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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 (35⁰35′E, 32⁰55′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.

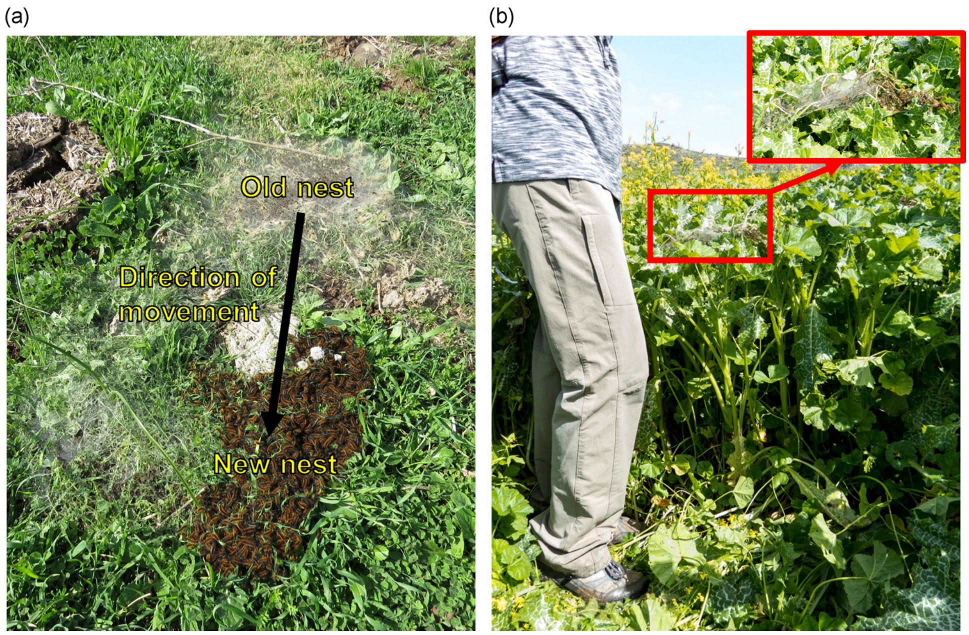

Fig. 1. The location of webworm nests on grazed and non-grazed vegetation. (a) Typical (and most common) nest on low, grazed vegetation (~5 cm). The black arrow marks the direction in which the gregarious caterpillars move as they feed (while continuously building a new nest), leaving their old nest behind. **(b)** A rare case of a nest positioned on the top (sun-exposed) of high, non-grazed vegetation (~80 cm). The nest is marked by a red rectangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4.1. The development of caterpillars on plants from grazed and non-grazed paddocks

We calculated the caterpillars' relative growth rate (RGR) when fed on plants from three grazed and three non-grazed paddocks. Prior to the experiment, we weighed solitary caterpillars (fourth instar) which were collected outside of the farm. Each caterpillar was placed in a round plastic container (12 cm diameter, 8 cm height) covered by a perforated lid. The containers were randomly divided into six groups (10 caterpillars per group, 60 in total) according to the paddocks and kept in room conditions. Each day we provided the caterpillars with a variety of fresh plants which were randomly collected from the paddocks. After five days, we reweighed the caterpillars and calculated their RGR as (lnW2–lnW1)/(t2–t1). W1 and W2 are the weights at the beginning (t1) and the end (t2) of the experiment.

2.5. The direct effect of cattle feeding on caterpillar survival

In order to check whether cattle consume caterpillars along with the plants we performed a dual choice feeding experiment in a cowshed (in Binyamina, Israel). We presented ten cows with a choice between 100 g *Malva* spp. (stems and leaves) only and 100 g *Malva* spp. with 30 solitary caterpillars (fourth-fifth instars, collected from natural populations outside the farm). The portions were placed randomly on the food alley 20 cm apart. One cow at a time was voluntarily allowed to feed from the alley. Once the cow walked away, we examined the fate of the caterpillars (intact, injured, ingested). The experiments were filmed with a high definition camera (GoPro© Hero 4 black edition, GoPro Inc., San Mateo, California, USA) for better detection of the caterpillars.

2.6. Caterpillar orientation towards sun-exposed areas

In preliminary observations, we noticed that gregarious nests and solitary caterpillars are mostly found in areas exposed to direct sunlight (Fig. 1). Using shade-manipulated experimental arenas, we examined whether the caterpillars prefer sunny over shaded areas. The experiment was conducted in Ramat Hanadiv Nature Park, Israel.

2.6.1. Orientation of gregarious caterpillars (nests)

We selected 20 nests (second to third instars), all exposed to direct sunlight within a 0.5 ha area in the park. We then positioned a small half-doughnut shaped canopy (outer diameter: 50 cm, inner diameter: 20 cm), made of black corrugated plastic with three skewer legs (20 cm high), over each nest, so that the nest was situated in the center of the doughnut, creating an arena that is half-shaded (Fig. 2a). The direction of the artificial canopy was randomized for each nest. As a control, we positioned three skewers without the black plastic cover opposite to the artificial canopy. Nest location (shade or sun) was recorded after 48 h (Fig. 2b).

2.6.2. Orientation of solitary caterpillars

We set 17 canopies (as described in subsection 2.6.1) in random locations within a 0.1 ha area in the park. We wrapped cellophane paper around the skewers (including those opposite the canopy) to create a transparent circular arena (half shaded and half sunny), and the upper rim of the arena was coated with Fluon® (AGC Chemicals Europe, Lancashire, UK) in order to prevent the caterpillars from scattering. We then placed 10 solitary caterpillars in the center of each arena and returned two hours later to document their location within it. Caterpillars that remained in the center of the arena were excluded from the experiment.

2.6.3. The effect of shaded vs. sun-exposed vegetation on solitary caterpillar orientation

We examined whether vegetation originating from sunny or shaded areas affected the caterpillars' movements and preferences. After completing the experiment above, we left the canopies standing for two weeks (shading the vegetation). We then removed the canopies (leaving only the transparent arena) and placed 10 solitary caterpillars in the center of the arena. We returned two hours later to document their location. Solitary caterpillars that remained in the center of the arena were excluded from the experiment.

2.7. Statistical analysis

All statistical analysis was performed with IBM SPSS software v.20 for Windows (IBM, Armonk, NY, USA). Data that did not follow the assumptions of parametric tests were tested with equivalent nonparametric tests.

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

The number of nests/solitary caterpillars recorded along the transects (subsection 2.3.1) in the different grazing treatments (moderate,

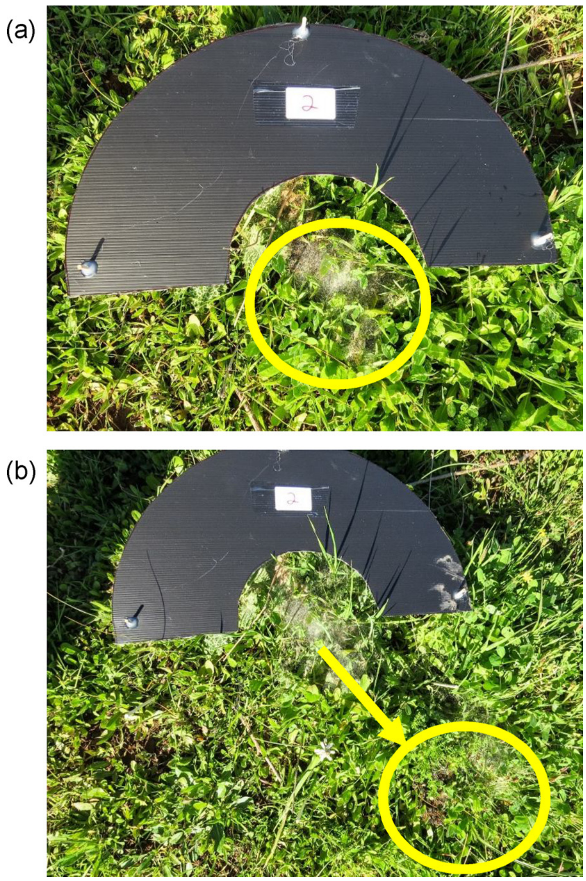

Fig. 2. Shade-manipulated experimental setup. (a) A nest in the center of the shade arena (marked by a yellow circle) at the beginning of the experiment. One side of the arena was shaded under a black plastic canopy. **(b)** The location of the nest 48 h after the experiment began. A yellow arrow marks the direction in which the nest moved (the sun-exposed side of the arena). The new location of the nest (currently constructed) is marked by a yellow circle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

heavy and non-grazed) was compared for each year (2014 and 2015) separately, using the Kruskal-Wallis test. The number of nests/solitary caterpillars between the paired plots (grazed and non-grazed, subsection 2.3.2), in heavy and moderate grazing intensities was compared using a mixed-model ANOVA, for each year separately (2014 and 2015, with the paired grazed and non-grazed plots as the repeated-measures factor). Since the data for solitary caterpillars did not follow a normal distribution, we compared their numbers in the paired plots separately for each grazing treatment (heavy or moderate), using a Wilcoxon signed-rank test. We also compared the number of solitary caterpillars between the grazing intensities for grazed and non-grazed plots separately, using the Mann–Whitney *U* test.

2.7.2. *The immediate effect of cattle grazing on the caterpillar population*

The number of nests/solitary caterpillars between the grazed and non-grazed plots (subsection 2.4) was compared over the weeks using a two-way repeated measures ANOVA (with the paired plots and weeks as the repeated-measures factors). This analysis was performed for each year and experiment separately (fences constructed in 2014 or in 2015). The RGR of caterpillars that fed on plants from grazed and non-grazed paddocks (subsection 2.4.1) was compared using a Student's *t*-test.

2.7.3. *Caterpillar orientation towards sun-exposed areas*

Gregarious nest locations (subsection 2.6.1) were compared using the Pearson chi-square test. The proportion of solitary caterpillars in each location (shade or sun in the first experiment and sunny *vs.* previously shaded vegetation in the second experiment, subsection 2.6.2 and 2.6.3 respectively) was compared using a paired samples *t*-test.

3. Results

3.1. *Long term effects of cattle grazing on the caterpillar population*

Both transect and plot sampling surveys showed that long-term cattle grazing had a positive impact on the caterpillar population, compared to non-grazed areas.

3.1.1. *Transect sampling*

Overall, the number of nests/solitary caterpillars was higher in grazed paddocks compared to non-grazed paddocks (Fig. 3). In 2014, the number of solitary caterpillars among the different grazing treatments was marginally insignificant, nonetheless, their numbers tended to be higher in the grazed treatments (Fig. 3b). In 2015 the number of nests was highest in moderately grazed paddocks by three and eight fold compared to heavily and non-grazed paddocks, respectively (Fig. 3a). The number of solitary caterpillars, however, was highest in heavily grazed paddocks by two and 12 fold compared to moderately and non-grazed paddocks, respectively (Fig. 3b).

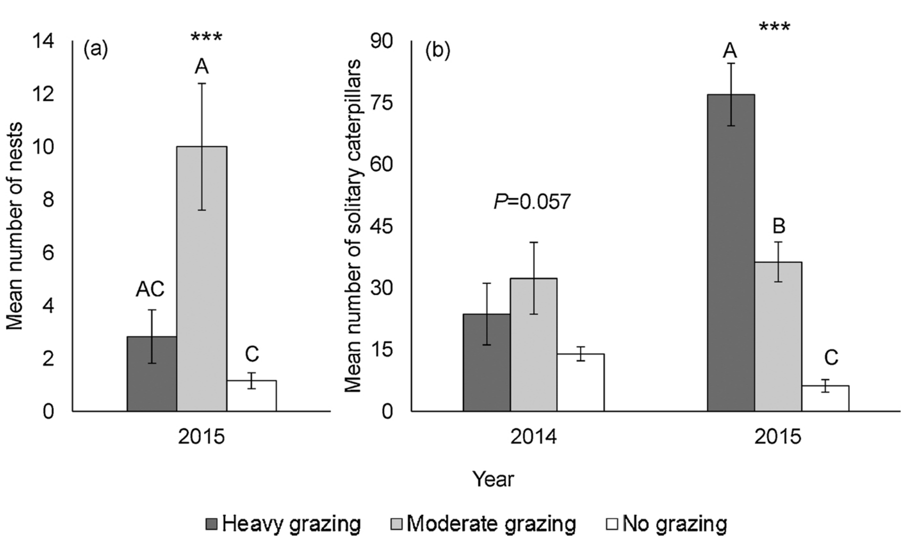

Fig. 3. The number of caterpillars sampled in various grazing regimes. The number of nests/solitary caterpillars was counted along three 20 m long transects. **(a)** Gregarious nests (Kruskal-Wallis, $\chi^2_2 = 13.963$, $P = 0.001$). The nests were not counted in 2014. **(b)** Solitary caterpillars (2014: the number of solitary caterpillars among the grazing treatments was marginally insignificant, Kruskal-Wallis, $\chi^2_2 = 5.74$, $P = 0.057$; 2015: Kruskal-Wallis, $\chi^2_2 = 19.482$, $P < 0.001$). Different letters above bars indicate significant differences. Bars indicate means ± SE. $^{***}P \le 0.001$.

Table 1
Two-way repeated measures ANOVA table examining the number of nests in paddocks of two grazing regimes.

Year	Effect	F	P
2014	Plots (grazing *vs.* no grazing)	45.235	**< 0.001**
	Grazing intensity (heavy *vs.* moderate)	18.669	**< 0.001**
	Plots × Grazing intensity	12.678	**0.002**
2015	Plots (grazing *vs.* no grazing)	24.880	**< 0.001**
	Grazing intensity (heavy *vs.* moderate)	9.008	**0.008**
	Plots × Grazing intensity	0.465	0.504

Each year was analyzed separately (with the paired plots as the repeated-measures factor). df = 1,18 for both years.

3.1.2. Plot sampling

Similar to the transects, the number of nests/solitary caterpillars was higher in grazed plots compared to non-grazed plots, regardless of grazing intensity (nests: Table 1, Fig. 4; solitary caterpillars: heavy intensity- Wilcoxon signed-rank test, $Z = -2.737$, $P = 0.006$, moderate intensity- Wilcoxon signed-rank test, $Z = -3.758$, $P < 0.001$, Fig. 5). While more nests were found within moderately grazed paddocks (as seen in the transect sampling, Fig. 3a), the number of solitary caterpillars was similar between the two grazing regimes (grazed plots: Mann-Whitney, $U = 782.5$, $P = 0.861$; non-grazed plots: Mann-Whitney, $U = 683.5$, $P = 0.254$, Fig. 5). A mixed-model ANOVA (Table 1) examining the number of nests in the paddocks showed that the interaction between plot type (grazed *vs.* non-grazed) and grazing intensity (heavy *vs.* moderate) was significant in 2014, but insignificant in 2015.

3.2. The immediate effects of cattle grazing on the caterpillar population

Cattle grazing had an immediate effect on the distribution of the caterpillar population, as it significantly changed within a week from cattle exclusion. Nests and solitary caterpillars actively moved from fenced plots to grazed areas (TS Berman personal observations, Fig. 6d), resulting in a low number of caterpillars in non-grazed areas compared to grazed areas.

Although the initial number of nests was similar between grazed and fenced (non-grazed) plots (paired *t*-test, $t_6 = 0.415$, $P = 0.693$, Fig. 6a), within a week, their numbers dropped in fenced plots as gregarious caterpillars actively moved to grazed areas (TS Berman personal observations, Fig. 6d). Consequently, the number of nests, and later solitary caterpillars, were more than twice as high in grazed plots

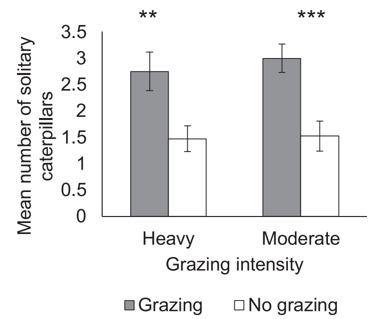

Fig. 5. The number of solitary caterpillars in paddocks of two grazing regimes. The sampling included two moderately and two heavily grazed paddocks, and 20 pairs of grazed and non-grazed plots (five in each paddock). Bars indicate means ± SE. ** $P \leq 0.01$, ***$P \leq 0.001$.

compared to fenced plots (Table 2). Naturally, the number of both nests and solitary caterpillars decreased over time (as gregarious caterpillars dispersed from the nests and solitary caterpillars pupated). A two-way repeated measures ANOVA (Table 2) showed that the interaction between plot type (grazed *vs.* non-grazed) and time was significant for solitary caterpillars, but not for nests. In the following year (2015, a year after the fences were constructed), a similar trend occurred for both nests and solitary caterpillars, however, more nests were evident in grazed plots straight from the start (Fig. 6b), as seen in the long-term experiment (Fig. 3b and 4).

In the second experiment (set up in 2015), the number of nests between grazed and fenced plots was similar to begin with (paired *t*-test, $t_5 = -0.89$, $P = 0.414$, Fig. 6c), yet it decreased in fenced plots over time (as observed in the previous experiment, Fig. 6a). Consequently, the number of nests/solitary caterpillars was higher in grazed plots compared to fenced plots (Fig. 6c and Table 3). The interaction between plot type (grazed *vs.* non-grazed) and time was significant for nests but not for solitary caterpillars (Table 3).

3.2.1. The development of caterpillars on plants from grazed and non-grazed paddocks

The relative growth rate of caterpillars feeding on vegetation from grazed and non-grazed paddocks was similar (0.118 ± 0.008 and 0.105 ± 0.006 $mg \times mg^{-1} \times d^{-1}$ respectively, Student's *t*-test, $t_4 = -1.697$, $P = 0.215$).

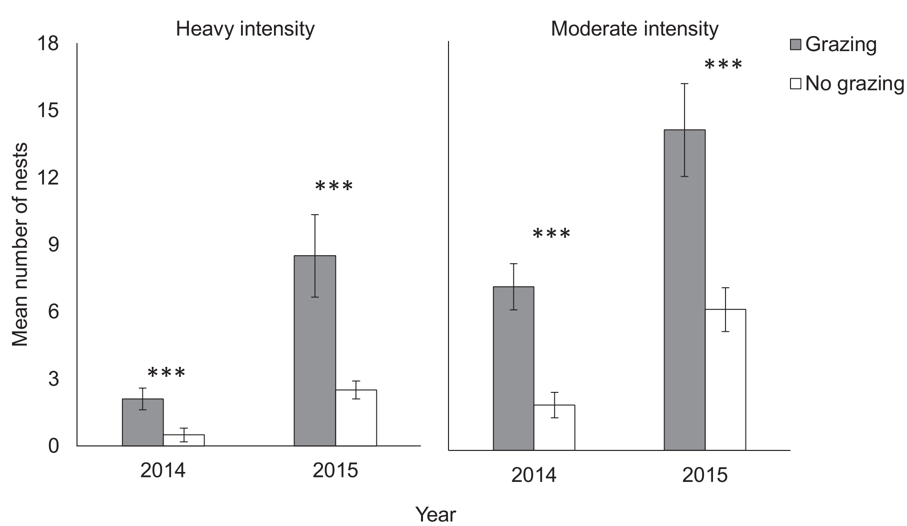

Fig. 4. The number of gregarious nests in paddocks of two grazing regimes. The sampling included two moderately and two heavily grazed paddocks, and 20 pairs of grazed and non-grazed plots (five in each paddock). Bars indicate means ± SE. ***$P \leq 0.001$.

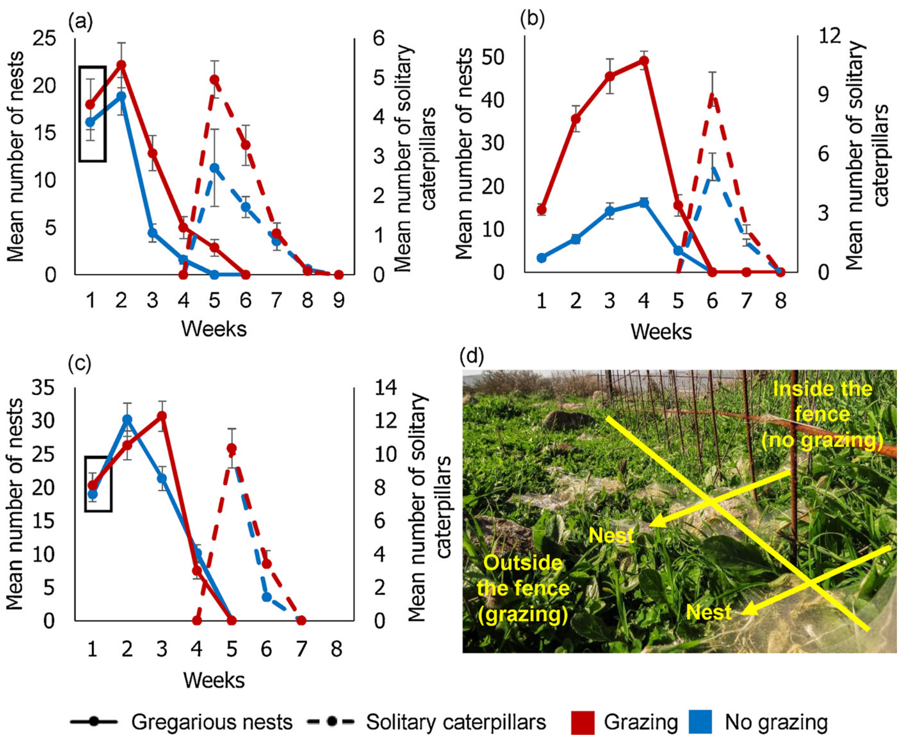

Fig. 6. The number of caterpillars in grazed and fenced (non-grazed) plots. The initial number of nests was similar between grazed and fenced plots (marked by a black rectangle). **(a,b)** Experiment set up in 2014. The caterpillars were also counted in the following year (2015). The sampling included seven pairs of grazed and fenced plots in 2014 (total of 14 plots) and six pairs in the following year (total of 12 plots). **(c)** Experiment set up in 2015. The sampling included six pairs of grazed and fenced plots (total of 12 plots). **(d)** The direction in which the nests moved (marked by yellow arrows), from the fenced plot to the grazed area. The border of the fence is marked by a yellow line. Points indicate means ± SE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Two-way repeated measures ANOVA table examining the number of caterpillars in grazed and fenced (non-grazed) plots constructed in 2014.

Year	Caterpillar stage	Effect	F	*P*
2014	**Nests**	Plots (grazing *vs.* no grazing)	521.344	**< 0.001**
		Time	3.695	**0.048**
		Plots × Time	1.926	0.188
	Solitary caterpillars	Plots (grazing *vs.* no grazing)	59.321	**< 0.001**
		Time	8.186	**0.002**
		Plots × Time	3.929	**0.026**
2015	**Nests**	Plots (grazing *vs.* no grazing)	120.655	**< 0.001**
		Time	5.703	**0.012**
		Plots × Time	47.559	**< 0.001**
	Solitary caterpillars	Plots (grazing *vs.* no grazing)	24.993	**0.015**
		Time	26.949	**0.014**
		Plots × Time	58.556	**0.005**

Fences were constructed in January 2014 (the caterpillars were also counted in 2015). Each year and caterpillar stage were analyzed separately (with the paired plots and weeks as the repeated-measures factors). df = 1,6 for both years.

Table 3
Two-way repeated measures ANOVA table examining the number of caterpillars in grazed and fenced (non-grazed) plots constructed in 2015.

Caterpillar stage	Effect	Statistic values		
		F	df	*P*
Nests	Plots (grazing *vs.* no grazing)	17.787	1,5	**0.005**
	Time	6.472	1,5	**0.007**
	Plots × Time	55.989	1,5	**< 0.001**
Solitary caterpillars	Plots (grazing *vs.* no grazing)	194.827	1,3	**0.001**
	Time	0.129	1,3	0.743
	Plots × Time	0.872	1,3	0.419

Fences were constructed in January 2015. Each caterpillar stage was analyzed separately (with the paired plots and weeks as the repeated-measures factors).

3.3. The direct effect of cattle feeding on caterpillar survival

The presence of caterpillars on the *Malva* spp. did not deter the cows, as they readily fed on it while avoiding caterpillar ingestion (Supplementary material Movie 1). Remarkably, 90% of the caterpillars remained intact (271/300), one was injured and only two were actually ingested (others were lost, i.e., were not ingested but could not be located).

3.4. Caterpillar orientation towards sun-exposed areas

Both gregarious nests and solitary caterpillars moved towards the sunny side of the arenas; nests within less than 48 h and solitary caterpillars within less than two hours, indicating a clear preference for sun-exposed over shaded areas (nests: Chi square, $\chi^2_1 = 12.8$, $P < 0.001$; solitary caterpillars: paired *t*-test, $t_{16} = 2.236$, $P = 0.04$, Fig. 7). Vegetation originating from sunny or shaded areas did not affect the solitary caterpillars' preference, as they were found distributed equally around the arena (paired *t*-test, $t_{16} = -0.126$, $P = 0.901$).

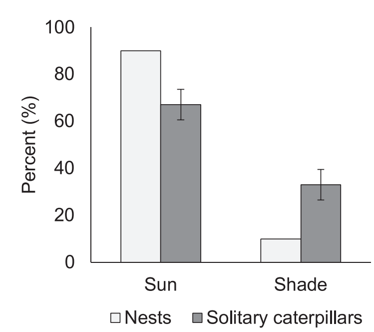

Fig. 7. Caterpillar preference for sunny *vs.* shaded areas. Both nests and solitary caterpillars preferred sun-exposed over shaded areas. N = 20 canopies (one nest per canopy, no average calculated), and N = 17 arenas (average of 10 solitary caterpillars per arena). Bars indicate means ± SE.

4. Discussion

We found that cattle grazing had an immediate and long-term facilitative effect on the population of the spring webworm, which thrived in grazed paddocks during the gregarious and solitary stages of the caterpillar. Within a week from the exclusion of cattle, the caterpillars changed their feeding location from fenced plots to grazed areas, increasing their numbers by two-fold on average in the latter. The high abundance of caterpillars in grazed paddocks persisted over the years, as seen in the long-term experiments, regardless of grazing intensity, implying that even heavily grazed areas can sustain the requirements of caterpillars for food and shelter.

4.1. The mechanism of facilitation

By consuming large quantities of plant material, the cattle considerably reduce vegetation height, exposing it to sunlight and consequentially to higher temperatures. Spring webworm caterpillars develop under relatively low temperatures, thus finding suitable microclimates within their habitat is essential for their growth. The rapid movement of caterpillars from fenced plots to grazed areas and to their favored sun-exposed vegetation indicates that they actively seek warm temperatures in the short vegetation created by cattle grazing. Direct sunlight is known to promote growth of caterpillars in cold climates (Bryant et al., 2000; Kukal et al., 1988; Porter, 1982) as they actively select such spots. For example, caterpillars preferred the south-facing side of trees where they were exposed to direct sunlight for longer periods (Alonso, 1997). Spring webworm caterpillars actively seek sun-exposed areas (subjected to higher temperatures, Figs. 1, 2 and 7) which most probably promote their development during the winter.

Mammalian herbivores can positively influence insects through changes in the composition and quality of plants (van Klink et al., 2015b). A long-term study carried out in 'Karei-Dehse' farm, showed that cattle grazing reduced the cover of tall annual grasses and increased the cover of short grasses (Sternberg et al., 2015). Nonetheless, it is unlikely that a shift in plant functional group composition can explain the abundance of caterpillars in grazed areas, since the caterpillars changed their feeding location within a week from fenced plots to grazed plots, a period in which the vegetation composition probably did not change. In addition, the polyphagous spring webworm caterpillar can cope with changes in vegetation composition, as it does not depend on specific plants for food and shelter. Indeed, it has been reported that polyphagous insects tend to survive better in grazed areas compared to specialist insects (Nickel and Hildebrandt, 2003). Mammalian herbivore grazing may positively affect plant quality through regrowth (McNaughton, 1976). However, the fact that the caterpillars showed no particular preference for vegetation originating from sunny areas and that their development (RGR) was not affected by diet (from grazed or non-grazed vegetation) indicates that plant quality was not the reason caterpillars' preferred grazed areas.

In some cases, grazing by a mamalian herbiovre may positivly affect insects by reducing their predation by arthropod predators that are less abundant in short vegetation (Langellotto and Denno, 2004; Woodcock and Pywell, 2009). On the other hand, the abundance of predators that hunt more efficiently in short vegetation, such as birds, may increase (Belovsky et al., 1990). In the future it would be interesting to examine the effects of cattle grazing on the predator assemblage in the habitat.

4.2. The effect of grazing intensity

Gregarious nests (unlike solitary caterpillars) were more abundant in moderately grazed paddocks (Figs. 3a, 4). The intermediate disturbance hypothesis (Fox, 1979), predicts that moderate grazing will positively affect insects. Indeed, moderate grazing maintains high insect diversity, species richness and abundance (e.g. Dumont et al., 2009; Wallis De Vries et al., 2007), mostly since it enhances vegetation heterogeneity (Adler et al., 2001; Hobbs, 1996) and the regrowth of plant tissue (McNaughton, 1976). The fact that gregarious nests were more abundant in moderately grazed paddocks means that the females laid more eggs there. Since females are flightless and show low mobility, the location of the nest actually reflects the site where the solitary caterpillar pupated (and the female emerged). The number of solitary caterpillars in moderately grazed paddocks, however, was lower or similar compared to heavily grazed paddocks (Figs. 3b and 5). It is likely therefore that less pupae survived in heavily grazed paddocks. The survival of pupae in the soil may be negatively affected by compaction associated with cattle trampling (as seen with other arthropods, van Klink et al., 2015a), which decreases pore space and oxygen transport (Beylich et al., 2010). It is also possible that intensive cattle grazing uncovered soil patches, exposing the pupae (and final stage caterpillars) to increased predation.

4.3. Direct influence of cattle feeding on caterpillar survival

Large mammalian herbivores can directly harm insects through ingestion or trampling (Gish et al., 2017), yet this effect was rather negligible in our system. We experimentally found that cattle hardly cause the caterpillars any damage while grazing (90% of caterpillars survived). They can probably detect and avoid caterpillar ingestion while feeding (Supplementary material, Movie 1), as seen in goats (Berman et al., 2017). Spring webworm caterpillars are covered with long setae, which can cause skin irritations and allergic responses in mammals upon contact (Campbell, 2001). Ingestion of such caterpillars may even lead to teratogenic diseases (Volpato et al., 2013; Webb et al., 2004). Since ingesting certain insects may harm mammalian herbivores (e.g. Nunamaker et al., 2003; Schmitz, 1989; Webb et al., 2004), the ability to avoid it, as seen in cattle, is critical. Incidental ingestion of nest webs by grazing mammals has been documented (van Noordwijk et al., 2012). In our system we did not witness ingestion of gregarious nests, but the cattle may trample them. Trampling can harm caterpillars (van Noordwijk et al., 2012), but it seemed to be rather negligible in our system (TS Berman personal observations).

In addition to the cattle's ability to avoid caterpillar ingestion, the mobile caterpillars themselves may be able to actively avoid ingestion by escaping from the grazed plants on time, as seen in other insect species, including caterpillars (Ben-Ari and Inbar, 2013; Brackenbury, 1997; Castellanos and Barbosa, 2006; Gish et al., 2010; Ohno and Miyatake, 2007).

4.4. Broader ecological interactions

The high caterpillar density in grazed areas may have additional complex effects on the community of animal and plants in the habitat. The combined impact of both cattle and caterpillar grazing should exert great pressure on the vegetation (Cao et al., 2015). This effect could be profound, especially during outbreaks (as seen in 2015, Fig. 6b), when caterpillar numbers were as high as 2 nests and 400 solitary caterpillars per square meter. In such cases, the reduced quantity (and even quality) of forage due to overgrazing may negatively affect other insect herbivores (Price et al., 2011; Tscharntke and Greiler, 1995) and potentially even the cattle themselves (Cao et al., 2015). During outbreaks, the ability of cattle to efficiently avoid ingesting caterpillars could be reduced, harming the cattle (see Campbell, 2001; Schmitz, 1989; Webb et al., 2004). The abundance of caterpillars in grazed paddocks could potentially affect the activity of the upper trophic level (natural enemies), such as predators (arthropods, reptiles and birds) and parasitoids. Grazing may also have multitrophic effects; we recently found that cattle grazing imposed cascading effects on the microbiome of the caterpillars in the habitat (Berman et al., 2018). Future studies should look into the broader ecological implications on communities in grazed habitats, and the complex impact of facilitative interactions between mammalian and insect herbivores.

5. Conclusion

Plant-mediated effects of mammalian herbivores on insects could be negative or facilitative (van Klink et al., 2015b). Our study emphasizes the need to thoroughly examine the detailed biology and limiting factors of a given insect species in order to understand how it would be affected by grazing mammals.

While most studies focused on the long-term effects of mammalian grazing on insect populations (Gish et al., 2017), only a few of them have examined the immediate effects (after grazing takes place, Bonal and Muñoz, 2007; van Noordwijk et al., 2012). In this study, we show that cattle grazing can have an immediate (within days) facilitative effect on spring webworm caterpillars. This positive effect later determines the distribution of the caterpillar population over the years. The caterpillars' rapid response suggests that the instant changes in plant traits caused by grazing are essential to the caterpillars. Indeed, by reducing vegetation height, the cattle created an open and warmer habitat that benefited the caterpillars during the cold winter months. This study demonstrates how changes in vegetation structure caused by mammalian herbivores can rapidly and positively affect the abundance and distribution of herbivorous insects. By indirectly affecting other trophic levels, mammalian herbivores may also influence the functioning of food webs within the habitat.

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Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2018.03.019.

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