



Research

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After the frass: foraging pikas select patches previously grazed by caterpillars

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Interactions among herbivores can shape the structure of their communities and drive their dynamics. However, detecting herbivore interactions can be challenging when they are deferred in space or time. Moreover, interactions among distantly related groups of herbivores, such as vertebrates and invertebrates, are poorly understood. We investigated the effect of invertebrate herbivory on the subsequent foraging choices of a small alpine-dwelling vertebrate, the collared pika (*Ochotona collaris*). We carried out a field experiment within pika territories, by presenting them with a choice of foraging sites following manipulation of invertebrate (caterpillar) herbivory. Pikas actively selected areas with increased, recent invertebrate herbivory. While the underlying mechanisms behind this interaction remain unknown, our results demonstrate a positive effect of invertebrate herbivores on subsequent vertebrate foraging preferences for the first time. Even among distantly related taxa, such interactions where one herbivore is cueing on the foraging of another, could drive the creation of herbivory hotspots, with cascading consequences for ecosystem processes.

1. Introduction

Indirect interactions are prevalent in biological communities, and can play a crucial role in their structure and dynamics [1]. Such interactions may be less conspicuous than direct ones and may occur among distantly related organisms. Taxonomic proximity can influence interaction strength among organisms because closely related species use resources more similarly [2], but strong interactions can also occur among distant taxa that share resources [3]. Among herbivores, interactions between vertebrates and invertebrates have been often ignored because of the intrinsic differences among them [4,5]. Larger body sizes of vertebrates have led to the assumption that they can affect invertebrates (more than the reverse) because vertebrates have greater impacts on vegetation [4]. Changes in the quality or quantity of vegetation or in habitat structure caused by vertebrate browsing can certainly affect invertebrate herbivores [6]. The effects of invertebrate herbivores on vertebrates have been less studied and usually reported when the invertebrate herbivore constitutes a pest. Less conspicuous invertebrate population levels may also affect sympatric vertebrate herbivores; however, to-date few studies have dealt with the effects of non-outbreak invertebrate populations on vertebrate herbivores or have failed to detect an effect [7].

Interactions among herbivores can be frequently delayed in time, when resource use by one herbivore earlier in the season affects subsequent use by another herbivore. For closely related species, previous grazing can enhance later use by other herbivores leading to a 'grazing succession' [8], but how this may apply for distantly related herbivores remains unknown. We investigated the effect of invertebrate herbivory on the subsequent foraging choices of a small vertebrate, the collared pika (*Ochotona collaris*). This is a suitable model system because pika foraging is constrained to meadows [9], where invertebrate herbivores (caterpillars) also occur. Relative intensity of foraging

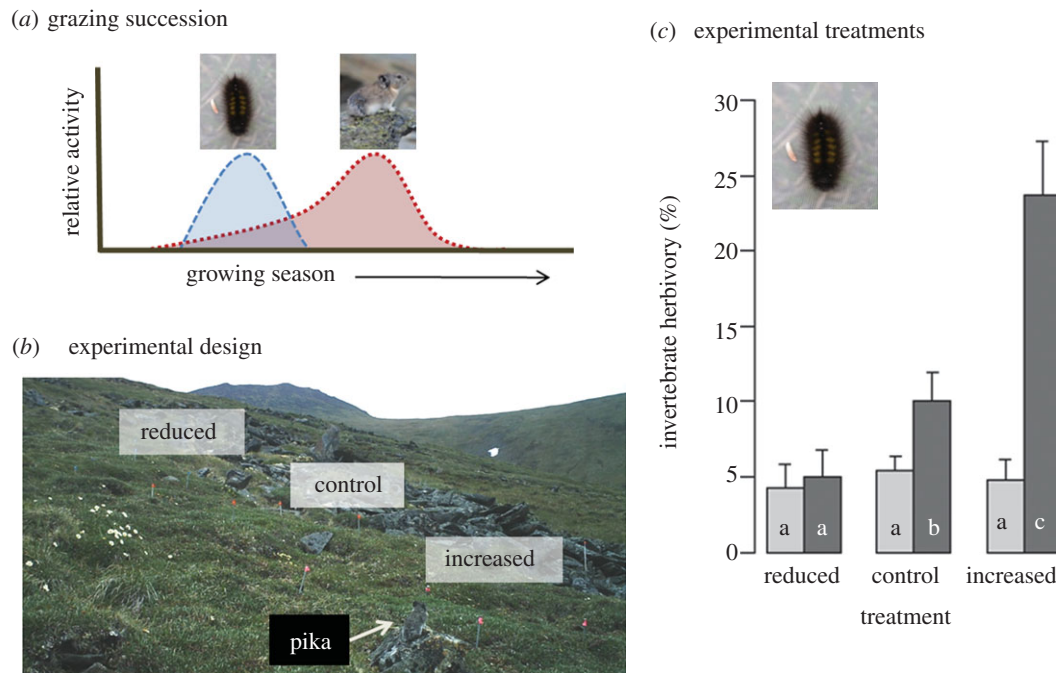


Figure 1. Experimental design. (a) Schematic of the relative activity of both herbivores along the growing season. (b) Photograph of pika and experimental plots in the field. (c) Effectiveness of experimental manipulation of invertebrate herbivory, showing percentage invertebrate herbivory before (light grey) and after (dark grey) manipulation. Experimental treatments either decreased (by using insecticide) or increased (by adding caterpillars for 7 days) invertebrate herbivory compared with the baseline levels of the control plots. Error bars indicate standard errors and letters indicate significant differences. (Online version in colour.)

activity of these herbivores varies during the growing season, with caterpillar activity peaking earlier and pikas later in the season ([10,11]; figure 1a). The aim of our study was to experimentally evaluate the effect of caterpillar herbivory on subsequent preferences of foraging collared pikas. We hypothesize that invertebrate herbivory will have an effect on foods available to pikas; this effect could be either positive or negative, depending on how invertebrate herbivory affects the availability and quality of shared resources.

2. Material and methods

(a) Study area and species

The study was conducted in an alpine valley in the Ruby Range (61°21' N, 138°28' W), SW Yukon, Canada. Landscapes comprise alpine meadows and tundra vegetation, interspersed with boulderfields. Collared pikas (*O. collaris*) are abundant in boulderfields, and use the adjacent meadows to forage and collect food caches (hay) for overwinter survival [11], creating over the years a well-defined grazing gradient from the boulderfield margin to the meadows [9]. Arctic moth *Gynaephora groenlandica* (Lymantriidae) caterpillars also occur in these meadows (mean density = 0.02 individuals per m², s.d. = 0.04) and use similar food resources, with their main hosts being *Salix* spp. and *Dryas* spp. [10].

(b) Experimental design

We constructed three experimental 1-m² plots on 10 foraging territories of actively haying pikas on 18 July 2012 (figure 1b). Invertebrate herbivory prior to the experiment was estimated using the point intercept method, with a 50 × 50 cm quadrat (5 cm grid, $n = 100$ interceptions) to determine the proportion of plants with obvious signs of invertebrate leaf damage. These pre-treatment levels of herbivory were low (mean \pm s.d. = 0.048 ± 0.021) and did not differ among plots (binomial

generalized linear mixed model (GLMM), $\chi^2 = 1.32$, d.f. = 2, $p = 0.520$; figure 1c). Plots were randomly allocated to one of three treatments: increased, reduced or baseline (control) invertebrate herbivory.

Increased herbivory was achieved by placing two similar-sized *G. groenlandica* caterpillars into each 1-m² plot. To prevent caterpillar escape, plots were covered with a 15 cm high net. Plots with decreased invertebrate herbivory were hand-sprayed once a week or after heavy rains with a commercially available Btk insecticide (*Bacillus thuringiensis* subspecies *kurstaki*, type HD-1; 6 ml of solution diluted in 1 l water), which is specific to a broad spectrum of caterpillars but innocuous to mammals. Baseline plots were sprayed with a similar volume of water as a procedural control. Baseline and reduced herbivory plots were temporarily fenced to exclude pika foraging while caterpillar enclosures were in place. After one week, treatments were discontinued and their effectiveness assessed; plots differed in the amount of invertebrate herbivory (binomial GLMM, $\chi^2 = 164$, d.f. = 2, $p = 0$; figure 1c).

Following removal of the caterpillars and fences from the plots, pikas had free access to the three experimental treatments. We evaluated pika foraging preferences within the plots after 7 days by quantifying pika herbivory (point intercept) based on two dominant plant species, *Dryas octopetala* and *Carex* sp., for which pika herbivory can be easily identified.

To ensure that pika foraging preferences were not related to the application of Btk insecticide, we conducted cafeteria trials [12]. Twenty-three pikas were presented for 3 consecutive days with two PVC tubes, each containing five fresh leaves of a preferred food plant, *Polygonum bistorta*, treated with insecticide or water (procedural control). No differences were found in the number of leaves removed by pikas from insecticide or control tubes (Poisson GLMM, $z = 0.386$, $p = 0.699$).

(c) Data analysis

Differences in pika herbivory among the experimental plots were analysed using a GLMM with binomial errors. Pika herbivory

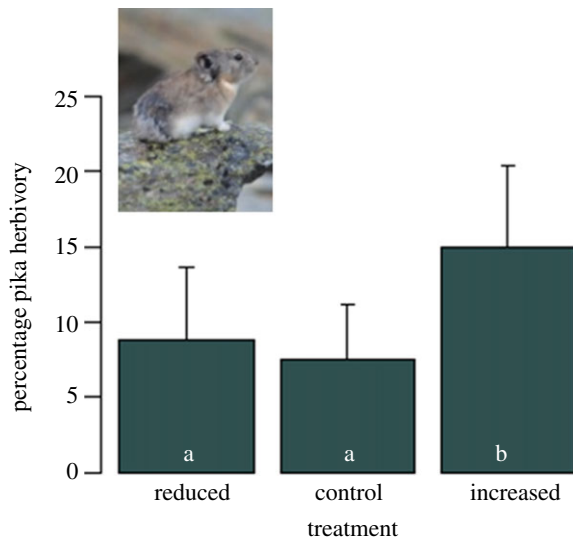


Figure 2. Pika foraging preferences following experimental manipulation of invertebrate herbivory, either decreasing (by using insecticide) or increasing (by adding caterpillars for 7 days) invertebrate herbivory compared with the control plots. Error bars indicate standard errors and letters indicate significant differences. (Online version in colour.)

(proportion of *Carex* sp. or *D. octopetala* damaged by pikas) was used as the response variable, foraging area ($n = 10$) as a random factor, and experimental treatment was included as a fixed factor. All analyses were conducted in R v. 2.14.0 [13]; all modelling assumptions were checked. Data are available as electronic supplementary material.

3. Results

Pikas showed significant differences in their use of the three types of experimental plots (binomial GLMM; $\chi^2 = 30.6$, d.f. = 2, $p = 0$; figure 2). Pika herbivory was highest in experimental plots with increased invertebrate herbivory (mean \pm s.d. = $14.91 \pm 8.82\%$; control versus increased: GLMM estimate = 0.844, $z = 5.02$, $p = 0$). There were no differences in pika herbivory between the control plots and plots with artificially reduced invertebrate herbivory ($z = 1.20$, $p = 0.230$).

4. Discussion

Our results showed that, when given a choice, pikas actively selected patches with increased recent invertebrate herbivory, demonstrating a positive interaction between distantly related, different-sized herbivores. Larger body and bite sizes often translate into vertebrates removing more biomass than insects, and the assumption that vertebrates have larger effects on plant population dynamics [4]. Although collared pikas are relatively small mammals (160 g), differences in body size with the relatively large *G. groenlandica* caterpillars (300 mg) could drive asymmetries in their interactions, with only the larger herbivore affecting the smaller one. However, we found a clear effect of the smaller herbivore on the larger one.

The mechanisms driving the positive selection of caterpillar grazed areas by pikas are still unknown, but a number of hypotheses can be suggested. Herbivorous insects typically consume a small fraction of the available plant foliage, so biomass removal by caterpillars is unlikely to be significant to pikas. However, even small amounts of invertebrate damage can have important ecological effects [14], not necessarily

deleterious to other herbivores. For example, invertebrate herbivory can induce secondary growth on their host plants, making more nutritious, new-growth tissues available to other herbivores [15]. Most of the plants eaten by caterpillars in this study have shown secondary growth and changes in morphology or phenology in response to mammalian herbivory [9]. Pikas may select foods based on leaf morphology, but their choice is affected by a complex suite of factors that are species-specific [12]. An alternative could be that caterpillar foraging induces changes in the chemistry of their host plants, through structural or volatile plant defences. Food-hoarding mammalian herbivores can take advantage of otherwise deterrent secondary chemical compounds because they can circumvent their toxicity through storing foods prior to consumption [16]. Plant chemical defences can influence foraging decisions of other pikas (e.g. *Ochotona princeps*; [16]), but seem less likely to influence forage selection of collared pikas living in colder and drier environments [17].

Besides a direct effect on the individual host plants, caterpillar herbivory may have a variety of impacts at the plant community level and on ecosystem processes. These effects have been largely (and typically) reported for vertebrate herbivores [4], and to a lesser extent for invertebrates. However, there is growing evidence of invertebrate herbivory altering competition abilities of plants, nutrient cycles and primary productivity [18]. Other activities of caterpillars could impact ecosystem processes at a local scale, such as soil nutrient cycling. For instance, frass of *G. groenlandica* caterpillars has a high proportion of phosphorus [10], which might be relevant in nutrient-limited environments such as the alpine tundra. The growth of tundra herbivores is more constrained by nutrient availability than energy [19], so locally enhanced nutrient availability could represent a potential way in which caterpillar foraging could indirectly benefit pikas. The mechanisms (or combinations of mechanisms) by which caterpillars affect nutrient cycling and tundra plant communities still require further investigation.

Whatever the underlying mechanism, our study demonstrates for the first time a positive interaction between two taxonomically distant alpine herbivores. Competitive (negative) interactions have been described for distantly related taxa [3], but positive interactions among herbivores may be more prevalent than previously thought [20]. Similar to facilitative interactions in grazing succession among ungulates [8], in our study caterpillars activate a cue that attracts foraging pikas. Given that these interactions were studied within pika foraging areas, they may favour the creation of herbivory hotspots, with potential cascading effects for ecosystem processes. The simultaneous impact of multiple herbivores, particularly those occurring at different spatial scales such as for vertebrate and invertebrate herbivores [5], can increase the heterogeneity of plant communities and enhance biodiversity [21]. Thus, these scarcely studied interactions can have important ecological consequences and represent an exciting avenue for future research.

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