Université de Montréal

Impacts de l'intensification agricole et de la structure du paysage sur les relations tri – trophiques entre un oiseau hôte, des mouches ectoparasites et leur parasitoïdes.

par
Simon P. Daoust

Département de sciences biologiques, Institut de recherche en biologie végétale
Faculté des arts et des sciences

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Université de Montréal
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Cette thèse intitulée :

Impacts de l'intensification agricole et de la structure du paysage sur les relations tri – trophiques entre un oiseau hôte, des mouches ectoparasites et leur parasitoïdes

présentée par :

Simon P. Daoust

a été évaluée par un jury formé des personnes suivantes :

Christopher Cameron Ph.D.
président-rapporteur

Jacques Brodeur Ph.D.
directeur de recherche

Jade Savage Ph.D.
co-directrice

Patrick James Ph.D.
membre du jury

Lenore Fahrig Ph.D.
examinateur externe

…………………………………………..
représentant du doyen

Résumé

L'intensification des pratiques agricoles a été identifiée comme cause majeure du déclin de la biodiversité. Plusieurs études ont documenté l'impact de la fragmentation du paysage naturel et de l'agriculture intensive sur la diversité des espèces, mais très peu ont quantifié le lien entre la structure du paysage et les interactions trophiques, ainsi que les mécanismes d'adaptation des organismes. J'ai étudié un modèle biologique à trois niveaux trophiques composé d'un oiseau hôte, l'hirondelle bicolore *Tachycineta bicolor*, de mouches ectoparasites du genre *Protocalliphora* et de guêpes parasitoïdes du genre *Nasonia*, au travers d'un gradient d'intensification agricole dans le sud du Québec. Le premier objectif était de déterminer l'abondance des espèces de mouches ectoparasites et de leurs guêpes parasitoïdes qui colonisent les nids d'hirondelles dans la zone d'étude. La prévalence de nids infectés par *Protocalliphora* spp. était de 70,8% en 2008 et 34,6% en 2009. Le pourcentage de nids comprenant des pupes de *Protocalliphora* parasitées par *Nasonia* spp. était de 85,3% en 2008 et 67,2% en 2009. Trois espèces de *Protocalliphora* ont été observées (*P. sialia, P. bennetti* et *P. metallica*) ainsi que deux espèces de *Nasonia* (*N. vitripennis* et *N. giraulti*). Il s'agit d'une première mention de *P. bennetti* et de *N. giraulti* dans la province de Québec. Mon deuxième objectif était d'évaluer l'impact de l'intensification agricole et de la structure du paysage sur les relations tri-trophiques entre les organismes à l'étude. Les résultats révèlent que les réponses à la structure du paysage de l'hirondelle, de l'ectoparasite et de l'hyperparasite dépendantent de l'échelle spatiale. L'échelle spatiale fonctionnelle à laquelle les espèces répondent le plus varie selon le paramètre du paysage modélisé. Les analyses démontrent que l'intensification des pratiques agricoles entraîne une diminution des populations d'oiseaux, d'ectoparasites et d'hyperparasites. De plus, les populations de *Protocalliphora* et de *Nasonia* sont menacées en paysage intensif puisque la dégradation du paysage associée à l'intensification des pratiques agricoles agit directement sur leurs populations et indirectement sur les populations de leurs hôtes. Mon troisième objectif était de caractériser les mécanismes comportementaux permettant aux guêpes de composer avec la variabilité de la structure du paysage et de la qualité des hôtes. Nos résultats révèlent que les femelles *Nasonia* ajustent la taille de leur ponte en fonction de la taille de la pupe hôte et de l'incidence d'hyperparasitisme. Le seul facteur ayant une influence déterminante sur le ratio sexuel est la proportion de paysage dédié à l'agriculture intensive. Aucune relation n'a été observée entre la structure du paysage et la taille des filles et des fils produits par les femelles *Nasonia* fondatrices. Ce phénomène est attribué aux comportements d'ajustement de la taille de la ponte et du ratio sexuel. En ajustant ces derniers, minimisant ainsi la compétition entre les membres de leur progéniture, les femelles fondatrices sont capables de maximiser la relation entre la disponibilité des ressources et la valeur sélective de leur progéniture. En conclusion, ce travail souligne l'importance de considérer le contexte spatial des interactions trophiques, puisqu'elles influencent la biodiversité locale et le fonctionnement de l'écosystème.

Mots clés : intensification agricole, échelle spatiale fonctionnelle, interactions trophiques, taille de ponte, ratio sexuel, hirondelle bicolore, *Protocalliphora*, *Nasonia*.

Abstract

Landscape fragmentation and homogenization are considered to be the main causes of the worldwide decline in biological diversity. The degradation of habitat quality is mainly caused by the expansion and intensification of human land-use activities, primarily for agricultural purposes. Many studies documented the impact of landscape fragmentation and agricultural intensification on the overall fitness of animals across various taxa, but few works have studied this phenomenon in relation to trophic interactions. Here, we investigated the effects of landscape structure on the tri-trophic interactions between a bird host (the Tree Swallow *Tachycineta bicolor* (Vieillot)), its blowfly ectoparasites (*Protocalliphora* Hough), and their parasitoid wasps (*Nasonia* Walker) along a gradient of agricultural intensification covering 10, 200 km^2 in southern Québec, Canada. The first objective was to describe the assemblages of *Protocalliphora* and *Nasonia* species found in Tree Swallow nests within our system. The prevalence of nest infestation by *Protocalliphora* was of 70.8% in 2008 and 34.6% in 2009. The percentage of nests containing *Protocalliphora* pupae parasitized by *Nasonia* spp. was of 85.3 % in 2008 and 67.2% in 2009. Three species of *Protocalliphora* were collected (*P. sialia*, *P. bennetti* and *P. metallica*) and two species of *Nasonia* (*N. vitripennis* and *N. giraulti*). Secondly, I evaluated the impact of landscape structure and agricultural intensification on the number of Tree Swallow fledglings, number of *Protocalliphora* per nest and the level of hyperparasitism by *Nasonia*. Our results revealed that organisms from different trophic levels perceived the landscape at distinctive spatial extents. This perception, however, differed based on whether the proportions of intensive or extensive culture in the landscape were considered. Furthermore, the number of Tree Swallow fledglings, the abundance of *P. sialia* and the level of hyperparasitism by *N. vitripennis* all decreased with an increase in the proportion of intensive culture in the landscape. *Protocalliphora* and *Nasonia* were more susceptible to extinction within highly intensive landscapes as they are confronted with both the direct effect of habitat degradation on their populations and the indirect effect of habitat degradation on their host populations. The last objective was to investigate how parasitoid wasps respond to environmental variability. We showed that the size of the *P. sialia* pupae hosts decreased in more intensive landscapes. Wasps clutch size was shown to increase within increasing host size and the sex ratio of offspring produced by *N. vitripennis* became more male biased as the proportion of intensive culture increased in the landscape. In addition, both female and male size was influenced by resource availability (size of host and number of competitors). Our data indicate that by producing smaller male biased clutches in the smaller hosts within intensive landscapes, females were able to respond to poor environments and maximize the size of their offspring. To conclude, this work highlights the importance of considering the landscape context of trophic interactions, as these interactions dictate local biodiversity and ecosystem function.

Key-words: agricultural intensification, functional spatial scale, trophic interactions, clutch size, sex ratio, Tree Swallow, *Protocalliphora*, *Nasonia*.

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AIC: critère d’information d’Akaike

AIC w_i: poids du critère d’information d’Akaike

ANOVA: analyse de variance

bp: paire de bases

***et al.*:** et autres

GIS: service informatique géographique

ID: identité

KW: analyse non-paramétrique Kruskal-Wallace

LMC: « local mate competition theory »

df: degré de liberté

MEGISD: « maternal effect gene imprinting sex determination »

msd: gène d’effet maternel

N: nombre de réplicas

p: probabilité

SD: écart type

spp.: abréviation latine indiquant plusieurs espèces

zsd: déterminant de sexe zygotique

∅: rayon

À ma mère,

parce que tu m’as toujours encouragé à rêver

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Après trois ans de maturation, ma thèse est finalement prête à éclore. Le moment est donc venu pour moi de vous remercier tous, vous qui m'avez guidé, soutenu et inspiré. Premièrement, ce travail n'aurait jamais vu la lueur du jour sans le soutien de mon directeur de thèse, Jacques Brodeur. Merci d'avoir encouragé toutes mes idées et mes initiatives. J'ai sincèrement apprécié de travailler avec toi et je te suis très reconnaissant pour le temps que tu m'as consacré et toutes les opportunités que tu m'as données depuis trois ans. Je suis aussi très reconnaissant envers ma co-directrice Jade Savage, qui a su partager avec moi sa passion et son enthousiasme pour la science et l'enseignement. Merci de m'avoir accueilli chez toi pendant ces semaines de 'bio-mol'. Mes remerciements vont aussi à Marc Bélisle et Dany Garant, les grands architectes du programme 'hirondelle et intensification agricole'; grâce à leur soutien, mon projet a pu prendre forme. Merci à tous de m'avoir guidé à travers la plus importante étape de ma vie intellectuelle.

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Plan de la thèse

Chapitre 1. Dans cette section, je contextualise et j'introduis le lecteur à la problématique de ma thèse de doctorat. Par la suite, je présente mes objectifs de recherche.

Chapitre 2. Cette partie comprend une revue de la littérature des thèmes pertinents aux objectifs de recherche afin de situer le lecteur et le familiariser avec les divers thèmes de recherche.

Chapitre 3. Dans ce chapitre, je décris ma contribution et celles des co-auteurs aux différents articles scientifiques inclus dans ma thèse.

Chapitre 4. Un premier article scientifique intitulé « Diversity and abundance of ectoparasitic blowflies *Protocalliphora* (Diptera: Calliphoridae) and their *Nasonia* parasitoids (Hymenoptera: Pteromalidae) in Tree Swallow nests within agricultural lands of southern Québec, Canada. »**.** Cet ouvrage représente une description de la communauté des mouches ectoparasites *Protocalliphora* et de leurs guêpes hyperparasitoïdes *Nasonia* provenant de nids de l'hirondelle bicolore.

Chapitre 5. Le deuxième article de recherche s'intitule « Diploid males in natural populations of *Nasonia vitripennis*: pervasive or jewel in the rough? ». Ce travail porte sur l'identification, à l'aide de techniques moléculaires, de mâles *Nasonia vitripennis* possédant un nombre aberrant de chromosomes.

Chapitre 6. Le troisième article scientifique s'intitule « Perception and response to landscape structure: insights from a tri-trophic system within agricultural lands. ». Ici, j'évalue l'impact de la structure du paysage et de l'intensification agricole sur le nombre d'hirondelles bicolores qui quittent le nid, l'abondance de mouches *Protocalliphora* *sialia* dans les nids et le niveau d'hyperparasitisme de *Nasonia vitripennis* sur *P. sialia* dans les nids.

Chapitre 7. Le dernier article de recherche s'intitule « Response of *Nasonia vitripennis* to agricultural intensification. ». Dans ce travail, j'examine les mécanismes par lesquels les parasitoïdes *Nasonia vitripennis* répondent à la variabilité dans la qualité de l'hôte et à la structure du paysage.

Chapitre 8. Ce chapitre constitue la discussion et la conclusion générale de la thèse. Je récapitule l'ensemble des nos découvertes et interprétations.

Chapitre 1 : Introduction générale

Au cours des cinquante prochaines années, la population mondiale pourrait dépasser les 9.1 milliards (United Nations Population Division 2009). Pour accommoder et nourrir cette population croissante, les habitats naturels et sauvages sont graduellement détruits ou modifiés pour faire place à l'expansion des villes et des fermes d'exploitations agricoles. A l'échelle mondiale, la superficie totale des terres cultivées a connu un impressionnant essor de 466% entre 1700 et 1980 (Matson *et al.* 1997) et ce phénomène a profondément modifié le paysage québécois. Avant l'arrivée des premiers européens, le sud du Québec était majoritairement forestier (Simard et Bouchard 1996; de Blois *et al.* 2001), alors que plus de 3.5 millions d'hectares sont aujourd'hui dédiés à l'agriculture dans la vallée du Saint-Laurent (Bélanger et Grenier 2002). De concert avec ces rapides changements environnementaux, les dernières décennies ont été marquées par une baisse inquiétante de la biodiversité ainsi que par une augmentation du taux d'extinction des espèces (Benton *et al.* 2003). Ce dernier phénomène s'est mérité l'épithète de « sixième extinction », puisqu'étant de magnitude comparable à celles des cinq autres épisodes d'extinction massive dénombrées au cours des dernières 500 millions d'années (Leaky et Lewin 1995; Frankham *et al*. 2007). Dans un tel contexte, il devient impératif de comprendre les facteurs déterminant la baisse de la biodiversité afin de développer des stratégies durables de protection et de gestion des habitats naturels.

Il est désormais clair pour les écologistes que la structure du paysage joue un rôle clé dans le maintien de la biodiversité et du bon fonctionnement des écosystèmes (Steffan-Dewenter 2002; Thies *et al*. 2003; Waldhardt 2003; Tscharntke et Brandl 2004; Burel et Baudry 2005; Bianchi *et al*. 2006). Ainsi, la fragmentation du paysage forestier est considérée comme étant la cause principale du déclin de la biodiversité mondiale (Wilcox et Murphy 1985; Argetlam 1997; Hunter 2002; Roschewitz *et al.* 2005). Elle entraîne des changements dans la configuration du paysage telles que la diminution de la surface des patchs naturelles, l'augmentation de l'isolation entre les patchs, l'augmentation de l'effet des bordures et la dégradation générale de la qualité de la patch (Freemark et Merriam 1986; Wilcove 1985; Dennis *et al*. 1994; Hunter 2002). Ces changements au niveau de la matrice originale de la forêt peuvent avoir des impacts négatifs au sein des différentes communautés animales, végétales et microbiennes et sur le fonctionnement de l'écosystème (Petit et Burel 1998; Blair 1999; Bélanger et Grenier 2002; Ghilain et Bélisle 2008).

De même, l'intensification des pratiques agricoles a été identifiée comme cause majeure du déclin de la biodiversité (Benton *et al.* 2003; Tscharntke *et al.* 2005). Les terres anciennement hétérogènes, cultivées de manière extensive, aux paysages complexes composés de terres cultivables, d'herbages, de forêts, de terres en friche, de haies et d'autres habitats semi-naturels, soutenant un niveau de biodiversité élevé, se transforment présentement en terres de culture homogène intensive, aux paysages simples, ne contenant que des fragments de terre arable. Ceci, en concert avec l'augmentation de l'intensité et de la fréquence des perturbations anthropogéniques, qui sont typiques d'un régime d'agriculture intensive, interfèrent avec le maintien de la biodiversité (Burel *et al.* 1998; Aviron *et al.* 2005; Green *et al.* 2005; Bianchi *et al.* 2006).

Plusieurs études ont documenté l'impact de la fragmentation du paysage naturel et de l'intensification agricole sur l'abondance et la diversité des espèces (Fuller *et al.* 1995; Chamberlain *et al.* 2000; Robinson et Sutherland 2002; Benton *et al*. 2002; Benton *et al.* 2003; Ghilain *et al*. 2008). Cependant, très peu d'entre elles ont établi et quantifié le lien entre la structure du paysage et le fonctionnement des écosystèmes (interactions trophiques) ainsi que sur les mécanismes d'adaptations des organismes (Roschewitsz *et al.* 1995; Tylianakis *et al.* 2007).

Afin d'examiner cette problématique, je propose d'étudier un modèle biologique à trois niveaux trophiques composé d'un oiseau hôte, l'hirondelle bicolore *Tachycineta bicolor*, des mouches ectoparasites du genre *Protocalliphora* et des guêpes parasitoïdes du genre *Nasonia*, au travers d'un gradient d'intensification agricole dans le sud du Québec. Les principaux objectifs de ma thèse sont les suivants : (1) identifier et déterminer l'abondance des espèces de mouches ectoparasites et de leurs guêpes parasitoïdes qui colonisent les nids d'hirondelles dans la zone d'étude, (2) évaluer l'impact de l'intensification agricole et de la structure du paysage sur les relations tri-trophiques entre les organismes à l'études et (3) caractériser les mécanismes comportementaux permettant aux guêpes de composer avec la variabilité de la structure du paysage et de la qualité des hôtes.

Chapitre 2 : Revue de la littérature

Dans ce chapitre, je résume la littérature pertinente aux objectifs de mon projet de recherche. En premier lieu, je décris le modèle biologique et la zone d'étude utilisés pour répondre à mes objectifs. Ceci fait, l'information appropriée relative à l'impact de la structure du paysage et de l'intensification agricole sur la biodiversité fait l'objet d'une courte discussion. Par la suite, la littérature portant sur la relation entre la valeur sélective et la taille des guêpes parasitoïdes, ainsi que celle sur les comportements de pontes adaptifs des femelles parasitoïdes sont traitées.

2.1. Le modèle tri-trophiques

2.1.1. L'hirondelle bicolore

L'hirondelle bicolore *Tachycineta bicolore* (Veillot) est un oiseau à reproduction estivale, communément retrouvé en Amérique du Nord. Il hiverne en Amérique Centrale, le long côte est des États-Unis jusqu'aux états de New York et du Massachussetts, en Californie dans sur la côte ouest (Bull et Farrand 1977; Udvardy 1977).

L'hirondelle bicolore est l'une des premières espèces d'oiseau migrateur à revenir sur sont aire de reproduction au début du printemps, arrivant à la mi-avril dans la province de Québec. Son nid est typiquement construit dans des cavités naturelles ou dans des nichoirs artificiels. La construction du nid dure de quelques jours à quelques semaines, selon les conditions climatiques; ce sont les femelles qui construisent le nid avec peu ou aucune aide des mâles (Turner 1989). La période d'incubation est de 13 à 16 jours (Bent 1963). Les oisillons restent dans le nid de 19 à 20 jours (Hussel 1983). Seul la femelle couve les oisillons, mais les deux parents participent à leur alimentation (Bent 1963; Turner 1989). Les adultes sont des chasseurs aériens et ce jusqu'à quelques kilomètres du nid. Ils sont principalement insectivores, se nourrissant de mouches, de coléoptères et de fourmis, mais supplémentent occasionnellement cette diète d'une variété de graines et de baies (Bent 1963; Quinney et Ankney 1985).

La zone de reproduction de l'hirondelle bicolore varie selon les saisons : avant l'incubation des œufs cette zone couvre plus de 60 km^2 et après l'incubation des œufs elle est réduite à 2-5 km^2 (Robertson *et al.* 1992). À la fin de la saison reproductrice, avant la migration automnale, l'hirondelle bicolore évalue couramment la qualité (grosseur, présence d'oisillons morts) des nids utilisés au cours de la saison reproductrice, un comportement appelé « prospection », lui permettant d'acquérir de l'information sur des futurs sites de reproduction. (Robertson *et al.* 1992; Doliguez *et al.* 2004)

2.1.2. Protocalliphora

Les mouches ectoparasites du genre *Protocalliphora* sont des insectes holarctiques, distribués en prédominance dans l'hémisphère nord. Dans la région Néarctique, elles sont présentes en Alaska, à travers le Canada, au Groenland et dans le reste des États-Unis. À l'extrémité sud de leur aire de distribution, ces mouches sont souvent trouvées en altitude, à des températures plus propices à leur développement. Ceci dit, l'information disponible sur l'aire de distribution des différentes espèces est très limitée, principalement en raison d'une absence d'échantillonnage dans les régions plus isolées (Sabrosky *et al.* 1989). Neuf espèces de *Protocalliphora* ont été recensées dans le sud-ouest du Québec: *P. braueri* (Hendel), *P. aenea* Shannon et Dobroscky, *P. avium* Shannon et Dobroscky, *P. rognesi* Thompson et Pont, *P. hirundo* Shannon et Dobroscky, *P. metallica* Townsend, *P. shannoni* Sabrosky, Bennett et Whitworth, *P. bennetti* Whitworth et *P. sialia* Shannon et Dobroscky (Sabrosky *et al.* 1989; Whitworth 2003).

Le cycle de vie des *Protocalliphora* n'a pas encore été entièrement décrit. Ils hivernent comme adultes, mais il n'est pas encore déterminé si l'accouplement se produit avant l'hiver ou au printemps. Lorsque la femelle gravide trouve un nid contenant des oisillons, elle dépose ses œufs directement sur, ou à proximité des oisillons. La majorité des espèces de *Protocalliphora* ont un court développement embryonnaire d'une durée approximative de 24-48 heures et 7-15 jours s'écoulent entre le premier et le troisième stade larvaire. La durée de la pupaison varie considérablement, soit de 9 à 36 jours. Généralement, la durée du développement de ces parasites reflète la durée de nidification de l'oiseau hôte. Plusieurs espèces de mouches peuvent parasiter un même nid (Sabrosky *et al.* 1989; Bennett et Whitworth 1991).

Les mouches *Protocalliphora* sont des ectoparasites hématophages obligatoires à tous les stades larvaires. Elles utilisent les crochets antérieurs de leurs pièces buccales pour couper la chair des oisillons et s'ancrent par la suite de façon superficielle à l'aide de leurs franges pro-thoraciques. La consommation de sang par la larve se fait très lentement, nécessitant plus de 45 minutes pour remplir le tiers du jabot. Les larves du troisième stade requièrent en général un minimum de trois repas pour initier la métamorphose, sans lesquels elles deviennent des adultes sous-développés et stériles, communément appelés « runts » (ou avortons) (Sabrosky *et al.* 1989; Bennett et Whitworth 1991).

Il n'y a pas de consensus quant à l'impact des larves de *Protocalliphora* sur la survie et la valeur sélective de leurs oiseaux hôtes. Certaines études ne démontrent aucun effet négatif de ce parasite sur la fitness des oisillons hôtes (Roby *et al*. 1992; Descamps *et al*. 2002), tandis qu'une majorité de travaux supportent des conclusions contraires (Simon *et al.* 2003; Charmantier *et al.* 2004; Puchala 2004; Hannam 2005; Simon *et al.* 2005; Gentes *et al*. 2007). Généralement, l'alimentation des larves entraine une baisse du niveau d'hématocrites et de l'hémoglobine chez l'oisillon hôte (O'Brien *et al.* 2001) et réduit significativement le taux de croissance chez certaines espèces (Whitworth et Bennett 1992; Simon *et al*. 2005). Les femelles de certaines espèces de *Protocalliphora* déposent leurs œufs dans la cavité nasale ou auditive de l'oisillon, ce qui peut entrainer la mort de l'oisillon lorsqu'elles pénètrent la cavité crânienne par inadvertance (Sabrosky *et al*. 1989).

2.1.3. Nasonia

Les guêpes du genre *Nasonia* (Hymenoptera: Pteromalidae) sont de petits parasitoïdes grégaire de pupes de diptères. À ce jour, quatre espèces ont été décrites: *N. vitripennis* (Walker), *N. longicornis* Darling et Werren, *N. giraulti* Darling et Werren et *N. oneida* Raychoudhury et Desjardins (Darling et Werren 1990; Raychoudhury *et al.* 2010).

Nasonia vitripennis est la plus commune des espèces avec une distribution mondiale, tandis que *N. longicornis* et *N. giraulti* sont endémiques respectivement au nord-est et au nord-ouest de l'Amérique (Whiting 1967; Darling et Werren 1990). L'aire de distribution complète de *N. oneida* n'est pas connue et l'unique population identifiée à ce jour se retrouve dans l'état de New York, USA (Raychoudhury *et al.* 2010).

La femelle *Nasonia* perce la cuticule rigide de la pupe avec son ovipositeur et pond de 20 à 50 œufs par hôte. Elle injecte aussi du venin, qui éventuellement tue la mouche en développement. Les guêpes adultes émergent, après une période de 14 jours, en cisaillant la cuticule de la pupe de l'hôte à l'aide de son ovipositeur. L'accouplement se produit dès l'émergence chez *N. vitripennis* et il arrive parfois que *N. longicornis* et *N. giraulti* s'accouplent avant d'émerger (Whiting 1967; Grillenberger *et al*. 2009). Suivant la copulation, si le patch natal est appauvri d'hôtes potentiels, les femelles se dispersent. Chez *N. vitripennis,* les mâles ont des ailes réduites et ne peuvent se disperser, contrairement aux mâles de *N. longicornis, N. giraulti,* et *N. oneida* qui possèdent des ailes fonctionnelles (Whiting 1967; Grillenberger *et al*. 2009; Raychoudhury *et al.* 2010). Dû à leur très petite taille, ces parasitoïdes ont une capacité de vol limitée, et profitent probablement des courants aériens pour se disperser (Whiting 1967; Grillenberger *et al.* 2009). Une étude a démontré que les femelles peuvent se disperser sur une distance de 2 km en 48 heures (Grillenberger *et al*. 2009). Puisque l'abondance et la distribution de pupes de diptères varient grandement dans le temps et l'espace, les guêpes parasitoïdes ont évolué des mécanismes efficaces pour détecter leurs hôtes, incluant un sens olfactif très développé (Whiting 1967).

La diapause est facultative chez *Nasonia*. Si les conditions sont favorables (température élevée, longue photopériode, hôtes et ressources alimentaires abondantes) ces guêpes n'entrent pas en diapause. Cependant, lorsque les femelles gravides sont exposées à de courtes journées, de basses températures, ou qu'elles sont privées d'hôtes, elles produisent des œufs en diapause. Ces derniers peuvent cesser leur développement jusqu'à un an dans la pupe de l'hôte (Whiting 1967).

Comme la majorité des hyménoptères (fourmis, guêpes, abeilles, mouches à scie), les *Nasonia* ont un système de reproduction haplodiploïde; les mâles haploïdes se développent à partir d'œufs non-fertilisés alors que les femelles diploïdes proviennent d'œufs fertilisés. Les mécanismes de détermination des sexes dans un système haplodiploïde ne sont toujours pas complètement résolus (Beukeboom et van de Zande 2010). Chez *Nasonia*, il est généralement accepté que la détermination des sexes se fait selon le modèle « maternal effect gene imprinting sex détermination » (MEGISD). Sous MEGISD, le gène d'effet maternel (*mds*) exprime un déterminant de sexe zygotique (*zsd*). L'expression seule du *zsd* maternel a pour conséquence le développement masculin du zygote; les œufs haploïdes non-fertilisés, possédant seulement la copie maternelle du *zsd*, se développent donc en mâle. Puisque le *msd* est un gène d'effet maternel, il n'est pas activé lors de la spermogenèse, et donc le gène *msd* hérité du père n'est pas exprimé. Les œufs diploïdes fertilisés, qui eux possèdent en plus une copie paternelle non-exprimée du *zsd*, se développent en femelle (Beukeboom *et al*. 2007).

Il est important de mentionner que le modèle MEGISD a seulement été validé à l'aide de *Nasonia vitripennis* polyploïdes, provenant d'une souche de laboratoire aberrante (Beukeboom *et al*. 2007). L'unique souche de polyploïdes a été identifiée en laboratoire dans les années 50 et est composée de femelles triploïdes stériles et de mâle diploïdes fertiles (Whiting 1960). Les mécanismes gouvernants la transition à la polyploïdie ne sont pas connue (Beukeboom *et al*. 2007).

2.2. Zone d'étude

La zone d'étude était composée de 400 nichoirs artificiels distribués dans 40 fermes (10 nichoirs par ferme) à l'intérieur d'un territoire de 10 200 km^2 dans le sud du Québec, entre Montréal et Sherbrooke. La région se caractérise par un gradient d'intensification agricole est – ouest, où les fermes laitières et les fermes familiales de petite taille sont graduellement remplacées par des fermes de grande taille pratiquant une gestion intensive de leurs cultures. Le gradient de pratiques agricoles extensives à intensives était aussi marqué par une augmentation de la fragmentation des zones « naturelles » (forêts, marécages, etc). Les fermes ont été choisies au hasard, selon une méthode d'échantillonnage stratifié (Ghilain et Bélisle 2008).

Les nichoirs artificiels ont été construits selon les spécifications du « North American Bluebird Society » et ont été installés durant l'hiver de 2004. Ils sont espacés de 50 mètres, le long des fossés et des lignes de clôtures qui séparent les fermes. Tous les nichoirs ont été montés sur un poteau métallique de 1.5 mètres, et leur ouverture fait face au sud-est (Ghilain et Bélisle 2008).

2.3. La structure du paysage, l'intensification agricole et la biodiversité

Malgré le fait que l'expansion des terres agricoles ait ralentie, le rendement des cultures a augmenté drastiquement au cours des 30 dernières années. Cette augmentation est principalement attribuable à l'intensification des pratiques de production sur les terres déjà dédiées à l'agriculture (Matson *et al.* 1997). La gestion, le type et l'abondance des cultures ont beaucoup changé au cours des dernières décennies: la gestion des pâturages a progressé de la production de foin à un système de sillage, l'application de produit chimiques (pesticides et fertilisants) a augmenté considérablement, la planification dans le temps des opérations agricoles a connu des changements majeurs, les habitats marginaux (boisés et marécages) ont été significativement restreints ou oblitérés, et finalement, la diversité des espèces en cultures a été largement réduite (Chamberlain *et al*. 2000). En diminuant considérablement l'hétérogénéité du paysage, cette transition au niveau des pratiques agricoles a entraîné une baisse de la biodiversité régionale (Benton *et al.* 2003), et ce chez plusieurs taxons (Burel *et al*. 1998; Tscharntke *et al*. 2002; Benton *et al*. 2003; Tscharntke et Brandl 2004; Burel *et al*. 2004).

Une préoccupation récente concerne le dépérissement des populations d'oiseaux en milieu agricole (Fuller *et al*. 1995; Chamberlain *et al*. 2000; Donald *et al*. 2001; Johst *et al.* 2001; Benton *et al*. 2002; Murphy 2003). Au Royaume-Uni, dix millions d'individus reproducteurs issus de dix espèces d'oiseaux retrouvées en milieu agricole ont disparu au cours de la période de 1980 à 1999 (Krebs *et al.* 1999). Plusieurs chercheurs ont postulé que la chute des populations d'oiseaux en milieu agricole serait attribuable à la fragmentation et à la destruction des habitats ainsi qu'à une baisse de l'entomofaune (Chamberlain *et al*. 2000; Brickle *et al*. 2002; Benton *et al.* 2002).

Toujours au Royaume-Uni, Brickle *et al*. (2002) ont démontré que le déclin des populations de bruant proyers, *Miliaria calandra* (L.), est lié aux changements des pratiques agricoles qui ont réduit la disponibilité des invertébrés utilisés par les adultes pour nourrir leurs jeunes. Ces auteurs ont aussi documenté une baisse importante des larves de symphytes (mouches à scie) et de lépidoptères dans les régions d'agricultures intensives.

Quelques études récentes ont quantifié l'impact de la structure du paysage sur le patron d'occupation et le succès reproducteur de l'hirondelle bicolore à travers un gradient d'intensification agricole au Québec où les fermes laitières et de petites tailles et caractérisé par une agriculture extensive (présence de pâturages, de friches et d'habitats marginaux) sont remplacées par de grandes fermes aux pratiques agricoles intensives (fermes à haut rendement, monocultures de grains, maïs et soya) (Ghilain et Bélisle 2008; Lamoureux 2010; Baeta *et al*. 2011; Rioux-Paquette et Bélisle 2011). Ghilain et Bélisle (2008) on démontré que les hirondelles ont des tailles de couvées semblables quel que soit le niveau d'intensification agricole, mais que les couvées retrouvées dans des zones principalement extensives présentent deux fois plus d'oisillons qui quittent le nid que celles en milieu intensif. Travaillant sur le même système expérimental, Lamoureux (2010) a rapporté que les oisillons grandissent significativement plus lentement et que les parents passent moins de temps autour des nids en milieu intensif. Baéta *et al*. (données non publiées) ont noté une diminution linéaire de deux grammes dans la masse corporelle (8.9%) des hirondelles bicolores adultes aux cours de la période d'incubation entre 2005 et 2009 dans les zones intensives.

La structure du paysage peut aussi avoir un impact important sur les fonctions écosystémiques comme la prédation, le parasitisme, et la pollinisation (Steffan-Dewenter *et al*. 2002). La grande majorité des études sur ce sujet ont mesuré l'impact de la structure du paysage sur les services écosystémiques, tel que la lutte biologique naturelle. Parmi ces études, plusieurs se sont penchées sur l'impact de l'intensification agricole sur les populations de guêpes parasitoïdes (Steffan-Dewenter 2002; Thies *et al*. 2003, 2004; Tscharntke et Brandl 2004; Tscharntke *et al.* 2005; Bianchi *et al.* 2006). Généralement, les populations de guêpes parasitoïdes sont négativement affectées par l'intensification agricole, et plus précisément par la disparition des habitats marginaux; la diminution de refuges, de sites d'hivernation et de sources alimentaires entrainent un déclin significatif dans la taille des populations de parasitoïdes et donc du niveau de parasitisme des insectes nuisibles en milieu agricole (Thies *et al*. 2003; Tscharntke et Brandl 2004; Holzschuh *et al* 2009, 2010).

2.4. La taille, la ponte, et la valeur sélective chez les guêpes parasitoïdes

2.4.1 Taille et valeur sélective

La relation entre la taille corporelle et la valeur sélective chez les parasitoïdes a été le sujet de multiples études (Godfray 1994; Rivero et West 2002; Burton-Chellew *et al*. 2007; Sykes *et al*. 2007). La théorie prédit que cette relation influence des comportements tels que la sélection de l'hôte, l'alimentation sur l'hôte, la taille de la ponte, le superparasitisme et l'allocation des sexes (Godfray 1994).

Dans la majorité des cas, le lien entre la taille et la valeur sélective diffère entre les mâles et les femelles. La valeur sélective d'une femelle parasitoïde est fortement corrélée au nombre d'hôtes qu'elle a pu parasiter ou, dans le cas des parasitoïdes grégaires, le nombre d'œufs pondus par hôte (Rivero et West 2002; Sykes *et al*. 2007). La taille de la femelle peut influencer sa valeur sélective en affectant sa capacité à chercher des hôtes, sa longévité et son succès reproducteur (Rivero et West 2002; Sykes *et al*. 2007). La valeur sélective des mâles est plutôt déterminée par le nombre d'œufs fécondés. La taille du mâle peut avoir un impact sur sa longévité et sa capacité à localiser et à inséminer les femelles. Il est aussi possible que les plus petits mâles soient défavorisés dans un contexte de compétition intrasexuelle pour des partenaires (Godfray 1994).

Chez plusieurs parasitoïdes, la taille corporelle est influencée par la disponibilité de ressources lors du développement larvaire, laquelle dépend de la taille et de la qualité de l'hôte ainsi que du nombre et du ratio sexuel des autres guêpes se développant dans l'hôte (Godfray 1994; Rivero et West 2002; Sykes *et al*. 2007). Les femelles de grande taille bénéficient d'une longévité supérieure grâce à des réserves lipidiques plus importantes, et sont plus fécondes en raison de leur capacité à stocker d'avantage d'œufs (Godfray 1994; Sykes *et al*. 2007). Chez *N. vitripennis*, le lien entre la taille corporelle et la valeur sélective est aussi fortement dépendant de l'état nutritionnel de la femelle; les petites femelles souffrent disproportionnellement des coûts d'une alimentation inadéquate puisqu'elles émergent avec très peu de réserves lipidiques et de vigueur, dépendant spécialement des sources de pollens (glucides) quelles obtiennent suite à l'émergence pour leur survie (Rivero et West 2002; Sykes *et al*. 2007). Curieusement, la taille ne semble pas avoir d'impact sur la valeur sélective des mâles *N. vitripennis*; Burton-Chellew *et al* (2007) ont démontré que le succès reproducteur (nombres copulations) des mâles était indépendant de leur taille.

2.4.2. Ajustement de la taille de la ponte

Chez les parasitoïdes grégaire, la taille de la ponte est définie comme étant le nombre d'œufs déposés dans un hôte lors d'un effort reproducteur (Godfray 1994). Lack (1947), travaillant sur les oiseaux, fut le premier à suggérer que les femelles devraient pondre juste assez d'œufs pour maximiser la valeur sélective de leur progéniture. Les parasitoïdes grégaires sont rapidement devenus le modèle de prédilection pour l'étude de l'ajustement adaptatif de la taille de ponte (Godfray 1986; Hardy *et al*. 1992; Godfray 1994; Zaviezo et Mills 2000).

En principe, la taille de ponte optimale pour la femelle parasitoïde est celle qui maximise la valeur sélective combinée de toute la progéniture d'une même ponte. Il existe donc un compromis entre la taille de la ponte et la valeur sélective combinée de la progéniture (Charnov et Skinner 1984; Godfray 1994); plus la taille de ponte est importante, plus le niveau de compétition pour les ressources sera élevé entre les larves, ce qui entraîne une diminution de la taille adulte de la progéniture (Hardy *et al.* 1992; Godfray 1994; Rivero et West 2002). Puisque chez les parasitoïdes la taille de l'individu est intimement liée à sa valeur sélective, surtout chez la femelle, (voir Rivero et West 2002), la sélection naturelle devrait donc favoriser l'évolution de mécanismes comportementaux visant à maximiser le compromis entre la taille de ponte et la taille adulte de la progéniture.

Dans ce contexte, plusieurs études ont démontré que les femelles parasitoïdes sont non seulement capables d'évaluer la qualité de l'hôte mais aussi d'ajuster la taille de la ponte en conséquence (Hardy *et al.* 1992; Godfray 1994; Rivero et West 2002). En effet, les femelles de plusieurs espèces de parasitoïdes déposeront moins d'œufs dans des hôtes plus petits (Hardy *et al.* 1992; Godfray 1994; Rivero et West 2002). De plus, les femelles de plusieurs espèces de parasitoïdes sont aussi capables de détecter si l'hôte est déjà parasité, et réduiront le nombre d'œufs injectés dans un hôte déjà exploité (Hamilton 1967; Godfray 1994; Grillenberger *et al*. 2008).

2.4.3. Ajustement du ratio sexuel

Un champ d'étude qui suscite beaucoup d'attention dans le domaine de l'écologie évolutive est l'allocation des sexes de la progéniture par la mère. Fisher (1958) proposa qu'au sein de grandes populations panmictiques, où la reproduction se fait aléatoirement entres individus, les deux sexes sont produits en nombre égal. Son raisonnement est simple; supposons que dans une population, le nombre de mâles produits est inférieur au nombre de femelles produites. Un mâle a une plus grande probabilité de s'accoupler dans une telle population, produisant donc plus de descendants que la femelle. Par conséquent, les parents génétiquement prédisposés à produire des mâles auront tendance à avoir, en moyenne, plus de petits-enfants. Éventuellement, les gènes favorisant la production de mâle se propageront dans la population et la production de mâles deviendra plus commune, jusqu'à ce que le ratio sexuel approche de 1 :1 et que l'avantage à produire des mâles disparaisse. Le même raisonnement s'applique si nous substituons les mâles par des femelles. Par conséquent, le ratio sexuel de 1:1 représente une condition à l'équilibre.

La théorie du « local mate competition » (LMC) a été développée pour expliquer l'observation de ratios sexuels biaisés en milieu naturel (Hamilton 1967). Cette théorie assouplit la condition de la théorie de Fisher concernant la reproduction aléatoire au sein d'une grande population. La théorie du LMC assume que : (1) la femelle contrôle le sexe de sa progéniture et peut maximiser sa propre valeur adaptative en diminuant la compétition entre ses fils, (2) l'accouplement se fait sur le patch natal, (3) l'accouplement sur le patch natal se déroule au hasard et (4) les femelles sont celles qui se dispersent (Hamilton 1967; Grillenberger *et al*. 2008). Sous ces conditions, le ratio sexuel devrait donc varier selon la somme et la qualité d'information que la femelle peut obtenir de son environnement (Burton-Chellew *et al.* 2008). L'une des sources d'information utilisées par la femelle peut être la présence de femelles additionnelles sur le même patch (d'où le nom de la théorie). Quand une seule femelle fondatrice dépose ses œufs sur le patch, les fils produits sont tous des frères, il est donc bénéfique pour la mère fondatrice de produire plus de femelles que de mâles pour réduire la compétition entre ses fils. Ceci étant dit, quand le nombre de femelles fondatrices augmente, la compétition entre les mâles non-apparentés augmente aussi. Dans ce contexte, la sélection naturelle favorise les femelles qui produisent plus de mâles (Hamilton 1967; Grillenberger *et al*. 2008). Plusieurs espèces de guêpes parasitoïdes, dont *N. vitripennis*, ont la capacité d'ajuster le ratio sexuel de leur progéniture suivant la théorie du « LMC » (Werren 1990; Godfray 1994; Grillenberger *et al*. 2008).

La condition physiologique et le contexte écologique (conditions environnementales, disponibilité des hôtes) de la femelle fondatrice peuvent aussi influencer le ratio sexuel de sa progéniture (King 1987; Godfray 1994; Rivers et Denlinger 1995). Par exemple, chez certaines espèces de parasitoïdes, plus la femelle fondatrice est âgée, plus elle produit de fils (revue par King 1987); un phénomène qui serait lié à l'épuisement des réserves de sperme ou à la réduction de la viabilité du sperme. La taille et la qualité de l'hôte peuvent aussi influencer le ratio sexuel lors de la ponte (Godfray 1994; Rivers et Delinger 1995). Effectivement, le ratio sexuel de la progéniture d'une femelle fondatrice dans un hôte de petite taille ou d'une espèce inappropriée est fortement biaisé en faveur de la production de mâles (Godfray 1994; Rivers et Delinger 1995). Chez *N. vitripennis*, étant donné que la taille affecte la valeur sélective des femelles de façon beaucoup plus prononcée que chez les mâles (Rivero et West 2002; Sykes *et al.* 2007), la sélection naturelle devrait favoriser les mères qui produisent des ratios sexuels maximisant la taille des filles. Des travaux précédents ont démontré que les femelles provenant de pontes composées majoritairement de femelles sont en moyenne plus petites, cet effet étant plus important dans des conditions où les ressources sont fortement limitées (petits hôtes) (Rivero et West 2002; Sykes *et al*. 2007).

Chapitre 3 : Contribution de l'auteur et des co-auteurs

Ce projet de recherche unique et multidisciplinaire est le fruit d'une collaboration entre trois groupes de recherche dirigés par Jacques Brodeur de l'Université de Montréal, Jade Savage de Bishop's University, Marc Bélisle et Dany Garant de l'Université de Sherbrooke et moi-même. Le programme de recherche a d'abord été initié à l'Université de Sherbrooke au début des années 2000 par les professeurs Bélisle et Garant. L'étude portait essentiellement à l'origine sur l'impact de l'intensification agricole sur l'hirondelle bicolore. En 2007, les professeurs Savage et Brodeur se sont joints au groupe, lequel a par la suite obtenu du CRSNG (Programme des subventions stratégiques) une subvention de recherche intitulée 'Impacts of agricultural intensification on wild animal populations interactions : from individuals to communities'. L'un des objectifs était d'étendre la recherche aux insectes. Par la suite, les idées principales ont été développées au cours de multiples discussions entre l'équipe de chercheurs et moi-même. C'est dans ce contexte que j'ai élaboré mon projet de doctorat. Jacques Brodeur, à titre de directeur recherche, a contribué son savoir sur les interactions trophiques et l'écologie des parasitoïdes. Jade Savage, siégeant comme co-directrice, a partagé son savoir sur la taxonomie et l'écologie des diptères. Marc Bélisle, agissant aussi comme co-directeur, a contribué à ce travail de par son expertise en écologie du paysage et sa connaissance du système à l'étude. Finalement, Dany Garant a contribué au développement des idées et aux approches méthodologiques pour tous les aspects concernant l'écologie moléculaire et la génétique des populations. Ces professeurs ont soumis mes idées et ma façon de penser à une grande rigueur intellectuelle, suggérant des pistes de recherche intéressantes et m'incitant à préciser et à redéfinir le champ de mes réflexions et à améliorer mon travail. Cette thèse n'aurait jamais vu le jour sans la participation soutenue de ce groupe de chercheurs.

Étant le premier auteur de chacun des articles scientifiques incluent dans cette thèse, j'ai été responsable de la conception et du développement des idées, ainsi que de l'acquisition, du traitement, de l'analyse et de l'interprétation des données. J'ai aussi rédigé intégralement les articles.

Chapitre 4 : Daoust, S.P., Savage, J., Whitworth, T.L., Bélisle, M. and J. Brodeur. (2011). Diversity and abundance of ectoparasitic blowflies *Protocalliphora* (Diptera: Calliphoridae) and their *Nasonia* parasitoids (Hymenoptera: Pteromalidae) in Tree Swallow nests within agricultural lands of southern Québec, Canada.

Le Dr. Jade Savage, spécialiste en taxonomie des diptères, m'a guidé lors de la conception du projet, de l'échantillonnage et de l'identification des spécimens. Elle a aussi participé à la rédaction du manuscrit. Le Dr. T.L. Whitworth est l'autorité mondiale des mouches *Protocalliphora*; il a participé à l'identification des mouches lors d'un stage que j'ai réalisé dans son laboratoire. Il a aussi commenté les premières versions du manuscrit. Le Dr. Marc Bélisle, responsable de la genèse du projet et du réseau de fermes et de nid d'oiseaux, a participé à l'élaboration du projet, à la conception expérimentale, aux échantillonnages et à la rédaction du manuscrit. Le Dr. Jacques Brodeur, directeur de thèse, a participé à la conception et à l'élaboration du projet, financé sa réalisation et sa participation au processus de rédaction du manuscrit fut indispensable.

Chapitre 5: Daoust, S.P., Garant, D. Presseault-Gauvin, H., Savage, J., Bélisle, M. and J. Brodeur. (2011). Diploid males in natural populations of *Nasonia vitripennis*: pervasive or jewel in the rough?

L'équipe du Dr. Dany Garant m'a accueilli lors de plusieurs séjours pour l'analyse moléculaire de mes guêpes. Le Dr. Dany Garant a assumé les coûts de l'utilisation de son équipement ainsi que le temps de sa professionnelle de recherche, il a commenté les différentes versions du manuscrit. Ses connaissances en génétique moléculaire se sont avérées essentielles à la compréhension des stratégies de reproduction au sein de notre modèle biologique. Mme Hélène Presseault-Gauvin m'a guidé tout au long du développement des protocoles au laboratoire et lors de l'analyse des données. Sans son expertise en biologie moléculaire, ce projet n'aurait pu être réalisé. Les Dr. Jade Savage et M. Bélisle ont commenté les différentes versions du manuscrit. Le Dr. Jacques Brodeur a participé à la conception et à l'élaboration du projet et sa participation au processus de rédaction du manuscrit fut indispensable.

Chapitre 6: Daoust, S.P., Savage, J., Bélisle, M., Robillard, A., Baeta, R. and J. Brodeur. (2011). Perception and response to landscape structure: insights from a tri-trophic system within agricultural lands.

En plus de son rôle de codirectrice, le Dr. Jade Savage est spécialiste en taxonomie des diptères. Ella m'a donc guidé et conseillé lors de la conception du projet, de l'identification des spécimens et a participé à la rédaction du manuscrit. Le Dr. Marc Bélisle est responsable de la genèse du projet et d'une partie de la conception expérimental (le réseau de fermes et de nid d'oiseaux a été développé par son groupe). Sa contribution fut essentielle lors de l'analyse et de l'interprétation des données en écologie spatiale. Il a aussi participé à la rédaction du manuscrit. Mme Audrey Robillard et le Dr. Renaud Baéta ont amassé et m'ont transmis toutes les informations biologiques sur les hirondelles bicolores dans le système. De plus, Mme Robillard a activement contribué au traitement des informations de la structure de paysage recueillies sur GIS (geographical information system). Le Dr. Jacques Brodeur a, participé à la conception et l'élaboration du projet et assumé les dépenses; sa participation au processus de rédaction du manuscrit fut indispensable.

Chapitre 7: Daoust, S.P., Garant, D., Savage, J., Bélisle, M., Presseault-Gauvin, H. and J. Brodeur. (2011). Response of natural populations of *Nasonia vitripennis* to agricultural intensification.

L'équipe du Dr. Dany Garant m'a accueilli pour l'analyse moléculaire de mes guêpes. Le Dr. Dany Garant a assumé les couts de l'utilisation de son équipement ainsi que le temps de sa professionnelle de recherche, il a commenté aussi les différentes versions du manuscrit. La contribution de Mme Hélène Presseault-Gauvin a été indispensable au laboratoire lors de la mise au point des manipulations et de l'analyse des données. Les Drs. Jade Savage et Marc Bélisle ont commenté les différentes versions du manuscrit. Le Dr. Jacques Brodeur a participé à la conception et l'élaboration du projet et sa participation au processus de rédaction du manuscrit fut indispensable.

Chapitre 4

Diversity and abundance of ectoparasitic blowflies *Protocalliphora* (Diptera: Calliphoridae) and their *Nasonia* parasitoids (Hymenoptera: Pteromalidae) in Tree Swallow nests within agricultural lands of southern Québec, Canada

Daoust, S.P.[1], Savage, J.[2], Whitworth, T.L.[3], Bélisle, M.[4] and J. Brodeur[1]

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Abstract

We described the community composition of the ectoparasitic flies *Protocalliphora* and their *Nasonia* hyperparasitoids collected from Tree Swallow *Tachycineta bicolor* (Vieillot) nests in southern Québec, Canada, in 2008 and 2009. The prevalence of nest infestation by *Protocalliphora* was of 70.8% in 2008 and 34.6% in 2009. The average parasitic burden of *Protocalliphora* was estimated at 5.53 (± 5.61SD) pupae/nestling for 2008 and 4.66 (± 9.31) pupae/nestling for 2009. The percentage of nests containing *Protocalliphora* pupae parasitized by *Nasonia* spp. was of 85.3 % in 2008 and 67.2% in 2009. Three species of *Protocalliphora* were collected (*P. sialia* Shannon & Dobroscky, *P. bennetti* Whitworth and *P. metallica* (Townsend)) and two species of *Nasonia* (*N. vitripennis* (Walker) and *N. giraulti* Darling & Werren). This is the first record of *P. bennetti* and *N. giraulti* in the province of Québec. Our findings provide further evidence to the observation made by Bennett & Whitworth (1992) that bird nests are more frequently and more heavily infested by blowflies in western than in eastern North America. Our data also suggest that more than a quarter of the bird hosts within the study area are exposed to high levels of ectoparasitism that could negatively affect the Tree Swallow.

Introduction

Larvae of Holarctic bird blow flies in the genera *Protocalliphora* Hough and *Trypocalliphora* Peus (Diptera: Calliphoridae) are obligate blood feeding parasites of nestling birds, a unique life history among the Calliphoridae. To date, 28 species of *Protocalliphora* and one species of *Trypocalliphora* parasitizing 139 bird species have been recorded from the Nearctic region (Sabrosky *et al.* 1989; Whitworth 2003). Birds with the highest infestation rates are those that nest repeatedly in a given area and build large nests, such as hawks (*Buteo* spp.), magpies (*Pica* spp.), crows (*Corvus* spp.) and cavity nest breeders such as European Starlings (*Sturnus vulgaris*) and Tree Swallows (*Tachycineta bicolor* Vieillot) (Bennett & Whitworth 1992).

Adult *Protocalliphora* are rarely collected in the field and immatures (larvae and pupae) are typically found following close examination of nestlings or nest materials. There is a paucity of information on the life history of these bird ectoparasites as most of the existing literature on *Protocalliphora* focuses on taxonomy, host records, and host fitness costs following parasitism (Dawson *et al*. 2005; Simon *et al*. 2005; Hannam 2006). Generally, both male and female *Protocalliphora* overwinter as adults and females lay their eggs as soon as nestlings hatch (T.L. Whitworth pers. com.), which can vary greatly depending on bird species (Gauthier & Aubry 1995). Development from egg to adult takes on average 23-38 days, and while most *Protocalliphora* species are univoltine, some are capable of parasitizing the second broods of bird species having more than one breeding cycle per season (Bennett & Whitworth 1991).

Blowfly larvae are typically anchored to the most accessible part of the nestling (feet, legs and belly), some species can also be found in the auditory and nasal cavities (Whitworth & Bennett 1992). *Protocalliphora* larvae must take two to three blood meals in order to complete their development (Sabrosky *et al.* 1989). Amounts of blood ingested vary according to species, reaching on average 0.0809g in the large *Protocalliphora rognesi* Thompson & Pont (Bennett & Whitworth 1991). In the most extreme scenario, 5 or 6 of the largest *P. rognesi* larvae, capable of each ingesting 0.201g of blood, could exsanguinate an 18-day-old Bank Swallow (*Riparia riparia*) in a single day (Whitworth & Bennett 1992). However, most instances of nestling mortality have been associated with organ damage due to parasitism by obligate subcutaneous larvae of *Trypocalliphora braueri* Hendel (Sabrosky *et al*. 1989; Howe 1992; Matsuoka *et al*. 1997).

At the upper trophic level, puparia of *Protocalliphora* are often found parasitized by small, gregarious "jewel wasps" of the genus *Nasonia* (Walker) (Hymenoptera: Pteromalidae). All four species of *Nasonia* are found in the Nearctic region and only *Nasonia vitripennis* (Walker), a generalist that develops in the pupae of a variety of calyptrate Diptera species (Whiting 1967), is also found in the Palaearctic region. The three other *Nasonia* species only parasitize *Protocalliphora* pupae and are restricted to eastern (*Nasonia giraulti* Darling & Werren, *Nasonia oneida* Raychoudhury & Desjardins) and western North America (*Nasonia longicornis* Darling & Werren) (Darling & Werren 1990; Raychoudhury *et al*. 2010). For the last 40 years, *Nasonia* parasitoids, especially *N. vitripennis*, have been extensively used as model organisms for studies investigating mating behavior, genomic, speciation and especially sex allocation and sex ratio distorters (see Werren & Loehlin 2009; Godfray 2010). However, very little is actually known of their ecology and behavior in their natural habitat.

Although the literature has been divided with regards to the impact of *Protocalliphora* larvae on their bird hosts, it now seems clear that they can negatively influence the health and survivorship of nestlings and fledglings by exacerbating the effects of unfavorable environmental conditions (e.g., low food abundance). Such negative impacts are more likely to occur in species that can be frequently afflicted by high loads of *Protocalliphora* larvae, such as the Tree Swallow (Bennett & Whitworth 1992; Hannam 2006; Thomas *et al*. 2007). Indeed, Tree Swallows renest in the same area interannually; conditions conducive to the maintenance of large *Protocalliphora* populations (Bent 1963; Bennett & Whitworth 1992). To date, 11 species of *Protocalliphora* have been recorded to parasitize Tree Swallow nestlings, 6 of which occur in the Eastern Nearctic (Sabrosky *et al*. 1989; Whitworth 2002, 2003). Moreover, the population of this bird species, like that of most aerial insectivores found in North America and Europe, has been found to decrease over most of its range during the last 30 years (Benton *et al*. 2002; Nebel *et al*. 2010). This generalized population decline of aerial insectivores is hypothesized to be linked to a decrease in flying insect abundance caused by large-scale ecosystem modifications, notably agricultural intensification (Benton *et al.* 2002; Ghilain & Bélisle 2008; Nebel *et al.* 2010). In the event that *Protocalliphora* abound in agricultural landscapes, these blowflies have the potential to exacerbate the negative impact that agricultural intensification has on aerial insectivores through reduced prey abundance. Nevertheless, the impact of *Protocalliphora* birds on aerial insectivores inhabiting farmlands will also depend on the capacity of *Nasonia* parasitoids to control these blowflies in agricultural landscapes.

The faunistics and ecology of the *Protocalliphora* and *Nasonia* associated with Tree Swallows are poorly known in eastern Canada where Tree Swallows show their most important population decline (Nebel *et al*. 2010). The objectives of this study were to: 1) describe the assemblages of *Protocalliphora* and *Nasonia* species found in Tree Swallow nests in 40 farms in southern Québec, Canada; 2) estimate the parasitic burden of *Protocalliphora* on their bird hosts; and 3) establish levels of hyperparasitism by *Nasonia*.

Materials and Methods

Study area and nest box network

The 10 200 km^2 study area included a network of 400 bird nest boxes distributed among 40 farms within the Montérégie and Estrie regions in Southern Québec (Fig. 1). The area is characterized by an east–west gradient of agricultural intensification where dairy farming and small-scale, familial farms are replaced by large-scale, continuous row cropping with full mechanization and high input of pesticides as well as of organic and chemical fertilizers (Bélanger & Grenier 2002; Jobin *et al*. 2005; Fig. 1). Nest boxes were built according to North American Bluebird Society's specifications (i.e., Eastern/Western Bluebird model) and were installed in the winter of 2004. Boxes were put up 50 m apart along drainage ditches or fence lines that bordered agricultural fields or pastures. All boxes were mounted on a metal post 1.5 m above the ground and with the opening facing southeast. See Ghilain & Bélisle (2008) for the detailed farm selection protocol.

Specimen collection and identification

Prior to their fall migration, Tree Swallows typically visit nests that were used during the breeding season, likely to ascertain the quality of potential future breeding sites (Bent 1963; Ghilain & Bélisle 2008). In order to avoid interference with the bird's habitat quality assessment, insect specimens were collected from the field using two protocols. First, 2 out of the 10 available Tree Swallow nests in each of the 40 farms were examined for *Protocalliphora* pupae immediately upon fledging, i.e. between June 25 and July 16 in both 2008 and 2009. The nest was carefully removed from the box and all pupae present in nest material and in the nest box were collected. The nest was put back into the box upon completion of sampling. Pupae were individually placed into meshed capped plastic bottles (4 cm X 7 cm) for rearing. They were maintained in a mixture of sawdust and 1% boric acid at room temperature (~ 22 ºC) until the emergence of the adult flies or their parasitoids (5 to 12 days). Adults were kept alive for a period of 48 hours for maturation and hardening of the integuments and killed by freezing (-30 ºC) for seven days. Adult *Protocalliphora* were pinned and air-dried and their puparia stored individually in 90% ethanol. Adult *Nasonia* were stored in 90% ethanol at -20 °C.

The second sampling protocol took place during the winters of 2008-2009 and 2009-2010, several months after the birds had left. All nests (including those sampled in the first place) were collected and brought back to the laboratory for examination. Empty *Procalliphora* puparia were removed from nest material, air dried and subsequently stored at room temperature in vials. Pupae from which insects failed to emerge were dissected and examined.

Adult *Protocalliphora* were sexed and keyed to species using Sabrosky *et al.* (1989) and Whitworth (2003). As *Protocalliphora* adults are rarely caught and most specimens in collections consist of puparia, much effort has been invested into developing reliable identification keys based on morphological structures of puparia (Whitworth 2006). The puparia of emerged adults as well as those collected during the winter were first examined with a stereomicroscope for markings associated with either adult fly emergence (missing or broken emergence cap) or wasp emergence (exit holes 0.5-1mm in diameter) and then keyed to species using Whitworth (2002, 2003). All puparia that could not be identified at low magnification were mounted on slides (see

Whitworth 2002) for examination with a compound microscope. All *Nasonia* specimens were examined and photographed for measurements necessary to identification using a stereomicroscope equipped with a digital camera. Measurements were taken using PixeLINK® imaging software and all specimens keyed to species using Darling & Werren (1990) and Raychoudhury *et al*. (2010). Voucher specimens have been deposited to the Ouellet-Robert entomological collection at Université de Montréal.

Results

A total of 202 nests from 37 farms were occupied by Tree Swallows in 2008 and 185 nests from 37 farms in 2009; remaining nest boxes were left empty or occupied by either Eastern Bluebirds (*Sialia sialis*) or House Sparrows (*Passer domesticus*) and were not considered in this study. A total of 3 601 and 1 275 *Protocalliphora* pupae and puparia were collected from 33 and 24 of these farms in 2008 and 2009, respectively; most being sampled during the winter period (82.40% in 2008 and 74.82% in 2009).

Protocalliphora

The prevalence of nest infestation by *Protocalliphora* was twice as high in 2008 (70.8%, N = 143) than in 2009 (34.6%, N = 64). Yet, the number of *Protocalliphora* pupae per nest or per nestling was only 15.9% and 25.2% higher in 2008 compared to 2009, respectively (Table 1). The number of *Protocalliphora* pupae per nest and per nestling, which were both inherently highly variable, showed, however, twice as much variation in 2008 than in 2009 (pupae per nest CV = 91.7-199.8%; pupae per nestling CV = 101.4-199.8%; Table 1). Overall, the observed within and between year levels of variation imply that most *Protocalliphora*-infested Tree Swallow broods experienced low to high parasitic burdens (Table 1).

Adults were reared from 283 of 333 collected pupae in 2008 and 110 of 204 pupae in 2009. Three species of *Protocalliphora* were identified (Table 1). *Protocalliphora sialia* Shannon & Dobroscky was by far the most prevalent and abundant, found in 96.51% of infested nests in 2008 and 87.58% in 2009 (Table 1).

Protocalliphora bennetti Whitworth was found in 21.11% of infested nests in 2008 and 31.29% in 2009, while *P. metallica* (Townsend) was only sampled in 10.03% of infested nests in 2008 and 4.82% in 2009. Nest infestation by *P. sialia* alone was the most frequent pattern, accounting for at least two thirds of nest parasitism in 2008 and 2009 (Table 2). Mixed infestations of *P. bennetti* and *P.sialia* accounted for almost a fifth of infestations while *P. bennetti* and *P. metallica* were predominantly found in mixed nest infestations with *P. sialia* and only rarely sampled in single or mixed infestations with each other (Table 2). Only 1 nest out of 143 in 2008 and 1 out of 64 in 2009 were simultaneously infested by the three *Protocalliphora* species.

Nasonia

Overall, more than two thirds of the nests containing *Protocalliphora* pupae were parasitized by *Nasonia* (Table 3). Nonetheless, the proportion of *Protocalliphora*-infested nest that incurred parasitism by *Nasonia* was 27% higher in 2008 than in 2009 (Table 3). Similarly, the level of hyperparasitism (proportion of pupae parasitized in *Nasonia*-infested nests), which nearly reached half of the pupae over the two years, was 28% greater in 2008 than in 2009 (Table 3). While the levels of hyperparasitism by *Nasonia* on *P. sialia*, *P. bennetti* and *P. metallica* were similar in 2008, *P. bennetti* experienced a level of hyperparasitism about twice as high as those of the other species in 2009 (Table 3).

Adult *Nasonia* emerged from 52.4% (N=635) of the *Protocalliphora* pupae collected following bird fledging in 2008 and from 63.6% (N=321) of collected pupae in 2009. Of the pupae sampled in the winter, based on the nature of exit holes, *Nasonia* were inferred to have emerged from 49.9% of pupae in 2008 (N=2966) and 31.1% of pupae in 2009 (N=954). Table 4 summarizes the prevalence of nest infestation by *Nasonia* species and the representation of each species of *Nasonia* among the parasitized pupae obtained from the first collecting effort. Two species of *Nasonia* were identified, *N. vitripennis*, by far the most common species, and *N. giraulti* (Table 4). In most cases, only *N. vitripennis* was found per nest (Table 4).

A mean of 30.66 ± 20.78SD (Range: 1-152) *N. vitripennis* wasps emerged per pupa in 2008 and 27.83 ± 14.82 (1-89) in 2009. For *N. giraulti*, 29.64 ± 9.24 (14-43) individuals per pupa emerged in 2008 and 20.63 ± 10.01 (10-36) in 2009.

Discussion

Our study presents a description of the *Protocalliphora* and *Nasonia* species composition and abundance from Tree Swallow nests within agricultural lands of southern Québec, Canada. We identified three species of *Protocalliphora* (*P. sialia, P. bennetti* and *P. metallica*) and two species of *Nasonia* (*N. vitripennis* and *N. giraulti*). This is the first record of both *P. bennetti* and *N. giraulti* in the province of Québec.

Protocalliphora

Protocalliphora infestations in bird nests have been reported to be higher in western than in eastern North America (Sabrosky *et al.* 1989; Bennett & Whitworth 1992). In their seminal work investigating the *Protocalliphora* fauna of 73 bird species, Bennett & Whitworth (1992) documented that 52% of the 1862 nests sampled in the west (i.e., Utah, USA) were infested with *Protocalliphora*, whereas only 24% of the 2806 nests in the east (Ontario, Canada) were infested. Accordingly, in three studies on the *Protocalliphora* of Tree Swallows within anthropogenically modified habitats of western Canada, Rendell & Verbeek (1996), Dawson *et al*. (2005) and Gentes *et al*. (2007) reported that 93%, 89% and 100% of the nests were infested, respectively. These numbers are notably higher than what was observed in our study (70.8% in 2008 and 34.6% in 2009). Not only are bird nests more frequently infested with *Protocalliphora* in western North America, they also appear to be more heavily infested with *Protocalliphora*. For instance, Rendell & Verbeek (1996), Dawson *et al.* (2005) and Gentes *et al.* (2007) reported mean abundances of *Protocalliphora* per nest that were 152%, 101% and 199% higher than from our study and this, for bird host species laying clutch sizes similar to that of Tree Swallows. Our findings thus provide further support for this east vs. west pattern of *Protocalliphora* infestation in North America. Ecological factors accounting for this geographical difference in levels of nest infestation remain to be explored.

Several studies have investigated the effect of blood feeding by *Protocalliphora* larvae on developing nestlings. In some cases, parasitized nestlings have been shown to have lower hematocrit and haemoglobin levels (Whitworth & Bennett 1992; O'Brien *et al*. 2001; Hannam 2006), reduced growth rates (Whitworth & Bennett 1992), decreased body temperatures and metabolic rates (Simon *et al.* 2005), and lower fledging survival and reduced dispersal in the first days following fledging (Thomas *et al.* 2007, Streby *et al.* 2008). Conversely, other works have reported no significant effects of *Protocalliphora* ectoparasitism on any of the aforementioned parameters (Johnson *et al.* 1991; Wittmann & Beason 1991; Roby *et al*. 1992; Miller & Fair, 1997). These latter studies, however, did not follow nestlings throughout their early developmental stages, when nestlings may be the most sensitive to *Protocalliphora* ectoparasitism. Negative effects on bird hosts have been observed at levels of ectoparasitism ranging from 7.2 - 13.73 pupae per nestling (Whitworth & Bennett 1992; O'Brien *et al*. 2001; Simon *et al.* 2005; Streby *et al.* 2008) and more specifically at 13.3 pupae per nestling for *P. sialia* on the Eastern Bluebird (Hannam 2006). For the Tree Swallow we measured on average 5.5 and 4.7 pupae per nestling in 2008 and 2009, respectively, but with considerable variation among infested broods. For instance, in 2008 and 2009, 38 of the 143 and 10 out of 64 infested nests had levels of ectoparasitism greater than to 7.5 pupae per nestling, the highest being 47 pupae per nestling. Although not intended to assess the effect of *Protocalliphora* on Tree Swallows, our data suggest that some birds are exposed to high levels of ectoparasitism that could influence breeding success.

We observed considerable interannual variation in the prevalence of *Protocalliphora* infestation in 2008 (70.8% of infested nests) and 2009 (34.6%). This should be interpreted with caution as the study was conducted solely over two field seasons. Yet, Johnson *et al.* (1991), Bennett & Whitworth (1992), Roby *et al.* (1992) and Germaine & Germaine (2002) also reported differences in prevalence of infestation between sampling years of 16%, 75%, 22% and 38%, respectively. When studying the conditions favoring parasitism by *Protocalliphora* within the Algonquin Provincial National Park in Ontario, Canada, Bennett & Whitworth (1992) suggested that the experimental removal from the field of immature stages of *Protocalliphora* prior to adult emergence decreases the rate of nest infestation the following year. This might partly explain the observed interannual variability described in the previously referenced studies, as they all removed nest material and *Protocalliphora* pupae within days of bird fledging. However, our sampling protocol was designed in such as way as to minimize the removal of adult *Protocalliphora* from the field. Indeed, only 16.8% of the pupae were removed from the field in 2008 and it is therefore unlikely that the interannual variation we observed resulted from oversampling. Long term monitoring would be necessary to elucidate the underlying mechanisms governing the population dynamics of *Protocalliphora*.

Of the seven *Protocalliphora* and the one *Trypocalliphora* species known to parasitize Tree Swallows in eastern North America, we sampled three (*P. sialia, P. bennetti* and *P. metallica*). This is not entirely surprising as the other three species are seldom found in Tree Swallow nests. The predominance of *P. sialia*, both in terms of nest infestation and abundance (Table 1), is consistent with other studies on Tree Swallows from across North-America (Wittmann & Beason 1991; Roby *et al.* 1992; Smar 1994; Dawson *et al.* 2005), as is the low prevalence and abundance of the two other species collected within our study system, *P. bennetti* and *P. metallica* (Bennett & Whitworth 1992; Whitworth 2002). Bennett & Whitworth (1992) and Whitworth (2002) suggested that females of some species of *Protocalliphora* have either a "nest site preference" or a "host preference," and possibly an interaction of the two, when ovipositing. *Protocalliphora bennetti,* for instance, are host specific, being most frequently found in cavity nests of either wrens or chickadees but rarely in nests of Tree Swallows (Bennett & Whitworth 1992; Whitworth 2002). In contrast, *P. metallica* seem to prefer habitats with open canopies rather than forested areas (Sabrosky *et al.* 1989; Bennett & Whitworth 1992). In addition, *P. metallica* have been shown to preferentially oviposit in open nests such as those of ground nesting birds but rarely in cavity-nesting birds (Sabrosky *et al*. 1989; Bennett & Whitworth 1992). Thus, the pattern of *Protocalliphora* species collected from Tree Swallow nests within the agricultural lands of southern Québec conforms to those reported in other works on Tree Swallows.

Two or more species of *Protocalliphora* were found in 24.5% of the infested nests (data from both years combined); this value is above what was reported in Bennett and Whitworth (1992) who found an average mixed infestation rater of 12.5% in Algonquin Provincial National Park, Ontario, Canada. The determinants governing this phenomenon have not yet been elucidated.

Nasonia

During the first sampling effort, the collected pupae were hyperparasitized by two species of *Nasonia* (*N. vitripennis* and *N. giraulti*). *Nasonia vitripennis* was the most prevalent and abundant of the two for each of the three *Protocalliphora* species. *Nasonia giraulti* was usually found in association with *N. vitripennis*. These data are consistent with those reported by Grillenberger *et al.* (2009) who identified *Nasonia* wasps emerging from *Protocalliphora* pupae collected from Tree Swallow and Eastern Bluebird nests in upper New York State; the majority of the nest contained single *N. vitripennis* infestations (67%), whereas 29% of nest contained mixed infestations of both *N. vitripennis* and *N. giraulti*. No single infestations of *N. giraulti* where observed. Historically, this pattern of relative abundance between *N. vitripennis* and *N. giraulti* might have been different as *N. giraulti* had once been more common within its range (J.H. Werren pers. comm.). A recent study proposes that the appearance of a new species, *N. oneida* in New York State, as well as the introduction of *N. longicornis* into eastern North-America, could play a role in the decrease of *N. giraulti* populations within that region (Raychoudhury *et al*. 2009). Whether or not this is the case for southern Québec remains unknown as there is a complete absence of historical data.

To our knowledge, only three field studies have been conducted on *Nasonia*. Grillenberger *et al*. (2008) (Europe), Grillenberger *et al.* (2009) (upper New York State) and Bennett & Whitworth (1991) (across North-America) observed that 60%, 91% and 72% of bird nests contained *Protocalliphora* pupae that were parasitized by *Nasonia* with levels of hyperparasitism (i.e., parasitized pupae) of 46.8%, 48.0% and 22.1%, respectively. Similarly, 85.3% and 67.2% of our nests contained parasitized pupae in 2008 and 2009, respectively, with levels of hyperparasitism of 49.8% and 35.7%.

Ecological factors determining levels of hyperparasitism by *Nasonia* under field conditions remain to be explored.

Nasonia do not appear to discriminate between *Protocalliphora* species, as *P. sialia, P. bennetti* and *P. metallica* experienced comparable levels of hyperparasitism (Table 4). The higher value observed for *P. bennetti* in 2009 was due to an exceptionally high level of hyperparasitism in a single nest, where all pupae from a single infestation of *P. bennetti* were hyperparasitized.

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Table 1. Abundance (number of *Protocalliphora* / nest) and estimated parasitic burden (number of *Protocalliphora* / nestling) of *Protocalliphora* spp. sampled from Tree Swallow nests (N=143 in 2008; N=64 in 2009) in 2008 and 2009 within the Montérégie and Estrie regions of southern Québec, Canada.

	2008		**2009**	
Parameters	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
Average number of *Protocalliphora* pupae / nest	25.43 ± 23.33	(1 - 110)	21.95 ± 43.86	(1 - 148)
P. sialia pupae / nest	24.20 ± 23.38	(0 - 110)	19.63 ± 39.20	(0 - 146)
P. bennetti pupae / nest	0.99 ± 3.21	(0 - 27)	1.8 ± 3.59	(0 - 18)
P. metallica pupae / nest	0.23 ± 0.896	(0 - 7)	0.188 ± 0.375	(0 - 4)
Average number of *Protocalliphora* pupae / nestling	5.53 ± 5.61	(0.15 - 45)	4.66 ± 9.31	(0.2 - 37)
P. sialia pupae / nestling	5.26 ± 5.51	(0 - 43)	4.20 ± 8.38	(0 - 36)
P. bennetti pupae / nestling	0.220 ± 0.703	(0 - 5.4)	0.364 ± 0.727	(0 - 3.6)
P. metallica pupae / nestling	0.051 ± 0.191	(0 - 1.33)	0.041 ± 0.082	(0 - 0.8)

Table 2. Level (%) of single and mixed infestations of *Protocalliphora* spp. in Tree Swallow nests (N=143 in 2008; N=64 in 2009) in 2008 and 2009 within the Montérégie and Estrie regions of southern Québec, Canada.

Parameters	**2008**	**2009**
Nest with single *Protocalliphora* infestations	73.43%	78.17%
P. sialia	71.33%	65.63%
P. bennetti	1.40%	10.94%
P. metallica	0.70%	1.60%
Nests with mixed infestations	26.58%	21.95%
*P. bennett*i + *P. sialia*	17.48%	18.75%
P. metallica + *P. sialia*	7.00%	1.60%
P. bennetti + *P. metallica*	1.40%	0
P. bennetti +*P. metallica* + *P. sialia*	0.70%	1.60%

Table 3. Prevalence of nest infestation and the total level of hyperparasitism of *Protocalliphora* pupae (N=3601 in 2008; N=1275 in 2009) by *Nasonia* spp. in Tree Swallow nests in 2008 and 2009 within the Montérégie and Estrie regions of southern Québec, Canada.

Parameters	**2008**	**2009**
Nests containing *Protocalliphora* pupae parasitized by *Nasonia* spp.	85.31%	67.19%
Protocalliphora pupae parasitized by *Nasonia* spp.	50.35%	39.29%
P. sialia	53.88%	34.71%
P. bennetti	47.45%	60.68%
P. metallica	46.67%	30.00%

Table 4. Percentage of hyperparasitism of *Protocalliphora* pupae by *Nasonia* spp. As determined from pupae collected during the first sampling effort (N = 333 pupae for 2008; N=204 for 2009) in Tree Swallow nests in 2008 and 2009 within the Montérégie and Estrie regions of southern Québec, Canada.

Parameters	**2008**	**2009**
Nests containing parasitized *Protocalliphora* pupae infested with *N. vitripennis*	63.13%	89.29%
Nests containing parasitized *Protocalliphora* pupae infested with *N. giraulti*	8.80%	25.00%
Protocalliphora pupae parasitized by *N. vitripennis*	93.01%	94.61%
Protocalliphora pupae parasitized by *N. giraulti*	3.90%	2.96%
Single *N. vitripennis* infestation	90.01%	92.65%
Single *N. giraulti* infestation	0.90%	1.00%
Mixed *Nasonia* infestations	3.00%	1.96%

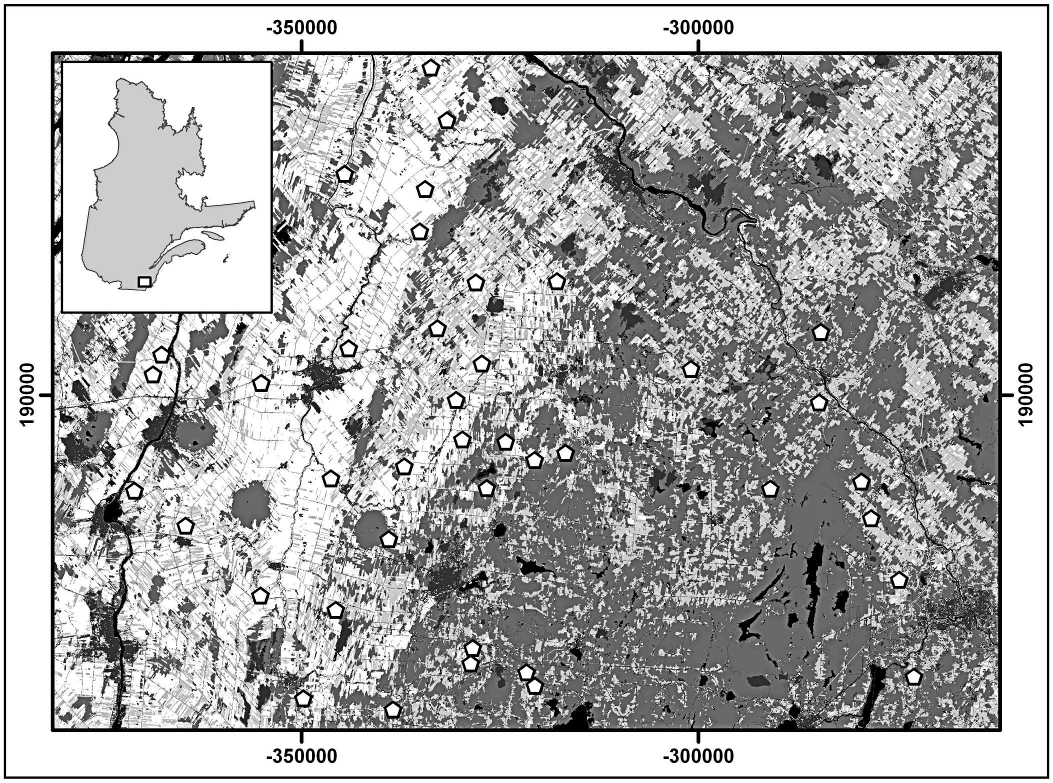

Fig.1. Distribution of the 40 farms along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. Land cover types are based on a mosaic of classified LANDSAT-TM satellite images (Canadian Wildlife Service 2004) and include water (black), urban (dark gray), forest (mid-tone gray), extensive cultures (e.g., hayfields and pastures; light gray), and intensive cultures (e.g., maize, cereals, and soybeans; white). Open pentagons indicate farm locations. Coordinates are Lambert Conic Conform and refer to the number of meters from a reference point.

Chapitre 5

Diploid males in natural populations of *Nasonia vitripennis*: pervasive or jewel in the rough?

Simon P. Daoust[1], Dany Garant[2], Hélène Presseault-Gauvin[2], Jade Savage[3], Marc Bélisle[2] and Jacques Brodeur[1]

Ready to be submitted to *Current Biology*

Abstract

Sex determination in *Nasonia* is best described by the maternal effect genomic imprinting sex determination model. This model was validated using a laboratory "aberrant" polyploid strain of *N. vitripennis*; polyploids having appeared in a lone strain more than 50 years ago. Here, we report for the first time diploid males collected from natural populations of *N. vitripennis.* Polyploidy appears to be common as diploid males were collected from 59% of the nests accounting for 17% of the total genotyped males. Our results suggest that spontaneous mutations leading to polyploidy in *N. vitripennis* occur frequently and are maintained in natural populations.

Brief scientific communication

Due to their haplodiploid mode of sex determination and the absence of heteromorphic sex chromosome, how gender is regulated in hymenopteran insects has been of great interest for researchers. For instance, *Nasonia* parasitoids, especially *Nasonia vitripennis* Walker, have been extensively used as model organisms for studies investigating sex determination (Beukeboom & van de Zandel 2010). To date, it is widely agreed that sex determination in *Nasonia* spp. is described by the maternal effect genomic imprinting sex determination (MEGISD) model (Beukeboom & van de Zandel 2010). Under MEGISD, the maternal effect gene (*msd*) imprints a zygotic sex determiner (*zsd*). Maternal imprinting of the *zsd* gene causes male development in the zygote. Haploid eggs only contain a maternally-derived *zsd* copy and develop into males, whereas diploid fertilized eggs additionally contain a non-imprinted paternal allele of *zsd* resulting in female development (Beukeboom *et al*. 2007b). To date, this model has only been validated using a laboratory reared "aberrant" polyploid strain of *N. vitripennis* (Beukeboom *et al*. 2007b). Polyploids (diploid males and triploid females) were reported in a lone strain, some 50 years ago, within Dr. Whiting's laboratory stock culture (Whiting 1960). The strain has been maintained in laboratory since (Beukeboom *et al*. 2007a). It was proposed that mutations resulting in polyploidy arise spontaneously in laboratory cultures of *N. vitripennis* due to occasional non-disjunction in oogenesis (Beukeboom *et al*. 2007b). Here, we report for the first time diploid males collected from natural populations of *N. vitripennis.*

Nasonia wasps were collected from parasitized *Protocalliphora* pupae in nests of Tree Swallows (*Tachycineta bicolor*) nests breeding in farmlands of southern Québec, Canada. Wasps were initially sexed based on morphological characters and the ploidy level was determined using three polymorphic microsatellites (Tables 1, 2). There were no obvious morphological differences between diploid and haploid males (Fig.1A, B) (hind tibia length; $t_{278} = 0.66$, $p = 0.51$) a finding contrary to Whiting (1960), who noted that diploid males from his culture were slightly larger than their haploid counterparts.

Though rare in the laboratory, polyploidy in our sampled populations appears to be relatively common as diploid males were collected from 59% of the sampled nests

(N=27; 1 nest per sampling site), accounting for 17% of the total genotyped males (N=280). Furthermore, diploid males were collected from sites which were separated by as much as 100 km, suggesting that polyploidy has appeared and been maintained in different *N. vitripennis* populations (Fig. 1C). Supporting this hypothesis is the fact that 23 out of 79 genetically distinct founding females were shown to produce diploid male offspring. These females produced clutches averaging 16.66 ± 6.81 (mean ± SD; range: 1 – 25) wasps with an average of 4.33 ± 4.17 (mean ± SD; range: 1 – 18) males (N=91) with diploids accounting for 45% of the males.

With the recent sequencing of its genome (Werren *et al*. 2010), *N. vitripennis* has reached the "model system" status; its biology in wild populations has been far less documented. Contrary to reports from laboratory studies (Whiting 1960), our results suggest that spontaneous mutations leading to polyploidy in *N. vitripennis* occur relatively frequently and are maintained in natural populations. These observations provide strong support for the MEGISD model to explain sex determination in polyploid *Nasonia*. Together with the recent discovery of a wild Canadian strain producing haploid females (*Beukeboom et al.* 2007a), our findings suggest that natural populations of *N. vitripennis* could differ significantly and unexpectedly from laboratory culture strains. More effort should therefore be devoted to investigate the biology of natural *Nasonia* populations to reconcile laboratory results with natural occurrences.

Material and Methods

Nasonia vitripennis were obtained from *Protocalliphora* pupae parasitizing Tree Swallow nests within a network of 400 nest boxes distributed among 40 farms over an area of 10 200 km^2 in the Montérégie and Estrie regions in Southern Québec, Canada (*S1*).

Two Tree Swallow nests in each of the 40 farms were examined for *Protocalliphora* pupae immediately upon fledging between June 25th and July 16th 2008 and 2009. Pupae were individually placed into (4 cm X 7 cm) meshed capped plastic bottles for rearing. They were maintained in a mixture of sawdust and 1% boric acid at room temperature (~ 22 C) until the emergence of the adult flies or their parasitoids (5 to 12 days). Adult *Nasonia* were stored in 90% ethanol at -20°C. Measurements were taken using PixeLINK® imaging software and all specimens keyed to species and sexes identified (Darling & Werren 1990; Raychoudhury *et al.* 2010).

A total of 805 *N. vitripennis* wasps (525 females and 280 males) from 54 parasitized *Protocalliphora* sp. pupae were genotyped. Parasitized pupae were collected from 27 farms (2 pupae from one nest per farm). DNA extraction was conducted following the streamlined prepGEM (ZyGEM, Hamilton, New Zealand) protocol for small insects. Genotyping was performed using polymorphic microsatellite loci (dinucleotide repeats) (Table 1). The length of the amplified fragments was determined using an AB 3130 Genetic Analyzer (Applied Biosystems) and GeneMapper ® (Applied Biosystems, Version 4.0).

Sibling status and founding *Nasonia* sp. female identity were determined from the offspring genotypic information following the protocol described in Grillenberger *et al.* (2008): (i) A female (mother) can supply up to two alleles per locus; (ii) The male (father) provides one allele per locus (being haploid) that is shared by all full sisters. (iii); sons can only have an allele from their mother, as they develop from unfertilized eggs. As in Grillenberger *et al* (2008), if several foundress genotypes were possible based on the microsatellite profile, we favoured the solution with the lowest number of foundresses. The analysis yielded data on the number of foundresses per host, as well as on the individual clutch sizes and sex ratio produced by individual founding females.

Hind tibia lengths fulfilled conditions for normality. Welch two sample t-tests were used to determine the difference in mean hind tibia length between diploid and haploid males with α =0.05. T-tests were run in the R statistical environment (version 2.4.0; R Development Core Team 2006).

Acknowledgments

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Table 1. Information related to the three microsatellite primer sets used.

Primer name	Annealing temperature (°C)	Chromosome	Sequence 5' - 3'	Fragment length (bp)	Allele number	Observed heterozygocity (H_O)	Dye	GenBank accession no.	Reference
Nv-17	46	-	F: AAG AAT GTA TCA AGT ATG AGC C R: TCA GTT CTT GAA ACG TTG C	207-244	13	0.4	NED	AY262049	Pietsch *et al*. 2004
Nv-41	56	V	F: GTC AGA CGT GGG CTT TGT C R: TTA TGC GCC ACA CAC ACC	321-341	11	0.38	FAM	EU155141	Grillenberger *et al*. 2008
Nv-46	58	IV	F: TTA CGT CAA GGT ATA GCT GC R: GAA TAA GTG GCT GAA AGT TCC	232-262	15	0.51	FAM	EU155142	Grillenberger *et al*. 2008

Table 2. Microsatellite profiles of diploid males sampled

Wasp ID	Farm	Nest	Founding female ID	Allele Nv-17a (bp)	Allele Nv-17b (bp)	Allele Nv-41a (bp)	Allele Nv-41b (bp)	Allele Nv-46a (bp)	Allele Nv-46b (bp)
17	2	7	1	207	215	333	337	242	244
21	2	7	1	207	207	337	337	244	262
68	5	2	7	231	231	323	325	248	250
107	5	4	9	207	207	337	337	244	252
155	9	5	16	207	207	333	333	244	252
163	9	5	16	207	207	333	333	244	252
166	9	5	15	207	213	333	339	244	252
176	11	6	18	207	207	333	333	244	248
187	11	6	18	207	213	333	337	244	244
192	11	6	20	207	213	333	337	244	244
208	11	7	22	207	207	335	337	252	252
212	11	7	21	207	215	335	337	244	252
272	14	3	28	207	237	331	337	242	244
301	14	3	32	207	207	333	337	244	254
333	15	4	36	207	215	337	337	244	252
337	15	4	38	213	213	335	337	240	252
338	15	4	37	215	215	337	339	252	252
340	15	4	38	207	213	337	337	244	252
342	15	4	38	207	213	335	337	240	252
345	15	4	38	207	217	337	339	252	252
478	23	3	53	213	213	335	339	244	248
481	23	3	53	213	213	335	339	244	248
492	23	3	55	213	213	335	339	244	248
498	23	3	54	207	213	337	337	240	248
501	23	3	55	213	213	335	339	244	248
504	24	1	56	207	213	331	337	250	250
505	24	1	56	207	207	331	337	252	252
506	24	1	56	207	207	331	337	240	250
507	24	1	56	207	215	331	337	240	244
509	24	1	56	213	213	329	331	250	250
510	24	1	56	207	215	331	331	244	252
542	24	4	59	207	213	337	337	244	252
544	24	4	59	207	207	337	337	244	252
565	25	3	62	207	207	337	337	240	240
579	25	3	62			333	337	244	248
632	30	3	66	207	213	337	337	244	244
646	30	3	66	207	240	337	337	244	244
648	30	3	66	207	240	337	337	244	244
686	38	2	72	207	215	333	337	240	240
728	39	6	77	213	215	333	339	244	248
733	39	6	77	213	215	333	339	244	248
736	39	6	77	213	215	333	337	244	248
739	39	6	77	213	215	337	339	244	248
746	39	6	79	213	215	337	339	244	248

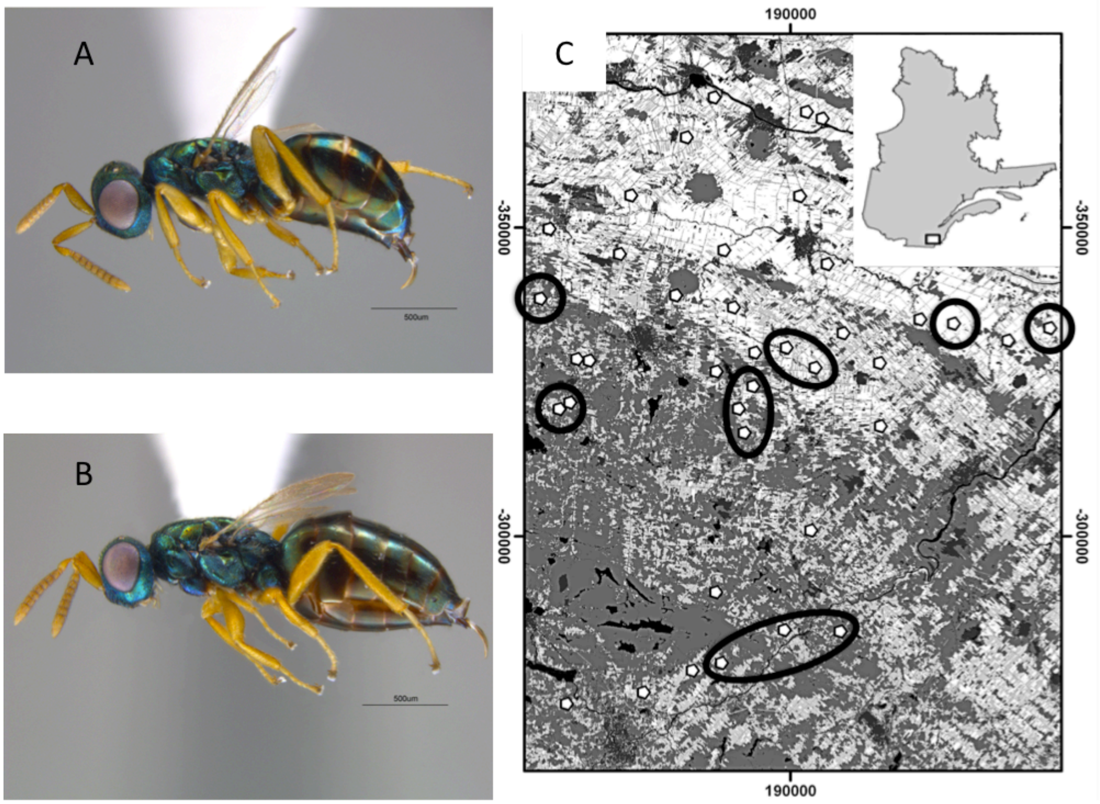

Fig. 1. (A) Haploid male *N. vitripennis*, **(B)** diploid male *N. vitripennis*, **(C)** Distribution of the 40 sampling sites (farms) along a gradient of agricultural intensification in southern Québec, Canada, 2009. Open pentagons indicate farm locations, circled pentagons represent where diploid males were collected. Map was rotated so that the north points right. Coordinates are Lambert Conic Conform and refer to the number of meters from a reference point.

Chapitre 6

Perception and response to landscape structure: insights from a tri-trophic system within agricultural lands

Daoust, S.P.[1], Bélisle, M.[2], Savage, J.[3], Robillard, A.[2], Baeta, R[2]. and J. Brodeur[4]

Abstract

1. Although many works have examined the influence of agricultural intensification and landscape structure on species abundance and diversity, few have addressed how agriculture impacts populations across multiple trophic levels.

2. In this two-year study, we investigated the effects of landscape structure on the tri-trophic interactions between a bird host (the Tree Swallow *Tachycineta bicolor* (Vieillot)), its blowfly ectoparasites (*Protocalliphora* Hough), and their parasitoid wasps (*Nasonia* Walker) across 13 spatial extents, along a gradient of agricultural intensification covering 10, 200 km^2 in southern Québec, Canada.

3. Interacting organisms at different trophic levels perceive the landscape at distinctive spatial extents. This perception, however, differs based on which landscape parameter is considered. The number of Tree Swallow fledglings, the abundance of *P. sialia* and the level of hyperparasitism by *N. vitripennis* are negatively affected by agricultural intensification.

4. Our data do not support the prediction that organisms at the higher trophic levels are more susceptible to habitat loss and degradation. We show that the organisms at the second trophic level that are disproportionally affected by agricultural intensification; the number of *P. sialia* per nest were shown to decreases by 74% from low to high intensive farms as compared to a 14% and 33% reduction in the number of Tree Swallow fledglings and in the level of hyperparasitism by *N. vitripennis*, respectively.

5. Our work highlights the importance of designing protocols that take spatial aspects of trophic interactions into account, as it is these interactions that dictate local biodiversity and community function. Furthermore, our results highlight the importance of considering multiple landscape parameters when identifying the functional spatial scales of organisms, a failure to do so could lead to an underestimation of the area used by organisms.

Introduction

The significance of spatial context in understanding local ecological processes is increasingly recognized by ecologists (Wiens 1989; Wheatly & Johnson 2009; Fahrig *et al*. 2011); species abundance, community structure and trophic interactions in a habitat may rely on processes at larger spatial scales (Tscharntke & Brandl 2004; Fisher *et al.* 2005; Thies *et al*. 2005; Bianchi *et al*. 2006; Holzschuh *et al*. 2010). The surrounding matrix of a habitat fragment may increase the amount of available resources or provide additional resources that do not occur within the local habitat fragment. It can also influence the connectivity of habitat patches, thereby potentially influencing local population density and extinction risk (Marshall & Moonen 2002; Steffan-Dewenter 2003; Tscharntke *et al*. 2005; Fahrig 2007). This notion is especially important in the context of recent changes to the agricultural landscape (Robinson & Sutherland 2002). Formerly heterogeneous, extensively cultured lands composed of complex landscapes with well-balanced proportions of arable land, grassland, forests, fallows, hedgerows and other semi-natural habitats are being transformed to homogenous intensively cultured lands with simple landscapes containing only fragments of natural or semi-natural land (Matson *et al*. 1997).

Although many studies have quantified the influence of agricultural intensification and landscape structure on species abundance and diversity (Burel *et al.* 1998; Benton *et al*. 2003; Burel *et al*. 2004; Tscharntke *et al*. 2005; Donald *et al*. 2006) few have empirically addressed how agriculture impacts populations across multiple trophic levels. It is relatively well understood that the responses of organisms to changes in landscape structure are contingent on the species' size and trophic level (Holt *et al*.1999; Tscharntke *et al*. 2004; Thies *et al.* 2005). Holt *et al.* (1999) postulated that organisms at higher trophic levels should respond to larger spatial-scale processes. Typically, predator populations utilize several prey populations and therefore must switch between patches colonized by the prey (Tscharntke *et al*. 2004). While this holds true for vertebrate-invertebrate food chains where species at the highest trophic rank are larger, the predictions by Holt *et al*. (1999) are not supported by parasite and parasitoid interactions where the species at the highest trophic ranks are much smaller (Thies *et al.*

2003, 2005). Notwithstanding size, species at higher trophic levels may be more susceptible to extinction after habitat loss due to agricultural intensification as they are confronted with both the direct effect of habitat degradation on their populations and the indirect effect of habitat degradation on their host populations (Cagnolo *et al.* 2009). Within each trophic level mechanisms driving species' response to landscape structure have been shown to be species specific (Fisher *et al.* 2006). This specificity is often attributed to behavioural differences, degree of habitat specialization and levels of adaptive flexibility (Fisher *et al.* 2006). Accordingly, in order to understand the relationship between landscape structure and species-specific responses, experimental protocols must include components and metrics relevant to the target species and landscape metrics should be quantified at the appropriate spatial scales (Thies *et al.* 2003; Wheatly & Johnson 2009; Whealty 2010).

In this two-year study, we investigated the effects of landscape structure on the tri-trophic interactions between a bird host (the Tree Swallow *Tachycineta bicolor* (Vieillot)), its blowfly ectoparasites (*Protocalliphora* Hough), and their parasitoid wasps (*Nasonia* Walker) along a gradient of agricultural intensification covering 10, 200 km^2 in southern Québec, Canada. Some of these taxa have already been shown to be susceptible to agricultural intensification. Previous works within our study system reported that nest box occupancy and breeding success of Tree Swallows are negatively correlated with the proportion of intensive culture in the landscape (Ghilain & Bélisle 2008). Similar findings have also been reported for several other regional bird species; Jobin *et al.* (1996) reported that many species associated with dairy farming, such as the Savannah Sparrow *Passerculus sandwichensis* (Gmelin), the Bobolink *Dolichonyx oryzivorus* L., the Brown-headed Cowbird *Molothrus ater* (Boddeart) and the Eastern Meadowlark *Sturnella magna* L., show decreasing population abundances within the intensively cultured agricultual lands of southern Québec, Canada. Although very little is known of the ecology of *Protocalliphora* within agricultural land, it is well established that the diversity and abundance of many flying insects, such as non-biting midges, sawflies and moths, are negatively affected by agricultural intensification (Burel *et al*. 1998, 2004; Wickramasinghe *et al.* 2004). Parasitoids do not fare any better, as several studies reported decreased levels of parasitism and parasitoid diversity within intensively cultured landscapes (Steffan-Dewenter 2003; Thies *et al*. 2003, 2004; Tscharntke & Brandl 2004; Tscharntke *et al.* 2005; Bianchi *et al.* 2006). The decreases of the various insect taxa were attributed to lower host diversity, fewer sources of nectar and shelter sites and the application of pesticides associated with intensively farmed lands (Burel *et al*. 1998, 2004; Tscharntke & Brandl 2004; Wickramasinghe *et al.* 2004; Tscharntke *et al.* 2005).

In order to investigate how host availability and landscape structure influence our tri-trophic model, the spatial scales at which the organisms maximally respond to landscape structure must be determined. To obtain these functional spatial scales, we used a multi-scalar design, categorizing the proportion of landscape dedicated to extensive (fallows, pastures, grasslands) and intensive cultures (monoculture crops such as grains, corn and soya) at 13 spatial extents. We measured the influence of landscape structure across these 13 spatial extents on the number of Tree Swallow fledglings. We then measured the impact of landscape structure and host availability on the abundance of *Protocalliphora* pupae per nest and on the number of *Protocalliphora* pupae per nest parasitized by *Nasonia* (level of hypeparasitism by *Nasonia*)*.* The effects of agricultural landscape characteristics were modelled while controlling for variables pertaining to clutches or broods (e.g., hatching date), nest weight and year.

Firstly, it is predicted that habitat loss associated with an increase in the proportion of intensive agriculture in the landscape should lead to reductions in the number of Tree Swallow fledglings, in the number of *Protocalliphora* pupae per nest and the level of hyperparasitism by *Nasonia*. Secondly, as *Protocalliphora* nest abundance is positively correlated with bird clutch size (Eeva *et al*. 1994) and the level of hyperparasitism is generally positively correlated with host density (Hassel 1982) it is predicted that these should increase in response to an increase in host abundance. Lastly, in accordance with Holt *et al.* (1999), it is predicted that organisms at higher trophic levels should be more negatively affected by the strong “bottom-up” effects (habitat loss and reduced host abundance) associated with agricultural intensification.

Materials and Methods

Model organisms

The Tree Swallow is an obligate secondary cavity nester and is primarily insectivorous, (Quinney & Ankney 1985; Robertson *et al.* 1992). Its breeding home range fluctuates throughout the season: prior to incubation, the range spans >60 km^2, but after incubation, it falls to 2-5 km^2 (Robertson *et al.* 1992).

Larvae of Holarctic bird blow flies are obligate blood-feeding parasites of nestling birds. To date, 28 species of *Protocalliphora* and one species of *Trypocalliphora* parasitizing 139 bird species have been recorded from the Nearctic region (Sabrosky *et al.* 1989; Whitworth 2003). Adult *Protocalliphora* are rarely collected in the field, while immatures (larvae and pupae) are typically found following close examination of nestlings or nest materials. Development from egg to adult takes on average 23-38 days, and while most *Protocalliphora* species are univoltine, some are capable of parasitizing the second-brood nests of bird species having more than a single breeding cycle per season (Bennett & Whitworth 1991). Feeding blowfly larvae are typically anchored to the most accessible part of nestlings (feet, legs and belly), although some species can be found in the auditory and nasal cavities (Whitworth & Bennett 1992). Parasitized nestlings have been shown to have lower hematocrit and haemoglobin levels (Whitworth & Bennett 1992), reduced growth rates (Whitworth & Bennett 1992), lower fledging survival and reduced dispersal in the first days following fledging (Streby *et al.* 2008), and decreased body temperature and metabolic rates (Simon *et al.* 2005).

Nasonia are small insects (approximately 2mm in length) commonly referred to as “jewel wasps”. There are currently four identified species in the genus *Nasonia*: *N. vitripennis, N. giraulti* Darling & Werren*, N. longcornis* Darling & Werren and *N. oneida* Raychoudhury & Desjardins (Darling & Werren 1990; Raychoudhury *et al* 2009). Adult females sting and lay their eggs within the puparium of various fly species. Venoms injected into the host modify host physiology and eventually killing it. Developing wasps typically emerge 2–3 weeks later, depending on temperature. Whereas *N. vitripennis* is a generalist that parasitize blowflies, fleshflies, houseflies and others, the other three species preferentially parasitize blood-sucking blowflies of the genus *Protocalliphora* (Werren & Loehlin 2009).

Study region and nest box network

The 10, 200 km^2 study area included a network of 400 nest boxes distributed among 40 farms within the Montérégie and Estrie regions in Southern Québec, Canada (Fig. 1). The area is characterized by an east–west gradient of agricultural intensification where dairy farming and small-scale, familial farms have been replaced by large-scale, continuous row cropping with full mechanization and high input of pesticides as well as of organic and chemical fertilizers (Ghilain & Bélisle 2008; Fig. 1). The agriculture gradient ranges from extensive (hayfields and pastures) to intensive (maize, cereals, and soybean). Nest boxes were built according to North American Bluebird Society's specifications (i.e., Eastern/Western Bluebird model) and were installed in the winter of 2004. Boxes were put up 50 m apart along drainage ditches or fence lines that bordered agricultural fields or pastures. The distance to the nearest building thus varied substantially among boxes (119 ± 93 m, mean = 1 SD; N = 400 boxes). All boxes were mounted on a metal post 1.5 m above the ground and with the opening facing southeast (Ghilain & Bélisle 2008). Farms were equally distributed between intensive and extensive agricultural zones. See Ghilain & Bélisle (2008) for the detailed farm selection protocol.

Nest box monitoring

We monitored the breeding of Tree Swallows during each breeding season (early May to mid-July) of 2008 and 2009. Each year, all nest boxes were visited every two days to determine occupancy, laying date of first egg, clutch size, brood size at hatching, and number of chicks fledged. We considered a nest box occupied when it contained at least one egg. We opted for this conservative operational definition of occupancy because of the difficulty in differentiating between two consecutive breeding attempts where the first one had been abandoned at the nest building stage. We determined the laying date of the first egg based on the assumption that Tree Swallows lay one egg per day until clutch completion (Robertson *et al.* 1992).

Specimen collection and identification

At the end of their breeding season, and prior to their fall migration, Tree Swallows typically assess the quality (size, presence of dead nestlings) of the nests that were used during the breeding season to ascertain potential future breeding sites (Robertson *et al.* 1992), a behaviour also called "prospection" (Doligez *et al*. 2004). In order to avoid interference with the bird's habitat quality assessment, insect specimens were collected using the following protocol: two out of the ten available tree swallow nests in each of the 40 farms were examined for *Protocalliphora* pupae immediately upon fledging, i.e. between June 25th and July 16th in 2009. Nests were carefully removed from the box and all pupae present in nest material and in the nest box were collected. Nests were put back into the box upon completion of sampling. Pupae were individually placed into (4 cm X 7 cm) meshed capped plastic bottles for rearing. They were maintained in a mixture of sawdust and 1% boric acid at room temperature (~ 22 ºC) until the emergence of the parasitoids (5 to 12 days). Adult *Nasonia* were stored in 90% ethanol at -20 °C.

All *Protocalliphora* adults and pupae and *Nasonia* specimens were examined and photographed for measurements necessary to identification using a stereoscope equipped with a digital camera. Measurements were taken using PixeLINK® imaging software. The second sampling protocol took place during the winters of 2008-2009 and 2009-2010, several months after the birds had fledged. All nests, including those sampled in the first place, were returned to the laboratory for examination. Empty *Procalliphora* puparia were removed from nest material, air dried and subsequently stored at room temperature in vials. Pupae from which insects failed to emerge were dissected and examined.

Specimens were keyed to species following Sabrosky *et al.* (1989), Darling & Werren (1990), Whitworth (2003) and Raychoudhury *et al.* (2009).

Landscape characterization

We characterized the level of spatial heterogeneity around each nest box by measuring the relative cover of intensive and extensive cultures (Burel *et al.* 2004) within radii of 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 1, 2, 3, 4, 5, 10, and 20 km, using both visual field characterisation (up to 0.5km radii) and estimates based on a mosaic of georeferenced classified Landsat-7 satellite images taken between August 1999 and May 2003 (pixel resolution 25 m x 25 m; Canadian Wildlife Service 2004) for radii between 1 and 20 km. The latter were chosen based on the findings of a previous work, where Tree Swallow fledging success was shown to respond to broader spatial scales (Ghilain & Belisle 2008). We included smaller radii (0.05-0.5 km) in the study as the level of parasitism by parasitoid wasps was shown to respond to landscape structure at smaller spatial scales than birds (Steffan-Dewenter 2003; Holzschuh *et al*. 2010). Measurements of relative land cover were obtained with ArcView GIS Spatial Analyst 2.0a (ESRI 2005).

Statistical analyses

In order to identify how the relative cover of intensive culture and extensive culture change over the different spatial extents measured (13 radii) we followed the protocol described in Wheatly (2010). Initially we intended to use standard analysis of variance (ANOVA) with an associated post-hoc multiple comparisons, however, even after transformation, the data did not satisfy the conditions for normality (Sokal & Rohlf 1995). Thus, we conducted a non-parametric ANOVA (Kruskal Wallis; KW) to determine whether differences existed among observational scales for each landscape parameter. For those with significant overall group KW tests, we determined differences between scales based on multiple non-parametric KW comparisons among all potential combinations of observational scales using the kruskalmc (package pgirmess version 1.4.7) function run in R (version 2.1.11; R Development Core Team 2010).

Pearson correlations between the percentages of extensive and intensive agriculture across the 13 spatial extents within the 40 farms were obtained using the cor function in R. Percentages were arcsine square root transformed to satisfy the conditions for normality (Sokal & Rohlf 1995).

We selected the number of Tree Swallow fledglings, the number of *Protocalliphora* pupae per nest and the level of hyperparasitism by *Nasonia* on *Protocalliphora* pupae as our response variables. Due to the hierarchical sampling design (i.e., nest boxes nested within farms), we modelled the three response variables using generalized linear mixed models using a logit link for poisson error distribution with farm identity as random factor fitted with the lmer (package lme4 version 0.999375-36) function in R (version 2.1.11; R Development Core Team 2010).

An information theoretic approach was employed to examine model sets for each response by calculating a sample size-corrected form of Akaike's information criterion (AICc) following recommendations in Anderson (2008). We built a series of five competing models for each response variable, composed of combinations of scalar landscape structure explanatory variables and non-scalar explanatory variables that are descriptive of the nest. The composition and justification of these groups of variables are found in Table 1, and the lists of models considered are included in Appendices A, B and C. As in Ghilain and Belisle (2008), we were unable to include the two types of cultures in the same model, with or without the interaction, as it lead to multicollinearity among explanatory variables and prevented model convergence. Hence, we built simpler models including only one type of culture. Explanatory variables included in a given model were never strongly correlated ($0.01 < r < 0.46$).

Functional spatial extents were determined by fitting two general models (Nest + Intensive and Nest + Extensive) at each of the 13 spatial extents and contrasting them between spatial extents using the aictab.mer (package AICcmodavg version 1.11) function. In order to identify which of the 5 candidate models were best at describing the response variables, we contrasted models between the previously determined functional spatial extents using the aictab.mer (package AICcmodavg version 1.11) function in R. Contrasts were based on the second-order variant of the Akaike information criterion (AIC*c*), which corrects the number of estimated parameters with respect to the sample size (Anderson 2008). The lower the AIC*c* value of a model, the better that model describes the information contained in the data. We also computed the weight of evidence of each model (w_i) which represents the likelihood that a model was the best ranked within the set of competing models (Anderson 2008). To evaluate the goodness-of-fit of the final models, a linear regression of the fitted values vs observed values was calculated to obtain R^2 values.

For each model set where no single candidate model stood out significantly above others ($w_i \geq 0.95$), model averaging with weighted support calculated on the basis of the ΔAICc of the five models was performed with the modavg (package AICcmodavg version 1.11) where parameter estimates for each predictor are averaged only over models which include this predictor (Anderson 2008).

In order to test our final prediction, Wilcoxon sign-ranked tests were used to compare the number of Tree Swallow fledglings, the number of *Protocalliphora* and the level of hyperparasitism by *Nasonia* per nest between the nest within high ($\geq$ 80% intensive culture in the landscape) and low ($\leq$ 20% intensive culture in the landscape) intensive farms. Non-Parametric tests were used because the data were highly skewed and failed to satisfy the conditions for normality even after transformation (Sokal & Rohlf 1995).

Results

Landscape structure

Two landscape metrics (relative cover of intensive and extensive cultures) were characterized at 13 spatial extents (Fig. 2a, b). The proportion of intensive culture in the landscape was high in the intensive zone of the study, ranging from 60-90% and low in the extensive zone, ranging from 0-50% (Fig. 2a). Similarly, the proportion of extensive culture was elevated in the extensive zone of the study, ranging from 45-90% and low in the intensive portion of the study, ranging from 2-20% (Fig. 2b). Clear breaks in the scale continuum (domains of scale as per Wiens 1989 and Wheatly 2010) were identified for both the relative cover of intensive culture (KW ANOVA: $\chi^2 = 777.36$, $df = 12$, $p = < 2.2 \times 10^{-16}$) and extensive culture (KW ANOVA: $\chi^2 = 319.51$, $df = 12$, $p = < 2.2 \times 10^{-16}$). Domains of scale in these two metrics were defined as observational scales that were statistically unique and did not transition in terms of similarities to scales either above or below the scale continuum. Two distinct domains of scale were identified for relative cover of intensive culture, the first between 0.05 and 2 km and the second between 3 and 20 km (Fig. 2a). Three domains of scale were recognized for the relative cover of extensive culture, the first between 0.05 and 0.3 km, the second between 0.4 and 2 km and the third between 4 and 20 km.

Tree Swallow fledging

Within nest boxes where at least one egg hatched, the number of fledglings averaged 4.29 (± 1.71SD) in 2008 and 4.04 (± 1.88SD) in 2009. Contrasts between spatial extents revealed that the Nest + Extensive model performed best at the spatial extent of 0.3 km (w_i: 0.35) (Fig. 3a) whereas the Nest + Intensive model performed best at the extents of 0.3 and 5 km (w_i: 0.26 and w_i: 0.26, respectively) (Fig. 3a). The percentage of intensive culture in the landscape at 0.3 km is strongly correlated with the percentage of extensive culture at 5 km (r = 0.691) (Appendix D, Table D1).

Contrasting the five candidate models within the spatial extents which performed best revealed that fledging number was best explained by the Nest + Intensive model at radii of 0.3 km (w_i: 0.31, R^2: 0.26) and 5 km (w_i: 0.12, R^2: 0.26), the Nest + Extensive model at 0.3 km (w_i: 0.20, R^2: 0.24) and 5 km (w_i: 0.28, R^2: 0.28) and by the Nest model at 0.3 km (w_i: 0.49, R^2: 0.22) and 5 km (w_i: 0.6, R^2: 0.22) (Appendix A, Table A1). Both nest and landscape components influenced the number of Tree Swallow hatchlings that fledged from the nest. Model parameters were estimated at each of these spatial extents from these three models using model averaging (Table 2). At the spatial extent of 0.3 km the only parameter that was shown to influence the number of Tree Swallow fledglings was the hatching date, where fewer birds fledged later in the season. Although the presence of intensive culture increased the parsimony of the model at this scale (Figure 3a), it was not shown to influence the number of Tree Swallow fledglings (Table 2). At the spatial extent of 5 km, the two model parameters influencing the number of Tree Swallow fledglings were the hatching date and the proportion of extensive culture in the landscape (Table 2). Based on these models, the number of fledglings increased with the amount of extensive culture within 5 km in the landscape (Fig. 4) and decreased as the season progressed (hatching date) (Table 2).

Protocalliphora abundance

Protocalliphora sialia Shannon & Dobroscky represented > 95% of collected specimens within our study system (Daoust *et al.* 2011 submitted). We therefore chose to model *Protocalliphora* abundance within Tree Swallow nests using only this species.

Within nest boxes where at least one egg hatched, the number of *P. sialia* pupae averaged 25.43 (± 23.33SD) in 2008 and 21.95 (± 43.86SD) in 2009. Contrasts between spatial extents revealed that the Nest + Extensive model performed best at the spatial extent of 2 km (w_i: 1) (Fig. 3b) whereas the Nest + Intensive model performed best at the extents of 0.2 (w_i: 1) (Fig. 3b). The percentage of intensive culture in the landscape at 0.2 km is weakly correlated with the percentage of extensive culture at 2 km (r = -0.352) (Appendix D, Table D1).

Contrasting the five candidate models within the spatial extents which performed best revealed that the number of *P. sialia* pupae per nest was best explained by the Nest + Extensive model at radii of 2 km (w_i: 1, R^2: 0.43) and the Nest + Intensive model at 0.2 km (w_i: 1, R^2: 0.44) (Appendix B, Table B1). Both nest and landscape components influenced the number of Tree Swallow hatchlings that fledged from the nest. Within the Nest + Intensive model at the spatial extent of 0.2 km, the number of *P. sialia* pupae per nest was shown to decrease between sampling years (Table 3), increase with the number of fledglings per nest (Fig. 5a; Table 3), increase with hatching date (Fig. 5b; Table 3) and decrease with the percentage of intensive culture in the landscape (Fig. 5c; Table 3). Within the Nest + Extensive model at the spatial extent of 2 km, the number of *P. sialia* per nest also increased with the number of Tree Swallow fledglings per nest (Table 3), the hatching date (Table 3) and the proportion of extensive culture within 2 km in the landscape (Fig. 4d; Table 3).

Level of hyperparasitism by Nasonia

Two species of *Nasonia* were identified, *N. vitripennis* (Walker) and *N. giraulti* Darling and Werren. *Nasonia vitripennis* represented >98% of the specimens collected in our study system (Daoust *et al*. submitted). We therefore modelled the level of hyperparasitism by *Nasonia* on *P. sialia* using only this species

Within nest boxes where at least one *P. sialia* pupae was found, the level of hyperparasitism by *N. vitripennis* on *P. sialia* pupae was 50.35 % in 2008 and 39.29% in 2009. Contrasts between spatial extents revealed that the Nest + Extensive model performed best at the spatial extent of 0.05 and 0.3 km (w_i: 0.26 and w_i: 0.61, respectively) (Fig. 3c) whereas the Nest + Intensive model performed best at 0.2 km (w_i: 0.91) (Fig. 3c). The percentage of intensive culture in the landscape at 0.2 km is strongly correlated with the percentage of extensive culture at 0.05 and 0.3 km ($r = -0.804$ and $r = -0.844$, respectively) (Appendix D, Table D1).

Contrasting the five candidate models within the spatial extents which performed best revealed that number of *P. sialia* pupae per nest parasitized by *N. vitripennis* was best explained by the Nest + Extensive model at radii of 0.05 km (w_i: 0.99, R^2: 0.81), 0.2 km (w_i: 0.66, R^2: 0.81) and 0.3 km (w_i: 0.40, R^2: 0.81) and by the Nest + Intensive model at radii of 0.2 km (w_i: 0.34, R^2: 0.84) and 0.3 km (w_i: 0.60, R^2: 0.84) (Appendix C, Table C1). Both nest and landscape components influenced the number of Tree Swallow hatchlings that fledged from the nest. Parameter estimates for the Nest + Extensive model at the spatial extent of 0.05 were used as it had a $w_i \geq 0.95$ (Table 4). Model parameters were estimated for the spatial extents of 0.2 and 0.3 km from the Nest + Extensive and Nest + Intensive models using model averaging (Table 4). Within the Nest + Extensive model at the spatial extent of 0.05 km, the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* were only shown to increase with the number of Tree Swallow fledglings per nest and the number of *P. sialia* pupae per nest (Table 4).

At the spatial scale of 0.02 km, the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* increased with the number of Tree Swallow fledglings, the number of *P. sialia* pupae per nest and with nestling hatching date and decreased with the percentage of intensive culture in the landscape (Table 4). Lastly, at the spatial scale of 0.3 km, the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* increased with the number of Tree Swallow fledglings (Table 4), with nestling hatching date (Fig. 6a; Table 4) the number of *P. sialia* pupae per nest (Fig. 6b; Table 4) and the percentage of extensive culture in the landscape (Fig. 6c; Table 4) and decreased with the percentage of intensive culture in the landscape.

Trophic rank and susceptibility to agricultural intensification

The number of Tree Swallow fledglings per nest decreased significantly between the least and most intensive farms by 13.89% ($W_{211} = 4270$, $p = 0.0377$) (Fig. 7). A significant reduction of 74.36% in the number of *P. sialia* pupae per nest was also observed between the least and most intensive farms ($W_{132} = 2293.5$, $p < 0.00001$) (Fig. 7). Although the difference is not statistically significant, probably due to the small number of replicates in the highly intensive farms (n=14) and the highly conservative nature of the non-parametric test, there was a reduction of 33.6% in the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* per nest between the most and least intensive farms ($W_{88} = 397$, $p = 0.1687$) (Fig. 7).

Discussion

To our knowledge, this is the first study to investigate the effects of agricultural intensification using a tri-trophic animal system. Our work reveals that the relative covers of both intensive and extensive cultures change across spatial extents. Furthermore, we show that not only do interacting organisms at different trophic levels perceive the landscape at distinctive spatial extents, but this perception can also differ based on which landscape parameter is considered. Lastly, the number of Tree Swallow fledglings, the abundance of *P. sialia* and the level of hyperparasitism by *N. vitripennis* were shown to be negatively affected by agricultural intensification.

Many studies have documented the effects of landscape structure on biodiversity but few have quantified the landscape structure within their study sites (Wheatley 2010; Wheatley & Johnson 2010). Wiens (1989) was one of the first to recognize that although patterns and processes change with spatial scale (extent or grain), they do not always change evenly. Our data is in agreement with these observations, as the proportions of intensive and extensive cultures in the landscape did not change evenly across all 13 spatial scales. Indeed, the proportion of intensive culture remained relatively continuous from 0.05 to 2 km, but then sharply increased from 2 to 3 km, at which point it stabilized (Fig. 2). Likewise, the proportion of extensive cover decreased and stabilized across three domains of scale. These findings are significant as they inform us that interacting organisms in our study system encounter a landscape structure that is unpredictable across the spatial continuum. This might be reflected in how organisms respond to the landscape structure, thereby influencing their functional spatial scales (Fahrig 2007).

We reported that the functional spatial extents perceived by the organisms of interest differed between landscape parameters modelled. Indeed, the spatial extent at which Tree Swallows perceive landscape structure differed between parameters; the most parsimonious model including intensive culture was found to be at a relatively small extent (0.3 km) whereas the one including extensive culture was at a much larger extent (5 km). As with the Tree Swallows, the functional spatial extents at which *P. sialia* perceived landscape structure was much smaller for intensive culture (0.2 km) than for extensive culture (2 km). In contrast, the functional spatial extents experienced by *N. vitripennis* were relatively similar between landscape parameters (0.2 and 0.3 km for intensive and extensive cultures, respectively). There is no clear explanation for these observations. One possibility is that this differential perception of the two landscape parameters could be a correlation artefact. Analysis revealed considerable correlation between the percentages of intensive agriculture and smaller extents and those of extensive agriculture at larger extents (Appendix D, Table D1). Indeed, we reported strong correlations between the small spatial extents perceived by both Tree Swallows and *N. vitripennis* in response to intensive culture and the larger scales perceived in response to extensive culture. However this is not true for *P. sialia*, as there was little correlation between the spatial extents it perceived. In this case, we attribute this differential perception to the underlying variations in the landscape structure between the intensive and extensive portions of our study system. As previously stated, the landscape matrix surrounding a patch significantly influences the structural connectivity of the habitat (Steffan-Dewenter 2003). For instance, the spatial distribution of crop and non-crop habitat in the surrounding landscape may affect extinction and recolonization patterns within patches via dispersal of organisms over the landscape (Jonsen & Fahrig 1997). The intensive portion of our study system is characterized by very high proportions of intensive culture (70 – 90%) within the first 2 km surrounding the nest. High levels of intensive culture around our nests could be construed as a hostile environment (as per Bianchi *et al.* 2006) and might serve as a barrier to the dispersal to *P. sialia*. We postulate that the functional spatial extent of 0.2 km identified when modelling intensive agriculture represents a maximal threshold for the negative effects associated with intensive culture. Conversely, the proportion of extensive cultures within the extensive zone of the study decreased gradually across spatial extents, reaching its lowest level (~ 40%,) between radii of 2-20 km. Non-crop habitats such as fallows, pastures, hedgerows and woodlots, which are characteristic of extensive farming, act as biodiversity reservoirs providing alternate food sources, shelters, overwintering sites to many species and facilitates dispersal (Matson *et al.*1997). It is therefore possible that the 2 km extent identified when modelling extensive culture in the landscape represents the true functional spatial extent to which *P. sialia* perceives and utilizes habitat.

The spatial scales experienced by the organisms in our study were also a function of their trophic rank. Holt (1999) proposed that organisms at higher trophic levels experienced the landscape at larger spatial scales. Our data do not support this hypothesis. Indeed, we report the exact opposite. The higher up the trophic ladder, the smaller the spatial extents were to which the organisms respond to the proportion of extensive culture. These findings, however, are consistent with studies on other parasitoid-host models (Thies *et al.* 2003; Holzschuh *et al*. 2010). The body size of the organisms within our study system, as with other parasitoid-host models, did not increase with trophic level as is often the case in vertebrate predator – prey interactions. Foraging range and dispersal ability determine which landscape elements contribute to population dynamics and trophic interactions, but these characteristics tend to be more related to body size than to trophic position. Roland & Taylor (1997) showed the larger the body size of the tachinid parasitoid species, the larger the spatial scale at which forest structure had its greatest effect. Thus, in parasitoid host models, body size and not trophic rank should be used as an indicator of the spatial scale used.

In agreement with our first prediction, we demonstrated that the number of Tree Swallow fledglings was positively associated with the proportion of extensive culture in the landscape but decreased as the breeding season progressed. These results parallel those reported by Ghilain & Bélisle (2008) in which the higher number of fledglings in more extensive landscapes was attributed to an increase availability of insect prey as food availability is a major determinant of Tree Swallow nestling growth and survival (McCarty & Winkler 1990; Ghilain & Bélisle 2008).

Protocalliphora sialia abundance was shown to decrease as the proportion of intensive culture in the landscape increased. The current literature is replete with examples reporting lower population abundances of various taxa within intensively cultured lands (Burel *et al.* 1998; Benton *et al*. 2003; Burel *et al*. 2004; Tscharntke *et al.*

2005; Donald *et al*. 2006). Due to its life history, *P. sialia* is potentially more sensitive to agricultural intensification than other organisms at lower trophic levels as it is directly and indirectly affected by agricultural intensification. First, agricultural intensification can act directly on *P. sialia* populations by reducing their sources of nectar as well as the number of shelter and overwintering sites necessary for adult survival; second, it can act indirectly by diminishing its bird host population (Bianchi *et al*. 2006; Ghilain & Bélisle 2008). Interestingly, the number of *P. sialia* pupae per nest increased as the bird breeding season progressed. This observation has been reported in several other studies (Bortolotti 1984; Roby *et al*. 1996). Aside from diapausing as adults, very little is known about the overwintering behaviour of *P. sialia,* especially the environmental factors leading to their emergence in the spring. It is possible that bird hosts nesting early in the season, such as Tree Swallows, may benefit from the fact that many *P. sialia* have not yet emerged from diapause.

Protocalliphora sialia also benefitted from increased bird host availability, supporting our second prediction. Indeed, there was a very strong link between *P. sialia* nest abundance and the number of Tree Swallow fledglings. As in many other parasitic insect models (Hassel 1982; Walde & Murdoche 1988), host patch density could influence the ovipositing behaviour of *P. sialia*, with individual females laying fewer eggs in less dense patches. Alternately, as *P. sialia* cue primarily on host odors (Bennett & Whitworth 1991), it is also possible that high densities of hosts emit stronger olfactory cues, thereby attracting more founding *P. sialia* females, a behaviour which has been reported in other parasitic insects (Turlings *et al*. 1993; Mackauer & Michaud 1996; Sullivan *et al.* 2000). Both hypotheses are not mutually exclusive as they may act in concert with each other. More laboratory studies are needed in order to elucidate the ovipositing behaviour of *Protocalliphora*.

In agreement with our first two predictions, the level of hyperparasitism by *N. vitripennis* on *P. sialia* was shown to decrease with the amount of intensive cultural in the landscape and increase with the number of *P. sialia* pupae per nest. Like *P. sialia*, *N. vitripennis* is directly affected by agricultural intensification as it is dependent on sources of nectar and shelter sites, which are diminished in intensively cultured lands (Steffan-Dewenter 2003; Tscharntke *et al*. 2005). As with *P. sialia*, greater levels of hyperparasitism by *N. vitripennis* when host density is high may be attributed to individual females ovipositing in a greater number of hosts and/or to the higher number of founding females visiting the patch due to stronger olfactory cues.

Lastly, our data do not support the prediction made by Holt *et al*. (1999) that organisms at the higher trophic levels should be more susceptible to habitat loss and degradation than those at the lower trophic levels. Indeed, we showed that it is the organisms at the second trophic level that are disproportionally affected by agricultural intensification; the number of *P. sialia* per nest were shown to decreases by 74% from low to high intensive farms as compared to a 14% and 33% reduction in the number of Tree Swallow fledglings and in the level of hyperparasitism by *N. vitripennis*, respectively. This disproportionate reduction could be attributed to the trophic breadth of *P. sialia* in combination with an important "top-down" effect by *N. vitripennis*. Flies of the genus *Protocalliphora* have a unique life-history, as larvae, they are obligate blood-feeding parasites of nestling birds. Although considered a generalist, as it can develop on several species of bird hosts, *P. sialia* remains highly dependent on a handful of altricial farmland bird species for their survival, most of which are negatively affected by agricultural intensification (Jobin *et al.* 1996). On the other hand, *N. vitripennis* is a generalist parasitoid of calyptrate flies, which are very common in our system. Although agricultural intensification has been shown to negatively affect fly populations, the decrease in fly host availability is probably smaller than the decrease in bird host availability, thus potentially contributing to the greater decrease in *P. sialia*. In addition, as with virtually all parasitoids (see Maure *et al.* 2011 for exception), parasitism by *N. vitripennis* leads to the death of the developing *P. sialia* pupa and therefore also contributing to the reduction in *P. sialia* abundance.

To conclude, habitat loss and degradation associated with the intensification of agricultural practices disrupt trophic processes by contributing to the reduction in the number of Tree Swallow fledglings per nest as well as the level ectoparasitism by *P.sialia* and the level of hyperparasitism by *N. vitripennis*. Interestingly, not only was the spatial extent perceived by the organisms shown to increase with the organism's size, it was also shown to change depending on the landscape parameter modelled. With croplands and pastures occupying >40% of the land surface (Foley *et al.* 2005), it is critical for researchers, and especially conservation biologists, to design research protocols that take spatial aspects of trophic interactions into account as it is these interactions that dictate local biodiversity and community function. Furthermore, our results highlight the importance of considering multiple landscape parameters when quantifying the functional spatial scales of organisms. This is especially important for conservation biologists who use functional spatial scales as a method of delineating conservation areas; here, using only one landscape parameter could lead to underestimation of the area used by the organism of interest.

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Table 1. Definition and justification of explanatory variables used to quantify the influence of landscape structure on number of Tree Swallow fledglings, the number of *P. sialia* pupae per nest and the level of hyparasitism by *N. vitripennis* on *P. sialia* pupae per nest.

Explanatory variable	Definition (units)	Justification		
		No. Tree Swallow Fledgings	***Protocalliphora sialia* abudance**	**Level of hyperparasitism by *Nasonia vitripennis***
Year		interannual variation	idem	idem
Hatching date	Julian date	clutch size decreases through the season (1)	*Protocalliphora* abundance increase through the season (2)	higher levels of hyperparasitism through the season (3)
Nest weight	grams (g)		no. *Protocalliphora* may increase with nest size (2)	levels of hyperparasitism may increase with nest size
No. fledglings	number of Tree Swallow fledglings/nest		no. *Protocalliphora* may increase with number of fledglings (2)	levels of hyperparasitism may increase with number of fledglings
No. *P. sialia* pupae	number of *P. sialia* pupae/nest	nestling survival decreases with number of *Protocalliphora* (4)		levels of hyperparasitism may increase with number of *Protocalliphora* pupae
Intensive culture	relative amount of cover within a given exent around a nest box (%)	breeding success decreases with culture type (5)	no. *Protocalliphora* may decreases with with culture type (6)	levels of hyperparasitism may decrease with culture type (6)
Extensive culture	relative amount of cover within a given exent around a nest box (%)	breeding success increases with culture type (5)	no. *Protocalliphora* my increase with culture type (6)	levels of hyperparasitism may increase with culture type (6)

(1) Winkler & Allen 1995, (2) Bennett & Whitworth 1992, (3) Bennett & Whitworth 1991, (4) Streby *et al*. 2008, (5) Ghilain & Bélisle 2008, (6) Tscharntke & Brandle 2004.

Table 2. Parameters of the averaged models explaining the number of Tree Swallow hatchlings that fledged from the nest within nest boxes along a gradient of agricultural intensification in southern Québec. (N = 387).

Parameter	Estimate	Unconditional SE	Lower CI	Upper CI
∅=0.3 km				
Number of *P. sialia* pupae	0.002	0.002	-0.001	0.005
Year	-0.159	0.682	-1.496	1.178
Hatching date	-0.021	0.056	-0.032	-0.098
Nest weight	0.001	0.001	-0.001	0.004
Intensive culture	-0.095	0.176	-0.249	0.439
Extensive culture	0.015	0.066	-0.115	0.145
∅=5 km				
Number of *P. sialia* pupae	0.002	0.002	-0.001	0.005
Year	-0.159	0.682	-1.496	1.178
Hatching date	-0.021	0.056	-0.032	-0.098
Nest weight	0.001	0.001	-0.001	0.004
Intensive culture	-0.209	0.258	-0.296	0.715
Extensive culture	0.180	0.082	0.020	0.341

Table 3. Parameters of the most parsimonious models explaining *P. sialia* abundance within the nest boxes along a gradient of agricultural intensification in southern Québec. (N = 387).

Parameter	Estimate	Unconditional SE	Lower CI	Upper CI
Model 1: Nest + Intensive ⌀=0.2 km				
Year	-1.162	0.045	-1.250	-1.074
Number of fledglings	0.254	0.017	0.221	0.287
Hatching date	0.052	0.004	0.044	0.06
Nest weight	0.006	0.007	-0.007	0.0018
Intensive culture	-2.688	0.191	-3.062	-2.314
Model 4: Nest + Extensive ⌀=2 km				
Year	-1.147	0.045	-1.235	-1.059
Number of fledglings	0.277	0.017	0.244	0.31
Hatching date	0.052	0.004	0.044	0.06
Nest weight	0.005	0.001	0.004	0.006
Extensive culture	1.496	0.180	1.144	1.848

Table 4. Parameters of the most parsimonious and averaged models explaining the level of hyperparasitism by *N. vitripennis* on *P. sialia* within nest boxes along a gradient of agricultural intensification in southern Québec. (N = 207).

Parameter	**Estimate**	**Unconditional SE**	**Lower CI**	**Upper CI**
Nest + Extensive *⌀=0.05 km*				
Number of fledglings	0.128	0.027	0.076	0.180
Number of *P. sialia* pupae	0.036	0.001	0.034	0.038
Year	-0.019	0.077	-0.170	0.132
Hatching date	0.027	0.059	-0.089	0.142
Nest weight	-0.002	0.001	-0.004	0.000
Intensive culture	-0.063	0.127	-0.311	0.186
Extensive culture	0.073	0.117	-0.157	0.303
⌀=0.2 km				
Number of fledglings	0.135	0.027	0.081	0.188
Number of *P. sialia* pupae	0.036	0.001	0.033	0.038
Year	-0.010	0.077	-0.161	0.014
Hatching date	0.028	0.006	0.016	0.040
Nest weight	-0.002	0.001	-0.004	0.000
Intensive culture	-0.589	0.217	-1.013	-0.164
Extensive culture	0.278	0.178	-0.071	0.628
⌀=0.3 km				
Number of fledglings	0.138	0.027	0.084	0.192
Number of *P. sialia* pupae	0.035	0.001	0.033	0.038
Year	-0.011	0.077	-0.162	0.140
Hatching date	0.028	0.006	0.016	0.041
Nest weight	-0.002	0.001	-0.004	0.000
Intensive culture	-0.802	0.252	-1.295	-0.308
Extensive culture	0.367	0.128	0.116	0.618

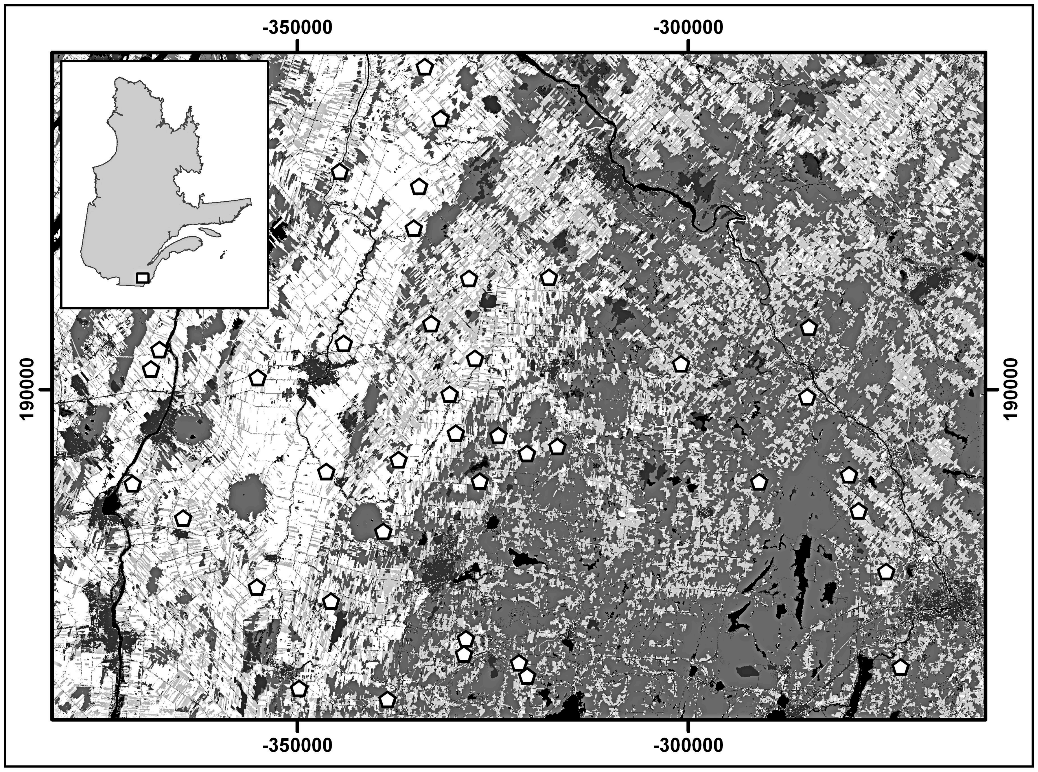

Fig. 1. Distribution of the 40 farms along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. Land cover types are based on a mosaic of classified LANDSAT-TM satellite images (Canadian Wildlife Service 2004) and include water (black), urban (dark gray), forest (mid-tone gray), extensive cultures (e.g., hayfields and pastures; light gray), and intensive cultures (e.g., maize, cereals, and soybeans; white). Open pentagons indicate farm locations. Coordinates are Lambert Conic Conform and refer to the number of meters from a reference point.

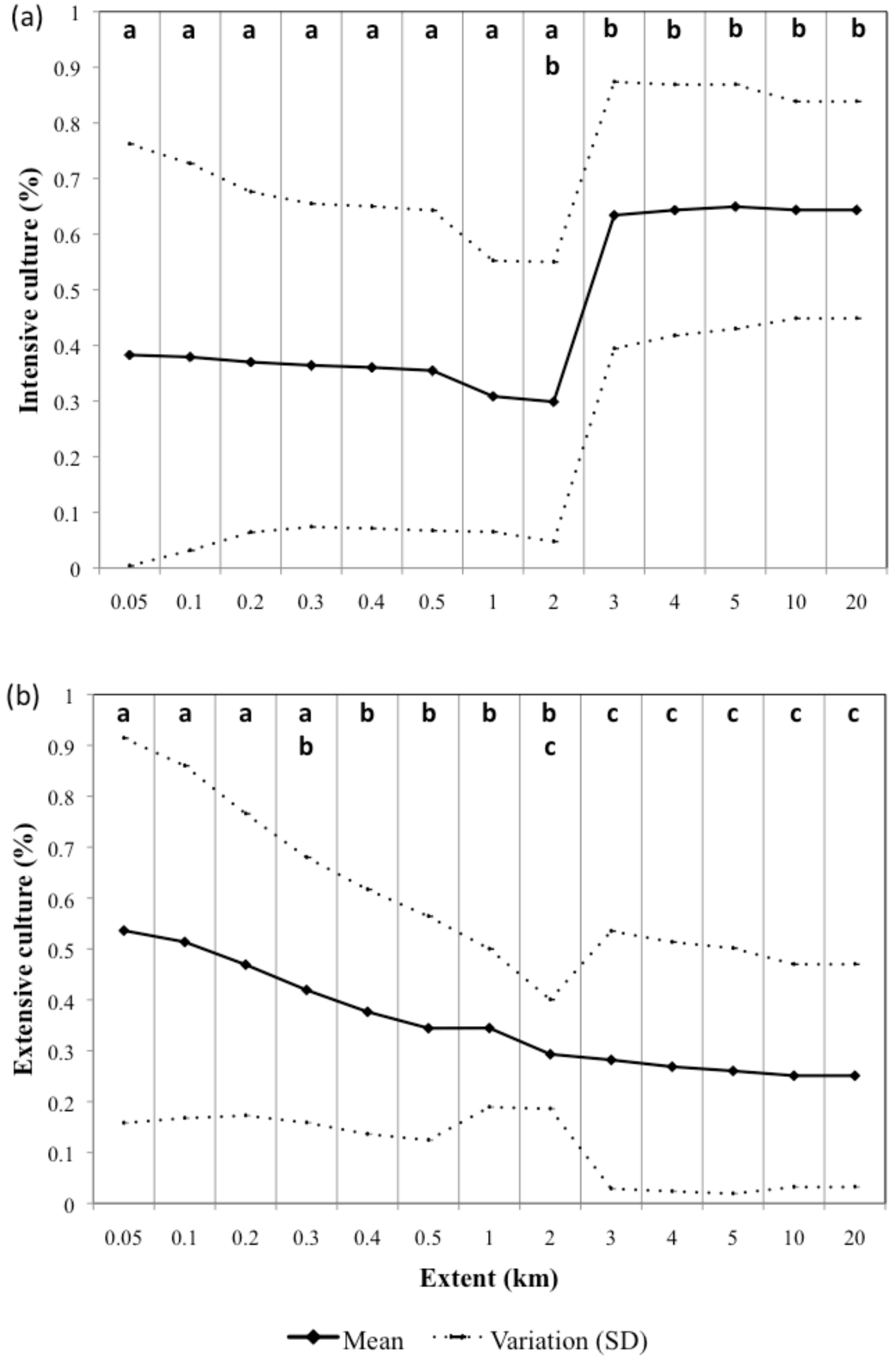

Fig. 2. Average values and associated variation (SD) for two landscape parameters (proportion of intensive and extensive culture in the landscape) across 13 spatial extents (while holding grain constant) from 40 farms along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. The number of scale domains within each metric is denoted for each figure using lowercase alphabet, as determined using Kruskal-Wallis non-parametric post-hoc tests.

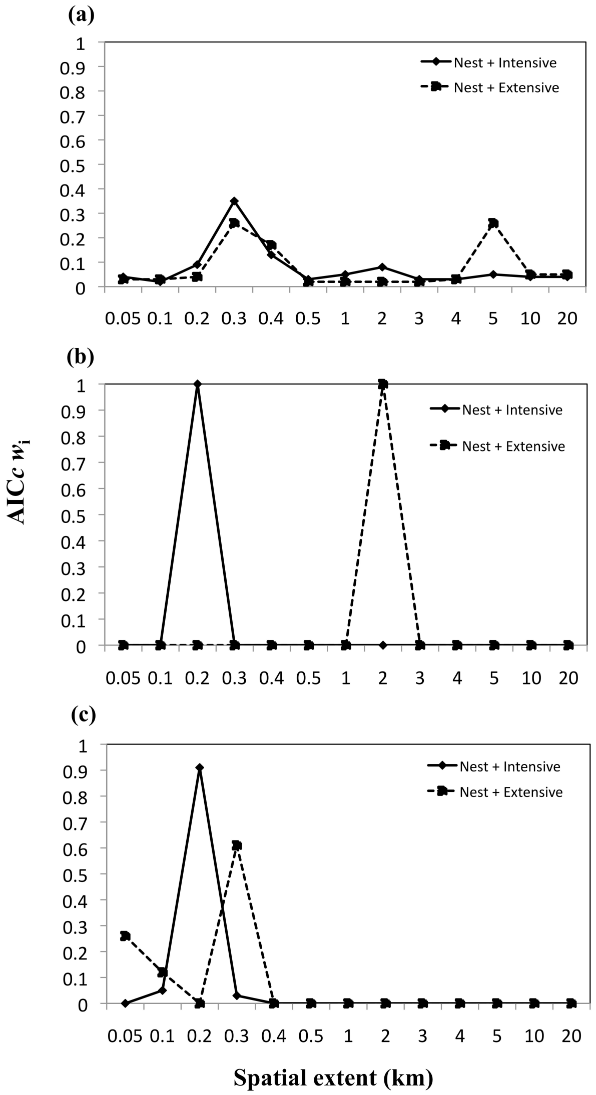

Fig. 3. Akaike weights of the models explaining (a) the number of Tree Swallow hatchlings that fledged (N=286), (b) abundance of *P. sialia* pupae (N=285) and (c) level of hyperparasitism by *N. vitripennis* on *P. sialia* (N=157) from the nest within the experimental nest boxes at 13 extents scales along a gradient of agricultural intensification in southern Quebec, 2008-2009. Models are generalized mixed models with a logit link for binomial error distribution with farm ID as random factor (N=286). See table 1 for variable definition and justification.

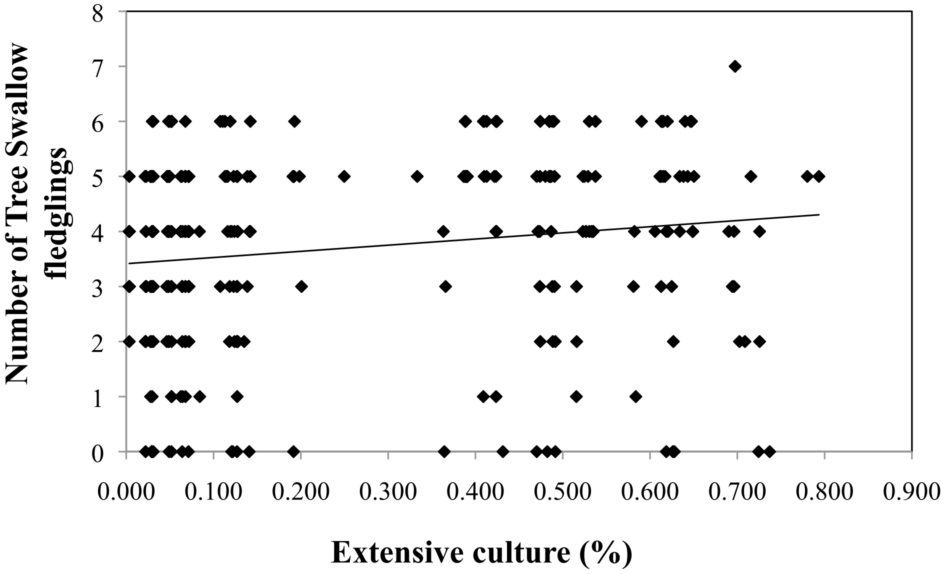

Fig. 4. Influence of landscape composition on number of Tree Swallow fledglings per nest along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. Effect of the proportion of extensive culture within a 5 km radius of the nest on number of Tree Swallow fledglings per nest (N = 286).

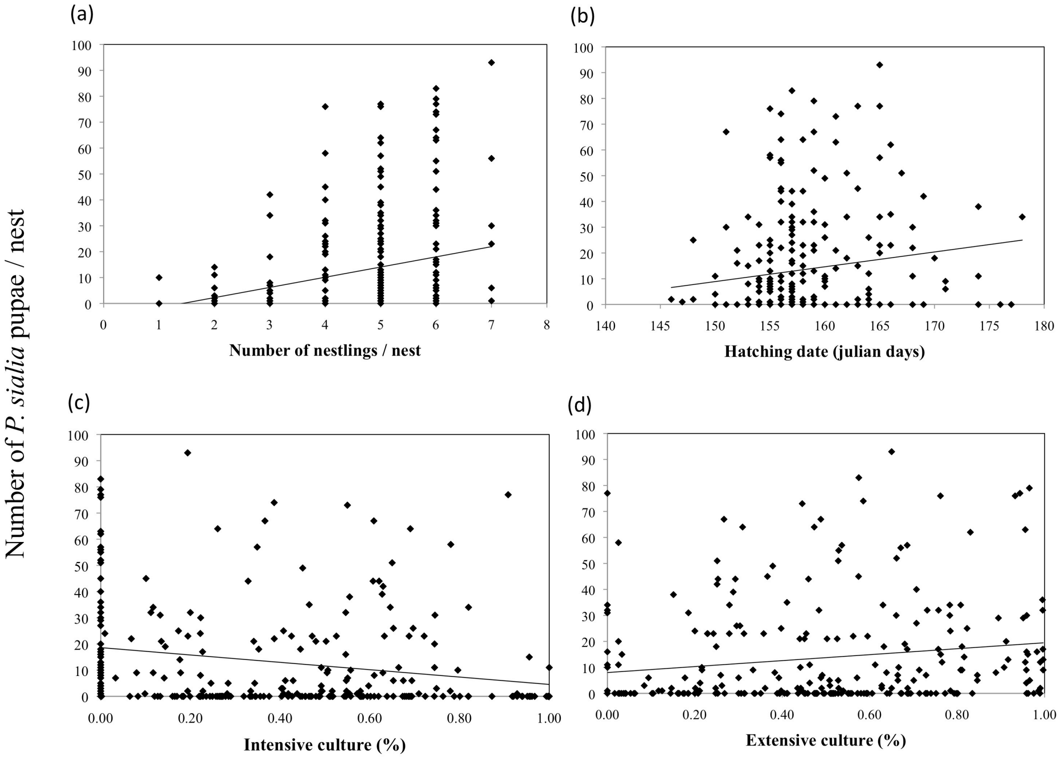

Fig. 5. Influence of landscape composition on number of *P. sialia* pupae per Tree Swallow nest along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. (a) Effect of the number of Tree Swallow nestlings per nest on the number of *P. sialia* per nest based on the Nest+Intensive model in Appendix C. (b) Effect of the Tree Swallow nestling hatching date on the number of *P. sialia* per nest based on the Nest+Intensive model in Appendix C (c) Effect of the proportion of intensive culture within a 0.2 km radius of the nest on the number of *P. sialia* per nest based on the Nest+Intensive model in Appendix C. (d) Effect of the proportion of extensive culture within a 2 km radius of the nest on the number of *P. sialia* per nest based on the Nest+Extensive model in Appendix C. (N = 387).

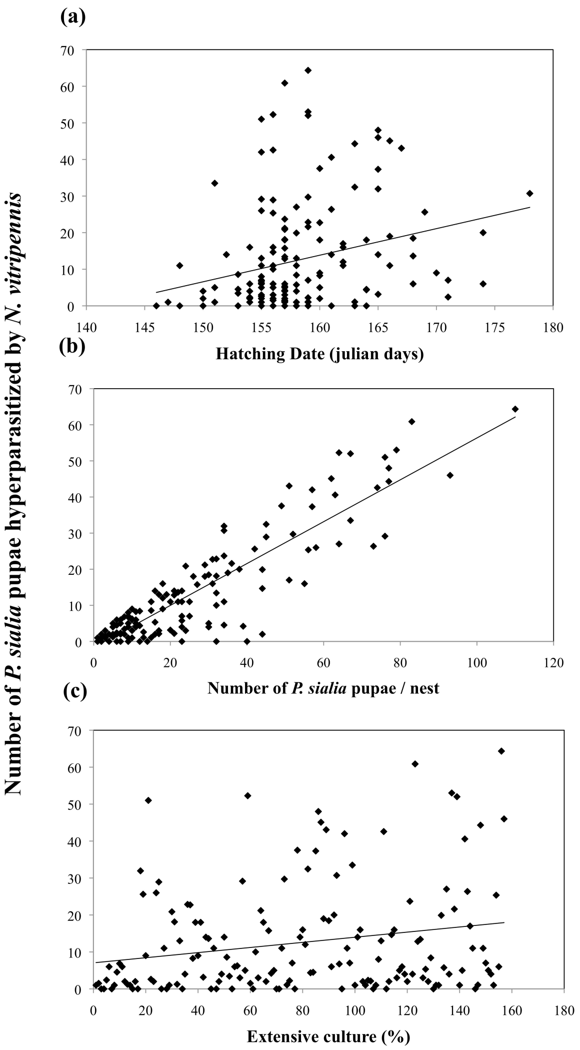

Fig. 6. Influence of landscape composition on number of *P. sialia* pupae hyperparasitized by *N. vitripennis* per Tree Swallow nest along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. (a) Effect of the Tree Swallow nestling hatching date on the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* per nest based on model averaged estimates at spatial extent of 0.3 km. (b) Effect of the number of number of *P. sialia* pupae per nest on the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* per nest based on model averaged estimates at spatial extent of 0.3 km. (c) Effect of the proportion of extensive culture on the number of *P. sialia* pupae hyperparasitized by *N. vitripennis* per Tree Swallow nest based on the based on model averaged estimates at spatial extent of 0.3 km (N = 207).

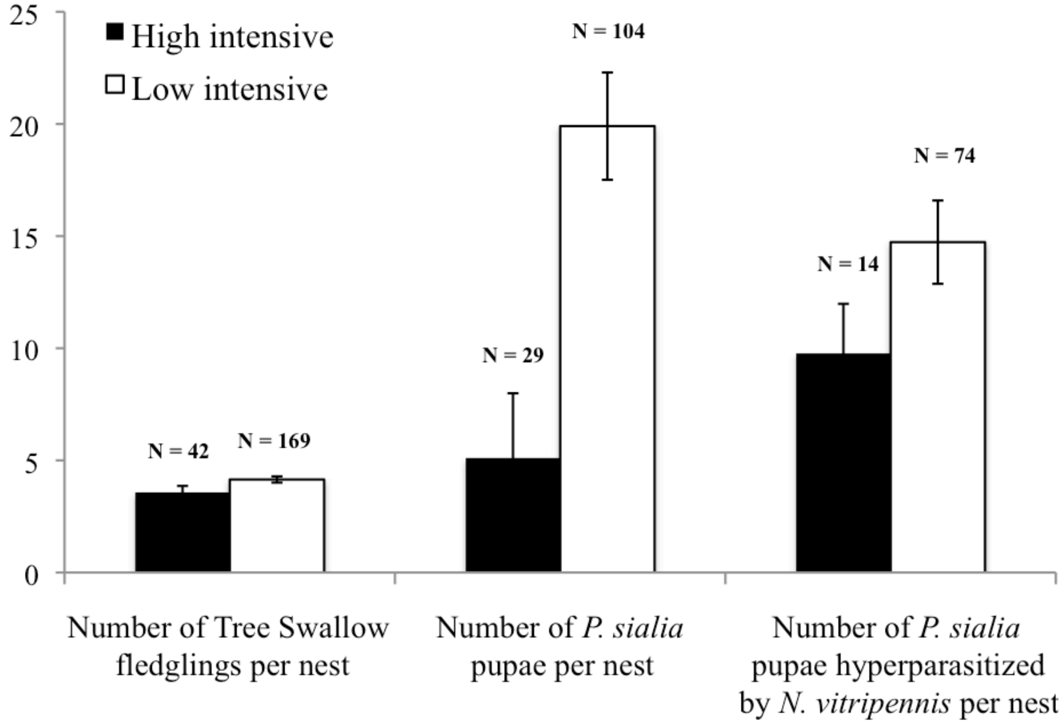

Fig. 7. The mean number of Tree Swallow fledglings, *P. sialia* pupae and *P. sialia* pupae parasitized by *N. vitriepennis* per nest within high (≥ 80% intensive culture in the landscape) and low (≤ 20% intensive culture in the landscape) intensive farms along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. (± SE).

Appendices

Appendix A. Akaike weights of the models explaining number of Tree Swallow hatchlings that fledged from the nest within the experimental nest boxes at the spatial extents of 0.3 km and 5 km along a gradient of agricultural intensification in southern Quebec, 2008-2009.

Table A1. Akaike weights of the models explaining number of Tree Swallow hatchlings that fledged from the nest within the experimental nest boxes at the spatial extents of 0.3 km and 5 km along a gradient of agricultural intensification in southern Quebec, 2008-2009. Models are generalized mixed models with a logit link for binomial error distribution with farm ID as random factor (N=286). See table 1 for variable definition and justification.

Spatial Extent (km)	Nest + Intensive		Nest		Intensive		Nest + Extensive		Extensive	
	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2
0.3	0.31	0.26	0.49	0.22	0	0.16	0.2	0.24	0	0.16
5	0.12	0.26	0.6	0.22	0	0.16	0.28	0.22	0	0.16

Notes: AIC_c weights depict the relative strength of each model for a given spatial extent.

List of models and their variables:

Nest + Intensive = number of *P. sialia* pupae + year + hatching date + nest weight + intensive culture

Nest = number of *P. sialia* pupae + year + hatching date + nest weight

Intensive = intensive culture

Nest + Extensive = number of *P. sialia* pupae + year + hatching date + nest weight + extensive culture

Extensive = extensive culture

Appendix B. Akaike weights of the models explaining the abundance of *P. sialia* pupae within the experimental nest boxes at the spatial extents of 0.2 km and 2 km along a gradient of agricultural intensification in southern Quebec, 2008-2009

Table B1. Akaike weights of the models explaining the abundance of *P. sialia* pupae within the experimental nest boxes at the spatial extents of 0.2 km and 2 km along a gradient of agricultural intensification in southern Quebec, 2008-2009. Models are generalized mixed models with a log link for poisson error distribution with farm ID as random factor (N=285). See table 1 for variable definition and justification.

Spatial Extent (km)	Nest + Intensive		Nest		Intensive		Nest + Extensive		Extensive	
	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2
0.2	1	0.44	0	0.39	0	0.16	0	0.41	0	0.15
2	0	0.40	0	0.39	0	0.15	1	0.43	0	0.16

Notes: AIC_c weights depict the relative strength of each model for a given spatial extent.

List of models and their variables:

Nest + Intensive = number of fledglings + year + hatching date + nest weight + intensive culture

Nest = number of fledglings + year + hatching date + nest weight

Intensive= intensive culture

Nest + Extensive= number of fledglings + year + hatching date + nest weight + extensive culture

Extensive= extensive culture

Appendix C. Akaike weights of the models explaining the level of hyperparasitism by *N. vitripennis* on *P. sialia* within the experimental nest boxes at the spatial extents of 0.05 km, 0.2 km and 0.3 km along a gradient of agricultural intensification in southern Quebec, 2008-2009.

Table C1. Akaike weights of the models explaining the level of hyperparasitism by *N. vitripennis* on *P. sialia* within the experimental nest boxes at the spatial extents of 0.05 km, 0.2 km and 0.3 km along a gradient of agricultural intensification in southern Quebec, 2008-2009. Models are generalized mixed models with a log link for poisson error distribution with farm ID as random factor (N=157). See table 1 for variable definition and justification.

Spatial Extent (km)	Nest + Intensive		Nest		Intensive		Nest + Extensive		Extensive	
	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2	AICc w_i	R^2
0.05	0.01	0.81	0	0.78	0	0.20	0.99	0.81	0	0.20
0.2	0.34	0.84	0	0.78	0	0.19	0.66	0.81		0.20
0.3	0.6	0.84	0	0.78	0	0.19	0.4	0.81	0	0.45

Notes: AIC$_c$ weights depict the relative strength of each model for a given spatial extent.

List of models and their variables:

Nest + Intensive = number of fledglings + number of *P. sialia* pupae + year + hatching date + nest weight + intensive culture

Nest = number of fledglings + number of *P. sialia* pupae + year + hatching date + nest weight

Intensive = intensive culture

Nest + Extensive = number of fledglings + number of *P. sialia* pupae + year + hatching date + nest weight

Extensive = extensive culture

Appendix D. Correlations between the percentages of extensive and intensive agriculture between spatial extents within 40 farms along a gradient of agricultural intensification in southern Quebec, 2008-2009.

Table D1. Pearson correlations of the arcsine square root transformed percentages of extensive and intensive agriculture between spatial extents within 40 farms along a gradient of agricultural intensification in southern Quebec, 2008-2009.

	Extensive 0.05 km	**Extensive 0.1 km**	**Extensive 0.2 km**	**Extensive 0.3 km**	**Extensive 0.4 km**	**Extensive 0.5 km**	**Extensive 1 km**	**Extensive 2 km**	**Extensive 3 km**	**Extensive 4 km**	**Extensive 5 km**	**Extensive 10 km**	**Extensive 20 km**
Intensive 0.05 km	-0.925	-0.891	-0.765	-0.697	-0.636	-0.590	-0.352	-0.281	0.360	0.337	0.326	0.369	0.357
Intensive 0.1 km	-0.904	-0.919	-0.837	-0.772	-0.714	-0.668	-0.400	-0.320	0.470	0.449	0.439	0.467	0.465
Intensive 0.2 km	-0.804	-0.860	-0.878	-0.844	-0.799	-0.758	-0.442	-0.352	0.611	0.590	0.585	0.608	0.607
Intensive 0.3 km	-0.698	-0.764	-0.812	-0.829	-0.810	-0.776	-0.439	-0.367	0.711	0.693	0.691	0.706	0.706
Intensive 0.4 km	-0.620	-0.695	-0.759	-0.789	-0.791	-0.765	-0.449	-0.387	0.760	0.748	0.747	0.761	0.761
Intensive 0.5 km	-0.586	-0.665	-0.731	-0.763	-0.771	-0.753	-0.460	-0.403	0.798	0.788	0.787	0.801	0.800
Intensive 1 km	-0.413	-0.506	-0.570	-0.593	-0.598	-0.584	-0.481	-0.445	0.895	0.887	0.875	0.870	0.871
Intensive 2 km	-0.370	-0.471	-0.544	-0.580	-0.590	-0.583	-0.468	-0.485	0.948	0.974	0.961	0.940	0.941
Intensive 3 km	0.300	0.410	0.500	0.545	0.558	0.558	0.443	0.453	-0.985	-0.975	-0.964	-0.938	-0.934
Intensive 4 km	0.281	0.397	0.490	0.534	0.548	0.549	0.461	0.470	-0.983	-0.985	-0.980	-0.953	-0.953
Intensive 5 km	0.269	0.382	0.490	0.536	0.553	0.561	0.491	0.493	-0.970	-0.979	-0.982	-0.963	-0.963
Intensive 10 km	0.301	0.415	0.515	0.560	0.584	0.604	0.547	0.542	-0.943	-0.952	-0.960	-0.971	-0.971
Intensive 20 km	0.304	0.415	0.516	0.560	0.584	0.604	0.548	0.542	-0.943	-0.952	-0.960	-0.972	-0.971

Chapter 7

Testing optimality models under natural conditions within a gradient of agricultural intensification

Simon P. Daoust[1], Dany Garant[2], Jade Savage[3], Marc Bélisle[2], Guy Boivin[4], Hélène Presseault-Gauvin[2] and Jacques Brodeur[1]

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Abstract

1. Optimality models have been developed to predict how animals should behave in order to maximize their lifetime fitness gain. However, most have been tested under artificial conditions that simplify the complex situation individuals face under natural conditions.

2. We investigated how founding females within populations of *Nasonia vitripennis* (Walker) parasitic wasps respond to environmental variability caused by agricultural intensification by testing predictions made from the Marginal Value Theorem (MVT), Local Mate Competition (LMC) and Host Quality (HQ) models. For this purpose, we used a tri-trophic biological model composed of a bird host, the Tree Swallow *Tachycineta bicolor* (Vieillot), the ectoparasite *Protocalliphora sialia* Shannon & Dobroscky (Diperta: Calliphoridae) and the parasitoid wasp *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae).

3. Habitat loss and degradation associated with the intensification of agricultural practices directly influence *P. sialia* and *N. vitripennis* populations as well as their interactions. The pupal length of the *P. sialia* fly hosts was shown to be smaller in more intensive landscapes. Female *P. sialia* were shown to oviposit following MVT and LMC, producing smaller broods in smaller hosts and adjusting the sex ratio of their offspring in order to minimize competition between their sons. When controlling for the number of founding females and founding female rank, females in areas of intensive agriculture produced more male biased broods than those in extensive landscapes.

4. We showed that the size of *N. vitripennis* wasps was affected by host size and by the number of conspecifics within the host; smaller wasps emerged from smaller hosts regardless of the brood size adjustments made by the founding females and both female and males were smaller when developing with a greater number of competitors.

5. To conclude, we showed that agricultural intensification disrupts trophic level processes by reducing both habitat and host quality. This in turn influences the

behavior of founding female wasps, resulting in smaller, more male biased broods, composed of smaller individual wasps within areas of intensive agriculture.

Introduction

The behaviors associated with resource acquisition and investment have a major impact on the distribution, movement and population dynamics of most organisms. In a behavioral ecology context, several optimality models have been used to predict how animals should behave in order to maximize their lifetime fitness gain (Giraldeau 2005). However, most organisms were tested under artificial conditions that simplify the complex situation individuals face under natural conditions. This is rather surprising as it is the ecology of the individuals that drives population level processes (Begon *et al.* 1996) and the response of individuals to modification of their habitat should translate into changes of the population dynamics of a population.

The intensification of agricultural production has resulted in a dramatic change in the agricultural landscape (Robinson & Sutherland 2002). Formerly heterogeneous, extensively cultured soils with well-balanced proportions of arable lands, grasslands, and forests are being transformed into homogenous, intensively cultured areas with simple landscapes containing only fragments of semi-natural lands (Bélanger & Grenier 2002). These changes have been shown to influence a variety of ecological responses, including animal movement (reviewed in Fahrig 2007), population persistence (Donald *et al.* 2001; Tscharntke *et al.* 2005), species interactions (Tscharntke & Brandl 2004) and ecosystem function (Matson *et al.* 1997; Tscharntke *et al.* 2005), resulting in a loss of local biodiversity (Benton *et al*. 2003).

These effects are likely to be magnified at higher trophic levels. Insect parasitoids, that develop on or in a single host, generally an herbivore, and kill it during its development (Eggleton & Gaston 1990), are influenced by the agricultural landscape. Their population density and their impact on herbivore populations decreases in inverse proportion with intensive culture in the landscape (Thies *et al.*

2003, 2004; Tscharntke & Brandl 2004; Tscharntke *et a*l. 2005; Bianchi *et al*. 2006). Occupying a high trophic rank, parasitoids can be directly affected by agricultural intensification through the loss of overwintering sites, shelters and sources of nectar, and indirectly through changes in abundance and quality of their host populations (Thies *et al*. 2003; Tscharntke *et al*. 2004; Holzschuh *et al*. 2010).

Several optimality models have been proposed to predict how parasitoid females should respond optimally to changes in factors such as host quality, host density and intraspecific competition but the predictions of three models will be examined here. The Marginal Value Theorem (MVT) was originally proposed to predict the optimal behavior of an organism that encounters resources that are clumped (Charnov 1976). The organism should exploit this patch of resource until its instantaneous rate of gain reaches the habitat average. In parasitoids, this model has been used to predict the optimal patch residence time and the optimal allocation of progeny in a host for gregarious parasitoid species (Charnov & Skinner 1984, 1985). Female parasitoids should therefore continue to allocate progeny within a host until the instantaneous rate of fitness gain obtained from an additional progeny invested in a host reached the habitat average. A parasitoid female is thus expected to stay for a shorter period of time, and therefore to invest fewer progeny, in low quality hosts compared to high quality hosts. The quality of the host can vary based on its species, size, age, sex, parasitization status (Boivin 2010).

The Local Mate Competition (LMC) model (Hamilton 1967; Taylor & Bulmer 1980; Werren 1980) predicts, for species whose populations are structured and where mating is limited to individuals present in a sub-population represented by the individuals emerging on the same patch, the optimal sex ratio that females should deposit according to the level of competition perceived on the patch. When a female is alone exploiting a patch, she should deposit just enough sons to mate with the daughters that will emerge from that patch. As the competition between ovipositing females increases, the females should gradually increase the sex ratio (proportion of males) deposited until it approaches equality. At this point the population also approaches panmixy on the patch. The factor driving this optimality model is mostly the competition perceived by the female as she exploits a patch but sib-mating on the emergence patch has also the effect of increasing the relatedness between mother and offspring, a phenomenon known to select for a more female-biased sex ratio (Ode & Hardy 2008). However, the predictions of the LMC model can be altered if there is competition for resources during larval development (Godfray 1986).

The Host Quality model (HQ) predicts that if the response of sons and daughters to host quality differs, then female should allocate to low quality hosts the sex that suffers the less (Charnov 1979; Charnov *et al.* 1981). The fitness of females is generally more affected by host quality and therefore males are allocated to low quality hosts in several species (King 1992; Ueno 1999; Sykes *et al*. 2007). although exceptions have been reported (King 1989, Ode *et al*. 1996, Godin & Boivin 2000). An important prediction of the HQ model is that the sex allocation in relation to host quality is not absolute but rather relative (West 2009). Theoretically, when only one host quality is available on a patch, the female should allocate the sex ratio predicted by the LMC model. It is only when a range of host qualities is available that females should allocate differently sons and daughters based on the perceived host quality.

The gregarious parasitoid *Nasonia vitripennis* (Walker) has been extensively used as a model organisms for the study of adaptive sex ratio and clutch size adjustment and has been shown to follow the MVT (indirectly tested by Rivers & Denlinger 1995) and the LMC model (Werren 1980; 1984; Orzack & Parker 1990; Drapeau & Werren 1999; Shuker & West 2004; Shuker *et al*. 2004; 2006) under laboratory conditions. Interestingly, *N. vitripennis* females do not follow the HQ model (King 1992; Sykes *et al.* 2007), as females do not to adjust the sex ratio deposited based on host quality. The prediction of these models however have only rarely been studied in the field (but see Werren 1980; Molbo & Parker 1996; Grillenberger *et al*. 2008; Burton-Chellew *et al*. 2008).

In this paper, we used an integrative approach combining behavioral, molecular, population, community and landscape ecology to investigate how founding females within populations of parasitoid wasps respond to environmental variability caused by agricultural intensification. We used a tri-trophic biological model composed of a bird host, the Tree Swallow *Tachycineta bicolor* (Vieillot), the ectoparasite *Protocalliphora sialia* Shannon & Dobroscky (Diperta: Calliphoridae) and the parasitoid wasp *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). Their interactions were studied within a gradient of agricultural intensification covering 10, 200 km^2 in southern Québec, Canada. Previous work revealed that agricultural intensification leads to a significant decrease in the abundance of *P. sialia,* the fly hosts of *N. vitripennis* (S.P. Daoust, unpublished data). Thus, *N. vitripennis* were confronted with different resources whether they forage within areas of intensive or extensive agriculture. The first objective was to quantify the effect of agricultural intensification on the quality of the *P. sialia* host populations, using pupal size as a proxy of host quality (Rivers & Denlinger 1995). In Diptera, poor maternal diet and increased age have been shown to reduce the size of the egg as well as the amount of maternal contribution (yoke), which in turn lead to smaller offspring (Jann & Ward 1999; Chapman & Goulson 2000; McIntyre & Gooding 2000). Areas of intensive agriculture provide fewer and more isolated sources of host, nectar and shelter, which translate in an increase in foraging time and a reduction in the energy reserves of founding females within these areas. In addition, nestlings within areas of intensive culture have been shown to contain higher pesticide levels in their blood, which could also potentially affect the development of the hematophagous larvae of *P. sialia* (Burgess *et al.* 1999; Bishop 1998a,b). Within this context we predict that *Protocalliphora* host size would be negatively affected by agricultural intensification. The second and major objective of this work was to identify the mechanisms through which *N. vitripennis* females respond to variations in resource quality and availability associated with agricultural intensification within the study system. In order to answer this objective, we used molecular tools to differentiate between the individual wasp families parasitizing the fly hosts. We focused on two behavioral traits, brood size and sex ratio adjustment by *N. vitripennis* females, as they allowed us to test predictions made from the MVT, LMC and HQ models. We also assessed the effect of these reproductive traits on offspring size, a good proxy of parasitoid fecundity and longevity (Roitberg *et al*. 2001; Rivero & West 2002; Sykes *et al.* 2007). Within the framework of the MVT model and in accordance with our first prediction, we postulate that *N. vitripennis*, within areas of intensive agriculture, should respond to the presence of smaller hosts by producing smaller broods. Previous work revealed significant reduction in the level of parasitism by *N. vitripennis* in areas of intensive agriculture (S.P. Daoust, unpublished data). This, in association with our first prediction provides the context from which the following predictions based on LMC and HQ models can be made: (1) there should be fewer founding females in areas of intensive culture, (2) females within natural populations should follow the LMC but not the HQ model and lastly, (3) the size of *N. vitripennis* females should be smaller in hosts where a higher proportion of the offspring are female, this effect being greater at larger clutch sizes.

Materials and Methods

Model organisms

The Tree Swallow is a common and widely distributed summer breeding bird in North America. It is one of the first migratory bird species to arrive on its breeding grounds in the spring, usually during the first two weeks of April within southern Québec, Canada. The Tree Swallow is predominantly insectivorous; feeding on flies, beetles and ants, but can also feed on a few varieties of seeds and berries (Quinney & Ankney 1985). To date, they are one of the farmland bird species in Canada that are the most impacted by agricultural intensification, with a total population annual decline of 2.5% since 1986 (Rioux Paquette & Bélisle 2011).

Protocalliphora sialia larvae are obligate blood-feeding parasites of nestling birds. As adults, they have been shown to feed on nectar producing flowers. Although infrequently collected in the field as adults, *P. sialia* larvae and pupae are typically found following close examination of nestlings or nest materials. While feeding, the larvae are characteristically anchored to the most accessible part of nestlings (feet, legs and belly) (Whitworth & Bennett 1992). Blood feeding by *Protocalliphora* larvae on developing nestlings has been shown to lower hematocrit and haemoglobin levels (Whitworth & Bennett 1992; O'Brien *et al*. 2001; Hannam 2006), reduce growth rates (Whitworth & Bennett 1992), decrease body temperatures and metabolic rates (Simon *et al*. 2005), lower fledging survival and reduce dispersal in the first days following fledging (Thomas *et al.* 2007, Streby *et al.* 2008). The prevalence of infestation by *Protocalliphora* in the Tree Swallow nests within our field system was of 34.6% in 2009 (S.P. Daoust, unpublished data). Of these infested nests, 87.88% were infested with *P. sialia*, with an average number of 19.63 ± 39.20SD pupae per nest (S.P. Daoust, unpublished data).

Nasonia vitripennis is a small gregarious parasitoid (females approximately 2mm in length) commonly referred to as "jewel wasp". Females are synovigenic, they emerge with a limited number of mature eggs, and egg production and maturation are continuous throughout the life of the female (Rivero & West 2002). They are generalists, adult females oviposit within the puparium of several cyclorraphous fly species (Whiting 1967). Females seek out the host puparia, paralyse the fly pupa within and can oviposit over 60 eggs on the pupa's surface. The flightless males emerge before the females and mate with them as they emerge. Females are winged and need to disperse after mating to find new, suitable hosts in which to lay eggs (Whiting 1967). Until a food source is found (source of carbohydrates such as nectar or honeydew), females must rely on the resources accumulated as a larva (Rivero & West 2002). Temporal starvation is thus a likely scenario in the field, and its duration will greatly depend on the quality of the environment in which the females forage (Rivero & West 2002). Once a host is parasitized, there is a window of approximately 48 h during which further females tend to parasitize the host (superparasitism). Superparasitism rarely occurs after this period because by then the first brood will have developed sufficiently to start utilizing the host's resources, leaving too little food for later larvae (Werren 1984).

Study region and nest box network

The 10,200 km^2 study area included a network of 400 nest boxes distributed among 40 farms within the Montérégie and Estrie regions of southern Québec, Canada (Fig. 1). The area is characterized by an east–west gradient of agricultural intensification where dairy farming and small-scale, familial farms are replaced by large-scale, continuous row cropping with full mechanization and high input of pesticides as well as organic and chemical fertilizers (Bélanger & Grenier 2002; Jobin *et al*. 2003; Fig. 1). The gradient which ranges from extensive (hayfields and pastures) to intensive (maize, cereals, and soybean) cultures is also characterized by gradually smaller and more fragmented forest cover, by an increase in the drainage of wetlands, and a canalization of streams (Bélanger & Grenier 2002; Jobin *et al*. 2003; Fig. 1). Nest boxes were built according to North American Bluebird Society's specifications (i.e., Eastern/Western Bluebird model) and were installed in the winter of 2004. Boxes were put up 50 m apart along drainage ditches or fence lines that bordered agricultural fields or pastures. The distance to the nearest building thus varied substantially among boxes (119 ± 93 m, mean = 1 SD; n = 400 boxes). All boxes were mounted on a metal post 1.5 m above the ground and with the opening facing southeast (Ghilain & Bélisle 2008). Neither the boxes nor the posts were fitted with antipredator devices. Farms were equally distributed between intensive and extensive agricultural zones. See Ghilain & Bélisle (2008) for the detailed farm selection protocol.

Specimen collection, identification and measurement

At the end of their breeding season, and prior to fall migration, Tree Swallows typically assess the quality (size, presence of dead nestlings) of the nests that were used during the breeding season to gather public information and ascertain potential future breeding sites (Robertson *et al.* 1992), a behaviour also called "prospection" (Doligez *et al*. 2004). To avoid interference with the bird's habitat quality assessment, insect specimens were collected using the following protocol: 2 Tree Swallow nests per farm were randomly selected in each of the 37 farms where Tree Swallows were shown to be present and were examined for *Protocalliphora* pupae immediately upon fledging, i.e. between June 25 and July 16 in 2009. Nests were carefully removed from the box and all pupae present in nest material and in the nest box were collected. Nests were put back into the box upon completion of sampling. *Protocalliphora* pupae were only collected from 27 of the 37 farms sampled. Pupae were individually placed into (4 cm X 7 cm) meshed capped plastic bottles for rearing. They were maintained in a mixture of sawdust and 1% boric acid at room temperature (~ 22 ºC) until the emergence of adult flies or parasitoids (5 to 12 days). Adult *Nasonia* were stored in 90% ethanol at -20 °C.

All *Protocalliphora* pupae and *Nasonia* specimens were identified and measured using a stereoscope equipped with a digital camera. Measurements were taken using PixeLINK® imaging software. Specimens were identified to species following the protocol described in Daoust *et al*. (unpublished data). *Protocalliphora sialia* and *Nasonia vitripennis* were by far the most abundant species collected within our study system, representing 98.5% and 99.3% of the sampled specimens (Simon P. Daoust unpublished data).

Protocalliphora sialia pupae length was measured from the tip of the prothoracic fringe to base of the stigmatal area (refer to Whitworth 2003). Female and male *N. vitripennis* size was determined by measuring the length of the right hind tibia, the most commonly used measure of body size in parasitic wasps (Roitberg *et al.* 2001) including *N. vitripennis* (Burton-Chellew *et al.* 2007).

Landscape characterization

We characterized the level of spatial heterogeneity around each nest box by measuring the relative cover of intensive and extensive cultures (Marshall & Moonen 2002; Burel *et al.* 2004) within radii of 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 1, 2, 3, 4, 5, 10, and 20 km, using both visual field characterisation (up to 0.5km radii) and estimates based on a mosaic of georeferenced classified Landsat-7 satellite images taken between August 1999 and May 2003 (pixel resolution 25 m X 25 m; Canadian Wildlife Service 2004) for radii between 1 and 20 km. The latter were chosen based on the findings of a previous work on Tree Swallows in which they were shown to respond to broader spatial scales (Ghilain & Belisle 2008). We included smaller radii (0.05-0.5 km) in the study as parasitoid abundance has been shown to respond to landscape structure at smaller spatial scales than birds (Steffan-Dewenter 2003; Holzschuh *et al*. 2010). Measurements of relative land cover were obtained with ArcView GIS Spatial Analyst 2.0a (ESRI 2005).

Genetic analysis

More than one *N. vitripennis* female can parasitize the same host (Grillenberger *et al.* 2008). Individual wasps were thus genotyped in order to identify sibling status and the identity of founding *N. vitripennis* females in order to determine the brood size of individual females. We subsampled by randomly selecting one nest per sampled farm (N=27) and then by randomly selecting two parasitized pupae per nest (N=54). We further subsampled by randomly selecting a percentage of wasps per pupa based on a sliding scale; for pupa containing: (1) ≤ 10 wasps, all wasps were sampled, ≤ 30 wasps, 95% were sampled, ≤ 50 wasps, 90% were sampled, ≤ 75 wasps, 85% were sampled and ≤ 110 wasps, 80% were sampled (N=805). DNA extraction was conducted following the streamlined prepGEM (ZyGEM, Hamilton, New Zealand) protocol for small insects. Genotyping was performed using polymorphic microsatellite loci (dinucleotide repeats) (Table 1). A total of 805 *Nasonia* sp. wasps (525 females and 280 males) from 54 parasitized *P. sialia* pupae were genotyped using 3 microsatellites loci (Table 1). The length of the amplified fragments was determined using an AB 3130 Genetic Analyzer (Applied Biosystems) and GeneMapper ® (Applied Biosystems, Version 4.0).

Sibling status and founding *N. vitripennis* female identity was determined from the offspring genotypic information following the protocol described in Grillenberger *et al.* (2008): (i) A female (mother) can supply up to two alleles per locus. (ii) The male (father) provides one allele per locus (being haploid) that is shared by all full sisters. (iii) Sons can only have one allele from their mother, as they develop from unfertilized eggs. As in Grillenberger *et al.* (2008), if several foundress genotypes were possible based on the microsatellite profile, we favored the solution with the lowest number of foundresses. The analysis yielded data on the number of foundresses per host, per nest, as well as on the individual brood sizes and sex ratio produced by each founding females. Foundress rank was determined following predictions derived from the LMC model: (1) the broods of the females ovipositing in unparasitized hosts (rank 1) should be the largest and the most female biased, (2) as LMC increases, brood size should decrease and become more male biased, females ovipositing second (rank 2) should have larger broods and slightly less male biased broods than those ovipositing third (rank 3). Brood size in gregarious parasitoids is defined as the number of sibling wasps emerging from a host. Within this context we used the tertiary sex ratio (the sex ratio of the progeny upon emergence from the host). Previous work revealed that *Nasonia* females make their oviposition decisions (sex ratio and brood size adjustment) at the host (pupa) level as opposed to the nest box level (Grillenberger *et al.* 2008; Burton-Chellew *et al*. 2008). Accordingly, our analysis was thus conducted at the host level.

Statistical analyses

Due to the hierarchical nature of our sampling design (pupae within nest within farm) we used a mixed model approach. Generalized linear mixed models using a logit link function for Poisson error distribution were used to analyze *P. sialia* pupa size with farm ID (farm identity) as a random factor. The same models were used to analyze the number of founding *N. vitripennis* females per pupae, per nest with farm as a random factor as well as for *N. vitripennis* brood size with pupa nested within farm set as random factors. Generalized linear mixed models using a log link for binomial error distribution with pupa nested within farm set as a random factor were used to analyze *N. vitripennis* sex ratio. Models were fitted with the lmer (package lme4 version 0.999375-36) function run in the R statistical environment (version 2.1.11; R Development Core Team 2010).

We built a series of three models for each response variable (*P. sialia* pupal size; number of founding *N. vitripennis* females per pupa and per nest; *N. vitripennis* brood size, progeny sex ratio and size); the first model (global model) is composed of a combination of variables that characterized the surrounding landscape and resource availability (host size and number of wasps per pupae), the second (resource model) and third (landscape model) models are composed solely of the resource variables and the landscape variables respectively. To investigate the direct effect of landscape structure on sex ratio without and with the effect of local mate competition, we modeled the progeny sex ratios produced by *N. vitripennis* females in the absence and in the presence of other founding females (1 founding female / pupa vs 2-3 founding females / pupa). The composition and justification of these groups of variables are found in Table 2 and the lists of models considered are included in Appendices A - H. Previous experiments showed that *P. sialia* and *N. vitripennis* abundance responds maximally to the proportion of intensive culture within a radius of 0.3 km and 0.2 km in the surrounding landscape, respectively (SP Daoust, unpublished data). We therefore only included these radii in our analyses. As in Ghilain & Belisle (2008), we were unable to include extensive and intensive cultures in the same model, with or without the interaction as it leads to multicollinearity among explanatory variables and prevented model convergence. We therefore built simpler models that included only one culture type (intensive culture). Explanatory variables included in a given model were never strongly correlated ($0.01 < r < 0.46$).

Competing models for each response variable were contrasted in order to identify which model(s) was the most parsimonious using the aictab.mer (package AICcmodavg version 1.11) function in R. Contrasts were based on the second-order variant of the Akaike information criterion (AIC*c*), which corrects the number of estimated parameters with respect to sample size (Anderson 2008). This quantity estimates the relative amount of information lost when a given model is used to describe reality (Anderson 2008). The lower the AIC*c* value of a model is, the better it is at summarizing the information contained in the data. AIC*c* values are relative and can only be used to compare models fitted to the exact same data set (Anderson 2008). Competing models were compared based on their difference in AIC*c* relative to the model that shows the lowest AIC*c* value. We also computed the weight of evidence of each model (w_i), which represents the likelihood that a model was the best ranked within the set of competing models, given the data (Anderson 2008). When no single model was revealed to be the most parsimonious through model comparisons, model averaging was performed using the model.avg (package MuMin version 0.23.21) function in R, using the "natural average" method.

Results

Protocalliphora pupal size

The global model ($w_i = 0.768$) was the most parsimonious at explaining the length of *P. sialia* pupae (Appendix A). When controlling for each of the tested explanatory variable, the only factor that influenced the size of the pupae within the global model was the proportion of intensive culture within the landscape (Table 3). *Protocalliphora sialia* pupal size decreased with an increase of intensive culture in the landscape (Fig. 2). The average pupal length within the areas with the least amount of intensive culture (< 20% intensive cultures) was 8.23 mm ± 0.27 (mean ± SD) compared to 7.49 mm ± 1.01 (mean ± SD) in the highly intensive areas (> 80% intensive cultures).

Number of founding N. vitripennis females per pupa and per nest

The landscape model was the most parsimonious at explaining the number of founding *N. vitripennis* females per pupa ($w_i = 0.69$) and per nest ($w_i = 0.64$) (Appendices B and C, respectively). The number of founding females per pupa and per nest decreased as the proportion of intensive culture increased in the landscape (Fig. 3a, Table 4a) and (Fig. 3b, Table 4b), respectively. For example, the number of founding females per pupae within the areas with the least amount of intensive culture (< 20% intensive cultures) was 2.04 ± 0.82 (mean ± SD) compared to 1.25 ± 0.5 (mean ± SD) in the highly intensive areas (> 80% intensive cultures). Furthermore, 70% of pupa within areas with the least amount of intensive culture were parasitized by more than one female as compared to 25% within highly intensive areas.

Nasonia brood size and sex ratio

No single model was shown to best explain *N. vitripennis* brood size (Appendix D). We thus used a model averaging all explanatory variables. When controlling for each of the tested explanatory variable, brood size was shown to increase with *P. sialia* pupal length (Fig. 4a, Table 4c) and decrease with the founding female rank (Fig. 4b, Table 4c).

Model comparisons revealed that the landscape model was by far the most parsimonious model ($w_i = 0.859$) in explaining the sex ratio pattern in *N. vitripennis* in the absence of other founding females (no LMC) (Appendix E). The proportion of males in the progeny increased with the proportion of intensive culture in the landscape (Fig. 5, Table 4d).

No single model was shown to best explain the sex ratio pattern in *N. vitripennis* in the presence of other founding females (LMC) (Appendix F). We thus used a model averaging all explanatory variables. The proportion of males in the progeny increased with founding female rank (Fig. 6a, Table 4e) and with the proportion of intensive culture in the landscape (Fig. 6b, Table 4e).

Nasonia size

Contrasting candidate models showed that *N. vitripennis* female size was best explained by the resource model ($w_i = 0.630$) (Appendix G). When controlling for the other explanatory variables in the model, *N. vitripennis* female size increased significantly with increasing progeny sex ratio; females were smaller in hosts where a higher proportion of the offspring were female, and this effect was greater at larger clutch sizes (interaction between sex ratio and brood size) (Fig. 7a; Table 4f) and where larger with increasing *P. sialia* pupal size (Fig. 7b; Table 4f). *Nasonia vitripennis* female size decreased significantly with number of competitors (Fig 7c; Table 4f).

As with female size, *N. vitripennis* male size was best explained by the resource model ($w_i = 0.790$) (Appendix H). When controlling for other explanatory variables in the model, male size decreased significantly with the number of competitors within the pupae (Fig. 8a; Table 4g) and increased significantly with *P. sialia* pupae length (Fig. 8b; Table 4g). However, contrarily to females, sex ratio did not influence male size.

Discussion

We used an integrative methodology combining aspects of behavioural, molecular, population, community and landscape ecology to determine how *N. vitripennis* female wasps respond to variations in host and environmental quality associated with agricultural intensification. This is one of the first studies to test predictions from the MVT, LMC and HQ models using natural wasp populations.

Trophic processes have a significant impact on community composition. Indeed, within our system, the decrease in Tree Swallow population size associated with agricultural intensification resulted in a concomitant reduction in *P. sialia* as well as *N. vitripennis* populations within these regions (Ghilain & Bélisle 2008; S.P. Daoust, unpublished data). Within this context, the first objective of this study was to quantify the effect of agricultural intensification on the quality of the *P. sialia* host. In accordance with our prediction, *P. sialia* pupae were smaller in more intensive landscapes. However, *P. sialia* larvae density and Tree Swallow nestling availability had no effect on *P. sialia* pupal size in our study, contrary to other Diptera models, such as the yellow dung fly *Scatophaga stercoraria* L. (Amano 1983; Blanckenhorn 1998), the house fly *Musca domestica* L. (Black & Krafsur 1986) and the blow fly *Calliphora vicina* Robineau-Desvoidy (Saunders & Bee 1995) whose sizes decrease with increasing competition. This suggests that competition for resources is not the determining factor influencing pupae size in this species. The impact of intensive agriculture on *P. sialia* pupal size could be explained by the reduced accessibility to food and ovipositing sites that increased the average age of the female and the likelihood of starvation when they discovered hosts. The habitat in which a female forage for host has been shown to influence offspring size and fitness in other fly species. Maternal age, size and nutritional status have all been shown to influence egg size and the amount of yoke contributed, which in turn affect adult size and fitness (Jann & Ward 1999; Chapman & Goulson 2000; McIntyre & Gooding 2000). Within our study system, areas with high proportions of intensive culture had very little non-crop habitat, resulting in a decrease in food sources (nectar producing flowers), shelter sites and Tree Swallow hosts. Furthermore, as Tree Swallow nestling blood pesticide levels were not measured, we cannot exclude the possibility that the observed reduction in size of *P. sialia* pupae was due to higher levels of pesticides in the blood of the Tree Swallow nestlings.

Through genotypic analysis we are able to identify the number of females that oviposited within each pupa. Here, in agreement with our prediction, we confirm that fewer founding *N. vitripennis* females were ovipositing in areas of intensive agriculture as compared to those in areas of extensive culture resulting in a decrease in the level of parasitism and superparasitism by *N. vitripennis* within the former areas. The effect of agriculture intensification on the number of females attacking host pupae can be attributed to differences in the landscape composition between areas of intensive and extensive agriculture (Bianchi *et al*. 2006). Areas of extensive agriculture are largely composed of perennial fallow strips, pastures, hay fields and higher proportions of marginal habitats such as hedgerows networks and small forests stands which have been shown to support higher densities of parasitoids (Kruess & Tscharntke 1994; Bianchi *et al*. 2006; Holzschuh *et al*. 2009). Furthermore, perennial fallow strips and other edge habitats are important for local recolonization processes from field edges into field centers as wasps have been shown to prefer flying along fallow strips instead of crossing conventionally managed cereal fields (Holzschuh *et al.* 2009).

Because the differences in *P. sialia* pupal length observed were attributed to changes in the landscape composition due to agricultural intensification, this not only allowed us to test predictions based the Marginal Value model in the field but also enabled us to test how landscape composition can influence trophic interactions. In line with our prediction and following the MVT model, *N. vitripennis* females deposited smaller broods in smaller hosts. This is the first demonstration of the MVT model in a wild population of *N. vitripennis*. Furthermore, these findings also elegantly demonstrate how the negative effects associated with agricultural intensification on one population can be transferred to another population at a higher trophic level. Although landscape composition was not shown to have a direct effect on *N. vitripennis* brood size, it did however, indirectly influence brood size through the reduction of host quality within areas of intensive agriculture. This, in combination with the decrease in the number of founding females per pupa, can serve to explain, at least in part, the observed reduction in hyperparasitism by *N. vitripennis* within these areas as compared to those in areas of extensive agriculture.

As predicted by the MVT and LMC models, *N. vitripennis* females laid smaller and more male biased broods when ovipositing in a previously parasitized pupa. Although frequently observed in laboratory (Werren 1980; 1983; 1984; Orzack & Parker 1990; Drapeau & Werren 1999; Shuker & West 2004; Shuker *et al*. 2004;

2006), this represents one of the few studies showing that *N. vitripennis* females make oviposition decisions following LMC in the wild. Of interest, when controlling for the number of founding females and founding female rank, the sex ratio of the progeny was not influenced by *P. sialia* pupal length; a finding confirming previous laboratory work that *N. vitripennis* do not follow HQ. That being said, the analysis did reveal that females in areas of intensive agriculture produced more male biased broods than those in extensive landscapes. This is, to our knowledge, the first report of an environmental effect on sex ratio in parasitoids from natural populations. Here, we propose a new model to explain this phenomenon, the Habitat Quality model (an extension of the Host Quality model), where the founding female assesses habitat and not host quality. In poor quality habitats, where sources of nectar and/or hosts are scarce, periods of starvation are likely to occur. Within this context, assuming that mating occurs at the natal patch and that females are the dispersing sex, it is advantageous for mothers to produce a sex ratio that will maximize the size of her daughters. In *N. vitripennis* specifically, small females suffer disproportionately the costs of not feeding as they are born with small lipid reserves and thus need to rely more heavily on carbohydrates for survival and reproduction (Rivero & West 2002). Large unfed females, on the other hand, rely heavily on their large lipid reserves, which provide roughly twice the amount of calories per unit as carbohydrates giving them more time to locate a host before their fecundity is lowered due to starvation (Rivero & West 2002). It is also important to note, that this shift towards male biased broods within areas of intensive agriculture could also be a factor contributing to the reduction of hyperparasitism by *N. vitripennis* within these areas.

Finally, we examined how offspring size varied across the gradient of agricultural intensification, as this would give an indication of the adaptive nature of the founding female's responses to landscape structure and resource availability. We showed that the size of both sexes was affected by *P. sialia* pupa length; smaller wasps emerged from smaller hosts and this regardless of the fact that *N. vitripennis* females adjusted their brood size in response to host quality. It is therefore possible that factors other then competition for resources are affecting the size of developing wasps. One such possibility is the presence of pesticides within the hemolymph of the developing pupa, which were acquired from the bird host's blood (Bishop 1998a,b; Burgess *et al.* 1999). Offspring size was also affected by competition, as both female and males were smaller when developing with a greater number of competitors; whilst females were smaller in hosts where a higher proportion of the offspring where female. These data indicate that females do not adjust the sex ratio and brood size of their progeny in order to maximize the size of their daughters. These findings are in agreement with those of Sykes *et al.* (2007), who concluded that the effects of LMC were the overriding factors influencing *N. vitripennis* female brood size and sex ratio adjustment.

To conclude, we showed that agricultural intensification disrupts trophic level processes by reducing both habitat and host quality. First, *P. sialia* hosts are of poorer quality in areas of intensive agriculture. In response to this and in line with the MVT, LMC and HQ models, *N. vitripennis* females lay smaller and more male biased broods within areas of intensive culture. This reduction in the abundance of *N. vitripennis* females translates to a decrease in the level of hyperparasitism by *N. vitripennis* on *P. sialia* in areas of intensive agriculture. To our knowledge, this is the first study to link optimality models to ecosystem function.

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Table 1. Information regarding the three microsatellite primer sets used to identify sibling status, and the identity of founding *N. vitripennis* females and siblings.

Primer name	Annealing temperature (°C)	Chromosome	Sequence 5' - 3'	Fragment length (bp)	Allele number	Observed heterozygocity (H_O)	Dye	GenBank accession no.	Reference
Nv-17	46	-	F: AAG AAT GTA TCA AGT ATG AGC C R: TCA GTT CTT GAA ACG TTG C	207-244	13	0.4	NED	AY262049	Pietsch *et al*. 2004
Nv-41	56	V	F: GTC AGA CGT GGG CTT TGT C R: TTA TGC GCC ACA CAC ACC	321-341	11	0.38	FAM	EU155141	Grillenberger *et al*. 2008
Nv-46	58	IV	F: TTA CGT CAA GGT ATA GCT GC R: GAA TAA GTG GCT GAA AGT TCC	232-262	15	0.51	FAM	EU155142	Grillenberger *et al*. 2008

Table 2. Definition and justification of explanatory variables used to quantify the influence of landscape structure on *P. sialia* pupal size, *N. vitripennis* progeny sex ratio and on *N. vitripennis* size.

			Justification				
Explanatory variable	**Definition (units)**	**Variable type**	***P. sialia* pupae length**	**Number of *N. vitripennis* founding females**	***N. vitripennis* brood size**	***N. vitripennis* sex ratio**	***N. vitripennis* size**
No. of Tree Swallow nestlings	number of Tree Swallow nestlings per nest	resource	host availability influences *Protocalliphora* size (1)				
No. *P. sialia* pupae	number of *P. sialia* pupae per nest	resource	competition for resources influences *Protocalliphora* size (1)	encounter rate may influence level of superparasitism (3)			
P. sialia pupae length	(mm)	resource		host quality may influences level of superparasitism (3)	brood size may be influenced by host size (3)	sex ratio may be influenced by host size (5)	wasp size is influenced by host size (3)
Number of competitors	number of *N. vitripennis* within one host pupae	resource				sex ratio is influenced by brood size (3)	wasp size is influenced by brood size (3)
Founding female rank	order in which founding female oviposited within the same host	resource			brood size is influenced by local mate competition (3)	sex ratio is influenced by local mate competition (3)	
N. vitripennis progeny sex ratio	number of male offspring over the total number offsprings (%)	resource					female size is influenced by sex ratio of brood (6)
Intensive culture	relative amount of cover within a given extent aroung the nest box (%)	landscape	size may be reduced in homogeneous landscape (2)	ecological context may influence the level of superparasitism (4)	ecological context experienced by females may influence brood size (5)	ecological context experienced by females may influence sex ratio (5)	ecological context experienced by founding females may influence offsring size (7)

(1) Sabrosky *et al.* 1989, (2) Jann & Ward 1999, (3) Godfray 1994, (4) SP Daoust, unpublished data, (5) King 1987, (6) Sykes *et al*. 2007, (7) Mousseau & Dingle 1991.

Table 3. Parameters of the most parsimonious models explaining *Protocalliphora sialia* pupal length within Tree Swallow nests along a gradient of agricultural intensification in southern Québec, Canada, in 2009 (N = 54).

Parameter	**Estimate**	**SE**	**CI (95%)**
Number of Tree Swallow nestlings	-0.5646	0.297	- 1.147 to 0.018
Number of *P. sialia* pupae	0.501	0.348	- 0.182 to 1.183
Intensive culture (%)	-0.104	0.022	-0.147 to -0.061

Table 4. Parameters of the most parsimonious models explaining (a) number of founding *N. vitripennis* females / pupae (N = 54), (b) number of founding *N. vitripennis* females / nest (N = 27), (c) the brood size produced by *N. vitripennis* females (N=79), (d) the sex ratio of the progeny produced by *N. vitripennis* females in the absence of competing females (N = 32), (e) the sex ratio of the progeny produced by female *N. vitripennis* in the presence of competing females (N = 81), (f) the length of the right hind tibia of female *N. vitripennis* (N = 525), (g) the length of the right hind tibia of male *N. vitripennis* (N = 280), within Tree Swallow nests along a gradient of agricultural intensification in southern Québec, Canada, in 2009 (N = 54).

Dependent variable	**Parameter**	**Estimate**	**SE**	**CI (95%)**
(a) Numbre of founding *N. vitripennis* females / pupae	Intensive culture (%)	-0.27	0.094	-0.800 to -0.454
(b) Numbre of founding *N. vitripennis* females / nest	Intensive culture (%)	-0.23	0.028	-0.681 to -0.285
(c) *N. vitripennis* brood size	*P. sialia* pupal length (cm)	0.144	0.082	-0.705 to -0.365
	Founding female rank (2nd)	-0.062	0.076	0.001 to 0.973
	Intensive culture (%)	0.121	0.13	-0.912 to 0.704
(d) *N. vitripennis* sex ratio in absence of competition	Intensive culture (%)	0.323	0.128	0.072 to 0.574
(e) *N. vitripennis* sex ratio in the presence of competition	*P. sialia* pupal length (cm)	-0.118	0.119	-0.351 to 0.115
	Number of competitors	-0.376	0.275	-0.915 to 0.163
	Founding female rank (2nd)	0.42	0.123	0.179 to 0.661
	Intensive culture (%)	0.229	0.058	0.115 to 0.343
(f) *N. vitripennis* female size	*P. sialia* pupal length (cm)	0.169	0.019	0.131 to 0.065
	Number of competitors	-0.781	0.275	-0.132 to -0.210
	Sex ratio (%)	0.14	0.022	0.010 to 0.183
	Sex ratio (%) X Number of competitors	0.182	0.0462	0.091 to 0.273
(g) *N. vitripennis* male size	*P. sialia* pupal length (cm)	0.075	0.011	0.053 to 0.097
	Number of competitors	-0.233	0.099	-0.427 to -0.039
	Sex ratio (%)	-0.228	0.308	-0.831 to 0.376
	Sex ratio (%) X Number of competitors	0.07	0.037	-0.003 to 0.142

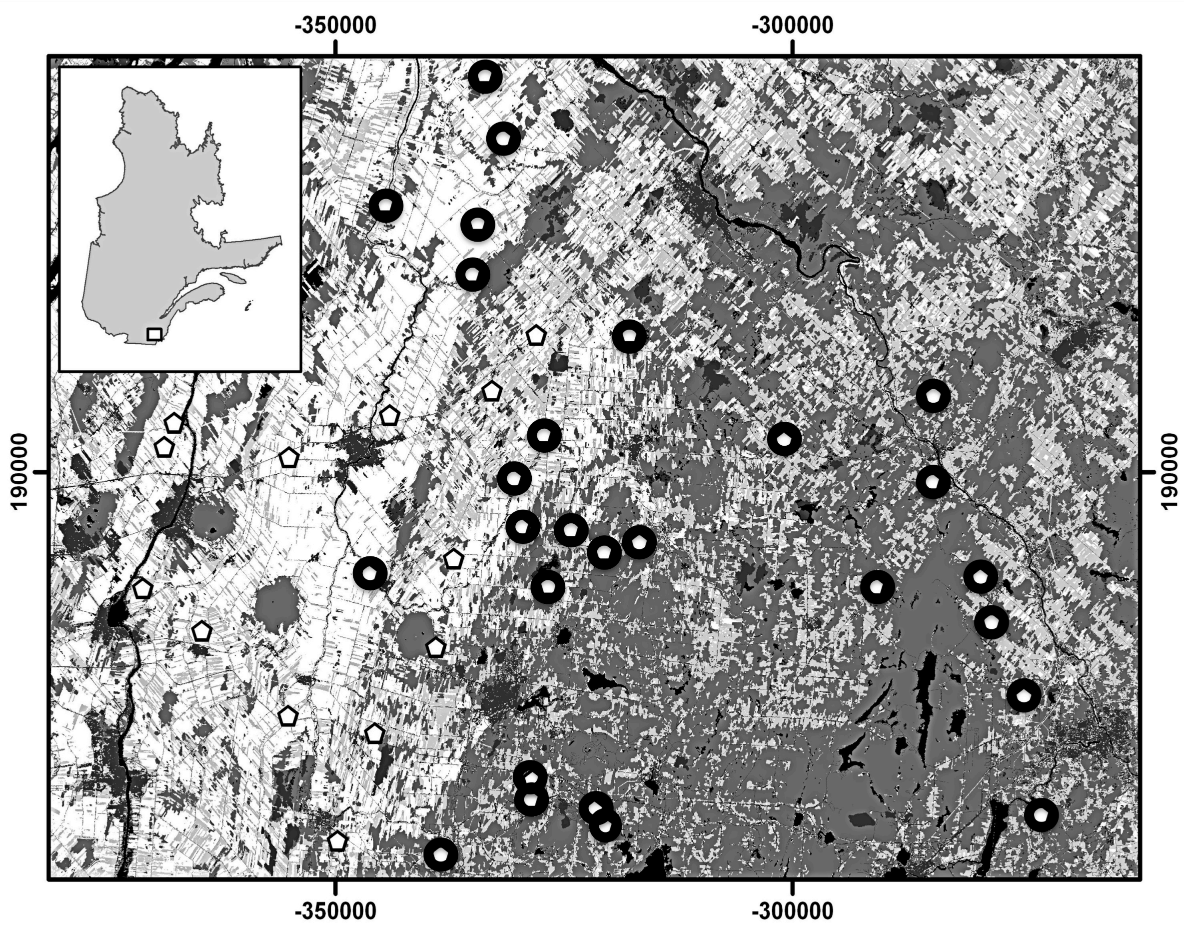

Fig. 1. Distribution of the 27 sampled farms along a gradient of agricultural intensification in southern Québec, Canada, 2008–2009. Land cover types are based on a mosaic of classified LANDSAT-TM satellite images (Canadian Wildlife Service 2004) and include water (black), urban (dark gray), forest (mid-tone gray), extensive cultures (e.g., hayfields and pastures; light gray), and intensive cultures (e.g., maize, cereals, and soybeans; white). Open pentagons indicate farm locations. Black circles indicate farms where *N. vitripennis* were obtained. Coordinates are Lambert Conic Conform and refer to the number of meters from a reference point.

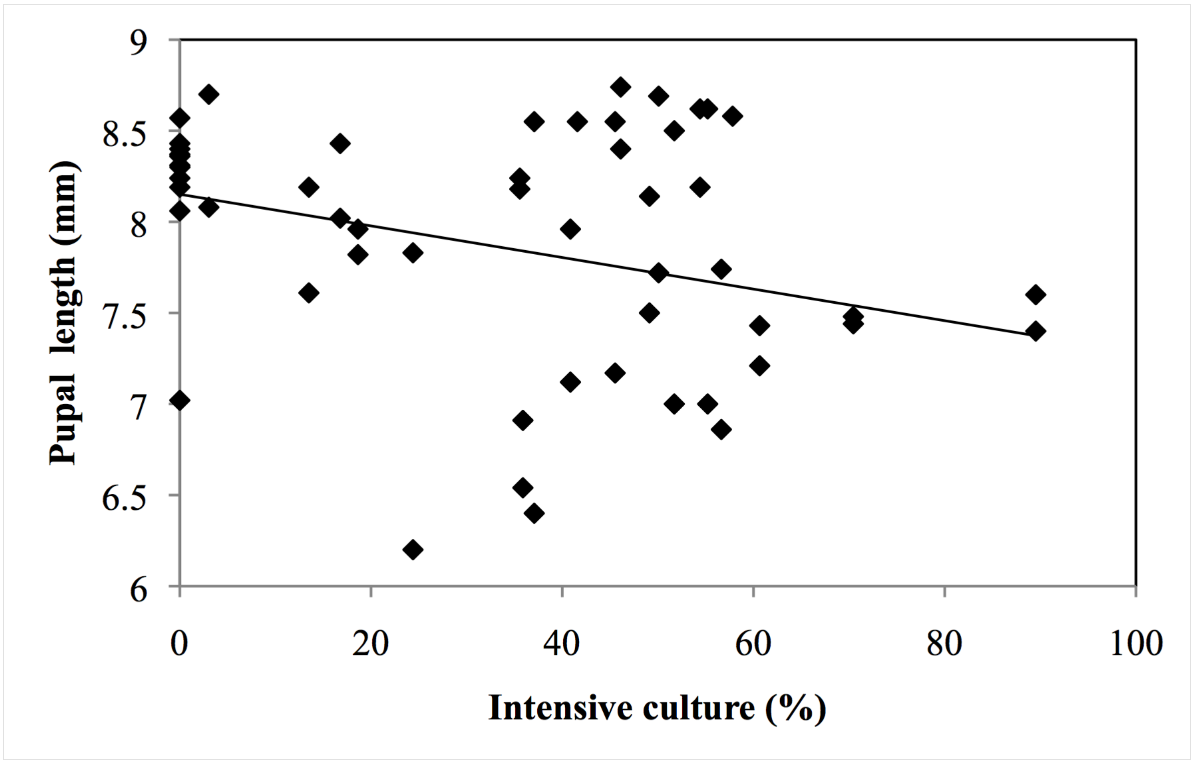

Fig. 2. Effect of the percentage of intensive culture on *Protocalliphora sialia* pupal length along a gradient of agricultural intensification in southern Québec, Canada, 2009, (N=54). Based on model 1 in Appendix A.

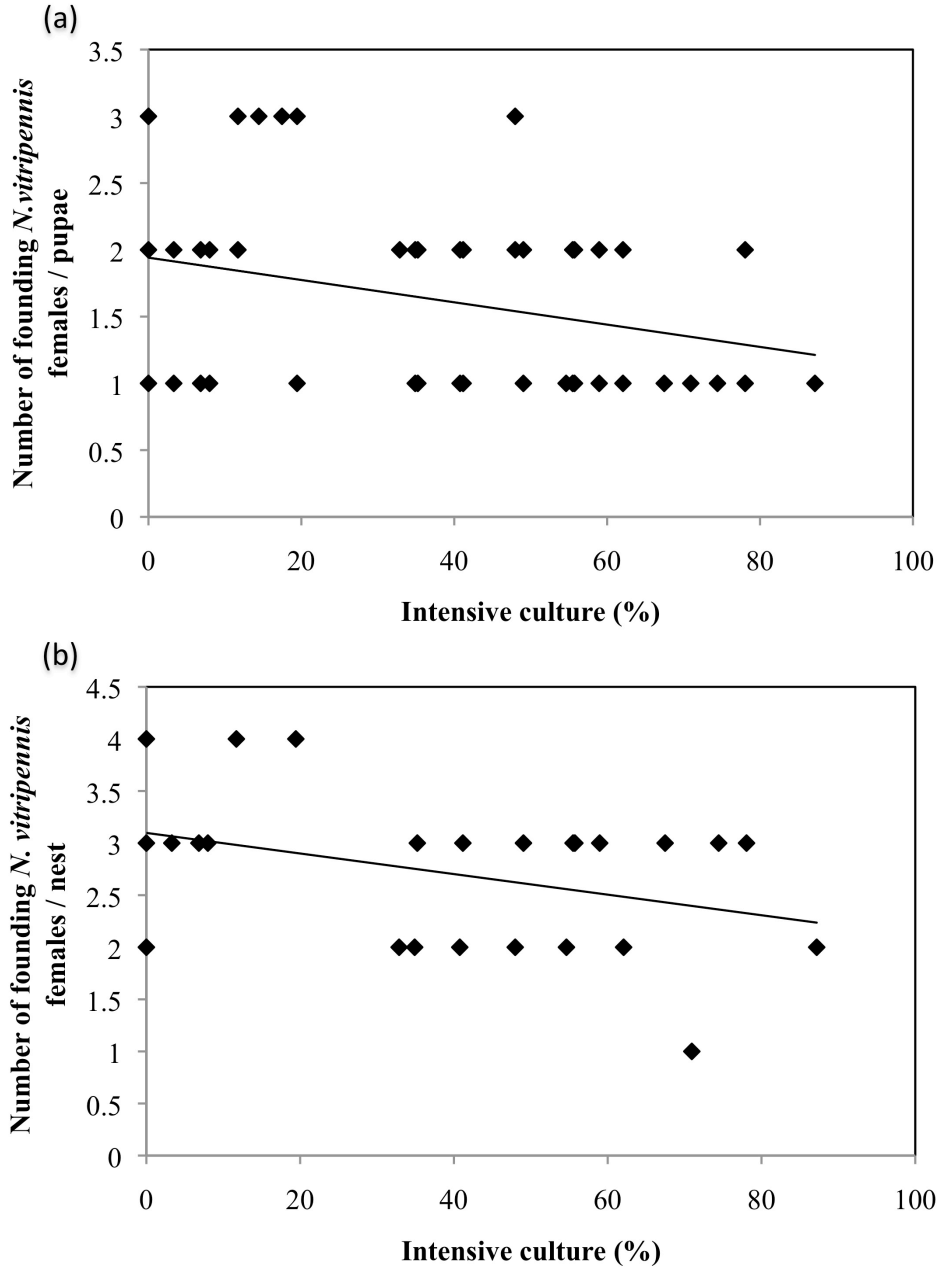

Fig. 3. Effect of the percentage of intensive culture on (a) the number of founding *Nasonia vitripennis* females / pupae (N = 54) based on model 3 in Appendix B and (b) the number of founding *N. vitripennis* females / nest (N = 27) based on model 3 in Appendix C, along a gradient of agricultural intensification in southern Québec, Canada, 2009.

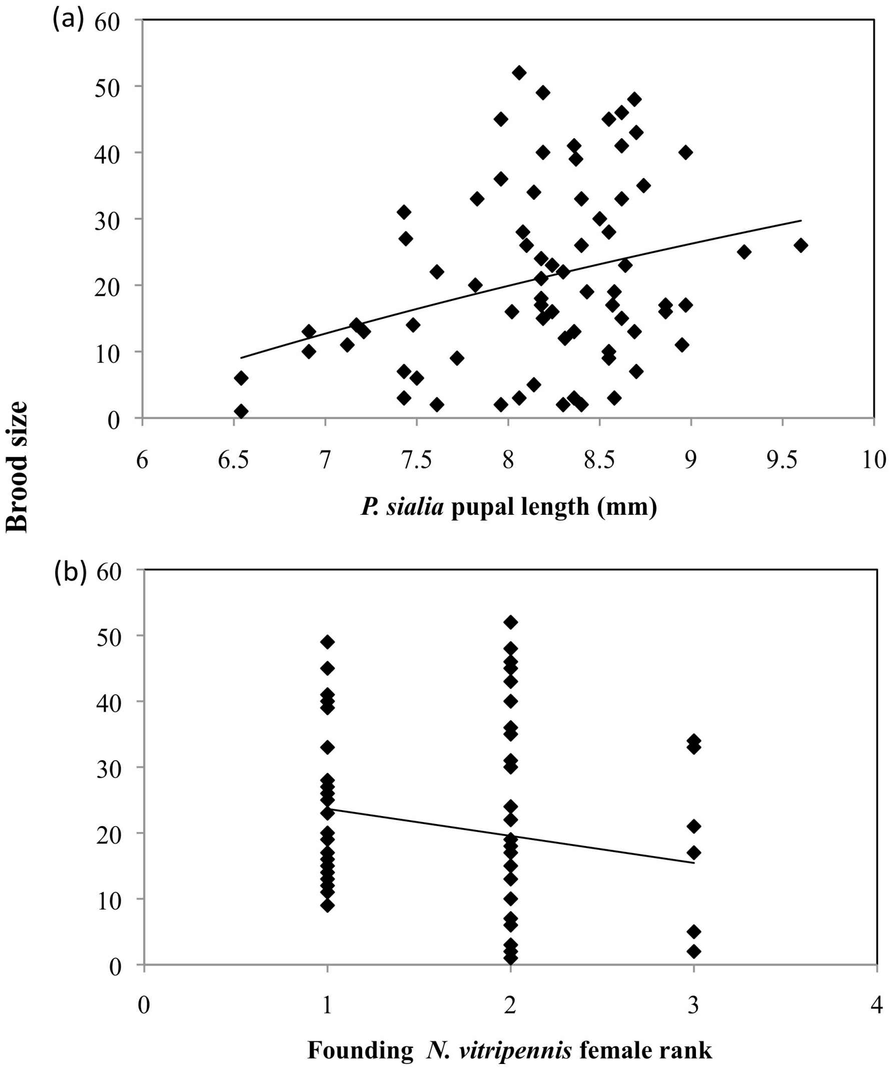

Fig. 4. Effect of the *Protocalliphora sialia* pupal length and the number of founding *Nasonia vitripennis* females on *Nasonia vitripennis* brood size along a gradient of agricultural intensification in southern Québec, Canada, 2009, (N=79). (a) Effect of the *P. sialia* pupal length on *N. vitripennis* brood size based on model 2 in Appendix B. (b) Effect of the number of founding females on *N. vitripennis* brood size based on model 2 in Appendix B.

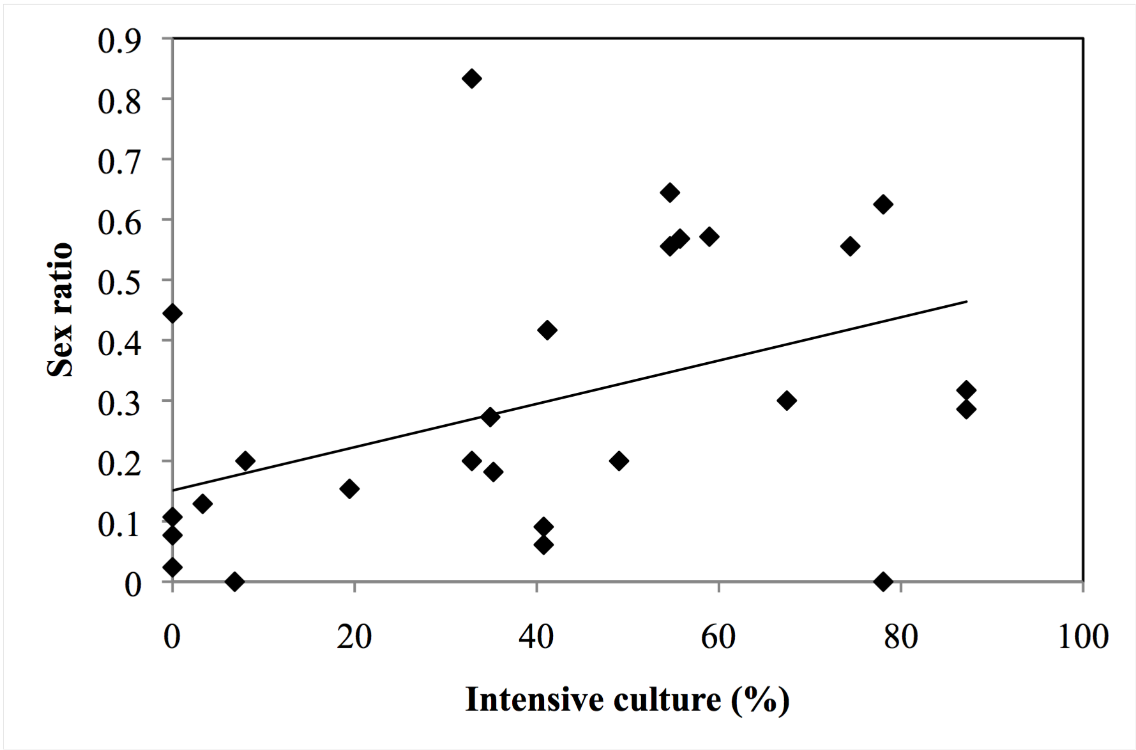

Fig. 5. Effect of the proportion of intensive culture on the sex ratio (% of males) of the progeny produced by *Nasonia vitripennis* in the absence of competing females (1 founding female) based on model 3 in Appendix C, (N = 32).

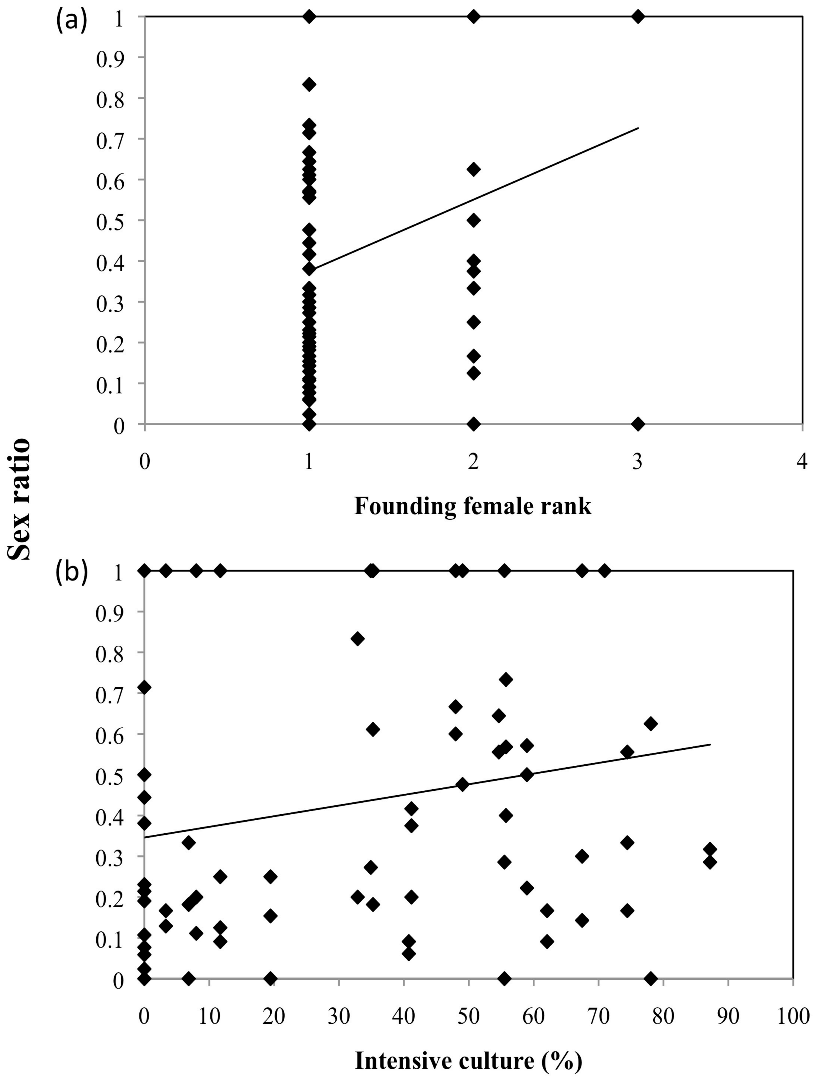

Fig. 6. Effect of (a) the founding female rank and (b) the proportion of intensive culture on the progeny sex ratio (% of males) produced by *Nasonia vitripennis* females based on model 1 in Appendix F (N = 81).

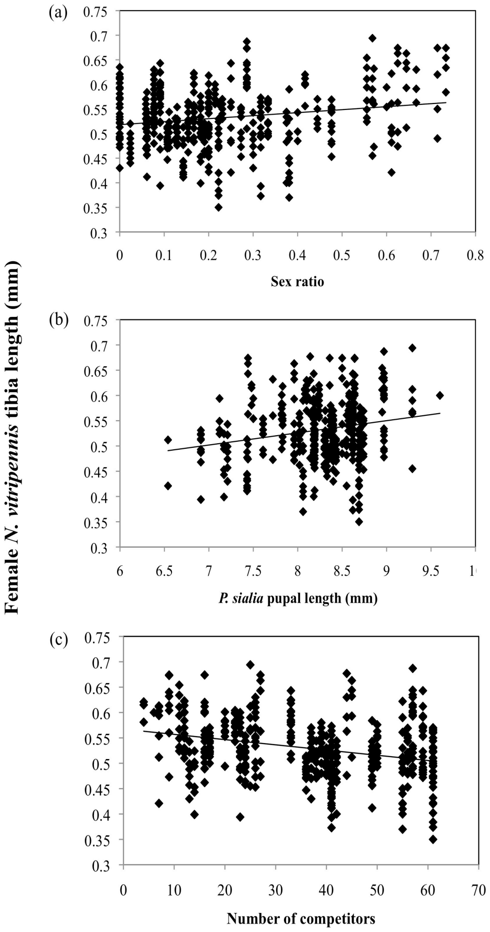

Fig. 7. Influence of the sex ratio, *Protocalliphora sialia* pupal length and the number of *Nasonia vitripennis* wasps competing within the pupae on the right hind tibia length (mm) of female *Nasonia vitripennis* along a gradient of agricultural intensification in southern Québec, Canada in 2009 (N = 525). (a) Effect of the sex ratio of the progeny produced by *N. vitripennis* on the right hind tibia length (mm) of female *N. vitripennis* within the agricultural landscapes based on model 2 in Appendix D. (b) Effect of the *P. sialia* pupal length on the right hind tibia length (mm) of female *N. vitripennis* within the agricultural landscapes based on model 2 in Appendix D. (c) Effect of the number of *N. vitripennis* wasps competing within the pupae on the right hind tibia length (mm) of female *N. vitripennis* within the agricultural landscapes based on model 2 in Appendix D.

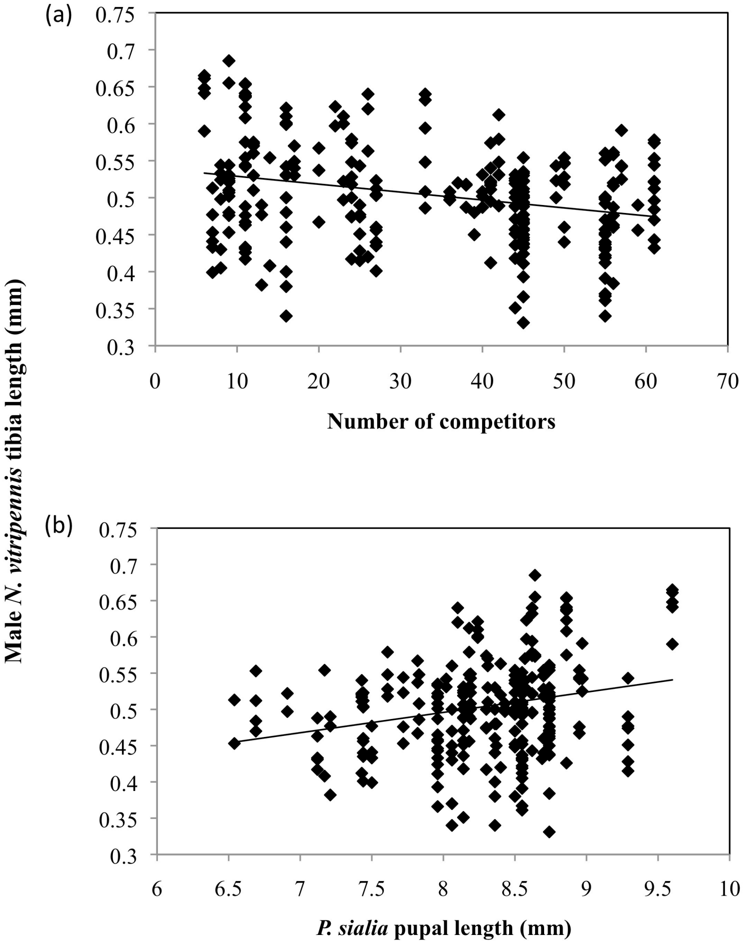

Fig. 8. Influence of the number of *Nasonia vitripennis* wasps competing within the pupae and *Protocalliphora sialia* pupae length on the right hind tibia length (mm) of male *Nasonia vitripennis* along a gradient of agricultural intensification in southern Québec, Canada, 2009 (N = 280). (a) Effect of the number of *N. vitripennis* wasps competing within the pupae on the right hind tibia length (mm) of male *N. vitripennis* within the agricultural landscapes based on model 2 in Appendix E. (b) Effect of the *P. sialia* pupae length on the right hind tibia length (mm) of male *N. vitripennis* within the agricultural landscapes based on model 2 in Appendix E.

Appendix A. Comparison of models explaining the length of *P. sialia* pupae within experimental nest boxes at a spatial extent of 0.3 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table A1. Comparison of models explaining the length of *P. sialia* pupae within experimental nest boxes at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID as random factor (N=65). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	**-45.6**	**98.42**	**0.768**
2	-43.33	103.05	0.076
3	-45.19	101.61	0.156

List of models and their variables:

Model 1 (global model): Number of Tree Swallow Hatchlings + Number of *P. sialia* pupae / nest + Intensive culture (%)

Model 2 (resource model): Number of Tree Swallow Hatchlings + Number of *P. sialia* pupae / nest

Model 3 (landscape model): Intensive culture (%)

Appendix B. Comparison of models explaining the number of founding *N. vitripennis* females per pupae at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table B1. Comparison of models explaining the number of founding *N. vitripennis* females per pupae at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID as random factor (N=54). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	-7.362	25.97	0.07
2	-7.362	23.54	0.24
3	**-7.361**	**21.43**	**0.69**

List of models and their variables:

Model 1 (global model): *P. sialia* pupae length + Number of *P. sialia* pupae + Intensive culture (%)

Model 2 (resource model): *P. sialia* pupae length + Number of *P. sialia* pupae

Model 3 (landscape model): Intensive culture (%)

Appendix C. Comparison of models explaining the number of founding *N. vitripennis* females per nest at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table C1. Comparison of models explaining the number of founding *N. vitripennis* females per nest at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID as random factor (N=27). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	-3.15	18.9	0.07
2	-3.15	15.96	0.29
3	**-3.73**	**14.43**	**0.64**

List of models and their variables:

Model 1 (global model): *P. sialia* pupae length + Number of *P. sialia* pupae + Intensive culture (%)

Model 2 (resource model): *P. sialia* pupae length + Number of *P. sialia* pupae

Model 3 (landscape model): Intensive culture (%)

Appendix D. Comparison of models explaining the brood size produced by female *N. vitripennis* at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table D1. Comparison of models explaining the brood size produced by female *N. vitripennis* at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID and pupae ID as random factor (N=79). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	-43.69	102.87	0.205
2	**-44.07**	**101.31**	**0.447**
3	-45.49	101.81	0.35

List of models and their variables:

Model 1 (global model): *P. sialia* pupae length + Number of founding females + Intensive culture (%)

Model 2 (resource model): *P. sialia* pupae length + Number of founding females

Model 3 (landscape model): Intensive culture (%)

Appendix E. Comparison of models explaining the sex ratio of the progeny produced by female *N. vitripennis* in the absence of competing females at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table E1. Comparison of models explaining the sex ratio of the progeny produced by female *N. vitripennis* in the absence of competing females at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID and pupae ID as random factor (N=33). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	-0.84	17.88	0.113
2	-3.9	20.66	0.028
3	**-2**	**13.82**	**0.859**

List of models and their variables:

Model 1 (global model): *P. sialia*. pupae length + Number of competitors + Intensive culture (%)

Model 2 (resource model): *P. sialia* pupae length + Number of competitors

Model 3 (landscape model): Intensive culture (%)

Appendix F. Comparison of models explaining the sex ratio of the progeny produced by female *N. vitripennis* in the presence of competing females at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009.

Table F1. Comparison of models explaining the sex ratio of the progeny produced by female *N. vitripennis* in the presence of competing females at a spatial extent of 0.2 km (intensive culture) along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID and pupae ID as random factor (N=81). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	-51.28	120.57	0.392
2	**-52.23**	**119.97**	**0.523**
3	-57.55	123.62	0.085

List of models and their variables:

Model 1 (global model): *P. sialia*. pupae length + Number of competitors + Founding female rank + Intensive culture (%)

Model 2 (resource model): *P. sialia* pupae length + Number of competitors + Founding female rank

Model 3 (landscape model): Intensive culture (%)

Appendix G. Comparison of models explaining the length of the right hind tibia of female *N.*
vitripennis along a gradient of agricultural intensification in southern Quebec, 2009.

Table G1. Comparison of models explaining the length of the right hind tibia of female *N. vitripennis* along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID, pupae ID and founding female ID as random factors (N=525). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	947.84	-1873.16	0.37
2	**946.29**	**-1874.24**	**0.63**
3	928.98	-1845.79	0

List of models and their variables:

Model 1 (global model): *P. sialia* pupae length + Number of competitors + Sex ratio + Intensive culture (%) + Sex ratio X Number of competitors

Model 2 (resource model): *P. sialia* pupae length + Number of competitors + Sex ratio + Sex ratio X Number of competitors

Model 3 (landscape model): Intensive culture (%)

Appendix H. Comparison of models explaining the length of the right hind tibia of male *N. vitripennis* along a gradient of agricultural intensification in southern Quebec in 2009.

Table H1. Comparison of models explaining the length of the right hind tibia of male *N. vitripennis* along a gradient of agricultural intensification in southern Quebec in 2009. Models are generalized linear mixed models with farm ID, pupae ID and founding female ID as random factors (N=280). See table 2 for variable definition and justification.

Model	Log-Likelihood	AICc	AICcWt
1	424.26	-825.53	0.171
2	**424.63**	**-828.59**	**0.79**
3	420.67	-822.67	0.041

List of models and their variables:

Model 1 (global model): *P. sialia* pupae length + Number of competitors + Sex ratio + Intensive culture (%) + Sex ratio X Number of competitors

Model 2 (resource model): *P. sialia* pupae length + Number of competitors + Sex ratio + Sex ratio X Number of competitors

Model 3 (landscape model): Intensive culture (%)

Chapitre 8 : Discussion et conclusion générale

L'intensification des pratiques agricoles a été identifiée comme une cause majeure du déclin de la biodiversité végétale et animale (Benton *et al.* 2003; Tscharntke *et al*. 2005). Plusieurs études ont documenté l'impact négatif de la fragmentation du paysage naturel et de l'intensification agricole sur l'abondance et la diversité des espèces (Fuller *et al*. 1995; Chamberlain *et al*. 2000; Robinson et Sutherland 2002; Benton *et al*. 2002; Benton *et al.* 2003; Ghilain *et al.* 2008). Cependant, très peu d'entre elles ont établi et quantifié le lien entre la structure du paysage et le fonctionnement des écosystèmes (interactions trophiques et intraguildes) ainsi que les mécanismes d'adaptation des organismes (Roschewitsz *et al.* 1995; Tylianakis *et al*. 2007).

J'ai voulu contribuer à combler ce manque en étudiant un modèle biologique à trois niveaux trophiques composé d'un oiseau hôte, l'hirondelle bicolore *Tachycineta bicolor* (Vieillot), de mouches ectoparasites du genre *Protocalliphora* Hough et de guêpes parasitoïdes du genre *Nasonia* (Walker), au travers d'un gradient d'intensification agricole dans le sud du Québec. Je me suis concentré sur (1) l'identification et l'abondance des espèces de mouches ectoparasites et de leurs guêpes parasitoïdes qui colonisent les nids d'hirondelles dans la zone d'étude (**Chapitres 5 et 6**), (2) l'évaluation de l'impact de l'intensification agricole et de la structure du paysage sur les relations tri-trophiques entre les organismes à l'étude (**Chapitre 7**) et (3) la caractérisation des mécanismes comportementaux permettant aux guêpes de composer avec la variabilité de la structure du paysage et de la qualité des hôtes (**Chapitre 8**).

Tout d'abord, nous avons décrit la composition de la communauté des mouches ectoparasites *Protocalliphora* et de leurs guêpes hyperparasitoïdes *Nasonia* provenant de nids de l'hirondelle bicolore (**Chapitre 5**). Trois espèces de *Protocalliphora* ont été observées (*P. sialia, P. bennetti* et *P. metallica*) ainsi que deux espèces de *Nasonia* (*N. vitripennis* et *N. giraulti*). Il s'agit d'une première mention de *P. bennetti* et de *N. giraulti* dans la province de Québec. Ceci dit, *P. sialia* et *N. vitripennis* sont de loin les espèces les plus communes dans les systèmes étudiés à ce jour.

Un examen de la structure génétique des populations de guêpes *N. vitripennis* nous a permit de faire une découverte inattendue, soit la présence de mâles diploïdes dans notre système d'étude (**Chapitre 6**). Ceci représente la première identification de mâles polyploïdes en milieu naturel chez cette espèce. Les guêpes ont généralement un système de reproduction haplodiploïde; les mâles (haploïdes) se développent d'œufs non-fécondés et les femelles (diploïdes) d'œufs fécondés (Whiting 1967). À ce jour, l'unique mention indiquant la présence d'individus polyploïdes chez *Nasonia* provient d'une source qui a plus de 50 ans. Whiting (1960) a rapporté l'apparition spontanée d'individus polyploïdes dans une colonie de laboratoire. Les mécanismes d'une telle transition à la polyploïdie demeurent toujours incompris. Non seulement avons nous identifié la présence de mâles diploïdes, mais nous avons aussi documenté une grande fréquente de ces derniers dans nos populations, soit 57% des nids échantillonnés. Il est important de noter, que la présence des guêpes polyploïdes en milieu naturel demeure toujours un mystère. Il serait donc intéressant d'examiner en profondeur cette population, qui est à ce jour, unique. Une étude profitable serait de comparer la population naturelle de guêpe diploïde à celle découverte et maintenue dans la culture de Whiting (1960). L'examen de la valeur sélective des mâles polyploïdes comparativement à leurs confrères haploïdes éluciderait potentiellement la raison pour laquelle la polyploïdie semble persister en milieu naturel, notant que les femelles polyploïdes sont stériles.

Un aspect primordial des résultats présentés dans cette thèse est la mise en évidence du rôle que joue la structure du paysage sur la composition des communautés et des relations trophiques. Premièrement, nos analyses démontrent que les réponses à la structure du paysage de l'hirondelle, de l'ectoparasite et de l'hyperparasite sont dépendantes de l'échelle spatiale. Mais plus important encore, nous sommes les premiers à démontrer que l'échelle spatiale fonctionnelle à laquelle les espèces répondent le plus varie selon le paramètre du paysage modélisé. Plus précisément, les organismes perçoivent le paysage à très petites échelles (0.2-0.3 km) lorsque nous modélisons la proportion de terre dédiée à l'agriculture intensive, mais généralement à grandes échelles (2-5 km) quand nous modélisons la proportion de terre dédiée à l'agriculture extensive. Nous attribuons cette perception différentielle des deux paramètres de la structure du paysage utilisés à deux facteurs: (1) la divergence dans leurs compositions à travers les différentes échelles spatiales dans notre zone d'étude et (2) une dissimilitude quant à leur impact sur la dispersions des espèces. Les conséquences d'une telle observation sont importantes, spécialement dans le contexte de l'établissement d'aires de conservation. Nos résultats mettent à l'évidence la nécessité de considérer plusieurs paramètres de la structure du paysage de la zone de conservation afin de ne pas sous-estimer les superficies auxquelles les organismes répondent aux paysages.

En deuxième lieu, nos résultats indiquent que le rang trophique qu'occupe l'organisme influence sa perception et sa sensibilité à la structure du paysage. Contrairement à Holt *et al*. (1999), qui avaient proposé que les organismes des rangs trophiques supérieurs devraient percevoir le paysage à plus grandes échelles, nous avons observé que l'échelle spatiale perçue est plus petite aux niveaux trophiques supérieurs. Nos résultats sont en accord avec d'autres travaux étudiant l'impact de la structure du paysage dans des systèmes où un parasitoïde occupe le rang trophique supérieur (Thies *et al.* 2003; 2005; Holzschuh *et al*. 2010). Il semble que, dans de tels systèmes, la taille et non le rang trophique constitue le facteur déterminant de l'échelle spatiale fonctionnelle de l'organisme.

De façon générale, nos analysent révèlent que l'intensification des pratiques agricoles entraîne une diminution des populations d'ectoparasites et d'hyperparasites à l'étude. Nos résultats démontrent également que le nombre d'oisillons quittant le nid diminue avec l'augmentation de la proportion de terre dédiée à l'agriculture intensive dans le paysage. Cette observation confirme celle de Ghilain et Bélisle (2008), qui ont étudié l'impact de l'intensification agricole sur le succès reproducteur de l'hirondelle bicolore dans notre zone d'étude. Puisque la taille de la couvée ne varie pas en fonction du paysage (Ghilain et Bélisle 2008), la différence dans le nombre d'oisillons quittant le nid est due à l'augmentation de la mortalité des oisillons en milieux intensifs. Le niveau élevé de mortalité est corrélé à la diminution de l'entomofaune en milieu intensif (Rioux-Paquette et Bélisle 2011). Plus précisément, Rioux-Paquette et Bélisle (2011) ont démontré que dans notre zone d'étude, durant la période où l'hirondelle bicolore sélectionne son site de nidification, l'abondance de diptères ne diffère pas entre les régions intensives et extensives. Toutefois, pour la durée de la période comprise entre l'éclosion des oisillons et l'envol du nid, l'abondance des diptères est significativement moindre en milieu agricole intensif; entraînant une diminution importante des ressources alimentaires primaires de l'hirondelle. De plus, l'abondance de mouches *P. sialia* ainsi que le niveau d'hyperparasitisme par *N. vitripennis* par nid diminuent en fonction du nombre d'hôtes et de la portion de terre dédiée à l'agriculture intensive. Ces résultats sont en accord avec ceux d'études similaires (Burel *et al*. 1998; Burel *et al.* 2004; Benton *et al.* 2002; Holzschuh *et al*. 2010). De façon générale, la perte d'habitats marginaux (haie, forêt, marécage) servant d'abris et comprenant des sources alimentaires, l'homogénéisation des cultures, l'application de pesticides et la diminution d'hôtes qui sont associées à l'intensification des pratiques agricoles, entraînent une réduction des populations de mouches ectoparasites et des parasitoïdes (Burel *et al.* 1998, 2004; Wickramasinghe *et al.* 2004; Tscharntke *et al.* 2005; Bianchi *et al.* 2006).

Suite aux travaux présentés dans le **Chapitre 7**, il est clair que les populations de guêpes parasitoïdes dans notre zone d'étude font face à des conditions différentes lorsqu'elles exploitent des zones intensives ou extensives. Nous nous sommes donc intéressés aux mécanismes par lesquels les parasitoïdes *N. vitripennis* répondent à la variabilité dans la qualité de l'hôte et à la structure du paysage (**Chapitre 8**). Nos résultats révèlent, en accord avec d'autres travaux (Godfray 1994; Rivers et Denlinger 1995; Burton-Chellew *et al.* 2008), que les femelles *Nasonia* ajustent la taille de leurs pontes en fonction de la taille de la pupe hôte et de l'incidence d'hyperparasitisme (une condition où l'hôte est déjà parasité). Étonnamment, en contrôlant pour le nombre de femelles *Nasonia* fondatrices, le seul facteur ayant une influence déterminante sur le ratio sexuel est la proportion de paysage dédié à l'agriculture intensive. Ceci représente la première démonstration de l'impact du paysage sur l'ajustement du ratio sexuel d'une guêpe parasitoïde. Malgré le fait que les pupes de *Protocalliphora* soient plus petites en milieu intensif, nous n'avons pas observé de lien entre la structure du paysage et la taille des filles et des fils produit par les femelles *Nasonia* fondatrices. Nous attribuons ce phénomène aux comportements d'ajustement de taille de ponte et de ratio sexuel. En ajustant ces derniers, minimisant ainsi la compétition entre les membres de leur progéniture, les femelles fondatrices sont capables de maximiser la relation entre la disponibilité des ressources et la valeur sélective de leur progéniture.

Suite à ces résultats, il serait fort intéressant d'examiner les stratégies d'exploitations du patch (le nid) par les femelles fondatrices à travers le gradient agricole. Par exemple, une comparaison du nombre d'hôtes parasités par la même femelle à travers le gradient agricole, en contrôlant pour le nombre de femelles fondatrices ainsi que le nombre d'hôtes par patch, révèlerait l'impact du paysage sur un autre aspect du comportement de ponte chez *Nasonia*.

Conclusion

L'utilisation des terres à des fins agricoles modifie une grande partie de la surface terrestre. Depuis 2005, les terres cultivées et les pâturages occupent près de 40% de la surface terrestre mondiale (Foley *et al*. 2005). Pour la conservation de la biodiversité à l'intérieur des ces régions dominées par l'homme, il est très important de comprendre comment la structure des communautés naturelles, l'abondance des populations et les interactions entre les espèces répondent aux changements de la structure du paysage associés à différents régimes agricoles. Dans ce travail, il a été confirmé que les changements dans la structure du paysage associés à l'intensification des pratiques agricoles affectent de façon négative les organismes de trois niveaux trophiques, et plus particulièrement ceux aux niveaux supérieurs. De plus, nous avons constaté que les différents paramètres de la structure du paysage sont perçus à différentes échelles spatiales par les organismes à l'étude ; une observation inédite. Nos résultats démontrent aussi que les populations, par l'entremise de la plasticité comportementale des individus, sont capables de répondre de façon adaptative à des variations dans la qualité des ressources et de l'environnement.

Suite à ces résultats, nous proposons qu'une façon de remédier aux effets négatifs de l'intensification agricole et d'améliorer la biodiversité et le fonctionnement des écosystèmes en milieu d'agriculture intensif, serait d'y intégrer d'avantages d'habitats marginaux. L'addition de haies et des petites zones semi naturelles (boisés) en périphérie des terres agricoles intensives, aurait un impact positif sur les populations animales dans la région (Tscharntke *et al.* 2005; Fahrig *et al*. 2011). De plus, ceci pourrait aussi augmenter les services de l'écosystème tels que la pollinisation et la lutte biologique naturelle, menant à de meilleurs rendements agricoles (Cardinale *et al.* 2003)

Une nouvelle avenue de recherche très prometteuse dans le domaine de la biodiversité et de l’hétérogénéité du paysage fut récemment proposée par Fahrig *et al.* (2011). Ces auteurs suggèrent l’utilisation de l’ « hétérogénéité fonctionnelle du paysage », où les différents types de recouvrements sont caractérisés selon les différentes dépendances en ressources des espèces ou des groupes d’espèces, contrairement à l’approche traditionnelle où les recouvrements sont séparés selon leurs caractéristiques structurales. Une telle approche pourrait clarifier notre compréhension du rôle que joue le paysage dans le maintien de la biodiversité et contribuer à améliorer les mesures visant à promouvoir la biodiversité en milieux anthropogéniques.

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Appendice 1 : Autres réalisations durant le doctorat

Publications

*Maure, F. ***Daoust**, S.P., Brodeur, J. and F. Thomas. (2011). Diversity and Evolution of bodyguard-type manipulation. En préparation pour soumission à *Journal of Evolutionary Biology* * participation égale.

Mader, B.J., **Daoust, S.P**., Cardinal-Aucoin, M., Bauce, E. and E. Despland. (2011). Larval experience induces aversion in adult to rearing host-plant, a novel behaviour opposing Hopkin's Host Selection Principle. *Soumis à Oikos* (ID:o20022)

Thomas, F., **Daoust, S.P.** and M. Raymond. (2011). Can we understand modern humans without considering parasites? Soumis à *Evolutionary Applications* (ID: EVA-2011-148-S)

Despland, E., Gundersen, M., **Daoust, S.P.**, Mader, B.J., Delvas, N., Albert, P. and Eric Bauce. (2011). Taste receptor activity and feeding behaviour reveal mechanisms of white spruce natural resistance to Eastern spruce budworm *Choristoneura fumiferana*. *Physiological Entomology* **36**: 39-46

Daoust, S.P., Mader, B.J., Maure, F., McLaughlin, J.D., Thomas, F. and M. E. Rau. (2010). Experimental evidence of size/age-biased infection of *Biomphalaria glabrata* (Pulmonata: Planorbidae) by an incompatible parasite species: consequences for biological control. *Infection, Genetics and Evolution* **10**: 1008-1012.

Projet de recherche

QCBS (Quebec Center for Biodiversity Science) Seed Grant Award (5000$). Projet financé: "Distribution, abondance et spécificité parasitaire des mouches protocalliphoridées". Chargé du projet: Simon P. Daoust. Membres associés: Jacques Brodeur Ph.D., Jade Savage Ph.D., Anne Bruneau Ph.D. and Terry L. Whitworth Ph.D