Research Note

Effects of Rock Climbing on the Land Snail Community of the Niagara Escarpment in Southern Ontario, Canada

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Abstract: *The cliffs of the Niagara Escarpment provide habitat for extremely diverse communities of land snails that may be at risk as a result of recreational rock climbing. We examined the effects of rock climbing on the density, richness, diversity, and community composition of snails on the Niagara Escarpment in southern Ontario, Canada. We sampled from randomly selected climbed and unclimbed sections of cliffs on the plateau (cliff edge), cliff face, and talus (cliff base). Snail density, richness, and diversity were lower along climbing routes than in unclimbed areas, and community composition differed between climbed and unclimbed samples. These results suggest that rock climbing has significant negative effects on all aspects of the snail community on cliffs; therefore, we recommend the inclusion of gastropods in conservation plans for protected areas containing cliffs.*

Efectos del Alpinismo en la Comunidad de Caracoles Terrestres del Acantilado del Niagara en Ontario Meridional, Canadá

Resumen: *Las barrancas del acantilado del Niagara proveen hábitat para comunidades extremadamente diversas de caracoles terrestres que pueden estar en riesgo debido al alpinismo recreativo. Examinamos los efectos del alpinismo en la densidad, riqueza, diversidad y composición de comunidades de caracoles del acantilado del Niagara en Ontario Meridional, Canadá. Tomamos muestras de las mesetas (bordes de acantilados), la cara del acantilado y el talud (base del acantilado) de secciones de barrancas usadas y no usadas para el alpinismo y seleccionadas al azar. La densidad, la riqueza y la diversidad de caracoles fueron más bajas en las rutas escaladas que en aquellas áreas no escaladas y la composición de la comunidad difirió entre muestras escaladas y no escaladas. Estos resultados sugieren que el alpinismo tiene impactos negativos significativos en todos los aspectos de la comunidad de caracoles en acantilados; por lo tanto, recomendamos la inclusión de gasterópodos en los planes de conservación para áreas protegidas que contengan acantilados.*

Introduction

Since its introduction to eastern North America 50 years ago, recreational rock climbing has continually increased in popularity, with the most dramatic increases occurring over the past 20 years (Valis 1991). Cliff ecosystems contribute greatly to the regional biodiversity of plants and animals (Larson et al. 2000). Research conducted thus far has demonstrated that rock climbing can lead to decreased abundance and richness of vascular and nonvascular plants and lichens (Nuzzo 1995; Herter 1996; Nuzzo 1996; Kelly & Larson 1997; Camp & Knight 1998; Farris 1998; McMillan & Larson 2002), suggesting that the entire biotic community might be affected.

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The potential exists for rock climbing to have a particularly strong influence on land snails because land snail diversity is generally higher on limestone outcrops than in other habitats (Burch 1962; Baur et al. 1995). In fact, maximum global richness levels for terrestrial gastropods are often associated with wooded carbonate cliffs and talus slopes. This has been demonstrated in New South Wales (Stanisic 1997), Scotland (Cameron & Greenwood 1991), Germany (Schmid 1966), Sweden (Waldén 1981), the Appalachian mountains (Getz & Uetz 1994), and the Great Lakes region of North America (Nekola 1999).

The Niagara Escarpment is a series of dolomitic limestone outcrops that extends from the Bruce Peninsula to the Niagara Region in Ontario and through Michigan, Wisconsin, Illinois, and Iowa. These cliffs support the most ancient forest ecosystem east of the Rocky Mountains (Larson & Kelly 1991), with eastern white cedar trees (*Thuja occidentalis*) living in excess of 900 years (Larson et al. 2000). These cliffs also support extremely high levels of snail diversity. Up to 34 species have been observed in soil collected from a surface area of 1000 m^2, up to 23 species in 1 m^2, and up to 21 species in 0.04 m^2 (Nekola 1999; Nekola & Smith 1999). Unfortunately, these cliffs are also exposed to the highest levels of recreational rock climbing in Ontario (Bracken et al. 1991).

The importance of the Niagara Escarpment as a reservoir for biotic biodiversity necessitates the creation of formal conservation policies that protect this community. Here, we document the effects of rock climbing on the density, richness, diversity, and community composition of land snails on dolomitic limestone cliffs in Ontario.

Methods

Study Site

We conducted field work from late August to early October 1998 along a 35-km section of the Niagara Escarpment near Milton, Ontario (Universal Transverse Mercator Zone 17, 4806800–4818000 mN, 587500–591500 mE). The public and privately owned cliffs we sampled are composed of Silurian dolomitic limestone (Niagara Escarpment Commission 1979) surrounded by a green belt of second-growth deciduous forest that runs through larger areas of urban development and agricultural land.

Climbed cliffs were sampled at Buffalo Crag (90 graded routes), Rattlesnake Point (142 graded routes), Mt. Nemo (236 graded routes), and Kelso (54 graded routes) conservation areas. Unclimbed cliffs were sampled at Mt. Nemo and Crawford Lake conservation areas and from an adjacent cliff on the property of Milton Limestone Incorporated. Sections of climbed and unclimbed cliffs were within 15 km of one another.

Sampling Design

We determined the impact of climbing through the comparison of "climbed" and "unclimbed" areas. A region was classified as climbed when climbing manuals described an established climbing route for that area (Bracken et al. 1991; Oates & Bracken 1997). A section of the cliff was classified as unclimbed when no routes were described for the area and when no other obvious signs of climbing were present (e.g., implanted climbing hardware, chalk marks on hand holds).

We sampled from 50 vertical belt transects, each 1 m in width, that extended the height of the cliff. Twenty-five climbed transects were chosen randomly from a pool of 101 climbing routes, and 25 unclimbed transects were chosen randomly from a pool of 106 transects. The pool of climbed transects included all documented climbing routes for the area with a difficulty rating between 5.7 and 5.9 and a star rating in the climbing manual (Bracken et al. 1991). We chose these routes because they represented the best routes for climbers with an intermediate skill level. As such, they likely attract higher and more regular amounts of climbing activity than other routes. We restricted unclimbed transects to sections of the cliff that were $\geq$7 m wide, that appeared physically suitable for climbing, and that two experienced climbers and the first author agreed would be rated between 5.7 and 5.9 if graded. Climbed and unclimbed transects were rejected if they were $<$10 m in height or contained a roof or overhang of more than 1 m, continuous water seeps, or loose rocks.

Land snails were sampled from three positions within each transect for a total of 150 observations: cliff face (vertical surface), plateau (or cliff edge), and talus (cliff base). These adjacent habitats were sampled in addition to the cliff face because they are also subjected to climbing-related disturbances such as being used as a place from which to belay (hold the ropes for the climber), to anchor climbing ropes, to store packs and other equipment, and for climbers to rest between ascents.

Transects extended from 2 m beyond the cliff face on the plateau to 2 m beyond the cliff base in the subtending talus. We collected 250 mL of soil from each of the three positions within each transect. In plateau and talus habitats, we collected soil from the upper 5 cm of the organic soil horizon within a 1 $\times$ 2 m area. Because of the paucity of soil on the cliff face, we collected soil samples from ledges and cracks extending the entire height of the cliff within the 1-m transect (ranging from 11.5 to 30 m). Although the sample extent for the cliff-face samples was greater, the total surface area over which the samples were taken did not exceed 2 m^2. To minimize the effects of sampling on the cliff community, no ledge was deprived of more than half its soil.

Each 1 $\times$ 2 m quadrat sampled from the plateau and talus was divided into 50 20 $\times$ 20 cm subquadrats, and

Table 1. Frequency (% of quadrats) in which each species of land snail was present for unclimbed (U) and climbed (C) quadrats sampled in 1998 from the Niagara Escarpment in southern Ontario, Canada.

Species	*G rank*[a]	*S rank*[b]	*Freq. (%)*		$\chi^{2c,d}$	*Species*	*G rank*[a]	*S rank*[b]	*Freq. (%)*		$\chi^{2c,d}$
			U	*C*					*U*	*C*	
Anguispira alternata	G5	S5	49.3	24.0	9.30*	*Nesovitrea binneyana*	G?	S4-S5	28.0	2.7	16.64**
Carychium exile	G4?	S3-S4	28.0	9.3	7.42	*Paravitrea multidentata*	G4-G5	S2-S3	6.7	2.7	0.60
Carychium nannodes	G4-G5	S1-S2	6.7	1.3	1.56	*Punctum minutissimum*	/	/	85.3	2.7	50.03****
Cochlicopa lubrica	G4-G5	S5	14.7	0.0	9.81*	*Pupilla muscorum*	/	/	1.3	32.0	23.23****
Cochlicopa lubricella	G4-G5	S4	2.7	1.3	0.00	*Stenotrema fraternum fraternum*	/	/	5.3	0.0	2.31
Columella simplex	/	/	28.0	0.0	22.15***	*Striatura exigua*	G4	S4	17.0	1.3	9.53*
Discus catskillensis	G3-G5	S5	72.0	32.0	22.46****	*Striatura ferrea*	G4-G5	S5	1.3	0.0	0.00
Euconulus fulvus	G4-G5	S4-S5	28.0	0.0	22.15***	*Striatura milium*	G4	S4-S5	40.0	2.7	28.96****
Euconulus polygyratus	G?	S4	6.7	0.0	3.31	*Strobilops labyrinthica*	G5	S5	18.7	10.7	1.33
Gastrocopta contracta	G5	S5	14.7	18.7	0.19	*Succinea ovalis*	G5	S3-S4	20.0	0.0	14.52**
Gastrocopta corticaria	G4-G5	S2	32.0	38.7	0.47	*Triodopsis albolabris*	/	/	2.7	0.0	0.51
Gastrocopta holzingeri	G4-G5	S2-S3	53.3	49.3	0.11	*Triodopsis denotata*	/	/	1.3	0.0	0.00
Gastrocopta pentodon	G5	S5	61.3	17.3	28.61****	*Triodopsis tridentata*	G5	S3-S4	6.7	4.0	0.13
Glyphyalinia indentata	/	/	4.0	1.3	0.26	*Vallonia costata*	G4-G5	S5	0.0	1.3	0.00
Glyphyalina rhoadsi	G5	S3-S4	16.0	4.0	4.74	*Vallonia gracilicosta*	G?	S1-S2	65.3	72.0	0.50
Guppya sterkii	G4-G5	SH	5.3	1.3	0.83	*Vallonia pulchella*	G4-G5	S5	0.0	1.3	0.00
Hawaiia miniscula	G5	S3	0.0	8.0	4.34	*Vertigo bollesiana*	G3	S3	26.7	5.3	11.16*
Helicodiscus parallelus	G5	S5	12.0	6.7	0.71	*Vertigo gouldi*	G4-G5	S3	78.7	33.3	29.46****
Helicodiscus shimeki	G4	S4-S5	2.7	6.7	0.60	*Vertigo paradoxa*	G2-G4	S2-S3	76.0	42.7	15.91**
Mesomphix cupreus	G5	S3	1.3	0.0	0.00	*Zonitoides arboreus*	G5	S5	50.1	26.7	8.12

[a] *Global conservation rank: G1, extremely rare; G2, very rare; G3, rare to uncommon; G4, common; G5, very common; G?, unranked or not listed.*

[b] *Provincial conservation ranking: S1, extremely rare; S2, very rare; S3, rare to uncommon; S4, common; S5, very common; SH, historically present in Ontario but not observed recently (typically not recorded for 20 years) or not listed.*

[c] *Adjusted using Yates' correction for continuity as suggested for cases in which there is a single degree of freedom. The Bonferroni correction for multiple comparisons was used to calculate significance levels (Ministry of Natural Resources 2002).*

[d] *Probability:* * $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

the number of subquadrats containing exposed rock was recorded. A 1 × 2 m quadrat was similarly sampled from the vertical center of each cliff-face transect. We recorded this data prior to soil collection.

We collected soil samples in muslin bags. We placed fresh samples in a drying oven at 80° C for 4–7 days and then stored them at room temperature for several months. We soaked each bag in water from 12–24 hours, after which we removed the soil and washed it through a graduated sieve series (4, 2, 1, and 0.42 mm). We discarded particles that passed through the smallest sieve. We returned the soil to muslin bags and redried them. We then dry-sieved the soil through the graduated sieve series and examined the factions of soil under an 8× dissecting microscope against a neutral brown background. We removed intact shells from the soil with a moist paintbrush and identified them to species (or subspecies) following the nomenclature of Hubricht (1985). We checked our identifications against the Hubricht Collection at the Field Museum of Natural History and the second author's reference collection at the University of Wisconsin, Green Bay. We counted and recorded the number of shells for each species. We also calculated the species richness and heterogeneity (Shannon-Wiener index) of each sample. The reference collection from this study is housed in the Department of Botany at the University of Guelph.

Statistical Analysis

We used a split-plot experimental design (Steel & Torrie 1980; Kuehl 1994) to compare the density, richness, and heterogeneity of the sampled snails. We used climbing intensity (climbed vs. unclimbed) as the whole-plot factor and habitat (plateau, cliff face, and talus) as the split-plot factor.

To minimize the impact of factors other than climbing and habitat on the outcome of the statistical analysis, we included cliff height, percent canopy cover, and compass direction of the cliff face in the model as covariates. The compass direction of the cliff was broken down into a north component and an east component, with the former being equal to the cosine (compass reading * π) and the latter being equal to sine (compass reading * π). We used these conversions because the use of an untransformed compass reading would determine 1° and 359° to be very different from one another, when they are both almost due north.

We analyzed the effects of rock climbing and habitat type on snail density, richness, and heterogeneity through analysis of variance (ANOVA) tables generated by SAS computer software (Anonymous 1995). We used the MIXED procedure due to the combination of covariates within the split-plot design. We analyzed the results for both main and simple effects, the main effects with F statistics and the simple effects with Tukey's procedure (Steel & Torrie 1980).

We employed chi-square tests to determine the impact of climbing and habitat type on the abundance of individual species. We used the Bonferroni correction for multiple comparisons (Kuehl 1994) and Yates's correction for continuity when there was only a single degree of freedom (Steel & Torrie 1980).

Results

We retrieved 14,023 intact shells from the 37.5 L of soil collected. These individuals belonged to 40 different species, which represents almost half the diversity of land snails in Ontario (88 taxa). The species varied in global conservation ranking from G3 (*Vertigo bollesiana*) to G5 and in provincial ranking from S1/S2 (*Carychium nannodes, Vallonia gracilicosta*) to S5 (Table 1).

Most of the species were <5 mm at their widest point and are thus referred to as "minute" snails (Emberton 1995). We found a large amount of broken shell material but did not include this in our analysis.

Shell density was over five times greater in unclimbed samples than in climbed samples (78.26 vs. 14.86 individuals per 250 mL of soil; $p < 0.00001$). Shell density was significantly lower along climbing routes in each of the three habitat positions (Fig. 1). In addition, shell density varied significantly between the three habitat positions ($p < 0.005$). The average density of shells found in

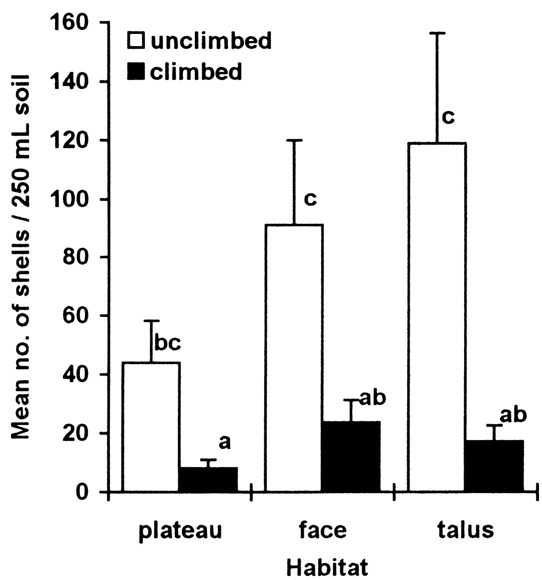

Figure 1. Mean density of land snails per 250 mL soil sample collected from the Niagara Escarpment, Ontario, Canada. Each bar represents the mean from 25 samples. Bars that share a letter code are not significantly different from one another at $\alpha = 0.05$.

cliff face and talus samples (46.63 and 45.41 individuals per 250 mL soil) was more than twice the average density of shells found in plateau samples (19.15 individuals per 250 mL soil; $p < 0.005$).

The species richness of land snails was significantly lower along climbing routes ($p < 0.00001$). Unclimbed areas supported almost two times more species than undisturbed areas (9.84 vs. 5.20 species per 250 mL soil). This significant reduction in richness along climbing routes occurred in all habitat positions (Fig. 2). Similarly, climbed areas showed significantly lower levels of Shannon-Wiener diversity than did unclimbed areas (1.11 vs. 1.53; $p < 0.001$). Species richness was lowest on the plateau (4.94 species per 250 mL soil) and highest on the talus (10.56 species per 250 mL soil; $p < 0.00001$).

Fourteen of the 40 species had significantly greater frequency in unclimbed samples, whereas only one species had a significantly greater frequency in climbed areas (Table 1). The remaining species showed no statistical preference for either climbed or unclimbed areas.

The proportion of subquadrats containing exposed rock was significantly higher in climbed than unclimbed quadrats (79.6% vs. 48.0%; $p < 0.00001$). This trend occurred in each of the three habitat types, but was significant for the plateau (10.6% vs. 66.8%; $p < 0.0001$) and talus (40.2% vs. 73.9%; $p < 0.0001$) habitats only. Unclimbed and climbed quadrats contained similar amounts of exposed rock (93.1% vs. 98.0%; $p = 0.98$).

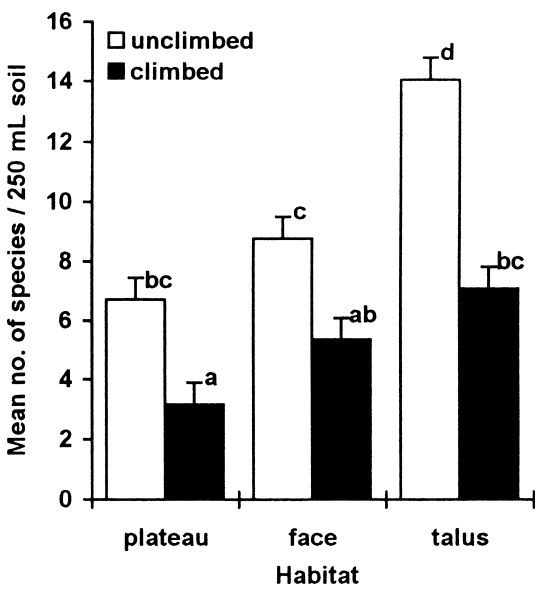

Figure 2. Mean number of land snail species present in 250 mL soil samples collected from the Niagara Escarpment, Ontario, Canada. Each bar represents the mean from 25 samples. Bars that share a letter code are not significantly different from one another at $\alpha = 0.05$.

Discussion

Our results suggest that rock climbing has strong negative effects on the extremely diverse and abundant community of land snails that normally occurs on undisturbed cliffs of the Niagara Escarpment. Snail density, richness, and diversity were all significantly lower in climbed areas than in undisturbed areas, in spite of the fact that the amount of soil collected was constant. Because the surface area of soil was also lower in climbed areas, it is likely that rock climbing has an even larger impact on land snails than is suggested by our results.

The enormous local abundance of land snails and the unusually high species richness in undisturbed sites suggest that snails may be processing energy and matter at high rates and therefore may be important natural components of cliff-ecosystem food webs. Whatever their role, their recolonization and the subsequent restoration of function are likely to occur very slowly on denuded cliffs in view of the slow rates of dispersal of such snails (Baur & Baur 1994).

Rock climbing also appears to affect the composition of land snail communities. There are several possible mechanisms that might account for this change. First, the ledges and cracks in the vertical rock surface that are the primary habitat for cliff land snails are also the primary means by which climbers ascend the cliff face. The use of these microsites for hand and foot holds causes removal of unconsolidated soil and organic matter, thereby decreasing the amount and quality of available habitat for snails. In some instances, climbers purposefully remove soil to increase the security of the hold and to reduce the chance of slipping. The soil that is left is then subject to direct pressure from the hands and feet of climbers, which probably causes soil compaction and a reduction in organic material, as is found in other disturbed sites. Soil compaction and removal from staging areas in the talus and at tie-off sites on the plateau also decrease the amount of habitat and resources available for these species. Future research is required to determine the effects of climbing on physical soil properties and chemistry.

Due to the detrimental effect of rock climbing on the land snail community we observed in this study, we recommend that management plans for the Niagara Escarpment be modified to include specific policies regarding recreational rock climbing. The most effective management practices for the protection of gastropod species on the Niagara Escarpment would limit the aerial extent of climbing activity. We believe that land snail communities on other cliffs may react similarly to climbing pressure, because other cliffs around the world also support extremely diverse communities of terrestrial gastropods (Schmid 1966; Waldén 1981; Cameron & Greenwood 1991; Getz & Uetz 1994; Stanisic 1997; Nekola 1999). We therefore recommend that gastropods also be included in management policies for other areas containing cliffs. Special attention should be given to areas in which rare species are known to exist.

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Literature Cited

Anonymous. 1995. SAS system for Windows. Version 6.11. SAS Institute, Cary, North Carolina.

Baur, B., and A. Baur. 1994. Dispersal of the land snail *Chondrina avenacea* on vertical rock walls. Malacological Review **27:**53–59.

Baur, B., L. Fröberg, and A. Baur. 1995. Species diversity and grazing damage in a calcicolous lichen community on top of stone walls in Öland, Sweden. Annales Botanici Fennici **32:**239–250.

Bracken, M., J. Barnes, and C. Oates. 1991. The escarpment: a climbers guide. Borealis Press, Toronto.

Burch, J. B. 1962. How to know the eastern land snails. WM.C. Brown, Dubuque, Iowa.

Cameron, R. A. D., and J. J. D. Greenwood. 1991. Some montane and forest molluscan fauna from eastern Scotland: effects of altitude, disturbance, and isolation. Pages 437–442 in Proceedings of the tenth international malacological congress. Unitas Malacologica, Tübingen, Germany.

Camp, R. J., and R. L. Knight. 1998. Effects of rock climbing on cliff plant communities at Joshua Tree National Park, California. Conservation Biology **12:**1302–1306.

Emberton, K. C. 1995. Land-snail community morphologies of the highest-diversity sites of Madagascar, North America, and New Zealand, with recommended alternatives to height-diameter plots. Malacologia **36:**43–66.

Farris, M. A. 1998. The effects of rock climbing on the vegetation of three Minnesota cliff systems. Canadian Journal of Botany **76:** 1981–1990.

Getz, L. L., and G. W. Uetz. 1994. Species diversity of terrestrial snails in the southern Appalachian mountains, U.S.A. Malacological Review **27:**61–74.

Herter, W. 1996. Die Xerothermvegetation des Oberen Donautals—Gefaerhrdung der Vegetation durchMensch und Wild sowie Schutz—und Erhaltungsvorschlaege. Veroeffentlichungen des projekts AAngewandte Oekologie@ PAoe 10. Veroef, Karlsruhe, Germany.

Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana **24:**1–191.

Kelly, P. E., and D. W. Larson. 1997. Effects of rock climbing on populations of presettlement eastern white cedar (*Thuja occidentalis*) on cliffs of the Niagara Escarpment, Canada. Conservation Biology **11:**1125–1132.

Kuehl, R. O. 1994. Statistical principles of research design and analysis. Wadsworth Publishing, Belmont, California.

Larson, D. W., and P. E. Kelly. 1991. The extent of old-growth *Thuja occidentalis* on cliffs of the Niagara Escarpment. Canadian Journal of Botany **69:**1628–1636.

Larson, D. W., U. Matthes, and P. E. Kelly. 2000. Cliff ecology: pattern and process in cliff ecosystems. Cambridge University Press, Cambridge, United Kingdom.

McMillan, M. A., and D. W. Larson. 2002. The effects of rock climbing on the vegetation of the Niagara Escarpment in Southern Ontario, Canada. Conservation Biology **16:**389–398.

Ministry of Natural Resources. 2002. Natural heritage information centre list of Ontario mollusks. Ministry of Natural Resources, Peterborough, Ontario, Canada. Available from http://www.mnr.gov.on.ca/MNR/nhic/nhic.html (accessed March 2002).

Nekola, J. C. 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the great lakes region of North America. Malacologia **41:**231–252.

Nekola, J. C., and T. M. Smith. 1999. Terrestrial gastropod richness patterns in Wisconsin and carbonate cliff communities. Malacologia **41:**253–269.

Niagara Escarpment Commission. 1979. Geology: the Niagara Escarpment. Niagara Escarpment Commission, Georgetown, Ontario, Canada.

Nuzzo, V. A. 1995. Effects of rock climbing on cliff goldenrod (*Solidago sciaphila* Steele) in Northwest Illinois. American Midland Naturalist **133:**229–241.

Nuzzo, V. A. 1996. Structure of cliff vegetation on exposed cliffs and the effect of rock climbing. Canadian Journal of Botany **74:**607–617.

Oates, C., and M. Bracken. 1997. A sport climbers guide to Ontario limestone. Borealis Press, Toronto.

Schmid, G. 1966. Die mollusken des Spitzbergs. Der Spitzberg bei Tübingen, Natur und Landschaftsschutzgebiete. Baden-Würtemburg **3:**596–701.

Stanisic, J. 1997. An area of exceptional land snail diversity: the Macleay Valley, north-eastern New South Wales. Memoirs of the Museum of Victoria **56:**441–448.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. 2nd edition. McGraw-Hill, New York.

Valis, T. 1991. Escarpment climbing history. Pages 3–6 in M. Bracken, J. Barnes, and C. Oates, editors. The escarpment: a climbers guide. Borealis Press, Toronto.

Waldén, H. W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. Journal of Conchology **30:**351–372.