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Herbivory in Rocks and the Weathering of a Desert

MOSHE SHACHAK, CLIVE G. JONES,* YIGAL GRANOT

Two species of snail, *Euchondrus albulus* and *Euchondrus desertorum*, eat endolithic lichens growing under the surface of limestone rocks in the Negev Desert, Israel. This unusual type of herbivory has the unexpected and major impact of weathering this rocky desert at a rate of 0.7 to 1.1 metric tons per hectare per year. The biotic weathering contributes to the process of soil formation at a rate that is similar to wind-borne dust deposition. These findings demonstrate that herbivores can have a significant regulatory impact on ecosystem processes, even in cases where the total amount of primary production consumed is small.

PLANTS HAVE MANY CHARACTERISTICS that make consumption by herbivores difficult. Features of particular importance are low availability of nutrients and water, low digestibility, toughness, and high concentrations of defensive chemicals (*1*). Lichens possess all of the above characteristics, and it has been suggested that lichens should be difficult to consume (*2*). Endolithic lichens that occur under the rock surface should be an even more difficult food to use than epilithic or surface lichens. We report an unusual form of herbivory by two snail species in the Negev Desert. These animals feed on endolithic lichens in the limestone rock. An unexpected consequence of this consumption is that the snails are major agents of rock weathering and soil formation in this desert, despite the relatively small amount of primary production that they consume. The disproportionate impact of the consumption of lichens by snails arises because snails must physically disrupt and ingest the rock substrate in order to consume the lichens. These findings show that herbivores can play an important regulatory role in ecosystem processes, even if they consume small quantities of primary production.

The Negev Desert Highlands, Israel, is a hilly limestone rock desert 500 to 1000 m above sea level with an annual rainfall of 90 mm/year. Seventy percent of the ground area is covered by rocks of various sizes from 10^1 to 10^8 cm^2 (*3*). These rocks are partially covered by epilithic lichens and contain extensive areas of endolithic lichens. Endolithic lichens are the dominant cryptogamic elements in limestone in extreme environments. They consist of a fungal cortex, algal layer, and fungal medulla and occur at depths between 1 and 7 mm in rock (*4*). We observed snails of two species, *Euchondrus albulus* Mousson and *Euchondrus desertorum* Roch, foraging on these rocks. A close examination of foraging areas showed white trails that were the color of raw limestone (limestone without any endolithic lichens); we also saw small piles of feces of the same color. We postulated that snails were feeding on endolithic lichens, which occur within the upper 1 to 3 mm of these rocks (*4*), and were ingesting rock in the process of obtaining food.

We videotaped the foraging behavior of snails on rocks in the laboratory (Fig. 1). Our findings showed that snails moved over the rock surface in what appeared to be a searching behavior, then stopped and changed body orientation so that the shell became almost vertical. They then began a series of short, rapid, side-to-side motions. Snails continued this activity for about 20 minutes per foraging period while moving slowly along the rock, leaving a white mark in the rock. We do not know what cues are used by the snails in selecting a feeding area. One of these white marks was a gouge in the rock surface about 10.3 mm long, 1.1 mm wide, and 0.4 mm deep (Fig. 2). The sides of this gouge clearly showed layers of fungus and algae in the rock, with the white limestone beneath. The depth of the trail appeared to depend on the number of times an old trail had been re-browsed (Fig. 2). It is possible that snails re-browse trails to consume the fungal hyphae that grow into the trail within 48 hours of initial browsing. The radula of both snail species appears to be typical of the family. Cutting teeth have a large cusp with a blunted and curved tip. Injuries and deformities to the teeth are common, presumably as a consequence of feeding. However, there is no evidence of any special radula adaptations in these two species. We presume that teeth are continually regrown to repair those that have been damaged (*5*). We analyzed the calcium content of snail feces and compared the values to those of samples from the top 1 mm of the rock and lichen layer that was removed by the snails. The calcium content was 0.33 mg of Ca^{2+} per milligram of feces and 0.31 mg of Ca^{2+} per milligram of rock and lichen

Fig. 1. *Euchondrus desertorum* foraging on a limestone rock containing endolithic lichens. The snail shell is 150 mm long; white feces are on top right-hand side of the rock. The feeding trails scraped in the rock by the snail are the white lines running down the rock between the snail and the feces. [Photograph by Alan Rokach]

M. Shachak, Mitrani Center for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boquer Campus, Israel 84990, and Institute of Ecosystem Studies, New York Botanical Garden, Mary Flagler Cary Arboretum, Millbrook, NY 12545.
C. G. Jones, Institute of Ecosystem Studies, New York Botanical Garden, Mary Flagler Cary Arboretum, Millbrook, NY 12545.
Y. Granot, Mitrani Center for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boquer Campus, Israel 84990.

*To whom correspondence should be addressed.

layer (*6*). These results supported our hypothesis that snails ingested the rock material they had removed.

We determined the rate of removal of rock by snails in a field enclosure experiment and in the field (*7*). In the enclosure, where snails were at densities of ten per stone, rock surface was removed at an estimated rate of 15 mm^3 per snail per day, which is about 7% of the surface area of the rock to a depth of about 1 mm per year (*8*). Our estimate of weathering from the field was 4% of the rock surface area to a depth of 1 mm per year and a feeding rate of 9 mm^3 per snail per day (*8*). On the basis of these estimates of annual grazing rates in the field and enclosure, we calculated the rates of biological weathering of rock by snails for the whole desert as 69.5 to 110.4 g/m^2 per year (0.695 to 1.104 metric tons per hectare per year; about 0.626 to 0.994 m^3 per hectare per year) (*9*).

To help evaluate the magnitude of the impact of weathering due to snails on the process of soil formation, we compared our estimates to dust deposition. Deposition of dust from other areas, such as the Arabian and Sinai peninsulas, has been considered to be one of the main sources of soil in the Negev Desert Highlands (*3*). We determined dust deposition on stones in the same general area where *E. albulus* was abundant (*10*) and estimated a mean (± 1 SD) dust deposition rate of 36 (± 11) g/m^2 per year. This value, together with estimates of dust deposition in the Negev and other deserts (*10*), is similar to that calculated for biological weathering due to snails. Clearly, snail consumption of lichen and rock has a major effect on the ecosystem processes of weathering and soil formation. A live biomass of snails of only about 0.575 g/m^2 (based on an abundance of 21 snails per square meter) has about the same impact on soil formation as dry dust deposition by wind—a major physical factor in arid zones (*11*).

Researchers debate the issue of whether or not consumers can affect or regulate ecosystem processes; it is frequently assumed that if a regulatory role is possible, it will occur only when herbivores overconsume the resource, as in insect outbreaks or overgrazing (*12*). Our data show that snail herbivory in the Negev Desert has an extensive impact. The amount of herbivory here is similar to or less than that found in other ecosystems (*13*). The disproportionate impact of these herbivores on processes other than trophic relations arises because the rock abiotic substrate must be disrupted in order for the snails to consume food. Our findings suggest that a more comprehensive understanding of the role of herbivores will be gained from a recognition that consumers can significantly affect ecosystem processes and that the magnitude of the impact does not necessarily relate to the amount of resource consumed.

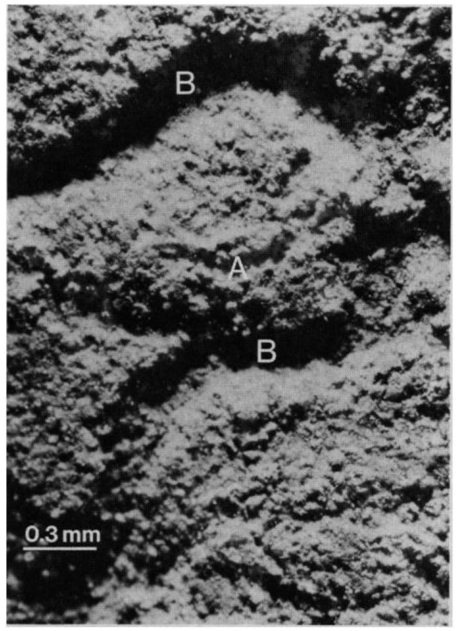

Fig. 2. Feeding trails caused by foraging of *E. albulus* on endolithic lichens in limestone rock. (**A**) A new trail, (**B**) old trails. [Photograph by Robert Mickler]

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5. Observations on radulae are based on SEM preparations from both species (A. Solem, personal communication).
6. Feces (20.3 mg) were collected after snail feeding. We used an engraving tool to scrape 22.7 mg of rock containing lichen from the top 1.0 mm of the same rock that the snails had been feeding on. Samples were digested in 30% HNO_3 and analyzed for Ca^{2+} by using inductively coupled plasma emission spectroscopy.
7. Ten stones [mean upper surface area (± 1 SD) 7206 (± 1232) mm^2] with endolithic lichens were randomly placed in a fiberglass open-top field enclosure, 6 m by 9 m, with 100 *E. albulus*. The enclosure was sprayed with 3 liters of water per square meter per day to activate snails. At the end of 3 weeks the area on the stones that had been grazed was estimated by measuring the trail length with a map measuring wheel and the trail width with a dissecting microscope. Mean (± 1 SD) area grazed was 3141 (± 420) mm^2 per stone, equivalent to a grazing rate of 15 mm^2 per snail per day. We assumed trail depth to be a minimum of 1 mm, on the basis of laboratory measurements and because these endolithic lichens occur at depths between 1 and 3 mm (*4*). We also estimated snail and stone density and snail grazing rates in the field in the Negev Desert Highlands (34°46′15″E, 30°52′30″N). We randomly sampled 150 quadrats 1 m by 1 m. Mean (± 1 SD) snail density was 21 (± 5) snails per square meter with a mean stone density of 32 (± 9) stones per square meter (that is, 0.66 snail per stone). Mean area grazed was directly estimated by measuring length and width of all trails that were bright white on 100 randomly selected stones. The bright white color is an indication of new trails (Fig. 1). This value was 1300 (± 400) mm^2 per stone, equivalent to 1300 mm^2 per stone per year, because measurements were carried out immediately after the active snail season (December through April). Depth was again assumed to be 1 mm.
8. For the enclosure experiment, annual rate of stone material removal (R_r) (66,100 mm^3/m^2 per year) equals daily grazing rate (R_g) (15 mm^3 per snail per day) times snail density (D_s) (21 per square meter) times number of days of snail activity per year (A) (210 days). Snail activity occurs during the season when dew formation occurs, that is, 7 months a year. For the field estimate, R_r (41,600 mm^3/m^2 per year) equals annual grazing amount (1,300 mm^3 per stone per year) times stone density (32 per square meter); R_g (9 mm^3 per snail per day) equals R_r (41,600 mm^3/m^2 per year) divided by D_s (21 per square meter) times A (210 days).
9. For the enclosure experiment, annual weathering rate by snails R_w (110.4 g/m^2 per year) = R_r (66,100 mm^3/m^2 per year) times density per unit volume of stone material (measured directly by displacement) (D_d) (1.67 g/cm^3). For the field estimate, R_w (69.5 g/m^2 per year) = R_r (41,600 mm^3/m^2 per year) times D_d (1.67 g/cm^3).
10. Ten stones that had been washed with distilled water [mean upper surface area (± 1 SD) 9351 (± 1950) mm^2] were placed in a local area of the highlands known to have a low snail density (more than one snail per square meter) during the dry season (May through November), 5 months of which have no snail activity. The upper surface of stones was washed off once a month with 20 liters of distilled water per square meter. Dust weight in the wash was determined gravimetrically from evaporated samples. Mean (± 1 SD) dust deposition rate was 3 (± 0.917) g/m^2 per month. Our estimates of dust deposition are representative, because we assume that accumulated dust does not turn over on rocks over the 1-month sampling period and that all dust is new input and not redistribution of local dust. There are common problems in estimating dust deposition [T. L. Pewe, *Geol. Soc. Am. Spec. Pap.* **186**, 1 (1981)]. Nevertheless, our estimates for dust deposition are very similar to other values for the Negev of 50 to 200 g/m^2 per year [D. H. Yaalon and J. Dan, *Z. Geomorphol.* **20**, 91 (1974); D. H. Yaalon and E. Ganor, *Int. Congr. Sedimentol.* **19**, 169 (1975)] and for deserts of New Mexico (42 to 164 g/m^2 per year) [L. H. Gile, F. F. Peterson, R. B. Grossman, *Soil Sci.* **101**, 347 (1966)] and Arizona (54 g/m^2 per year) [T. L. Pewe, E. A. Pewe, R. H. Pewe, A. Journeaux, R. M. Slatt, *Geol. Soc. Am. Spec. Pap.* **186**, 169 (1981)].
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13. On average, about 10% of net primary production is consumed by herbivores [M. J. Crawley, *Herbivory* (Blackwell Scientific, Oxford, 1983)]. Snails consume about 4 to 7% of the surface of rock that is capable of supporting primary production to a depth of 1 mm per year.
14. We thank S. Rosen and S. Brand for technical assistance; A. Rokach and R. Mickler for photography; A. Solem for examination of radulae; G. Likens, S. T. A. Pickett, and D. L. Strayer for advice and critical comment. Contribution to the program of the Institute of Ecosystem Studies (IES), New York Botanical Garden. Publication no. 61 from the Mitrani Center for Desert Ecology. Financial support, including support for visiting scientist at IES (M.S.) provided by the Mary Flagler Cary Charitable Trust.

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