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Immediate and long-term facilitative effects of cattle grazing on a polyphagous caterpillar

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ABSTRACT

Mammalian herbivores induce changes in the composition, abundance, architecture and chemistry of vegetation which can affect insects in their habitat. Many studies addressed the long-term effects of mammalian grazing on insect herbivores, yet few examined the effects during grazing (or right after it takes place). We investigated the immediate and long-term effects of cattle grazing on the abundance and distribution of the herbivorous spring webworm caterpillar (*Ocnogyna loewii*), via excluding cattle (by fencing) within a grazed paddock. In addition, we estimated the caterpillar density in replicated grazed and non-grazed paddocks (maintained as so for dozens of years), in moderate and heavy grazing intensities. Since the caterpillars develop during the cold winter months, we predicted that cattle grazing would positively affect them by reducing plant height and increasing their exposure to direct warm sunlight. Therefore, we examined caterpillar preference for sun-exposed areas using shade-manipulation experiments. Overall, cattle grazing positively affected the caterpillars, increasing their numbers two-fold on average, regardless of grazing intensity. This effect was immediate, as the caterpillars rapidly responded to exclusion of cattle by moving away from non-grazed areas. Caterpillar growth rate was similar when feeding on grazed and non-grazed vegetation. Most caterpillars (over 80%) preferred sun over manipulated shaded microhabitats. Furthermore, we found that cattle usually do not ingest caterpillars while feeding. Cattle grazing likely benefited the caterpillars that develop under low temperatures by reducing plant cover, thus creating a warmer habitat. This study demonstrates how changes in vegetation structure caused by mammalian herbivores can rapidly and positively affect the abundance and distribution of herbivorous insects.

1. Introduction

Large mammalian herbivores widely affect the function, productivity and diversity of grasslands (Crawley, 1983; McNaughton et al., 1989). By consuming large quantities of plant material, they reduce plant biomass and induce changes in the abundance, distribution, phenology, architecture and chemistry of plants in their habitats (Skarpe and Hester, 2008). These effects can later indirectly influence insects that depend on these plants for food and shelter. Mammalian herbivores can also directly affect insects through trampling or ingestion (Gish et al., 2017; van Klink et al., 2015b).

The indirect influence of mammalian herbivores on insect diversity and abundance may be negative (e.g. Kruess and Tscharntke, 2002a,b; Pöyry et al., 2004; Rambo and Faeth, 1999), neutral (e.g. Hofmann and Mason, 2006) or positive (facilitative, e.g. Joern, 2005; Woodcock and Pywell, 2009; Zhong et al., 2014). Mammalian and insect herbivores may feed on the same plant, but since they greatly differ in size, the competition between them is usually assymetrical (Gómez and González-Megías, 2007). Mammalian herbivores may reduce the availability of shared plant resources. Grazing induces plant defense responses that may harm herbivorus insects (Gómez and González-Megías, 2002). Furthermore, short grazed vegetation provides less shelter from harsh climatic conditions (van Klink et al., 2015b) and exposes insects to predators (e.g. Belovsky et al., 1990). On the other hand, the lack of shelter and stalking opportunities in grazed areas may reduce predation of insect herbivores by arthropod predators (Langellotto and Denno, 2004; Woodcock and Pywell, 2009).

Mamalian grazing can also positively affect insect herbivores by inducing nutrient-rich regrowth of plants (Martinsen et al., 1998; McNaughton, 1976) and reducing predation, as mentioned above. Positive effects on insect diversity and abundance are more likely to occur under moderate grazing pressure which enhances vegetation and microhabitat heterogeneity (e.g. Adler et al., 2001; Dumont et al., 2009; Hobbs, 1996; Stewart, 2001; Wallis De Vries et al., 2007).

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While most studies focused on the long-term effects of mammalian grazing on insect populations (Gish et al., 2017), only a few have examined the immediate effects while or shortly after grazing takes place (Bonal and Muñoz, 2007; van Noordwijk et al., 2012). In the current study we investigated the immediate and long-term effects of cattle grazing on the population of the spring webworm (*Ocnogyna loewii,* Lepidoptera: Erebidae), a common polyphagous caterpillar in Mediterranean-type habitats. These caterpillars hatch at the end of winter (January) when temperatures are relatively low. Temperature strongly affects caterpillar growth and activity, thus finding suitable thermal conditions is critical for their development (Casey, 1993). Caterpillars developing in cold climates are behaviorally adapted to utilize sunlight for growth (Kukal et al., 1988). They elevate their body temperature by orientating towards the sun (Alonso, 1997); by basking (Porter, 1982); or by seeking warmer microhabitats provided by variable vegetation structures (Turlure et al., 2011). Some caterpillar species (including the first instars of the spring webworm) live gregariously within nests that increase heat (Bryant et al., 2000). Since spring webworm caterpillars develop during the cold winter months, we expected cattle grazing, which increases exposure to sunlight, to have an overall facilitative effect on the caterpillars despite the potential competition over food resources.

Using a replicated field experiment of grazed and non-grazed paddocks, we investigated how long-term (years) cattle (*Bos taurus*) grazing affects the natural populations of spring webworm caterpillars and whether this effect occurs immediately, as both feed simultaneously. In addition, we tested the preference of caterpillars for sun-exposed areas. We also examined whether cattle ingest caterpillars while feeding (see Gish et al., 2017; van Klink et al., 2015b). Specifically, the following questions were addressed: (1) How does cattle grazing affect the caterpillar population in the long-term? (2) Does cattle grazing have an immediate effect on the distribution of the caterpillars? (3) Do caterpillars prefer sun-exposed over shaded areas? (4) Do cattle ingest caterpillars while feeding?

2. Materials and methods

2.1. Study organism

The spring-webworm (*O. loewii,* henceforth “caterpillars”) is a polyphagous moth species common in Mediterranean-type habitats (especially grasslands). These caterpillars feed on a wide variety of plant families (e.g. Brassicaceae, Asteraceae and Poaceae), including crops, such as alfafa and wheat (Swailem and Amin, 1979). The caterpillars hatch at the end of winter and complete their development in spring (January-March). Shortly after hatching, they form a communal web nest, which extends and moves (a few dozen meters) on the vegetation as the caterpillars feed and grow (Fig. 1a). During the later instars (fourth-sixth), the highly mobile caterpillars scatter and feed solitarily. The mild Mediterranean winter enables the caterpillars to be active most days (TSB personal observation). Pupation belowground takes place at the end of spring and adults emerge in late autumn. Winged males mate with wingless females, which lay numerous eggs under stones or on the soil surface (close to where they emerged from the pupa) to complete their univoltine life cycle (Swailem and Amin, 1979; Yathom, 1984).

2.2. Study site

The study was conducted during the years 2014–2015 in ‘Karei-Deshe’ experimental farm, in the eastern Galilee, Israel (35^{0}35′E, 32^{0}55′N). The topography is hilly, with a basaltic rock cover of about 30%. The climate is Mediterranean, characterized by a mild, rainy winter (temperature range: 7–14 °C) and a hot, dry summer (temperature range: 19–32 °C). The grassland vegetation is dominated by the perennial species hemicryptophytes *Bituminaria bituminosa* (L.) C.H. Stirton*, Echinops gaillardotii* Boiss.*, E. adenocaulos* Boiss.*, Ferula communis* L. and *Hordeum bulbosum* L. Most other species are annuals of the families Poaceae, Fabaceae, Asteraceae, Brassicaceae and Apiaceae (Noy-Meir et al., 1989; Sternberg et al., 2000).

Since 1994, the farm (covering about 1450 ha) has been divided into paddocks that are subjected to moderate (0.55 cows.ha^{-1}) and heavy (1.1 cows.ha^{-1}) grazing throughout the year (Henkin et al., 2015). In addition, the farm has enclosures from which cattle have been excluded for dozens of years.

2.3. Long-term effects of cattle grazing on the caterpillar population

In order to investigate how long-term cattle grazing influences the caterpillar population, we counted the number of active gregarious nests (containing caterpillars, henceforth “nests”) and solitary caterpillars, in the grazed and non-grazed paddocks described above (see subsection 2.2). The counts were performed separately once a year (during January and March) for each caterpillar stage.

2.3.1. Transect sampling

We sampled in two moderately and two heavily grazed paddocks (~27 ha each), and in four non-grazed enclosures (~0.5–4 ha). Within each paddock, we randomly selected three 20 m long transects and recorded the number of nests/solitary caterpillars encountered while walking (counts were averaged for each grazing treatment). Nests were not counted in 2014 (the first sampling year).

2.3.2. Plot sampling

We sampled plots in the two moderately and two heavily grazed paddocks (see subsection 2.3.1). In each paddock, we sampled five fenced plots (10 × 10 m, total of 20 fenced plots in all paddocks) from which cattle have been excluded for over 10 years. For comparison, we marked a 10 × 10 m grazed plot set three meters apart from each fenced plot (in random cardinal directions for each plot), using tape measure, and counted all the nests within these paired plots. Since there could be hundreds of solitary caterpillars in each plot, we tossed a square frame (30 × 30 cm) from three random locations in the plot and counted the solitary caterpillars within the frame (counts from the frames were averaged). Solitary caterpillars were not counted in 2014 (the first sampling year).

2.4. The immediate effect of cattle grazing on the caterpillar population

In order to investigate whether cattle grazing has an immediate effect on the caterpillar population, we constructed fenced plots (to exclude cattle grazing) within a heavily grazed paddock (~50 ha, grazed by 60 cows) and continuously examined the nest/solitary caterpillar numbers and distribution over the course of several weeks.

Fences were constructed in January (when nests started appearing throughout the farm) in 2014 and 2015. This enabled us to examine the immediate effect of cattle grazing on caterpillar numbers in two consecutive years. We selected a random area in the paddock and constructed 6 × 6 m fenced plots within it, 12 m apart from one another (seven plots in 2014 and six plots in 2015). We then marked identically sized unfenced grazed plots set three meters apart from each fenced plot, in random cardinal locations for each plot. The initial number of nests (at the beginning of each experiment) between the paired plots (grazed and non-grazed) was similar (see Results). Once a week, we counted the number of nests, and later the number of solitary caterpillars, in all plots (as described in subsection 2.3.2), until solitary caterpillar numbers reached zero. The caterpillars in the experiment constructed in 2014 were also counted in 2015. Fences breached by cattle were excluded from the experiment, together with their paired grazed plot.