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Standard Paper

A new experimental approach to investigate grazing on epiphytic lichens by gastropods in a controlled laboratory environment

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Abstract

The grazing impact on epiphytic lichens by a non-native gastropod species is documented and quantified for the first time in the province of Newfoundland and Labrador using a unique combination of a multiple-choice feeding design with lichen transplant techniques under controlled laboratory conditions. The feeding experiment included three arboreal lichen species sewn onto a mesh and attached to red maple sticks inside a terrarium where four *Cepaea nemoralis* snails were introduced and allowed to graze over a five-day period. The three lichen species used in the feeding trials included the green-algal *Platismatia glauca*, the cephalolichen *Lobaria pulmonaria*, and the cyanolichen *Lobarina scrobiculata.* The trials also included two sets of *L. pulmonaria* from different regions of the island of Newfoundland. The levels of grazing and preference by the snails was very high. Herbivory was high for all lichen species but was highest for *Platismatia glauca*, for which 70% of thalli were consumed after only 24 hours. Our results show that *C. nemoralis* is probably affecting the distribution and abundance of epiphytic lichens in the forests of Newfoundland and Labrador. Furthermore, our observations of intense herbivory on reproductive structures challenges the universal application of the optimal defence theory in lichens.

Keywords: *Cepaea nemoralis*; herbivory; *Lobaria*; *Lobarina*; Newfoundland; *Platismatia glauca*

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Introduction

Epiphytic lichen communities are sensitive to environmental change and are often used as indicators to monitor the effect of different stressors on the integrity of forest ecosystems (McCune 2000; Nimis *et al.* 2002; Thormann 2006; Giordani *et al.* 2012; Li *et al.* 2013; Nascimbene *et al.* 2013). Examples of stressors affecting lichen communities include air pollution (LeBlanc & Sloover 1970), the removal of suitable habitat (Arsenault & Goward 2016), change in microclimate through natural and anthropogenic disturbances (Boudreault *et al.* 2013), conversion of old-growth forests to younger forests and plantations (Goward & Arsenault 2018), interspecific competition (Armstrong & Welch 2007), and grazing (Smith 1921).

Epiphytic lichens are also an important food source for a wide variety of animals, ranging from large vertebrates such as mountain caribou (Goward & Campbell 2005) and deer (Hodgman & Bowyer 1985; Ward & Marcum 2005; Lefort *et al.* 2007) to voles (Dubay *et al.* 2008), squirrels (Maser *et al.* 1985; Hayward & Rosentreter 1994) and invertebrates such as mites, collembola, woodlice and gastropods (Gerson 1973; Gerson & Seaward 1977; Seyd & Seaward 1984; Lawrey 1987; Reutimann & Scheidegger 1987; Prinzing 1997; Wieners *et al.* 2018).

In Europe, gastropods have received considerable attention as important lichen grazers (Benesperi & Tretiach 2004; Gauslaa 2005, 2008; Gauslaa *et al.* 2006; Asplund & Gauslaa 2008; Asplund 2010; Asplund *et al.* 2010*a*, *b*, *c*; Vatne *et al.* 2010; Fröberg *et al.* 2011; Černajová & Svoboda 2014; Boch *et al.* 2015, 2016). Lichenivorous gastropods can influence epiphytic lichen abundance, diversity and distribution. Grazing can influence the distribution of lichen species in forest canopies, with more susceptible species being restricted to higher positions on trunks (Asplund *et al.* 2010*b*), on thin *Picea* twigs (Gauslaa 2008), on trees with lower bark pH and available calcium (Asplund *et al.* 2018), and to areas where there is less grazing pressure (Gauslaa 2008; Vatne *et al.* 2010). For instance, gastropods have been shown to limit the distribution of *Lobaria pulmonaria* (L.) Hoffm. in calcareous deciduous forests and to limit establishment of the species by feeding on juvenile lobes (Asplund & Gauslaa 2008; Vatne *et al.* 2010). Fröberg *et al.* (2011) found that snail grazing decreases overall lichen diversity along cracks in limestone pavement, while another study by Boch *et al.* (2016) showed that gastropod grazing maintained lichen species richness on European beech over a six-year period by controlling the growth of algae and crustose lichens.

In North America, there has been comparatively little research on lichen grazing by invertebrates. Here most reports of lichen grazing seem to be in eastern North America (Clyne *et al.* 2019) but see Cornejo & Dillman (2017), who suggest herbivory on *Ricasolia quercizans* (Michx.) Stizenb. specimens obtained from Alaska, USA. Although several reports have identified gastropods as a

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threat to rare lichens in Canada (e.g. Richardson *et al.* 2015), it appears that this information is mostly anecdotal or inferred from damage patterns on thalli and presence of gastropods, with little or no direct evidence of feeding (Cameron 2009). It has also been hypothesized that some damage to *Erioderma mollissimum* (Samp.) Du Rietz may be due to mites (Cameron *et al.* 2009) but this has not yet been clearly documented. In Nova Scotia, Cameron (2009) observed damage on one thallus of *Erioderma pedicellatum* (Hue) P.M. Jørg. consistent with feeding tracks of gastropods and in subsequent surveys of gastropods on trees found that the dominant species was the non-native slug *Arion subfuscus.* Although Cameron's study also found other species of lichen with similar damage, including *Lobaria pulmonaria*, *Parmelia squarrosa* Hale, *Parmelia sulcata* Taylor and *Platismatia glauca* (L.) W.L. Culb. & C.F. Culb., no direct lichen grazing by gastropods was observed *in situ.* The only published record of direct gastropod grazing on lichens was in New Brunswick, where Asplund (2010, 2011*a*) observed a species of snail, *Anguispira alternata*, and a species of slug, *Arion subfuscus*, grazing *Lobaria pulmonaria* thalli.

While carrying out lichen surveys throughout Newfoundland, we have observed grazing marks on many of the epiphytic lichen thalli we encountered. Grazing marks have been observed in many forest regions of Newfoundland, including Central and Western Newfoundland, and the Avalon and Great Northern Peninsulas. The level of observed grazing damage varies, but in some areas can be quite severe, with some *Lobaria pulmonaria* thalli having a lacy appearance and some *Parmelia squarrosa* thalli completely missing an upper cortex. Occasional sightings of slugs and snails grazing on these epiphytes give rise to questions about the grazers responsible for the damage being observed.

One snail observed grazing on *Lobaria* species locally was *Cepaea nemoralis* (Fig. 1), a species that was introduced to North America from Europe (Örstan 2010). Layton *et al.* (2019) indicate that the distribution of *C. nemoralis* in Canada is the result of multiple introductions. *Cepaea nemoralis* is a generalist known to feed on lichens (Peake & James 1967). It occurs in a wide range of habitats, including dunes, meadows and woodlands, and shows a preference for habitats associated with humans (Cook 1998; Rosin *et al.* 2017). Observations of grazing damage by gastropods suggest that they may present a threat to epiphytic cyanolichens (Gauslaa 2008; Cameron 2009; Asplund 2011*a*). However, there has been no research into how gastropods may be influencing lichen populations and communities in Canada and almost none in North America, except for one study in New England by Clyne *et al.* (2019).

Figure 1. *Cepaea nemoralis* on a thallus of *Ricasolia quercizans* transplant in Corner Brook, Newfoundland and Labrador.

In this study, we use a new experimental approach combining lichen transplant techniques with a multiple-choice feeding experiment in the laboratory to investigate the preferences of *C. nemoralis* for three local epiphytic lichen species, a common chlorolichen species and two less common *Lobariaceae* species (a cephalolichen and a cyanolichen). The aim of the study is to quantify for the first time in the province the level of grazing and preference by this non-native gastropod on epiphytic lichens, using an experimental approach under controlled laboratory conditions.

Methods

Three foliose lichen species were used in the feeding experiment: *Platismatia glauca*, *Lobarina scrobiculata* (Scrop) Nyl. and *Lobaria pulmonaria. Platismatia glauca* is a common epiphyte on the boles and branches of conifers in Newfoundland, while the *Lobariaceae* species are less common, being found predominantly on deciduous trees but also on some conifers under special conditions. *Platismatia glauca*, *L. scrobiculata* and one set of *L. pulmonaria* (A) thalli were collected in the autumn of 2017 from *Abies balsamea* branches within a treed bog, in Hall's Gullies, south-eastern Newfoundland (47.37549°N, 53.44069°W). A second set of *L. pulmonaria* (B) thalli was collected in August 2018 from *Acer rubrum* stems in a mixed forest stand in the Corner Brook area of western Newfoundland (48.93001°N, 57.9095013°W). The *L. pulmonaria* A from Hall's Gullies had little to no previous grazing damage while the Corner Brook thalli had moderate grazing damage. All lichen thalli were air-dried and stored in paper bags at room temperature before the start of the experiment in the autumn of 2018.

Approximately one week before the start of the experiment, 16 snails (*Cepaea nemoralis*) were collected opportunistically from the trunk of *Prunus padus* and a garage siding in the city of Corner Brook. The snails were kept in plastic containers with perforated lids and fed a mixed diet of lettuce, *Lobarina scrobiculata*, *Lobaria pulmonaria* and *Platismatia glauca.* The snails were not starved before the experiment.

Experimental design

In the laboratory, lichen thalli were cleaned of tree bark and bryophytes, then cut into pieces of roughly similar sizes. Twenty-five pieces/thalli of each lichen species (for simplicity, *L. pulmonaria* A and B will be referred to here as separate species) were weighed and the air-dry weights recorded. The air-dry weights were also converted to oven-dry weights (oven-dried at 70 °C for 24 h) using a correction factor, obtained by using the oven-dry weights from five additional, sacrificed thalli. The mean dry weights for the lichen thalli used in the experiment were 0.147 g for *Lobaria pulmonaria* A, 0.148 g for *L. pulmonaria* B, 0.143 g for *Lobarina scrobiculata*, and 0.057 g for *Platismatia glauca.* The thalli were hydrated for at least 15 min, then each thallus was quickly patted dry to remove excess water and the wet weight was recorded. While still hydrated, each thallus was flattened under a piece of Plexiglass with a 1 cm scale and photographed using a Nikon DSLR D5100 camera equipped with an AF-S Micro-Nikkor 105 mm f/2.8G lens. Before and after photographs were later used for reference purposes and to help describe grazing patterns.

The *Lobaria pulmonaria* A thalli, collected from Hall's Gullies in 2017, were observed to produce a reddish brown discoloration on

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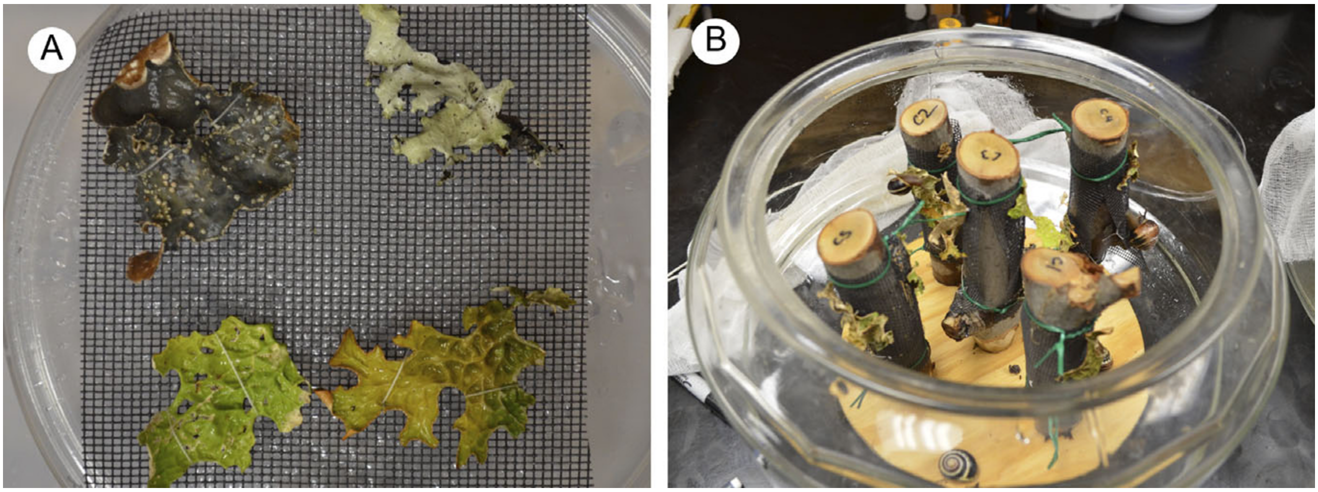

Figure 2. Experimental set-up. A, the four lichen thalli sewn onto a mesh. B, the mesh attached to maple sticks and placed upright in a glass terrarium.

the paper towel when hydrated, an observation not seen in any of the other species.

Four thalli, one of each lichen species, were randomly positioned and sewn onto a 10 cm × 10 cm piece of nylon mesh using nylon thread (Fig. 2A). Twenty-five mesh were prepared in this way. Each mesh was sprayed with distilled water to hydrate the thalli, photographed and then fastened to a section of young *Acer rubrum* stem, *c.* 3 cm in diameter × 15 cm in length, using twist ties. We chose to mount the transplants on *Acer rubrum* sticks because studies have shown that there is a greater amount of grazing on lichens growing on deciduous trees and that slugs and snails are more apt to climb on trees rather than artificial substrata (Asplund & Gauslaa 2008; Asplund 2010; Asplund *et al.* 2018). Five glass terrariums were set up with a flat, round, wooden disc placed at the bottom into which five holes had been pre-drilled. A stick with an attached mesh was inserted into each of the five holes in the wooden disc so that the sticks stood upright in the terrariums (Fig. 2B). The experiment consisted of five terrariums, each containing five sticks with one attached mesh and one thallus of each lichen species per mesh so that there were five thalli per species per terrarium.

Our approach requires the snails to feed while climbing the maple stick to consume lichens. To our knowledge, this is the first laboratory experiment of this kind, since all others have placed lichens and snails together directly into containers.

Four snails were placed in each of four terrariums, leaving the 5th terrarium as a control. To account for individual snail feeding variability and variation in snail size, we randomly chose the four snails to add to each terrarium. Snail size, however, has been shown to have little effect on consumption in feeding trials (Hanley *et al.* 2003). A piece of cheesecloth was secured over the top of each terrarium, and they were sprayed liberally with distilled water 2 to 3 times daily. The terrariums were kept at room temperature in a laboratory without natural light, so the lights were left on for *c.* 6–8 h during the day.

After 24 h, each mesh was carefully removed, the lichen thalli were hydrated, and the mesh photographed. The mesh was then carefully re-affixed to its corresponding stick. The number of thalli that were completely consumed was noted at this time. A thallus was considered completely consumed if no biomass remained on the mesh. This procedure was repeated after 48 h and finally after 120 h, at which time the snails and all mesh were removed from the terrariums. Any remaining thalli were collected from the mesh and the final hydrated thallus weights were obtained. The remaining thalli were individually photographed under plexiglass at the end of the experiment. The thalli were air-dried for at least 48 h before final dry weights were measured.

The experiment was repeated a second time using new thalli from the same collections of lichen material and using the same snails which were again randomly distributed between the four experimental terrariums. In between trials, snails were fed a mixed diet of lettuce, *Lobaria pulmonaria*, *Lobarina scrobiculata* and *Platismatia glauca.*

Data analysis

The amount of snail grazing was calculated as the mean percent loss in lichen air-dry mass. We did not perform an analysis on absolute weight loss because initial weights between species were different due to their morphology. The dry mass was summed for each species on the five sticks/mesh per terrarium before and after grazing. A single value for mean percent dry mass change was then calculated for each species per terrarium and for each species per trial. The terrarium was used as the sample unit to report mean and standard error of dry mass loss of each species, separately for each trial session (Appendix A). We used this approach instead of a nested analysis design to avoid pseudoreplication (Hurlbert 1984). The assumption of normality for each lichen was evaluated in Excel by comparing the mean and median of percentage dry mass loss for all experimental terrariums combining both trials ($n = 8$) and examining box plots and normal probability plots. We also conducted Shapiro Wilk tests. An Anova was performed using the same data and post-hoc paired *t*-tests; however, because one of the lichen taxa examined had no variance, we used a non-parametric Kruskal-Wallis test and post-hoc Mann-Whitney U test and are not presenting the results of the Anova in this paper. All statistical tests were performed with SYSTAT 13. There was a single control value for each species and trial session. A slight loss in dry mass in the control thalli was observed by the end of the experiment, indicating that some autogenic changes had occurred, but experimental differences were robust and clear between controls and three of the grazed lichen species. One species, *Lobaria*

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pulmonaria B, clearly showed no difference with the control. Due to the robustness of the experiment and the unequivocal experimental response, no statistical tests are presented on the difference between the experimental terrariums and the control.

The consumption rate was given as the total number of lichen thalli completely consumed after 24, 48 and 120 h of snail grazing. Consumption rate of the four lichen species was compared for trials 1 and 2. Complete consumption meant that no thallus remnants remained on the mesh. Although some remnants of all lichen thalli grazed by the snails fell to the bottom of the terrariums, we considered that as being lost, as it would be in nature if it fell to the forest floor. In addition, these thallus remnants represented very small amounts, *c.* 4% of original wet weight. This was assessed only in the first trial since the patterns were similar in the second trial.

To determine the amount of extractable carbon-based secondary compounds (CBSCs) in the thalli used in the feeding trials, the acetone rinse method described by Solhaug & Gauslaa (2001) was employed. Four extra, intact thalli of each species were placed in separate glass vials with 5 ml of 100% acetone and left at room temperature. After 20 min, each thallus was removed and placed in a clean vial. The extraction was repeated three more times for a total extraction time of 80 min. After acetone extraction, the thalli were allowed to air-dry for 48 h and a final dry weight was recorded. The mean percentage loss in air-dry mass was calculated for each species and compared between species using paired *t*-tests.

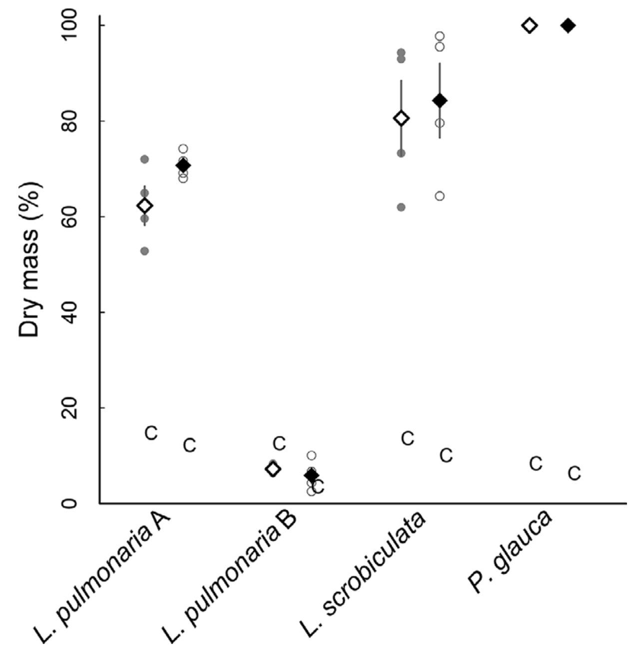

Figure 3. The mean percentage loss in dry lichen mass after 120 h of exposure to grazing by *Cepaea nemoralis.* ◇ = trial 1, ◆ = trial 2, C = control. Means ± SEs; *n* = 4 grazed terrariums per trial, *n* = 1 control per trial. Small symbols are results for individual terrariums. Lichen species included in the trials were *Lobaria pulmonaria*, *Lobarina scrobiculata* and *Platismatia glauca.*

Results

The severity of grazing on lichen thalli for all species used was extreme except for *Lobaria pulmonaria* B, which was collected locally in Corner Brook before the start of the experiment (Appendix A, Fig. 3). The differences between the relative dry weight consumption of all four lichen types used in the experiment were significant (Kruskal-Wallis test statistic: 27.633, $P < 0.001$). *Cepaea nemoralis* appeared to show a preference for *Platismatia glauca* early in the experiment. In trial 1 of the experiment, it was observed that when the snails were introduced into the terrariums they began to climb towards the top and, after just 30 min, 77% of snails occupying positions on lichen thalli were located on *P. glauca.*

The mean percentage loss in dry mass for *P. glauca* was 100% by the end of trials 1 and 2, significantly more than for the other species (Appendix A, Fig. 3). At the end of trials 1 and 2, the percentage loss in dry mass of *L. scrobiculata* and *L. pulmonaria* A was also quite high. Biomass loss was 80.6% and 84.3% for *L. scrobiculata* and 62.3% and 70.8 % for *L. pulmonaria* A for trials 1 and 2, respectively (Appendix A, Fig. 3). Among all species, the level of grazing was significant using the paired *t*-test and Mann-Whitney U test, pooling the eight replicates across the two trial sessions (Table 1).

To demonstrate the observed preference for *P. glauca* more clearly, the number of thalli that were completely consumed was tallied after 24, 48, and then finally after 120 h of exposure to grazing (Fig. 4). It was observed that in trials 1 and 2 respectively, 80% and 60% of the *P. glauca* thalli were consumed within the first

Table 1. Results from a paired *t*-test (left) and Mann-Whitney U test (right) comparing the loss in dry mass between lichen species after 120 hours of grazing by *Cepaea nemoralis.* Data was pooled for the 8 replicates across the two trial sessions. The distributions of lichens across the 8 replicates were normal using a Shapiro-Wilk test (LPA $P = 0.31$, LPB $P = 0.82$, LS $P = 0.13$) except for *Platismatia glauca.* Note that for comparisons involving *P. glauca* for which there is no variance, there is no sampling error and hence 0% chance that sampling error created the observed difference. LPA = *Lobaria pulmonaria* A; LPB = *L. pulmonaria* B; LS = *Lobarina scrobiculata*; PG = *Platismatia glauca.*

	Paired Differences					Mann-Whitney statistics, df = 1		
	Mean	Std of difference	*t*	df	*P*	Rank	U Stat	*P*
LPA - LPB	59.936	7.97	21.269	7	0.000	100–36	64	0.01
LPA - LS	15.907	5.958	2.670	7	0.032	49–87	13	0.04
LPA - PG	33.463	7.199	13.147	7	0.000	36–100	0	0
LPB - PG	93.399	2.304	114.65	7	0.000	36–100	0	0
LPB - LS	75.843	14.949	14.350	7	0.000	36–100	0	0.001
LS - PG	17.556	14.624	3.396	7	0.012	36–100	0	0

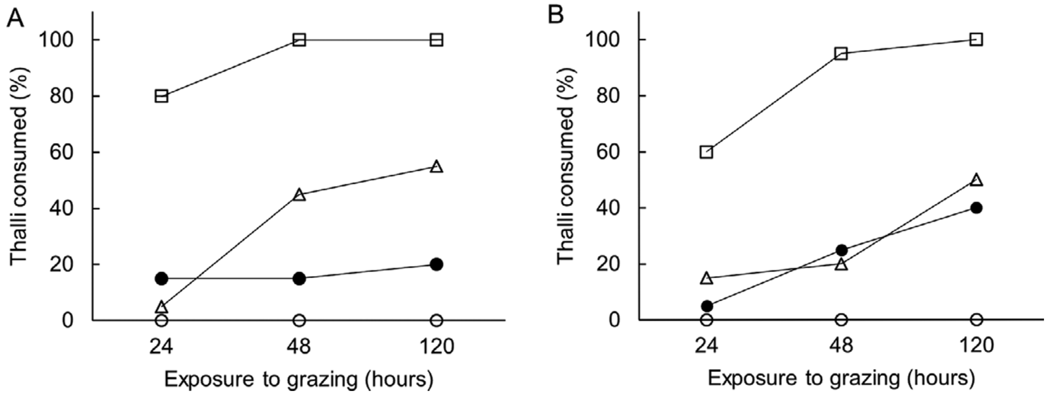

Figure 4. The percentage of lichen thalli completely consumed by *Cepaea nemoralis* over a 120-h period. A, trial 1. B, trial 2. ● = *Lobaria pulmonaria* A, ○ = *L. pulmonaria* B, Δ = *Lobarina scrobiculata*, □ = *Platismatia glauca*. *n* = 20 thalli of each species per trial.

24 h; after 48 h, 100% and 95% of *P. glauca* thalli had been completely consumed. Once the snails had consumed all the *P. glauca* thalli, they were forced to feed on the other species. There was an increase in the number of *L. scrobiculata* and *L. pulmonaria* A thalli consumed between 48 and 120 h, with 55% and 50% of the *L. scrobiculata* thalli and 20% and 30% of the *L. pulmonaria* A thalli completely consumed by the end of trials 1 and 2, respectively. None of the *L. pulmonaria* B thalli were completely consumed over the course of the two trials. The trends were consistent across all the experimental terrariums (Appendix B). We could not statistically compare the absolute mass loss consumed because the initial weights of the lichens were different and using equal weights with our experimental set-up would have been impossible. However, in another experiment where we used equal weights of a *Lobariaceae* lichen and *Platismatia glauca*, we observed the same grazing preference by the snails.

We observed interesting variations in the patterns of grazing on *L. pulmonaria* A and *L. scrobiculata* by *C. nemoralis.* On some of the *L. pulmonaria* A there were grazing marks along the ridges where just the upper cortex and photobiont layer were removed, but most of the grazing marks consisted of holes through all layers of the thallus. On *L. scrobiculata*, grazing marks consisted of holes through the upper cortex exposing the white medulla beneath, and white rimmed holes through all thallus layers. The soralia of *L. scrobiculata* were often grazed by the snails (Appendix C). On two occasions, snails removed apothecia from *L. pulmonaria* B but did not graze the thallus. These observations are consistent with damage seen on lichen thalli in the forests of Newfoundland, although the level of damage varies considerably across the island.

The mean percentage of lichen dry mass of extractable compounds in the four lichens used in the feeding experiment are presented in Appendix A. *Lobarina scrobiculata* had a significantly greater percentage of secondary compounds than did *P. glauca*, which had the lowest amount ($P = 0.002$). According to paired *t*-tests, there were no significant differences in the % dry mass of extractable compounds between the other pairs of lichen species.

Discussion

Using the multiple-choice feeding experiment, we were able to observe and document the feeding of an introduced snail species on three local epiphytic lichen species. We found that *Cepaea nemoralis* prefers the common green-algal lichen *Platismatia glauca* compared to the two generally less common, N-fixing *Lobariaceae* species. Several other studies using feeding trials have found that gastropods prefer the more abundant lichen species (Baur *et al.* 1995; Boch *et al.* 2015; Clyne *et al.* 2019). Clyne *et al.* (2019) found that the two most abundant lichen species used in their feeding trials, *P. glauca* and *Hypogymnia physodes* (L.) Nyl., were grazed more heavily by both the native and non-native slugs. Our results also agree with the findings of Asplund & Wardle (2013), who carried out feeding bioassays using the snail species *Cepaea hortensis* and 28 different lichen species, including *P. glauca* and *L. pulmonaria.* They found that for foliose lichens, consumption rates were significantly higher for chlorolichens than for N-fixing lichens.

Platismatia glauca used in this experiment had a lower % dry mass of CBSC's than the other species, although only significantly less than *L. scrobiculata.* This could have been a reason why *P. glauca* was preferred by the snails but the relationship between palatability and the concentration of secondary compounds is a complex one (Asplund *et al.* 2010*c*). *Platismatia glauca* contains atranorin and caperatic acids, whereas the *Lobariaceae* species contain stictic acid and related compounds (Gauslaa 2005; Asplund *et al.* 2010*c*). Stictic acid is known to deter herbivores, whereas atranorin does not (Gauslaa 2005). In addition, the thallus of *P. glauca* is thin and soft when wet so thallus texture also may have influenced snail preference. Speiser (2001) mentioned that softer plant leaves tend to be more readily eaten by gastropods.

Surprisingly, the snails grazed on older *L. pulmonaria* A thalli from eastern Newfoundland but almost completely avoided fresher *L. pulmonaria* B from western Newfoundland. It is especially surprising since almost all the *L. pulmonaria* B thalli had been previously grazed by gastropods. The *L. pulmonaria* A thalli from eastern Newfoundland had been collected months prior to the experiment and stored at room temperature in paper bags. It was noticed that during processing the thalli produced a rusty brown discoloration when hydrated. Asplund & Wardle (2012) found that senesced thalli of *L. pulmonaria* and *L. scrobiculata* produce a red leachate when moistened. They found that senescence in *L. pulmonaria* thalli decreases the concentration of secondary compounds, such as stictic acid, making the lichen more palatable. The *L. pulmonaria* B thalli did have a higher %

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Table 2. List of studies using laboratory feeding trials and transplant experiments in the field to investigate gastropod grazing on epiphytic lichens.

Author(s)	Location	Experimental design	Herbivore	Lichen species	Grazing metric	Duration	Thallus dry weight or size used
Laboratory Feeding Experiments							
This paper	Canada	Multiple-choice – 4 thalli on 5 separate mesh on sticks in a container with 4 snails	*Cepaea nemoralis*	*Lobaria pulmonaria* *Lobarina scrobiculata* *Platismatia glauca*	Loss in dry mass and # of thalli consumed	5 d	57–148 mg
Clyne *et al*. 2019	USA	Multiple-choice – 1st exp. – 4 thalli in a container with 1 snail or slug 2nd exp. – 7 thalli in a container with 1 slug	4 gastropod taxa	7 species including *Lobaria pulmonaria* *Plastismatia glauca*	Total biomass consumed for each species and relative consumption by gastropod biomass	4 d	N/A
Asplund *et al*. 2016	Norway	2-choice – 1 thallus pair in a container with 3 snails	*Cepaea hortensis*	*Lobaria pulmonaria* *Lobarina scrobiculata*	Preference (%)	48 h	N/A
Boch *et al*. 2015	Switzerland	No choice – 1 thallus in a container with 1 snail	2 snail taxa	24 species	Consumed lichen mass	48 h	*c*. 200 mg
Černajová & Svoboda 2014	Slovakia	2-choice – 1 thallus pair in a container with 2 snails or slugs	*Cochlodina cerata* *Lehmannia marginata*	8 species	Biomass consumed calculated as difference in thallus weight and area	48 h (slugs) 72 h (snails)	219–1150 mm^2
Asplund & Wardle 2013	Norway	No choice – 1 thallus in a container with 3 snails	*Cepaea hortensis*	28 species including *Lobaria pulmonaria* *Platismatia glauca*	Biomass consumed	24 h	187 ± 3.4 mg (mean ± SE)
Asplund & Wardle 2012	Norway	2-choice – 1 thallus pair in a container with 4 snails	*Cepaea hortensis*	*Lobaria pulmonaria* *Lobarina scrobiculata*	Preference (%)	24 h	N/A
Asplund 2011*a*	Norway	2-choice – 2 thalli in a container with 3 snails	*Helicigona lapicida*	*Lobaria pulmonaria*	Preference (%)	6 h	99.6 ± 4.8 mg (mean ± SE)
Asplund 2011*b*	Norway	No choice – 1 thallus in a container with 3 snails	*Cochlodina laminata*	*Lobaria pulmonaria* *Lobarina scrobiculata*	Ratio between % area grazed and % biomass grazed	24 h	N/A
Asplund *et al.* 2010*a*	Norway	2-choice – 1 thallus pair in a container with 2 snails or 3–5 slugs 3-choice – 3 thalli in a container with 2 snails or 3–5 slugs	*Cepaea hortensis* *Arion fuscus*	4 species including *Lobarina scrobiculata* *Platismatia glauca*	Preference (%)	24 h	N/A
Asplund *et al.* 2010*c*	Norway	No choice – 1 thallus in a container with 3 snails	*Cochlodina laminata*	*Lobarina scrobiculata*	% area consumed	48 h	N/A
Gauslaa 2005	Norway	2-choice – 1 thallus pair in a container with 2 snails	*Cepaea hortensis* *Arianta arbustorum*	17 species including *Lobaria pulmonaria* *Plastismatia glauca*	% dry mass consumed relative to start weight and actual dry mass consumed	24 h	26–365 mg

(*Continued*)

Table 2. (*Continued*)

Author(s)	Location	Experimental design	Herbivore	Lichen species	Grazing metric	Duration	Thallus dry weight or size used
Field Experiments							
Gauslaa *et al.* 2018	Sweden	Transplants – 3 treatment pairs on a mesh	N/A	*Lobaria pulmonaria* *Lobaria amplissima*	Loss in dry mass and grazing marks	1 yr	300–400 mm^2
Čermajová & Svoboda 2014	Slovakia	Transplants – 6 thalli on a mesh	N/A	*Parmelia sulcata* 4 *Melanelixia* spp.	Area consumed	112–114 d	N/A
Asplund *et al.* 2010*b*	Norway	Transplants – 8 thalli, 2 per species, on a mesh	N/A	4 species including *Lobaria pulmonaria* *Lobarina scrobiculata*	Area consumed & preference (%)	137–139 d	N/A
Asplund & Gauslaa 2008	Norway	Transplants – 1 piece of bark with many juvenile thalli & 2 pairs of mature thalli on a board	N/A	*Lobaria pulmonaria*	Relative change in dry matter, grazing classes, % loss in juvenile thalli	104 d	50–300 mg
Gauslaa 2008	Norway	Transplants – 4 *L. pulmonaria thalli* & 2–3 *P. crocata* thalli on a frame holder	N/A	*Lobaria pulmonaria* *Pseudocyphellaria crocata*	% area consumed	110 d	35–315 mg

dry mass of CBSCs compared to *L. pulmonaria* A but this was not statistically significant, although close (P = 0.056). The *L. scrobiculata* and *P. glauca* thalli used in the experiment had been collected at the same time and stored in the same way as *L. pulmonaria* A, and did not show any signs of senescence. Gauslaa *et al.* (2016), when growing *L. pulmonaria* on filter paper in growth cabinets, also observed browning. He attributed the browning to some sort of damage, but thalli were not senesced as growth did still occur. It is also possible that the *L. pulmonaria* A thalli leaked K+ ions which reacted with stictic acid to cause the reddish discoloration.

Lobaria pulmonaria A was collected from a treed bog, dominated by conifers, with poor, more acidic soil. *Lobaria pulmonaria* B, on the other hand, was collected in a mixed forest stand with a larger component of broadleaf trees and probably richer, less acidic soil. Gastropod abundance is generally considered higher in deciduous forests compared to more acidic coniferous forests (Asplund *et al.* 2010*b*; Vatne *et al.* 2010). *Lobaria pulmonaria* A may have been exposed to lower grazing pressure than *L. pulmonaria* B, as evidenced by few grazing marks on the thalli. Based upon the difference in habitat and grazing pressure, the two sets of *L. pulmonaria* possibly differed in their content and concentration of CBSCs. Other studies have shown that intraspecific variation in the content and concentration of CBSCs does occur (Vatne *et al.* 2010) and can even occur across relatively short distances (Bokhorst *et al.* 2024). Asplund (2011*a*) described how two chemical races of *L. pulmonaria* in New Brunswick differed in their palatability to gastropods and found that chemical race I was avoided by gastropods. It is not possible to determine in our study why *L. pulmonaria* B was avoided but it was probably another gastropod, possibly slugs, which caused the previous grazing damage. Future work on the role of secondary metabolites in the mediation of herbivory is warranted for Newfoundland.

In the feeding trials, we found only a slight difference in *C. nemoralis* preference for *L. scrobiculata* and *L. pulmonaria* A. It was noticed that more *L. scrobiculata* than *L. pulmonaria* A thalli were completely consumed, after the *P. glauca* had been eaten. Others have shown that gastropods prefer *L. scrobiculata* to *L. pulmonaria* (Asplund 2010; Asplund *et al.* 2010*b*, 2018). Stictic acid and related compounds deter grazing of *L. pulmonaria* and these compounds are found in much lower concentrations in *L. scrobiculata*, making it more palatable (Gauslaa 2005; Asplund & Gauslaa 2008; Asplund *et al.* 2010*b*). The *L. scrobiculata* thalli used in our feeding experiment had the highest percentage of dry matter of total acetone-extractable CBSCs, although it was not significantly higher than that of the *L. pulmonaria* A thalli. This may have been due to differences in the effectiveness of using whole thalli to extract secondary compounds. Asplund *et al.* (2010*c*) found that acetone rinsing of intact *L. scrobiculata* was able to extract *c.* 80% of the stictic acid and related compounds, while acetone rinsing of intact *L. pulmonaria* thalli was only able to extract *c.* 64%, with 36% of the original concentration remaining (Asplund & Gauslaa 2008).

We also found that *C. nemoralis* grazed the soralia of *L. scrobiculata* (before and after grazing pictures are shown in Appendix C). During feeding trials with another snail species, *Cochlodina laminata*, Asplund *et al.* (2010*c*) found that soralia of *L. scrobiculata* were avoided and preferred only after the secondary compounds had been removed. They argued that this observation provided strong evidence supporting the 'optimal defense theory' (Stamp 2003). This potentially suggests differences in the content

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and concentration of secondary lichen compounds in the thalli studied in Europe and Newfoundland, and perhaps different tolerances between the different gastropod species examined. Further work is needed to verify how widespread the optimal defence hypothesis is in lichens (Hyvärinen *et al.* 2000).

We summarized 16 experimental studies that have been published over the last 20 years on different aspects of gastropod herbivory on epiphytic lichens (Table 2). These experiments have been carried out in the laboratory and include no-choice feeding experiments (n = 4), 2-choice feeding experiments (n = 6), 4-choice feeding experiment (n = 1), and field experiments using transplant techniques where gastropods are not controlled or necessarily known to species (n = 5). Our new experimental approach blends lichen transplant techniques used in field studies with a multiple-choice grazing experiment under controlled laboratory conditions. Although results from multiple-choice experiments can present some challenges for statistical analysis because the consumption of one food can be dependent on the neighbouring food choices (Roa 1992; Manly 1993; Lockwood 1998), they are more representative of feeding choices in nature. In this study, our multiple-choice design was unique in that it allowed the snails to climb on a natural substratum to search amongst a variety of lichen species. The replication of feeding choices and snails within each experimental terrarium provides a robust experimental approach to address previous criticisms of multiple-choice experiments. During the experiment, the snails ran out of the preferred lichen species after 48 hours. The experiment was continued, however, forcing the snails to feed on the less preferred species. Some might argue that this does not accurately reflect food consumption in nature, but it did allow us to observe how the snails fed upon the less preferred species and the potential grazing impact. One limitation of our approach is that the weights of lichens used differed due to their morphology, which meant that we had to use relative weights consumed as opposed to absolute weights. Other published studies also used different weights of lichens in their experiments (Table 2) and many used extremely small amounts of lichens, which one could argue offers only a restricted perspective on lichen preferences by gastropods. Our study also showed that, for *L. pulmonaria*, snails preferred thalli that had been stored for longer, which could suggest that lichens with less vitality could be more susceptible to grazing by snails. This study has provided interesting observations on the preferences and possible impacts of lichen grazing by an introduced snail species in the province of Newfoundland and Labrador. Further investigation is needed to elucidate the concentration of secondary compounds, as well as the nutritional contents of the lichen species studied, and how that may affect gastropod grazing. In addition, little is known about the distribution and abundance of *C. nemoralis* in the forests of Newfoundland and Labrador. However, this study has shown that non-native gastropods could potentially be affecting the abundance and distribution of epiphytic lichen communities in the province, similar to what other studies have shown in Europe (Gauslaa *et al.* 2018).

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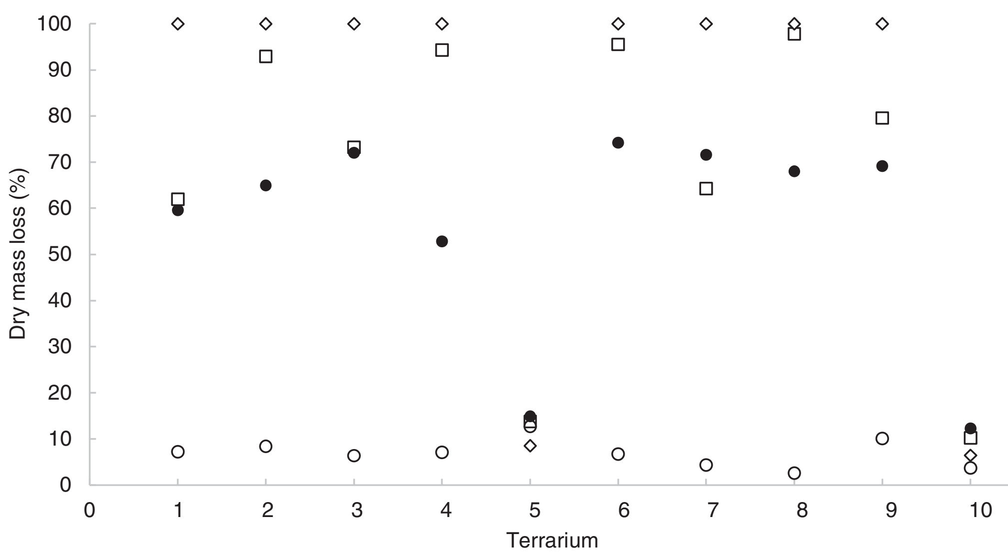
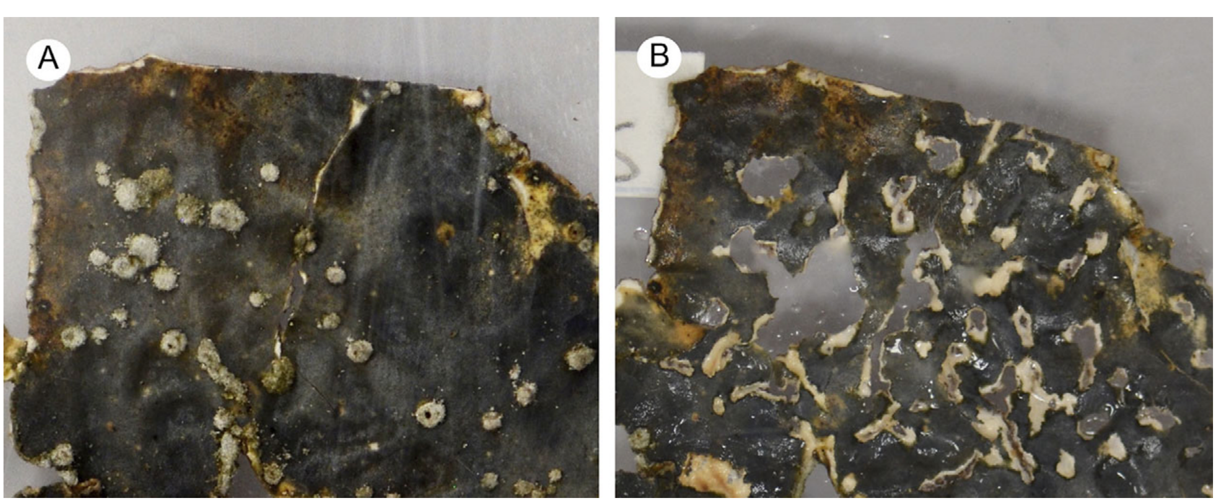
Appendix A. Results of a multiple-choice feeding trial comparing the mean percent loss in lichen dry mass of grazed and ungrazed thalli and the content of acetone-extractable compounds (*n* = 4). DM = dry mass. Means ± SE are given; *n* = 4 for grazed terrariums, *n* = 1 for controls.

	% loss in DM				
	Trial 1		Trial 2		
Species	Grazed	Control	Grazed	Control	Extractable compounds (% of DM)
Lobaria pulmonaria A	62.33 ± 4.07	14.88	70.74 ± 1.38	12.30	2.01 ± 0.58
Lobaria pulmonaria B	7.26 ± 0.41	12.70	5.94 ± 1.62	3.67	2.87 ± 0.76
Lobarina scrobiculata	80.60 ± 7.86	13.78	84.29 ± 7.79	10.18	3.29 ± 0.50
Platismatia glauca	100	8.51	100	6.46	0.45 ± 0.26



Appendix B. The total percent loss in lichen dry mass for all grazed terrariums after 120 h of exposure to grazing by *Cepaea nemoralis.* Terrariums 1 to 5, trial 1; terrariums 6 to 10, trial 2; terrariums 5 and 10, controls; ● = *Lobaria pulmonaria* A, ○ = *L. pulmonaria* B, □ = *Lobarina scrobiculata*, ◇ = *Platismatia glauca. n* = 5 thalli per terrarium.



Appendix C. Soralia of *Lobarina scrobiculata* before (A) and after (B) grazing by *Cepaea nemoralis*. In colour online.