolution* **35**: 1251–1260.
- Sakal AK, Weller SG, Chen M, Chou SY, Tسانونت C. 1997.** Evolution of gynodioecy and the maintenance of females. The role of inbreeding depression, outcrossing rates and resource allocation in *Schiedea adamantis* (Caryophyllaceae). *Evolution* **51**: 724–736.
- Schluter D. 1996.** Ecological causes of speciation. *American Naturalist* **148**: S40–S64.
- Schoen DJ. 1981.** The evolution of self-pollination in *Gilia achilleifolia* (Polmoniaceae). Unpublished PhD Thesis, University of California, Berkeley.
- Schrag SJ, Read AF. 1996.** Loss of male outcrossing ability in simultaneous hermaphrodites – phylogenetic analysis of pulmonate snails. *Journal of Zoology* **238**: 287–299.
- Solbrig OT, Rollins RC. 1977.** The evolution of autogamy in *Leavenworthia*. *Evolution* **31**: 265–281.
- Smith TB, Wayne RK, Girman DJ, Bruford MW. 1997.** A role for ecotones in generating rainforest biodiversity. *Science* **276**: 1855–1857.
- Stebbins GL, Major J. 1965.** Endemism and speciation in the California flora. *Ecological Monographs* **35**: 1–35.
- Tauber CA, Tauber MJ. 1977.** A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* **268**: 702–705.

- Tompa AS. 1984.** Land snails (Stylommatophora). In: Tompa AS, Verdunk NH, Van Den Biggelaar JAM. *The Mollusca, Reproduction*, Vol 7. New York: Academic Press, 47–140.
- Waldén HW. 1983.** Systematic and biogeographical studies in the terrestrial Gastropoda of Madeira. With an annotated check-list. *Annales Zoologici Fennici* **20**: 255–275.
- Willig MR, Sandlin EA, Gannon MR. 1998.** Structural and taxonomic correlates of habitat selection by a Puerto Rican land snail. *Southwestern Naturalist* **43**: 70–79.