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Lichen Recovery Following Heavy Grazing by Reindeer Delayed by Climate Warming

David R. Klein and Martha Shulski

Abstract

Introduced reindeer, *Rangifer tarandus*, over exploited lichen-rich plant communities on St. Matthew Island in the Bering Sea. A die-off of the reindeer followed, exacerbated by extreme weather in 1964, resulting in extirpation of the reindeer. A similar pattern of removal of lichens as major components of plant communities has occurred following introductions of reindeer to other islands at high latitudes. By 1985, two decades following die-off of the reindeer, total lichen biomass was only 6% of that in similar plant communities on adjacent Hall Island, not reached by the reindeer. By 2005, 41 y after the reindeer die-off, lichen regrowth on St. Matthew was only 12% of lichen biomass in the Hall Island communities. A warmer, drier climate and decreased fog in recent decades contributed to deterioration of conditions favoring lichen growth on St. Matthew Island.

Introduction

Introductions of large herbivores to island ecosystems, where none had been present, can lead to major changes in plant community structure and associated ecosystem dynamics (1–4). At the plant community level, these ecosystem changes occur because the new herbivores selectively exploit some plant species as forage differentially and beyond their sustainability as major components within the plant community structure. Similarly, the alternating presence or absence of reindeer/caribou (a Eurasian vs. North American semantic distinction for the same species, *Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) on islands or comparable insular habitats in the high Arctic appears to be tied to the interplay between wide climatic extremes and the differing ability of plant types to sustain continuing tissue loss to large herbivores under high arctic conditions (5–9).

The introduction of reindeer to St. Matthew Island in 1944, a remote subarctic island in the Bering Sea, set the stage for a classic population eruption and subsequent crash die-off of the reindeer following their overexploitation of the limited forage resources of the island (7). Lichens, the primary winter forage in the diet of the reindeer, were the most severely affected components in the plant communities of the island. Systematic monitoring of the effects of the reindeer on the vegetation of the island was begun in 1957 (10) and continued for nearly 50 y through occasional visits to the island before and following the crash die-off of the reindeer in the winter of 1963–1964 (2–3). A visit in 2005 to St. Matthew Island and adjacent Hall Island provided the opportunity to assess the influence of pronounced climate warming in the region in recent decades (11) on the regrowth and reestablishment of lichens in the

formerly lichen dominated plant communities of the island.

Study Area and Background

St. Matthew and Hall Islands (608150N, 1728300W), which have no permanent human habitation, lie in the northern Bering Sea and are components of the Alaska Maritime National Wildlife Refuge (Fig. 1). The islands have an area of 332 and 23 km², respectively, and are separated by a 4-km-wide strait. The terrain of St. Matthew and Hall Islands is dominated by mountains, generally lower than 450 m, and intervening lowlands.

No detailed description of the plant communities of St. Matthew Island had been made prior to the introduction of reindeer in 1944. In 1874, H.W. Elliott (12) described the plant cover of the lichen-dominated landscape of low-lying areas of St. Matthew Island as “a simple coat of cryptogamic gray.” Later visitors to St. Matthew Island, before the reindeer were introduced, commented on the thick mats of lichens in well drained lowlands and on lower mountain slopes (13–14). The vegetation of St. Matthew and Hall Islands is listed as “prostrate dwarf-shrub tundra” in the Circumpolar Arctic Vegetation Map (15). The rich diversity of lichen taxa on St. Matthew has been described by Talbot et al. (16). Plant communities on adjacent Hall Island are similar to those on St. Matthew. Moist sedge meadows, however, are more common on St. Matthew, associated with the longer drainage systems than on smaller Hall Island. Pack ice normally surrounds the islands during six to seven months of winter (17).

The US Coast Guard introduced the reindeer to St. Matthew Island as an emergency food source for personnel stationed there during World War II. At the end

Figure 1. Location of St. Matthew and St. Paul Islands in the Bering Sea. The continental shelf is shown in white. (Map: The Nature Conservancy in Alaska)

of the war, the Coast Guard station was abandoned, and the reindeer were left to increase in the absence of natural predators. Studies of the population dynamics of the introduced reindeer and their impact on the plant communities of St. Matthew Island were begun in 1957 (10). From the original 29 animals introduced, the reindeer increased to 6000 by the summer of 1963. A nearly complete die-off of the reindeer occurred in the following winter in association with an extreme and aberrant weather event (2). Only 42 reindeer survived, including 41 females and one nonviable male. Without breeding and recruitment of new animals, the remnant population declined to extirpation.

In 1957, groups of four 1 m² plots were established at three locations on southern St. Matthew Island, and ground cover of lichens, predominately *Cladonia* spp., in these lichen-dominated plant communities in the lowlands was found to be 75.6% $\pm$ 4.89% SD at Station 1

Figure 2. The thick mats of fruticose lichens that dominated much of the landscape in the southern portion of St. Matthew Island prior to the introduction of reindeer had been greatly depleted by reindeer grazing 13 y after their introduction when vegetation plots were established (a) (Station 2) in early August 1957. (Photo: D. R. Klein) Only fragments of fractured lichens and moss remained on the ground surface in the depressions between the dark-green willow hummocks. Similar lichen-dominated plant communities with scattered hummocks of willow on Hall Island in 2005 (b), never reached by the reindeer, served as controls for assessing grazing impact of reindeer on similar communities on St. Matthew Island. (Photo: E. Witten)

and 73.2% $\pm$ 12.02% SD at Station 2 (10). Lichens in these lowland communities, however, had already been substantially altered by the grazing and trampling effects of the reindeer (Fig. 2a). Where thick mats of lichens had presumably existed before the reindeer arrived, only a thin layer of fractured lichens and mosses remained. At Station 3, located on a ridge top $\sim$ 60 m higher than the plots at the lowland stations, lichen cover in plant communities was 28.3% $\pm$ 15.79% SD, and *Dryas octopetala* and *Empetrum nigrum* occupied substantial proportions of the remaining ground cover.

At the time of establishment of the vegetation plots, total biomass of lichens had already been markedly reduced in the 13 y that followed the introduction of the reindeer. Although the lichen mats had been reduced to a thin layer of fractured lichens, ground cover of lichens appeared similar to that prior to reindeer introduction. This observation was based on the similarity of the lichen-dominated plant communities to those on adjacent Hall Island, which had never been reached by the

Table 1. Lichen biomass measurements from 1985 and 2005 taken in similar plant communities on St. Matthew and Hall Islands (g m⁻² $\pm$ SD).

	St. Matthew Island	Hall Island
1985	35 $\pm$ 18	550 $\pm$ 144
2005	62 $\pm$ 32	507 $\pm$ 86

Figure 3. Changes in vegetation reflected in mean percent ground cover 6SE in the four 1 m² plots at Stations 2 (right) and 3 (left) as measured in 1957, 1985, and 2005.

reindeer, where lichen mat thicknesses were, and have remained, at 70–80 mm (3) (Table 1, Fig. 2b). In 1957, lichens within the plots consisted of a layer of fractured fragments of both living and dead lichens. By 1963, however, when reindeer numbers peaked at 6000, ground cover of lichens in the plots at Stations 1 and 2 and in the surrounding areas was visually estimated at less than 13%. The fragments of forage lichen species present in 1957 had been almost entirely removed by the continued effects of grazing and trampling by the increasing numbers of reindeer until the crash die-off in 1964 and/or removal of remaining unattached fragments of lichens by the strong cross-island winds. By 1985, in those portions of the plots that originally had been dominated by lichens, virtually no evidence of the prior presence of the

forage lichen species remained. No reestablishment of forage lichen species (predominantly *Cladina* spp.) had occurred by 1985, although pioneering lichen species (predominantly *Cetraria delisei*, *Sphaeophorus globosus*, and *Stereocaulon* spp.) were becoming established and comprised 31% of the ground cover in these plots (3).

Assessment Procedure Associated with the 2005 Island Visit

During visits to St. Matthew and Hall Islands in 2005 (July 18–28), eight permanent 1 m² plots established within previously lichen-dominated plant communities in 1957 (10) were reexamined, four at Station 2 and four at Station 3. Photo images were taken of each of the

Figure 4. Time-series plots of the mean summer (June–July–August) precipitation (mm), temperature (8C), relative humidity (%), and frequency of occurrence for low cloud-ceiling heights (below 160 m) in July for St. Paul Island. Included in each plot is a five-year moving average and the best-fit linear trend line. The Student's *t*-test performed on all four time series revealed that the temperature trend is statistically significant at the 95% confidence level. The others were not statistically significant.

plots to enable assessment of vegetation changes and to measure percent cover within these plots for comparison to similar measurements recorded in 1963, 1966 (2), and 1985 (3). Photo images were also taken at the site of a 1954 photo by Rausch and Rausch (18), which showed extensive areas of severely depleted and fragmented lichens being replaced by *Empetrum nigrum*.

Lichen biomass sampling, using randomly placed 0.25 m² sample plots, was conducted in 1985 and 2005 in plant communities located in the southern portion of St. Matthew Island where lichens had been most abundant prior to introduction of the reindeer. Similar lichen biomass sampling was done in comparable lichen-dominated plant communities on Hall Island, which has no previous reindeer grazing history (Fig. 2b). The lichen biomass samples were placed in plastic bags and transported to the University of Alaska-Fairbanks, where they were sorted to remove fragments of mosses, air dried (relative humidity 20%), and weighed.

Weather data recorded on St. Paul Island, 400 km south-southeast of St. Matthew and the closest weather station with a long and uninterrupted series of climatic data (1949–present), were used in comparison to the limited data at St. Matthew. St. Matthew daily temperature and precipitation data were only available for the period October 1942 through August 1944, when military observation stations were located there. Since the corresponding observations for St. Paul are missing for this time period, the closest years (1949 to 1954) were used in the station comparison. St. Paul is currently an automated National Weather Service first-order meteorological station and is located at the airport (578100N, 1708130W, 10.7 m above sea level). All climatological data used include, where available, hourly observations of cloud-ceiling height, daily precipitation totals and temperature, and monthly average relative humidity (19). Cloud-ceiling height measurements (reported to the nearest 33 m, or 100 ft) were used as a determinant for fog frequency by analyzing the occurrence of heights less than 160 m (500 ft). Continuous low clouds and thick fog are commonplace for summer in this Bering Sea island location because of abundant moisture availability, a cool ocean, and relatively warm atmosphere. Precipitation, temperature, and relative humidity were totaled or averaged, respectively, for each month. A simple time-series analysis of the data was conducted over the period of record, and the best-fit linear trend was determined. A t-test was used to indicate significance of the trend at the 95% confidence level.

Assessment of Change

Vegetation Changes

When the plots at Stations 2 and 3 were visited in 2005, relatively little change had taken place in the vegetative cover on the plots in the 20 y that had elapsed since 1985 (Fig. 3). Within the plots at Station 2, the proportion of

the area that had only a thin covering of fragmented lichens and moss when the plots were established in 1957 had become diminished in area by 1985 through establishment of pioneering lichen species and encroachment by vascular plants, and moss. In 2005, in all eight plots, vascular plants, primarily *Salix arctica* (previously *S. crassijulis* x *ovalifolia*), *Dryas octopetalla*, *Empetrum nigrum*, sedges, grasses, and occasional forbs, which had increased following removal of the lichens, continued to dominate the vegetated portions of the plots.

In 2005, it was evident that many vascular plant species had responded positively to the warmer climate. Among the prostrate shrubs, willows appeared particularly robust, with leaf expansion continuing through late July, although this apparently enhanced growth may have been at least partly related to the warm summer temperature on St. Matthew in 2005 (Fig. 4). Plants of some herbaceous species appear to have increased their presence in many plant communities, presumably by the opening of new niches for seed establishment by the reindeer, and by increased seed production and dispersal following the disappearance of the reindeer (3). *Pedicularis kanei*, *Oxytropis nigrescens*, and *Rumex arcticus* were noteworthy in this regard. In 2005, lichens and mosses, however, did not show responses similar to vascular plants. This appeared to be a consequence of the warming climate in recent decades. Although it was apparent in 1985 that ground cover of mosses had initially increased following removal of lichens by the reindeer, by 2005, mosses had decreased on moister sites through the shading effect of expansive growth of willows and other vascular plants. On well-drained and drier sites, the composition of moss species had changed from predominately green-colored species in 1985 with high moisture requirements, such as *Polytrichum piliferum*, dead tissues of which were still present, to gray-white species that are more adapted to dry conditions or to periodic drought, such as *Racomitrium lanuginosum*.

Lichen biomass measurements made in 2005 in similar areas as in 1985 (3) on both St. Matthew and Hall Islands showed that on St. Matthew there had been surprisingly little regrowth of lichen biomass within the plots in the 20 y that had elapsed (Table 1). In the 42 y that had elapsed following the crash dieoff of the reindeer, the percent of lichen biomass in the previously lichen-dominated plant communities on St. Matthew was only 12% of that of comparable lichen-dominated communities on Hall Island.

An old beach ridge between the northeastern shore of Big Lake and the sea was photographed by R. L. Rausch and V. R. Rausch in 1954 (18) (Fig. 5a). They described the plant community there as a “Stabilized beach grown to lichens and *Empetrum nigrum*,” and further commented that the lichens “. . . in general had suffered severe fragmentation by the reindeer.” The photograph provided a baseline for assessment of the subsequent influence of

the reindeer on this unique plant community. In 1957, Klein (10) described this plant community as "An almost pure stand of crowberry, *Empetrum nigrum*. . ." The reindeer had completely removed the remaining lichens in this plant community in three years as the reindeer population increased from an estimated 400–500 (18) to 1350 animals (10). A photograph from 2005 in the same location shows that, surprisingly, no lichens had become reestablished in this plant community after 48 y (Fig. 5b).

Changing Climate

A comparison of weather data recorded at St. Paul on the Pribilof Islands, 400 km southeast of St. Matthew Island, shows that St. Paul is warmer and wetter than St. Matthew. The difference in temperature is most pronounced during winter, and there is only a slight difference during summer. The likely attribution for the greater winter discrepancy is the difference in sea-ice conditions. During May through September, the period of the year when lichen growth is most likely to take place, monthly mean temperature was 1.28°C cooler and monthly mean precipitation was 13.8 mm less on St. Matthew. Though only two years of temperature data and one year of precipitation data were available for St. Matthew, this comparison provides at least some quantitative assessment of the climatological differences in the two locations.

Weather data from St. Paul Island show a pronounced warming trend associated with a climatic regime shift initiated in the late 1970s, a pattern that has been observed in relation to declining extent of sea-ice coverage in the northern Bering Sea (17). This shift in 1976 corresponds to a change in the phase of the Pacific Decadal Oscillation from negative prior to 1976 to a positive mode since that time. Dramatic changes have been documented not only for the Bering Sea region, but for Alaska as a whole, such as a significant increase in temperature for the post-1976 period (11). While the change is most pronounced in the cold seasons, the shift is noticeable for the summer (June–July–August) period as well. Two prominent features are evident in the long-term summer temperature time series for St. Paul: an overall increase in temperature over time of almost 28°C since 1949, and a stepwise change around 1976 (Fig. 4).

Along with the general warming trend, there has also been a drying trend for the summer months at St. Paul. The total summer precipitation, while showing high variability, exhibits a decline of ~30 mm over the 58 y time period. There is a normal seasonal cycle to the precipitation pattern: a minimum in late spring and a maximum in autumn. Of the summer months, August has the highest precipitation, with about 76 mm on average, and the total annual average precipitation for this area is just over 584 mm. Relative humidity values have been normally quite high in this climate region with a strong maritime influence, especially during the warm season. A time-series plot of the average summer relative

humidity shows high values of around 92%, on average, and a gradual decline, indicating a slight drying of the atmosphere. Finally, the occurrence of low-lying clouds and fog has been common for this environment. During June and July, the frequency of cloud ceiling height less than 160 m shows a decrease during this long-term time sequence, indicating higher cloud heights, a reduction in cloud cover, or both. All of the climatological data point toward warmer and drier conditions at or near the surface in recent decades, which, in combination, are known to be less favorable for lichen growth. A marked decline of about 2 m in the water level of the largest lake on the island in recent decades is also a reflection of the drying climate.

Discussion

Overexploitation of the Lichens by the Reindeer

Why did the forage lichens that were so heavily grazed by the reindeer fail to show significant recovery in the 41 y following the crash die-off of the reindeer? Of foremost importance, is the reindeer themselves, which, in the 19 y from their introduction to the crash die-off, had exploited virtually all of the standing biomass of forage lichens available in the lowlands of the southern one-third of the island where the lichen-dominated plant communities were concentrated. This was the area where reindeer derived from Nunivak Island were released in 1944, and it remained the area of major focus of use by the reindeer throughout their presence on the island. This area initially provided optimal foraging conditions for reindeer on a year-round basis, including abundant lichens as winter forage, and in moister, less well-drained sites, sedges and other vascular plants, which were of importance in the summer diet. The original animals were derived from stock brought from the Chukchi Peninsula of Russia to the Seward Peninsula during 1891–1902 (20), from which animals were moved to Nunivak Island in the 1920s (21). The Chukchi reindeer are noteworthy among the semi-domestic reindeer of the Russian North for their strong fidelity to a fixed grazing area and for their tendency to aggregate into large groups (22). Herders consider these characteristics desirable when the reindeer are closely herded. In the absence of herders to move the animals, however, these characteristics tend to result in localized overexploitation of forage resources. This sedentary tendency of the St. Matthew reindeer, derived from their Chukchi lineage, led to their tendency to remain in the area of their release on the island and accelerated the destruction of the previously unexploited lichens there. It was only when the reindeer had reached their peak numbers in 1963 that increased evidence of use of the northern portion of island, primarily by groups of adult males, became apparent.

Assuming that the entire island was suitable for grazing, the stocking level of ~5.5 ha per reindeer when the

population peaked at 6000 greatly exceeded that recommended by Palmer (20) for Alaskan coastal tundra. He recommended 13.4 ha per animal, if herded, and 18.2 ha for free-ranging animals. It is likely that at the time of their introduction, not more than one-third of St. Matthew Island would have included plant communities that collectively would have been considered suitable for supporting reindeer on a year-round basis, in which case, the recommended maximum stocking level by Palmer's standards would have been 600 reindeer. On St. Paul Island, 400 km to the southeast of St. Matthew and one-third the size, reindeer introduced in 1911 increased to 2000 animals in 27 y with only relatively small annual harvests; the reindeer population then declined to 2 animals in the subsequent 12 y in association with removal of virtually all lichens by the sustained heavy grazing pressure of the reindeer (23). A similar pattern of introduced reindeer altering plant community structure through removal of lichens and preferred vascular plant species occurred on South Georgia Island in the Antarctic (4).

Vulnerability of the Lichens to Exploitation

Another important factor contributing to the nearly irreversible overexploitation of the lichens on St. Matthew Island was the nature of the thick lichen mats at the time of introduction of the reindeer. Lichens on St. Matthew were at a climax stage when the reindeer were introduced because of the ideal conditions that had existed for lichen growth in the foggy maritime climate of these islands in the absence of any large herbivores. The lichens in these lichen-dominated plant communities were mostly those species highly favored by reindeer as winter forage.

Although polar bears were resident in summer on these islands in the past and had been observed grazing on green vegetation in sedge-dominated areas (12), the summer resident bears had been eliminated by the 1890s (24). Prior to their elimination, possible impacts of the polar bears on the lichens through trampling apparently had been minimal. Well-defined trails were used by the bears when traveling through lichen-rich areas, limiting their primary impact to the trail itself, or perimeters of lichen-rich areas of the lowlands (Fig. 5). The rich lichen mats, in the absence of exploitation by large herbivores, were presumably in a relatively stable state, where growth at the top equaled decomposition of the older lichen material underneath as it became deprived of light. In this condition, these thick lichen mats were vulnerable to overexploitation by the introduced reindeer because the living portions that were sought by the reindeer were not directly attached to the mineral soil substrate, as is usually the case where there has been a history of moderate to heavy grazing (25). Grazing of the lichens by the reindeer, therefore, often removed all living portions of the lichens, leaving behind only decomposing dead lichen tissues from which regrowth could not occur. This

vulnerability of virgin lichen stands to damage when first grazed by reindeer has been described in Sweden by Skuncke (25). On St. Matthew, trampling of living portions of the lichens also contributed to the fracturing and dislocation of the lichens from their attachment to the ground, especially when they were dry in summer, rendering the unattached lichen fragments vulnerable to dispersal by wind. Although living fragments of lichens dispersed by wind can be a factor in reestablishment of lichens vegetatively, on St. Matthew, prevailing cross-island winds undoubtedly resulted in large amounts of the lichen fragments that remained on the ground following grazing by the reindeer being blown to sea.

The unique plant community restricted to an area lying between Big Lake and the sea (Fig. 5a), described as a lichen *Empetrum* community in 1954 by Rausch and Rausch (18), had become "grown almost exclusively to *Empetrum nigrum*" by 1957 (10). The reindeer had increased almost threefold during this three-year period. There was no evidence of reestablishment of lichens in this *Empetrum* community when visited 21 y after the reindeer die-off in 1985, as well as when visited again in 2005, a total of 41 y without reindeer grazing pressure. Patches of dead *Empetrum* were evident in 1957 that presumably had died from the shading effect of the lichens that had previously grown there. By 2005, these patches had become grown over with living *Empetrum*, creating a relatively uniform green ground cover, and only an occasional other plant species was present (Fig. 5b). Also noteworthy, lichens had not become established in the old polar bear trail overgrown by *Empetrum* evident in the 1954 photo in the more than 50 previous years without polar bears on the island (18), emphasizing the difficulty for lichen establishment on the densely growing *Empetrum*.

Substrate Limitations on Lichen Reestablishment

The nature of the remaining ground surface following excessive grazing pressure appears to have played a major role in the delayed reestablishment of fruticose lichen species on St. Matthew Island. Dead and decomposing plant material appears to be favored for attachment of fragments of fruticose lichens that may be transported by wind, as well as for establishment of early seral stage foliose, fruticose, and possibly crustose lichen species through *propagules* (*soredia* and *isidia*) commonly transported by wind, birds, or other animals (26). Dead organic material that remained on the ground surface following removal of the thick mats of *Cladina* spp. by the intensive grazing pressure of the reindeer was subsequently removed by wind in exposed sites, along with the finer soil particles that had been on the soil surface. The coarse, gravelly soil surface remaining apparently did not provide a suitable substrate for reestablishment of lichens. This was particularly evident in the wind-exposed plots established at Station 3 (Fig. 3). Live tissues

of vascular plants are rarely sites of establishment of new lichen growth, and this appears to have been a factor in the failure of lichen reestablishment in the *Empetrum*-dominated old beach ridge near Big Lake, 41 y after the demise of the reindeer (Fig. 5).

Climate Change Effects on Lichen Recovery

Has the warming climate in recent decades at St. Matthew and Hall Islands had an effect on the seasonal growth of vegetation there? Lichen recovery was slow in the 21 y following the crash die-off in the southern portion of the island that had been most heavily grazed by reindeer (3). Recovery was primarily limited to species characteristic of early succession stages of lichen establishment following extreme disturbances to the ground cover. In the same area of the island, surprisingly little change in lichen ground cover, biomass, and species composition had occurred in the 20 additional years since 1985. Initial recovery of lichens from the grazing effects of the reindeer after 1964 to 1985 appeared to be primarily related to the vulnerability of the pristine lichen stands to destructive grazing by the reindeer. The extremely slow rate of continued recovery of the lichens from 1985 to 2005, however, appears to have been tied to changing climatic conditions associated with a climatic regime shift to warmer temperatures initiated in the late 1970s (17, 27). This assumption is supported by extrapolation of past weather data from the St. Paul weather record on St. Matthew. The regional climate warming effect, through lengthening of the plant growth season, warmer ambient temperatures during summer, and a decrease in precipitation and fog during this season, has affected growth of lichens and vascular plants differently on St. Matthew (Fig. 4). Lichens, unlike rooted vascular plants, are dependent on atmospheric moisture for growth. They enter dormancy and a growth stasis when their tissues become dry. Although lichens are well adapted to undergo drying during extended periods of low humidity in the absence of rain and fog, no growth can occur under such conditions.

Reduced rates of lichen growth associated with climate warming have also been observed in recent decades in northwestern Alaska (28). The response of lichens to the changing climate at northern latitudes is proving to be markedly different and often opposite that of vascular plants, which has major potential consequences for the dynamics of northern ecosystems, where lichens have played critical roles in plant community processes and structure, and where they have been of major importance in the winter diet of caribou and reindeer.

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