

Lichenologist 25(1): 83–95 (1993)

DIFFERENTIAL HERBIVORE DAMAGE TO CALCICOLOUS LICHENS BY SNAILS

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Abstract: A laboratory experiment was conducted to determine the damage caused by snail grazing to 35 calcicolous lichen species and cyanobacteria from the Baltic island of Öland, Sweden. Individuals of four species of land snails (*Balea perversa*, *Chondrina clienta*, *Clausilia bidentata* and *Helicigona lapicida*) were allowed to graze on identified lichen species growing on pieces of limestone. Snail grazing on thalli and ascocarps was classified into four categories ranging from no damage to completely eaten. In general, some lichen species were heavily grazed, whereas others were only slightly damaged or not injured. *Aspicilia calcarea*, *Tephromela atra* and *Verrucaria nigrescens* were preferred by all snail species except *Chondrina clienta*. In general, lichen thalli that were not immersed in the calcareous rock and cyanobacteria were preferred, whereas ascocarps were avoided by one of the snail species (*C. clienta*). Immersed perithecia with a carbonized outer layer were avoided by all snail species except *C. bidentata*. Possibilities of chemical and mechanical defence properties in calcicolous lichens are discussed.

Introduction

The effects of herbivory on lichens and their subsequent regeneration have been briefly mentioned in Poelt (1969), Ozenda & Clauzade (1970), Wunder (1974) and Wirth (1980). Among invertebrates, various species of terrestrial gastropods have been reported as lichen grazers (Schmid 1929; Plitt 1934; Frömring 1954; Coker 1967; Peake & James 1967; Yom-Tov & Galun 1971; James & Henssen 1976; Gerson & Seaward 1977; Lawrey 1980, 1983*a, b*; Seaward 1988). Lawrey (1980, 1983*a, b*) showed that the preference for lichens by a slug depended on the chemical content of the thalli. However, in these investigations of lichen-herbivore relationships, estimation of the damage to individuals was not made.

One-hundred-and-eight calcicolous lichen species have been reported from the Great Alvar, a limestone grassland on the Baltic island of Öland, Sweden (Fröberg 1988, 1989). On a 1.2 ha limestone pavement in the Great Alvar, 17 species of terrestrial gastropods have been found, four of them being potential lichen feeders (Baur 1987). Experiments demonstrated that (1) these snail species grow and reproduce when kept on pieces of limestone covered with lichens and cyanobacteria, and (2) both intra- and interspecific competition for lichens occur among these snail species (Baur 1988; Baur 1990; Baur & Baur 1990).

In this study, we have quantified the damage to various species of calcicolous lichens by snail grazing. Pieces of limestone covered with lichens were offered

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to individuals of four species of rock-dwelling land snails (*Balea perversa* (L.), *Chondrina clienta* (Westerlund), *Clausilia bidentata* (Ström), and *Helicigona lapicida* (L.)) for a period of defined length, after which the damage to the lichens was examined as well as the snails' faeces. In particular, the following questions were addressed:

(1) Are endolithic and epilithic lichens differently grazed by individuals from different snail species?

(2) Are lichens with green photobionts or cyanobacteria preferred by any of the snail species?

(3) Are thalli or ascocarps preferentially grazed by the snails?

(4) Are apothecia or perithecia differentially grazed by the snails?

Materials and Methods

Study area

The lichens studied were collected in the limestone grassland Great Alvar in the southern part of the Baltic island of Öland, Sweden (56°33'N, 16°36'E) on 12 September 1990. Vegetation, climate and geomorphology of the Great Alvar have been described in detail by Rosén (1982). Samples of lichens were collected at three sites:

(1) Tornrör, Gårdby parish, on scattered rocks and a stone wall (made of flat pieces of limestone arranged in horizontal layers).

(2) 10 km E of Mörbylånga, on a limestone pavement (50 m × 40 m).

(3) 1.4 km W of the southernmost tip of the marsh area Möckelmossen, on a stone wall on the southern side of the road connecting Resmo and Stenåsa.

Lichens

The lichen nomenclature follows Santesson (1984), except for *Aspicilia contorta* subsp. *contorta*, *A. contorta* subsp. *hoffmanniana* Ekman & Fröberg ined., *Bagliettoa baldensis* (Massal.) Vězda, *Clauzadea immersa* (Hoffm.) Hafellner & Bellem., *Collema fuscovirens* (With.) Laundon, *Farnoldia jurana* (Schaer.) Hertel, *Gyalecta subclausa* Anzi, *Lecania rabenhorstii* (Hepp) Arnold and *Tephromela atra* (Huds.) Hafellner. *Lecanora dispersa* II and *Verrucaria glaucina* correspond to *L. dispersa* type 2 and *V. glaucina* auct., non Ach. in Fröberg (1989).

Snails

Specimens of the land snails *Balea perversa*, *Chondrina clienta*, *Clausilia bidentata* and *Helicigona lapicida* were collected at the sites described above. *Balea perversa* (Fig. 1A) is characteristic of dry places among rocks and old stone walls, occurring occasionally on stems of trees. It is widespread in western Europe, and in Scandinavia it occurs mainly along the coast (Kerney & Cameron 1979). *Chondrina clienta* (Fig. 1B) occurs in open limestone areas of central and south-eastern Europe and in three isolated areas of Sweden (Kerney & Cameron 1979; Baur 1988). *Clausilia bidentata* is a widespread species in Europe, occurring among rocks and in woods and hedgerows. Its slender conical shell is sinistral and in adults is 9–12 mm high (Kerney & Cameron 1979). *Helicigona lapicida* is common in holes and crevices in rocky ground, and in old woodland and hedgerows in western and central Europe. Fully-grown snails have a flattened, sharply keeled shell measuring 12–20 mm in diameter (Kerney & Cameron 1979). All species are particularly well adapted to rocky habitats; they are very resistant to drought with activity confined to periods of high air humidity, and their specialized radulae enable them to graze epi- and endolithic lichens from rock-faces (Schmid 1929; Gittenberger 1973; Breure & Gittenberger 1982). Snail grazing on endolithic lichens contributes to the erosion of rocky habitats (Danin 1986; Shachak *et al.* 1987; Jones & Shachak 1990).

Experimental methods

To investigate damage due to grazing, individuals of the four snail species were kept on pieces of limestone covered with 1–11 lichen species for periods of 10–25 days (Table 1). For this purpose the

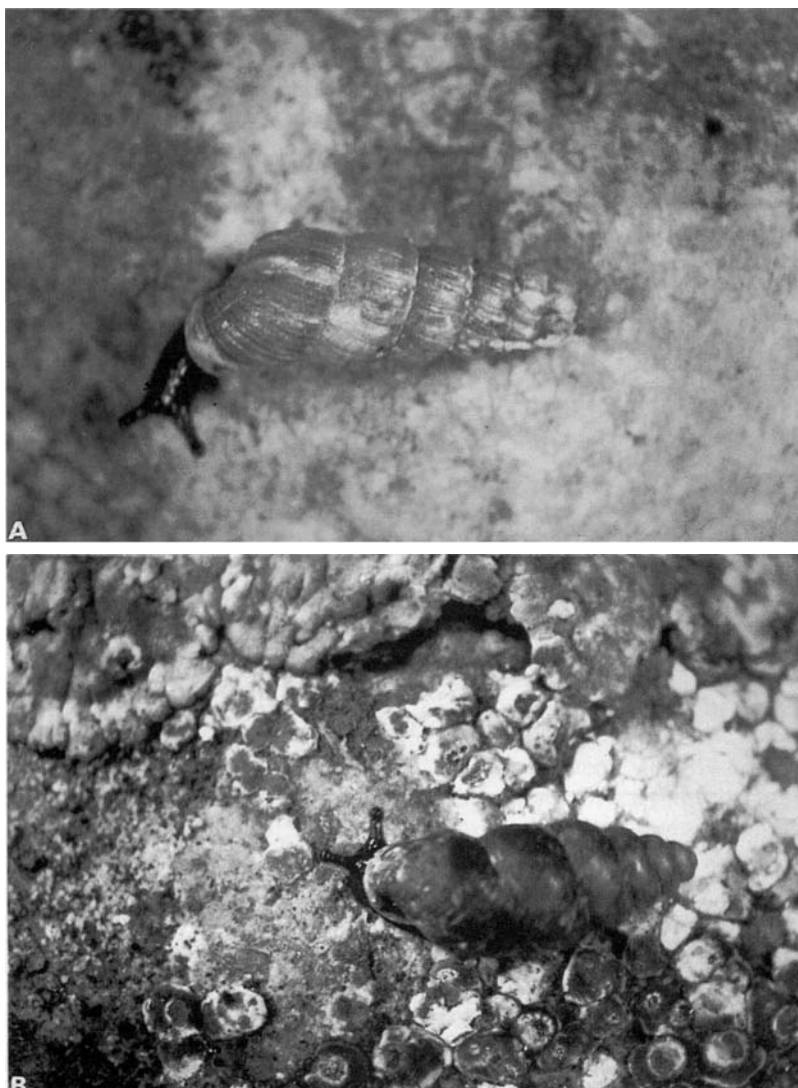


FIG. 1. Adult snails. A, *Balea perversa* (shell height 9.8 mm); B, *Chondrina clienta* (shell height 6.1 mm).

lichen samples were placed in transparent plastic containers lined with paper towelling. Two to 50 adult snails were put on the pieces of limestone (Table 1).

All snails belonged to the same species within each container. To stimulate periodic snail activity, the containers were moistened and kept wet for 12 h and subsequently allowed to dry out for 36 h. For details of snail maintenance see Baur & Baur (1990). To compare grazed and ungrazed lichens on the same piece of stone at the end of the experiment, approximately half of the area with lichen vegetation was covered with opaque tape.

Lichen species were identified microscopically and the damage caused by snail grazing was carefully examined using a dissecting microscope. The level of grazing was classified as follows:

TABLE 1. Number of snails and days they were allowed to graze on a piece of limestone; each line represents one trial

Snail species	No. of snail individuals	No. of grazing days per snail	Size of limestone (mm ²)	No. of lichen species present
<i>Balea perversa</i>	10	10	800	2
	5	10	150	2
	10	25	800	4
<i>Chondrina clienta</i>	10	10	600	5
	10	10	900	6
	7	10	450	2
	5	10	350	3
	10	10	550	2
	5	10	350	1
	3	10	60	1
	3	10	50	2
	7	10	450	2
	10	10	1100	11
	10	10	1400	6
	40	10	1700	6
	10	10	1700	3
50	10	3500	7	
10	6	800	2	
<i>Clausilia bidentata</i>	2	6	200	4
<i>Helicigona lapicida</i>	4	6	2000	8
	7	6	3500	7
	7	6	5000	5
	7	6	3200	4
	2	6	800	3

lichen thalli without photobiont layer exposed (0 = no grazing); less than half of lichen thalli with photobiont layer exposed (+, low level of grazing); more than half of lichen thalli with photobiont layer exposed (++, moderate level of grazing); lichens with most of the thallus including the photobiont layer removed (+++, high level of grazing). If earlier grazing damage had occurred, the damage during the experiment could be determined by comparison with that in the area covered with tape. A four-grade scale was also used to judge ascocarp damage and damage to free-living cyanobacteria. Two slides with faeces were made for each trial to search microscopically for any identifiable remains of lichens and cyanobacteria.

Interspecific comparisons of snail grazing were based on damage to the thalli, except in *Caloplaca holocarpa* and *C. velana*. In the latter species, the ascocarps dominate the surface of the individuals and thus damage to them was used instead. Preferences for type of thallus (endolithic/epilithic), type of alga (green photobiont/cyanobacteria), part of lichen (thallus/ascocarp) and type of ascocarp (apothecium/perithecium) were tested for each snail species with the exception of type of alga in *H. lapicida* and *C. bidentata* and type of thallus in *C. bidentata* where the sample sizes were too low. In another experiment, a mixed-species group (ten *B. perversa* and ten *C. clienta*) were allowed to graze on the lichens on a piece of limestone. However, these data were exclusively used for illustrations (Fig. 2C, D) and not in statistical analyses.

We defined grazing pressure as the total number of snail days a lichen was exposed to grazing (number of individuals multiplied by number of grazing days per snail; Table 1). Since grazing pressure varied among lichen samples (Table 1), we calculated the relative grazing defined as the level of grazing (see above) divided by the grazing pressure and multiplied by 100 (i.e. relative grazing = [level of grazing/grazing pressure] × 100). Relative grazing was used in all comparisons of grazing among the lichens. All statistical analyses were performed using the SAS program package (SAS Institute 1990).

Results

Grazing damage

In most cases, grazing damage by the snails could be easily observed, since the green photobiont layer, which was more or less exposed when grazed, contrasted against the normal thallus colour (Fig. 2C–E). In some cases, the whole thallus was removed (Fig. 2E, F). When the ascocarps were grazed, the hypothecium or lower part of the hymenium was exposed, exhibiting a lighter colour (Fig. 2E). Cyanobacteria were also grazed, as indicated by the lighter colour of the exposed underlying rock surface (Fig. 2B). In a few cases, cyanobacteria on *Aspicilia calcarea* were grazed without the photobiont layer of the underlying lichen being exposed (Fig. 2E).

Table 2 summarizes the damage to various species of lichens due to snail grazing. The damage varied considerably, depending both on the lichen and the snail species. Several lichen species differed in damage to the thallus and ascocarp, even within the same individual.

Faecal remains

Faecal remains and mucous trails from the snails were frequently observed. Faeces were either blackish (containing mainly cyanobacteria), greenish (containing mainly green photobionts from lichens), or whitish (containing mainly limestone granules) (Fig. 2A). In microscopic preparations of the faeces, cyanobacteria were frequently found in large amounts. Free-living cyanobacteria belonged to the genera *Chroococcus*, *Gloeocapsa* and *Gloeotheca* of the family Chroococcaceae (identified by direct microscopic observation of areas previously covered by tape). Cells seemed intact, although the surrounding mucilaginous sheaths were reduced to some extent. In one case, a few *Nostoc* cells of *Collema fuscovirens* were also observed. Green photobionts of the lichens were usually found in small amounts, and almost always damaged. Furthermore, algal cells belonging to the genus *Trentepohlia* were recorded in one case, but no fungal hyphae were observed in the faeces. In a few cases, lichen remains were identified, including a fragment of an apothecium of *Rinodina immersa* consisting of paraphyses and asci with spores. A few *Caloplaca* spores, a spore of *Polyblastia diminuta* and a piece of a hymenium, possibly belonging to a species of *Aspicilia*, were also recorded.

Selective grazing by different snail species

The damage caused by a particular snail species varied among lichen species and, most interestingly, also to some extent between thallus and ascocarp of the same lichen, indicating selective grazing (Table 2). Both *A. calcarea* and *Verrucaria nigrescens* were intensively grazed by *Balea perversa*, *Helicigona lapicida* and *Clausilia bidentata*, and *Tephromela atra* by *B. perversa* (cf. Fig 2C & E), while *Chondrina clienta* did not feed on these three lichen species (Table 2).

Table 3 presents the preferences of the four snail species to epilithic/endolithic lichens, green photobionts/cyanobacteria, thalli/ascocarps and apothecia/perithecia. *Balea perversa* showed no overall preference for endolithic or epilithic lichens, type of alga, or for part of lichen. However,

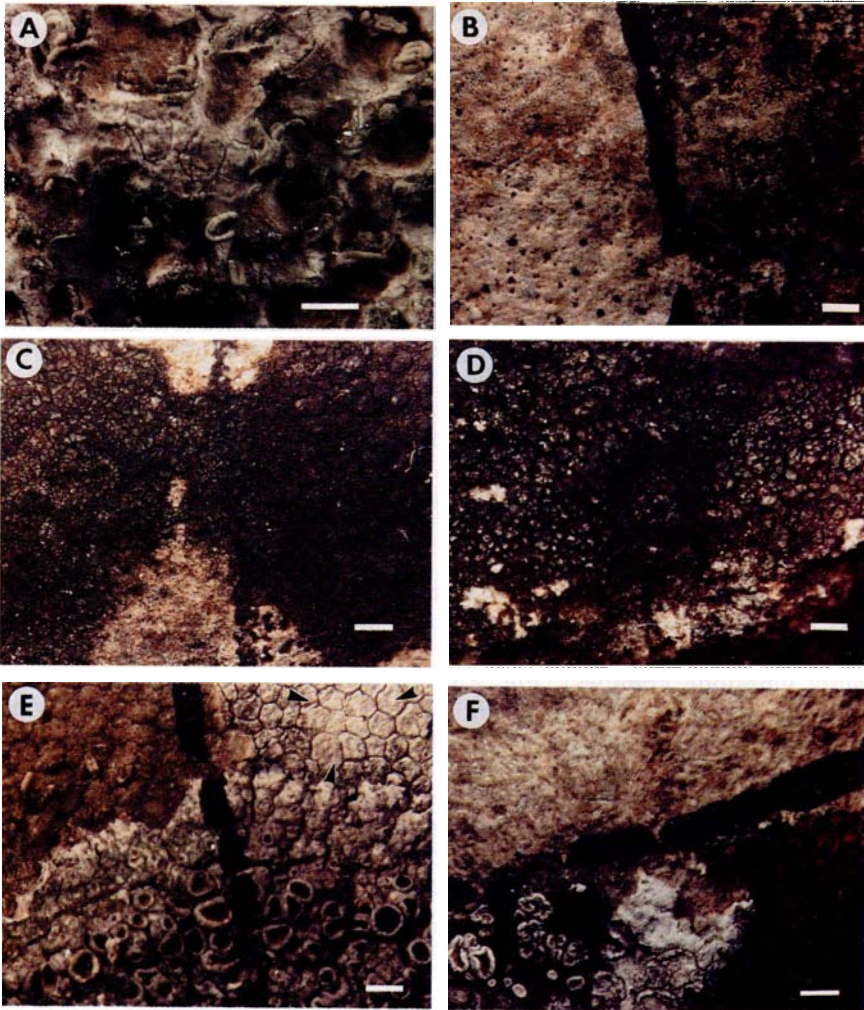


FIG. 2. A, Faecal remains and mucous trails of *Balea perversa*. The faeces are either white (containing mainly limestone granules), green (containing mainly green photobionts) or black (containing mainly cyanobacteria). B, Cyanobacteria grazed by *Chondrina clienta* (left half). The black line separates the grazed and ungrazed areas. The underlying lichen *Clauzadea immersa* is exposed due to grazing. C, *Verrucaria nigrescens* grazed by *B. perversa* and *C. clienta* (left half). The photobiont layer can be seen as green patches where grazing has occurred. D, *Verrucaria glaucina* grazed by *B. perversa* and *C. clienta* (right half). The photobiont layer can be seen as green patches where grazing has occurred. The perithecia that are immersed in the photobiont layer are visible as minute dots within green patches. E, *Tephromela atra* (lower part) and *Aspicilia calcarea* (upper part) grazed by *B. perversa* (left half). The thallus edge of *T. atra* has been more grazed than the central parts, and the apothecia are also slightly grazed, exhibiting a lighter colour. *Aspicilia calcarea* has completely vanished due to the grazing. Note the cyanobacteria on the upper right part of the illustration, growing in thread-like colonies on *A. calcarea*. They have been grazed prior to the experimental grazing, probably by *C. clienta*, without the snails penetrating the lichen beneath (grazed parts indicated by arrows). F, *Lecanora dispersa*, *Aspicilia calcarea* and *Caloplaca velana* grazed by *Helicigona lapicida* (upper half). The epilithic lichen cover has completely vanished due to snail grazing. Scale = 1 mm.

individuals of *B. perversa* preferred to graze on apothecia. *Chondrina clienta* grazed more on epilithic than on endolithic lichens and preferred cyanobacteria to lichens with a green photobiont. Furthermore, *C. clienta* preferred to graze on lichen thalli rather than on ascocarps and on apothecia rather than perithecia. Individuals of *H. lapicida* showed no preferential grazing with respect to type or part of thallus, but preferred to graze on apothecia. *Clausilia bidentata* showed no preferential grazing with respect to part of lichen and type of ascocarp.

Discussion

Several differences in grazing damage were found among the lichen species in this study. In general, *Aspicilia* species, *Caloplaca* species and cyanobacteria were heavily grazed, whereas *Bagliettoa baldensis*, *Clauzadea immersa* and *Verrucaria calciseda* as well as other endolithic species were not or only slightly grazed. Snail grazing may affect the life-history and population dynamics of lichen species, but so far no quantitative information is available on the damage to lichen individuals, or on what happens to lichens after grazing has occurred. If only the upper part of the thallus has been grazed, regeneration of the lichen individual may occur. If the whole thallus has disappeared, either the original lichen individual may recolonize the grazed area, or colonization by other lichens occurs. It has often been argued that regenerated lichen individuals can exhibit new characters. For example, Wunder (1974) claims that *Caloplaca variabilis* may even transform from an epilithic to endolithic appearance when regenerated from severe grazing damage. However, such deductions must be based on careful observations of the different stages during regeneration. Genetic variation within *C. variabilis* is more likely the most important reason for the occurrence of both epilithic and endolithic morphotypes (cf. Fröberg 1989).

The differential grazing damage observed indicates selective snail grazing. The occurrence of species-specific grazing preferences suggests different adaptations of snails to a particular lichen species or, alternatively, differential ingestive conditioning (cf. Wood 1968; Hall *et al.* 1982). The lack of hyphae in the faeces as well as the occurrence of partially digested green photobionts suggest that the grazed lichens provide the snail with nutrients. Furthermore, avoidance of grazing can, in many cases, be explained by the chemical content of the lichen. Lawrey (1980, 1983a) showed that *Aspicilia gibbosa* and *A. cinerea*, both containing the fatty acid aspicilin, were heavily grazed by the slug *Pallifera varia*. In contrast, lichens containing stictic or protocetraric acid were avoided. *Aspicilia calcarea*, which also contains aspicilin, was heavily grazed by three species in this study, but avoided by *C. clienta*.

On coastal cliffs on the island of Bornholm, Denmark, mites and Collembola were associated with *Tephromela atra*, which contains atranorin and α -collatolic acid (Gelstrup & Søchting 1984; Søchting & Gelstrup 1985). Other lichen species containing atranorin were eaten by the slug *P. varia* (Lawrey 1980, 1983a). Similarly, in the present study *B. perversa* fed on *T. atra*, but *C. clienta* avoided this lichen. More detailed experiments are needed to evaluate the underlying mechanisms for these snails' feeding preferences. *Tephromela atra*

TABLE 2. Summary of damage to various species of calcicolous lichens, cyanobacteria and one green alga, due to snail grazing by four species of land snails

Species	Snail species‡	Level of grazing*			
		Thallus	N§	Ascocarp	N
<i>Aspicilia calcarea</i>	<i>Bp</i>	+++	1	+++	1
	<i>Cc</i>	(+)	5	(+)	5
	<i>Cb</i>	+++	1	—	
	<i>Hl</i>	+++	3	+++	2
<i>A. contorta</i> agg.	<i>Hl</i>	+++	1	+++	1
<i>A. contorta</i> subsp. <i>contorta</i>	<i>Cc</i>	+	1	++	1
<i>A. contorta</i> subsp. <i>hoffmanniana</i>	<i>Cc</i>	++	2	++	2
	<i>Hl</i>	+++	1	+++	1
<i>Bagliettoa</i> cf. <i>baldensis</i>	<i>Cc</i>	0	2	0	2
<i>Buellia epipolia</i>	<i>Cc</i>	+	1	0	1
<i>Caloplaca citrina</i>	<i>Cc</i>	++	1	+	1
	<i>Hl</i>	+++	3	+++	1
<i>C. holocarpa</i>	<i>Cc</i>	0	1	++	1
<i>C. saxicola</i>	<i>Hl</i>	+++	1	+++	1
<i>C. variabilis</i>	<i>Bp</i>	+++	1	+++	1
	<i>Cc</i>	++	1	0	1
<i>C. velana</i>	<i>Cc</i>	++	2	+	2
	<i>Hl</i>	+++	1	+++	1
<i>Catillaria lenticularis</i>	<i>Cc</i>	+	1	0	1
	<i>Hl</i>	+++	1	+++	1
<i>Clauzadea immersa</i>	<i>Cc</i>	0	8	(+)	8
<i>Collema fuscovirens</i>	<i>Bp</i>	+	1	—	
	<i>Cc</i>	0	1	—	
Cyanobacteria	<i>Cc</i>	++	7	—	
<i>Farnoldia jurana</i>	<i>Cc</i>	+	1	—	
<i>Gyalecta subclausa</i>	<i>Cc</i>	0	1	0	1
<i>Lecania rabenhorstii</i>	<i>Cc</i>	++	1	++	1
<i>Lecanora albescens</i>	<i>Cc</i>	+	1	0	1
	<i>Hl</i>	+++	2	+++	2
<i>L. crenulata</i>	<i>Cc</i>	0	1	0	1
<i>L. dispersa</i> s. lat.	<i>Hl</i>	+++	1	+++	1
<i>L. dispersa</i> type II	<i>Cc</i>	0	1	+	1
<i>Phaeophyscia nigricans</i>	<i>Hl</i>	+++	2	—	
<i>Physcia adscendens</i>	<i>Cc</i>	0	1	—	
<i>Protoblastenia rupestris</i>	<i>Cb</i>	+++	1	+++	1
<i>Rimodina bischoffii</i>	<i>Cc</i>	0	1	0	1
<i>R. immersa</i>	<i>Bp</i>	+	1	++	1
	<i>Hl</i>	++	3	++	3
<i>Staurothele caesia</i>	<i>Cc</i>	0	1	0	1
<i>S.</i> cf. <i>guestphalica</i>	<i>Bp</i>	+	1	0	1
<i>Tephromela atra</i>	<i>Bp</i>	++	1	++	1
	<i>Cc</i>	0	1	0	1
<i>Thelidium decipiens</i>	<i>Cc</i>	+	4	0	4
	<i>Hl</i>	++	2	++	2
<i>Trentepohlia</i> sp.	<i>Cc</i>	++	1	—	
<i>Verrucaria calciseda</i>	<i>Cc</i>	0	3	0	3
	<i>Hl</i>	+	2	+	2
<i>V. caerulea</i>	<i>Cc</i>	+	2	+	2
<i>V. dufourii</i>	<i>Cc</i>	+	2	0	2
<i>V. glaucina</i>	<i>Cb</i>	++	1	++	1

TABLE 2. *Continued*

Species	Snail species‡	Level of grazing*			
		Thallus	N§	Ascocarp	N
<i>V. macrostoma</i>	<i>Hl</i>	++	1	++	1
<i>V. muralis</i>	<i>Bp</i>	+	1	0	1
<i>V. nigrescens</i>	<i>Bp</i>	++	1	++	1
	<i>Cc</i>	+	3	0	1
	<i>Cb</i>	++	1	++	1
	<i>Hl</i>	++	3	++	3

*Four levels of grazing were distinguished: no grazing (0), low (+), moderate (++), and high (+++) grazing.

‡*Bp* = *Balea perversa*, *Cc* = *Chondrina clienta*, *Cb* = *Clausilia bidentata*, *Hl* = *Helicigona lapicida*.

§N = Number of observations.

and *A. calcarea* are most abundant on stone walls, where *B. perversa* occurs at high densities. Most interestingly, the grazing damage by *B. perversa* on *T. atra* was more severe at the edge of the thallus (Fig. 2E), which presumably is the youngest part of the lichen. The arguments by Lawrey (1984: 254) that the protection against grazers by secondary metabolites is most important in young, metabolically active parts of the thalli stresses the fact in our study that none of the secondary metabolites in *T. atra* acts as an antiherbivore agent against *B. perversa*.

Verrucaria nigrescens does not contain any secondary metabolites. Consequently, other factors might be responsible for the low grazing rate of *C. clienta*. Perhaps the carbonized tissue of *V. nigrescens* is less attractive to snails than non-carbonized tissues of other lichens. All *Caloplaca* species were intensively grazed by the snails. Thus, their content of parietin and related substances does not seem to adversely affect snail grazing (cf. Fröberg 1989).

Collema fuscovirens, the only lichen in this study with cyanobacteria as photobiont, was not grazed by *C. clienta* and hardly by *B. perversa*. This contrasts with the finding that *C. clienta* readily fed on free-living cyanobacteria. Gerson (1973) reported the resistance of gelatinous lichens to invertebrate feeders. This could also be a reason for the avoidance by the snails in the present investigation. Avoidance of lichens with cyanobacteria as photobiont by *Clausilia* species, was also reported in the case of *Sticta canariensis-dufourii* by James & Henssen (1976).

The grazing damage caused by the four snail species was compared with some properties of the lichens (Table 3). The damage to epilithic lichens by *Chondrina clienta* was significantly larger than that to endolithic ones. The high proportion of endolithic species on calcareous rocks in the area studied may in part be induced by invertebrate herbivores. However, neither the grazing of *Balea perversa* nor *Helicigona lapicida* showed any significant damage as to type of thallus.

Chondrina clienta also showed a significant preference for cyanobacteria (mainly free-living), compared with green photobionts in lichens (Table 3).

TABLE 3. Grazing preferences of four species of land snails with respect to type of thallus, type of alga, part of lichen, and type of ascocarp

Comparison*	Snail species						
	<i>Balea perversa</i>		<i>Chondrina clienta</i>		<i>Helicigona lapicida</i>		
	Preference	P†	Preference	P	Preference	P	
Type of thallus (endolithic/epilithic)	None	>0.8	Epilithic	<0.001	—	None	>0.1
Type of alga (green photobiont/cyanobacteria)	None	>0.6	Cyanobacteria	<0.001	—	—	—
Part of lichen (thallus/ascocarp)	None	>0.9	Thallus	<0.05	None	None	>0.6
Type of ascocarp (apothecium/perithecium)	Apothecium	<0.05	Apothecium	<0.05	None	Apothecium	<0.05

*Preferences are based on differences in relative grazing on lichen species listed in Table 2 (see Materials & Methods).

†P = values from Mann-Whitney U-tests.

Although the cyanobacterial cells in the faeces were intact, their sheaths, presumably containing polysaccharides (Mehta & Vaidya 1978), were probably consumed. Furthermore, free-living cyanobacteria leak both polysaccharides and combined nitrogen (Mehta & Vaidya 1978). For example, *Anabaena* sp. was reported to secrete polypeptides and shorter peptides, with a high proportion of serine, and polysaccharides, mostly consisting of galactose and glucose (Paerl 1982). In this way the snails can benefit from the cyanobacteria without the energy-consuming breakdown of their cell walls. The cover of cyanobacteria on limestone pavements has almost completely vanished in the vicinity of certain crevices inhabited by individuals of *C. clienta*. The snails graze on the rock surface under conditions of high air humidity, leaving a conspicuous light zone on both sides of the crevice, which is dominated by *Clauzadea immersa*. An illustration of these crevices is given in Fröberg (1989: 9), where the light zone was wrongly inferred to be caused by weathering processes. No significant preference for type of alga was found in the grazing damage caused by *B. perversa*.

When comparing grazing damage to different parts of the same lichen, the thallus was more grazed than the ascocarps by *C. clienta* (Table 3). Lawrey (1984: 254) argued that protection against grazing is expected to be larger in the reproductive tissue than in vegetative tissue. It is possible that some of the lichen species contain substances in the hymenium that prevent grazing to some extent. The other three snail species showed no preference for different parts of the lichen.

Finally, the grazing damage to the apothecia was significantly higher than to the perithecia in the case of *B. perversa*, *C. clienta* and *H. lapicida* (Table 3). This is most probably due to the fact that perithecia in most of the lichen species studied are immersed in the substratum and thus protected. However, the carbonized excipulum surrounding the generative tissue in almost all species with perithecia could also play an important role for protection against grazers. The apothecia of *Clauzadea immersa*, which are immersed and have a carbonized excipulum, were almost completely avoided by the snails. Further investigations are needed to understand the complex interactions between lichens and their herbivores in the area studied.

We are grateful to Prof. V. Ahmadjian for comments on the manuscript. We also thank the staff at the Ecological Research Station of Uppsala University on Öland for their hospitality. Financial support has been provided by Lunds Botaniska Förening (grant to L. Fröberg), and the Swiss National Science Foundation (grant No. 31-26258.89 to B. Baur).

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Accepted for publication 26 March 1992

