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
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 (haying) 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 (Lymantridae) 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 ± s.d. = 0.048 ± 0.021) and did not differ among plots (binomial generalized linear mixed model (GLMM), χ² = 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 thuringensis 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, χ² = 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
assumptions were checked. Data are available as electronic
All analyses were conducted in R v. 2.14.0 [13]; all modelling
factor, and experimental treatment was included as a fixed factor.

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consume a small fraction of the available plant foliage, so bio-
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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 bio-
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 her-
bivory 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 herbi-
ory [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 forage
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, cater-
pillar 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 her-
bivores [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 nutri-
ent cycling. For instance, frass of G. groenlandica caterpillars
has a high proportion of phosphorus [10], which might be rel-
levant 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 mechan-
isms (or combinations of mechanisms) by which caterpillars
affect nutrient cycling and tundra plant communities still
require further investigation.

Whatever the underlying mechanism, our study demon-
strates for the first time a positive interaction between two
taxonomically distant alpine herbivores. Competitive (negative) interactions have been described for distinctly 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 simul-
taneous 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
scarce studies can have important ecological consequences and
represent an exciting avenue for future research.

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