

Exotic grass invasion impacts fitness of an endangered prairie butterfly, *Icaricia icarioides fenderi*

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Abstract Fender's blue butterfly is an endangered species restricted to fragmented, grassland remnants that are becoming increasingly dominated by tall, invasive grasses in western Oregon, USA. I performed a removal experiment to assess the impacts of structural degradation accompanying the invasion of *Arrhenatherum elatius*, tall oat grass, on butterfly fitness and fitness related behaviors. Clipping of *A. elatius* to native grass sward height resulted in 2.5–5 times as many eggs laid per leaf of host plant. Both male and female butterflies basked more frequently in areas removed of *A. elatius* inflorescences and upon encountering the treatment edge butterflies had a high rate of return into a large area removed of the grass inflorescences. Although butterfly behavior appeared to be affected by the change in sward height on the treatment edge, there was no evidence for the edge causing a disproportionate egg load. Invasion and dominance by *A. elatius* appeared to diminish host plant apparency which may result in overloading of eggs on conspicuous host plants, increased incidence of emigration, and a decrease in the likelihood of colonization because female butterflies appeared indifferent to larval resources beneath *A. elatius* inflorescences. Dominance of natural shortgrass prairies by tall stature grasses like *A. elatius* may be an insidious form of habitat degradation for grassland Lepidoptera worldwide, but it may go largely unnoticed because larval and adult resources can persist under the unnaturally tall grass canopy.

Keywords Invasive species · Grassland · Oviposition preference · Habitat quality · Thermoregulation · Butterfly behavior

Introduction

Exotic plant invasion may change the behavior of animals by modifying fundamental aspects of the invaded native habitat. For example, invasion and dominance by exotic plants that change the structure of open spaces may be detrimental to fauna requiring open habitats. Butterflies are sensitive to changes in habitat structure such as the edges of grasslands (Reis and Debinski 2001; Schultz and Crone 2001), hilltops (Shields 1967; Lederhouse 1982), forest edges (DeVries et al. 1999; Haddad 1999), perches taller than the surrounding habitat (Rutowski 2000), roads (Munguira and Thomas 1992), and microtopographic changes that afford protection from wind and access to basking sites (e.g., Thomas et al. 1986). Butterfly sensitivity and preference for specific habitat features suggests that exotic plants that change habitat structure may directly impact butterfly behavior. For example, changes in vegetation structure may degrade basking site quality and subsequently interfere with thermoregulation. This may further impact reproductive related behaviors like mate searching, territorial defense, predator avoidance, oviposition, and nectaring (Clench 1966; Heinrich 1986; Shreeve 1986; Stutt and Willmer 1998; Ide 2002; Berwaerts and Van Dyck 2004). Host plant apparency may diminish if the presence of taller plants physically obscures the host plant (Wiklund 1984; Karban 1997; Floater and Zalucki 2000) or oviposition likelihood may decline if the taller plants alter preferred egg laying environments (Williams 1981; Thomas et al. 1986).

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Grassland quality and butterfly diversity are thought to be related, such that floristically degraded grasslands tend to be less diverse and have lower relative butterfly abundance than higher quality prairies (Pollard et al. 1998; Maes and Van Dyck 2001; Collinge et al. 2003). Although a lack of floral diversity is often the assumed link between the degree of grassland degradation and low butterfly diversity, changes in vegetation stature have been linked with population declines and extinction in grassland butterflies. Due to an increase in the overall sward height with respect to the native condition, *Hesperia comma* L. (Thomas et al. 1986; Thomas and Jones 1993) and *Polyommatus bellargus* Rottemburg (Thomas 1983) declined in numbers from decreased larval survival and a lack of suitable oviposition sites. Populations of *Euphydryas editha bayensis* Sternitzki were invaded by exotic grasses and herbaceous plants, which culminated in the loss of larval host plants and subsequent population extinction (Weiss 1999 and references therein). Dominance of shortgrass prairies by exotic plants that increase the sward height may alter the behavior of butterflies, especially when host plants are visually obscured by taller vegetation. In prairies dominated by tall, native grasses some butterflies drop eggs while in flight or after alighting on the ground when their host plant is physically obscured or has senesced, leaving larvae to encounter host plants through exploration (Scott 1986; Kopper et al. 2000). However, in grasslands that are naturally dominated by shorter grasses where host plants are conspicuous, shading and visual obstruction of host plants by taller, invasive grasses, may significantly alter butterfly behavior related to survival and reproduction, particularly in butterfly species that oviposit directly on their host plant.

Willamette Valley upland prairie, of western Oregon, USA, is a highly fragmented and degraded grassland that is under increasing pressure by exotic, invasive grasses (Wilson and Clark 2001; Wilson et al. 2003). One of the dominant invasive grasses, *Arrhenatherum elatius* (L.) Beauv. ex J. & K. Presl, is two to three times the height of the historically dominant native grasses *Festuca roemerii* Pavlick (Alexeev) and *Danthonia californica* Boland. Over the last decade, *A. elatius* has invaded remnant parcels of upland prairie throughout the Willamette Valley that support an endangered butterfly *Icaricia icarioides fenderi* Macy (hereafter Fender's blue) and its primary, threatened larval host plant, *Lupinus sulphureus* ssp. *kincaidii* [Smith] Phillips (hereafter Kincaid's lupine). In higher quality Willamette Valley upland prairies, native bunch grasses are approximately equal in height to the leaves of Kincaid's lupine plants and do not visually obscure host plant foliage. However *A. elatius* is nearly three times the height of Kincaid's lupine foliage and inflorescences, and the presence of the exotic, invasive grass shades and visually

obscures the host plant. Fender's blue butterfly populations fluctuate greatly between years and the amount of habitat available is limited (Schultz et al. 2003; Schultz and Hammond 2003). If tall stature, invasive grasses negatively impact butterfly oviposition and fitness related behaviors, then the quantification of this effect is necessary for understanding how to properly conserve Fender's blue butterfly and other Willamette Valley grassland butterflies that are now rare (Severns and Villegas 2005; Severns et al. 2006).

I selected three populations of Fender's blue butterfly to investigate the impacts of *A. elatius* invasion and dominance on butterfly fitness related behaviors by removing small and large areas of the exotic grass to a native sward height. Fender's blue lays an increasing number of eggs with the relative host plant size (Severns unpublished data), suggesting that host apparency is important for oviposition. If host plant apparency is diminished by the presence of *A. elatius* then the observed number of oviposition events and the number of eggs laid per unit of host plant should be lower when compared to similar adjacent habitat without *A. elatius*. Moreover, because *A. elatius* creates an unnaturally tall canopy and may cause physical obstruction to bare patches of ground that are important for thermoregulation, the presence of *A. elatius* should reduce the frequency of basking and the amount of time butterflies spend in *A. elatius* dominated habitat.

Primary invasion of *A. elatius* in remnant prairies is often patchy and can leave small groups of lupines amongst native, short stature grasses, but invasion can also advance like a phalanx, completely covering large, continuous patches of host plants. Both situations may be perceived differently by ovipositing females and both situations exist in invaded habitats. If *A. elatius* exerts a strong edge effect on butterfly oviposition, then the number of eggs laid per unit of host plant should be spatially distributed in relation to the invasion edge when *A. elatius* is removed from a large, continuous area. Alternatively, if host plant apparency is more important than the *A. elatius* edge then there should be no spatial pattern of oviposition with respect to the edge. Understanding how oviposition is related to host plant apparency and the invasion edge is important for planning how to conserve the remaining populations of Fender's blue butterfly in invaded habitats.

Materials and methods

Study species

Fender's blue butterfly was once considered to be an extinct taxon in the Willamette Valley of western Oregon, USA, but was rediscovered in the late 1980s nearly

60 years after the last butterflies were observed. Fender's blue is endemic to upland prairies in the Willamette Valley and the primary larval host plant of the butterfly is Kincaid's lupine, also an endemic Willamette Valley species (Wilson et al. 2003). Kincaid's lupine is a long-lived perennial, deciduous plant that generally sends up multiple, unbranched, blue-flowered racemes, approximately 0.5 m in height, from late May through early July. Butterflies are distributed in 16 populations scattered and fragmented throughout the nearly 200 km length of the Willamette Valley (Schultz et al. 2003). In 2000, Fender's blue was listed as endangered and Kincaid's lupine was listed as threatened.

Fender's blue normally flies from early May through mid June, with adults living 10–14 days (see Schultz et al. 2003 for detailed life history information). Females lay eggs singly on the underside of Kincaid's lupine leaflets from late May through early June but more than one egg may be laid on a leaf during an oviposition event. Occasionally, <1% of observations, (Severns unpublished data) eggs are laid on lupine peduncles, pedicels and the upper side of leaflets. Another lycaenid butterfly, *Glaucopsyche lygdamus columbia* Skinner, also uses Kincaid's lupine as a host plant, but eggs of this species are laid primarily on lupine inflorescence. Upon hatching from the egg, Fender's blue larvae do not consume the eggshell so the remnants are persistent on lupine leaflets and can be counted after larvae hatch.

Arrhenatherum elatius is native to Eurasia where it does not commonly dominate grasslands (Liancourt et al. 2005) but is invasive throughout western North America, New Zealand, and Australia (Pfitzenmeyer 1962; Wilson and Clark 2001). *Arrhenatherum elatius* forms rhizomatous tussocks and the inflorescence can bolt to nearly 2 m in height, approximately two to three times the height of the dominant native Willamette Valley grasses *Danthonia californica*, *Festuca roemerii* (Wilson 1997), *Festuca rubra* s.l., three times the height of Kincaid's lupine inflorescences, and up to five times the height of the tallest Kincaid's lupine leaves. *Arrhenatherum elatius*, in most years, bolts and blooms concurrently with Fender's blue oviposition, although the butterfly may emerge and enter peak flight before *A. elatius* bolts in exceptionally dry, warm springs. In the Willamette Valley, *A. elatius* is most effectively controlled by mechanical mowing in the spring (Wilson and Clark 2001), but since the mowing occurs during the peak butterfly flight period and lupine flowering, invaded patches of host plant are not treated.

Study sites

Three sites invaded by *A. elatius* over the past decade that are now dominated by the grass were selected for study.

The Shore, Spires, and North Eaton study sites are located in the southern Willamette Valley, approximately 10 km west of Eugene, Oregon, USA and are managed by the US Army Corps of Engineers. These sites are part of a larger system of small, fragmented remnant upland prairie habitat (Severns 2003a) that have a history of repeated colonization and extinction events by Fender's blue butterfly (Severns unpublished data). All three study sites have similar cover of Kincaid's lupine and parcels (1–5 ha) are bordered by fir and deciduous forests, 10–15 m tall hedgerows, and residential developments (Severns 2003a). Study sites housed between 100 and 200 Fender's blue butterflies in the spring of 2004, but were about half the size in 2005 (Severns unpublished data).

Vegetation treatments

In the first week of May 2004, when Fender's blues began their flight, four pairs of plots were randomly selected in each of the Shore and Spires study sites. Each plot was 1 m in radius and the epicenter of each plot pair was 2.5 m apart. The orientation of plot pairs was based off a random compass bearing and I visually estimated lupine cover inside each treatment plot to help ensure that the amount of larval resources was approximately equal within a plot pair. Furthermore, no nectar plants grew and flowered in the plots over the course of the experiment. Plot pairs were separated by at least 10 m to avoid spatial autocorrelation between other plot pairs. One of the plots in each pair was randomly selected to have *A. elatius* inflorescences removed and the other was an untreated control. Grasses in the treatment plots were clipped with shears to the same height of the Kincaid's lupine leaves, all other plants were not cut. There was no need for subsequent vegetation treatments in the *A. elatius* removal plots because the grass did not bolt until after the butterfly flight season was finished.

On 6-May-2005, approximately half of a patch of lupine in North Eaton was cleared of *A. elatius* while the other half was left as an untreated control. The area cleared was broadly oval measuring 22 m × 17 m. Similar to vegetation treatments in paired plots of the previous year, *A. elatius* was clipped to the height of native grasses, approximately 1–2 dm from ground level.

Butterfly behavior

In the third week of May in 2004, butterfly behavior was quantified in plot pairs at the Shore and Spires study sites (small patch removal) under optimal butterfly flight conditions, when butterflies were observed to be the most active. Optimal weather conditions for butterfly observations included mostly sunny weather and temperatures above

23°C. Unfortunately, only 3 h of optimal weather conditions co-occurred with dates for behavioral observations, so observations were taken at three of the four plot pairs at each study site. Each plot within a pair was observed simultaneously for 50 min outside of the actual plot areas and care was taken to not disturb the butterflies during the observation period. For each individual that flew into the plot boundary the choice to fly over the plot (flythrough), bask, or oviposit (females only) was recorded. A flythrough was defined as a straight-line flight over the plot or a flight over the plot where the butterfly changed its horizontal trajectory but did not obviously dip into the plot on an exploratory flight. Basking was recorded when perched butterflies opened their wings and oriented towards the sun, gathering incident light with the dorsal wing surfaces. Oviposition was recorded if the female curled her abdomen and deposited an egg on any lupine plant within the plot. I used a stopwatch to record the total time (in seconds) that females spent in the plots.

On four separate occasions throughout May of 2005, butterfly behavior was observed for a total of 2 h in the large grass removal area at North Eaton. For both male and female Fender's blue butterflies, the behavior of butterflies flying out of the *A. elatius* removed area into the area with *A. elatius* (as well as the reverse situation) was recorded. When a butterfly encountered the *A. elatius* edge flying from the treatment area, I recorded whether or not the butterfly turned around and flew back into the treatment area or kept flying into the *A. elatius* dominated habitat within the first 3 m of the treatment edge. I recorded whether or not butterfly flight dipped on encountering the treatment edge within the first 2 m or flew at the same height after flying in from an area with *A. elatius* into the treatment area. I assumed that relatively rapid flight in a straight line without turns are an indication that Fender's blue butterfly interprets the habitat it is flying over as "unsuitable" and that slower flights with turns downward or sideways indicate interest in the habitat (*sensu* Schultz and Crone 2001).

Measuring oviposition

Eggs were counted in the first and second weeks of June at both study sites with the paired plots (Shore and Spires) after the flight season was finished. All Kincaid's lupine plants within the 2 m diameter of each plot were searched for eggs by visual inspection of both the upper and lower leaf surface. Additionally, non-host plant vegetation near to lupine plants was also searched for eggs because occasionally females were observed to oviposit on entangled non-lupine vegetation. For each plant within the plots the number of leaves and eggs laid were recorded. A lupine "plant" was defined as a cluster of aboveground leaves

with >10 cm of ground without lupine leaves separating it from another cluster of leaves.

In North Eaton, where a large area of *A. elatius* was removed, lupine plants were selected off an edge treatment transect (24 m in length) where I randomly selected 15 points and placed another transect on a compass bearing that ran perpendicular to the edge transect. I extended a meter tape on both sides of the edge transect throughout the area occupied by lupine, on both the unmanipulated control and *A. elatius* removed areas, and any plant that intersected this line was selected for measurement. I measured the distance of the plant from the treatment edge to the nearest decimeter and counted all leaves and butterfly eggs on the plant. In 2005, due to an abnormal weather year, eggs of the other butterfly using Kincaid's lupine, *Glaucopsyche lygdamus columbia*, had hatched and larvae were active 2 weeks before Fender's blue began to lay eggs. I assumed that the eggs counted on the lupine racemes were those of Fender's blue and not those of *G. l. columbia*.

Statistical analyses

To test for differences between *A. elatius* removed and unmanipulated control habitats, all plot pair data from the two sites were pooled, and two-tailed paired *t*-tests were used for the number of leaves and eggs laid per leaf. The number of butterflies that flew through each of the plot pairs during the observation periods were not equal, cover by *A. elatius* at both study sites appeared similar, and the target was to understand general behavioral responses to habitat differences, so I pooled the behavior data. The number of seconds that females spent in the *A. elatius* removed and unmanipulated control plots (flythroughs omitted) was ln-transformed and analyzed for statistical difference with a two-tailed *t*-test. I performed a proportions test (Ramsey and Schafer 2002) on the percentage of butterflies that basked, flew through the area, and oviposited for the two habitat types.

Although Fender's blue females lay solitary eggs, they often lay more than one egg on the same leaf during the same egg laying event. To describe how female butterflies view host plants within an area cleared of *A. elatius* and one with *A. elatius* present, plants within each habitat type were grouped into different categories based on leaf number, <6 leaves, 6–15 leaves, 16–25 leaves, 26–50 leaves, 51–100 leaves, and >100 leaves. The median number of eggs laid per plant in each plant size category (25th and 75th quartiles) was plotted against increasing plant category size. Medians, instead of means, were used because the median was a better estimate of central tendency within plant size classes. The median number of eggs laid in each plant size class was used as a point to investigate the relationship between host plant size and egg load in unmanipulated and *A. elatius* removed habitat.

I used a two tailed *t*-test to quantify differences in the number of eggs laid per leaf of Kincaid’s lupine that was attributable to *A. elatius* removal and differences in the mean number of leaves per plant (ln-transformed) in the treatment and control areas. To detect an edge effect, I performed a linear regression between the number of eggs laid per leaf and the distance in meters from the *A. elatius* edge in the treatment area.

Results

Butterfly behavior

In the study sites with a paired plot design, females oviposited and basked more frequently in plots that were cleared of *A. elatius* than they did in unmanipulated plots (Fig. 1). Females flew over plots containing *A. elatius* more frequently than they did over plots without *A. elatius*, suggesting that females do not detect the larval host plant nor prefer habitats with *A. elatius* (Fig. 1). Females also spent more time in plots without *A. elatius* than they did in plots with *A. elatius* present, however the difference was not statistically significant (two sample *t*-test: n females control (without flythroughs) = 24, mean time control = 73.8 s (back transformed); n females treatment (without flythroughs) = 59, mean time treatment = 117 s (back transformed), df = 81, *t* = 1.797, *P* = 0.08). Males behaved similarly to females, they basked more frequently in plots with *A. elatius* removed and a greater percentage of individuals flew-through plots with *A. elatius* compared to plots with *A. elatius* removed (Fig. 2).

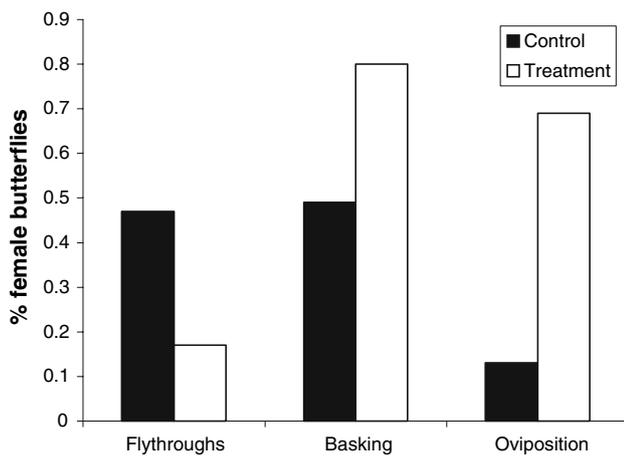


Fig. 1 Female butterfly behavior in paired plots. Number of individuals observed: control = 45, treatment = 71. Results of proportions test: flythroughs *Z* = 3.62, *P* = 0.0003; basking *Z* = 3.54, *P* = 0.0002; oviposition *Z* = 5.87, *P* < 0.0001

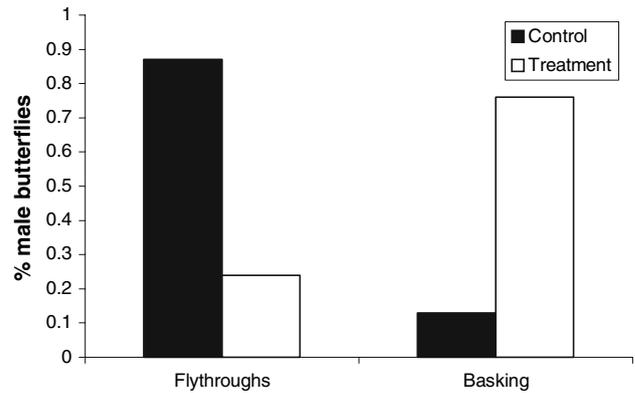


Fig. 2 Male butterfly behavior in paired plots. Number of individuals observed: control = 60, treatment = 95. Results of proportions test: flythroughs *Z* = 7.57, *P* < 0.0001; basking *Z* = 7.57, *P* < 0.0001

In the study site with a large treatment area (North Eaton), both male and female butterflies showed similar behavioral patterns when the treatment edge was encountered on a flight from either the unmanipulated habitat (*A. elatius* present) into the treatment area or vice versa. The majority of butterflies that started their flight from inside the treatment area and encountered the edge turned back into the treatment area within the first 3 m of the edge (Table 1). A few butterflies flew out of the treatment area into *A. elatius* dominated habitat, in a straight line approximately 1 m above the height of the *A. elatius* canopy, and out of sight. When flying from a habitat with *A. elatius* into the treatment area, nearly all of the butterflies engaged in exploratory flights within the first meter of the edge (Table 1).

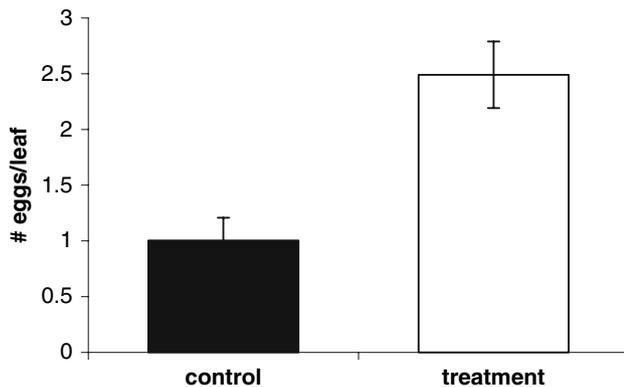
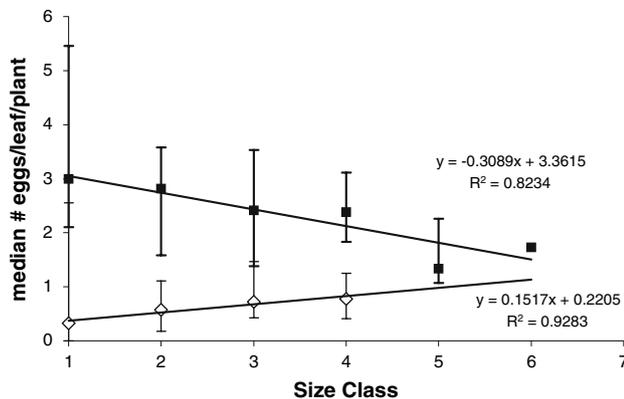
Oviposition

In paired plots, females laid on average about 2.5 times as many eggs per leaf in plots with *A. elatius* removed than in plots with *A. elatius* present (Fig. 3). The mean number of lupine leaves per plot was greater in *A. elatius* removal treatments but this difference was not statistically significant (paired *t*-test: mean removed = 292 leaves, mean control = 172 leaves, df = 6, *t* = -2.34, *P* = 0.06). Plotting the median number of eggs laid per leaf against host plant size classes, suggested a different relationship in oviposition patterns within the treatment and unmanipulated areas. It appeared that more eggs were laid per leaf when the leaf number per plant increased in the plots with *A. elatius* present (Fig. 4), although the error about the smallest plant size class was large. The number of eggs laid per leaf decreased with the plant size class (Fig. 4) in the plots with *A. elatius* removed, suggesting that the butterflies detect and oviposit on host plants differently between the two habitat conditions.

Consistent with egg laying patterns in the paired plots, Fender’s blue laid significantly more eggs per leaf in the

Table 1 Summary of butterfly behavior in the large area removal study site (North Eaton) on the treatment edge

Butterfly behavior	Sex	% of observations	# of observations
Exploratory flight when flying from the habitat with <i>A. elatius</i> over the edge into the treatment area	♂	98.7	77
	♀	94.7	19
Return into the treatment area within the first 3 m of the treatment edge	♂	83.7	104
	♀	87.0	23

**Fig. 3** The mean number of eggs laid per leaf in paired plots with *A. elatius* removed and present (control) \pm 1 SE. Results of paired *t*-test: $n = 7$ pairs, mean control = 1.004 eggs/leaf, mean treatment = 2.49 eggs/leaf, $t = -7.15$, $P = 0.0004$ **Fig. 4** Median number of eggs laid per leaf with upper and lower quartile ranges by host plant size class (class 1 = <6 leaves, class 2 = 6–15 leaves, class 3 = 16–25 leaves, class 4 = 26–50 leaves, class 5 = 51–100 leaves, class 6 > 100 leaves) in paired plots with *A. elatius* present (\diamond) and plots with *A. elatius* removed (\blacksquare). A best fit linear trend line to the median values for each habitat is also presented

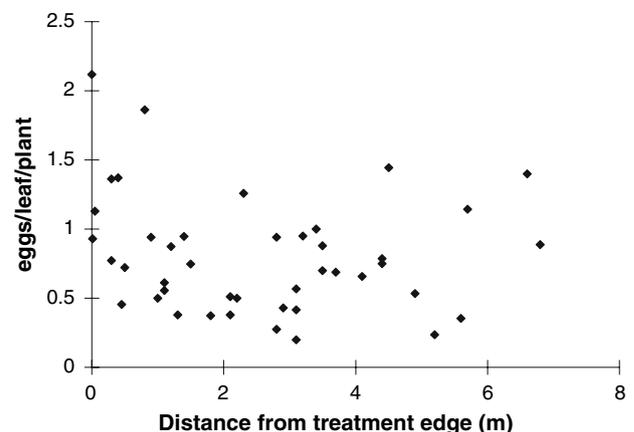
large area without *A. elatius* than on plants in the area dominated by *A. elatius* (two sample *t*-test: control $n = 34$ plants, mean control = 0.229 eggs/leaf; treatment $n = 43$ plants, mean treatment = 0.803 eggs/leaf, \pm 0.06 SE, $df = 75$, $t = -6.86$, $P < 0.000001$). There was no statistical difference in the mean number of leaves per lupine sampled for eggs between the treatment and control areas, however the treatment plants averaged more leaves (mean treatment = 3.1 leaves/plant (ln transformed), $n = 43$ plants; mean control = 2.82 leaves/plant (ln transformed), $df = 75$,

$t = 1.6$, $P = 0.12$). Within the large *A. elatius* removal area, there was no relationship between the number of eggs laid per leaf and distance from the treatment edge (Fig. 5), indicating that there was not preferential oviposition on plants near the treatment edge. In the process of observing butterfly behavior in the control area, three different Fender's blue females were observed laying eggs directly on the inflorescences of Kincaid's lupine while 4th and 5th instar larvae of *Glaucopsyche lygdamus columbia* were consuming flowers on the same inflorescence. These females landed first on lupine inflorescences, crawled down the inflorescence towards the leaves but walked instead on the peduncles of *A. elatius* that grew across and atop of the lupine leaves. They then crawled or flew back to the lupine inflorescence and oviposited single eggs. No Fender's blue eggs were found on inflorescences of host plants in the area lacking *A. elatius* (935 eggs from 43 plants), but five of 150 eggs (34 plants) were laid on inflorescences in the *A. elatius* dominated area.

Discussion

Effects of *A. elatius* removal on butterfly fitness and host plant response

When *A. elatius* was clipped to the height of native grasses in both small (paired plots) and large areas, Fender's blue laid more eggs per unit of host plant in the treatment areas

**Fig. 5** Linear regression results from the large *A. elatius* removal area ($n = 43$ plants, $F = 1.19$, $P = 0.281$)

than on host plants under the tall canopy of *A. elatius*. Moreover, the percentage of females that flew over host plants covered by *A. elatius* was significantly greater than when females flew over areas with the grass removed (Fig. 1). Depending upon the study site and year, the number of eggs laid per leaf of lupine was about 2.5–4 times greater without *A. elatius*. The large difference in reproductive effort between habitats in different years and under different sized treatment areas indicates that there is a strong preference for oviposition habitats with native stature grasses when habitats are invaded by *A. elatius*. Egg load increased with the host plant size class when *A. elatius* inflorescences were present but egg load decreased with host plant size class when inflorescences were removed (Fig. 4). If host plant apparency is diminished by the presence of *A. elatius*, then larger host plants should receive a higher egg load compared to smaller plants, female butterflies should not use areas covered by *A. elatius* as frequently, and butterflies should display flight behavior suggesting that they do not detect the resources available beneath the canopy of *A. elatius*. All three of these predictions appear to be supported because results from the paired plots show that egg load increased with plant size in the presence of *A. elatius* (Fig. 4), females had a higher percentage of flythroughs over *A. elatius* dominated habitat (Fig. 1), and they spent less time in plots when *A. elatius* was present. However, I cannot explain why smaller lupine plants received a higher egg load per leaf when the inflorescences of *A. elatius* were removed (Fig. 4). It may be that the smaller lupine plants have some properties that are attractive to ovipositing females, like higher water/nitrogen content or less concentrated defensive compounds, which are known to receive oviposition preference by insects (White 1984; Pilson and Rausher 1988; Price 1991). If similar mechanisms exist in Fender's blue then they may impact lupine recruitment and butterfly population growth rates, so investigation into host plant quality and oviposition preference is warranted.

Removal of *A. elatius* inflorescences also appeared to affect the host plants. The number of leaves that were produced in the *A. elatius* removal paired plots was greater (but not statistically significant) than the control area, despite my attempt to assure that the relative amount of host plant was equal within a plot pair when the vegetation treatments began. Vigorous growth following neighbor removal and competitor release occurs in plants (Graham and Turkington 2000; Baumann et al. 2001) so the response of increased leaf production to *A. elatius* inflorescence removal is not entirely unexpected. If release from competition did result in more lupine leaves being produced, then areas without *A. elatius* could be a more attractive area for ovipositing butterflies due to a larger host plant display, yielding an inflated difference in egg

load between habitats with and without *A. elatius* inflorescences. Kincaid's lupine vegetation is structured so that more leaves may not necessarily correspond with a larger host plant display. Petioles arise from a rhizome node just below the surface of the ground forming a dome-like crown of vegetation (Severns 2003b). Lupines growing in the *A. elatius* treatment plots had more leaves, but when anecdotally compared with lupines in the control plots (vegetation was etiolated) the leaves were smaller and filled the internal space of the foliage where butterflies are less likely to oviposit when compared to the outer leaves. By producing more leaves that are unlikely to be used by ovipositing butterflies, the difference in egg load between plants growing with and without *A. elatius* should decrease, but did not. Moreover, the patterns of egg load versus host plant size classes (Fig. 4) suggests that oviposition is not disproportionately driven by leaf number in the areas lacking *A. elatius* because plants with fewer leaves received a greater egg load. Regardless of whether or not host plants averaged larger in the plot pairs with *A. elatius* removed, the effect of grass inflorescence removal on maternal investment was dramatic.

Thermoregulation

In addition to differences in oviposition, the incidence of basking was greater in plots where *A. elatius* was removed (Fig. 1). Observations of butterflies in the paired plots suggested that the access to suitable basking habitats nearer to the ground is an important behavior perturbed by the presence of *A. elatius*. Basking immediately preceded all observed oviposition events, implying that maintaining a warm body temperature is important for egg laying Fender's blue, which has also been suggested for other Lepidoptera in temperate zones (Wiklund 1977; Williams 1981; Thomas 1983; Shreeve 1986; Thomas et al. 1986; Betzholtz 2003). Fender's blue landed and basked in the treatment areas on low-lying vegetation that would normally be shaded in the presence of *A. elatius*. When Fender's blue oviposited, they folded their both fore- and hindwings above the thorax and exposed their whitish ventral wing surface, which reflects sunlight and likely lowers body temperature. They then crawled to the underside of lupine leaves to oviposit beneath the shade of leaflets, which likely further lowered body temperatures which was increased by basking immediately before egg laying began. Following oviposition, females again basked before flying away, further indicating the importance of thermoregulation. It appeared that the presence of *A. elatius* interfered with butterfly access to optimal basking sites that are close to the ground, where the ambient temperature is likely to be greater and microhabitats are more sheltered from winds that are likely to convectively cool butterflies. Basking in

plots with *A. elatius* generally occurred on the apices of bent *A. elatius* inflorescences, from 0.5 to 1.0 m above the ground, and butterflies were exposed to frequent wind gusts. These individuals appeared to convectively cool to temperatures that did not enable flight. When Fender's blue did perch near the ground in the plots with *A. elatius*, it was under partial shade and dappled sunlight, not full exposure to sun as in the plots without *A. elatius*. These individuals crawled to patches of sunlight or up grass inflorescences where they likely experienced suboptimal basking conditions. It appears that accessibility to sufficient basking sites is a key feature linked to oviposition because weather during the Fender's blue flight period typically consists of brief sun-breaks between clouds and rain. It is likely that I underestimated the frequency of basking in the treatment areas because observations were made when the butterflies showed the greatest flight activity, not the ephemeral periods of warmth between spring rains that are common during the Fender's blue flight period. Since basking and maintenance of body temperature in female butterflies is linked with fecundity (Watt 2003) and flight performance (Berwaerts and Van Dyck 2004), the invasion and dominance of any vegetation that interferes with basking is likely to be detrimental to Fender's blue and may ultimately affect population growth rates.

Potential vegetation \times weather interactions

The behavioral differences in basking frequency that are related to sward height suggest that there may be an interaction between *A. elatius* and weather. During 2004, when Fender's blue laid approximately 2.5 times as many eggs per leaf in paired plots with *A. elatius* removed (Fig. 3), the percentage of females observed ovipositing in plots without *A. elatius* was nearly five times greater than in plots with *A. elatius* (Fig. 1). This difference between the egg load and percentage of females observed laying eggs can be explained by the early emergence of Fender's blue females during the study year and the growth phenology of *A. elatius*. The spring of 2004 was unseasonably warm in mid to late April, which resulted in butterflies hatching nearly 2 weeks ahead of the earliest recorded flights at these study sites over the previous 7 years (Severns unpublished data). In early May, when females began to oviposit, *A. elatius* inflorescences were as tall or slightly taller than the Kincaid's lupine inflorescences, and did not visually obscure host plants as they did in late May when butterfly behavior was recorded in 2004. In general, the peak Fender's blue oviposition period is late May and early June, which corresponds with *A. elatius* inflorescence elongation and flowering. The difference in the number of eggs per leaf per plant from the large treatment area in 2005 is approximately four times greater than in the habitat

with *A. elatius* inflorescences present. This difference in egg load is comparable to the difference in the percentage of females ovipositing in the paired plots from the previous year (Fig. 1), when the weather in 2005 was more typical. Butterflies in 2005 emerged and peaked in the last week of May when interference with host plant apparency by *A. elatius* would be the greatest. Different between year patterns in egg laying, butterfly flight times, and *A. elatius* flowering suggest that there is likely a relationship with the weather. On one hand, the effects of invasion by tall grasses like *A. elatius* could be minimal if butterflies emerge and lay eggs before grass inflorescences bolt. However, cool weather could produce strong negative interactions on population growth rates if weather conditions result in the peak oviposition period overlapping with fully expanded grass inflorescences and the early lifestages are negatively impacted by the tall grass canopy. The chances of stochastic based weather extinctions could be magnified by the dominance of *A. elatius* and may contribute to large between year population fluctuations observed in Fender's blue populations (Schultz et al. 2003).

Exotic grass invasion and edge effects

Butterflies responded strongly to the treatment edge when there was an absence of *A. elatius* inflorescences over a relatively large treatment area. The difference in grass sward height appeared to reinforce the retention of adults in areas without *A. elatius* inflorescences. Both males and females had a high rate of return into the treatment area when they encountered the treatment edge and nearly all individuals observed engaged in exploratory flights immediately upon encountering areas without *A. elatius* when flying from the adjacent habitat dominated by the tall grass (Table 1). Despite the marked exploratory behavior on encountering the treatment edge, this behavior did not result in a greater egg load on host plants near the *A. elatius* edge in the treatment area (Fig. 5), indicating that there was no edge effect on egg laying. While butterflies preferred to stay in the large area removed of *A. elatius* (Table 1), butterflies in smaller areas removed of *A. elatius* (paired plots) readily flew in and out of the treatment area, but females still targeted plants surrounded by low stature grasses for oviposition (Figs. 1, 2). These behavioral differences suggest that Fender's blue is likely to respond to varying spatial patterns of invasion by *A. elatius* differently. In the small paired plot removal areas, both males and females flew over the treatment areas about 20% of the time (Figs. 1, 2) but upon encountering the edge in the large removal area butterflies investigated the habitat about 95% of the time (Table 1). Moreover, butterflies turned back into the large removal area nearly 85% of the time (Table 1) indicating that the size of the area free from *A.*

elatus inflorescences impacts residence time and site attraction when butterfly populations are invaded and dominated by the tall grass. Across the fragmented prairie landscape, there is likely a gradient of vegetation ranging from formidable physical barriers to butterfly dispersal, like forest edges, to more subtle changes in grass stature within a generally “suitable” piece of degraded prairie that may impact site residency. Habitat quality assessment by butterflies associated with subtle and conspicuous structural changes in open habitats has been suggested by others (Dover and Fry 2001; Thomas et al. 2001; Summerville et al. 2002; Ellis 2003; Dover and Rowlingson 2005) and these behaviors may be important for the survival of relatively weak flying, monophagous species as they may have to detect and use limited resources in specific habitat conditions (Dennis et al. 2004).

Implications for conservation

A reduction in host plant apparency and less frequent use of habitat dominated by *A. elatus* is likely to increase the chances of extinction in Fender’s blue because many of the host plant populations are small and fragmented (Severns 2003a; Wilson et al. 2003). The behavioral response of butterflies to host plants in *A. elatus* dominated conditions suggests that the amount of habitat butterflies perceive as available for reproduction is potentially much lower than what is actually available. If this is true then the encroachment of *A. elatus* into populations of Kincaid’s lupine likely decreases colonization probability and may lead to abnormally high rates of emigration when compared to sites without tall invasive grasses. Moreover, conspicuous lupines in patchy areas of shorter grasses surrounded by *A. elatus* may be overloaded with butterfly eggs, potentially leading to density dependant mortality of larvae (Stiling 1988; Zalucki et al. 2002) and population declines. Studies that have documented population decline of butterflies from structural changes in grasslands do not appear to be from a loss of host plant apparency. In the case of *Hesperia comma* the difference in sward height lead to the loss of suitable oviposition microsites while the larval resources were still abundant (Thomas et al. 1986). *Polyommatus bellargus* (Thomas 1983) and *Maculinea* spp. (Mouquet et al. 2005) have obligate myrmecophilous interactions that may change with sward height resulting in ant community shifts that result in decreased butterfly survival. Fender’s blue does not have obligate ant associations like other lycaenids (Schultz et al. 2003), so the invasion by *A. elatus* is not likely to affect survival of Fender’s blue by altering the butterfly-ant mutualism. *Arrhenatherum elatius* invasion does appear to directly interfere with Fender’s blue oviposition, thermoregulation, and habitat preference primarily by its tall growth habit.

For *Euphydryas editha bayensis* (Weiss 1999), the invasion and dominance of taller stature grasses culminated in the loss of butterfly host plants, whereas, in the case of Fender’s blue the host plant resources are still present but not as effectively detected by ovipositing females. Furthermore, the presence of *A. elatus* appears to lead to oviposition mistakes where Fender’s blue places eggs on lupine inflorescences instead of the underside of lupine leaflets. This oviposition “mistake” places first instar Fender’s blue larvae in direct competition with late instar caterpillars of *G. l. columbia*. Although, the two lycaenid butterflies generally feed on different parts of the lupine, late instar *G. l. columbia* larvae are often tended by ants (some of which are exotic) that occasionally prey upon first instar Fender’s blue larvae.

The overall decrease in host plant apparency and behavioral modifications related to butterfly fitness that accompanies *A. elatus* invasion and dominance indicates that the invasion and dominance of any tall stature grass species is likely to impact Fender’s blue similarly. These findings suggest that any naturally shortgrass prairies invaded by grass species that increase the overall sward height may impact other lepidopterans through a comparable mechanism. If habitat quality for grassland Lepidoptera is degraded by the cover of taller stature exotic grasses, as it appears to do in the case of Fender’s blue butterfly, then invasion by exotic grasses may be acting globally to degrade butterfly communities and contribute to the loss of biodiversity.

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