Univerzita Palackého v Olomouci

Přírodovědecká fakulta

Disertační práce

Klíčové biotické a abiotické faktory ovlivňující aktivitu predátorů herbivorního hmyzu v prostorových gradientech temperátních ekosystémů

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Olomouc 2013

Šipoš J. 2013: Klíčové biotické a abiotické faktory ovlivňující aktivitu predátorů herbivorního hmyzu v prostorových gradientech temperátních ekosystémů [doktorská dizertační práce]. Univerzita Palackého, Olomouc

Abstrakt:

Ekologové se shodují, že predátoři a rostliny společně ovlivňují populace herbivorů. Rostoucí počet studií poukazuje na to, že komplexnost stanoviště nebo vegetačního zápoje často zprostředkovává a ovlivňuje sílu top-down efektu na herbivory. Únik před predátorem a nalezení místa, kde se vyskytne predátor s menší pravděpodobností (enemy-free space), tak může být hlavním faktorem, determinujícím chování herbivorního hmyzu.

Pro samotné studium enemy-free space je nutné nejprve zjistit, jakým způsobem je predační tlak ovlivněn biotickými a abiotickými faktory prostředí v prostoru a čase. V předkládané práci jsem studoval změny v míře predace v průběhu vegetační sezóny v gradientech lesních a nelesních habitatů. Dále byl studován vliv abiotických faktorů na změny v predaci v prostorovém a časovém gradientu. Z výsledků mých pozorování vyplývá, že predační tlak je v lesním prostředí nerovnoměrný. Predátoři v interiéru lesa napadali instalované návnady bezobratlých nejčastěji při povrchu země, v lesní hrabance. Naproti tomu v prostředí lesních okrajů byla zvýšená aktivita predátorů zaznamenána na listech stromů. V oligotrofních lesních ekosystémech se predace soustředila do mechových polštářů.

Tyto výsledky je možno interpretovat ve vztahu k distribuci biomasy (organická hmota), jež v temperátních ekosystémech vzniká a kumuluje se převážně při zemi. Vysoká míra predace na listech v okrajových lesních částech byla pravděpodobně výsledkem silného vlivu teploty na létavé skupiny hmyzu. Vyšší proporce napadených návnad v interiéru lesa oproti lesnímu okraji lze vysvětlit nejen akumulací biomasy, ale taky abiotickými faktory (teplota, vlhkost). Komplexnost korunového zápoje byl další faktor s průkazným vlivem na predaci. Predátoři pohybující se na stromech s jednodušší korunou, napadli vetší proporci návnad. Tato práce taky odhaluje, že v otevřených a nelesních stanovištích má na míru predace větší vliv sezónnost a abiotické faktory, než na predaci v interiéru lesa.

Z výše uvedených důvodů vyvozuji, že efekt abiotických faktorů, komplexnosti koruny stromu, vertikálního lesního gradientu, gradientu v lesním zápoji, primární produktivity a jejich interakcí musí být zahrnut při predikci času a prostoru, ve kterém bude mít predace největší respektive nejmenší vliv.

Klíčová slova:

Architektura koruny, časová a prostorová variabilita, návnady, otevřené lesní habitaty, predační tlak, vertikální stratifikace.

Šipoš J. 2013: Key biotic and abiotic factors influencing activity of predators of herbivorous insect in spatial gradients of temperate ecosystems [doctoral dissertation]. Palacky University, Olomouc

Abstract:

There is consensus among ecologist that predators and plants affect population of herbivorous insect. Increasing number of studies shows that a habitat complexity and a vegetation canopy characteristic often mediate or influence the strength of top-down effect on herbivores. Escape from predators and search for “area without enemies” (enemy-free space), may be the main factors that dominantly influences the behavior of herbivorous insect.

To study enemy-free space, one must at first determine how the predation rate is influenced by biotic and abiotic environmental factors in space and time. In this thesis I have studied the changes in the predation rate during the growing season in the gradients of forest and non-forest habitats. Furthermore, I have studied influence of the abiotic factors on the changes in the predation rate in the temporal and spatial gradient. The results show that predators occurring in the forest interior attacked the baits set in the forest litter. High activity of predators was also recorded on the leaves of trees at the edge of the forest. In oligotrophic forest ecosystems predation was concentrated to the moss tussocks.

These results can be explained by the distribution of biomass (organic matter) which is mainly produced and accumulated on the ground in the temperate ecosystems. A high level of predation on the leaves in the forest margins was probably due to the strong influence of temperature in more open habitats. Higher proportion of attacked baits in the forest interior than on its edge can be explained not only by the accumulation of biomass, but also by abiotic factors (temperature, humidity). Canopy complexity was another factor with a significant effect on the predation rate. Predators foraging in the trees with a simple crown attacked a larger proportion of the baits. This thesis also reveals that the seasonality and abiotic factors have greater influence on the predation rate in an open and non-forest habitats than in a forest interior. Therefore, I conclude that abiotic factors, canopy complexity, forest strata, forest openness, primary productivity and their interactions have to be considered in attempting to predict a time and a space in which the predation will have the greatest or the smallest impact on herbivore populations.

Key words:

Baits, canopy architecture, forest openness, forest strata, predation rate, temporal and spatial variability.

OBSAH

Seznam originálních publikací

Disertační práce je založena na těchto článcích. Ty jsou v textu citovány tiskacími písmeny A-E.

A Šipoš J., Drozdová M. and Drozd P. 2012: Assessment of trends in predation pressure on insects across temperate forest microhabitats. *Agricultural and Forest Entomology*. Article in press.

B Šipoš J., Drozdová M. and Drozd P. 2012: Effect of canopy openness on the pressure of predatory arthropods and birds on epigeic insect. *Central European Journal of Biology* 7: 1021-1029.

C Drozdová M., Šipoš J. and Drozd P. 2013: Key factors affecting the predation risk of insects on leaves of trees in forests on a floodplain in the temperate region. *European Journal of Entomology.* Article in press.

D Šipoš J. and Kindlmann P. 2012: Effect of the canopy complexity of trees on the rate of predation of insect. *Journal of Applied Entomology*. Article in press.

E Drozdová M., Šipoš J. and Drozd P. 2009: Predation risk for insect living in moss cushions: comparison between different strata of mountain forest. *Nowellia Bryologica* 38: 31-35.

Autor se podílel na designu experimentu (A,B,D,E), na analýze dat (A,B,C,D,E), podílel se na sběru dat (A,B,D,E) a na psaní publikací (A,B,C,D,E).

Poděkování:

Chtěl bych poděkovat především mé mamce Ireně Šipošové, jejíž podpora a pomoc mi psaní této práce velice usnadnily. Za cenné rady a připomínky bych chtěl také poděkovat Tomáši Kurasovi, Monice Mazalové a Emilu Tkadlecovi. Tato práce by nemohla nikdy vzniknout bez přispění Pavla Drozda, který mi poskytoval velké množství rad a informací. Michaele Drozdové bych chtěl poděkovat za spolupráci na terénních výzkumech a sepisování publikací. Poděkování patří také Kateřině Havlíčkové za její trpělivost, povzbuzování a pomoc při terénních výzkumech.

Úvod:

Predátoři jako významný faktor regulace početností herbivorů

Predace je považována za jeden z klíčových faktorů ovlivňujících charakteristické rysy organizmů (životní strategie, chování), populací (velikost populace, stabilita populace) a společenstev (druhová bohatost, relativní a celková abundance) (Sih et al. 1985). Jedním z prvních autorů, který poukázal na roli predace, coby významného mechanismu regulace populačních početností kořisti byl Nicholson (1933, 1958)

Funkční a numerická odpověď predátorů na abundanci kořisti byla chápána jako důležitý faktor, který se pokouší vysvětlit klasickou otázku v ekologii „proč je svět zelený“ (*why the world is green*) (Hairston et al. 1960). Rostliny jsou jen málokdy zcela zahubeny herbivorním hmyzem, protože jeho populace jsou ovlivňovány aktivitou predátorů, patogenů a parazitoidů (Hairston et al. 1960). Tato hypotéza staví predaci z hlediska významu při regulaci populačních početností herbivorů, na první místo pomyslného pořadí před kompetici a vlivy primárních producentů. Zahájila také dlouhotrvající diskuzi na téma zda jsou herbivoři limitováni v trofickém řetězci výše postavenými predátory (*top-down effect*) nebo naopak zdola, z úrovně primárních producentů (*bottom-up effect*).

Z předpokladu dominantního vlivu predátorů na herbivory vychází také hypotéza o „prostoru bez nepřátel“ (*enemy-free space*) (Jefries & Lawton 1984). Autoři tuto hypotézu definují jako způsob života, který redukuje nebo eliminuje zranitelnost k jednomu nebo ke skupině predátorů. Scheirs & De Bruin (2005) uvádějí, že síla predačního tlaku se mění s časem. Kořist vlivem variability predace během dne nebo vegetační sezóny může svoji aktivitu soustředit do časového intervalu, ve kterém je aktivita predátorů nejmenší a žije tak v dočasném časovém refugiu (*enemy-free time*).

Schmitz (1997, 2004) ve svých studiích uzavírá, že dominantní vliv predátora se neodehrává prostřednictvím zabíjení kořisti, ale přes změny chování, fyziologie a životní historie kořisti. Až do nedávna ekologické studie vyzdvihovaly exploatační a interferenční mechanizmy řídící kompetici (Price et al. 2011). Jsou to ale nepřímé interakce, zprostředkované skrze rostliny nebo predátory, které dominantně ovlivňují naprostou většinu vztahů mezi herbivory (Kaplan & Denno 2007). Nepřímý vliv rostlin a predátorů na kompetici mezi herbivory také vyvrací předpoklad, že většina interspecifické kompetice je symetrická (Denno et al. 1995, Kaplan & Denno 2007).

Vliv primární produktivity na roli predátorů v trofických řetězcích

Oksanen et al. (1981) uvádí, že predátoři regulují abundanci herbivorů spíše v produktivních ekosystémech, které disponují dostatečnou primární produktivitou pro vytvoření většího počtu trofických stupňů v potravním řetězci. Ekosystémy s nízkou produktivitou, které nejsou schopny udržet dostatečné množství predátorů, jsou charakteristické vysokým stupněm spásání vegetace (viz stepi, polopouště, tundry, vysokohorské bezlesí) (Fretwell 1977).

Přestože klíčový vliv predátorů na nižší trofické úrovně byl prokázán, jejich role v trofických kaskádách a jejich významnost v ekosystémových procesech a funkcích stále zůstávají diskutabilní (Polis 1996, Polis 1999, Schmitz et al. 2000). Jedním z důvodů kontroverze je časté použití nevhodné metodiky při studiu trofických kaskád. Nevhodná metoda experimentálního studia pak mohla vést k chybným závěrům, tj. že společenstva herbivorů jsou výrazněji ovlivňována rostlinami, než predátory. Nedostatky v metodice vycházely z chybného faktu, že interakce mezi predátorem a kořistí jsou zprostředkovány hlavně změnou hustoty kořisti (Price at al. 1980, Power 1992, Schmitz & Suttle 1997, Schmitz 2004).

Skupina hypotéz propagujících limitaci společenstev herbivorů primárními producenty byla založena na skutečnosti, že rostlinná pletiva jsou velice chudá na dusík, který je potřebný pro tvorbu proteinů (White 1978, 1984). Rostliny také nejsou jen pasivními aktéry, ale umějí se cíleně bránit napadení. Za tím účelem vytvářejí velké množství obranných mechanizmů, jako jsou mechanické struktury (trny, trichomy) nebo sekundární metabolity (taniny, alkaloidy) (Van Der Meiden 1996, Coley & Barone 1996). Z tohoto předpokladu vychází kompromisní hypotéza, že herbivorní hmyz není regulován výhradně predátory, ale také rostlinami, jež jsou pro herbivory špatně stravitelné (White 1978).

Společný vliv rostlin a predátorů na dynamiku herbivorního hmyzu

V současné době se při studiu populační dynamiky stále častěji vyhodnocuje společný vliv predátorů (top-down effect) a primárních producentů (bottom-up effect) na populace herbivorů (Hunter and Price 1992, Forkner and Hunter 2000). Potvrdilo se, že vliv top-down nebo bottom-up efektu vykazuje sezónní variabilitu (Pitt 1999, Forkner and Hunter 2000, Boyer et al. 2003). Ukazuje se, že efekt rostliny na abundanci herbivorů zůstává silný během celého vegetačního období, zatímco predátoři vykazují silný vliv pouze na jeho začátku (Boyer et al. 2003). Ekologové se shodují, že predátoři a rostliny společně ovlivňují populace herbivorů, ale není upřesněno, jak se vliv top-down a bottom-up efektu na herbivory mění v prostoru a čase, a které faktory prostředí sílu těchto efektů ovlivňují (Denno et al. 1995).

Náhlé časově a prostorově ohraničené přemnožení herbivorů, způsobující zničení velkých ploch vegetace, poukazuje na selhání role predátorů jako jednoho z hlavních regulujících faktorů populací herbivorů (Maron et al. 2001). Jako nejpravděpodobnější viník těchto kalamitních stavů se zdá být interakce mezi prostorovými (fragmentace, izolovanost a komplexnost prostředí), abiotickými (teplota, vlhkost, sluneční radiace) a biotickými faktory (primární produktivita) na jedné straně a predátory a herbivory na straně druhé.

Nezastupitelná role struktury porostu

Vegetační struktura je jedním ze zásadních environmentálních faktorů, ovlivňujících herbivory a jejich predátory (Riihimaki et al. 2006). Můžeme ji vnímat na více hierarchických úrovních, sahajících od celých rostlinných společenstev přes jednotlivé rostliny, až k jejich částem (Halaj et al. 2000a, Riihimaki et al. 2006). Zvětšující se množství studií poukazuje na to, že komplexnost habitatu nebo vegetačního zápoje často zprostředkovává a ovlivňuje sílu top-down efektu na herbivory (Kruess & Tscharntke 1994, Hunter et al. 1997, Zabel & Tscharntke 1998, Halaj et al. 2000b, Liebhold et al. 2005, Tschasnz et al. 2005, Riihimäki et al. 2006). Komplexita prostředí ovlivňuje interakce mezi predátory a mezi predátorem a kořistí prostřednictvím (sensu Lawton 1983, Franklin & Van Pelt 2004, Gruner 2004, Langellotto & Denno 2004, Theunis et al. 2005, Tschanz et al. 2008):

a) refugií pro predátory, poskytujících ochranu před intra-guildovou predací a kanibalizmem;

b) alternativních zdrojů potravy (pyl, nektar);

c) dostatečného počtu vhodných míst pro přezimování a reprodukci;

d) stabilního prostředí, chránícího predátory před nepříznivými vlivy prostředí.

Takto heterogenní habitaty budou snižovat antagonistické interakce mezi predátory a umožní jim dostatek potravy a stabilního prostředí (Finke & Denno 2006, Rickers et al. 2006). Tscharntke (1994, 1998) poukazuje na zranitelnost organizmů stojících výš v trofickém řetězci. Řada studií potvrdila, že predátoři jsou náchylnější na disturbance habitatu (ve smyslu zvýšení fragmentace a izolovanosti) a na stres způsobený změnou počasí než herbivoři (Kruess & Tscharntke 1994, Zabel & Tscharntke 1998, Valladares et al. 2005, Hance et al. 2007). Teorie ostrovní biogeografie (MacArthur & Wilson 1967) jako jedna z prvních pracovala s vlivem rozlohy a izolovanosti dané plochy na společenstva organizmů.

Řada výzkumů dokládá, že vegetace často zprostředkuje vliv top-down efektu na herbivorní hmyz (Forkner & Hunter 2000, Denno et al. 2002). Stále málo studií se zabývá tím, jak se predace mění v čase a v prostoru a které faktory ji ovlivňují. Možným přístupem je studovat tuto variabilitu podél krajinných gradientů. Ty jsou reprezentovány (sensu Denno et al. 2005):

a) korunovým zápojem;
b) nadmořskou výškou;
c) abundancí predátorů a herbivorů;
d) primární produktivitou;
e) stářím porostu.

Hierarchicky níže než struktura rostlinných společenstev stojí komplexnost a architektura koruny jednotlivých stromů. Vliv struktury koruny na predátory a jejich aktivitu není jednoznačný (Riihimaki et al. 2006). Její heterogenní architektura poskytuje dostatek refugií pro herbivory, v důsledku čehož predátoři nejsou schopni zapříčinit lokální extinkci své kořisti (Price et al. 2011). Větší heterogennost dále způsobuje, že predátoři a parazitoidi jsou méně efektivní, a to z důvodu delší doby potřebné k nalezení potravy (Andow & Prokrym 1990, Riihimäki et al. 2006). Na druhé straně vyšší heterogenita pozitivně ovlivňuje populace predátorů, protože snižuje množství jejich negativních interakcí (intra-guildová predace a kanibalizmus) (Langelloto & Denno 2004).

Významná role času a proměnlivosti prostředí

Řada experimentů potvrdila, že efekt predátorů na populační dynamiku herbivorů se mění v prostoru a čase (Forkner & Hunter 2000, Denno et al. 2002, Stireman III & Singer 2002, Boyer et al. 2003). Tyto ekologické procesy jsou do značné míry ovlivňovány abiotickými faktory prostředí. Andrewartha & Birch (1954, 1960) jako první poukázali na dominantní roli abiotických faktorů coby regulátorů početnosti herbivorů. Jedním z těchto nejdůležitějších faktorů je klima, které sehrává zásadní roli při ovlivnění:

a) diverzity a pestrosti společenstev;
b) rozšíření druhů;
c) produktivity prostředí (Johansson et al. 1995).

Na menších prostorových škálách jsou mikroklimatické podmínky prostředí významnější, protože přímo ovlivňují většinu ekologických procesů (Chen & Franklin 1997).

Přestože se předpokládá, že „enemy-free space“ se chová jako dynamická mozaika měnící se v čase a prostoru, nikdo zatím přesně neformuloval potenciální kauzální vztahy mezi predátorem a faktory prostředí. Proto jedním z hlavních přínosů této práce je identifikace těch faktorů prostředí a jejich kombinací, které se jeví jako stěžejní z hlediska ovlivnění prostorové a časové variability v predačním tlaku. Mezi faktory prostředí, jejichž vliv na predační tlak byl analyzován v předkládané práci patří:

a) mikroklimatické podmínky prostředí (vlhkost, teplota, úhrn srážek, sluneční záření);
b) makroklimatické veličiny (NAO indexy);
c) biotické faktory (primární produktivita, abundance herbivorního hmyzu).

Příloha A se zaměřuje na sezónní proměnlivost v predačním tlaku podél gradientu vertikální a horizontální struktury porostu, tj. mezi lesními patry (pata stromu, kmen a koruna), resp. mezi okrajem a interiérem lesa. **Příloha B** se zabývá potenciálními rozdíly v predačním tlaku v závislosti na korunovém zápoji v lesních a nelesních ekosystémech. **Příloha C** je orientována na hlavní faktory, ovlivňující aktivitu predátorů. **Příloha D** zkoumá vliv komplexity koruny stromu na míru predace u herbivorního hmyzu. **Příloha E** je zaměřena na problematiku predačního tlaku mezi jednotlivými mikro-stanovišti troficky chudých smrkových monokultur.

Za účelem poskytnutí ucelenějšího náhledu do problematiky vztahu predátor-kořist jsem použil i dosud nepublikované výsledky.

Cíle:

(a) Zjistit rozložení predace mezi různými lesními patry

(b) Identifikovat trend v predačním tlaku podél gradientu vegetačního zápoje (i) v lesních a (ii) v nelesních ekosystémech.

(c) Determinovat vliv architektury koruny stromu na aktivitu predátorů

(d) Identifikovat stěžejní faktory prostředí, determinující fluktuace v predačním tlaku (i) v lesních a (ii) v nelesních ekosystémech.

(e) Porovnat vliv mikro a makroklimatických faktorů prostředí na míru predace

Metodika:

Vliv predátorů na kořist lze studovat dvěma hlavními metodickými přístupy: 1) s volným přístupem predátora; a 2) se zamezením vstupu predátora. Většina experimentů, zabývajících se vlivem predátorů na nižší trofické úrovně, používá tzv. „**oplocovací metody**“ (exclosure experiments) (Holmes et al. 1979, Marquis & Whelan 1994, Sipura 1999, Strong et al. 2000, Gibb 2003). Tyto výzkumy umožňují určit abundanci kořisti při zamezení přístupu predátora použitím sítí nebo klecí (Van Bael et al. 2003, Weseloh 1988). Stejného efektu lze docílit pomocí insekticidních přípravků, které významně zredukují početnost predátorů na daném území (Klimeš et al. 2011). Principem těchto metod je srovnání ploch s volným přístupem predátorů a ploch, kde bylo zabráněno vstupu predátorů. Uvedené metodické přístupy umožňují měřit absolutní predační tlak. Nevýhodou těchto experimentů je jejich omezená použitelnost při sledování menších ploch. Také neumožňují dohledat a identifikovat taxony predátorů a určit čas, ve kterém k napadení došlo.

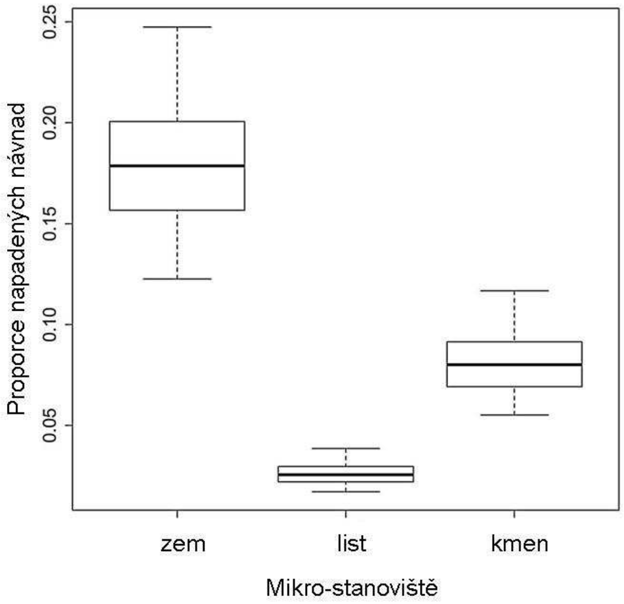
Druhým typem studia interakcí mezi predátorem a kořistí jsou **experimenty s volným přístupem predátora** ke kořisti. U těchto typů experimentů se používají buď živé (larvy dvoukřídlých, larvy motýlů, kukly, nebo termiti) nebo umělé návnady (plastelínové nebo umělohmotné modely kořisti) (Barton 1986, Olson 1992, Lichtenberg & Lichtenberg 2003, Liebhold et al. 2005, Koh & Menge 2006, Skoczylas et al. 2007, Remmel et al. 2009, Barbaro et al. 2012). Při měření predačního tlaku jsou návnady nejčastěji fixovány na určité místo (Novotný et al. 1999, Lichtenberg & Lichtenberg 2003). K jejich fixaci se využívají špendlíky

(Novotný et al. 1999, Lichtenberg & Lichtenberg 2003), lepidlo (Remmel et al. 2009), provázky (Strauss 1997), nebo sponky (Lill & Marquis 2001).

Pro můj experiment, srovnávající variabilitu proporce napadených návnad během dne a roku mezi různými mikro-stanovišti, bylo použití „oplocovacích“ metod nevhodné. Výhodnější tak bylo použití živých larev jako návnad, fixovaných pomocí entomologických špendlíků. Tento design experimentu mi umožňoval porovnat rizika predace v různých mikro-stanovištích, změřit fluktuaci relativní míry predace během dne a vegetačního období a zjistit vliv abiotických faktorů.

Terénní experiment probíhal následovně: na začátku každého vzorkování bylo náhodně vybráno 15 stromů (*Tilia* spp.), v jejichž okolí byly vymezeny vlastní vzorkovací plošky (mikro-stanoviště o rozměrech 50x50 cm). Rozměry byly definovány v závislosti na velikosti studovaných mikro-stanovišť a na počtu upevněných návnad. Na těchto ploškách bylo náhodně umístěno 20ks návnad (fixované návnady larev bzučivek, viz dále). Expozice larev na dané plošce byla bez opakování a trvala po dobu 30 min. Opakované měření probíhalo na nové plošce, jejíž vzdálenost byla vždy minimálně 10m od původně vzorkované plošky. Studium probíhalo na třech lokalitách v CHKO Poodří (Jistebnické rybníky, Polanský les a Oderské louky).

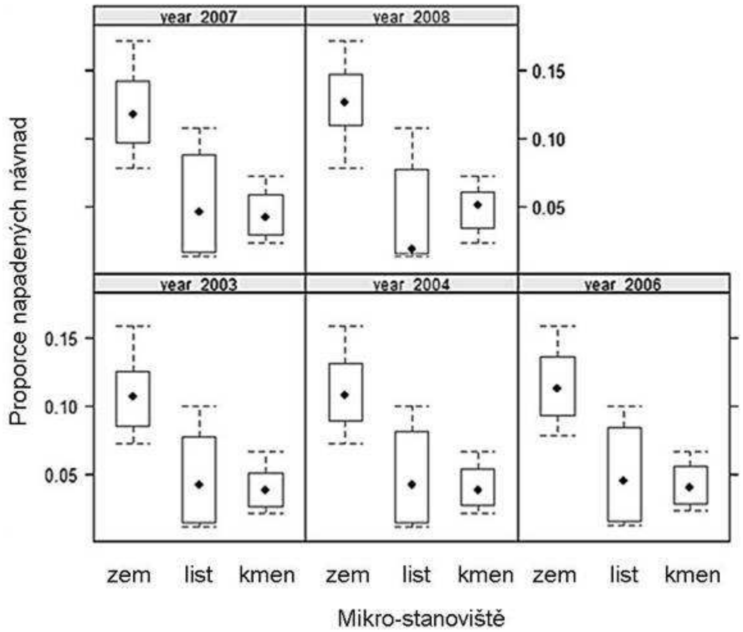
V popisovaném terénním experimentu je velmi důležité použití vhodné návnady (Weseloh 1988, Novotný et al. 1999). Výzkum byl veden v temperátním ekosystému, z toho důvodu byla vybrána návnada, která se v něm přirozeně vyskytuje. Další kritéria vhodnosti návnady reprezentují: (a) přirozený výskyt druhu, použitého jako návnada, během celého vegetačního období; (b) neexistence obranných mechanizmů; (c) dobrá palatabilita (Lundgren et al. 2009). Uvedeným kritériím nejlépe vyhovovaly larvy mouchy *Calliphora vicina*. Rovněž velikost této návnady (1,5 cm) je atraktivní pro velké množství druhů predátorů (Remel et al. 2009). Široké spektrum taxonů napadajících návnady dokládá, že typ návnady pro tento experiment byl vybrán správně.



Obr. 1. Vztah mezi mikro-stanovištěm a proporcí napadených návnad. Krabicový graf znázorňuje hodnotu mediánu, hranice krabice představují mezi-kvartilový interval a extrémní hodnoty jsou zobrazeny v podobě koncových úseček.

Během připevňování návnady jsem se snažil vyhnout jejímu velkému poškození, které by mohlo způsobit její předčasný úhyn a tím i atraktivitu pro nežádoucí taxony hmyzu. Ptáci a sociální hmyz jsou schopni se naučit lovit konkrétní kořist na určitém místě, z toho důvodu doba umístění návnady na konkrétním mikro-stanovišti nepřesáhla uvedený interval 30ti minut a opakované experimenty na stejných lokalitách byly odděleny delším časovým intervalem.

Některé používané abiotické faktory, vystupující v modelech jako vysvětlující proměnné, nebyly přímo měřeny, ale vypočítány nebo získány z internetových databází. Jako klimatický faktor byl použit tzv. zimní NAO index (North Atlantic oscillation). Ten byl kalkulován jako rozdíl v atmosférickém tlaku v úrovni moře mezi Lisabonem a Reykjavikem v období mezi prosincem a březnem 2002-2009. Pozitivní NAO index reprezentuje velké rozdíly v tlaku vzduchu, které způsobují převážně západní proudění vzdušných mas, v jehož důsledku v Evropě převládají chladná léta a mírné vlhké zimy (Hurrell 1995). Jako datový podklad jsem použil zdroj http://www.cgd.ucar.edu/cas/jhurrell. Pro vyjádření biomasy jsem použil index NDVI (Normalizovaný diferenční vegetační index), který pozitivně koreluje s biomasou, primární produktivitou a listovou plochou. Jako datový podklad jsem použil zdroj http://earthobservatory.nasa.gov/GlobalMaps.



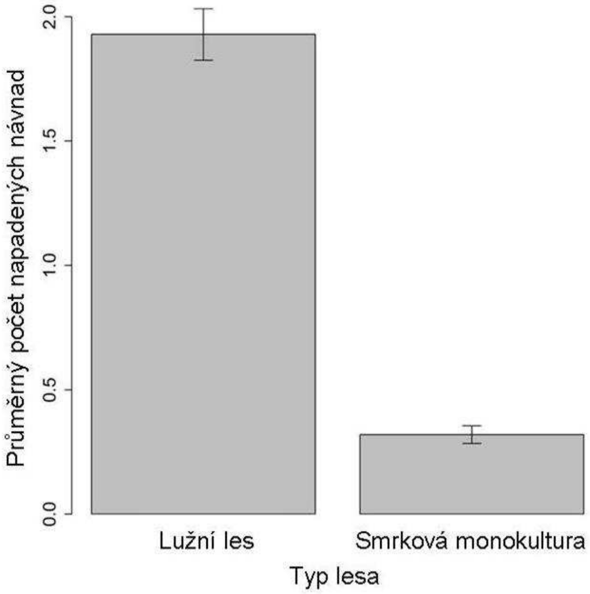
Obr. 2. Proporce napadených návnad v závislosti na roce a mikro-stanovišti. Krabicový graf znázorňuje hodnotu mediánu, hranice krabice představují mezikvartilový interval a extrémní hodnoty jsou zobrazeny v podobě koncových úseček.

Diskuze a výsledky vlastních výzkumů:

1. Rozložení predace v různých patrech lesa

Řada prací poukazuje na průkazné rozdíly v predačním tlaku na herbivorní hmyz mezi jednotlivými patry lesa (Weseloh 1988, Jeanne 1979, Olson 1992). Studie z tropického deštného lesa ukazují, že největší míra predace je soustředěna do horních pater lesa tzv. „canopy“ (Jeanne 1979, Olson 1992). Naopak nejmenšímu nebezpečí čelil hmyz na listech podrostové vegetace (Jeanne 1979, Olson 1992). V temperátních ekosystémech bylo však nejvyšší riziko napadení zjištěno na zemi v lesním opadu (Weseloh 1988, Jeanne 1979). Stejný trend v predačním tlaku jsem zaznamenal i v mém experimentu (Obr. 1.) (A). Jedním z možných důvodů rozdílně situované predace v tropickém a temperátním ekosystému by mohla být distribuce a tvorba rostlinné a živočišné biomasy (Van Bael et al. 2003). Vzhledem k nedostatku světla v podrostu je v tropickém deštném lese významná část produkce rostlinné biomasy soustředěna do vyšších lesních pater (Lowman 1995, Basset et al. 2003, Van Bael et al. 2003). Tento gradient odráží i distribuce herbivorního hmyzu. Ten pro svoji aktivitu také vyhledává nejvyšší lesní patra, protože je zde soustředěna tvorba mladých listů, které jsou na základě nižšího obsahu toxických sekundárních metabolitů a taninů preferovanou potravou (Basset 1994, Coley & Barone 1996, Basset et al. 2001, Basset et al. 2003, Van Bael et al. 2003). V temperátních ekosystémech je tvorba rostlinné biomasy rovnoměrněji rozdělena mezi podrostem a korunovým patrem, proto se aktivita herbivorního hmyzu tak intenzivně nesoustředí do nejvyšších pater lesa (Basset 1994, Coley & Barone 1996, Dyer & Coley 2002). Biomasa členovců je v temperátu spíše soustředěna do půdy a lesního opadu (Preisser et al. 1998, Basset et al. 2003). Dalším faktorem, který by mohl ovlivnit aktivitu predátorů, jsou abiotické podmínky prostředí, které jsou vzhledem k sezónní ztrátě olistění korunového patra v temperátu, stabilnější v rovníkových oblastech. (Lowman 1995, Basset et al. 1992, Preisser et al. 1998).

Výsledky měření predačního tlaku v různých patrech lesa mohou být ovlivněny poměrem mezi abundancí predátora a kořisti. Předchozí studie rovněž potvrdily, že různé gildy herbivorního hmyzu dosahovaly svého populačního maxima v různých obdobích během roku (Southwood et al. 2004, Stork & Hammond 2012). Southwood et al. (2005) zjistil, že některá společenstva členovců, vyskytujících se v korunovém patře, vykazují průkazný trend v počtech jedinců během vegetační sezóny. Různé rozložení diverzity a druhového složení společenstev podél vertikálního gradientu (patrovitosti) bylo zjištěno např. pro saproxylický hmyz nebo v rámci řádu Hymenoptera (Vance et al. 2007, Bouget et al. 2011). Fichter (1939) ve své práci zaznamenal nejnižší abundancí organizmů ve výšce 1-3 m nad zemí. Experimenty zahrnuté v Příloze A probíhaly v průběhu celé vegetační sezóny, od dubna do října po dobu pěti let. Časový interval této délky by měl odstranit možné zkreslení výsledků náhodnými časovými fluktuacemi v abundanci kořisti. Trend v rozložení predace mezi patry



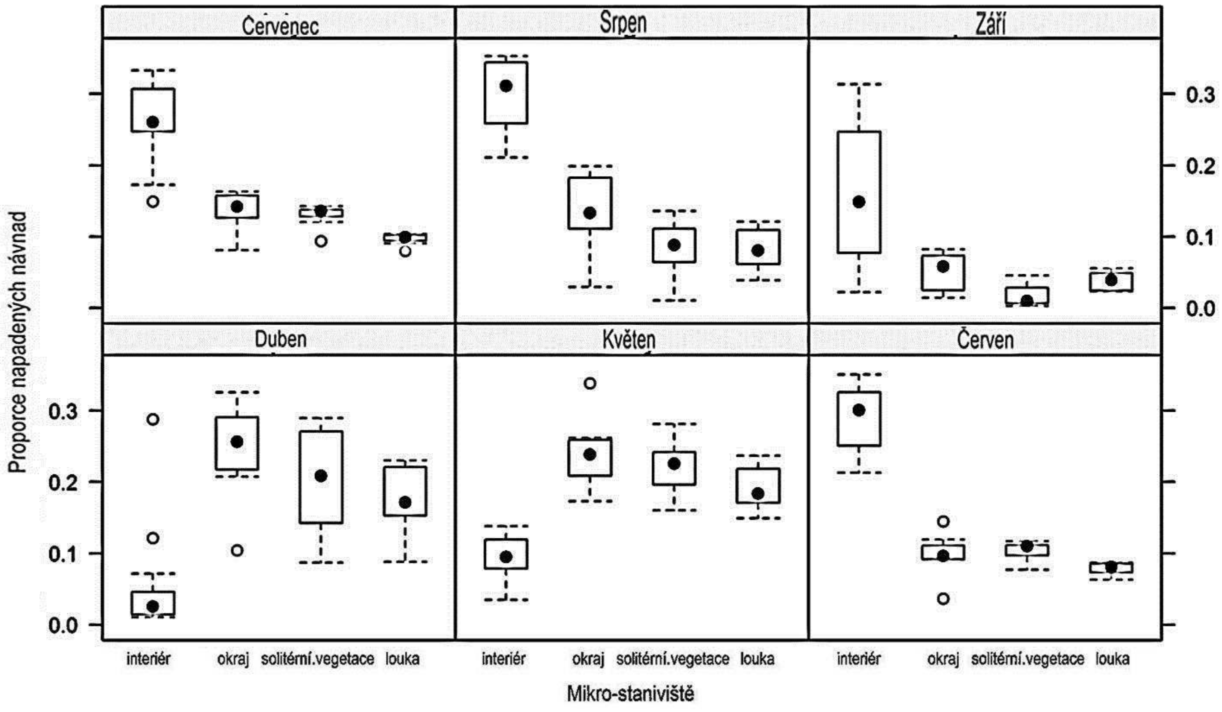
Obr. 3. Rozdíl v průměrném počtu napadených návnad mezi smrkovou monokulturou a lužním lesem. Chybové úsečky znázorňují střední chybu průměru.

lesa zůstával ve všech letech stejný (Obr. 2.).

V Příloze E se věnuji rozložení predačního tlaku mezi lesními patry ve smrkové monokultuře. Tyto lesní kultury mají nižší obsah živin a menší tvorbu organické biomasy než lesy lužních ekosystémů. Celkový počet napadených návnad byl vyšší v lužním lese ($P<0.01$, $F_{1,1045} = 189.25$) (Obr. 3.). Tento výsledek by potvrzoval hypotézu Oksanena et al. (1981), který uvádí, že predátoři kontrolují abundanci herbivorů jen v ekosystémech, které disponují dostatečnou primární produktivitou. Tomu by nasvědčovalo i časté přemnožení kůrovců a jiných škůdců v monokulturních hospodářských lesích. Ve smrkové monokultuře se predace soustředila do mechových polštářů, na rozdíl od lužních lesů, kde byla nejvyšší aktivita predátorů v lesní hrabance (A, E). Ta je ve smrkových monokulturách kompaktní, na živiny chudé mikro-stanoviště, které je těžko prostupné pro epigeické predátory. Mechové polštáře, které poskytují dostatečnou vlhkost, množství úkrytů a potravy pro predátory i herbivory, mohou sloužit jako vhodné mikro-stanoviště pro jejich aktivitu.

2. Trend v aktivitě predátorů v závislosti na hustotě vegetačního zápoje

Většina studií, zabývajících se vlivem gradientu v lesním zápoji na predátory, používá metodu zemních pastí, která se *apriori* zaměřuje pouze na epigeické organizmy (Greenslade



Obr. 4. Proporce napadených návnad mezi lesními a nelesními stanovišti s různou hustotou zápoje během celého vegetačního období. Krabicový graf znázorňuje hodnotu mediánu, hranice krabice představují mezi-kvartilový interval a extrémní hodnoty jsou zobrazeny v podobě koncových úseček a koleček.

1964, Chapman et al 1999, Halaj et al. 2008). Výsledkem takových studií bylo ve většině případů zjištění, že hustota vegetace pozitivně koreluje s množstvím a aktivitou epigeických predátorů. Experimenty měřící relativní predační tlak pomocí návnad zjistily průkazný rozdíl v napadení herbivorů mezi interiérem a okrajem lesa jen u některých predátorů (Lichtenberg & Lichtenberg 2003). V Příloze B se zaměřuji na kvantifikaci míry predace pro všechny skupiny hmyzích predátorů. Dosavadní studie zaměřené na vztah mezi predátory a hustotou vegetačního zápoje, byly prováděny pouze v lesních ekosystémech, aniž by si autoři kladli za cíl analyzovat tentýž vztah v nelesních prostředích (Greenslade 1964, Weseloh 1988,

Chapman et al 1999, Lichtenberg & Lichtenberg 2003, Halaj et al. 2008). Moje hypotéza, že predátoři budou více napadat návnady umístěné v prostředí s hustějším vegetačním patrem, jak v lesních, tak nelesních prostředích, byla založena na pozitivním vlivu heterogenity a komplexnosti prostředí na přežívání jedinců (De Vasconcelos 1990, Barbosa & Fernandes 2003, Franklin & Van Pelt 2004, Langelloto & Denno 2004). V okrajových a fragmentovaných lesních biotopech je menší množství nakumulovaného listí a dalšího rostlinného opadu než v lesních interiérech (Franklin & Van Pelt 2004, Halaj et al. 2008). Je známo, že korunové patro hraje důležitou roli ve vytváření prostorové heterogenity a stability lesního opadu (Kara et al. 2008). Z toho důvodu bude role korunového patra, resp. jeho schopnosti vytvářet biomasu, stěžejní i pro půdní biotu, vázanou na povrchové vrstvy rozkládajícího se rostlinného materiálu. (Zhao et al. 2011). Zásadní vliv na strukturu a bohatost hmyzích populací má totiž i mocnost vrstvy spadaného listí (Jabin et al. 2004). Její vertikální stratifikace dovoluje koexistenci většího množství predátorů, z důvodu snížené intragildové predace, kanibalizmu a dostupnosti alternativních zdrojů potravy (O`Neal et al. 2005, Theunis et al. 2005). Spadané listí nadto vytváří vhodné mikroklima s určitou vlhkostí a teplotou, které jsou důležité pro vývoj, vývin a přezimování některých druhů predátorů (De Vasconcelos 1990, Langelloto & Denno 2004, Theunis et al. 2005). V souladu s hypotézou jsem v lesním prostředí zaznamenal větší míru predace v interiéru lesa než na jeho okraji (B).

Tabulka č. 1. Výsledky analýzy deviance faktorů ovlivňujících proporci napadených návnad. Kombinace a pořadí faktorů bylo vybráno pomocí step wise selekce na základě nejmenšího AIC. Jako vysvětlující faktory byly použity pouze abiotické podmínky prostředí

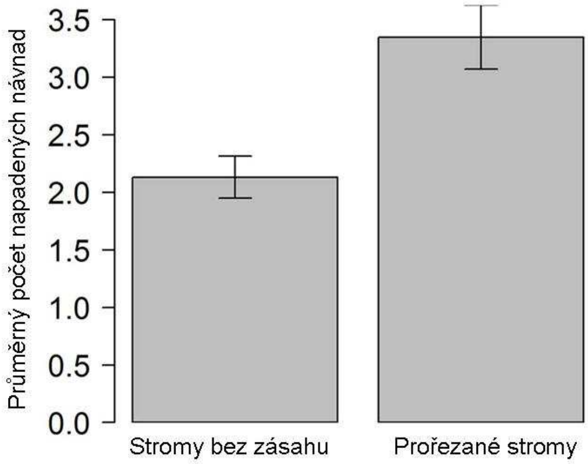
	Df.	Deviance	Residualni Df.	Residualni Deviance	F	P
NULL			1967	362.81		
poly(teplota, 2)	2	27.7768	1965	335.03	60.4012	<0.001
teplota v zimě	1	3.3292	1964	331.70	14.4786	<0.001
poly(NDVI,2)	2	3.9164	1962	327.78	8.5163	<0.001
poly(srážky,3)	3	4.5121	1959	323.27	6.5411	<0.001

Na druhé straně jsem nezjistil průkazný rozdíl v napadení návnad mezi nelesními biotopy s rozdílnou hustotou korunového zápoje (B). Podobná míra predace mezi ploškami s vyvinutým korunovým zápojem (solitérní stromy) a ploškami bez korunového zápoje v nelesních prostředích naznačuje, že koruny solitérních stromů nemají dostatečný dopad na společenstva predátorů, jako je tomu v interiérech lesa (Obr. 4.). Tento průkazný trend větší predace v lesních interiérech podporuje hypotézu, že abundance a aktivita predátorů se snižuje s rostoucí fragmentací a izolovaností lesních ekosystémů (Kruess & Tscharntke 1994, Zabel & Tscharntke 1998).

3. Vliv architektury koruny stromu na míru predace

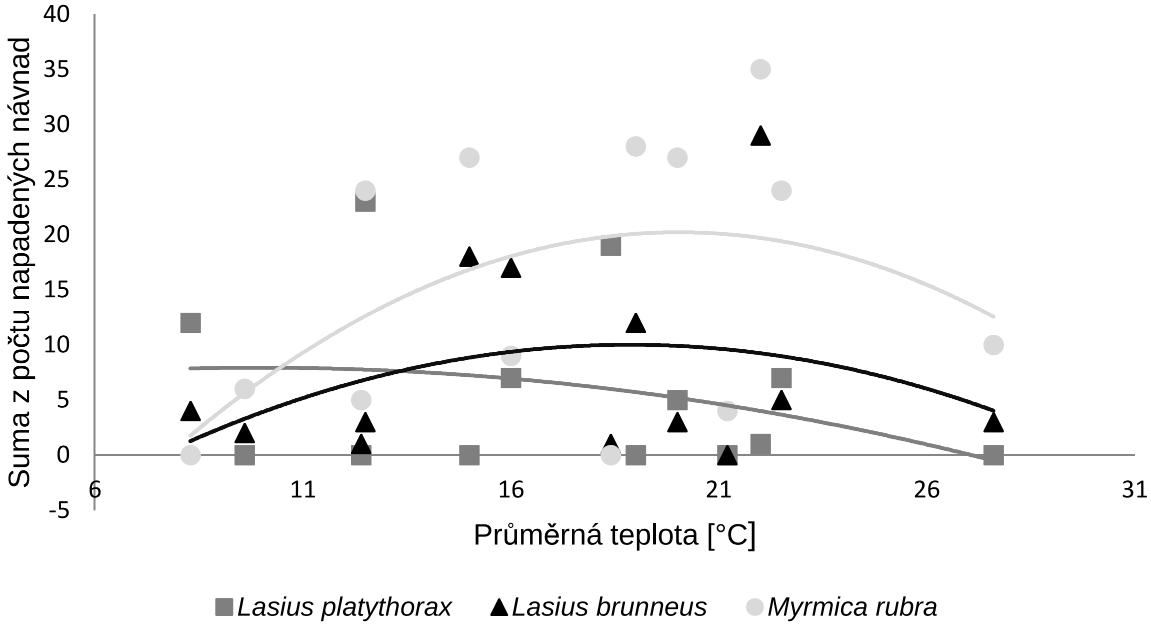
Jednotlivé rostliny se mohou lišit v architektonické komplexitě, která je determinována dvěma hlavními faktory. Prvním je velikost rostliny (rozložení rostliny v prostoru), druhou pak diverzita rostlinných částí (počet odlišných částí rostlinného těla, jako jsou listy, řapíky, stonky, pupeny nebo plody) (Price et al. 2011). Uvedené charakteristiky společně definují prostředí, na kterém se odehrávají interakce mezi predátory a jejich kořistí.

Populační dynamika herbivorního hmyzu může být někdy více ovlivněna prostorovou komplexitou než kvalitou rostlinné potravy (Van Valen 1973, Lawton 1983, Halaj et al. 2000a). Jedním z důvodů je architektura rostliny, která do značné míry ovlivňuje schopnost



Obr. 5. Průměrný počet napadených návnad na stromech ponechaných bez zásahu a s prořezanou korunou. Chybové úsečky znázorňují střední chybu průměru.

predátora ulovit kořist (Tschanz et al. 2005, Riihimaki et al. 2006). Takto heterogenní habitaty budou snižovat antagonistické interakce mezi predátory a umožní jim zisk dostatku potravy a zároveň dostatečně stabilní prostředí, umožňující rozvoj početných populací (Finke & Denno 2006, Rickers et al. 2006). Poslední výzkumy naznačují, že nepřímé interakce, zprostředkované přes rostlinu nebo predátora, dominantně ovlivňují naprostou většinu interakcí mezi herbivory (Kaplan & Denno 2007). Na druhé straně, velké rostliny se složitou strukturou často podporují velkou hustotu herbivorního hmyzu, protože jim poskytují velkou diverzitu míst pro: a) rozmnožování; b) shánění potravy; c) přezimování; a d) ukrytí se před predátorem (Denno 1995). Přestože rostliny hrají tak důležitou roli ve vztahu predátor × kořist, problematice vlivu struktury rostliny na predátory se věnuje překvapivě málo prací (Halaj et al. 2000a, Riihimaki et al. 2006). Zůstává také nezodpovězena otázka, zda staré, strukturně heterogenní stromy mohou způsobovat lokální přemnožení škůdců. Výsledky posledních studií překvapivě naznačují, že zvýšená komplexita zvyšující zákonitě dobu nalezení kořisti nemá negativní vliv na aktivně se pohybující predátory, ale jen na ty predátory, kteří číhají na potravu v úkrytu (Riihimaki et al. 2006). Tyto výsledky ale stojí proti předpokládané negativní korelaci mezi efektivitou predátorů a rostlinnou komplexností (Gingras et al.2002, Casas & Djemai 2002, Meiners & Obermaier 2004). Casas & Djemai



Obr. 6. Závislost mezi množstvím napadených návnad a mezi průměrnou denní teplotou. Regrese pro druh: a) *Lasius platythorax*: $y= 0.53x-0.027x^2+5.24$, $F_{2,477}= 1.11$, $P= 0.33$, $R^2= 0.09$; b) *Lasius brunneus*: $y=2.95x-0.07x^2-17.85$, $F_{2,477}= 0.91$, $P= 0.40$, $R^2= 0.10$; c) *Myrmica rubra*: $5.36x-0.13x^2-33.54$, $F_{2,477}= 4.12$, $P= 0.016$, $R^2= 0.24$.

(2002) uvádějí, že prostorová komplexita rostliny bude zvětšovat dobu, po kterou predátor hledá kořist. Efektivita predace má být negativně ovlivněna také nahloučenou distribucí kořisti v prostoru, která ještě může zvýšit čas nalezení potravy, a tím zapříčinit, že predátor dříve opustí dané stanoviště nebo se mu zcela vyhne (Casas & Djemai 2002). V Příloze D jsem došel k opačnému závěru než Riihimaki et al. (2006). Zjistil jsem, že herbivorní hmyz vyskytující se na rostlině s jednodušší strukturou, je ve větším nebezpečí před predátory aktivně vyhledávajícími kořist, než by byl na komplexnější rostlině (Obr. 5.). Výsledky ukazují průkazně větší míru predace na stromech s jednodušší strukturou (Obr. 5.) (D). To je v souladu s hypotézou, že větší heterogenita prostoru bude snižovat efektivitu predátora (Casas & Djemai 2002). Z výsledků také vyplývá, že napadení návnad mělo negativně binomické rozdělení (C). To by odpovídalo ostrůvkovitému rozložení míry predace v prostoru (C, D). Tuto hypotézu podporuje i způsob lovu dominantních predátorů herbivorního hmyzu (ptáci a sociální hmyz), kteří zvyšují svojí aktivitu v okolí své kořisti (Taylor & Taylor 1977, Tinbergen 1960, Bell 1991). Rozdílné výsledky mého výzkumu a studie Riihimakiho et al. (2006), pravděpodobně vycházejí z metodických odlišností měření predačního tlaku v obou pracích. Riihimaki et al. (2006) použil návnady, které zůstávaly připevněny na stejném místě po dlouhou dobu. Sociální hmyz (mravenci, vosy) se proto zřejmě naučil využívat tato místa častěji k vyhledávání potravy (Bell 1991, Nicolis & Deneubourg 1999). Také ptáci si mohou vyvinout tzv. „search image“ a mohou upřednostňovat nejčastější typ potravy na dané lokalitě (Tinbergen 1960, Church et al. 1997).

Uvedené okolnosti mohly uměle zvýšit efektivitu těchto predátorů a snížit tak efekt komplexity rostliny. V mém výzkumu byly návnady ponechány na jednom místě 30 min a

Tabulka č. 2. Výsledky analýzy deviance faktorů ovlivňujících proporci napadených návnad. Kombinace a pořadí faktorů bylo vybráno pomocí step wise selekce na základě nejmenšího AIC. Jako vysvětlující faktory byly použity abiotické podmínky prostředí spolu s charakteristikami stanoviště.

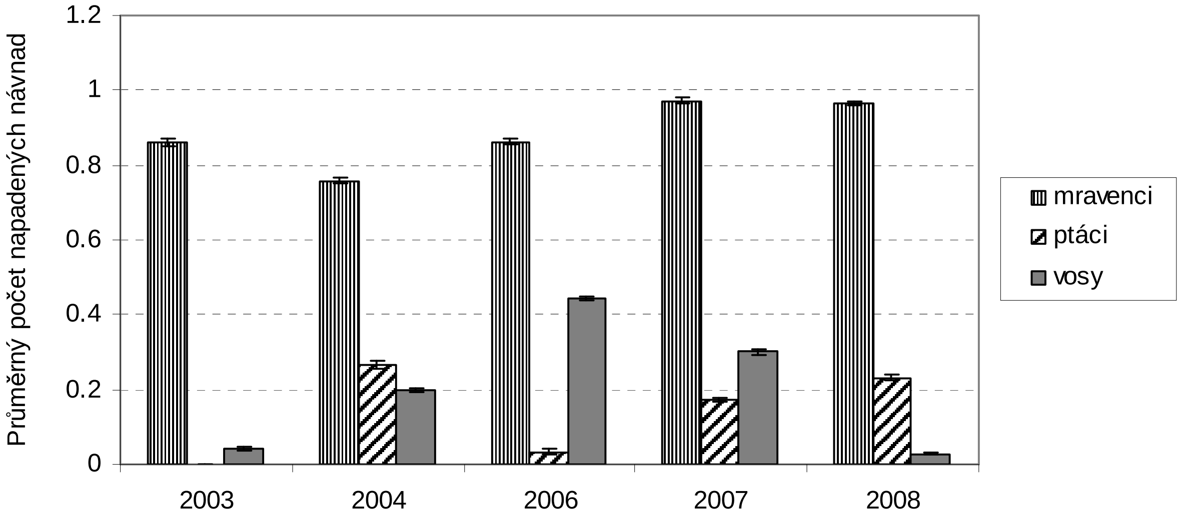
	Df.	Deviance	Residualni Df.	Residualni Deviance	F	P
NULL			1967	362.81		
lesní patra	2	62.830	1965	299.98	153.59	<0.001
poly(vegetační sezóna,2)	3	26.770	1962	273.21	43.62	<0.001
poly(teplota,2)	2	8.436	1960	264.77	20.62	<0.001
zimní teplota	1	3.933	1956	259.37	19.23	<0.001
poly(NDVI,2)	2	2.076	1954	257.29	5.07	0.006
hustota zápoje	1	0.863	1953	256.43	4.22	0.04

poté bylo spočítáno množství napadených návnad. Tato metodika by měla pro sociální hmyz i pro ptáky ztížit možnost naučit se vyhledávat kořist v místě experimentu.

4. Role druhového složení predátorů

Variabilita v predačním tlaku pravděpodobně je značně ovlivněna aktivitou dominantních predátorů. V pětiletém období našeho výzkumu byli nejaktivnějšími predátory bez výjimky mravenci (61%, N=1935), následováni vosami (11%, N=358), ptáky (10%, N=325), střevlíky (7%, N= 237) a sekáči (4%, N= 118). Naopak nejméně častými predátory byli pavouci (1%, N= 33), drabčíci (1%, N= 28), srpice (1%, N= 24) a celkově nejnižší počet návnad byl napaden plošticemi (1%, N= 20) (A, B, C, D). Z uvedených skupin byli na úroveň jednotlivých druhů determinováni pouze mravenci, jež byli daleko nejvýznamnější skupinou predátorů. Největší podíl napadených návnad mezi mravenci byl zjištěn u druhu *Myrmica rubra* (54%), významným mravenčím predátorem byl také *Lasius brunneus* (26%), nejméně napadení způsobil druh *Lasius platythorax* (20%).

Ordinační analýza CCA ukázala, že různé druhy predátorů směřují svou aktivitu do různých lesních pater (A). Pozorování v Příloze (A) ukazují, že největší predace byla naměřena v lesním opadu v interiéru lesa. Stejný trend v aktivitě vykazovali také mravenci, kteří si v temperátním pásmu staví svoje hnízda zpravidla na zemi nebo pod ní (A). Naopak v tropech si mravenci staví hnízda často v korunách stromů, které jim zde poskytují stabilnější prostředí než v temperátním ekosystému (Brühl et al. 1998, Floren et al. 2002). Tato rozdílná

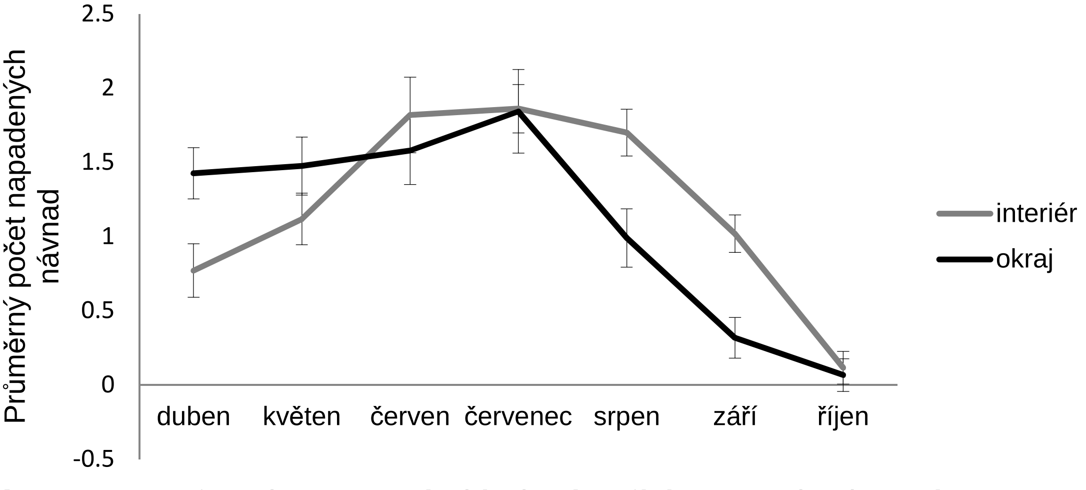


Obr. 7. Rozložení predačního tlaku dominantních predátorů v jednotlivých letech. Chybové úsečky znázorňují střední chybu průměru.

vertikální stratifikace v tvorbě hnízd mezi temperátním a tropickým deštným lesem může být příčinou rozdílného trendu v predačním tlaku v různých patrech lesa (Olson 1992, Floren et al. 2002, Davidson et al. 2003).

Vysvětlení vertikální stratifikace v predačním tlaku pomocí ekologických nároků jednotlivých druhů predátorů lze dobře dokumentovat rozložením predační aktivity v rámci taxonu mravenců (A). Aktivita druhu *Myrmica rubra* byla situována do lesního opadu (A). Tento druh má tendenci se v něm pohybovat, protože zde nachází většinu své potravy a také získává cukernou šťávu ze mšic, žijících na kořenech stromů (Wilson 1971, Depa & Wojciechowski 2008). Naopak *Lasius bruneus* soustřeďoval svou aktivitu podél kmenů (A). Na rozdíl od předchozího druhu si tento mravenec zpravidla nezakládá hnízda u země, ale staví je především nad zemí, v mrtvém dřevě nebo pod kůrou stromů (Pisarski & Vepsäläinen 1988). Konečně *Lasius platythorax* dává přednost hnízdění v zetlelém dřevě. Z toho důvodu tento druh zřejmě nevykazoval zřetelnou preferenci konkrétního lesního patra (A) (Savolainen & Vepsäläinen 1988). Dále byl u taxonu mravenců naměřen pozitivní trend v aktivitě směrem k interiéru lesa (B). Mravenci jsou většinou senzitivní k vyšším teplotám a preferují vlhčí a zastíněné habitaty (Holec et al. 2006) (Obr. 6.). Ve svém výzkumu jsem zaznamenal stabilní predaci, způsobenou mravenci během celé vegetační sezóny (Obr. 7.). Mravenčí predace dosahovala maximálních hodnot ve dvou obdobích vegetační sezóny. Prvním vrcholem aktivity mravenců byl měsíc květen, druhé maximum v predační aktivitě nastávalo v červenci. Intenzívní predace na začátku vegetační sezóny je vysvětlována velkými nároky na nutričně bohatou potravu na začátku léta, kdy mravenci vychovávají pohlavní jedince (Carroll & Janzen 1973, Puntilla et al. 2004).

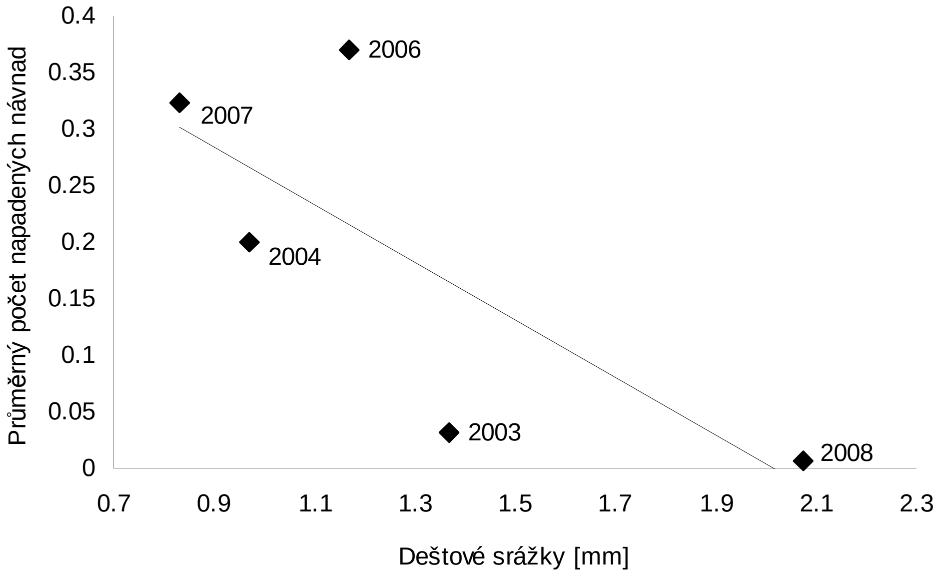
Zajímavá je vyšší míra predace na začátku vegetační sezóny na listech v lesních okrajích ve



Obr. 8. Změny v průměrném počtu napadených návnad v průběhu vegetační sezóny na okraji a v interiéru lesa. Chybové úsečky znázorňují střední chybu průměru.

srovnání s interiérem lesa (Obr. 8.). Důvodem může být výskyt herbivorního hmyzu, konzumujícího v této době převážně listy na okrajích nebo ve vrcholových partiích stromů, které zde na začátku vegetační sezóny začínají rašit (Kikuzawa 1983). Důležitou roli hraje také kvalita listů, která v průběhu vegetační sezóny nejdříve klesá na okrajích a v nejvyšších patrech lesa (Murakami et al. 2005). Posílení obranných vlastností listů způsobuje změny v abundanci a distribuci herbivorního hmyzu, který migruje do vegetace podrostu (Murakami 1998, Murakami et al. 2005). Dalším faktorem ovlivňujícím aktivitu predátorů a herbivorů je pravděpodobně teplota, která na otevřených stanovištích dosahuje vyšších hodnot (MacGarvin et al. 1986, Heithecker & Halpern 2007) (B). Celkově nižší predace mravenců na listech ve srovnání s lesní hrabankou může souviset s faktem, že v korunách stromů se mravenci živí hlavně cukrovou šťávou mšic (Carroll & Janzen 1973, Heads 1986, Mahdi & Whittaker 1993, Richard et al. 2001). Ostatní epigeičtí predátoři, jako střevlíci, drabčíci nebo sekáči, preferovali v lesním ekosystému opad (A). Mimo lesní stanoviště dominovali v počtu napadených návnad nad mravenci pavouci rodu *Pardosa* a střevlíci rodu *Amara* a *Poecilus* (B). Tyto zmiňované rody jsou aktivní za dne a preferují prosluněné a otevřené habitaty (Niemelä et al. 1993).

Druhou nejpočetnější skupinou predátorů po mravencích byly vosy (A). Naše výsledky tak odpovídají řadě studií, označujících vosy za jedny z nejdůležitějších predátorů herbivorního hmyzu (Stamp & Bowers 1988, Steward et al. 1988, Stamp & Bowers 1993). Vosy svoji

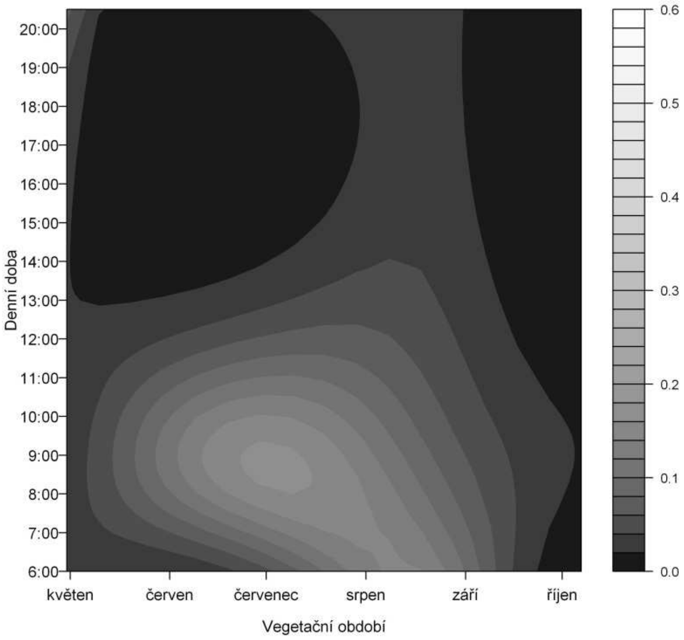


Obr. 9. Vztah mezi průměrnými srážkami v měsících dubnu a květnu a mezi průměrem v napadení návnad vosami v různých letech (y=-0.25x +0.51, R^2= 0.51)

aktivitu směřovaly zejména na listy a kmeny na okrajích lesního habitatu, pravděpodobně v důsledku vyšších teplot, které coby ektotermní živočichové potřebují pro snadný let (A) (Lichtenber & Lichtenberg 2003). Na rozdíl od mravenců, vykazoval predační tlak vos velkou variabilitu mezi roky (Obr. 7.). Tato fluktuace v početnosti byla pravděpodobně zapříčiněna vlivem rozdílných srážkových úhrnů během dubna a května v jednotlivých letech, kdy si vosy zakládají hnízda a jsou zranitelné ke změnám počasí (Obr. 9.) (Madden 1981).

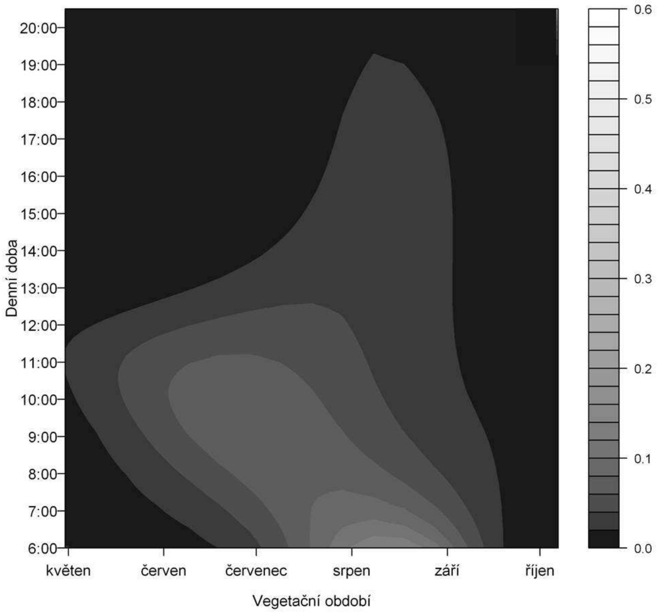
Interiér lesa

Kmen



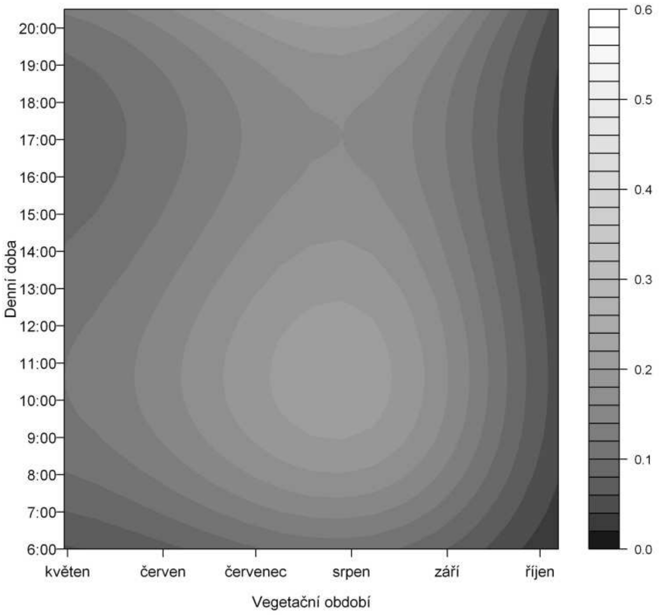
Obr. 10. Proporce napadených návnad na kmeni v interiéru lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,345}$=6.11, P<0.001, R^2=0.06. Pro faktor denní doba: $F_{3,345}$=4.78, P=0.002, R^2=0.03.

List



Obr. 11. Proporce napadených návnad na listě v interiéru lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,345}$=3.51, P=0.015, R^2=0.05. Pro faktor denní doba: $F_{3,345}$=1.95, P=0.12, R^2=0.02.

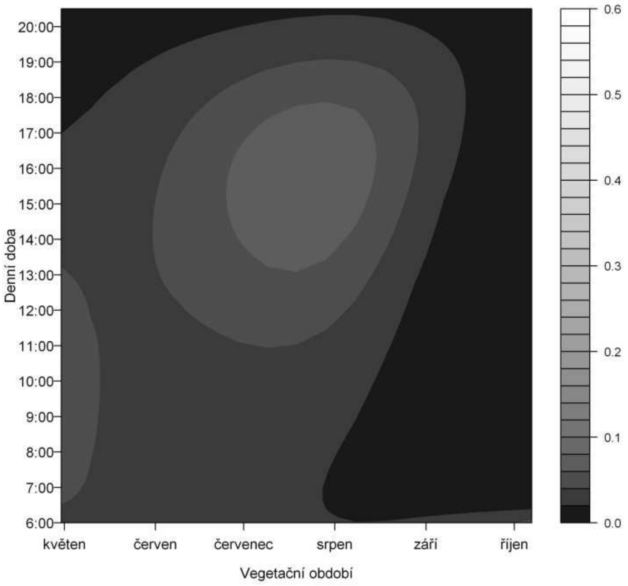
Zem



Obr. 12. Proporce napadených návnad na zemi v interiéru lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,345}$=13.21, P<0.001, R^2=0.09. Pro faktor denní doba: $F_{3,345}$=2.00, P=0.11, R^2=0.008.

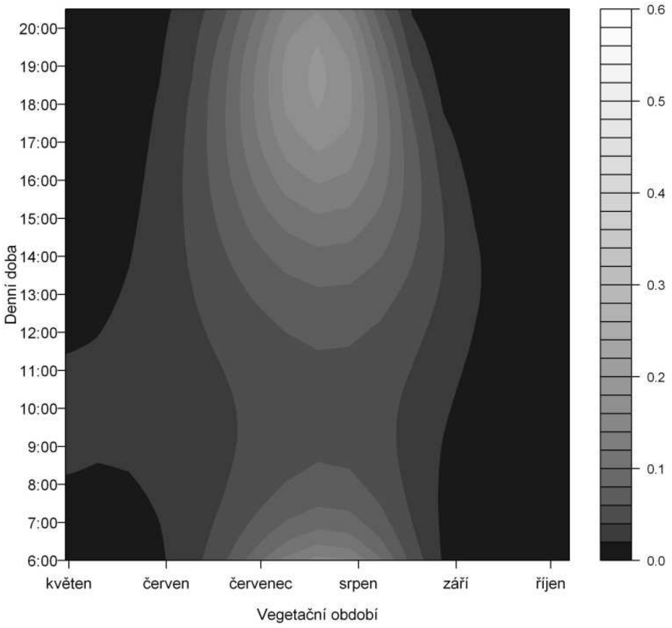
Okraj lesa

Kmen



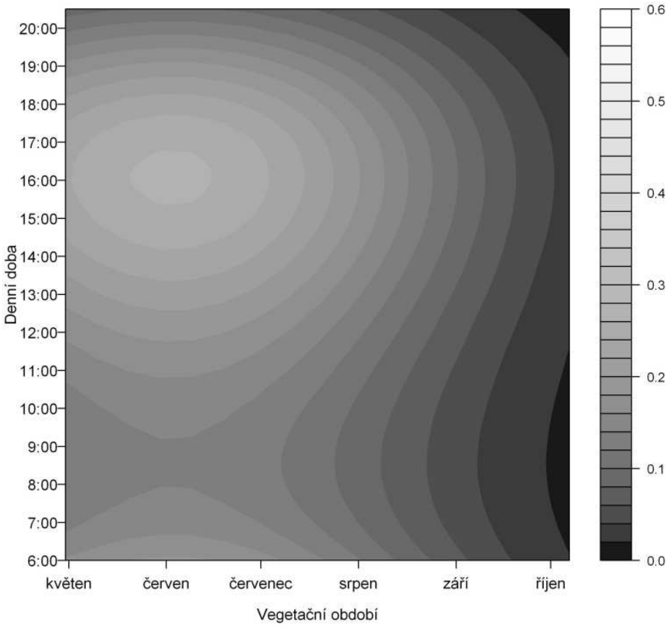
Obr. 13. Proporce napadených návnad na kmeni na okraji lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,303}$=6.90, P<0.001, R^2=0.11. Pro faktor denní doba: $F_{3,303}$=0.83, P=0.47, R^2=0.01.

List

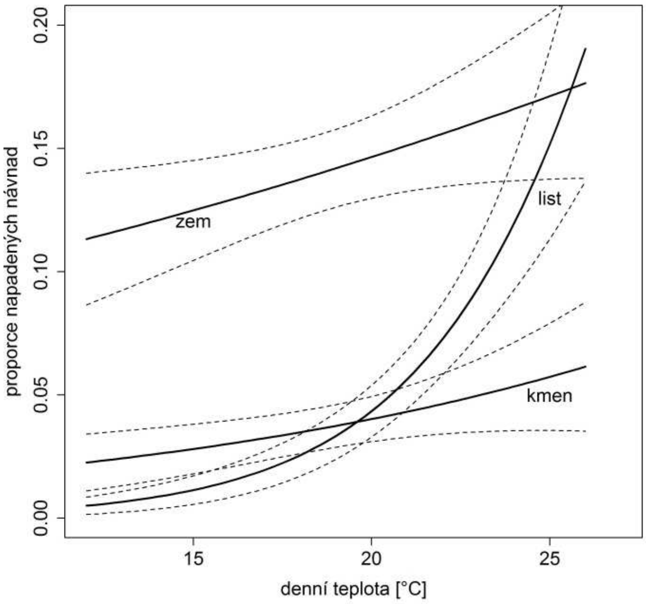


Obr. 14. Proporce napadených návnad na listě na okraji lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,303}$=12.32, P<0.001, R^2=0.25. Pro faktor denní doba: $F_{3,303}$=3.53, P=0.01, R^2=0.07.

Zem



Obr. 15. Proporce napadených návnad na zemi na okraji lesa. Výsledky analýzy deviance jsou: Pro faktor vegetační období: $F_{3,303}$=20.93, P<0.001, R^2=0.18. Pro faktor denní doba: $F_{3,303}$=4.41, P=0.004, R^2=0.04.



Obr. 16. Závislost proporce napadených návnad na teplotě ve studovaných mikro-stanovištích. Nejlépe fitující logistické regrese jsou: Pro faktor zem: $y= 1/[1+e^{(1.98x-2.07)}]$, $F_{1,66}=6.5$, $P= 0.02$, $R^2= 0.28$. Pro faktor kmen: $y= 1/[1+e^{(1.88x-2.07)}]$, $F_{1,66}= 5.8$, $P= 0.03$, $R^2=0.12$, Pro faktor list: $y= 1/[1+e^{(9.88x-4.22)}]$, $F_{1,66}=26.2$, $P<0.001$, $R^2=0.65$. Přerušované čáry znázorňují standardní chybu.

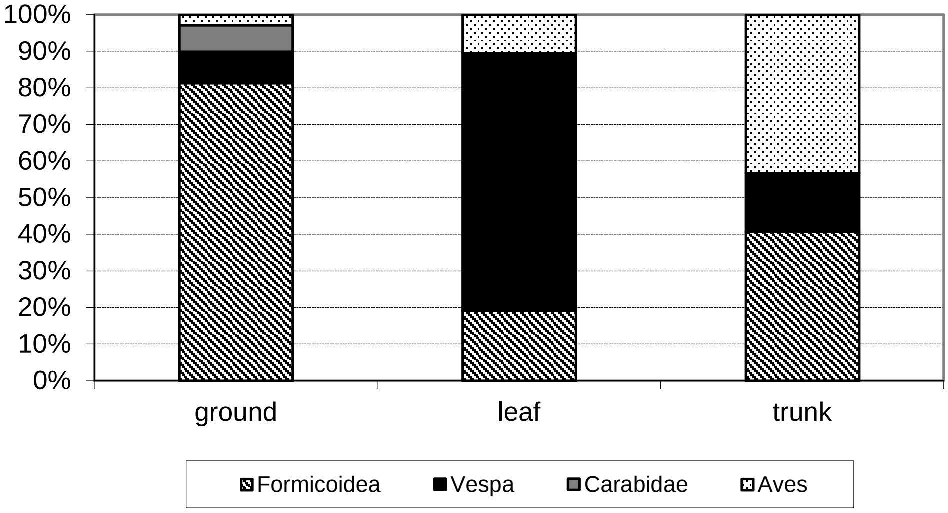
Většina napadení návnad vosami byla zaznamenána během měsíců červenece a září. Důvodem je charakteristický průběh životního cyklu této skupiny sociálního hmyzu, která dosahuje maxima populačních početností v průběhu července a srpna. Počet napadení návnad na listech způsobený vosami se v okrajových částech lesa vyrovnal množství návnad napadených mravenci na zemi (A). Z toho důvodu nebyl v lesních okrajích naměřen průkazný rozdíl v počtu napadených návnad mezi těmito mikro-stanovišti (A). Z obratlovců byly návnady napadány nejčastěji ptáky, kteří preferovali návnady umístěné na kmeni (A). Ptáci zkonzumovali v porovnání s hmyzími predátory průkazně méně návnad, protože preferují tento typ potravy jenom po krátkou dobu hnízdění a vyvádění mláďat (Tinbergen 1960, Royama 1970). To potvrdily i výsledky, které ukázaly, že hlavní napadení návnad ptáky probíhalo na začátku vegetační sezony (A). Na rozdíl od ostatních studií (Skoczylas et al. 2007, Barbaro et al. 2012), ve kterých ptačí predace rostla s lesní fragmentací, vzrůstal v tomto výzkumu počet ptáky napadených návnad směrem do interiéru lesa. Opačný trend, zjištěný ve výše zmiňovaných pracích, může být dán: a) jejich kratší dobou trvání experimentu (1 vegetační období); b) použitím nevhodných návnad (plastové nebo hliněné napodobeniny housenek); c) ponecháním návnad po delší dobu na stejném místě (ptáci se mohli naučit využívat některá místa častěji k vyhledávání potravy) (Tinbergen 1960, Church et al. 1997).

Z předchozích odstavců vyplývá, že v interiéru lesa většina predátorů lovila svou kořist dominantně na zemi v lesním opadu (A, B). Druhé mikro-stanoviště v interiéru lesa s největším počtem napadených návnad byl kmen, kde byli dominantními predátory ptáci (A). Na okrajích lesních porostů byly návnady nejvíce napadány nejenom mravenci, ale také vosami. Přesto predační tlak ostatních druhů predátorů nebyl dostatečný, aby změnil výsledný pattern vytvořený predačním tlakem mravenců, kteří svou aktivitu soustředili do opadu interiéru lesa (A, B).

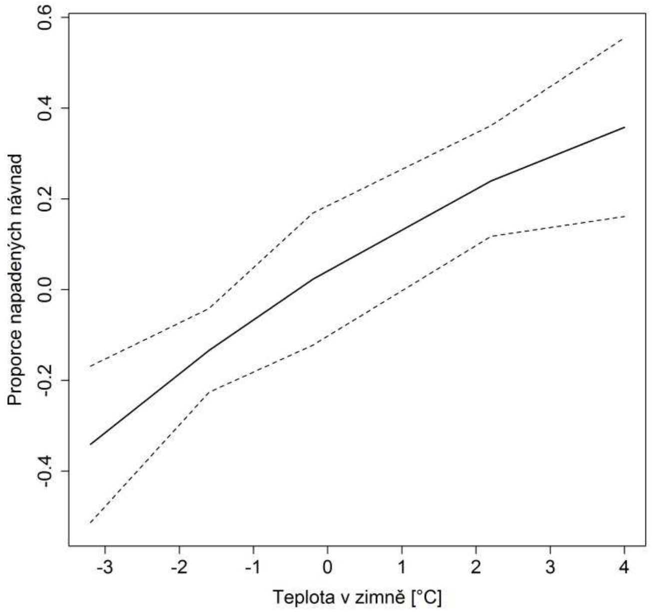
5. Environmentální faktory ovlivňující sezónní a časové změny v predaci

Celá řada autorů uvádí, že predační tlak se mění v čase a v prostoru v závislosti na faktorech prostředí (Floyd 1996, Forkner and Hunter 2000, Stireman III & Singer 2002, Scheirs & De Bruin 2005). Přesto jenom velmi málo prací bylo publikováno se zaměřením na diurnální a sezónní variabilitu v predačním tlaku (Novotny et al. 1999, Lichtenberg & Lichtenberg 2003, Berger & Wirthe 2004, Remmel et al. 2009). U převážné většiny těchto studií jsou diurnální fluktuace v predaci jen vedlejším výsledkem a jsou studované jen na krátkých časových škálách (maximálně 2. roky).

Aktivita predátorů je ovlivňována různými faktory prostředí (teplota, vlhkost), které jsou variabilní v prostoru a čase. Na základě těchto poznatků jsem předpokládal, že výsledný pattern v predaci bude dán kombinací faktorů prostředí v závislosti na prostorové struktuře



Obr. 17. Proporce dominantních taxonů predátorů v závislosti na daném mikro-stanovišti.

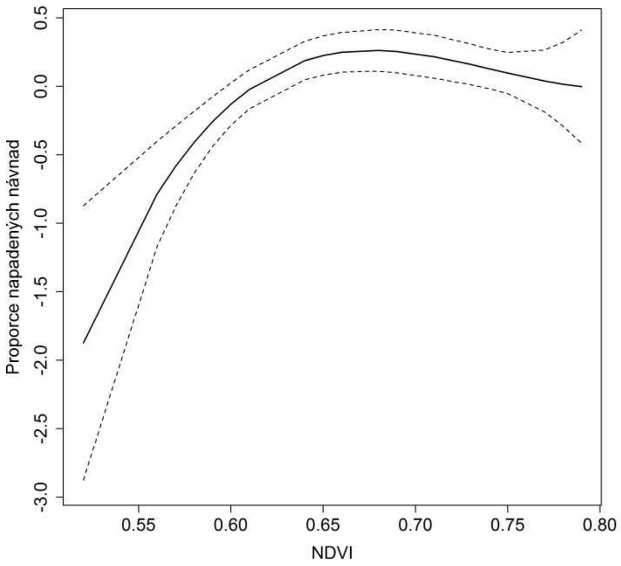


Obr. 18. Vztah mezi proporcí napadených návnad a průměrnou denní teplotou v zimním období. Logistická regrese pro faktor zimní teploty je: $y= 1/[1+e^{(4.6x+7.27x2-2.67)}]$, $F_{2,1965}= 9.73$, $P<0.001$, $R^2=0.013$. Přerušované čáry znázorňují standardní chybu.

habitatu (Stireman III & Singer 2002). Proporce napadených návnad se v tomto výzkumu průkazně měnila během dne a během vegetační sezóny (Obr. 10-15.).

Nejvýznamnějším faktorem prostředí, který ovlivňoval proporci napadených návnad, byla **průměrná denní teplota** okolí (Tabulka č. 1). Predační tlak rostl se vzrůstající teplotou ve všech studovaných mikro-stanovištích (Obr. 16.). Zajímavý průběh měla predace v závislosti na rostoucí teplotě na listě. Na rozdíl od ostatních mikro-stanovišť vykazovala exponenciální růst (Obr. 16.). Tento trend lze na listech zdůvodnit dominantní aktivitou vos (Obr. 17.), čímž je možno vysvětlit také velice malý podíl larev holometabolního hmyzu na listech tropických dřevin (Dyer & Coley 2002, Floren et al. 2002). Silný vliv teploty na míru predace může dokládat, proč je predační tlak tak důležitým faktorem mortality herbivorního hmyzu v tropickém deštném lese (Rabinowitz & Price 1976). Průkazný vliv teploty není překvapivý, protože je obecně pokládán za stěžejní faktor mezi abiotickými vlivy (Xu et al. 1997). Výrazný efekt externí teploty umocňuje fakt, že hmyz není schopen udržovat stálou tělesnou teplotu, a proto je jeho aktivita silně ovlivněna teplotními fluktuacemi (Dobley 1997, Perdikis et al. 1999).

V pořadí druhým faktorem, který nejlépe vysvětloval změny v predaci, byla průměrná denní **teplota v zimním období** (Tabulka č. 1). Nízká teplota v zimě má negativní vliv na přežívání



Obr. 19. Vztah mezi proporcí napadených návnad a NDVI. Logistická regrese pro faktor NDVI je: y= $1/[1+e^{(13.49x-16.58x2-2.73)}]$, $F_{2,1965}=33.29$, $P<0.001$, $R^2=0.04$. Přerušované čáry znázorňují standardní chybu.

hibernujícího hmyzu (Abdullah 1961). Tomu by odpovídala zjištěná pozitivní korelace mezi mírou predace a průměrnou denní teplotou v zimním období (Obr. 18.). Možný negativní efekt v podobě přežívání většího počtu potenciální kořisti, která by „konkurovala“ návnadám se neprojevil.

Dalším faktorem, který průkazně ovlivňoval proporci napadených návnad, bylo množství rostlinné biomasy (měřena prostřednictvím Normalizovaného diferenčního vegetačního indexu **NDVI**). Na Obr. (19.) můžeme vidět kvadratickou závislost mezi faktorem NDVI a proporcí napadených návnad. Množství biomasy může mít pozitivní vliv ve dvou rovinách:

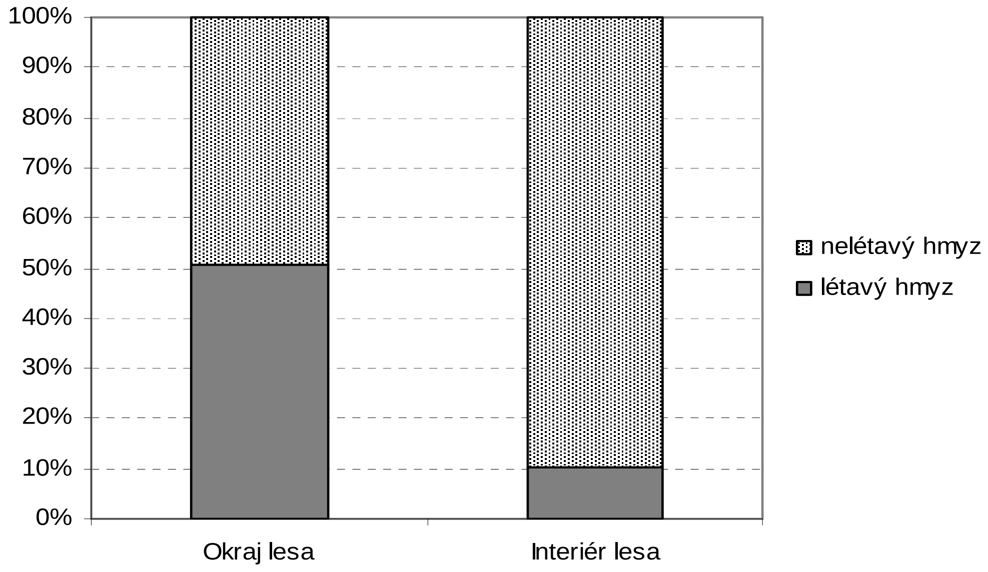
a) větší biomasa koreluje s množstvím vegetace, která vytváří životní prostředí hmyzu;

b) větší biomasa podporuje větší abundanci herbivorů a tedy potenciální kořisti;

(Franklin & Van Pelt 2004, Langelloto & Denno 2004).

Mírný pokles počtu zkonzumovaných návnad může být dán tím, že s větším množstvím biomasy narůstá i množství potenciální kořisti, která „konkurovala“ fixovaným návnadám (Obr. 19.) (Remmel et al. 2009).

Průběh proporce napadení návnad ve vegetační sezoně i během dne se průkazně lišil mezi jednotlivými mikro-stanovišti (list, kmen, zem), stejně jako mezi interiérem a okrajem lesa (Tabulka č. 2). V **opadu interiéru lesa** byla soustředěna největší aktivita predátorů do období července a srpna mezi 10:00 a 11:00 hod. a druhého maxima dosáhla ve večerních



Obr. 20. Proporce létavých a nelétavých predátorů v interiéru a na okraji lesa.

hodinách (Obr. 12.). Maximum napadených návnad v dopoledních hodinách korelovalo s aktivitou mravenců, ve večerních hodinách se k mravencům přidávali také střevlíci. Z obr. (10.) je zřejmé, že návnady umístěné na kmeni byly nejčastěji napadány ve dvou obdobích, a to na rozmezí června a července mezi 8:00 a 9:00 hod. a na přelomu srpna a září kolem 7:00 hod.. Na listech se pohybovalo nejvíce predátorů mezi červnem a červencem v období mezi 9:00 a 10:00 hod. a v ranních a odpoledních hodinách mezi červencem a srpnem (Obr. 11.).

Na **okraji lesa** v opadu dosahovala predace v průběhu vegetační sezóny dvou maxim v červnu, první mezi 16:00-17:00 hod. a druhé maximum nastávalo v ranních hodinách (Obr. 15.). Proporce napadených návnad na kmeni na okraji lesa měla dvě maxima a to na začátku vegetační sezóny (dominantní vliv aktivity ptáků) a v odpoledních hodinách mezi červencem a srpnem (dominantní vliv aktivity mravenců a vos) (Obr. 13.). Predace na listě měla během dne dvě maxima a to v ranních a odpoledních hodinách (Obr. 14.). Tato maxima pravděpodobně byla způsobena aktivitou mravenců a vos. Na rozdíl od výsledků publikovaných v této práci, v Příloze C dosáhla predace na listech tří vrcholů v průběhu vegetační sezóny. Tento nesoulad může být způsoben tím, že v studii uváděné v Příloze C probíhal výzkum jednu sezónu na více druzích dřevin a zároveň bylo napadeno jen malé množství návnad. Proporce napadených návnad měla rozdílný průběh v **interiéru** a na **okraji lesa** (Tabulka č. 2). Tento průběh predace během dne se dá vysvětlit měnící se proporcí létavých a nelétavých predátorů (Obr. 20.).

V interiéru lesa byla návnada napadána dominantně skupinou nelétavých predátorů (Obr. 20.). To mohlo způsobit relativně velkou predaci i v průběhu časných hodin (Obr. 10-12.). Na okraji lesa stoupá predační tlak pozvolněji a dosahuje svého maxima až mezi 15:00 - 16:00 hodinou (Obr. 13-15.). Pomalejší nárůst predace na okraji lesa je způsoben tím, že hlavní skupinu zde tvoří létaví predátoři (vosy), které jsou mnohem více vázány na denní chod teploty než epigeičtí predátoři (Lichtenber & Lichtenberg 2003) (Obr. 20.).

Druhým vysvětlením rozdílné míry predace mezi okrajem a interiérem lesa by mohl být vliv teploty na predátory v těchto prostředích. Teplota a dostupnost světla je větší v okrajových částech než v centrálních částech lesa, na druhou stranu půdní vlhkost roste směrem do interiéru lesa (Heithecker & Halpern 2007). V práci uvedené v Příloze B míra predace pozitivně korelovala s teplotou pouze v interiéru lesa, protože negativní efekt teploty zde není tak výrazný (Halaj et al. 2008) (B). Avšak na otevřených stanovištích predační tlak nerostl s teplotou v celém jejím gradientu, ale od hodnoty kolem 23°C přestal stoupat (B). Příčinou se jeví být negativní vliv vysokých teplot na hospodaření s vodou a jiné metabolické děje v těle, protože většina hmyzu není schopna svou teplotu regulovat (Abdullah 1961).

Další výsledky ukazují, že míra predace se mezi jednotlivými mikro-stanovišti mění v závislosti na vegetačním období (B). Aktivita predátorů byla na jaře intenzivnější na otevřených stanovištích než v interiéru lesa (Obr. 4.). Tento pattern může být způsoben vyššími teplotami na těchto stanovištích na začátku vegetační sezóny než v interiéru lesa (Heithecker & Halpern 2007). Predátoři, kteří zde hledají potravu, pak budou více aktivní, než ti, kteří potravu hledají v zástinu. Vyšší predace v otevřených stanovištích se projevila pouze na začátku vegetačního období (Obr. 4.). Efekt teploty je totiž na začátku vegetační sezóny pozitivní u velkého spektra druhů, kdy vyšší teploty urychlují ukončení diapauzy, líhnutí a aktivitu hmyzu, zatímco v letním období mohou mít vysoké teploty na některé druhy hmyzu

Tabulka č. 3. Výsledky analýzy deviance faktorů ovlivňujících proporci napadených návnad na okraji lesa. Kombinace a pořadí faktorů bylo vybráno pomocí step wise selekce na základě nejmenšího AIC.

	Df.	Deviance	Residualni Df.	Residualni Deviance	F	P
NULL			920	165.05		
poly(vegetační sezóna,3)	3	18.749	917	146.30	34.64	<0.001
lesní patra	2	25.487	915	120.81	70.64	<0.001
poly(zimní NAO index,3)	3	6.184	912	114.63	11.42	<0.001
poly(teplota,2)	2	1.654	910	112.98	4.58	0.01
poly(denní doba,2)	2	2.636	908	110.34	7.30	<0.001

(mravenci) spíše vliv negativní (Cerdá 2001) (Obr. 6., Obr. 21.) (B).

Predační tlak na okraji a v interiéru se nelišil jenom v množství napadených návnad, ale taky abiotickými faktory vysvětlujícími jeho variabilitu (Tabulka č. 3-4). Teplota zůstala v obou typech biotopů nejdůležitějším faktorem prostředí, ovlivňujícím aktivitu predátorů. Predace v otevřených biotopech byla do značné míry ovlivněna sezonalitou (signifikantní vliv vegetačního období na predaci) (Tabulka č. 3). Dále byl v těchto biotopech zjištěn průkazný vliv globálních klimatických jevů na predační tlak (NAO index). To by potvrzovalo velkou nestabilitu interakcí mezi predátorem a kořistí, probíhajících ve fragmentovaných biotopech, a náchylnost těchto interakcí k disturbancím a ke změnám klimatu (Kruess & Tscharntke 1994, Zabel & Tscharntke 1998).

V biotopech se zapojeným korunovým patrem mělo největší vliv na predaci umístění návnad v různých patrech lesa (Tabulka č. 4). V těchto biotopech faktor sezonality vysvětloval nejmenší procento variability ze všech proměnných a vliv klimatu nebyl průkazný (Tabulka č. 4).

Závěr:

Do této doby chybí ucelený pohled na sezonní a časové fluktuace v predačním tlaku. Většina dosavadních studií se věnuje tomuto tématu jen okrajově a analyzuje spíš krátké časové řady dat (Weseloh 1988, Novotný et al. 1999, Berger & Wirth 2004). Mezi hlavní nevýhody většiny dosavadních výzkumů patří:

(a) zaměřují se pouze na některé skupiny predátorů (mravenci, ptáci);

(b) probíhaly pouze v jednom nebo dvou vegetačních obdobích;

(c) nezabývají se interakcí mezi mikro-stanovištěm a diurnální nebo sezónní fluktuací v míře predace;

(d) nestudují vliv abiotických faktorů prostředí na aktivitu predátorů.

Tabulka č. 4. Výsledky analýzy deviance faktorů ovlivňujících proporci napadených návnad v interiéru lesa. Kombinace a pořadí faktorů bylo vybráno pomocí step wise selekce na základě nejmenšího AIC.

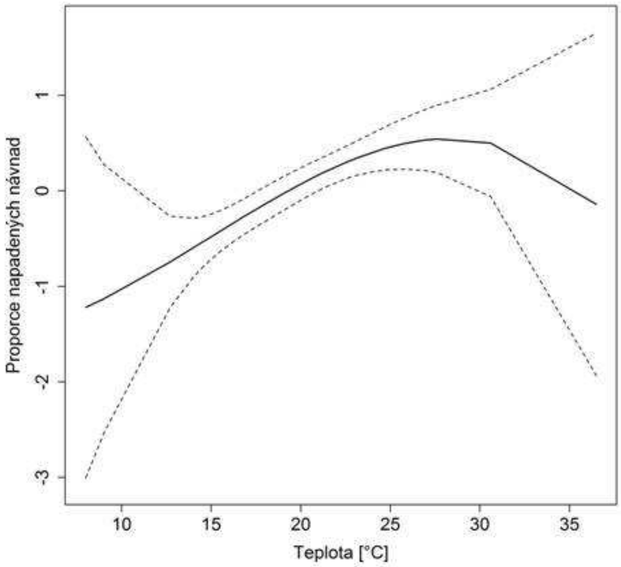
	Df.	Deviance	Residualni Df.	Residualni Deviance	F	P
NULL			1046	197.18		
lesní patra	2	43.24	1044	153.93	129.0	<0.001
poly(NDVI,3)	3	10.88	1041	143.04	21.6	<0.001
poly(teplota,3)	3	12.93	1035	121.61	25.7	<0.001
poly(vegetační sezóna,2)	2	0.24	1033	121.37	0.7	0.48

Z těchto nedostatků plyne také určitá nekonzistentnost výsledku dosavadních experimentů. Lichtenberg & Lichtenber (2003) nenaměřili průkazný rozdíl v celkovém predačním tlaku všech taxonů mezi interiérem a okrajem lesa v temperátu. Průkazný rozdíl v napadení návnad potvrdili pouze u taxonu vos. Koh & Menge (2006) nezjistili průkazný vliv hustoty zápoje na počet napadených návnad v tropickém deštném lese. Na druhou stranu Tschanz et al. (2005) zjistil průkazně větší míru napadení herbivorního hmyzu na rostlinách, rostoucích v otevřeném prostoru, než na rostlinách rostoucích v hustém zápoji. Studie, soustřeďující se pouze na ptačí taxony predátorů, potvrdily průkazně větší napadení v lesních okrajích (Skoczylas et al. 2007, Barbaro et al. 2012).

V předkládané práci jsem se zaměřil na široké spektrum predátorů, testována byla velká škála environmentálních faktorů. Významným přínosem a rozdílem oproti většině dosavadních prací na dané téma byla pětiletá délka terénního experimentu a velký počet opakování. Vše uvedené mi umožnilo otestovat s vyšší vypovídací hodnotou vliv abiotických a biotických faktorů na prostorovou a časovou variabilitu v predačním tlaku.

Hlavním cílem dizertační práce bylo vyhodnotit množství ekologických faktorů měnících se v čase a prostoru, determinujících míru predačního tlaku na herbivorní hmyz. Pomocí statistických modelů byla vybrána kombinace biotických a abiotických faktorů, nejlépe fitujících variabilitu v predaci (Tabulka č. 2).

Faktory výsledného modelu byly použity pro predikci času a prostoru, ve kterém bude mít



Obr. 21. Závislost mezi proporcí napadených návnad a průměrnými denními teplotami v letním období. Logistická regrese pro faktor letní teploty je: $y=1/[1+e^{(26.44x-9.52x2-2.71)}]$, $F_{2,1965}=58.54$, $P<0.001$, $R^2=0.096$. Přerušované čáry znázorňují standardní chybu.

predace největší respektive nejmenší vliv. Z výsledku této práce vyplývá, že na listech a na kmeni nabývá míra predace v průběhu vegetační sezóny dvou maxim a to v květnu a v srpnu. Na zemi dosahuje míra predačního tlaku v obou mikro-stanovištích vždy jednoho vrcholu - v interiéru lesa byla zjištěna maximální relativní míra predace v srpnu, zatímco na okraji lesa již v červnu. Z výsledků je také patrné, že relativní míra predace dosahovala na všech mikro-stanovištích dvou maxim také během dne.

Předložená práce zdůrazňuje jak význam interakcí mezi predátorem a abiotickými podmínkami prostředí (průměrná denní teplota v zimě a v průběhu vegetační sezóny, NDVI, množství dešťových srážek), tak i vztah predátorů ke komplexním charakteristikám stanoviště (korunový zápoj, lesní patrovitost, struktura koruny). Oba typy faktorů mohou definovat nebo ovlivňovat „prostor bez nepřátel“. Za klíčové výstupy práce považuji následující zjištění:

(i) Míra predace byla v nelesních stanovištích korelována s teplotou, v okrajové části lesa dominantně ovlivňována vegetační sezónou a v interiéru lesa se uplatňovala hlavně vertikální struktura porostu.

(ii) V interiéru lesa byl naměřen průkazný trend v proporci napadených návnad směrem k lesnímu opadu, v lesních okrajích byla největší proporce návnad napadena při zemi a na listě.

(iii) V nelesních stanovištích nebyl zjištěn průkazný rozdíl v proporci napadených návnad mezi ploškami s vyvinutým korunovým zápojem (solitérní stromy) a ploškami bez korunového zápoje.

(iv) Na otevřených stanovištích predační tlak nerostl s teplotou v celém jejím gradientu.

(v) Sezónními změnami počasí a klimatu byla predace více ovlivněna na otevřených stanovištích než v lese.

(vi) Složitá architektura rostliny negativně ovlivňovala efektivitu predátorů.

(vii) V oligotrofních ekosystémech smrkových monokultur byla aktivita predátorů soustředěna do míst spojených s produkcí organické hmoty, ať už živočišné nebo rostlinné. Produktivní plošky se v těchto ekosystémech často omezují na prameniště, mechové polštáře a rašeliniště.

(viii) Vznik refugií je velmi pravděpodobně funkcí druhového složení predátorů v daném prostředí. Jejich diurnální aktivita v rámci vegetační sezóny a mikro-stanoviště pak vytváří časo-prostorovou mozaiku vhodných míst s nízkou pravděpodobností napadení, která můžou sloužit jako refugium pro herbivorní hmyz.

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Příloha A

Assessment of trends in predation pressure on insects across temperate forest microhabitats.

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Agricultural and Forest Entomology

(Article in press)

Agricultural and Forest Entomology

Agricultural and Forest Entomology (2013), DOI: 10.1111/afe.12012

Assessment of trends in predation pressure on insects across temperate forest microhabitats

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Abstract

1 Experimental tests of whether predation pressure on insects is sometimes restricted to particular forest microhabitats have been carried out only in one or two vegetation periods and described for only a few predators. In the present study, we describe the seasonal dynamics of a wide spectrum of insect predators among forest microhabitats.

2 We also examine the impact of weather conditions on insect predation, and predict that forest openness would influence the predation trends among forest microhabitats.

3 The design of our experiments enabled direct measurement of relative predation pressure on bait (larvae of the blowfly *Calliphora vicina*) pinned onto selected microhabitats (the base, trunk and leaves of trees) within a temperate floodplain forest (Czech Republic).

4 The most parsimonious generalized additive model showed significant trends in the predation rate among the forest microhabitats. The highest predation rate for bait was at the base of trees and the lowest predation rate was on leaves.

5 We also observed significant differences in the species structure of predators in various microhabitats. The most common source of predation on trunks was from birds, whereas wasps were the most common predator on leaves and ants were the most common at the base of trees.

Keywords Forest layers, predation rate, refuge, spatial variability, temporal variability.

Introduction

Predation is considered one of the most important factors in determining species distribution and abundance (Hairston *et al*., 1960; Janzen, 1966; Sih *et al*., 1985; Scheirs & De Bruyn, 2002). Because prey availability is limited, predation pressure in specific habitats is affected by the efficiency of searching for prey. It is well established that biomass production and accumulation differ between forest layers in the forest litter, canopy, and understorey (Basset *et al*., 1992, 2003; Lowman, 1995; Malhi *et al*., 1999). Spatial heterogeneity and diet quantity are positively correlated with the amount of biomass (Polis *et al*., 1996). This correlation positively affects: (i) overwintering sites; (ii) the magnitude of abiotic stressors; and (iii) access to alternative prey (Halaj *et al*., 2000; Langellotto & Denno, 2004; Riihimäki *et al*., 2006). Therefore, differences in biomass partitioning among forest layers can influence the abundance of predators, with higher densities tending to be found in layers with the greatest amount of biomass (De Dijn, 2003; Vance *et al*., 2007).

This information can be useful when examining whether certain safe refuges for prey exist. For insects, spatial refuges can be located on different scales: (i) various habitats within a plant; (ii) different layers within the forest; and (iii) different types of forest habitat.

Studies from tropical and temperate forests imply that predation activity differs across forest layers (Jeanne, 1979; Olson, 1992; Loiselle & Farji-Brener, 2002). The main disadvantages of recent predation studies are that they: (i) focus only on a few predators (mostly ants and birds); (ii) are carried out only in one or two growing seasons; (iii) do not examine diurnal or seasonal variability in the predation rate in different forest layers; and (iv) do not examine the effect of abiotic conditions on predation (Weseloh, 1988; Olson, 1992; Floyd, 1996; Novotny *et al*., 1999; Lichtenberg & Lichtenberg,

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2003). Because insect predators are poikilothermic, factors such as temperature, humidity and solar radiation influence their activity. Therefore, it can be assumed that the forest layer with the highest predation rate will not be invariant but rather will change throughout the day and the growing season. Accordingly, the overall predation rate will be determined by the spatial and temporal interaction of biotic and abiotic factors (Floyd, 1996; Heard *et al*., 2006).

The majority of predation studies have been conducted using predator exclusion techniques (Holmes, 1979; Steward *et al*., 1988; Marquis & Whelan, 1994). Although these techniques can be used to evaluate absolute predation pressure, they (i) cannot identify particular carnivores; (ii) are rarely applicable in small microhabitats; and (iii) cannot assess the time when the prey was attacked. Direct measurement of predation pressure makes it possible to compare predation in different microhabitats (Olson, 1992; Novotny *et al*., 1999; Lichtenberg & Lichtenberg, 2003).

We predicted that predation pressure should vary in relation to: (i) various microhabitats within a plant; (ii) the gradient in forest openness; (iii) diverse predator abundance and species; and (iv) seasonal changes in weather conditions. To test these predictions, we measured relative predation on the base, trunk and leaves of trees. Our research provides more precise information on the spatio-temporal variability of insect predators, with a major emphasis on the differences in predator pressure and composition among forest microhabitats. These findings could have crucial implication for the design of managed landscapes aiming to increase the effect of natural enemies.

Materials and methods

Sampling

The research was conducted in a temperate floodplain forest along the River Odra in the Czech Republic. Three sites within the Poodri Protected Landscape Area were chosen for field experiments (NR Polansky les, Polanské louky and NNR Polanska niva). The size of the experimental area in each site was approximately 30 ha. Predation was measured during the daytime (between 06.00 h and 20.00 h), four times per month from April to September during the period 2003–2008, except for 2005.

Relative predation pressure was measured as the number of attacked baits (Novotny *et al*., 1999) pinned onto the base, trunk and leaves of trees, thus representing three different forest microhabitats along a vertical gradient. Each sample consisted of 20 baits that were fixed to the one particular microhabitat (50 × 50 cm) of a single tree. The baits on leaves were mounted on the upper surface. Before each experimental day, 15 trees were chosen in random order approximately 10 m apart from each other. Five sample replicates were set up for each microhabitat within a particular day. One replicate consisted of 20 baits on a particular vertically and horizontally specified microhabitat on a particular day and year. After 30 min, the majority of the insect predators were still on the baits and could be visually identified. Therefore, we did not have to be in the immediate vicinity of the baits to record predator attacks. Predation was calculated as the proportion of attacked larvae per 20 baits; that is why we used term 'predation rate'. We also observed the trees using binoculars to determine the species of avian predators. As bait, we used living larvae of the blowfly *Calliphora vicina* Robineau-Desvoidy, 1930 (Diptera: Calliphoridae). We pinned larvae through the abdomen using entomological pins; this allowed greater activity of the larvae and decreased their mortality during the experiments. The entomological pins were fitted with small coloured markers (red and yellow) for better visibility.

The experiment was performed on the two most abundant tree species: *Tilia cordata* and *Tilia platyphyllos*. The predation experiment was conducted only on understorey trees of approximately 1.5–2 m in height. To exclude the potential effect of forest openness, half of the experiments were performed at the forest edge and half within the forest interior. In total, we analyzed 3000 samples (47 640 baits) with 600 replications. In each type of habitat, environmental conditions (temperature, humidity and solar radiation) were measured using data loggers. Precipitation data were provided by the Czech Hydro-Meteorological Institute from a meteorological station approximately 5.5 km away from our site (Fig. 1).

Statistical analysis

Relationships between predation rate (treated as the probability of bait attack within one sample) and studied factors (microhabitats, forest openness, weather conditions and growing season) were examined using generalized additive mixed models using penalized quasi-likelihood (GAMM) with binomial error distribution (link logit). Standard errors were corrected using a quasi-binomial model to compensate for over-dispersion (Pinheiro & Bates, 2000). The best and the most parsimonious

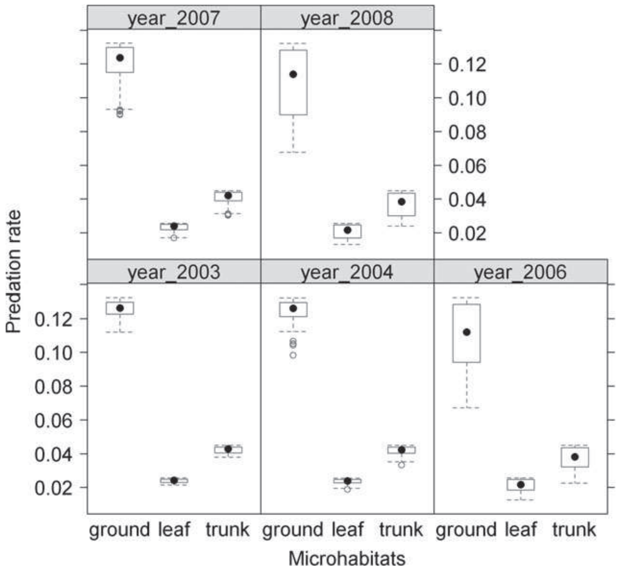

Figure 1 Proportion of attacked baits in the forest layers throughout the years. The *y*-coordinates are predicted by a generalized additive mixed model using penalized quasi-likelihood. Median values are shown with the quartile range (box) and total range (whiskers).

model based on the lowest Akaike information criterion was fitted by forward selection. Temporal correlation among samples was proved because predation experiments were repeated during the day and year. Therefore, the date of each sample nested within the year was used as a random effect in the mixed model to avoid pseudoreplication. The variables year, time, weather conditions and month were smoothed by cubic regression splines. The smoothing spline method was used because the shape of the response curve was not limited. The degree of smoothness for the GAMM model terms was estimated using the generalized cross-validation criterion. We used an F-test to determine the significance of the model because it is a robust test for over-dispersed data.

Because we did not expect a linear response of species, we used canonical correspondence analysis (CCA) to examine whether the structure of predator guilds differed between forest microhabitats. Species data were centred by species and the logarithmic transformation of predator frequency was used. The significance of the canonical axis and explanatory variables was determined using a Monte Carlo permutation test. Data were analyzed using R software (R Development Core Team, Austria) and CANOCO (Ter Braak & Smilauer, 1998) (Fig. 2 and Table 1).

Results

We recorded 3167 attacks on bait by predators in our study. Ants were the most active predator observed in our experiment (61%; $n = 1935$), followed by wasps (11%; $n = 358$), birds (10%; $n = 325$), Carabidae (7%; $n = 237$), Opilionidae (4%; $n = 118$), Araneidae (1%; $n = 33$), Staphylinidae (1%; $n = 28$), Mecoptera (1%; $n = 24$) and Heteroptera (1%; $n = 20$). Other predator taxa contributed to only a small proportion of the attacks. Three species of ants were distinguished in our experiment. The greatest proportion of predation by ants was by *Myrmica rubra* (54%), followed by *Lasius brunneus* (26%) and *Lasius platythorax* (20%).

The generalized additive model revealed that the predation rate varied significantly between the studied microhabitats (Table 1) and exhibited to the same pattern in all studied years (Fig. 1). A significant interaction between forest openness (forest edge versus interior) and forest microhabitats was shown (Table 1). In the forest interior, the predation rate was highest at the base of the tree (Fig. 2). However, the difference between predation rates at the base of the tree and on leaves was not significant at the edge of the forest (Fig. 2). The highest probability of attack was found at the base of the tree (Fig. 1), primarily by ants. In addition, CCA analysis showed that different species of predators directed their activity to different microhabitats within the tree (Fig. 3). The high

Table 1 Analysis of deviance for the generalized additive mixed model using a penalized quasi-likelihood model to test factors influencing the predation rate ('bs' indicates the cubic regression spline)

Factors	d.f.	*F*	*P*
Forest layer	2	16.735	< 0.001
bs (temperature)	3	15.263	< 0.001
bs (year)	3	9.291	< 0.001
bs (month)	3	5.529	< 0.001
Forest openness	2	4.778	0.008
Forest layer: forest openness	6	6.542	< 0.001
Forest layer: month	6	3.315	0.002
Forest layer: bs (year)	6	2.147	0.04542
r^2 (adjusted) = 0.259			
Dispersion parameter = 3.706828			

The month nested within the year was used as a random variable.

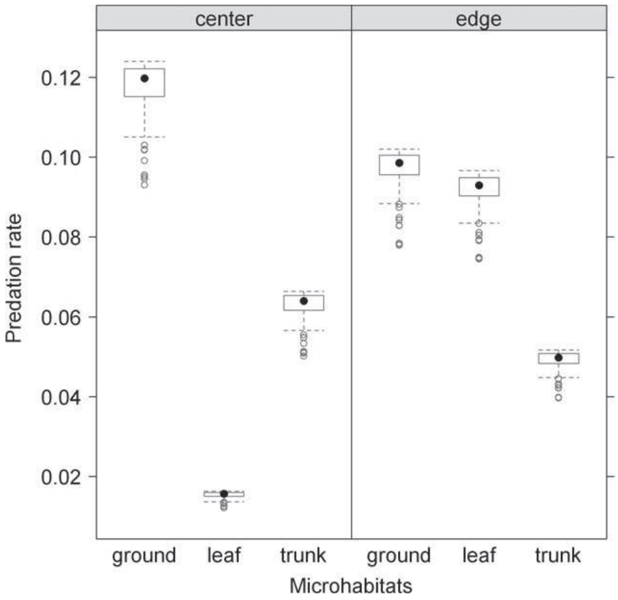

Figure 2 Interaction between the predation rate in forest layers (ground, leaves, trunk) and forest openness (edge, interior). The y-coordinates are predicted by a generalized additive mixed model using penalized quasi-likelihood. Median values are shown with the quartile range (box) and total range (whiskers).

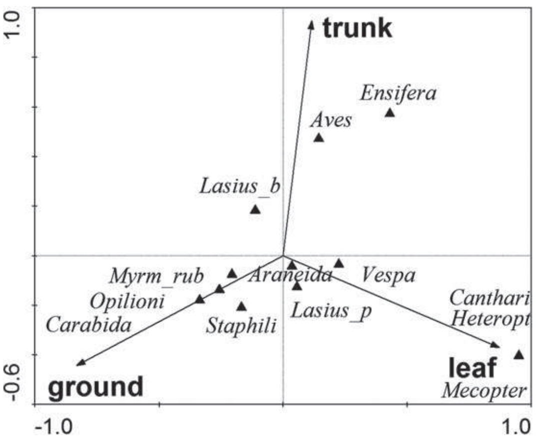

Figure 3 Canonical correspondence analysis ordination graph showing the different partitioning of dominant predators among forest layers. (Lasius_p, *Lasius platythorax*; Myrm_rub, *Myrmica rubra*; Lasius_b, *Lasius brunneus*; Mecopter, Mecoptera; Opilioni, Opilionidae; Carabida, Carabidae; Staphili, Staphylinidaec; Araneida, Araneida; Vespa, *Vespula vulgaris*; Heteropt, Heteroptera; Canthari, Cantharidae; Aves, Aves; Ensifera, *Meconema thalassinum*).

Table 2 Summary of the Monte Carlo test in the canonical correspondence analysis model

Axes	I	II	III	IV
Eigen values	0.333	0.209	0.091	0.787
Species–environment correlations	0.740	0.552	0.416	0.000
Sum of all eigen values	5.744	–	–	–
Sum of all canonical eigen values	0.633	–	–	–
Test of significance of first canonical axis	*F*-ratio = 11.022	*P* = 0.0005	–	–
Test of significance of all canonical axes	*F*-ratio = 7.393	*P* = 0.0005	–	–

Table 3 Significance of environmental variables in the canonical correspondence analysis model

Environmental variable	Lambda 1	Lambda A	*P*	*F*
Leaf	0.29	0.29	0.001	9.66
Ground	0.28	0.21	0.001	7.03
Trunk	0.20	0.13	0.001	4.80

significance of the environmental factors and the canonical axis in CCA confirmed the correctness of the ordination model (Tables 2 and 3).

The predation rate was significantly lower on the leaves and trunk (Fig. 1). The significantly lower predation in these microhabitats was a result of the correspondingly lower activity of ants (Fig. 3). Baits fixed on leaves and trunks were typically attacked by wasps (*Vespula vulgaris*) and birds (Passeriformes), respectively (Fig. 3). Predation by wasps was negatively correlated with the mean precipitation for April and May (Fig. 4).

There was also a seasonal effect (Table 1). The predation rate depended on the date and season of bait exposure (Table 1). The estimated predation pattern among forest microhabitats showed an invariant trend throughout the seasons. The dynamics of the predation rate varied among the three forest microhabitats during the growing season (Fig. 5). The predation rate on the trunk showed a trend towards the beginning of the growing season. The predation rate on the leaves was characterized by a hump-shaped curve with a maximum in July. Larvae fixed at the ground level showed a consistent trend in the predation rate until August (Fig. 5).

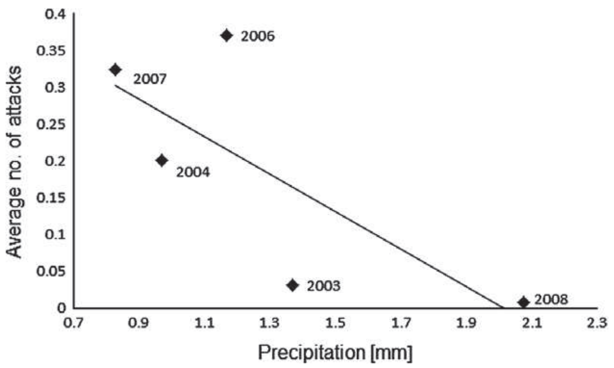

Figure 4 Relationship between mean precipitation during April and May and the average numbers of attack by wasps (Regression line: $y = -0.25x + 0.51$; $r^2 = 0.56$).

Our final model also included the effect of temperature, which was the second most important factor in explaining the predation rate (Table 1). Other environmental variables (sun radiation, humidity and precipitation) were eliminated by a stepwise regression procedure (Figs 3–5; Tables 2 and 3).

Discussion

Vertical stratification of predation

We found a significant positive trend in predation rate towards the forest floor. Studies from tropical rain forests have shown significant variability among forest levels, although the location of the highest predation rate differed from that of temperate regions (Olson, 1992; Novotny *et al*., 1999). In tropical rain forest, the greatest predation pressure is situated in the canopy and the lowest is on the understory leaves. The distribution of biomass production may be the reason why the predation probability does not have the same partitioning among vertically chosen patches in tropical and temperate ecosystems (Lowman, 1995; Basset *et al*., 2003). In tropical rain forest, the understory flora grows in permanent shade and biomass production is mainly in the canopy (Lowman, 1995). The activity of the majority of tropical insects is situated in the canopy, and this is why the predation pressure occurs mainly in this stratum (Basset *et al*., 1992, 2001, 2003). In a temperate ecosystem, forest litter supports a major component of the insect biomass (Preisser *et al*., 1998; Basset *et al*., 2003). Therefore, predation activity will be influenced by: (i) environmental conditions, which in temperate ecosystems are more stable and suitable in the understory than in the canopy, and (ii) the biomass of potential prey that is active at the ground level (Basset *et al*., 1992, 2003; Lowman, 1995; Preisser *et al*., 1998; Drozdová *et al*., 2009).

Another factor that significantly influenced the predation rate during the present study was forest openness. We observed a significant positive trend in the predation rate toward the forest interior. The more stable weather conditions and the greater accumulation of litter as a result of the higher canopy leaf area could lead to a higher predation rate in the central part of the forest (Andow, 1991; Perdikis *et al*., 1999; Kara *et al*., 2008). A significant difference in the predation rate between forest microhabitats was observed only in the central part of the forest. We did not observe any trend in predation pressure at the forest edge because the predation activity of wasps on the leaves was at a similar rate to the predation activity of ants, which preferred foraging in the leaf litter.

Variability in predation between forest layers can reflect the distribution in the activity of the dominant predator. The dominant predators of tropical and temperate ecosystems are ants (Olson, 1992; Lichtenberg & Lichtenberg, 2003). Ants build their nests and search for prey in different layers in tropical versus temperate forests (Olson, 1992; Floren *et al*.,

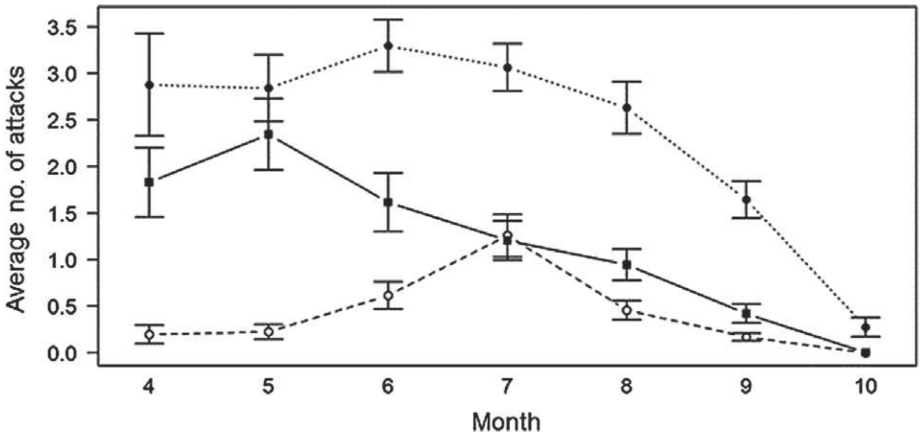

Figure 5 The mean ± SE number of baits attacked by predators in each of the three microhabitats during the growing season (estimated over the values calculated for a particular forest microhabitat × month replication). Open circles, leaves; filled squares, trunk; filled circles, ground.

2002; Davidson *et al*., 2003; Lichtenberg & Lichtenberg, 2003). In tropical forest, the canopy provides ants with a more stable environment for building nests and hunting prey (Brühl *et al*., 1998; Floren *et al*., 2002). In temperate regions, the majority of ant species show a strong affinity for foraging in forest litter (Lichtenberg & Lichtenberg, 2003). This is confirmed by the most common ant species in the present study, *M. rubra*, whose activity was significantly directed to the forest litter, showing behaviour that corresponds with the ecology of this species. These ants tend to forage in leaf litter because they find most of their prey there, and they can also obtain honeydew from aphids living on roots (Wilson, 1971; Depa & Wojciechowski, 2008). On the other hand, *L. brunneus* exhibits an apparent trend towards the trunk in its predation. *Lasius brunneus* builds its nests higher above the ground in dead wood or under bark, and therefore it mainly forages on trees (Pisarski & Vepsäläinen, 1989). *Lasius platythorax* builds its nests in rotten wood, and this may explain why we did not detect a clear affinity in this species for a particular habitat (Savolainen & Vepsäläinen, 1988). The predation rate of the two less active ant species was not so frequent as to alter the final predation pattern, which was oriented towards the leaf litter. After ants, the main predators in the forest litter were ground beetles, rove beetles and harvestmen. These types of predator tend to forage in moist habitats, mainly leaf litter. Other important predators observed in the present study were flying predators. These predators (*V. vulgaris*, Cantharidae and Mecoptera) direct their activity to the leaves and trunk at the forest edge, probably because of the higher temperature there, which they need to sustain flying (Lichtenberg & Lichtenberg, 2003). Predation by wasps started at the end of June and peaked in August. In our experiment, predation by wasps fluctuated among the years (data not shown). This fluctuation was probably mainly caused by the variation in precipitation during April and May because wasps search for a suitable nesting site during this time (Madden, 1981). Ants exerted high predation pressure throughout the entire growing season and had stable predation activity between years (data not shown). The predation activity of birds was negligible compared with that of arthropods because birds prefer insect food only for a short period during their nesting time (Tinbergen, 1960; Royama, 1970). In the present study, birds also attacked bait mainly at the beginning of the growing season.

Not only spatial, but also temporal stability in environmental conditions can be important. There is an increasing emphasis on the view that top-down effects cannot be rigorously tested unless between-season fluctuations in carnivores are taken into account (Scheirs & De Bruyn, 2002). Environmental conditions can change throughout the years, and changes are more pronounced in temperate ecosystems than in tropical ecosystems. The 5-year length of the present study enabled us to preclude the effect of seasonality and to predict that the pattern in vertical stratification of predation is invariant throughout the years (Fig. 3).

Knowledge about spatio-temporal patterns in predation rates in a fragmented landscape can be applied to woodland design in managed landscapes. We discovered that ground-dwelling predators increase their activity towards the forest interior. Ants, which are the dominant insect predators, are generally sensitive to high temperatures, and therefore they prefer not to forage in hot, open habitats (Holec *et al*., 2006). The canopy of hedgerows or solitary trees does not have as large an impact on predation rates compared with the canopy of the forest interior (Šipoš *et al*., 2012). Therefore, forest fragments in managed landscapes should have a sufficient central area to maintain a humid climate and forest litter. One of the findings of the present study was that the predation rate on the leaves showed a positive trend towards the forest edge. Therefore, forest fragments should also possess heterogeneous and diverse ecotones to support the large predator communities that are important for open habitats (e.g. wasps), and which can serve as biocontrol agents in adjacent patches (Lichtenberg & Lichtenberg, 2003; Sousa *et al*., 2011). Our results show that there is a wide range of potential predators of insects in the different parts of trees and a possibly high risk of predation at ground level. We cannot assess the relative predation rate in the forest canopy because the predation rate on leaves was studied only in the understorey layer. The high predation risk at ground level was mainly attributable to *M. rubra*. We showed that a wide spectrum of predators should be included in predation studies. The results of the present study suggest that ants, wasps and birds can be important predators of insects in temperate forests. These results also imply that we should not underestimate the effect of seasonal changes on the predation rate. Our results indicate a stable pattern in the predation rate among forest levels during the period 2003–2008.

Experimental design

The data collection technique employed in the present study did not allow us to assess the real predation rate because immobilization of the bait imposes the impossibility of its escaping from a predator and limits its ability to defend itself. Although we did not measure absolute predation, we nevertheless assume that the assessed differences reflect the real predation rate and the composition of predators.

During bait fixing, we aim to avoid the bias caused by larval immobility, and also strive not to damage the bait, because this can cause early death and attract unwanted insect taxa. Church *et al*. (1997) established that birds can distinguish between baits of different colour. Therefore, the experiments were performed repeatedly over longer periods of time.

Selecting the most suitable bait is very important for this type of experiment. For bait, Novotny *et al*. (1999) and Olson (1992) used worker termites, which are a typical prey in tropical ecosystems. Our experiment was situated in a temperate ecosystem, and therefore the bait had to comprise a species normally occurring in this type of ecosystem. Furthermore, the size our larvae (approximately 1.5 cm in length) appears to be sufficient for a wide range of predators (Lichtenberg & Lichtenberg, 2003; Remmel *et al*., 2009). The predatory species did not show a special preference for our bait because we studied the predation rate of generalist predators (Olson, 1992; Novotny *et al*., 1999; Lichtenberg & Lichtenberg, 2003). The high richness of predators attacking our bait convinced us that we chose an appropriate type of bait.

The major findings of the present study are that: (i) the predation rate of ground-dwelling insects tended to increase towards the forest interior; (ii) the predation rate on leaves significantly increased towards the forest edge; (iii) three different ant species directed their predatory activity towards separate microhabitats; (iv) the predation rate in particular microhabitats showed specific trends throughout the growing season; and (v) the predation of wasps was negatively correlated with the mean spring precipitation.

Acknowledgements

The present study was supported by Grant No. PrF_2010_021 from the Internal Grant Agency of Palacky University in Olomouc and MSMT grants CzechGlobe Reg. No. CZ.1.05/1.1.00/02.0073 and LC06073 from the Ministry of Education, Youth and Sports of the Czech Republic. Additional support was from the Grant Agency of the Czech Republic (GACR 206/99/1112, GACR 206/07/0811) and the Institute of Environmental Technologies Project (reg. no. CZ.1.05/2.1.00/03.0100).

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Accepted 7 February 2013

Příloha B

Effect of canopy openness on the pressure of predatory arthropods and birds on epigeic insect

Šipoš J., Drozdová M. & Drozd P.

Central European Journal of Biology 7: 1021-1029

Cent. Eur. J. Biol. • 7(6) • 2012 • 1021-1029
DOI: 10.2478/s11535-012-0093-5

VERSITA

Central European Journal of **Biology**

Effect of canopy openness on the pressure of predatory arthropods and birds on epigeic insects

Research Article

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Received 16 March 2012; Accepted 29 August 2012

Abstract: As canopy structure produces spatial heterogeneity of litter microclimatic conditions and thus is a crucial factor affecting ground insects, we hypothesized that low canopy openness has a positive effect on the activity of ground insect predators in forest and non-forest habitats. Blowfly larvae were used as bait along the canopy openness gradient (forest interior, forest edge, base of a solitary tree and meadow) and the attack rate was assessed after 30 min of exposure. Although the predation rate has a varying pattern throughout the year in different habitats, in contrast to previous studies, we observed a significant positive trend in predation rates toward the forest interior. A significant trend in predation rate was not observed in non-forest areas. We found that the trend was strongly influenced by ants as the most active taxon of predators (65%) attacking our baits, whereas ground beetles, the second-most active predators (21%), showed the opposite trend along the canopy openness gradient.

Keywords: *Predation rate • Weather conditions • Living baits • Temperate forest*

1. Introduction

There has long been debate over whether canopy openness significantly influences predation rates on arthropods [1-5]. It is known that canopy complexity in a wide range of habitats does play an important role in the formation of spatial heterogeneity and microclimate stability in leaf litter [6-8]. Thus, treetops provide stable conditions favoring the activity of arthropod predators which are sensitive to temperature and humidity fluctuations [9,10]. Moreover, accumulation of litter from a canopy leaf area has a positive effect on ground insect predators [7,11-13]. Generally, we can say that litter affects predator abundances through at least four mechanisms: (1) access to alternative prey; (2) reduction of interspecific competition and prevention of intraguild predation [9]; (3) provision of overwintering sites, places for reproduction, and shelters to hide from higher trophic level predators [13-15]; and (4) reduction of abiotic stressors [6,9,16-18]. The use of pitfall trapping to study activity of predators has confirmed that vegetation density positively correlates with activity and abundance of predators [19-23].

Stability of habitat conditions influences not only abundance, but also species composition of predator guilds. This results in different predation rate patterns in different habitats, and, consequently, in different spatial distributions of arthropod prey [24]. For example, flying predatory insects like wasps prefer a boundary layer between forest and open habitat as a major patch for their activity [3], whereas ants primarily focus on ground insects in forest habitats [25]. This indicates that changes in total predation activity in a given habitat are straightforwardly predictable if we are able to estimate

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the trends in predation rate for dominant predator guilds. Such findings are very important and applicable considering the recent and rapid forest fragmentation and frequent outbreaks of pests [2].

Despite many authors having studied changes in predator abundance and activity, and while we can expect significant connectedness between activity and predation rate, there are only a few studies which explicitly focused on this relationship by measuring direct predation rates on the ground. Experiments focused on the relationship between forest openness and predators measured predation rate only between the forest edge and forest interior, but did not compare predation among non-forest habitats. The effect of abiotic conditions on predation in forest and non-forest habitats is unknown [1,3]. Furthermore, such studies have focused on different strata (mainly the understorey) and found no significant differences in predation rate between the interior and forest edge. Such results are inconsistent with studies indicating that the higher trophic level organisms (predators and parasitoids) are more affected by fragmentation than are herbivores [2,26,27].

In our research, we focused on the following questions: (1) Does the total predation rate on the ground show any trend along a canopy openness gradient? (2) How does total predation rate vary along the gradient during the season? (3) Which major taxa of generalist predators are significantly affected by canopy openness, and can we observe the same trend for all taxa? (4) How does total predation rate vary among forest and non-forest habitats with different canopy openness? (5) Is predation rate more affected by abiotic conditions in non-forest than in forest habitats? Here we hypothesize that predation on an epigeic insect in forest habitats is negatively correlated with canopy openness and this trend will be the same for non-forest habitats.

2. Experimental Procedures

2.1 Study site

The study was conducted in a temperate floodplain forest near the towns of Studénka (49°41’44.949”N, 18°2’30.755”E) and Polanka nad Odrou (49°46’39.397”N, 18°11’18.639”E) in the Czech Republic. This area consists of large and small forest fragments with willows, oaks, lindens and poplars as the dominant tree species and of grassland with shrubs and solitary trees. We chose two forest habitat types which differ in canopy openness (forest interior and forest edge). The third type of habitat could be described as grasslands with sparsely scattered trees. Solitary trees were used as last type of habitat. Effect of forest openness on predation can be well studied among the first two habitat types. The remaining habitats were including in the research to study patterns in predation rate among habitats in the vicinity of the forest. We can exclude the effect of human pressure on the research because study was arranged in an area protected for more than 20 years.

2.2 Field experiment

Within each area we chose four different patches for each habitat type. The samples were exposed in all four patches each day. In both areas the predation rate was measured during the daytime (between 7:00 a.m. and 2:00 p.m.), 2 times per month from April to September during 2008. Live baits (larvae of the blowfly *Calliphora vicina* Robineau-Desvoidy, 1830) were affixed to the ground using entomological pins along the canopy openness gradient: forest interior, forest edge, base of solitary trees and meadow. These larvae are primarily used as baits for fishing therefore we do not see problematic affixing the living larvae by pins. The entomological pins were fitted with colored paper markers (0.5×0.5 cm) to facilitate counting. Twenty larvae exposed for 30 min comprised one sample, and the proportion of attacked baits was treated as predation rate. Larvae were placed approximately 10 cm apart from each other. The predation was calculated as proportion of attacked larvae per 20 baits, that is why we used term “predation rate”. Four sample replicates were made for each factor combination (habitat and day). After 30 min. the majority of the insect predators were still on the baits and therefore could be identified. Based on [3] and our own observation, missing baits were considered as predation by vertebrates (mainly birds). We also observed the trees using binoculars to determine the species of birds. Due to the risk that predators (particularly wasps, ants, as well as mammalian and bird predators) would adapt to bait location, we changed the placement of pinned baits within the habitat. In each type of habitat environmental conditions (temperature, humidity and solar radiation) were measured by data loggers to separate effect of abiotic conditions from the effect of canopy openness.

2.3 Data analysis

To determine whether canopy openness and climatic conditions affect predation rate, we developed generalized additive mixed models with binomial error distributions and logit link functions. Predation rate was always the dependent value. Generalized additive models were used because shape of the response curve is not limited. Regression lines were fitted using the cubic spline method. Degree of smoothness was estimated using the generalized cross-validation criterion [28].

Temporal correlation among samples was demonstrated because predation experiments were repeated across days and months. Therefore, date of each sample nested within the month was used as random effect in the mixed model to avoid pseudo-replication. Standard errors were corrected using a quasi-Binomial model to compensate for over-dispersion [28]. The predation rate was assumed to follow binomial distribution, because the sum of attacked baits was divided by the total number of baits for each sample. The final model was selected using a step wise procedure. The most parsimonious combination of environmental variables was selected based on lowest Akaike information criterion (AIC) by combining both forward and backward selection [29]. Effect of canopy openness and climatic conditions on predation was tested by analysis of deviance using an F test. We used the F test to check the significance of the model, because it is a robust test for over-dispersed data. To compare variability of predation rate between habitats types, the multiple comparison method using Tukey contrasts was applied. Effect of forest openness on predation rate of each predatory species was fitted by separate models. All analyses were done using the statistical program R [30].

3. Results

We recorded 741 predator attacks from the total of 5,040 baits (384 samples). The best model selected with AIC equals to 1026.46 and explained 42% of the model deviance. The most frequent predators were ants (65%, n=472), followed by ground beetles (21%, n=159), spiders (5%, n=40), vertebrates (4%, n=30), harvestmen (3%, n=23), and rove beetles (2%, n=16). The most active ants were *Myrmica rubra* and *Lasius platythorax* and most active spiders were *Pardosa palustris* and *P. amentata*. The beetle family *Carabidae* was represented by the genus *Pterostichus,* which were dominantly foraging in the forest interior, and the genera *Poecilus* and *Amara,* dominantly foraging in meadows. The vertebrate predators had peak activity during May and June, which probably is associated with the breeding season.

We found a significant effect of tree canopy gradient on predation rate (Table 1). According to our analysis, predation rate in forest areas was influenced mostly by temperature and canopy openness and in non-forest areas by sun radiation and seasonality (Table 2). In the forest, habitat predation rates decreased with canopy openness, whereas predation rate was similar among habitats in non-forest area (Figure 1). Multiple comparisons test showed that only predation rate in

	df	F	P-value
bs (temperature)	3	7.632	<0.001
habitats	3	7.185	<0.001
bs (month)	3	9.206	<0.001
bs (time of the day)	3	6.682	<0.001
habitats: bs (month)	9	4.945	<0.001

Table 1. Results of the analysis of deviance of the factors affecting predation rate included in the generalized additive mixed model ("bs" representing cubic regression spline). Month nested within year was used as a random variable. Factors were selected by the step-wise procedure.

Non-forest habitats	df	F	P-value
bs (global_rad.)	3	4.471	0.00518
bs (month)	3	4.501	0.00499
Forest Habitats	df	F	P-value
bs (temperature)	3	9.506	<0.001
habitats	1	5.471	0.021058
bs (time of the day)	3	7.852	<0.001
fortype: bs (time of the day)	3	7.174	<0.001

Table 2. Results of the analysis of deviance of the factors affecting predation rate included in the generalized additive mixed model ("bs" representing cubic regression spline). Month nested within year was used as the random variable. Factors were selected by the step-wise procedure.

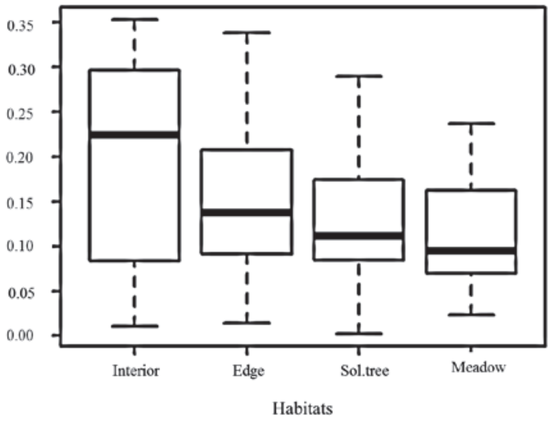

Figure 1. Proportions of predation predicted by generalized additive mixed models (with predation as the dependent variable, canopy openness as the explanatory variable and date nested within the month as the random factor) in the forest (interior, edge) and non-forest habitats (sol.tree, meadow). The proportions were predicted by using the function "predict"in the program R. Shown are median values with quartile range (box) and total range (whiskers).

the forest interior was significantly different from other habitat types (Table 3). This effect can be due to different abundances of major predators in different habitats (Figure 2). The taxon with highest number of attacks, ants, had its highest predation rates in the forest interior (F=9.771, P<0.001, n=252) (Figure 2). In other habitats, except for meadows, ants were also the predator with highest number of attacks, but their predation was less intensive than in the forest interior (Figure 2). There was a significant trend toward the meadow for predation by ground beetles (F=14.31, P<0.001, n=252) (Figure 2) and spiders (F=3.288, P=0.02, n=252) (Figure 2). The activity of predators culminated between 11:00 and 12:00, with no differences between higher predator taxa.

We observed that predation rate had a different pattern through the year in different habitats (Table 1) (Figure 3). At the beginning of the growing season (April to May), predation was highest on meadows and under solitary trees. During the rest of the season, the highest predation rates were observed in the interior of the forest. In our study, predation rate was positively correlated with temperature only in the forest interior

	Estimate	Std. Error	z value	Pr(>|z|)
interior - edge == 0	-0.4193	0.1929	-2.834	0.0479
meadow - edge == 0	-0.3674	0.2167	-1.696	0.3218
soliter - edge == 0	-0.2083	0.2476	-0.841	0.8324
meadow - interior == 0	-0.6595	0.1541	-3.788	<0.001
soliter - interior == 0	-0.5004	0.1813	-3.368	0.0316
soliter - meadow == 0	0.1591	0.2270	0.701	0.8951

Table 3. Multiple comparisons of predation rate between habitat types using Tukey contrasts of the generalized linear mixed model.

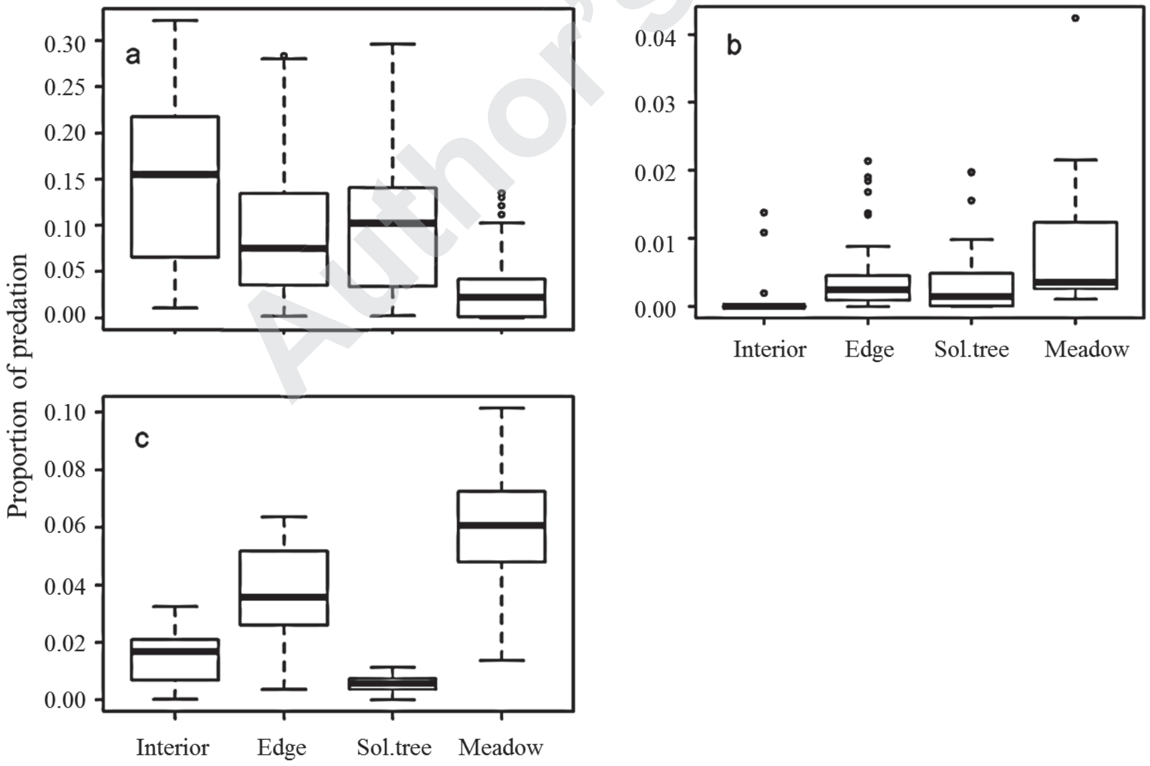

Figure 2. Proportions of predation predicted by generalized additive mixed models (with predation by particular species of predator as the dependent variable, canopy openness as the explanatory variable and date nested within month as the random factor) in the forest (interior, edge) and non-forest habitats (sol.tree, meadow): a) ants, b) spiders, c) ground beetles. Shown are median values with quartile range (box) and total range (whiskers).

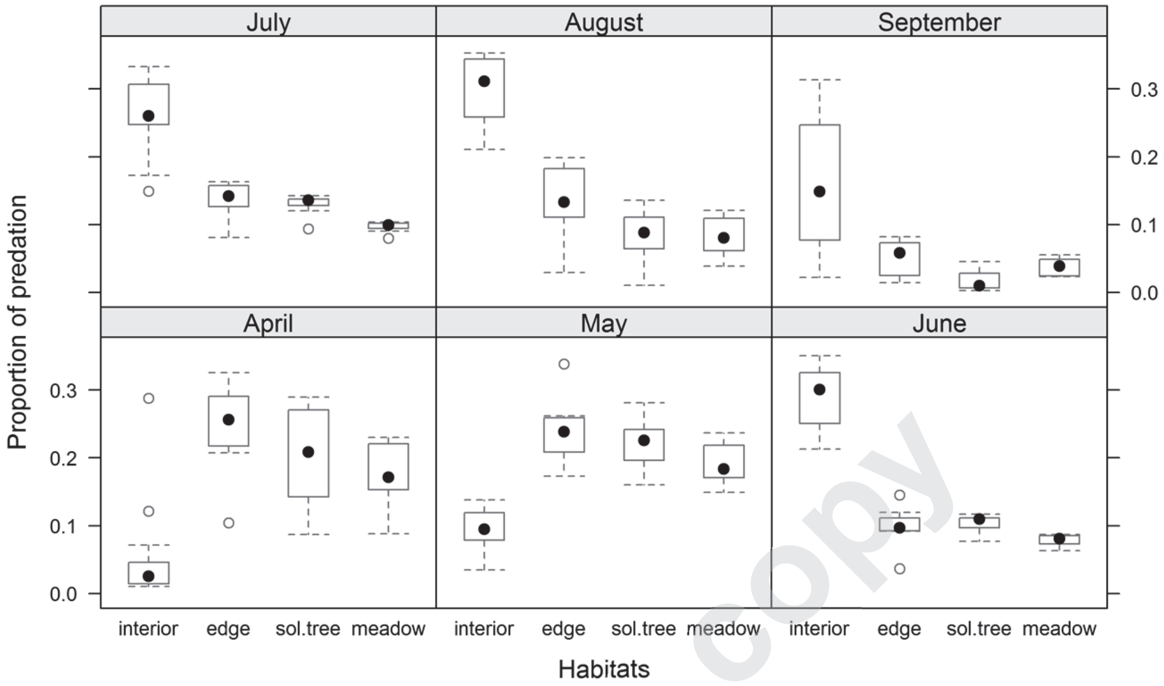

Figure 3. Proportions of predation predicted by generalized additive mixed models (with predation as the dependent variable, interaction between month and canopy openness as the explanatory variable and date nested within month as the random factor) in the forest (interior, edge) and non-forest (sol. tree, meadow) habitats throughout the growing season. Shown are median values with quartile range (box) and total range (whiskers).

(Figure 4). Optimal temperature during active feeding was about 30°C; above this temperature predation rate was starting to decrease in non-forest habitats (Figure 4).

4. Discussion

4.1 Experimental design

Our data collection technique did not allow us to assess real predation rates because immobilization of the baits imposes the impossibility of it escaping from a predator and limits its ability to defend itself. Although we did not measure absolute predation, we nevertheless suppose that the assessed differences reflect the real predation rate and composition of predators. Selecting the right baits is very important for this kind of experiment [25]. Our experiment was situated in a temperate ecosystem, and therefore the bait had to be a species normally occurring in this kind of ecosystem. Other requirements were that the bait had to (i) occur during the entire vegetation period, (ii) be one having no defensive mechanism, and (iii) be edible [3,31]. From that perspective, using of *Calliphora* larvae looks very appropriate. Also, the size of larvae (about 1.5 cm) seems sufficient for a wide range of predators [32]. High richness of predators attacking our baits convinced us that we chose right type of the bait. Predatory species did not show any special preference for our baits also because we studied predation rate of generalist predators [3,4].

4.2 Effect of canopy openness in forest and non-forest habitats on predation rate

The results indicate that we were able to detect diurnal activity for a large spectrum of arthropod and vertebrate generalist predators along the entire canopy openness gradient in forest and non-forest habitats through the growing season. This is in accordance with most studies focused on methodology of predation rate measurement [25,26,32]. Predation rate has predominantly been measured indirectly through predation exclosure techniques [26,33-36], which provide sufficient estimates of absolute predation risk. Although direct predation measurement has been employed only in a minority of studies [3,4,37,38], it is considered a better alternative for comparing different habitats, identifying predators, and estimating time of attack [3,26]. Our research was designed with emphasis on avoiding known issues of

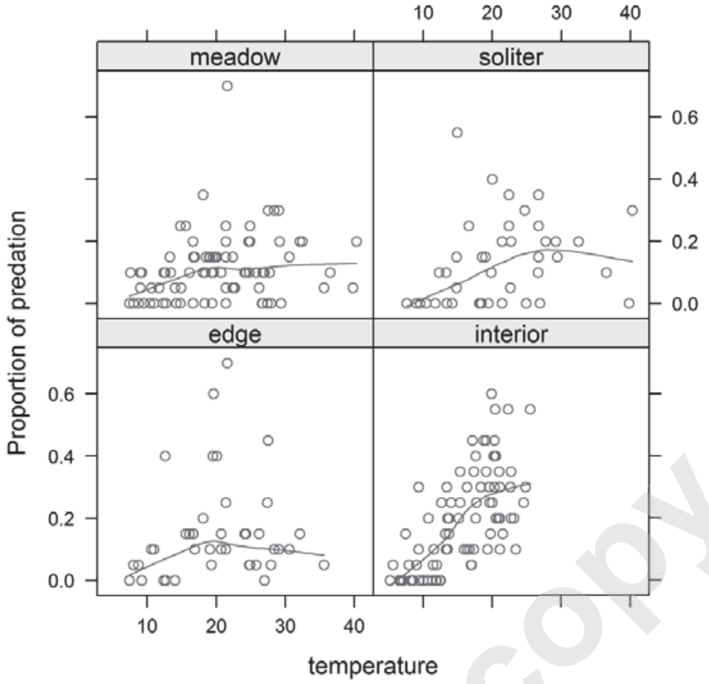

Figure 4. Proportions of predation predicted by generalized additive mixed models (with predation as the dependent variable, interaction between habitats and temperature as the explanatory variable and date nested within month as the random factor). Lines are fitted by a smoothing spline.

direct predation measurements mentioned in previous studies: a) we studied effect of canopy gradient in forest and non-forest patches; b) we did more replications for each month and hour; c) baits were exposed for just 30 min to allow identification of predator taxa; and d) we changed the placement of experiments during the season to avoid possible bias caused by the non-random searching pattern found in studies wherein predation experiments were at the same place for a long time period (with only missing or injured baits being replaced). It is known that social insects like wasps and ants can focus their activity upon locations with longer bait exposure time and that vertebrates, especially birds, may learn to find food there [39,40].

The majority of predation was by arthropods (96%), the rest by vertebrates. Among the arthropods, ants were the most active predators in our experiments. Similar results have been reported for most studied ecosystems and biomes [4,25,26]. We found an apparent trend in ant predation toward the forest interior, whereas the ground beetles, with second-highest predation rate, attacked more baits in open habitats. These results were caused by the proportion of attacks between species preferring forest and non-forest habitat within each taxon. Ground beetles showed a trend in predation rate toward open habitat because the most active genera, *Amara* and *Poecilus*, are active in daytime and predominantly prefer open habitats [41]. The most active ant species (*Myrmica rubra*) showed a trend in predation rate opposite to that of ground beetles, because they prefer moist forest habitats and build their nests and forage in leaf litter or rotten wood [42,43]. Spiders showed a trend in predation rate toward open habitat because most active species were wolf spiders, which preferred non-forest habitats. These results played only a marginal role in our experiments and are in contrast to predation experiments in temperate ecosystems where birds are assumed to be important predators [44-46]. The negligible predation effect attributable to birds could reflect behavioral activity of birds, which use leaf damage as clues in their searching effort for the caterpillars, which comprise the most preferred food for their nestlings [47,48]. Furthermore, birds prefer insect food only for the short period of nesting to feed their nestlings [45,46].

As we hypothesized, in the forest habitats we observed predation to be highest in the forest interior; on the other hand, we did not find significant difference in predation rate between patches in non-forest habitats. Similar predation rate between non-forest habitats implies that the canopy of solitary trees did not have sufficient impact on predation rate as does the canopy of the forest interior. The highest predation rate at the forest interior supports the assumption that abundance of predators also declines with increasing forest fragmentation and isolation [2]. Such findings are in agreement with outcomes of pitfall trap studies, which confirm positive correlations between low canopy openness and predation activity [19-22]. Differences between forest edge and interior in predation rate recorded in our experiments probably result from temperature variability within and between the two habitats. We found out that predation rate is positively correlated with temperature only in the forest interior, because negative effects of high temperature on insects are not fully pronounced in dense forest conditions. Predation rate in habitats with higher canopy openness did not increase over the whole temperature interval, but started to decrease after some threshold level. Temperature can negatively affect water distribution, water loss and other metabolic reactions in the body, because insects are not able to regulate body temperature [49]. Therefore, life is limited within a range of temperature [49].

We also found that predation risk among habitats differs during the growing season. This is in agreement with an assumption that predation is highly influenced by seasonal changes of weather [32]. The activity of predators was greatest in open habitats during spring. Such patterns can be caused by a higher temperature in open habitats at the beginning of the growing season. Predators that move in open habitats are more active than are carnivores which seek their prey in shaded places. In addition, the effect of temperature could be more apparent at the beginning of the season, because temperature speeds up hatching and emerging of predatory species from hibernation.

In conclusion, the results confirm the great importance of vegetation's spatial characteristics for patterns of predator–prey interactions and for corresponding predator activity. We found that total predation rate in non-forest habitats is lower than in forest habitats. These results correspond with the predation rate of ants as the most active group of predators. Although the most active taxons of ants predominate along the entire observed canopy openness gradient, increasing forest patchiness affects them negatively and thus the highest predation rate was found in forest interior where we can expect more stable environmental conditions. Furthermore, a canopy of sparsely scattered trees did not significantly increase predation rate in grassland habitats. By contrast, we did not find the same trend for other taxa of abundant predators, because taxons of spiders and ground beetles preferring non-forest habitats consumed a higher proportion of baits than taxons preferring forest habitats. The latter findings are, however, in agreement with those reported for other studies using different methods (e.g. pitfall traps). As the method of direct predation rate measurement is very simple, we propose to use this as an effective alternative method in estimating the impact of deforestation on epigeic arthropod fauna within areas of disturbance, and also in the vicinity of such habitats.

Acknowledgements

This study was supported by Grant No. PrF_2010_021 from the Internal Grant Agency of Palacky University in Olomouc and grant MSMT LC 06073 from the Ministry of Education, Youth and Sports of the Czech Republic, the Grant Agency of the Czech Republic (GACR 206/07/0811), and the Institute of Environmental Technologies project reg. no. CZ.1.05/2.1.00/03.0100. We thank Tawny Chandler, Renáta Pešátová, Filip Trnka, Michal Zedek, Kateřina Havlíčková and Irena Šipošová for their help with this project. This paper was written in connection with the MSMT grants CzechGlobe—Reg. No. CZ.1.05/1.1.00/02.0073, and LC06073.

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Příloha C

Key factors affecting the predation risk of insects on leaves of trees in forests on a floodplain in the temperate region

Drozdová M., Šipoš J. & Drozd P.

European journal of Entomology

(Article in press)

Eur. J. Entomol. **110**(3): 000–000, 2013
http://www.eje.cz/pdfs/110/3/@
ISSN 1210-5759 (print), 1802-8829 (online)

Key factors affecting the predation risk on insects on leaves in temperate floodplain forest

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Key words. Diptera, Calliphoridae, *Calliphora vicina*, insect predators, living prey, temporal and spatial differences, clumped dispersal of attacks

Abstract. The predation on insects on leaves was measured by direct observation using live larvae of *Calliphora vicina* (Diptera: Calliphoridae) as bait placed on 15 common species of woody plants in a floodplain forest in the temperate region. The predation rate was measured in terms of the proportion of the larvae that were missing or had been attacked after 30 min of exposure on leaves. Despite the fact that the important predators differed during the course of a season, the most frequently recorded predators were birds and ants and less frequently recorded wasps and spiders. Analysis of the pattern in the distribution of the attacks confirmed that it is best described by a negative binomial distribution, which corresponds to a clumped dispersal of predation. Based on the results of the best-fitted generalized additive model, we could not reject an equal probability of attacks on the different species of woody plants. Further, predation at the forest edge was notably higher than in the forest interior. The model also predicted marked variations in the incidence of attacks during the course of a day and a season, with the attacks occurring mainly in three periods during the year and two during the day. In general, the sampling method used could become the standard measure of the risk of insects living on trees being attacked by predators in future studies.

INTRODUCTION

Despite recent advances in ecological methodology and quantitative analysis for determining the nature of the complex interactions between organisms and their environment (Bolker et al., 2009; Kilkenny et al., 2009; Csillery et al., 2010), little attention has been paid to determining the potential of a multifactorial approach for studying the risk to insects from predation. Some aspects of predation risk on insects have been studied in both tropical (Olson, 1992; Berger & Wirth, 2004; Koh & Menge, 2006) and temperate ecosystems (Steward et al., 1988; Weseloh, 1988; Church et al., 1997; Haemig, 1999; Lichtenberg & Lichtenberg, 2003). However, mostly single factors (or a class of factors, e.g. spatial, temporal and taxonomical) are tested separately for different groups of predators (e.g. birds: Bernays, 1997; Strong et al., 2000; spiders: Riechert & Lawrence, 1997; Lang et al., 1999; ants: Barton, 1986; Leponce et al., 1999).

For example, there are significant differences in the predation risk on different species of trees because of differences in their attractiveness to predators, particularly for tropical rainforests (Janzen, 1966; Novotny et al., 1999; Basset, 2001). Differences in predation risk are correlated with the abundance of herbivores on three species of *Salix* (Ishihara & Ohgushi, 2008) in a temperate ecosystem. There are also experimental studies on spatial variability in predation risk along vertical (Weseloh, 1988; Basset, 2003) and horizontal gradients, such as in the interior of a closed canopy forest compared with that at the edge of the forest or in the open (Koh & Menge, 2006; Valladares et al., 2006). There are few studies on the diurnal and seasonal activity of predators (Barton, 1986; Kaspari & Joern, 1993; Reichert & Lawrence, 1997; Remmel et al., 2011) and these are only occasionally tested (temperate: Lichtenberg & Lichtenberg, 2003; Remmel et al., 2009; tropics: Richards & Coley, 2007). This is despite the logical expectation that the risk of predation is likely to vary depending on the time of day or year, for example, due to differences in temperature and seasonal changes in ecosystems (Bernays, 1997; Lill & Marquis, 2001).

The results of the experiments cited above have been criticised (e.g. Sih et al., 2000) for underestimating the interactions between the factors. Unfortunately, it is not possible to produce a simple synthesis or compare the results of the different studies because they were obtained using different methods. Two key methods are used for measuring the risk of predation on trees. Free access of predators to prey is prevented by using exclosure experiments (Marquis & Whelan, 1994; Sipura, 1999; Berger & Wirth, 2004). This method is used mainly to study complex multitrophic interactions, such as bottom-up effects and top-down effects, and fitness of the prey or host plant foraged by the herbivore (Gunnarsson, 1996; Strong et al., 2000). In contrast, experiments using various types of baits (Olson, 1992; Karhu & Neuvonen, 1998; Novotny et al., 1999; Lichtenberg & Lichtenberg, 2003) allow direct contact between the prey and predator and provide more information on the characteristics of the taxa or guilds of predators, such as their species structures and the effects of prey dispersal (Church et al., 1997; Beauchamp, 2002), vegetation structure (Gunnarsson, 1996) or seasonal changes (Lang et al., 1999; Lill & Marquis, 2001; Lichtenberg & Lichtenberg, 2003).

In addition to the aforementioned factors affecting the accumulative risk of predation in space and time, many authors note that the risk of predation is greater when prey is abundant (e.g. Crawley, 1975; Turchin et al., 1999; Abrams & Ginsburg, 2000; Lombaert et al., 2006). They found that predation risk affects prey behaviour and leads to avoidance and dispersal of the prey (Jeffries & Lawton, 1984, Berdegue et al., 1996; recently, Skelhorn et al., 2011; Gonthier, 2012). On the other hand, there is a lack of information confirming that the distribution in space of the attacks by predators is patchily distributed even though the searching patterns of predators are well known.

It is clear from the above that there are very few multifactorial models that include various predators and the interactions between factors and those published are mainly for tropical rainforests and there are no similar studies for temperate ecosystems. Our goal, therefore, was to identify the significant factors affecting predation on insects on the leaves of trees and then develop a complex model for assessing the predation risk. We tested the following ecological variables: (a) tree species (15 tree species with varying herbivore species abundances and diversities), (b) habitat (forest interior and edge), (c) time of day, and (d) time of year.

MATERIAL AND METHODS

Study site

This field study on predation was carried out in a lowland floodplain forest within the Poodri Protected Landscape Area (total, 300 ha; 18°03–13´E, 49°42–48´N; Northern Moravia, Czech Republic). The area included three fragments of primary floodplain forest in close proximity to the regional capital of Ostrava along a 20-km embankment of the meandering River Odra. The area is characterized by flooded meadows and a number of shallow ponds. The forest vegetation consists of *Quercus*, *Ulmus*, *Tilia*, *Prunus* and *Fraxinus*.

Field experiment

Our sampling design was that previously suggested for comparing the predation risk between temperate floodplain forest and tropical lowland rainforest (Novotny et al., 2006). For the experiments, 15 locally common species of woody plants (*Acer campestre* L., *Acer platanoides* L., *Alnus glutinos* (L.) Gaertn., *Alnus incana* (L.) Moench., *Carpinus betulus* L., *Corylus avellana* L., *Fraxinus excelsior* L., *Padus avium* Mill., *Populus tremula* L., *Quercus robur* L., *Sambucus nigra* L., *Swida sanguinea* (L.) Opiz., *Tilia cordata* Mill., *Ulmus glabra* Huds., and *Ulmus laevis* Pallas) typical of floodplain forests in the temperate region, were selected.

The ecological attributes of the above woody plants (i.e. the abundance and diversity of herbivores as well as the abundance and frequency of the trees) were adopted from our plant–herbivore study performed simultaneously with the predation experiments. Only those folivorous insects that were feeding were hand-collected from the foliage of 15 species of trees throughout the 1999–2001 growing seasons. This resulted in 150 m^2 of foliage being inspected per species of tree. The estimates of the species richness and frequency of woody plants were based on total number of woody stems in 62 25 × 25 m quadrats (for details, see Novotny et al., 2006).

Predation risk was estimated by recording whether bait placed on leaves is attacked or missing (see Olson, 1992; Novotny et al., 1999). The bait consisted of live larvae (last instar; size, 1–1.5 cm) of the blowfly *Calliphora vicina* Robineau-Desvoidy (Diptera: Calliphoridae). These larvae are palatable and very vulnerable to attack (Lundgren et al., 2009) and thus previously used as model artificial palatable prey in several predator–prey experiments (Wilson et al., 1990; Lundgren et al., 2009; Remmel et al., 2009). Further, the last instars are of a suitable size for both vertebrate and invertebrate predators (Lang et al., 1999).

In each experiment (sample), 25 living larvae were pinned onto each tree for 30 min (one larva per twig separated by a minimum distance of about 25–30 cm) at breast height using entomological pins inserted into veins on the upper surface of leaves. Attaching larvae by pins to leaf veins prevents them from accidental falling off leaves and makes the removal of the pins by invertebrate predators impossible. The pins were marked with small coloured tags to avoid missing those that were accidentally dislodged. Baits continued to move actively throughout the duration of the experiment. After 30-min, during which we moved away from the tree upon which the test was performed, the presence of predators or missing larvae were recorded (the proportion of larvae attacked per tree was used as a response variable). The experimental sites were systematically changed during the course of the year to eliminate the possibility of birds learning to find larvae by searching for tags. Based on our experiences from a preliminary study in 2001 and other published experiments (Lichtenberg & Lichtenberg, 2003), pins that disappeared (confirmed after carefully searching for baits on the ground and nearby vegetation) were assumed to reflect bird predation. On the other hand, ants and wasps, which were the most frequently recorded invertebrate predators, were always observed feeding on the baits.

In total, 300 experiments with 7500 baits were conducted from May–September 2002 between 09:00 to 18:00 h. The following factors were recorded in each experiment: time of day (Hour), time of year (Day), species of woody plant (Species) and habitat (MicHab, i.e. forest interior or edge). Samples that were more than 20 m away from the edge of the forest were regarded as being in the interior of the forest. To maximise the balance in the design, the experiments were replicated twice each month for each species of tree species and type of habitat.

Data analysis

As a patchy dispersal is very often recorded in nature because resources are not uniformly distributed (Potthoff et al., 2006), we expected that the dispersal of predator attacks would follow a negative binomial distribution. Thus, the index of dispersion (the variance-to-mean ratio), Morisita's index of dispersion and goodness of fit to a negative binomial distribution with aggregation parameter k estimated by maximum likelihood were used to identify the patterns in the distribution of the attacks (Krebs, 1999). Index values significantly higher than 1 (or 0 for Morisita's index) indicated clumped (patchy) distributions. The dispersal of the attacks was analysed separately for each combination of habitat (interior, edge), month and time interval (2 h per interval) to distinguish between spatial and temporal distributions. For this reason, we used additional data from 2001 (not applicable for the other analyses due to the low number of replications for each combination). This approach allowed us to increase the number of samples for each combination and

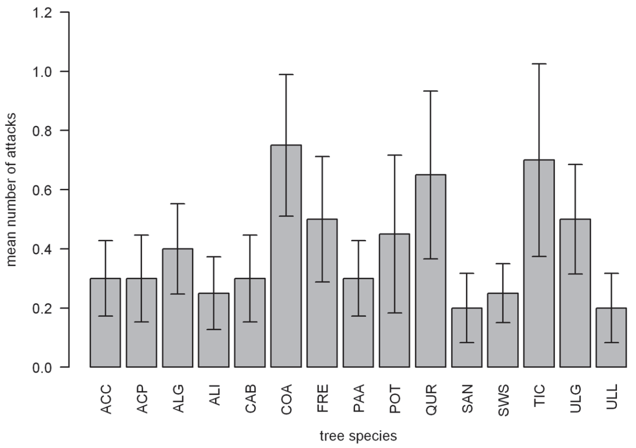

Fig. 1. The mean (± SE) of the number of attacks recorded per experiment on the different species of woody plants studied. ACC – *Acer campestre*; ACP – *Acer platanoides*; ALG – *Alnus glutinosa*; ALI – *Alnus incana*; CAB – *Carpinus betulus*; COA – *Corylus avellana*; FRE – *Fraxinus excelsior*; PAA – *Padus avium*; POT – *Populus tremula*; QUR – *Quercus robur*; SAN – *Sambucus nigra*; SWS – *Swida sanguinea*; TIC – *Tilia cordata*; ULG – *Ulmus glabra*; ULL – *Ulmus laevis*.

improve the validity of the results. However, we had to omit some combinations because of the low number of attacks.

Generalized additive models (GAM) were used to investigate the effect of the factors studied on the probability of attack. For those cases when the response variable was a probability and the model indicated overdispersion (the dispersion index was approximately 1.7 for our data), a quasibinomial distribution gave more reasonable results. The numerical variables Hour and Day were smoothed by using thin plate regression splines (Wood, 2006). The basis dimensions for both the terms were selected manually (k = 4 for Hour and k = 6 for Day) using the generalized cross validation (GCV) criterion, which is one of the best ways of estimating smoothing parameters. This criterion was also used for manual selection of the best parameters in the additive models (for more details, see Wood, 2006). All factors tested were added sequentially to the model using GCV and Cp Mallow's statistics criteria for model parameter selection (Mallows, 1973; Hocking, 1976) and the best fitting model comparisons (the lowest Cp and GCV values indicated the most parsimonious model).

The final model of the probability of attack was constructed based on the GCV, and Mallow's Cp ranking statistics. Both criteria are based on the maximum parsimony approach recently suggested for model selection, but mixing of criterion-based selection with standard measurement of significance is not recommended (Anderson, 2008).

All analyses were performed using R software 2.14.0 (R core development team, 2011) and several specific libraries: lattice 0.20-0 (Deepayan, 2008), vegan 2.0-1 (Oksanen et al., 2011), gam 1.04.1 (Hastie, 2011) and vcd 1.2-12 (Meyer et al., 2011).

RESULTS

A total 119 of the 7500 baits (1.6%) were attacked by predators, meaning that on average, 0.4 baits were attacked per experiment (standard deviation (SD) = 0.85; standard error (SE) = 0.05; maximum = 6 baits per experiment). The dominant groups of predators were birds (59.7%), ants (13.4%), Heteroptera (11.8%), Mecoptera (5.9%) and wasps (4.2%). Several other groups were recorded occasionally (spiders and carabid beetles). The maximum predation risk, measured as the average number of baits attacked per experiment, was recorded on *Corylus avellana* (0.75), *Tilia cordata* (0.7) and *Quercus robur* (0.65) and the minimum on *Ulmus laevis* (0.20) and *Sambucus nigra* (0.20) (Fig. 1).

Predation risk correlated neither with the abundance and frequency of particular species of trees nor with abundance and diversity of insect herbivores (Pearson's correlation coefficient was the highest for abundance of herbivores, r = 0.43; p > 0.1).

The results of all the tests used for determining the pattern of the attacks were consistent with our prediction of patchy dispersal. We found the variance-to-mean ratio of attacks per experiment to be significantly greater than 1 (I = 1.793, χ^2_{299} = 536.0, $p < 0.0001$) and the Morisita's

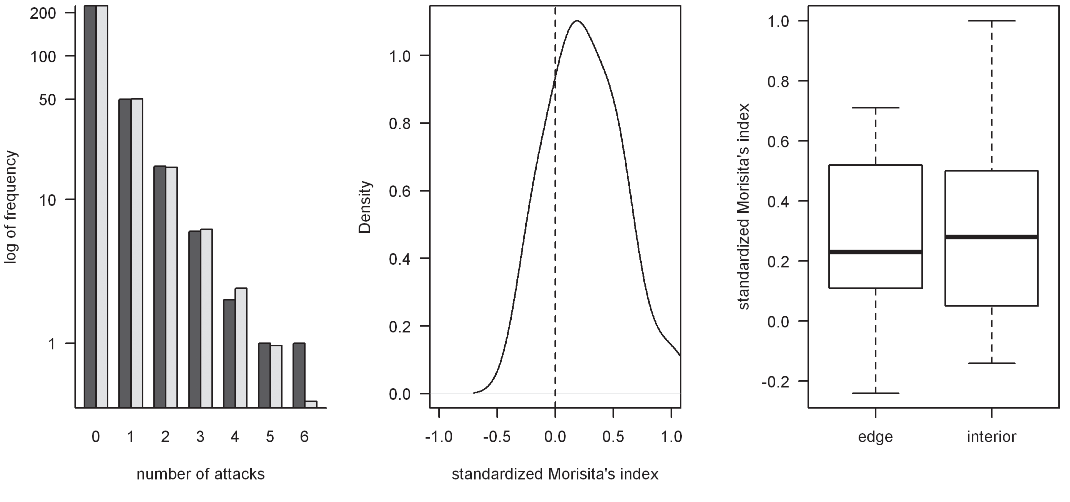

Fig. 2. The observed (dark grey) and theoretical negative binomially distributed (light grey) frequencies of attacks per tree plotted on a logarithmic scale (left), the probability density (empirical density function) of the standardized Morisita's indices (middle) for each combination of temporal and spatial variables (positive values indicates a patchy distribution), and a box plot comparing the standardized Morisita's indices for the edge and interior of the forest (right).

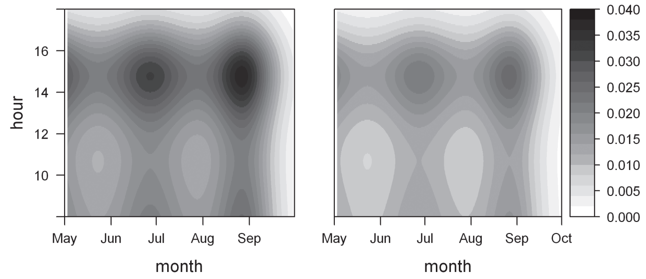

Fig. 3. A contour plot with predicted probabilities of attack by predators (grey scale on the right) for the most parsimonious model, including type of habitat (left, forest edge; right, forest interior), time of day and time of year.

index to be 2.98 (standardized Morisita's index = 0.5026); further, the goodness-of-fit test (maximum likelihood estimate of $k = 0.506$, $\chi^2_2 = 0.011$, $p = 0.995$) did not support a rejection of a negative binomial distribution (Fig. 2). Such outcomes can result from a patchy dispersal in time (attacks occur mainly within specific time intervals). However, we observed similar results for the pattern of distribution of attacks for each combination of the temporal and spatial variables. Nearly 75% of the standardized Morisita's indices calculated were positive (indicating a patchy dispersal). Negative indices (indicating a uniform dispersal) and indices equal to 0 (indicating a random dispersal) were found only for samples with a low number of attacks and the most frequent were for samples recorded in autumn.

The best fitting GAM model chosen by forward selection included three terms: microhabitat, time of day and day of the year (Table 1). All terms in the final model have weak but significant statistical support from the analysis of deviance (p-value$_{\text{MicHab}}$ = 0.096, p-value$_{\text{Hour}}$ = 0.067, p-value$_{\text{Day}}$ = 0.049). In contrast, we could not reject the hypothesis of an identical risk of predation on all species of woody plants. The final model predicts the risk of predation is highest at the edge of forest during late August and early September between 13:00–15:00 h (Fig. 3).

Table 1. Values of the statistics used in the selection of the best GAM model (GCV – generalized cross validation; Cp – Mallow's Cp; DevExpl – explained deviance).

Model	GCV	Cp	DevExpl
Null	1.2594	377.70	0.000
Species	1.3039	390.20	0.059
Hour	1.2358	370.67	0.037
MicHab	1.2328	369.82	0.028
Day	1.2098	362.79	0.070
MicHab + Hour	1.2182	365.37	0.057
MicHab + Day	1.2046	361.21	0.080
Hour + Day	1.1917	357.23	0.100
MicHab + Hour + Day	1.1903	356.74	0.107

Despite the overall low number of records of predation, we performed separate analyses for invertebrate and vertebrate predators, and found apparent temporal differences between predation by arthropods and birds. This was confirmed by the lack of a correlation between the two groups (Pearson's correlation coefficient r = –0.22, t = –0.99, df = 19, p-value = 0.3349). A peak in predation by birds was recorded during the morning in May and June while arthropods dominated in July between the hours of 09:00 to 11:00 and 15:00 to 17:00 (Fig. 4).

DISCUSSION

Our experiments on predation revealed that the distribution of attacks on bait attached to leaves was clumped, with no significant differences between species of trees but an important effect of habitat (higher predation risk at the edge than in the interior of the forest), time of the day and season. The important predators were birds and ants, but the frequency of their attacks varied during the year

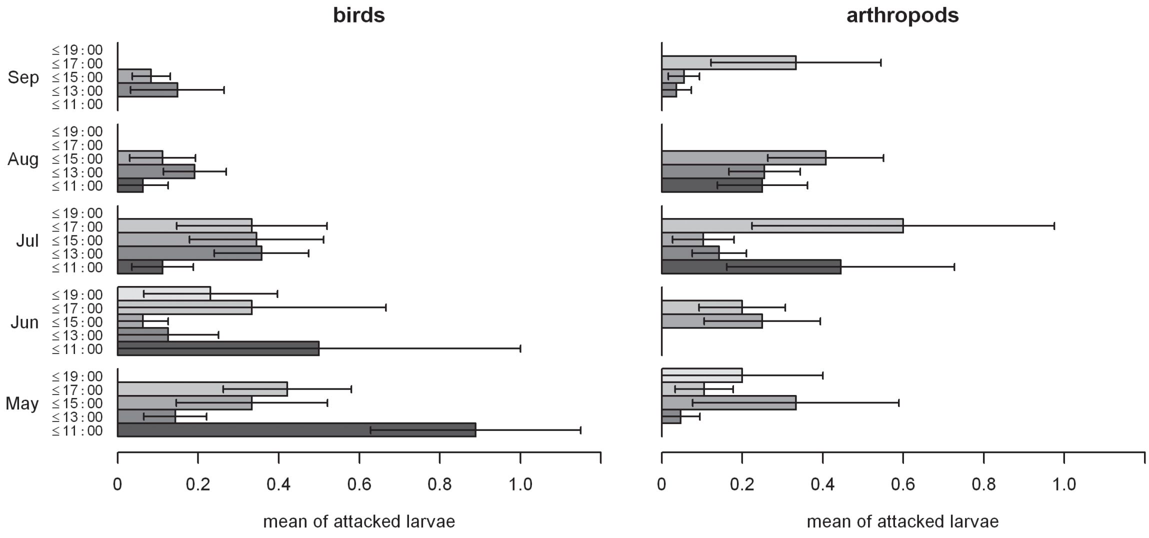

Fig. 4. A comparison of the mean (± SE) of the number of attacks recorded that were attributed to birds and arthropods at different times of the day in different months of the season (right-closed intervals).

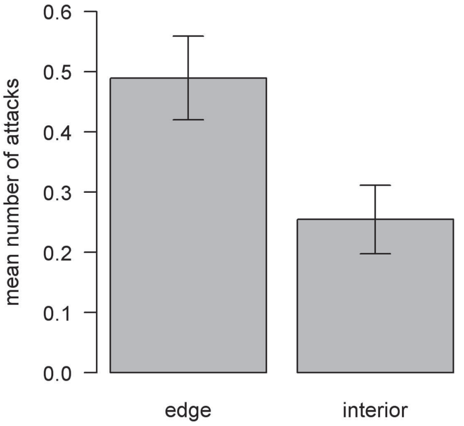

Fig. 5. The mean (± SE) of the number of attacks recorded on trees at the edge and interior of the forest.

and was dependent on their seasonal activity (cf. epigeic predators, Šipoš et al., 2011).

The analyses of the spatial distribution of attacks indicate that rates of predation in patches with equal densities of prey differed. This probably reflects random search for the first prey and then systematic searching in the surrounding area. Such behaviour is often mentioned as typical of birds and ants (Church et al., 1997; Beauchamp, 2002). On the other hand, these results should be interpreted cautiously, because very few attacks were recorded and we did not distinguish between these two groups in the analyses of the spatial distributions of the attacks.

As expected, our data did not provide a basis for rejecting the hypothesis of a non-random distribution of attacks on the different species of woody plants. This result is also supported by the non significant correlations between the average predation risk and features of the different species of trees (abundance, frequency, and number of herbivores and their diversity). Unlike parasitoids (Iwao et al., 2001), true predators probably have not evolved close interspecific interactions with plants in forests in temperate regions (Olsson et al., 2001) but have in tropical rainforests (Basset, 1995, 1996; Novotny et al., 1999). Significant differences were found only for those species like ants, which have a mutualistic relationship with plants (Janzen, 1966; Floren & Linsenmair, 1997; Fiala et al., 1994; Di Gusto et al., 2001).

The greater predation risk at the edge of the forest (Fig. 5) predicted by our final model, was previously recorded for the same predators as we studied (Olson, 1992; Haemig, 1999; Lichtenberg & Lichtenberg, 2003; Valladares et al., 2006). This may be due to a greater abundance and activity of insects (mostly herbivores) and more favourable microhabitat conditions at the edges of forests (Murcia, 1995; Didham et al., 1996; Cadenasso & Pickett, 2000; Zheng & Chen, 2000; Wirth et al., 2008). Moreover, wasps can have a notable effect at the edges of forest because it is warmer there than in forests (Steward et al., 1988; Lichtenberg & Lichtenberg, 2003).

Despite the fact that we could not include the entire range of diurnal and seasonal differences in predatory activity (see Fig. 3), our model did indicate three peaks of predation risk during the course of the growing season and two during the day. There are only a limited number of incidental records of the diurnal variation in the predation risk (Barton, 1986; Novotny et al., 1999; Berger & Wirth, 2004) and our model cannot predict the risk of predation either at night or early in the morning when there is a peak in the incidence of predation by birds (e.g. Hutto, 1981). However, a greater incidence predation early in the morning was partially apparent in the prediction of our model (i.e., the decline in the rate of predation that occurred after the expected early morning peak) and particularly notable was a shift in peak predation during the course of the year (Fig. 3, dark grey areas at the bottom of the left figure). Montllor & Bernays (1993) state that the high predation risk recorded at midday is due to the greater activity of invertebrates then because both the temperature and relative humidity are high at that time. At night the expectation is that the foraging activity of ants and other invertebrate predators is likely to be very low in ecosystems in temperate regions (Bernstein, 1979; Traniello, 1989). Moreover, for predators that orientate visually (including insectivorous birds) searching for prey is less effective at night. However, there is little experimental data on this, because recording attacks by predators at night is difficult. Novotny et al. (1999) used termites (*Microcerotermes biroi*) as bait to determine the risk of herbivorous insects being killed by predators during day and night in Papua New Guinea rainforests. They record marked differences in the composition of predators, but the differences in the probabilities of being attacked were not significant. Their results differ from those of Berger & Wirth (2004) who used exclosure experiments and revealed that the predation pressure on phasmids in rainforest in Panama was significantly higher at night than during the day (p-value < 0.001).

Consistent with the results of Holmes et al. (1979), Lill & Marquis (2001) and Lichtenberg & Lichtenberg (2003) and our unpublished data from the previous year (not used because of an unbalanced design for species and daytime), we recorded a greater predation risk at the beginning of May (using extrapolation, we estimated that the peak occurred at the end of April), with birds at that time the most important predators, at the end of June it was birds and ants and at the end of August wasps, as colonies of these insects were large and very active (MacDonald & Matthews, 1981; Stamp & Bowers, 1996).

Measuring the risk of predation is technically difficult and it is likely that the method used and the features measured could have biased the results. For this reason, exclosure and predator removal experiments are generally regarded as the best way of estimating the real effect of predation (absolute predation risk). However, it is important to note that our experiments were performed under identical conditions for each factor combination and that, it is thus possible to correlate relative differences in the number of attacks with predator activity within a study site (Novotny et al., 1999). Another issue usually discussed is the most suitable bait (Kaspari & Joern, 1993;

Berger et al., 2006). For generalist predators like birds and ants, size (Lang et al., 1999; Di Giusto et al., 2001; Mänd et al., 2007; Remmel & Tammaru, 2009; Remmel et al., 2011), palatability (Skelhorn & Rowe, 2006; Lundgren et al., 2009), mobility (Eubanks & Denno, 2000) and colour (Church et al., 1997) are the main characteristics determining the probability of a bait being attacked. The most widely used baits in studies in tropical forest are termites, which are highly palatable prey for ants and all the other important predators of herbivorous insects in the tropics (Olson, 1992; Leponce et al., 1999; Novotny et al., 1999). However, the baits most widely used in ecosystems in temperate regions are caterpillars (Bernays, 1997; Lill & Marquis, 2001; Lichtenberg & Lichtenberg, 2003). The larvae of *Calliphora vicina*, which we used in our experiments, are probably analogous to termite baits used in the tropics (see Lundgren et al., 2009). A very important characteristic is that the larvae attached to leaves are highly active and therefore likely to attract predators that orientate visually when searching for prey. It is known that the mobility of prey can increase their risk of predation by beetles (e.g. Marston et al., 1978; Eubanks & Denno, 2000) and spiders (Reichert & Lawrence, 1997). Finding prey by responding to visual stimuli is recorded for birds (Beauchamp, 2002) and wasps (Bernays, 1997). In most cases, the mobility of the prey seems to be more important than its nutritional quality (Bernays, 1997; Eubanks & Denno, 2000; Beauchamp, 2002). Although *Calliphora* larvae are not herbivores, the range of predators we recorded attacking them does not differ from the predator composition recorded in the previously cited experiments that used caterpillars. The low frequency of bird predation recorded by Lichtenberg & Lichtenberg (2003) may be because they did not include in their results the baits that disappeared and the baits were attached to the undersides of the leaves.

Despite these difficulties, our complex model of the risk of insects being killed by predators in forests in temperate regions is based on the results of very simple experiments using baits that are suitable for most insectivorous generalists. We consider this method to be very useful and believe that it is suitable for use as a standard method for directly measuring predation risk in the future.

ACKNOWLEDGEMENTS. We are very grateful to T. Kocurek and B. Varkockova for help with the field experiments and three anonymous referees for their constructive comments. The project was supported by the Grant Agency of the Academy of Sciences of the Czech Republic (GAAV B6187001), the Grant Agency of the Czech Republic (GACR 206/99/1112, GACR 206/07/0811), CzechGlobe, reg. no. CZ.1.05/1.1.00/02.0073, LC06073 and the Institute of Environmental Technologies project, reg. no. CZ.1.05/2.1.00/03.0100.

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Received February 27, 2012; revised and accepted December 20, 2012

Příloha D

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Journal of Applied Entomology

(Article in press)

JOURNAL OF APPLIED ENTOMOLOGY

J. Appl. Entomol.

ORIGINAL CONTRIBUTION

Effect of the canopy complexity of trees on the rate of predation of insects

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Keywords
baits, enemy-free space, enemy-free time
tri-trophic interactions

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Received: May 10, 2012; accepted: September 17, 2012

doi: 10.1111/jen.12015

Abstract

The effect of the complexity of tree canopies on the effectiveness of biological control of tree-dwelling insect herbivores by predators has been neglected. A complex canopy provides a greater variety of resources than a simple canopy, which may result in an increase in the abundance of both herbivores and predators in complex canopies and a higher predation rate. On the other hand, it may be more difficult to locate prey in trees with a complex canopy, which may lower the predation rate. The main aim of this study is to determine the relationship between predation rate and canopy complexity. We have used a system consisting of lime trees, larvae of blowflies as prey and naturally occurring predators (mainly birds and ants). The complexity of the canopy of 12 of the lime trees was reduced by pruning, and the predation rate was determined by recording the fate of prey pinned on each of the trees for 30 min several times during the course of a year. The predation rate was negatively associated with canopy complexity. We compare these results with those reported in the literature and contrary to the widely held view conclude that a negative relationship between predation rate and canopy complexity is a common phenomenon and can be expected to be reported in studies not only on ambush but also on predators that actively search for prey.

Introduction

Population dynamics of insect herbivores may sometimes be more affected by spatial complexity than the food quality of their host plants (Van Valen 1973; Lawton 1983; Halaj et al. 2000a; Riihimäki et al. 2005; Obermaier et al. 2008). This is because differences in canopy complexity may affect predator–prey interactions (Hunter and Price 1992; Tscharntke 1992; Clark and Messina 1998; Sipura 1999; Halaj et al. 2000b; Casas and Djemai 2002; Langellotto and Denno 2004; Tschanz et al. 2005; Riihimäki et al. 2006). It is unclear, however, whether this effect is positive or negative.

On the one hand, predators may survive better in more complex patches because in such patches there are more places where they can (i) find safe places for resting (Polis 1996), (ii) escape from intraguild predation and cannibalism (Langellotto and Denno 2004), (iii) find stable microclimatic conditions (Halaj et al. 2000a,b), (iv) find alternative food sources (Polis 1996) and (v) encounter more potential prey (Polis 1996; Langellotto and Denno 2004). High number of refuges, prey and alternative food sources can potentially enable predators to reach large abundances. This may result in a positive correlation between predation rate and canopy complexity (Lawton 1983; Halaj et al. 2000b; Kondoh 2003; Langellotto and Denno 2004; Nouhuys 2005).

On the other hand, locating prey on trees with complex canopies is more difficult; therefore, herbivores are less likely to be discovered there, and also residence time of predators is negatively correlated with tree canopy complexity (Clark and Messina 1998; Hawkins et al. 1993), which indicate it is more likely that the correlation between canopy complexity and predation rate is negative (Carroll and Janzen 1973; Andow and Prokrym 1990; Bell 1991; Clark and Messina 1998; Geitzenauer and Bernays 1996; Langellotto and Denno 2004).

Evidence from empirical studies is also contradictory (table 1). The results of most studies indicate that herbivores survive better in more complex habitats (Hartvigsen et al. 1995; Halaj et al. 2000b; Casas and Djemai 2002; Gingras et al. 2002). Riihimäki et al. (2006) also report a negative correlation between predation rate and canopy complexity for ambush predators, like spiders, but no correlation for actively searching predators, which visually scan the environment, like ants. Stamp and Bowers (1993) observed that predation activity of wasps and stinkbugs was negatively influenced by the size of the plant. They hypothesize that this is because plant size is positively correlated with number of refuges. Birds, which are also actively searching predators, use visual cues like damaged leaves or leaf shape during the foraging (Heinrich and Collins 1983; Murakami 1999). These visual cues are likely to be more difficult to detect in larger or more complex plants. Foraging behaviour of parasitic wasps was also influenced by plant complexity: on average, wasps spend more time on plants with low structural canopy complexity (Mackauer and Völkl 1993).

Table 1 Review of hypotheses on the relationship between habitat complexity and predation. The first column indicates whether the hypothesis 'habitat complexity is negatively correlated with predator and parasitoid activity' is confirmed (+) or not supported (–) by empirical data

	Detailed description of the variables measured	References
+	Parasitism was higher on plants with a simple structure	Gingras et al. 2002
+	Parasitism rate was higher on simple surface of plant parts	Andow and Prokrym 1990
+	Height and density of the vegetation affected beetle oviposition positively and egg parasitism negatively	Obermaier et al. 2008
+	The probability that egg clutches will be present increasing with decreasing habitat complexity	Meiners and Obermaier 2004
+	Predators captured aphids at higher rates on plants with less complicated architecture	Clark and Messina 1998
+	Predators are more effective on smaller-sized plants	Hartvigsen et al. 1995
–	Larvae survived worse in more complex trees, if predation by ants was not prevented	Riihimäki et al. 2006
–	Needle density reduction and branch thinning led to decline in both prey and predator abundance	Halaj et al. 2000b
–	Increased habitat complexity resulted in large and significant increase in natural enemy abundance	Langellotto and Denno 2004

Here, we hypothesize that a negative correlation between predation rate and canopy complexity is a common phenomenon and show that it occurs in actively searching predators like birds and ants.

Materials and Methods

Field experiment

The study was conducted in a temperate flood-plain forest near the village of Grygov, Czech Republic (49° 41′44.949″N, 18°2′30.755″E). This area consists of a large homogeneous fragment of original flood-plain forest (fig. 1). Typical tree species in the study area are lime, ash, oak and hornbeam.

Predation rate was measured three times per month from April to October 2010, that is, 21 times, and measured at a randomly chosen 30-min interval between 8 a.m. and 2 p.m. Predation rate was calculated as proportion of attacked larvae per 20 baits. The tree chosen for this study was lime (*Tilia* spp.), because it is characteristic of this biotope and abundant. Twenty-four trees, each about 2 m tall, with similar crown complexity were chosen. Twelve of these trees (control group) were left untouched and the crown complexity of the remaining 12 trees reduced by removing all third and higher order branches (Riihimäki et al. 2006). Canopy complexity is represented by the density of twigs and leaves which form canopy of the tree. Canopy complexity can be artificially reduced by the reduction in branchiness (clipping the higher order branches) or by reduction in foliage (clipping the first-order branches to avoid changing the branching pattern itself) (Riihimäki et al. 2006). Predation by ants is determined to a large extent by whether the saplings are within the territory of ants. To minimize the effect of the distribution of ant colonies in the study area pair sly adjusted trees were selected one which was the control and the second was pruned. In temperate ecosystems, ants build their nests on the ground and are active during the whole growing season (Floren et al. 2002; Lichtenberg and Lichtenberg 2003). The branches were removed before bud burst to minimize the chance of the trees responding to pruning. Pruning the tree can induce growth changes in leaves and buds. Therefore, we have chosen similar-sized trees with similar canopy complexity, and after pruning, we still controlled the canopy size of all trees. The predation rate was measured by pinning twenty blowfly larvae to branches on each tree and recording the number eaten by predators after 30 min. After 30 min, the majority of the insect predators was still on the baits and therefore could be identified. Predation was attributed to birds when the bait plus pin were missing. We also observed the trees using binoculars to determine the species of birds. Live larvae of *Calliphora vicina* Robineau Desvoidy, 1930 (Diptera, Calliphoridae) were used as the bait and were each attached to a branch of a tree by an entomological pin inserted through the caudal region of their body. Our experiment was situated in a temperate ecosystem; therefore, the bait had to be a species normally occurring in this kind of ecosystem. Furthermore, the size of larvae (about 1.5 cm) seems to be sufficient for a wide range of predators and larvae are lacking any type of defence mechanism (Lichtenberg and Lichtenberg 2003; Remmel et al. 2009).

Data analysis

Data were analysed using the statistical program R (R Development Core Team 2009). The generalized linear model (GLM) was used with binomial error distribution and link function logit (dispersion parameter was 1.414) to investigate relationships between the variables, month and day (continuous variables), canopy complexity and individual trees (nominal variables). Standard errors were corrected using a quasi-binomial distribution to compensate for over-dispersion (Pinheiro and Bates 2000). We used binomial distribution because the response variable was calculated as the proportion of attacked larvae per 20 baits. The variables in the GLM model were ordered using stepwise procedure. The most parsimonious combination of environmental variables was selected based on lowest Akaike information criterion (AIC) by combining both forward and backward selection (Burnham and Anderson 2002).

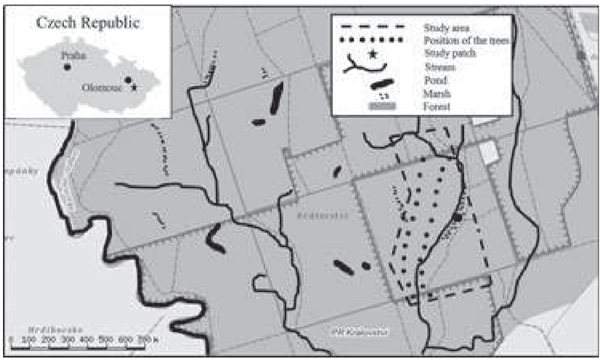

Fig. 1 Map of the research area.

To test the effect of tree structure on predation rate, function in R-generalized linear mixed models using penalized quasi-likelihood (glmmPQL, part of MASS package) with quasi-binomial error distribution was used (Venables and Ripley 2002). Predation rate was the dependent value and canopy complexity the explanatory variable. Effect of the tree was proved because predation experiments were repeated on each tree throughout the season. Therefore, we used each tree as random effect, and each tree was nested within the particular tree-pair in the mixed model to avoid pseudo-replication.

To analyse diurnal and seasonal variation in predation, we used the generalized additive model (GAM). The variables time and day were smoothed using a cubic regression spline. Degree of smoothness for GAM model terms was estimated using the generalized cross validation criterion. Generalized additive model with spline methods was used because the response curve was not constrained. Effect of explanatory variables on predation was tested by the analysis of deviance using F-test, because it is a robust test for over-dispersed data.

Results

We recorded 789 predator attacks on a total of 5760 baits (252 samples). The most abundant species of ants were *Myrmica rubra*, *Lasius brunneus* and *Lasius platythorax* and most abundant species of birds *Parus major*, *Cyanistes caeruleus*, *Sitta europaea* and *Dendrocopos* spp. The best and the most parsimonious model based on the lowest AIC was fitted by forward and backward selection including the following variables: Time of the season + Time of the season 2 + Experiment + Time of the day + Tree (table 2). Model explained 49.3% (adjusted R^2) of the data deviance.

Predation rate was significantly higher in the pruned trees (d.f. = 2, resid. d.f. = 11, F = 323.19, $P < 0.001$; fig. 2). Ants (77%) and birds (20%) were the predominant predators, followed by Dermaptera (2%) and Hemiptera (1%). Both the diurnal and seasonal patterns of predation by ants and birds differed (figs 3 and 4). Birds showed a diurnal variability in predation rate ($\text{d.f.}_{\text{spline}} = 3$, F = 26.46, $P < 0.001$; fig. 3) but not ants ($\text{d.f.}_{\text{spline}} = 3$, F = 0.693, P = 0.557; fig. 3). Birds attacked baits mainly in the

Table 2 Results of the analysis of deviance of the factors influencing predation rate included in the generalized linear model

	d.f.	Deviance	Resid. d.f.	Resid. dev.	F	Pr(> F)
NULL			287	51.064		
Time of the season	1	15.4336	286	35.630	157.4729	< 0.001
Time of the season 2	1	2.0811	285	33.549	21.2339	< 0.001
Experiment	1	2.4271	284	31.122	24.7643	< 0.001
Time of the day	1	0.0314	283	31.091	0.3089	0.57886
Tree	22	3.5854	261	26.710	1.6629	0.034127

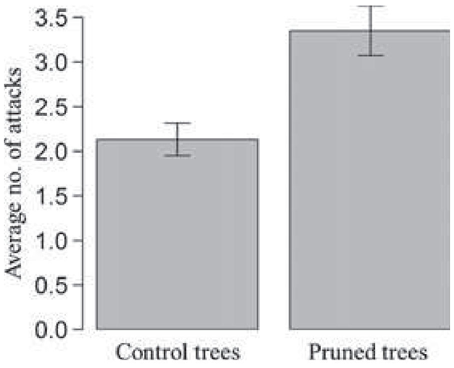

Fig. 2 Average number of attacks recorded on control and pruned trees. Vertical bars show standard error.

morning at around 8:00 (fig. 3). Predation by birds attained its maximum in May, while predation by ants increased exponentially throughout the entire season ($d.f._{spline} = 3$, $F = 146.4$, $P < 0.001$; $d.f._{spline} = 3$, $F = 56.74$, $P < 0.001$; fig. 4).

Discussion

Contrary to previous results from Riihimäki et al. (2006), we conclude that insects feeding on trees with a reduced branchiness are in greater danger of being eaten by predators. More complex patches provide, not only spatial, but also temporal refuges, which means that a predator must search longer to find prey in a more complex space. This means that herbivorous insects living in the large complex canopies of old trees have a greater chance of escaping from their enemies in space and time. We also conclude that in studies of predation similar to that presented here, baits for attracting predators should not be fixed at the same place for a long time, because this might lead to predators memorizing the positions of the baits.

Riihimäki et al. (2006) report a negative correlation between predation by spiders and tree canopy structure but not for ants and hypothesize that this is because ants forage actively in the canopy. They conclude that such correlation is more likely to hold for ambush predators, like spiders, than for actively searching predators, like ants. This contradicts, however, the negative correlation recorded between the rate of predation by parasitoids and tree canopy structure, as parasitoids also actively search for hosts (Gingras et al. 2002; Meiners and Obermaier 2004; Riihimäki et al. 2006), and other results (Hartvigsen et al. 1995; Halaj et al. 2000b; Casas and Djemai 2002; Gingras et al. 2002).

Predation rate on the trees can be influenced by the predator–prey ratio. Previous studies of species richness on the trees proved that the abundance of insect guild structure peaked in different times of the year (Southwood et al. 2004; Stork and Hammond 2012).

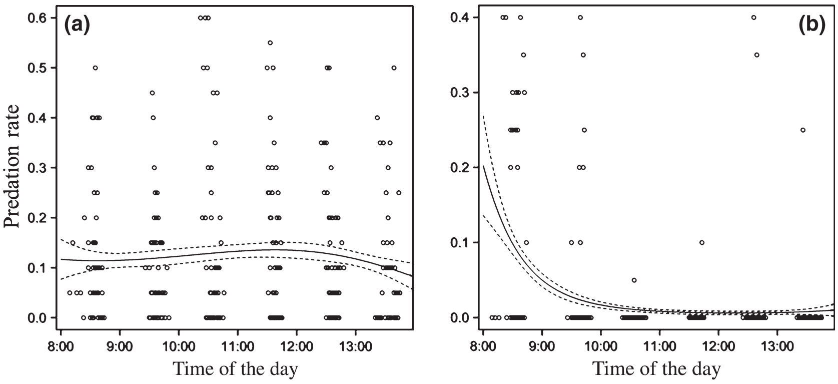

Fig. 3 Relationships between predation rate and the time of the day for (a) ants and (b) birds. The standard error of the regression curve is indicated by the dashed lines. Predation rate was calculated as the proportion of the attacked larvae out of the total number of baits. Smoothed line and standard errors were predicted by the generalized additive model.

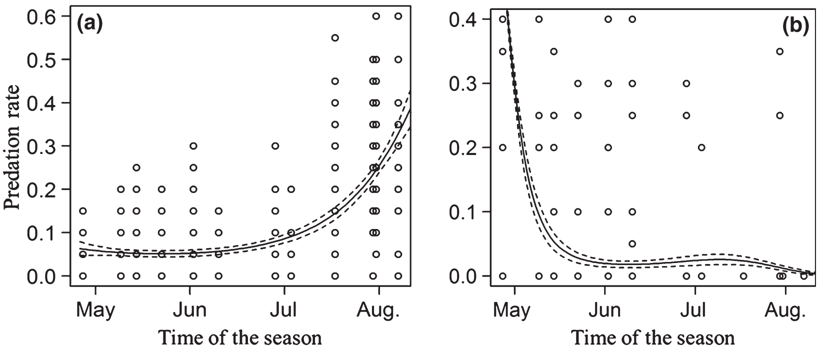

Fig. 4 Relationships between predation rate and the time in the season for (a) ants and (b) birds. The standard error of the regression curve is indicated by the dashed lines. Predation rate was calculated as the proportion of the attacked larvae out of the total number of baits. Smoothed line and standard errors were predicted by the generalized additive model.

Predator–prey ratio also shows a significant trend during the growing season (Southwood et al. 2005). In our study, we measured predation rate during the whole growing season. Therefore, our outcomes are not biased by its temporal fluctuations.

Our method enabled us to monitor the diurnal and seasonal activities of predators, which yielded some additional interesting results. In particular, increased temperature boosts the running speed of ants, and therefore, they can forage over a larger area (Taylor 1977), which is in accord with the exponential increase in the rate of predation by ants during the growing season. The colonies also increase in size and require more food. Birds exerted the highest predation rate in late May, which coincides with their nesting period (Tinbergen 1960; Royama 1970).

In our experiments, ants and birds were the main predators and they attacked fewer larvae in control than in pruned trees, which indicate that there is a negative correlation between the rate of predation by birds and ants and tree canopy structure. Explanation of the discrepancy between our and Riihimäki et al. (2006) results may be in the different methods used to measure predation. Riihimäki et al. (2006) used baits that were located at the same place for a long period. Therefore, ants could have learned to find food at this place (Bell 1991; Nicolis and Deneubourg 1999). It is well documented that many social hymenoptera recruit other foragers if they find a rich food source (Bell 1991). Similarly, birds can develop a search image and as a consequence they spend more time by foraging in areas, where prey is abundant (Church et al. 1997).This could have resulted in equal larval survival they record on both the control and experimental trees. In our experiment, we measured predation rate after 30 min of larval exposure. This makes a learning response to the availability of prey by either the birds or ants unlikely. We feel that this is more realistic, as in the field the abundance of prey is not artificially maintained at the same level for a long period of the time.

Acknowledgements

This study was supported by Grant No. PrF_2010_021 from the Internal Grant Agency of Palacky University in Olomouc, grant MSMT LC 06073 from the Ministry of Education of the CR and by CzechGlobe – Centre for Global Climate Change Impacts Studies, Reg. No. CZ.1.05/1.1.00/02.0073. We would like to thank Prof. Anthony F. G. Dixon for his help with language and for valuable comments on the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Supplement table of original data.

Příloha E

Predation risk for insect living in moss cushions: comparison between different strata of mountain forest

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Nowellia Bryologica 38: 31-35

Predation risk for insects living in moss cushions: comparison between different strata of mountain forest

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Résumé

Le risque de prédation est un des plus importants facteurs pouvant affecter la vie de chaque espèce animale. Il existe bon nombre d'adaptations qui permettent d'éviter la détection ou la capture par des prédateurs et qui sont la conséquence directe des effets de la prédation.

Nous appelons ces manières de vivre réduisant ou éliminant le risque de prédation (ou la vulnérabilité des espèces) «l'espace sans ennemi».

De récentes études mettent en évidence que la distribution spatiale de la proie peut également être le résultat de la prédation, spécialement quand les espèces préfèrent «s'échapper du champ de bataille» vers des refuges au faible risque de prédation occasionné par plusieurs facteurs.

L'hypothèse principale de notre recherche est que les coussins de mousses sont un habitat unique qui peut servir de refuge contre les prédateurs. En nous basant sur la comparaison du risque de prédation dans deux habitats montagneux et micro-habitats au sol (coussins de mousse vs. litière), nous avons découvert la structure spécifique des prédateurs d'insectes, probablement unique pour les micro-habitats composés de mousses.

Cette étude a été subventionnée par le grant NO. 206/07/0811 (spécificité des hôtes et diversité des espèces des communautés d'insectes bryophages – analyse des facteurs clé) de la Grant Agency de la République tchèque.

Abstract

Predation is a process of a major importance affecting the distribution, abundance, and diversity of species in ecosystems. Thus ecological research of predation is very intensive at present and very sophisticated designs are proposed to measure complex phenomena such as existence of an enemy-free space and tritrophic interactions. In our research we used living baits for a measurement of the predation risk in various microhabitats along vertical gradient (surface level, moss cushions, bushes and trunk of trees). The main hypothesis of our research is that moss cushions are unique habitat that can provide a shelter against predators. Based on the comparison of the predation risk in different strata in two mountain habitats and ground microhabitats (moss cushions vs. litter) we tried to describe specific structure of insect predator guild probably unique for the moss microhabitats.

Introduction

Predation risk is one of the very important factors affecting the whole life history of each

animal species (Hairston et al., 1960). The existence of predation strongly influences the host--enemy coevolution (Kniskern & Rausher 2001). As the consequence of a predation pressure there is a number of various adaptations to avoid detection or capture by predator (Lichtenberg & Lichtenberg 2003, Novotný et al. 1999). These ways of living that reduce or eliminate predation risk or species vulnerability are commonly called “enemy free space” (Jeffries & Lawton 1984, Strong et al. 2000, Weseloh 1988, Denno et al. 1990). Recent studies give us evidence that also spatial distribution of the prey can be the result of predation especially when species prefer to “escape from the battlefield” to refugees with low predation risk caused by various factors (Novotný et al. 1999, Schuler 1990).

The most of the studies that tested predation pressure measure the predator impact by comparison of sites where predator is eliminated and control sites (e.g. Gunnarsson 1996, Haemig 1999). Various cages or boxes that avoid the access of natural enemies are often used in these "enclosure" experiments (Low & Conner 2003). Contrary we can study the contrast between a number of baits attacked by predator under different conditions. First method is more sufficient for total predation pressure estimates when second method can measure relative predation rate and it is more flexible and less difficult. Of course there is also a problem with the type of the bait (Church et al. 1997).

Despite a number of predation studies concerned tritrophic interactions of predator, prey and major plant taxonomic groups, especially woody species important for pest management and plant herbivorous studies (Bianchi et al. 2005, Jones & Sieving 2006) informations about predation risk within moss cushions are very sporadic (Wotton & Mcrritt 1988). Although mosses are mentioned as potential shelters for arthropods and bryophytes provide them great camouflage (Gerson 1982).

The main object of our study was to describe diversity and structure of insect predators within moss cushions in comparision with other vertical strata.

Methods

Experiments were performed on two sites in the submontane forest of the Beskydy Mountains and the Jeseníky Mountains in the Northern Moravia (Czech Republic) during the years 2004-2008. Living larvae of blowfly *Calliphora vicina* (Calliphoridae, Diptera) that are palatable and tasteful for most of insect predators were used as a baits. The great advantage is also their agility during all exposition interval. All the time 20 baits for each test were pinned on leaves, trunk, phyloids or forest floor in studied microhabitats: bushes of blueberries (*Vaccinium myrtillus*), moss cushions (*Polytrichastrum formosum*, *Polytrichum commune*, *Dicranella* sp.), trunk of spruce (*Picea abies*). Attacked and missing larvae were counted and presence predators were identified into higher taxonomical levels after 30 minutes of the exposition time.

Results and discussion

Taxonomical structure of predators is approximately same for similar microhabitats at the both localities (Fig 1 and Fig 2). The most dominant taxa of predators on the surface level are Formicoidea and Araneida - the major groups of diurnal surface active invertebrate predators in temperate forests. Ecological dominance of ants is represented by their biomass, and estimation for different environments shows that they contribute 15–20% of the total temperate ter-

restrial animal biomass (Schultz 2000). Also spiders are established in all terrestrial ecological niches (Platnick & Norman 2009, Greenstone 1999).

Predation rate inside the moss cushions is almost same to rate on the ground (litter), but there are obvious differences in the taxonomical structure of the predators (cf. Fig 1 and Fig 2). Millipedes (Chilopoda) were found as a dominant predators on *Dicranella* and inside the cushions of *Polytrichum* followed by spiders and beetles (Carabidae and Staphylinidae). Simultaneously Chilopoda were recorded also from the ground below *Vaccinium*, where mosses occurred. It is evident that they are well adapted to dense vegetation typical for moss cushions.

Bird predation that dominated on the leaves of *Vaccinium* can be explained by better accessibility for birds in the Jeseníky site where the sampling was maintained near forest clearance.

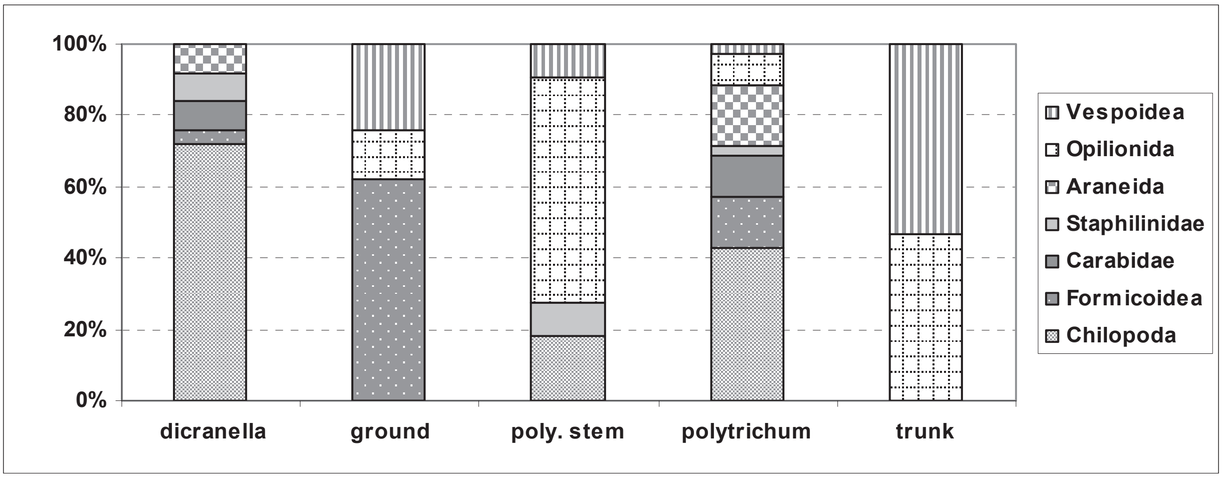

Fig 1: Proportion of predator taxa in different microhabitats in the Beskydy Mountains. (poly.stem = terminal part of *Polytrichum*, polytrichum = inside cushion of *Polytrichum*)

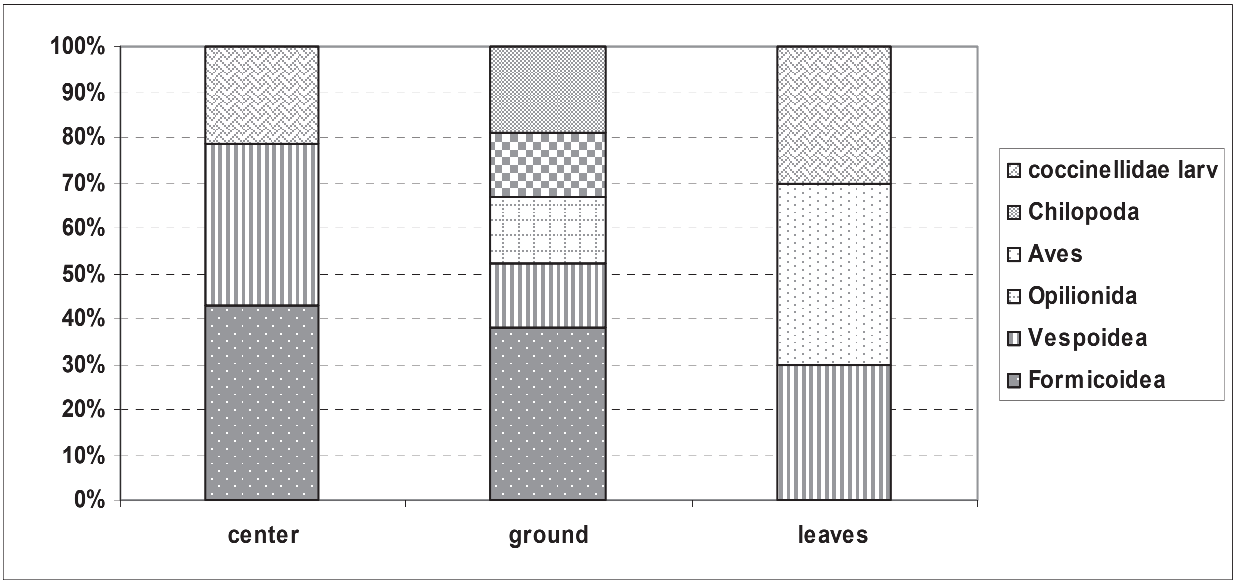

Fig 2: Proportion of predator taxa in different microhabitats within *Vaccinium* in the Jeseníky Mountains.

Analysis of variance shows significant differences of predation risk between different microhabitats within moss cushion and other strata in the Beskydy site ($p<0.001$, Fig 3). The highest probability of predation was found inside the cushion of *Polytrichum*. Predation of the baits

mounted on the terminal parts of *Polytrichum* was same as predation rate on the trunk of trees.

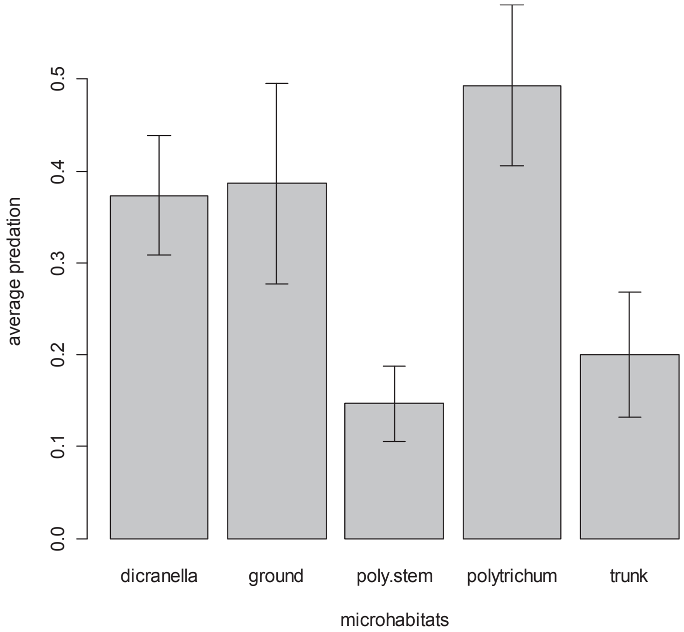

Fig 3: Mean number of attacks per experiment (with standard error).

The most intensive predation risk was recorded from the forest ground in the Jeseníky Mts site. Higher predation was probably caused by extreme abundance of ant nests (*Formica lugubris*) and relatively high heterogeneity of the habitat in comparison with spruce wood monoculture in the Beskydy Mts. site.

Acknowledgements

This study was supported by the grant No. 206/07/0811 (Host specificity and species diversity of bryophagous insect communities – key factors analysis) from the Grant Agency of the Czech Republic.

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