Fld Stud. (1978), **4**, 715–728

TERRESTRIAL SNAIL FAUNAS OF THE MALHAM AREA

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Introduction

Since the last account of the ecology of the land Mollusca of Malham (Cameron and Redfern, 1972), more information has been collected as a result of four more field courses held at Malham Tarn Field Centre. The number of sites investigated has more than doubled, previously unworked habitats have been studied, and sites with doubtful or incomplete information revisited. This new information allows a more detailed analysis. Coupled with new work done elsewhere, this analysis leads to modification and amplification of the conclusions presented in Cameron and Redfern (1972). This paper presents the results and conclusions of this new analysis.

Since 1972, there has been further taxonomic revision of British land and freshwater Mollusca. The new check-list of land Mollusca has been used here (Waldén, 1976) and a new annotated checklist of the land Mollusca of Malham, with synonyms used in Cameron and Redfern (1972) is included as an appendix.

The Area

Figure 1 shows the extent of the area considered. Individual sites are not marked—details are available at the Field Centre or from the author. With the exception of Colt Park Wood, Cameron and Redfern (1972) considered only sites close to Malham Tarn and Malham village. This paper includes sites from the limestone plateaux around Ingleborough, from the west face of Pen-y-Ghent, and from Oxenber Wood, Austwick (the published list of Kerney and Fogan, 1969). This increase in the area results in certain geographical singularities which are discussed below. Further details of the area are given in Cameron and Redfern (1972).

Methods

Sampling was by searching by eye on site and by collecting soil and litter for examination in the laboratory (Cameron and Redfern, 1972). This method has given consistent qualitative results for snails in sites visited repeatedly, and the analysis is based on presence and absence data only. The method is not reliable for slugs (Wäreborn, 1969), and most of the analysis is restricted to snails. Slugs are considered briefly at the end. Only sites subjected to a thorough search are considered here. Details of others are available at the Field Centre.

Habitats

Field notes taken at the time of sampling have been used to allocate sites to the habitat categories described below. A few aberrant sites do not fit in the scheme, and are considered separately.

1. *Woods*

(a) **Old rocky woodland.** Areas of seminatural woodland on limestone rock. Of the four sites involved, two (Colt Park and Oxenber) are on limestone pavements, one (Malham Cove) is on large boulder scree, and the last (Janet's Foss), in a craggy gorge. Soils are all calcareous.

(b) **Plantations.** Most woods in the area are planted, and are very varied in topography, soil and tree species. The range is from rich mixed deciduous woods on rocky limestone soils (e.g. the upper parts of Tarn House Wood) to conifer plantations on acid, partly podzolised soils.

2. *Open Calcareous Habitats.* Mostly rocky areas on limestone, these sites can be classified by the structure of the rocks and by the amount of grazing.

(a) **Grassy screes.** Talus slopes below crags and cliffs where there is a mixture of rock and grassland. The nature of the terrain gives some protection from grazing, at least in small pockets, and no division into grazed or ungrazed was possible.

(b) **Bare screes.** Substantial areas of bare scree with no, or very few higher plants. Samples were made in the centre of such areas.

(c) **Ungrazed crags.** Crags and cliffs with grassland, in sites inaccessible to, or little used by sheep. Most sites in this category are from the higher crags of Gordale Scar.

(d) **Grazed crags.** Areas like (c) above, but subject to sheep grazing.

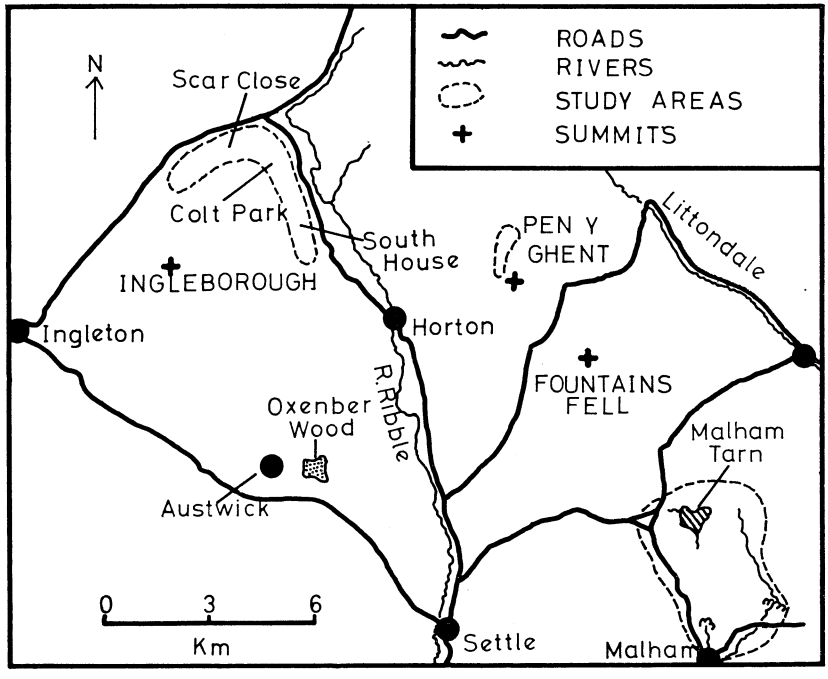

FIG. 1.

A map of the area referred to in this paper.

(e) **Grazed grassland with boulders.** Includes both limestone and drift grassland with occasional limestone boulders—talus or erratics. Soil pH frequently 6·0–6·5 away from boulders.

(f) **Grazed grassland.** Grassland with no exposed rocks. Surface soil pH nearly always acid—pH 5·5–6·5.

(g) **Ungrazed limestone pavements.** Lack of grazing on limestone pavements is due to a variety of causes. Some sites, with large clints and deep, narrow grykes are dangerous and inaccessible to sheep. The best examples are to be seen at Scar Close. Such areas, or areas containing patches of this type, are frequently fenced or walled to prevent sheep gaining access. Other areas (e.g. Highfolds Scar) have been fenced for experimental reasons, and were grazed in the recent past. Ungrazed limestone pavements are not stable habitats—some, such as Scar Close, appear to be developing into woodland of the type seen at Colt Park nearby, while others (parts of South House Pavement, Highfolds Scar) seem to be reverting to rather acid grassland—the grykes filling up, and coarse grasses, bilberry *Vaccinium myrtillus* and bracken *Pteridium aquilinum* spreading over the surface.

(h) **Grazed limestone pavements.** Typically, the grykes are wider and the clints smaller than in (g) above; the grykes are nearly filled with soil carrying grazed grass. Woodland plants and other tall herbs are rare, and confined to a few narrower and deeper grykes inaccessible to sheep.

3. *Wetlands.* Only moderately rich sites are considered here—fens (on peaty soil) and mires (on mineral soil). The raised bog on Tarn Moss has been searched; only the slug *Arion ater* has been found. The fens and mires have been further subdivided by their dominant vegetation.

(a) **Carex fens.** Fens in the Malham Fen complex dominated by sedges *Carex* spp (Proctor, 1974), mostly *C. nigra.*

(b) **Filipendula fens.** Fens in the Malham Fen complex dominated by Meadowsweet *Filipendula ulmaria.*

(c) **Willow carr.** Scrubby willow *Salix* spp. woods on fen peat. Excludes the more acid woodlands of the fen complex which have birch *Betula pubescens* and acidophilous mosses *Sphagnum* and *Polytrichum* spp.

(d) **Carex mires.** Sedge-dominated areas on waterlogged mineral soils (e.g. Great Close Mire).

(e) **Filipendula mires.** Usually transitional zones—between water and fully terrestrial habitats—e.g. on the shores of the Tarn.

Results

(a) General

A total of 107 sites are considered here. Full details of the fauna of each site are available at the Field Centre or from the author. A summary of the snail faunas of woods and open calcareous habitats is given in Table 1 and of wetlands in Table 2. Four aberrant sites are also included in Table 1. Nomenclature of freshwater species in Table 2 follows Kerney (1976*a*).

Three taxonomic difficulties should be mentioned. Cameron and Redfern (1972) questioned the validity of earlier records of *Hygromia liberta* (cf. Stratton, 1956),

synonomizing it with *Trichia hispida*. *H. liberta* (correctly *Trichia plebeia*, cf. Waldén, 1976) is now recognized as a species occurring in Britain. Recent records are probably of *T. hispida* only but more work is required. *Columella aspera* has recently

Table 1. *Frequencies of snail species recorded in woodland and open calcareous habitats, and occurrence in four aberrant sites*

	Old rocky woods	Other woods	Grassy screes	Bare screes	Ungrazed craggy grass	Grazed craggy grass	Grazed grass with few rocks	Grazed grass with no rocks	Ungrazed pavements	Grazed pavements	Site 39	Site 70	Site 64	Site 79
Carychium tridentatum	4	9	8						6	2	+			
Lymnaea truncatula	1	1												
Succinea putris		1												
Oxyloma pfeifferi		1												
Azeca goodalli	3		1											
Cochlicopa lubrica	4	6	9		4	6	2		12	4	+	+		+
Cochlicopa lubricella	4	4	11		4	9	1		10	6	+			
Pyramidula rupestris	4		15	4	4	11	2		12	10	+			
Columella edentula	2		2						10	4	+			
Columella aspera									1					
Vertigo pygmaea						3					+			
Abida secale	1								5	3				
Pupilla muscorum						3					+			
Lauria cylindracea	4	3	13		4	10			11	9	+	+		
Vallonia costata	1										+			
Vallonia pulchella										1	+			
Vallonia excentrica						6				1	+			
Acanthinula aculeata	3										+			
Ena obscura	4	1	9		3	3			3	2				
Punctum pygmaeum	2	4	1		1	2			2		+			
Discus rotundatus	4	14	15	4	4	12	2		12	9	+	+		+
Vitrina pellucida	4	13	10		3	2			7	2	+			+
Vitrea subrimata	3	1	4	1	2				4	1				
Vitrea crystallina	4	15	15	4	2	3			10	7	+	+	+	+
Vitrea contracta	4	9	15	3	3	12			11	10	+			+
Nesovitrea hammonis	4	2	8		2	8	3	4	7	4	+	+	+	
Aegopinella pura	4	9	10		3	3	1		7	4	+		+	+
Aegopinella nitidula	4	14	12	1	4	5			9	4	+		+	+
Oxychilus cellarius	4	16	14	4	4	10			11	4	+	+		+
Oxychilus alliarius	4	17	13	2	4	5	2		12	3	+			
Oxychilus helveticus	3	4	4		1				1		+			
Euconulus fulvus	4	11	2						9				+	+
Cochlodina laminata	1								1					
Clausilia bidentata	4	2	14		4	10	2		5	4	+			
Clausilia dubia	3	2	15	2	4	10	1		12	9		+		
Balea perversa	2		1											
Ashfordia granulata	1	2									+			
Trichia striolata	4	12	11		4	3			9	3	+		+	+
Trichia hispida	4	2	8		2	10			4	5	+			
Arianta arbustorum	4	4	8		2	2			9	3	+			
Helicigona lapicida			2											
Cepaea nemoralis	3	1	12		3	6			7	1	+			
Cepaea hortensis	4		5		3	1								
Helix aspersa											+			
No. of sites	4	17	15	4	4	12	3	4	12	10	1	1	1	1
No. of species recorded	35	28	30	9	24	25	9	1	29	26	30	7	6	10
Mean No. of species/site	28·25	–	17·8	6·25	18·5	12·9	5·3	1	18·25	11·4	–	–	–	–
Minimum	25	5	12	5	16	9	4	1	14	8				
Maximum	30	18	23	7	21	16	6	1	24	15				

been recognized as distinct from *C. edentula* (Paul, 1975*b*). *C. edentula* has been confirmed from most sites here, but the status of older records is in doubt, since *C. aspera* has been found at one site. Similarly, *Euconulus alderi* has been recognized as distinct from *E. fulvus* (Paul, 1975*a*). *Euconulus* material from Malham has not been examined critically. From what is known of the ecology of the two species, it is likely that wetland records of *E. fulvus* refer to *E. alderi*, but this requires confirmation.

Two species, *Abida secale* and *Cochlodina laminata* are included in Table 1, but are not included in most of the analysis because they are restricted to the Ingleborough massif, and are not found in the immediate vicinity of Malham.

Of the habitats sampled, plantations differ from all the rest in the great diversity of faunas found within them, and in the greater range of soil and vegetation types. They are therefore considered separately first, and excluded from the general analysis of habitats and their faunas.

(b) The faunas of plantations and old rocky woodland

Plantation faunas are poorer and less consistent than those from rocky woods.

Table 2. *Frequencies of occurrence of snail species in wetland habitats*

		Fens				Mires		
		Carex	*Filipendula*	Carr	Total	*Carex*	*Filipendula*	Total
	Carychium tridentatum	3	3	4	10		1	1
*	*Carychium minimum*	3	5	4	12	2	2	4
*	*Lymnaea truncatula*	2	3		5	3	3	6
F	*Lymnaea palustris*	2	2		4	1		1
F	*Aplexa hypnorum*	1			1			
F	*Anisus leucostoma*	2	1	3	6	1		1
F	*Bathyomphalus contortus*	1			1			
*	*Succinea putris*						1	1
*	*Oxyloma pfeifferi*	3	2		5	3	2	5
	Cochlicopa lubrica	3	4	4	11	3	3	6
	Columella edentula						1	1
*	*Vertigo antivertigo*	2			2	1		1
*	*Vertigo substriata*	2			2			
	Punctum pygmaeum	3	1	3	7			
	Vitrina pellucida						1	1
	Vitrea crystallina	3	5	4	12	3	3	6
	Vitrea contracta	2	3	1	6	1		1
	Nesovitrea hammonis	3	5	4	12	3	3	6
	Aegopinella pura			1	1			
	Aegopinella nitidula						2	2
	Oxychilus cellarius						1	1
	Oxychilus alliarius	1			1			
	Euconulus fulvus	3	3	4	10	1	1	2
	Clausilia bidentata					1		1
	Ashfordia granulata						1	1
	Trichia hispida					1	2	3
	Arianta arbustorum						1	1
	Number of sites	3	5	4	12	3	3	6
	Number of species	17	12	10	18	12	15	20

F = freshwater species.
* = obligate wetland species.

Many species occur at lower frequencies in the plantations, and *Azeca goodalli*, *Pyramidula rupestris*, *Columella edentula*, *Acanthinula aculeata*, *Balea perversa* and *Cepaea hortensis* occur in at least two of the old woods but in none of the plantations. The species common in both kinds of woodland tend to be small thin-shelled species of the litter.

Within the plantations, species diversity is related to soil pH (Figure 2), with the most alkaline sites having about three times as many species as the most acid (excluding slugs and wetland species). Five species are found only in alkaline sites, and only eleven are found at pH 5·0, mostly small "thin-shelled" species.

(c) General comparison of the faunas of different habitats

A convenient method to compare a number of faunas is to use an index of affinity which can be computed between all possible pairs of faunas (Southwood, 1966). Inspection of Table 1 suggests that many faunas are merely impoverished versions of others, lacking characteristic species. The faunas of each habitat have therefore been compared using the Maximum Similarity Index (M.S.I.) where:

$$\text{M.S.I.} = \frac{\text{number of species in common}}{\text{number of species in the less diverse of the two faunas}}$$

A fauna which is merely a reduced version of another will show 100% similarity on this index, and only the possession of unique species by both faunas will produce a lower figure.

The resultant matrix is shown in Table 3. Wetland faunas are clearly distinct

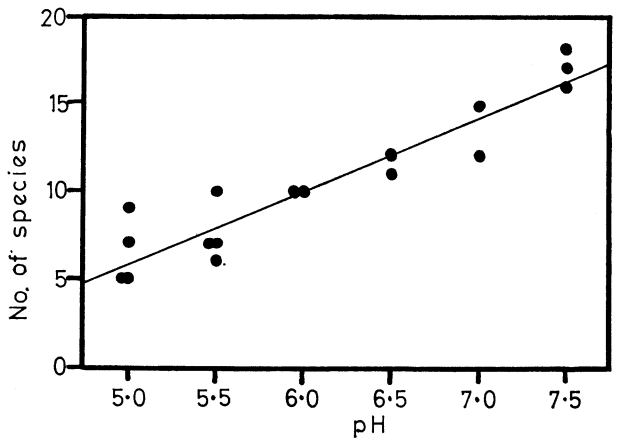

FIG. 2.

The scatter of number of species of snail on soil pH for sites from plantations. The calculated regression line is shown (slope, b. = $4{\cdot}14 \pm 0{\cdot}39$. $t_{15} = 10{\cdot}56$ $P < 0{\cdot}001$).

Table 3. *Maximum similarity index* (%) *matrix for comparison of the faunas of each habitat. Note that wetlands are only divided into fens and mires, and that plantations and rock-free grassland are omitted*

	Grassy screes	Ungrazed pavements	Ungrazed crags	Grazed pavements	Grazed crags	Bare screes	Boulders and grass	Fens	Mires
Old rocky woods	97	100	100	92	88	100	100	50	68
Grassy screes		100	100	92	88	100	100	50	64
Ungrazed pavements			96	92	84	100	100	50	64
Ungrazed crags				87	92	100	100	39	50
Grazed pavements					84	100	100	39	59
Grazed crags						89	100	39	50
Bare screes							44	33	44
Boulders and grass								44	33
Fens									77

from the remainder, fens more so than mires. They are considered separately below (section f). All the remaining habitats are very similar, the open ones being all reduced versions of that found in old rocky woods. The grazed habitats are slightly distinct, and the two most impoverished faunas, bare screes and bouldery grassland, are distinct from each other, although similar to all the rest. Rock-free grassland is omitted from the matrix; it contains only one species, *Nesovitrea hammonis*, found also in all the other habitats.

Inspection of Table 1 shows that old rocky woodland has much the richest fauna; the major ungrazed habitats are similarly richer than their grazed equivalents.

(d) The fauna of the major rocky habitats

The great similarity in the faunas of the major rocky habitats is partly spurious. Many species common to many habitats occur much less frequently in some than in others, and are hardly typical. A better comparison of these habitats can be made with an index of affinity which considers differences in frequency as well as occurrence. The one used here can be called a frequency similarity index (F.S.I.) where:

$$\text{F.S.I.} = 1 - \frac{\text{sum of differences in frequencies (\%) of each species between habitats}}{\text{sum of total frequencies (\%) in each habitat}}$$

The resultant matrix is shown in Table 4. This demonstrates greater differences between habitats. The grazed habitats are similar to each other, but rather distinct from woods, while the ungrazed open habitats resemble woods more closely than they do their grazed equivalents.

Differences between the grazed and ungrazed habitats are summarized in Table 5. The effects of grazing are consistent between crags and pavements, with a general

Table 4. *Frequency similarity index matrix for the comparison of faunas from the major rocky habitats*

	Grassy screes	Ungrazed pavements	Ungrazed crags	Grazed pavements	Grazed crags
Old rocky woods	0·77	0·76	0.80	0·57	0.61
Grassy screes		0·86	0·87	0·73	0·73
Ungrazed pavements			0·82	0·75	0·70
Ungrazed crags				0·67	0·70
Grazed pavements					0·80

reduction in typical woodland species and an increase in xerophils (see discussion below). The same trend is visible in the comparison of relative frequencies of closely related species pairs, with the "dry" member of each pair relatively more frequent in the grazed habitat (Table 5*b*) in 9 out of 10 cases ($\chi^2 = 6{\cdot}4$, $P < 0{\cdot}02$).

There are also differences in detail between the ungrazed habitats. Many species are more frequent in old rocky woods than elsewhere; *Azeca goodalli*, *Acanthinula aculeata* and *Oxychilus helveticus* are common in the woods but rare or absent elsewhere. *Columella edentula* and *Euconulus fulvus* are almost exclusive to pavements (amongst the open habitats), while *Ena obscura*, *Clausilia bidentata* and *Cepaea hortensis* are rare or absent there, but common in screes and crags. No species are exclusive to screes or crags, but *Carychium tridentatum* and *Vitrea crystallina* are absent or rare in crags and common elsewhere. Other species show only minor variations in frequency. The same trends are visible for six out of the seven species mentioned above in the comparison of grazed crags and pavements; the seventh, *Euconulus fulvus* is absent from all grazed habitats.

(e) Altitude

The sites range in altitude from 230–590 m above sea level. Some impoverishment occurs at the highest altitudes. All seven sites above 500 m have less than the median number of species for their habitat, and the four highest samples, at 575–580 m on Pen-y-Ghent show the biggest reduction. The most conspicuous absentees at this height are *Lauria cylindracea* (nearly universal on lower rocky sites) and all Helicids (*Trichia* and *Cepaea* spp.) except *Arianta arbustorum*. The four most xerophil species, typical of grazed calcareous grassland, *Vallonia costata* and *V. excentrica*, *Pupilla muscorum* and *Vertigo pygmaea* are found only below 360 m, and rarely above 300 m. Even below this they tend to occur only in sites with a southerly aspect.

(f) Wetland faunas (Table 2)

Carychium minimum, *Cochlicopa lubrica*, *Vitrea crystallina* and *Nesovitrea hammonis* occur in nearly all wetland sites; only the first is absent elsewhere. All the freshwater

species and *Vertigo* spp., *Carychium tridentatum*, *Punctum pygmaeum*, *Vitrea contracta* and *Euconulus fulvus* are much more frequent in fens than in mires. *Lymnaea truncatula* and *Oxyloma pfeifferi* are equally frequent in both (except in fen carr). The remainder, mostly terrestrial species of low frequency, are commoner in mires.

The chief distinction between the vegetation classes is that freshwater and obligate wetland species are most frequent in *Carex* and least in carr. The differences in their combined frequencies, relative to the remainder, between the three vegetation classes are significant ($\chi^2 = 6{\cdot}17$, $P<0{\cdot}05$ for fen and mire results combined). The carr lacks nearly all the freshwater species and *Oxyloma pfeifferi*, while *Vertigo* spp. and two freshwater species are restricted to *Carex*.

Table 5. *Comparisons of grazed and ungrazed crags and pavements*

Species reduced in frequency in both crags and pavements:
- *Cochlicopa lubrica*
- *Cochlicopa lubricella*
- *Lauria cylindracea*
- *Ena obscura*
- *Clausilia bidentata*
- *Clausilia dubia*
- *Arianta arbustorum*
- *Cepaea nemoralis*
- *Trichia striolata*
- *Punctum pygmaeum*
- *Vitrea crystallina*
- *Vitrea subrimata*
- *Oxychilus cellarius*
- *Oxychilus alliarius*
- *Oxychilus helvetius*
- *Aegopinella pura*
- *Aegopinella nitidula*
- *Vitrina pellucida*

Species remaining constant in one habitat and reducing in the other:
- *Discus rotundatus*
- *Pyramidula rupestris*

Species absent in one and reducing in the other
- *Carychium tridentatum*
- *Columella edentula*
- *Cepaea hortensis*
- *Euconulus fulvus*

Species increasing in one and decreasing in the other
- *Nesovitrea hammonis*

Species increasing in both crags and pavements
- *Vallonia excentrica*
- *Trichia hispida*
- *Vitrea contracta*

Species absent from one and increasing in the other
- *Vallonia pulchella*
- *Vertigo pygmaea*
- *Pupilla muscorum*

(a) Changes in frequency of species in grazed crags and pavements by comparison with their ungrazed equivalents.

	Crags	Pavements
Cochlicopa lubrica / *C. lubricella*	+	+
Trichia striolata / *Trichia hispida*	+	+
Arianta arbustorum / *Cepaea nemoralis*	+	−
Aegopinella nitidula / *Nesovitrea hammonis*	+	+
Vitrea crystallina / *Vitrea contracta*	+	+

(b) Relative frequencies of closely related species pairs as between grazed and ungrazed pavements and crags. The first species of each pair normally prefers more cover or humidity than the second. + = first species with higher relative frequency in ungrazed conditions, − = first species with higher relative frequency in grazed conditions.

(g) Slugs

Table 6 shows the frequencies of slugs found. Only the major habitat divisions of woods, open calcareous habitats and wetlands are used, because of the very low frequencies of many species. The low frequencies recorded in open sites is undoubtedly an artifact of the sampling technique used. Another species, *Milax budapestensis*, has been recorded from the gardens of the Field Centre. Early records of *Arion circumscriptus* are aggregates (Cameron and Redfern, 1972), and it should be noted that *Arion hortensis* is now known to be an aggregate species (Davies, 1977).

The woodland fauna is characterized by high frequencies of *Arion hortensis* and *Limax marginatus;* these and *Limax maximus*, *Arion fasciatus* and *A. silvaticus* are more or less absent from open sites. Wetlands are characterized by *Deroceras laeve*. The two most frequent slugs of open dry sites, *Arion ater* and *Deroceras reticulatum* are the most universal of all molluscan species in Britain.

Discussion

Cameron and Redfern (1972) concluded that woodland and wetland faunas at Malham were similar to those found elsewhere, but that those of open calcareous habitats were peculiar in resembling those of rocky woods, a similarity attributed chiefly to the exceptionally wet climate at Malham. These conclusions can now be amplified and modified.

Faunas of old rocky woods, and of the more calcareous plantations, are typical of calcareous woodland generally (Bishop, 1976*b*; Boycott, 1934; Cameron, 1973) and indeed differ only in detail from woodland faunas of the post-glacial Climatic Optimum (Kerney, 1976*b*; e.g. Tornewton). They remain amongst the richest of all known molluscan habitats in Britain, although they lack certain species with geographically restricted distributions.

In the plantations, the relationship of species diversity with soil pH is particularly striking. Acid woodlands can have much richer faunas than those seen here (Berry, 1973; Bishop, 1976*b*; Boycott, 1934; Chatfield, 1972; Waldén, 1955). The recent origin of many of these plantations on rock-free acid grassland, which carries very few snails, may be responsible, as many woodland snails have poor powers of dispersal (Waldén, 1955).

Table 6. *Frequencies of slug species recorded in each of the primary habitat categories*

	All woods	All grassland	All wetlands
Arion ater	11	8	5
Arion subfuscus	5	3	3
Arion circumscriptus	4 } 7	3	
Arion silvaticus	5		
Arion fasciatus	2		
Arion hortensis	15	1	4
Arion intermedius	5	6	6
Limax maximus	4		
Limax marginatus	12		
Deroceras laeve	2		17
Deroceras agreste	0	1	1
Deroceras reticulatum	16	8	2
Number of species	11	7	7
Number of sites	21	62	18

The faunas of open rocky habitats resemble those of calcareous woods very closely, but recent work suggests that Cameron and Redfern (1972) overemphasized the role of macroclimate as a causal factor. The presence of rocks creates different microclimates and affords local protection from grazing so that some of the soils and vegetation of a woodland can develop. The rocks and soil present sites of activity and rest not present in typical chalk grassland of southern England, but similar to those provided by logs, tree trunks and litter in woods. Cameron (1978) has shown that species living in the same habitat differ markedly in sites of activity, and that the woodland species of open rocky grassland at Malham are active on rocks and soil, and not on living vegetation. Tree trunks and logs in woods are suitable alternatives to rock in woods except for the obligate saxicole *Pyramidula rupestris*. Furthermore, even in dry southern England, the snail fauna of chalk grassland changes dramatically in the absence of grazing, with an increase in the woodland element, and a decrease in typical xerophils (Cameron and Morgan-Huws, 1975). Direct comparison of unrocky grazed grassland is difficult, because this habitat at Malham is usually slightly acid. Rocky open habitats in drier areas than Malham also have a high proportion of woodland species (Waldén, 1955; Evans and Jones, 1973), some of which tend to be cavernicolous and carnivorous (Cameron, 1976; Evans and Jones, 1973); it is these species which are found in bare screes.

The effects of grazing on open habitats are now clearer. In both crags and pavements, grazing decreases the proportion of woodland species found. Species of soil and litter (*Oxychilus*, *Aegopinella*, *Carychium*, *Vitrina*) are generally more affected than those of rocks (*Pyramidula*, *Lauria*, *Clausilia*, *Discus*). Loose soil and litter are much reduced in grazed sites. Sites 64 and 79, listed separately in Table 1, are in the ungrazed, "rock free" meadow of Tarn Close, with soil pH of *c.* 6·0. Their faunas are much richer than those of the four grazed sites without rocks. Conversely, the true open country element of the fauna (*Vallonia*, *Pupilla*, *Vertigo*) increases in grazed sites, particularly in those in the driest and sunniest places as do the relative proportions of species showing a "dry" habitat range by contrast with close relatives. Site 39 (listed separately in Table 1) is unique, in that it contains in a very small area a mosaic of grazed and ungrazed habitat types and damp patches, resulting in a small and externally undistinguished roadside verge having a fauna as diverse as that of ancient woodland.

The small differences between the three major open rock habitats—scree, crag and pavement—seem also to be in part due to differences in the availability of different surfaces. Limestone pavements have the greatest amount of damp soil and litter and crags the least—two litter dwelling species *Euconulus fulvus* and *Columella edentula* are nearly restricted to pavements, while two others—*Carychium tridentatum* and *Vitrea crystallina* are missing, or nearly so, from crags.

Ungrazed pavements are unstable habitats. Sites protected from grazing by their structure tend to develop into rich mixed woodland, and the two such sites at Scar Close with much scrub have the highest diversity (23 and 24 species compared to a mean for ungrazed pavements of 18). Fenced off sites may develop into acid grassland; the three sites on Highfolds Scar showing this tendency have the poorest faunas (14, 15 and 15 species). Site 70, listed separately in Table 1, shows an extreme form of this—an area of pavement at South House with grykes filled with soil and a dense cover of bracken. Except for *Discus*, rock dwellers have disappeared.

Conservation management of limestone pavements must take account of these differences.

Dance (1971) gives a catalogue of altitude limits for terrestrial mollusca. Many records here exceed the limits quoted, but it is clear that sites over 500 m have an appreciably reduced fauna.

The wetland faunas are typical, and similar ones are reported elsewhere (Boycott, 1934; Walden, 1955; Bishop, 1976*a*; Paul, 1976). The slight distinctions between different vegetation types correspond to successional stages in fen development (Proctor, 1974), with the later stages having lower frequencies of obligate wetland species. Litter dwelling species (*Punctum*, *Euconulus*, *Carychium*) are commoner in fens than in mires; the fens are protected from grazing, and have a much greater accumulation of litter.

Summary

1. A revised account is given of the terrestrial Mollusca of Malham and their ecology.
2. Woodland and wetland faunas are typical of those found elsewhere, but much of the variation within each can be attributed to various environmental and historical factors.
3. Open rocky calcareous habitats have faunas rather similar to those of woods, and this is probably due to the similar range of microhabitats provided. Minor differences between habitats are consistent with this explanation.
4. Grazing pressure reduces the woodland element of open habitat faunas and increases the xerophil element. Soil and litter dwelling species are most affected. Ungrazed limestone pavements are unstable habitats, and more than one immediate outcome of succession is possible.

APPENDIX

An annotated list of the species of terrestrial mollusc found in the area covered by the paper.

Carychium tridentatum (Risso)
Carychium minimum Müller
Succinea putris (L)
Oxyloma pfeifferi (Rossmässler) (*Succinea pfeifferi*)
Azeca goodalli (Férussac)
Cochlicopa lubrica (Müller)
Cochlicopa lubricella (Porro)
Pyramidula rupestris (Draparnaud)
Columella edentula (Draparnaud)
I *Columella aspera* Waldén
A *Vertigo pusilla* Müller
Vertigo antivertigo (Draparnaud)
Vertigo substriata (Jeffreys)
Vertigo pygmaea (Draparnaud)
AI *Abida secale* (Draparnaud)
Pupilla muscorum (L)
Lauria cylindracea (Da Costa)
Vallonia costata (Müller)
Vallonia pulchella (Müller)
Vallonia excentrica Sterki
Acanthinula aculeata (Müller)
Ena obscura (Müller)

Punctum pygmaeum (Draparnaud)
Discus rotundatus (Müller)
C *Arion ater* (L)
Arion subfuscus (Draparnaud)
Arion circumscriptus Johnston
Arion silvaticus Lohmander
Arion fasciatus (Nilsson)
Arion hortensis Férussac
Arion intermedius Normand
Vitrina pellucida (Müller)
Vitrea subrimata (Reinhardt) (*V. diaphana*)
Vitrea crystallina (Müller)
Vitrea contracta (Westerlund)
Nesovitrea hammonis (Ström) (*Retinella radiatula*)
Aegopinella pura (Alder) (*Retinella pura*)
Aegopinella nitidula (Draparnaud) (*Retinella nitidula*)
Oxychilus cellarius (Müller)
Oxychilus alliarius (Müller)
Oxychilus helveticus (Blum)
Milax budapestensis (Hazay)
Limax maximus L.
Limax marginatus Müller (*Lehmannia marginata*)
Deroceras laeve (Müller) (*Agriolimax laevis*)
Deroceras agreste (L) (*Agriolimax agrestis*)
Deroceras reticulatum (Müller) (*Agriolimax reticulatus*)
Euconulus fulvus (Müller)
B *Cecilioides acicula* (Müller)
I *Cochlodina laminata* (Montagu)
Clausilia bidentata (Ström)
Clausilia dubia Draparnaud
Balea perversa (L)
B *Helicella itala* (L)
Ashfordia granulata (Alder) (*Monacha granulata*)
Trichia striolata (C. Pfeiffer) (*Hygromia striolata*)
Trichia plebeia (Draparnaud) (*Hygromia liberta*)
Trichia hispida (L) (*Hygromia hispida*)
Arianta arbustorum (L)
Helicigona lapicida (L)
Cepaea nemoralis (L)
Cepaea hortensis (Müller)
Helix aspersa Müller

Notes: I = Ingleborough area only at present. A = not confirmed in Malham area this century. B = not confirmed in Malham area in last 10 years. C = All *Arion ater* found are black, but all 4 specimens dissected have genitalia appropriate to the subspecies *Arion ater rufus*. Note also that *Arion hortensis* and *Euconulus fulvus* are aggregate species (see text). This list follows Waldén (1976). Names in brackets are synonyms used in Cameron and Redfern (1972).

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