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ORIGINAL PAPER

Predation of larval Lepidoptera in habitat fragments varies spatially and temporally but is not affected by light pollution

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Abstract As human populations continue to expand, many more species are affected by habitat fragmentation and urbanization. One of the most common themes in studies of fragmented habitats is finding higher rates of predation along habitat edges. However, field studies supporting this pattern are heavily influenced by avian literature and may not apply similarly to other organisms, such as invertebrates. Field studies of predation are typically performed during the day or do not distinguish between day and night; these studies therefore overlook daily fluctuations in predation and may miss important effects that occur solely at night, such as light pollution from streetlights. We tested whether predation of larval Lepidoptera differed between edge and core habitats and also whether predation along the habitat edge varied in response to light pollution from streetlights. We placed larvae in the core of suburban habitat patches and along the habitat edge, both under streetlights as well as between streetlights where it was dark. We found that predation rate increased in both edge and core habitats over the summer. Early season, we found daily fluctuations in predation dynamics with greater predation along the habitat edge than in the habitat core during the day, but not at night. Additionally, we found that streetlights did not affect predation rate along the habitat edge. Our results suggest that increased predation along habitat edges may be a diurnal effect.

Keywords Anthropogenic disturbance · Arthropods · Conservation of Lepidoptera · Edge effects · Light pollution · Temporal variation

Introduction

Increased anthropogenic development of native landscapes leads to habitat loss and fragmentation, which may reduce biodiversity and change species interactions (Saunders et al. 1991; Fahrig 2003). One of the most pronounced changes in these altered habitats is that of increased edge habitat and its effects on species (Saunders et al. 1991; Ries and Sisk 2004; Lindenmayer and Fischer 2006). Changes in the abiotic environment along edges, such as wind, light exposure, and temperature, translate to a wide range of biotic responses (Saunders et al. 1991), including changes in ecosystem services, species distributions, and trophic interactions. For example, some smaller predators actively prefer habitat edges, while others require core habitat conditions to persist in the environment (Andren 1994; Didham et al. 1996). Increases in predator presence can translate to higher predation rates for prey living along the edge (Gates and Gysel 1978; Quinn and Harrison 1988; Chalfoun et al. 2002; Ries and Fagan 2003; Batary and Baldi 2004; Wimp et al. 2011). However, the general trend of increased predation rate along edges is based primarily on avian studies and should be applied cautiously to other systems until more studies on other species confirm its applicability to other systems (Wimp et al. in review).

Contrary to the consistent result of high predation rates along habitat edges in avian studies, empirical studies on arthropod communities have shown positive, negative or no change in invertebrate predation. For example, Bolger et al. (2000) found consistent distributions of species,

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including predators, between the edge and core, while Ries and Fagan (2003) found higher insect predation rates along habitat edges and Wimp et al. (2011) found declines in specialist predators along the edge but a positive response by generalist predators. Yet even in the insect literature, a bias towards diurnal studies or no distinction between diurnal and nocturnal predation ignores potentially important daily variation in predation and core–edge dynamics that could explain the divergent responses previously measured.

Abiotic conditions experienced by edge and core habitats in the day and night vary, and thus the types and abundances of predators in these habitats may also fluctuate temporally. For example, during the day, edges differ in the amount of solar radiation, wind, moisture, and temperature that they experience compared to core habitat (Saunders et al. 1991; Lindenmayer and Fischer 2006). Notably, previous research shows that temperature differences across patches may equalize during the night and provide less microhabitat variation nocturnally between edge and core (Daily and Ehrlich 1996; Ricketts et al. 2001). Variation in abiotic conditions that create microhabitats are important for small invertebrates as even the smallest changes may offer a refuge from environmental changes and predation (Bolger et al. 2000; Schoonhoven et al. 2005; Gibb and Hochuli 2006); overnight, microhabitat differences between the core and edge may dissipate (Daily and Ehrlich 1996; Ricketts et al. 2001). In habitat patches surrounded by urban and suburban development, the types of predators present, predator abundance, and behavior, may also be influenced by the presence of artificial light at night.

Artificial lighting can change predator communities and foraging habits. Visual hunters, such as diurnal shorebirds, for example, are able to extend their foraging periods when areas are lit at night (Santos et al. 2010). Some vertebrate predators, such as birds and bats, forage preferentially under street lights because their prey is attracted to artificial lights (Frank 1988; Rydell 2006) while other nocturnal species, like spiny mice, are photophobic and will avoid foraging in areas where they are also more readily seen by their own predators (Bird et al. 2004; Rotics et al. 2011).

Invertebrate predators appear to prefer artificially lit areas. In laboratory experiments, orb weaving spiders preferentially build webs in lighted environments (Heiling 1999) and in England, ground dwelling invertebrate predators are present in greater densities under street lights (Davies et al. 2012). For insects living along habitat edges, greater densities of invertebrate predators may translate to greater nocturnal predation pressure under streetlights not only due to predator preference for foraging along edges (Bolger et al. 2000; Ries and Fagan 2003; Davies et al. 2012), but also because of variation in illumination along the edge. Whether street lighting affects predation rates of ground-dwelling prey, like larval Lepidoptera, however, has not yet been tested.

In this study, we examine whether predation rates on ground-dwelling invertebrate larvae by vertebrate and invertebrate predators vary spatially and temporally in urban habitat fragments. We test the hypothesis that predation rate of larval Lepidoptera differs between edge and core habitats and also that predation along the habitat edge varies in response to light pollution from streetlights. We also test whether predation rate varies temporally between day and night. Because there are stark differences in abiotic conditions affecting predator distributions diurnally, we expect that predation rate in edge habitats will be higher than in core habitats during the day, but the difference in predation rate may disappear at night. Additionally, we examine whether the presence of artificial lighting influences predation rate. As light pollution has been shown to alter predator communities, we expect that predation rates should vary with the presence of artificial lighting, and that predation will be greatest under streetlights where predator density is likely to be highest.

Methods and materials

Study sites

The Denver-Metro area has many Open Space programs devoted to preserving and restoring native ecosystems along the Eastern Foothills of the Colorado Rocky Mountains. Open Spaces generally consist of patches of mixed grass prairie with a number of both native and exotic species of forbs and grasses; trees and other woody vegetation are limited to small riparian drainages (Nufio et al. 2010; Hinners et al. 2012). These patches are unique in that they are "islands" of natural prairie habitat in an otherwise residentially-developed landscape, but they are able to maintain a diverse community of insects including bees, butterflies, grasshoppers, and moths (Nufio et al. 2010; Hinners et al. 2012; Robinson et al. 2012, Grenis and Murphy unpublished data). For this study, we selected 8 prairie sites between 5 and 15 ha in size with 2–5 street lights along the edge of the habitat patch. Sites were located throughout the Front Range in the City and County of Broomfield, the City of Lakewood, the City of Louisville, and the South Suburban Parks and Recreation District (Appendix 1).

Experimental design

For our study, we used wax worm (*Galleria mellonella* Linnaeus) larvae as prey because they have minimal defenses and are readily consumed by generalist invertebrate predators (K. Grenis and B. Tjossem, *personal observation*). We obtained larvae for each experimental trial from pet stores in the Denver Metro area as wax worm larvae are commonly fed to insectivorous pets. We pinned each wax worm larva to a square of Styrofoam (10 cm × 10 cm × 1.5 cm) with a 00 size insect pin through one of the last two abdominal segments (methods adapted from Frank and Shrewsbury 2004). Prior to deploying larvae in the field, we conducted a pilot experiment in the laboratory to ensure that pinned larvae would remain alive for at least 24 h and also not be able to escape, thus ensuring that disappearances in the field would be due solely to predation. We found that none of the 30 wax worms pinned in the lab died or escaped after 24 h, which is the maximum amount of time a larva would spend in the field. Therefore, we reasonably assume that any wax worm disappearances in the field were caused by some predation event rather than by escape.

Field experiment

For each trial during our field experiment, we placed 15 individually-pinned wax worms at each site in one of three habitat treatments: 5 in the core of the patch (at least 30 m from edge), 5 along the edge under streetlights, and 5 along the edge at least 10 m from a streetlight. There was some variation in the number of larvae deployed among sites because not all sites had 5 streetlights (see Appendix 1). We placed individual larvae in the experimental treatments across the entire field site; for example, larvae in the unlit edge treatment were dispersed along multiple parts of the unlit edge and were not grouped together. The wax worm larvae placed along the patch edge were at least 1 m from the edge (usually a street or sidewalk) but no more than 4 m into the patch. Our method measures the maximum predation rate within each habitat treatment (non-experimental larvae may conceal themselves or modify their behaviors to avoid predation) and thus allows us to compare predation rates among treatments, but is not a measure of natural predation rate on unpinned larvae.

To investigate diurnal predation, we deployed wax worm larvae at dawn (~06:00, we adjusted the times for deployment and recovery throughout the season as day length lengthened and then shortened) using the Styrofoam square described above and nailing the square to the ground with a large 15 cm nail. We pinned only one wax worm larva to each Styrofoam square. We labeled the Styrofoam squares with a "please do not disturb" tag with information about the experiment to avoid manipulation from curious visitors. To facilitate recovery of wax worm larvae in the core where visible landmarks were scarce, we placed a surveyor's flag at least 3 m away from the Styrofoam square in a haphazardly chosen cardinal direction (N, S, E, or W) to ensure that predators would not associate the marker with food. After pinning each larva to its own Styrofoam square, we used calipers to measure body length (to the nearest 0.01 mm). We returned to each site at dusk (~19:00), and recorded the status of the wax worm (predated or not predated). Wax worm larvae were considered predated if they were completely missing, half gone, or showed evidence of predation such as necrotic tissue around an open wound. During our dusk and dawn collections, we also took note of any predators that we found feeding on the wax worm. Additionally, during the early July observation period, we spent 5 h (09:00–14:00) in three field sites observing predation events to learn predator identities. To examine nocturnal and streetlight predation, we replaced any wax worm larvae that had died during the day (either by predation or desiccation) at dusk (~19:00) and recorded the status of the wax worm (predated or not predated) the following morning at dawn (~06:00).

We repeated this entire experimental design twice per month (e.g. early June and late June) in June, July and August, 2013. Thus, we had a total of six collection periods, which allowed us to account for the appearance and emergence of various predators during the summer, and our sampling periods were temporally separated to prevent learning by predators. All eight sites were used in each trial except the nights of the second and sixth sampling periods because of inclement weather (Late June, n = 7 sites; Late August, n = 6 sites).

Statistical analyses

We used multiple logistic regressions to test our hypotheses. First, we examined whether predation rates varied between the day and night using a logistic regression with predation (binomial response: 1 for predated, 0 for alive) as the dependent variable and larval body *length* as the continuous independent variable. Our categorical independent variables were *site*, *sampling period* (early June, late June etc.), *time of day* (day or night), and the interaction effect of *sampling period* × *time of day*. Our model showed no evidence of overdispersion, so we continued to use *site* as a fixed effect, even though it was not a variable of particular interest for our primary research questions (Warton and Hui 2011).

For our analyses of how unlit core and unlit edge habitats differ in predation rate over time, we excluded larvae from the streetlight treatment in order to compare unlit core with unlit edge. We analyzed whether a larva was predated (binomial response: 1 or 0) using a logistic regression with larval body *length* as a continuous covariate and *site, sampling period*, *patch location* (core or edge), and the interaction effect of *sampling period x patch location* as categorical fixed effects.

For our analyses of how street-lit and unlit edge habitats differ in predation rate, we excluded larvae from the unlit core treatment. Again, we analyzed whether a larva was predated (binomial response: 1 or 0) using a logistic regression with larval body *length* as a continuous covariate and *site, sampling period*, *patch location* (lit or unlit edge), and the interaction effect of *sampling period* × *patch location* as categorical fixed effects. In all of our tests, we dropped the interaction effect from the final model if it was not significant. We used JMP v 10.0.0 for all analyses (SAS Institute Inc., Cary, NC).

Results

Over the course of the summer, we deployed 1366 wax worm larvae and 56 % of those larvae were predated. The most common observed predators were ants, during both diurnal and nocturnal time periods; of 761 observed predation events, 309 (40 %) were due to ants. Other predators that we observed included wolf spiders and wasps; wasps systematically divided and removed larvae in pieces from the Styrofoam platform. Scavengers, like earwigs, were found feeding on or near larvae after death. Birds are major predators of lepidopteran larvae in many systems, but we never observed them eating larvae during our experiments. Of our 141 trials, only 2 % (n = 4) had all of the larvae eaten in a single treatment at a site suggesting that it was not common for a single predator to follow the patch edge and consume all of the larvae.

Predation rate between day and night

When all habitat types are analyzed together, we found that there were no differences in predation rate during the day and night but there was an interaction between *sampling period* and *time of day* because predation rate was higher at night than during the day, but only during the first sampling period (Table 1; Fig. 1). Additionally, predation rate varied by field site, driven primarily by high levels of predation in two field sites (Coyote Run and Jackass Hill) and low levels of overall predation at another field site (The Field 1), but showed no discernable spatial patterns to explain the differences in predation rate (i.e. the high predation

Table 1 Logistic regression results from five tests

Comparison	Predictor variables	*df*	χ^2	*P*
Day–Night	Time of day	1	1.29	0.26
	Sampling period	**5**	**46.87**	**<0.0001**
	Time of day × sampling period	**5**	**18.17**	**0.003**
	Site	**7**	**61.96**	**<0.0001**
	Body length	1	1.75	0.2
Day: Core versus edge	**Patch location**	**1**	**5.40**	**0.02**
	Sampling period	**5**	**20.52**	**0.001**
	Site	**7**	**49.4**	**<0.0001**
	Body length	1	0.71	0.4
Night: Core versus edge	Patch location	1	3.35	0.06
	Sampling period	**5**	**25.45**	**<0.0001**
	Patch location × sampling period	**5**	**12.78**	**0.03**
	Site	**7**	**34.15**	**<0.0001**
	Body length	1	0.068	0.8
Day: Unlit versus Lit	Patch location	1	0.004	0.9
	Sampling period	**5**	**19.35**	**0.002**
	Site	**7**	**31.24**	**<0.0001**
	Body length	1	0.06	0.8
Night: Unlit versus Lit	Patch location	1	0.02	0.9
	Sampling period	**5**	**15.19**	**0.01**
	Site	**7**	**14.15**	**0.05**
	Body length	1	0.16	0.9

Bolded values are significant. If an interaction was not significant, it was dropped from the model and not reported sites were not close to each other; Appendix 2). Finally, larval body length had no effect on whether larvae were predated in any of our analyses (Table 1).

Predation rate in habitat core versus habitat edge

During the day, larval predation rate was 20 % greater along the patch edge compared to the core (Table 1; Fig. 2). Predation of larvae increased over the course of the summer in both edge and core habitats (Table 1; Fig. 2). Again, field site was a significant factor with similar patterns as those detailed above (Appendix 3). During the night, larval predation did not differ between the habitat core and edge but did increase throughout the summer (Table 1; Fig. 2); however, there was an interaction between habitat *patch location* and *sampling period* (Table 1). We attribute this interaction to particularly low predation in the habitat core from inclement weather in late June. Predation rate differed among field sites at night (Appendix 4).

Predation rate along unlit edge versus streetlit edge

We found no differences in larval predation between unlit and streetlit edges during the day but found that, in general, diurnal predation rate increased during the course of the summer in both types of edge habitat (Table 1; Fig. 3). Similar to our results during the day, at night we also found no influence of nocturnal streetlighting on larval predation and there was an increase in predation over the summer (Table 1; Fig. 3). Predation rate again differed among field sites during the day (Appendix 5) and night (Appendix 6).

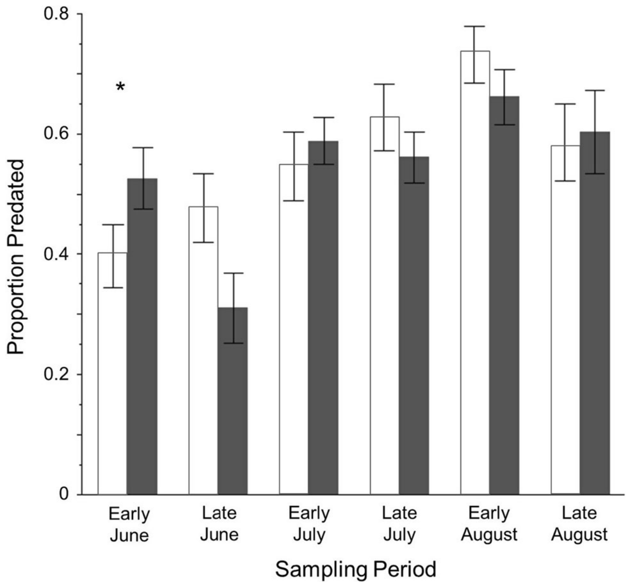

Fig. 1 Proportion of individual larvae (mean ± 1 SE) predated during the day (*white bars*) and the night (*black bars*) over the course of the summer of 2013. *Asterisks* denote significant differences in proportion of larvae predated between the day and night during a particular sampling period ($P < 0.05$ with a Bonferroni correction)

Discussion

Our results show that predation is significantly greater along habitat edges than in the habitat core, but only during the day. Notably, we found that nocturnal predation rates along the habitat edge are not affected by the presence of streetlights, which indicates that light pollution does not affect the strength of top–down pressures on lepidopteran larvae in fragments of mixed grass prairie surrounded by urban development. Furthermore, although predation rates increased throughout the summer in both habitat types, the greatest difference between edge and core habitats in predation risk for larvae occurred in early June. Thus, the generally accepted idea that edges are dangerous places for prey may instead be a pattern that is restricted to certain times of day and season.

We predicted that changes in predation rate associated with edge and core habitats would have consequences for their prey by increasing predation rate along the edge and these negative effects would vary temporally between day and night. We found that predation rates are higher along the edge as compared to the core, but only during the day, which may help explain why certain species are more sensitive to habitat fragmentation (Lindenmayer and Fischer 2006) and have varying responses to edges (Ries and Sisk 2004). Diurnal insects like butterflies, grasshoppers, and bees generally lose individuals and species richness as habitat sizes shrink and edge effects become more prominent (Nufio et al. 2010; Hinners et al. 2012; Robinson et al. 2012). However, organisms that are primarily nocturnal, like moths, do not respond negatively to habitat fragmentation and instead their species richness and abundance shows no discernable pattern with regard to habitat fragmentation (Ricketts et al. 2001; Summerville and Crist 2004; Schmidt and Roland 2006; Fuentes-Montemayor et al. 2012). We found diel fluctuations in edge and core predation rates, with predation greater in edge habitats than core habitats only during the day. Given that foraging and feeding are dangerous activities and expose herbivorous larvae to greater predation risk (Bernays 1997), lepidopteran species with larvae active during the day may be more negatively affected by predation in edge habitats than larvae active at night. Most studies of how Lepidoptera species respond to edges have focused on the adult stages (Ricketts et al. 2001; Summerville and Crist 2004; Schmidt and Roland 2006; Robinson et al. 2012; Fuentes-Montemayor et al. 2012), but our research demonstrates that

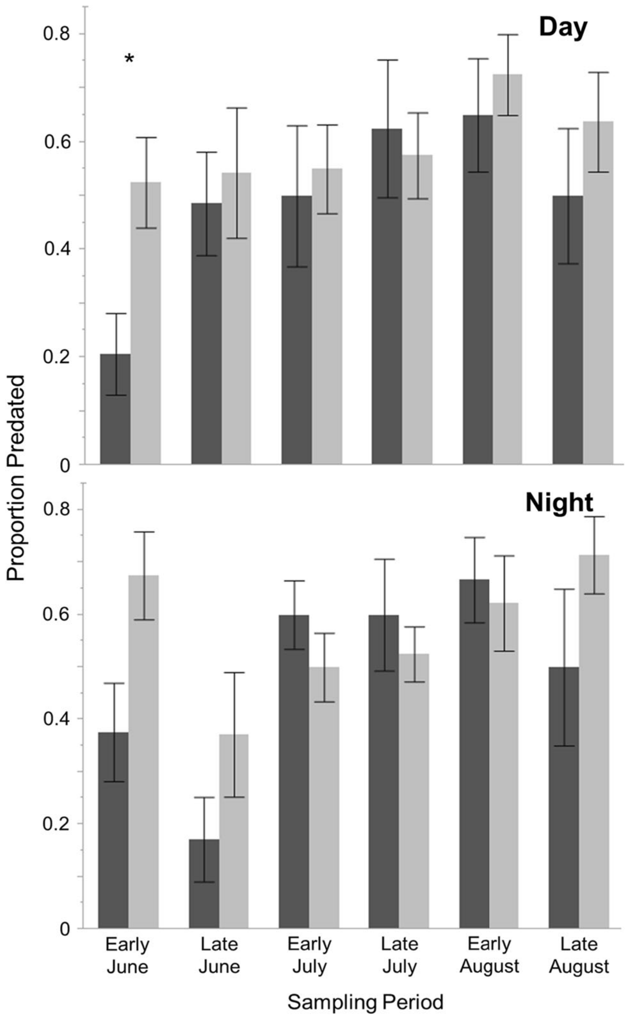

Fig. 2 Proportion of individual larvae (mean ± 1 SE) predated along the habitat edge (*black bars*) and in the habitat core (*gray bars*) during the day and night over the course of the summer of 2013. *Asterisks* denote significant differences in proportion of larvae predated between edge and core habitat types during a particular sampling period ($P < 0.05$ with a Bonferroni correction)

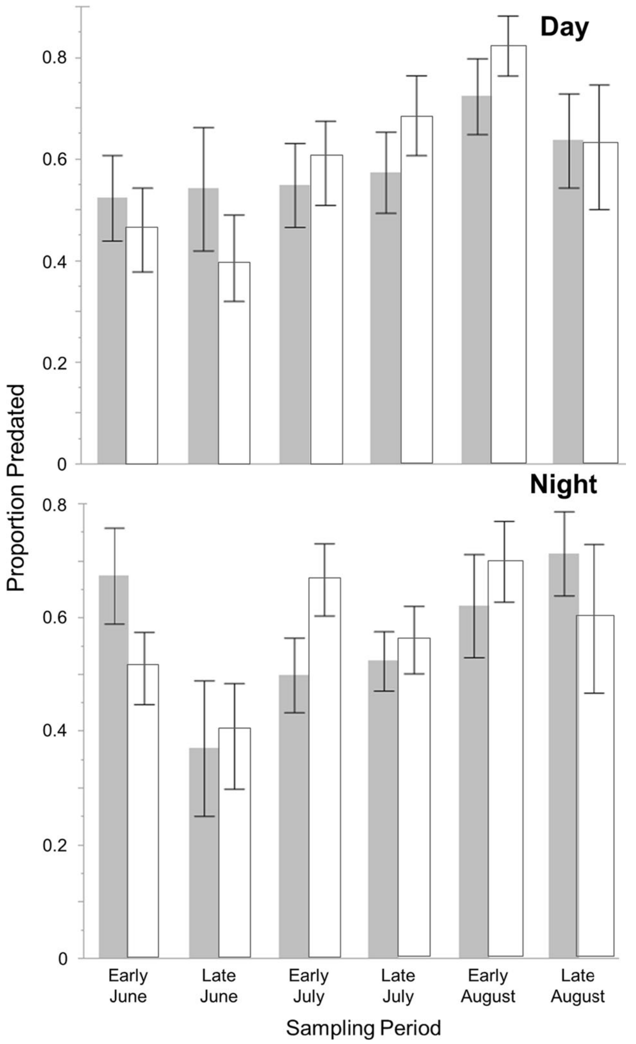

Fig. 3 Proportion of individual larvae (mean ± 1 SE) predated along the habitat edge in unlit areas (*black bars*) and under streetlights (*white bars*) during the day and night over the course of the summer of 2013

predation risk for the larval stage is also greatly affected by edges and may vary seasonally. Thus, how edges affect different ontogenetic stages needs further investigation as it may help to explain why butterflies and moths have such divergent responses to habitat fragmentation.

We found that light pollution from adjacent streetlights did not alter predation rates, which is surprising as light pollution has greatly altered the night time environment (Cinzano et al. 2001; Kyba et al. 2011) and has been shown to be an important effect in other studies (Bird et al. 2004; Tuxbury and Salmon 2005; Kriska et al. 2009; Santos et al. 2010; Rotics et al. 2011). On moonless, cloudless nights, patch edges near streetlights can receive light levels up to four times brighter than found during a full moon (Rich and Longcore 2006). Although we expected this change in nocturnal lighting regime to increase predation, our data show that the story might not be as simple. Research on predators demonstrates that some species are attracted to nocturnal artificial lighting while others respond negatively by avoiding lights or decreasing foraging time in lit areas (Heiling 1999; Bird et al. 2004; Santos et al. 2010; Davies et al. 2012). If predator foraging behavior has an additive effect on larval predation, we may find no net effect of street lights on predation risk for larvae despite significant positive and negative effects on different predator species' behavior and abundance. To further understand the impacts of light pollution on herbivores, we need more studies on the behavioral responses of predators to light pollution.

Although light pollution likely has important impacts on the functional and numeric responses of predators, our results suggest that artificial lighting may not alter overall predation rates on herbivorous larvae if the positive and negative effects of predation risk are evenly balanced.

We also found that predation increases throughout the summer, which may be due to accumulation in invertebrate predator individuals and species that emerge throughout the summer. Additionally, we may have observed a higher predation rate on our experimental larvae later in the summer if alternate prey decreased in abundance later in the growing season, but we did not measure alternate prey resources. Anecdotally, we noticed changes in vegetation structure throughout the summer that may make prey more visible. In early summer, vegetation in the prairie habitat fragments was lush, thick, and dense, and this vegetation complexity may provide hiding places for prey and obstacles for invertebrate predators. As the season became progressively drier, vegetation thinned and wilted, reducing the vegetation complexity, which may have made it easier for predators to find prey, but we did not specifically test this. Because predation rate in our study changed so drastically between the early and late summer, our results emphasize the importance of experimental repetition as patterns may vary not only year to year, but within a season as well.

Our data show that predation may be a cause of variation between nocturnal and diurnal invertebrate responses to habitat fragmentation. Because larvae are subject to greater rates of predation while feeding (Bernays 1997), larvae active during the day may be subject to more predation along habitat edges. We suggest that species with diurnal larvae in fragmented landscapes will suffer the effects of habitat fragmentation more than nocturnal species. Additionally, prairie species emerging later in the summer are also subject to greater predation. Our study suggests that late-season invertebrate larvae that are diurnal and live along the edge of a habitat patch will suffer the greatest amounts of predation and therefore will suffer the most from increased habitat fragmentation and subsequent increases in edge habitat, but this prediction needs to be tested in other natural and managed ecosystems accounting for prey evasion of predators.

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Conflict of interest Kylee Grenis: Dieter Hochuli, John Lill; Bergen Tjossem: n/a; Shannon M. Murphy: Yan Linhart, Paul Feeny, John Lill, Gina Wimp, Danny Lewis.

References

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitats: a review. Oikos 71:355–366

Batary P, Baldi A (2004) Evidence of an edge effect on avian nest success. Conserv Biol 18:389–400

Bernays EA (1997) Feeding by lepidopteran larvae is dangerous. Ecol Entomol 22:121–123

Bird BL, Branch LC, Miller DL (2004) Effects of coastal lighting on foraging behavior of beach mice. Conserv Biol 18:1435–1439

Bolger DT, Suarez AV, Crooks KR et al (2000) Arthropods in urban habitat fragments in Southern California: area, age, and edge effects. Ecol Appl 10:1230–1248

Chalfoun A, Thompson FR, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. Conserv Biol 16:306–318

Cinzano P, Falchi F, Elvidge CD (2001) The first World Atlas of the artificial night sky brightness. Mon Not R Astron Soc 328:689–707

Daily GC, Ehrlich PR (1996) Nocturnality and species survival. Proc Natl Acad Sci USA 93:11709–11712

Davies TW, Bennie J, Gaston KJ (2012) Street lighting changes the composition of invertebrate communites. Biol Lett 144:2274–2276

Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. Trends Ecol Evol 11:255–260

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Frank KD (1988) Impact of outdoor lighting on moths: an assessment. J Lepid Soc 42:63–93

Frank SD, Shrewsbury PM (2004) Effect of conservation strips on the abundance and distribution of natural enemies and predation of Agrotis ipsilon (Lepidoptera: Noctuidae) on golf course fairways. Environ Entomol 33:1662–1672

Fuentes-Montemayor E, Goulson D, Cavin L et al (2012) Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes. Biol Conserv 153:265–275

Gates JE, Gysel LW (1978) Avian nest dispersion and fledgling succes in field-forest ecotones. Ecology 59:871–883

Gibb H, Hochuli DF (2006) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv 106:91–100

Heiling AM (1999) Why do nocturnal orb-web spiders (Araneidae) search for light? Behav Ecol Sociobiol 46:43–49

Hinners SJ, Kearns CA, Wessman CA (2012) Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. Ecol Appl 22:1923–1935

Kriska G, Bernáth B, Farkas R, Horváth G (2009) Degrees of polarization of reflected light eliciting polarotaxis in dragonflies (Odonata), mayflies (Ephemeroptera) and tabanid flies (Tabanidae). J Insect Physiol 55:1167–1173

Kyba CCM, Ruhtz T, Fischer J, Hölker F (2011) Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. PLoS ONE 6:e17307

Lindenmayer DB, Fischer J (2006) Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press, Washington, p 328

Nufio CR, McClenahan JL, Deane Bowers M (2010) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. J Insect Conserv 15:409–419

Quinn JF, Harrison SP (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75:132–140

Rich C, Longcore T (2006) Ecological consequences of artificial night lighting. Island Press, Washington, p 458

Ricketts TH, Daily GC, Ehrlich PR et al (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conserv Biol 15:378–388

Ries L, Fagan WF (2003) Habitat edges as a potential ecological trap for an insect predator. Ecol Entomol 28:567–572

Ries L, Sisk TD (2004) A predictive model of edge effects. Ecology 85:2917–2926

Robinson N, Armstead S, Bowers MD (2012) Butterfly community ecology: the influences of habitat type, weather patterns, and dominant species in a temperate ecosystem. Entomol Exp Appl 145:50–61

Rotics S, Dayan T, Kronfeld-Schor N (2011) Effect of artificial night lighting on temporally partitioned spiny mice. J Mammal 92:159–168

Rydell J (2006) Bats and their insect prey at streetlights. In: Rich C, Longcore T (eds) Ecol. Consequences Artif. Night Light. Island Press, Washington, pp 43–60

Santos CD, Miranda AC, Granadeiro JP et al (2010) Effects of artificial illumination on the nocturnal foraging of waders. Acta Oecol 36:166–172

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32

Schmidt ABC, Roland J (2006) Moth diversity in a fragmented habitat: importance of functional groups and landscape scale in the boreal forest moth diversity in a fragmented habitat. Ann Entomol Soc Am 99:1110–1120

Schoonhoven LM, van Loon JA, Dicke M (2005) Insect-plant biology, 2nd edn. Oxford University Press, Oxford, p 421

Summerville KS, Crist TO (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. Ecography (Cop) 27:3–12

Tuxbury SM, Salmon M (2005) Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. Biol Conserv 121:311–316

Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10

Wimp GM, Murphy SM, Lewis D, Ries L (2011) Do edge responses cascade up or down a multi-trophic food web? Ecol Lett 14:863–870

Wimp, GM, Murphy SM, Lewis D, Ries L (in review) Do generalists always like edges? Habitat structure influences generalist predator responses to habitat edges. Ecology