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Vicuña dung gardens at the edge of the cryosphere

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The decline and subsequent recovery of the vicuña (*Vicugna vicugna*, wik'uña in Quechua), one of the few large, native herbivores in the Andes (Fig. 1), is one of the world's greatest conservation success stories. Over-exploited nearly to extinction by the 1960s, the current



FIG. 1. Vicuña latrine located at 5,320 m above sea level inside a rapidly deglaciating corridor in the Cordillera Vilcanota, southeastern Peru. The latrine is surrounded by characteristically unvegetated glacial till in front of the Puka outlet glacier descending from Nevado Hatun Rit'i.

population of these wild camelids is estimated at close to 500,000 animals, with nearly one-half of the global population in Peru (Acebes et al. 2018). Vicuñas are prized, noted for the high economic value of live-shorn wool from wild populations and their cultural significance among high-Andean indigenous pastoralist communities. The ecological roles of vicuñas are not well understood, although it is clear that predator–prey dynamics between puma (*Puma concolor*) and vicuña can have cascading effects on plant community composition and dynamics (Donadio and Buskirk 2016). One probable mechanism through which vicuñas have profound ecosystem effects is by traveling in large groups and defecating repeatedly in communal dung piles. These latrines persist for decades or more in the arid, alpine, rocky moraine landscape left in the wake of rapidly retreating Andean glaciers.

As part of a broader research program to understand community succession, phenology, and assembly following the rapid loss of glacier cover, in 2018 we began to study vicuña-mediated facilitation of primary succession in the recently deglaciated zone on their latrines. We studied properties of soil, plant, and microbial communities on latrines in newly deglaciated areas in one of the most heavily glaciated tropical mountain ranges on the planet, the Cordillera Vilcanota of southeastern Peru (13°45'44" S, 71°04'55" W). Over the last 15 yr, the Cordillera Vilcanota has become a living laboratory for understanding physical, social, and ecological responses to rapid climate change. We are finding evidence that nutrient subsidy by vicuñas accelerates the long (~100 yr) lag between glacier retreat and significant plant colonization in cold, arid, high-mountain landscapes (Darcy et al. 2018). Feces deposition by large herbivores shortcuts nutrient pathways in another cold and severely nutrient limited ecosystem, the tundra, where wide-scale deposition of reindeer feces across the landscape yields more food for reindeer (Van Der Wal et al. 2004).

Vicuña latrines become stunning islands of vegetation in a landscape otherwise comprised almost entirely of rocks and ice (Fig. 1). Vicuña latrines are thus facilitating the upward expansion of high-Andean grassland plants into glacial moraines and forefields on a timescale relevant to the rapid pace of anthropogenic climate change. In our study, we focused on vicuña latrines located from 4,950 m above sea level, near the toe of the rapidly retreating Puka outlet glacier of Nevado Hatun Rit'i, up to 5,450 m above sea level, near the current lower extent of the Osjollo Anante glacier. Ice has retreated from the corridor between these two glaciers at an accelerating pace over the last 40 yr (Seimon et al. 2017), allowing animals including vicuñas to move

across a landscape that was previously inaccessible under glacial ice and snow.

We placed a motion-activated camera (TrophyCam, Bushnell Corp., Kansas, USA) on one latrine located at 5,250 m above sea level from 1 May 2019 to 15 July 2019, during the pronounced dry season. We wanted to understand the frequency of vicuña defecation events and vicuñas visiting the latrine, and we were eager to confirm previous visual observations of vicuñas foraging on this and other latrines in tropical glacier forefields. The camera recorded vicuñas and other mammals (mountain viscacha, *Lagidium viscacia*, and Andean culpeo fox, *Lycalopex culpaeus*) visiting the latrine, suggesting that latrines are an important landscape feature for other wildlife, and may influence the spatial dimensions of predator–prey dynamics playing out in these island-like patches of vegetation. In addition, we made the surprising and significant discovery of a vicuña grazing on plants inside the latrine (Fig. 2). In a 16-photo sequence, we see a vicuña enter the latrine from the right and cross it while keeping its head below its shoulders and extending its open mouth near the lower stratum of plants. We interpret these photos as evidence of grazing behavior on the latrine. Vicuñas have morphological adaptations including special incisors and prehensile lips that allow them to graze the lowest stratum of forbs and perennial grasses close to the ground (Borgnia et al. 2010), which we observed.

Creation of latrines is ubiquitous in mammals (Eisenberg and Kleiman 1972, Brown and Macdonald 1985, Gorman and Trowbridge 1989), and latrines are hypothesized to function primarily as information centers that transfer social information between individuals and groups such as identity, health, social status, location information, and home range or territory boundaries (Buesching and Jordan 2019). Alternative hypotheses for latrine behaviors include avoidance of parasite transmission and predator avoidance (Hart 1994, Boonstra et al.

1996, Buesching and Jordan 2019). Alpacas, domesticated relatives of vicuñas, have been observed grazing at their latrine sites when forage was limited during the dry season (McGregor and Brown 2010). Among vicuñas, latrines are used for social communication and territoriality (Franklin 1980, Vilá 1994), but other uses are unknown.

Our evidence of vicuñas grazing on latrines suggests the discovery of a novel function of latrines for wild mammalian herbivores. By creating and maintaining latrines, vicuñas may be essentially creating resource patches, “gardens,” that facilitate their movement through the barren, high-Andean landscape (a Vicuña Gardening Hypothesis). The nutritional benefits of foraging at latrine sites is likely somewhat counter-balanced by the risks of encountering gastrointestinal parasites at these sites, but relatively little is known about these complex foraging trade-offs in wild mammals (Coulson et al. 2018). Because of the longstanding hypothesis that latrines broadly function to reduce fecal–oral transmission of otherwise undetectable gastrointestinal parasites that can have negative effects on hosts (Ezenwa 2004), it is surprising to observe a wild species foraging where the risk of parasite contamination may be relatively high. Our observations suggest that any parasite load cost to vicuñas from foraging near feces is outweighed by the benefits of nutrient intake in at least some situations.

The tradeoff between parasite risk and nutritional benefits of foraging in a feces-contaminated area may change under different environmental contexts (Hutchings et al. 1999). Exploiting nutritional resources on latrines may be especially important in the context of extreme environments (e.g., arid high mountains) where resources are exceedingly scarce and latrines provide reliable resources that persist for many years and throughout the pronounced dry season. Not only do vicuña latrines have profound environmental consequences in the Andean alpine ecosystem in the context of succession and climate change, latrine foraging behavior may provide these large herbivores with some of the only available grazing opportunities as they pioneer routes through glacier forefields and travel between grazing areas in the rapidly deglaciating high Andes. Ongoing research will investigate the potentially complex interactions of microbes, plants, and animals that determine the trade-offs between parasite risk and nutritional benefit of latrine foraging in this extreme environmental context. We will explore the relative importance of resources available on vicuña latrines for vicuña diets, as well as determine if vicuña latrines have an outsized contribution to resources for other animals eking out an existence at the edge of the rapidly shifting cryosphere.

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FIG. 2. Vicuña grazing low-growing plants on a latrine at 5,250 m above sea level on 4 June 2019.

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