ASSOCIATION OF SHELL BANDING AND HABITAT IN A COLONY OF THE LAND SNAIL *THEBA PISANA*

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SUMMARY

The Mediterranean snail *Theba pisana* is polymorphic for shell banding. In an introduced colony in Western Australia, the frequency of effectively unbanded shells is higher in exposed habitats than in adjacent thickets of *Acacia* bushes. This association holds for both unbanded shells and banded shells without upper bands. These results are most easily explained in terms of climatic selection.

1. INTRODUCTION

THE Mediterranean land snail *Theba pisana* (Müller) has a complex polymorphism for shell banding. In Israel, the frequency of pale shells increases in warmer and drier regions, which Nevo and Bar (1976) explain as the result of climatic selection similar to that proposed for *Cepaea nemoralis* and *C. vindobonensis* (Jones, 1973). On a microgeographic scale, this hypothesis predicts that in a heterogeneous environment with exposed and sheltered habitats, pale shells should be more common in the exposed areas.

T. pisana is widespread and abundant in coastal dunes in southern Western Australia, where it was introduced early in this century. The colonies are generally polymorphic, and occur in a variety of habitats. This paper reports a close association of banding morph frequencies with micro-habitat in a colony of *T. pisana* near Perth, Western Australia.

2. MATERIALS AND METHODS

(i) Shell variation

T. pisana displays a wide variety of colour and banding morphs (Taylor, 1914). In Australian colonies, the shell is white, with varying numbers and intensities of brown bands. The inheritance of the complicated banding patterns is unknown. The unbanded condition, however, is due to a single dominant allele (G. Lewis, personal communication). Banded shells vary from those with dark bands over most of the shell to those with only a series of dots along the midline. Some morphs are quite distinct, and presumably represent effects of single genes; others, however, grade into one another, suggesting polygenic control. Photographs in Hickson (1972) illustrate the banding variation such as found in the present study.

Faced with the complexity of the variation, I have adopted a functional classification similar to that used for *Cepaea* (Cain and Sheppard, 1954), using three categories:

- (1) Unbanded shells, which form a simple genetic class.
- (2) Partially banded, a heterogeneous class of banded shells in which bands are absent from the upper half of each whorl.
- (3) Fully banded, in which bands are present above the midline of each whorl.

Unbanded and partially banded shells comprise an "effectively unbanded" group, in which different genotypes underly similar phenotypes. Nevo and Bar (1976) score their samples as effectively unbanded or banded. Since there is frequently a flush of pigment on newly formed shells, even in otherwise unbanded shells, the last 90° of the outermost whorl was ignored while scoring the shells.

(ii) *Study area*

The study site is an area of coastal dunes at the southern boundary of City Beach, Western Australia (31°58'S; 115°45'E), adjacent to the Swanbourne Rifle Range. This area was chosen for study because *T. pisana* are abundant and occupy a mosaic of well defined, contrasting habitats. The two most obvious habitat types are thickets of *Acacia* scrub and areas of low, open vegetation. The 2 to 2.5 m tall *Acacia* bushes provide shade, but are sufficiently sparse to allow a grassy understory. *T. pisana* aestivate on the branches of the bushes, typically 0.5 to 1.5 m off the ground. The open habitat consists mainly of grasses and *Pelargonium*, which seldom exceed 0.5 m in height. The most extreme of the "open" areas are the foredunes, in which patches of prostrate succulent vegetation are surrounded by bare sand. Snails in the open areas are often directly exposed to the sun, and cannot aestivate far off the ground.

The *Acacia* and open habitats are interspersed, forming alternate zones roughly parallel to the shore. A sand track which runs eastwards (inland) from the shore and parallel to the fence of the rifle range provides a 600 m transect through a sequence of five transitions between open and *Acacia* habitats. The study area is thus divided naturally into 6 zones. Open I includes the foredunes, extending about 100 m eastwards. In the easternmost 25 m of Open I, the dune vegetation gives way to grass and *Pelargonium*. The transition from Open I to *Acacia* I is abrupt, occurring in about 5 m. This *Acacia* thicket is about 120 m wide, and is separated from *Acacia* II by Open II, a 50 m wide zone. *Acacia* II occupies both sides of a stable dune, about 175 m across. Open III extends 125 m eastwards from *Acacia* II, before grading into *Acacia* III. *Acacia* III is the least well defined of the zones, with smaller and more widely spaced bushes than in *Acacia* I or II; but it does provide a contrast to the open habitats.

Colonies of *T. pisana* are continuous along the transect, except in the foredunes, where the habitat is discontinuous. To ensure adequate sampling in the succulent vegetation, the transect was extended southwards for about 150 m along the foredunes. This extension was included in Open I.

To provide additional comparisons of sheltered and open habitats, two sites were chosen at which contrasting patches of vegetation are adjacent. The first was a 5 × 2 m patch of *Acacia* bushes surrounded by grass and succulent dune vegetation. The second was a single *Olearia axillaris* bush (2 m high, 2 m wide) within Open I, surrounded by grass and *Pelargonium*. In each case, snails were collected in the sheltered microhabitat and up to 5 m away in the open area.

(iii) Sampling

Except in the foredunes, samples were taken at 15 m intervals along the transect, adjacent to the track. Each sample was taken from a 5×5 m or smaller area. The vegetation and ground were searched thoroughly to avoid visual bias in sampling. Only live adults (>10 mm diameter) were collected. Where possible, 70 to 100 snails were taken from each sampling site. Movements of the snails undoubtedly make adjacent samples non-independent to some degree. On the other hand, I have observed significant changes in morph frequencies over distances of less than 5 m. The 15 m sampling interval is thus a compromise between the need for statistical independence of the samples and the recognition of the genetic responsiveness of the snails. In the southern transect (Open I), this problem is not as great, as samples were taken at approximately 50 m intervals through discontinuous *T. pisana* habitat.

A partial sampling of the transects was made in June 1977, followed by a complete sampling of 42 sites in July 1978. Although there were localised changes between years, the general pattern of morph frequencies was the same in the two years, and the data have been pooled for the present analyses.

3. RESULTS

All samples were polymorphic for shell banding, but the morph frequencies varied considerably along the transect (table 1). Considering all 42 of the transect samples, there is a clear association of higher frequencies of effectively unbanded shells with the open habitats ($P < 0.001$, Mann-Whitney U test). More importantly, the morph frequencies follow the habitat changes closely (fig. 1). The transect includes 5 transitions between

FIG. 1.—Proportions of effectively unbanded shells in samples of *T. pisana* from the City Beach transect. Open circles indicate samples from open habitats, solid circles samples from *Acacia* thickets. Vertical lines indicate standard errors.

TABLE 1
Composition of samples of T. pisana from the City Beach transect

Sample position (m)	Sample size	Unbanded	Partially banded	Fully banded	Percentage effectively unbanded
Open I					
165 south	46	15	9	22	52
112	75	28	27	20	73
68	105	26	41	38	64
0	103	47	21	35	66
30 east	75	25	20	30	60
45	102	46	19	37	64
80	135	47	22	66	51
95	119	19	26	74	38
Acacia I					
110	249	31	37	181	27
125	205	37	41	127	38
140	183	26	39	118	35
155	215	24	40	151	30
170	108	10	26	72	33
185	82	12	20	50	39
200	72	10	12	51	31
215	201	50	38	113	44
Open II					
230	149	35	61	53	64
245	197	48	54	95	54
260	91	22	34	35	62
275	203	45	43	115	43
Acacia II					
290	78	18	20	40	49
305	73	11	14	48	34
320	192	26	36	130	32
335	46	1	7	38	17
350	196	34	30	132	33
365	162	26	32	104	36
380	84	6	27	51	39
395	172	27	37	109	37
410	32	6	7	19	41
425	28	5	7	16	43
440	172	58	27	88	49
Open III					
455	97	30	23	44	55
470	96	18	40	38	60
485	93	20	41	32	60
500	102	15	46	41	60
515	51	22	14	15	71
Acacia III					
530	209	81	28	100	52
545	96	20	45	31	68
560	204	33	49	122	40
575	183	52	42	89	51
590	101	31	35	35	36
605	194	48	42	104	46

Acacia and open habitats. For each comparison of sets of samples from adjacent, contrasting habitats, there is a significantly higher proportion of effectively unbanded shells in the open area than in the *Acacia* (Mann-Whitney U test). The shifts in morph frequency are nearly as abrupt as the

shifts in the vegetation, with intermediate frequencies seldom occurring more than 30 m on either side of a habitat boundary. Consistent with the findings from the transect, in each of the paired microhabitat comparisons, the open area had a higher proportion of effectively unbanded shells (table 2). This difference was statistically significant in both cases.

TABLE 2

Comparisons of morph frequencies in samples of T. pisana from adjacent microhabitats

Vegetation	Effectively unbanded	Fully banded	χ^2	P
Acacia bushes	99 (65%)	53 (35%)	8.83	<0.01
Succulents/grass	103 (81%)	24 (19%)		
Olearia bush	24 (25%)	71 (75%)	25.12	<0.001
Grass/Pelargonium	54 (62%)	33 (38%)

FIG. 2.—Relationship of the proportion of effectively unbanded in banded shells and the proportion of unbanded shells in samples of *T. pisana* from the transect. Open circles indicate samples from open habitats, solid circles samples from *Acacia* thickets.

Effectively unbanded shells comprise two groups: genetically unbanded and genetically banded with the upper bands suppressed. Considering all of the transect samples, the frequencies of both unbanded shells and effectively unbanded in banded shells are higher in the open habitats than in the *Acacia* thickets (fig. 2). In the comparisons of adjacent zones, all pairs except Open III and *Acacia* III have significantly different frequencies for both traits (table 3). Thus, both mechanisms of producing pale shells contribute to the

TABLE 3
Comparisons of morph frequencies in Acacia and open habitats, based on Mann-Whitney U tests

Sets of samples	Banding morph		
	Effectively unbanded	Unbanded	Partially banded in banded
Entire transect	+++	+++	+++
Open I/ <i>Acacia</i> I	+++	+++	++
<i>Acacia</i> I/Open II	++	+	++
Open II/ <i>Acacia</i> II	++	+	++
<i>Acacia</i> II/Open III	+++	+	+++
Open III/ <i>Acacia</i> III	+	-	-

+++ , $P < 0.001$; ++ , $P < 0.01$; + , $P < 0.05$; - , nonsignificant.

increased paleness of colonies in the open areas. Although there is considerable scatter, the frequency of effectively unbanded in banded is correlated with the frequency of unbanded shells (fig. 2; for arcsine transformed frequencies, $r = 0.40$, $P < 0.05$).

4. DISCUSSION

The data from *T. pisana* add to a long list of associations between habitat and morph frequencies in land snails. In reviewing these studies, Clarke *et al.* (1979) emphasise the need for verification of such associations in several independent comparisons, to avoid spurious correlations. The patchiness of the environment at City Beach provides a test of consistency of the response of morph frequencies to habitat changes. The transect and microhabitat samples include a total of 7 comparisons between adjacent, contrasting habitats, all of which show significantly higher frequencies of effectively unbanded shells in the open area. Even ignoring the significance of individual comparisons, the occurrence of the same trend in all 7 cases has a probability of only 0.016 by chance alone. On a larger scale, the same trend occurs on Yorke Peninsula, South Australia, where populations of *T. pisana* from inland grassy sites are monomorphic for unbanded shells, but populations from the more bushy coastal vegetation are polymorphic (Butler and Murphy, 1977).

The variation of morph frequencies over short distances in the City Beach samples is as important as the association with habitat. This orderly responsiveness contrasts with Hickson's (1972) study of sand dune colonies of *T. pisana* in South Africa, in which he attributed variation in morph frequency to random drift. His samples were taken from an area similar to Open I in the present study. Consistent with Hickson's findings, there is significant heterogeneity (χ^2 test) among samples within 5 of the 6 habitat

zones of the City Beach transect (Open III is the only homogeneous group of samples). While such heterogeneity might represent drift, it more likely reflects the crudeness of the classification of habitats. In either case, the major variations in morph frequency correlate with environmental conditions, relegating drift to a minor role at most.

Although repeatable correlations of morph frequencies with environmental characteristics imply the operation of natural selection, the basis for that selection is generally elusive (Clarke, 1975). In the case of *T. pisana*, it is likely that selection is operating directly to favour pale shells in open habitats. The frequency of unbanded shells and the frequency of effectively unbanded in banded shells are genetically and statistically independent measures of the "paleness" of a population. Both of these genetic mechanisms contribute to the phenotypic responsiveness of the *T. pisana* populations, suggesting that the shell phenotype is the object of selection, as has been shown for *Cepaea* (e.g., Cain and Sheppard, 1954; Clarke, 1960; Richards and Murray, 1975). High frequencies of unbanded shells will reduce the effectiveness of selection on genetic modifiers of banding; likewise, high frequencies of suppressors of banding will reduce selection on the presence or absence of all bands. Consequently, the weak correlation between these two classes of effectively unbanded shells (fig. 2) is predictable.

The two obvious candidates for selective agents favouring pale shells in exposed habitats are microclimate and predation. Climate correlates with geographic variation of both allozymes and banding morphs of *T. pisana* in Israel, where the proportion of effectively unbanded shells increases in drier, warmer areas (Nevo and Bar, 1976). The data from City Beach confirm and extend this association on a finer scale.

Since *T. pisana* aestivate above ground through the summer, protection from overheating and dessication is crucial. The snails reduce the chances of overheating by climbing to escape high ground temperatures, and by selecting shadier sites (McQuaid *et al.*, 1979). At City Beach, the microclimates in *Acacia* and open areas are different. Not only are the open areas more fully exposed to the sun, they also offer little opportunity for escape from soil heat. If, as has been shown for *Cepaea vindobonensis* (Jones, 1973), individuals with pale shells heat up less rapidly than those with fully banded shells, the observed association of morph frequency with habitat is explicable in terms of climatic selection. However, visual selection by predators would also be likely to favour paler shells in the more exposed areas, and any firm interpretations of the mechanisms of selection must await experimental verification.

Whatever mechanism underlies the association of morph frequency with vegetation type, the sharp clines between adjacent habitats imply strong selection and/or very limited gene flow. An additional possibility is differential habitat selection by individuals with pale or dark shells. Indeed, selection in heterogeneous environments should result in selection for attraction of each genotype towards the habitat in which it is favoured.

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