LES EFFETS DIRECTS ET INDIRECTS DE LA STRUCTURE DU PAYSAGE SUR L'UTILISATION D'ÎLOTS FORESTIERS PAR LE COLIBRI À GORGE RUBIS (*ARCHILOCHUS COLUBRIS*)

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La structure des paysages peut influencer l'écologie d'une espèce directement, en contraignant ses mouvements, par exemple, de même qu'indirectement en affectant, entre autres, l'abondance de ses proies ou prédateurs. Quoique plusieurs études aient tenté de quantifier l'influence de la structure du paysage sur les patrons d'abondance, rares sont celles qui ont mesurer simultanément les effets directs et indirects du paysage. L'objectif de ce mémoire consiste à modéliser simultanément les effets directs de la structure du paysage sur l'abondance relative du Colibri à gorge rubis (*Archilochus colubris*) et sa consommation de nectar artificiel ainsi que les effets indirects par lesquels le paysage peut aussi agir tels la disponibilité en ressources alimentaires (communautés floristiques) et la relation interspécifique de commensalisme avec le Pic maculé (*Sphyrapicus varius*).

Pour ce faire, j'ai échantillonné 40 îlots forestiers (0,5 à >100 ha) dans la région de l'Estrie (Québec, Canada). À chacun d'eux, j'ai installé deux abreuvoirs (en bordure et 40 m à l'intérieur) durant les étés 2006 et 2007 et ont été visités de façon hebdomadaire. J'ai détecté une relation quadratique du couvert forestier dans le paysage avec l'abondance totale relative, celle des mâles et des femelles ainsi que pour la consommation quotidienne moyenne. Ces effets varient en fonction de la taille d'îlot sauf pour l'abondance relative totale. Les valeurs maximales se situent à des niveaux intermédiaires de couvert forestier et de taille d'îlots.

Certaines caractéristiques mesurées étaient à l'échelle locale comme la position de l'abreuvoir dans l'îlot forestier ou la structure de la végétation. J'ai détecté un effet de bordure pour toutes les variables sauf l'abondance des femelles. L'indice de structure de végétation n'avait d'influence que sur l'abondance des mâles. Concernant les effets indirects, l'ensemble des variables du paysage explique 69,61% de l'indice de communauté floristique et ce dernier a un effet significatif sur l'abondance totale et l'abondance des colibris mâles. Pour la relation avec le pic, les variables du paysage mesurées n'ont pas permis de détecter un effet. De plus, bien qu'étant une variable non significative, les modèles incluant la présence du Pic maculé étaient généralement parmi les plus performants. L'ensemble de ces résultats soutiennent l'importance de combiner l'écologie du paysage et l'écologie comportementale dans les mêmes modèles afin de tenir compte non seulement des effets directs mais aussi des effets indirects du paysage.

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La persistance d'une population pour toute espèce animale dépend essentiellement de la capacité de chaque individu à trouver un habitat adéquat où les ressources sont disponibles en quantité suffisante pour satisfaire ses besoins vitaux (Manly *et al.*, 2002). Ces ressources comprennent la nourriture, les partenaires sexuels ou même les caractéristiques générales et ponctuelles d'un habitat (tels que le couvert forestier, les haies, les marais, etc) pour répondre aux besoins comme l'alimentation, la reproduction ou l'utilisation d'abri pour l'évitement de prédateurs ou de conditions environnementales difficiles. Ainsi, la sélection d'habitat est d'abord un résultat de la sélection de ressources.

Plusieurs théories servent à appuyer l'étude de la sélection d'habitat (Rosenzweig, 1985) dont la théorie de l'approvisionnement optimal (« optimal foraging theory »; Stephens, 1986). Plusieurs modèles associés à la sélection d'habitat ont été mis de l'avant dans le cadre de cette théorie. On retrouve, entre autres, le modèle d'exploitation optimale des ressources(Charnov, 1976; MacArthur et Pianka, 1966). Une autre théorie d'importance est celle de l'approvisionnement social (*social foraging theory*), laquelle fait intervenir des notions de densité et de fréquence dépendances dans le cadre de la théorie des jeux (Giraldeau et Caraco, 2000). Parmi les modèles développés au sein de cette théorie, on retrouve ceux de distribution idéale libre, de distribution idéale despotique et de distribution idéale de préemption (Fretwell, 1972; Fretwell et Lucas, 1970; Pulliam et Danielson, 1991). Alors que les modèles de distribution idéale libre servent à prédire la distribution spatiale à l'équilibre d'individus voulant maximiser leur aptitude phénotypique alors qu'ils sont tous égaux et n'encourent pas de coûts de déplacement, ceux de distribution idéale despotique et de préemption tiennent compte des inégalités possibles entre les individus (coûts, monopolisation, interférence). La théorie de l'approvisionnement social fait aussi intervenir l'information sociale dans les processus de sélection d'un habitat du fait qu'un individu tire de l'information sur la qualité d'un habitat par la présence de conspécifiques ou encore via leur succès d'alimentation ou reproducteur (Nocera et Betts, 2010 et ses références). Par ailleurs, certaines études évaluent la sélection d'habitat d'une espèce en tenant compte de la compétition interspécifique et/ou utilisent les notions d'isolegs pour déterminer les densités optimales des différentes espèces dans un habitat (Lawlor et Maynard-Smith, 1976; Rosenzweig, 1981; Rosenzweig, 1985). Toutes ces théories suggèrent ainsi que la sélection d'habitat peut être influencée par une multitude de facteurs et de processus écologiques tels que la disponibilité en ressources alimentaires, la structure de la végétation, l'évitement de la prédation, le besoin d'abri contre les intempéries et la thermorégulation, l'accessibilité à des partenaires sexuels, la présence de compétiteurs intraspécifiques ou interspécifiques, la philopatrie et le succès reproducteur antérieur. Tous ces processus agissent directement ou interagissent sur les différentes ressources recherchées par un individu pour combler ses besoins (Cody, 1985; Jones, 2001).

En général, les ressources recherchées ne sont pas uniformément réparties dans l'espace et dans le temps et, par conséquent, contribuent à la structure des paysages (Manly *et al.*, 2002). Les processus écologiques liés à ces ressources sont eux aussi influencés par la structure du paysage; le tout n'interagissant pas forcément à la même échelle conduit à la nécessité d'intégrer l'écologie du paysage dans la notion de sélection d'habitat. Comme le suggère Johnson (1980), la sélection d'habitat résulte probablement d'un processus décisionnel hiérarchique. Johnson (1980) divise d'ailleurs ce processus décisionnel en 4 étapes. La sélection de 1er ordre est relative à la sélection de l'aire physique ou géographique d'une espèce qui s'évalue à macro-échelle. La sélection de 2^{e} ordre fait référence au domaine vital d'un individu ou d'un groupe d'individus. La sélection de 3^{e} ordre correspond à l'utilisation des différentes composantes du domaine vital. Alors que la sélection de 4^{e} ordre (micro-échelle) serait le choix de la ressource parmi celles disponibles.

Un tel processus hiérarchique de sélection est aussi reconnu en écologie du paysage (Kotliar et Wiens, 1990; Morris, 1995). En fait, la sélection des ressources dépendrait de la façon dont un individu perçoit la structure du paysage et comment il intègre et répond à cette information. Par conséquent, la composition et la configuration du paysage, ainsi que l’échelle spatiale à laquelle les caractéristiques sont perçues, pourraient modifier le comportement d'un individu quant à sa sélection ou l’utilisation d’un habitat. De plus, la structure du paysage peut également affecter les processus de sélection et d’utilisation des habitats en contraignant les mouvements et l’étendue de perception (*perceptual range*) des individus et ainsi leur processus d’échantillonnage (Bélisle, 2005; Lima et Zollner, 1996). C'est ce qui explique pourquoi les biologistes doivent accorder de l’importance à l’intégration de la composition et de la configuration des paysages lors des projets visant à documenter la disponibilité des différentes ressources et le lien entre elles afin de comprendre, par exemple, le comportement alimentaire, le succès reproducteur ou le comportement face à la compétition ou la prédation. La structure du paysage est donc le contexte géographique et évolutif, dans lequel la sélection d'habitat modifie la densité de population locale et la composition des communautés (Morris, 1995).

Les facteurs écologiques tels que la distribution des ressources, la compétition intra- ou interspécifique ainsi que les relations prédateur-proie peuvent influencer simultanément la sélection d'habitat. La structure du paysage, outre son effet direct sur les espèces, peut également influencer la sélection d’habitat par des effets indirects. De fait, la structure du paysage influence directement les processus et les patrons écologiques par des contraintes spatiales affectant, par exemple, les coûts de déplacement entre les parcelles de nourriture via leur niveau d'isolation, ou indirectement en modulant, entre autres, la répartition des ressources, des compétiteurs et des prédateurs. Ainsi, la compréhension de la sélection d’habitat d’une espèce doit considérer non seulement les effets directs de la structure du paysage, mais également les effets indirects de cette structure du paysage via les patrons et processus écologiques qu'elle affecte. Or, la majorité des études qui ont mesuré l'influence de la structure du paysage sur les patrons d'occurrence ou d'abondance, ou encore sur le succès d'appariement ou le succès reproducteur des individus, n'ont pas fait la distinction entre les effets directs et indirects du paysage (e.g., Ghilain et Bélisle, 2008; Mazerolle et al., 2005; Robinson et al., 1995). Il s'ensuit que les effets directs et indirects sont généralement confondus entre eux.

Mon intérêt était donc d'élaborer un projet qui permettait de quantifier simultanément des relations émanant directement et indirectement de la structure du paysage dans un même modèle. J'ai donc choisi de modéliser les impacts de la structure du paysage, de la disponibilité des ressources alimentaires et d'une interaction interspécifique sur l'abondance du Colibri à gorge rubis (*Archilochus colubris*) et, ce, tout en tenant compte des effets indirects de la composition et de la configuration du paysage sur la disponibilité des ressources alimentaires (abondance de fleurs) et la co-occurrence d'une espèce potentiellement commensale, le Pic maculé (*Sphyrapicus varius*).

LE CHOIX DE L'ESPÈCE MODÈLE

J'ai opté pour une espèce aviaire en tant que modèle d'étude puisque ce groupe possède plusieurs avantages pour l'étude de la sélection d'habitat et de l'effet de la structure du paysage. Les oiseaux sont généralement des espèces extrêmement mobiles et possèdent de larges aires de distribution. Par le fait même,ces organismes sont amenés à traverser une grande variété de types d'habitats. Malgré cette grande variété, les oiseaux semblent sélectionner des sites particuliers pour se nourrir ou nicher et, ce, selon une séquence de choix hiérarchiques (Hildén, 1965).

Le Colibri à gorge rubis (ci-après appelé colibri) est une espèce modèle utile pour étudier simultanément le rôle de plusieurs facteurs écologiques. Premièrement, c'est une espèce typiquement dépendante du nectar de fleurs (Bertin, 1982). De plus, les fleurs écloses sont relativement faciles à dénombrer (Fenster et Dudash, 2001). Les colibris s'alimentent de nectar en raison de sa haute teneur en saccharose qui peut répondre à leurs importants besoins énergétiques (Robinson *et al.*, 1996). Leur forte dépendance au nectar permet aux colibris d'être facilement enclins à l'utilisation de ressources alimentaires artificielles (Inouye *et al.*, 1991; McCaffrey et Wethington, 2008). Ceci est un atout pour notre étude puisqu'il garantie l'utilisation d'un dispositif d'abreuvoirs qui, à son tour, permet des prendre des données facilement mesurables via la quantité de nectar artificiel consommé ainsi que par l'observation d'individus en train de se nourrir. En fait, l'utilisation des abreuvoirs à nectar artificiel est essentielle pour étudier cette espèce dont les individus sont très difficiles à détecter dans les paysages forestiers naturels puisqu'ils sont petits, cryptiques et ne chantent pas comme la majorité des passereaux.

Deuxièmement, le colibri est connu pour interagir avec le Pic maculé (*Sphyrapicus varius*; ci-après appelé pic). En effet, certaines études ont rapporté des individus s'abreuvant à la sève des arbres s'écoulant des trous percés par ce pic (Freer et Murray, 1935; Kilham, 1953; Kattan et Murcia, 1985; Miller et Nero, 1983; Southwick et Southwick, 1980). Il est possible que le colibri utilise également ces trous pour y manger les insectes qui y sont attirés, voire s'y retrouvant collés, comme source de protéines. Il est suggéré que ces interactions de commensalisme surviennent quand le nectar est rare ou non disponible, comme à la fin du printemps (Robinson *et al.*, 1996). Il a même été suggéré que la limite nord de l'aire de nidification du Colibri à gorge rubis serait liée à celle du Pic maculé (Miller et Nero, 1983).

Troisièmement, le colibri est connu pour être une espèce de bordure (Freemark et Collins, 1992; Miller et Miller, 1971) ou, du moins, reliée aux forêts de début de succession (Imbeau *et al.*, 2003) et, ce, principalement parce qu'il a besoin à la fois des habitats ouverts pour les ressources alimentaires (fleurs) ainsi que des habitats forestiers pour sa nidification. D'ailleurs, le colibri est une espèce associée aux forêts mixtes et feuillues, mais également aux zones en friches, aux abords d'îlots forestiers, aux jardins et aux vergers (Robinson *et al.*, 1996). De plus, l'aire de distribution de colibri chevauche presque parfaitement certains types de forêts, mais ne coïncide pas avec 22 de ses plantes nectarifères préférentielles (Bertin, 1982). Également, cette espèce est très représentative de la sélection hiérarchique puisqu'elle passe par les quatre niveaux de sélection (Johnson, 1980). En effet, le colibri migre sur de très grandes distances et possède une grande aire de distribution (1er ordre), est considéré comme étant territorial (2^{e} ordre), utilise des composantes distinctes de son habitat selon s'il se nourrit ou s'il se reproduit (3^{e} ordre) et ajuste sa stratégie d'approvisionnement en nourriture selon le type de distribution des ressources (4^{e} ordre; Baum et Grant, 2001). Tous ces éléments nous portent à croire que le colibri répondra fortement à la composition et à la configuration du paysage.

LA BIOLOGIE DU COLIBRI À GORGE RUBIS

Le Colibri à gorge rubis est un oiseau migrateur néotropical de très petite taille (longueur 75-90 mm, 3,5 g en moyenne) et est la seule espèce de colibris se reproduisant dans l'est de l'Amérique du Nord. Il séjourne sur le territoire québécois du début mai jusqu'à la mi-septembre. Il présente un dimorphisme sexuel pour le poids (femelles : 3,8 g; mâles: 3,4 g) ainsi que pour la coloration du plumage de la gorge qui est d'un rubis métallique chez le mâle alors qu'elle est d'un blanc grisâtre chez la femelle. En outre, les rectrices externes des femelles ont les extrémités de couleur blanche tandis que celles des mâles ne le sont pas (Robinson *et al.*, 1996). Le colibri est une espèce polygyne, voire polygynandre, où le mâle ne prodigue aucun soin parental suite à l'accouplement. Les individus des deux sexes sont présumés fortement territoriaux; les territoires étant principalement associés aux sources de nourriture (Robinson *et al.*, 1996; Rousseu, 2010). Quoiqu'il s'agisse d'un nectarivore généraliste, le colibri possède un rôle clé comme pollinisateur pour certaines espèces de plantes (Fenster et Dudash, 2001).

Comme pour l'ensemble des colibris, le Colibri à gorge rubis possède un taux métabolique très élevé qui se reflète par leurs rythmes très élevés de battements d'ailes (53 battements / s) et cardiaque (au repos: 250 battements / min; en vol: 1220 battements / min) (Robinson *et al*., 1996). Les importants besoins énergétiques qui en découlent rendent les colibris fortement tributaires des sources de nectar qui leurs prodiguent un apport important en saccharose. En raison de leur vitesse de digestion, les colibris ont besoin de se nourrir approximativement aux 10 minutes (Robinson *et al*., 1996). Le Colibri à gorge rubis est une espèce diurne et qui, la nuit, entre en torpeur afin de réduire au minimum leur consommation d'énergie. Les colibris ont également besoin de se nourrir d'arthropodes (e.g., araignées, moustiques, moucherons et petites abeilles) afin d'avoir un apport en protéines (Robinson *et al.,* 1996).

OBJECTIF ET HYPOTHÈSES DU MÉMOIRE

L'objectif général de ce mémoire consiste à quantifier les effets directs et indirects de la structure du paysage sur l'utilisation de l'habitat et les patrons d'abondance du Colibri à gorge rubis. Ces effets indirects sont estimés par la disponibilité de la ressource floristique ainsi que par la co-occurrence du Pic maculé. Dans un premier temps, comme dans toute étude du paysage, il m'a fallu déterminer l'échelle spatiale à laquelle le colibri répond le plus aux caractéristiques du paysage utilisées dans le processus de sélection d'habitat (Baum et Grant, 2001; Kotliar et Wiens, 1990). Plusieurs aspects biologiques, comme sa forte territorialité ou son besoin de s'alimenter à des intervalles très courts, pourraient suggérer que le colibri intègre l'information du paysage et y répond dans un faible rayon. Toutefois, aucune étude n'a encore abordé cette question compte tenu de la difficulté à détecter les colibris avec les méthodes conventionnelles d'inventaires d'oiseaux et de l'impossibilité d'utiliser le suivi télémétrique. J'ai donc tenté une approche exploratoire où j'ai comparé, par approche statistique, une vaste gamme d'échelles variant de 1 à 20 km.

Afin de pouvoir modéliser les patrons d'abondance du colibri, j'ai sélectionné deux variables réponses relativement facile à mesurer, soient l'abondance relative de colibris observés autour des abreuvoirs à nectar artificiel ainsi que la consommation moyenne quotidienne de nectar artificiel à ces mêmes abreuvoirs. Compte tenu de la polygynie de cette espèce et de l'absence de soins parentaux prodigués par les mâles, j'ai suspecté une relation différentielle selon le sexe. J'ai donc également modélisé séparément l'abondance des mâles et des femelles observés aux abreuvoirs.

Concernant l'effet du paysage, je m'attendais à ce que l'abondance relative totale ainsi que la consommation atteignent leur maximum à des niveaux intermédiaires de couvert forestier dans le paysage, puisque ceux-ci possèdent la plus grande quantité d'habitat de bordure. En effet, il existe dans notre aire d'étude une forte relation quadratique entre le pourcentage de couvert forestier et la quantité de bordure (en km) dont les coefficients de détermination (R^2) varient entre 0,20 et 0,57 pour des échelles variant d'un rayon de 500 m à 16 km et de 0,16 à 0,09 pour les rayons de 17 à 20 km.

Cela m'a amené également à suspecter un impact de caractéristiques locales du paysage sur l'abondance du colibri. De fait, je m'attendais à retrouver un effet de bordure via la position de l'abreuvoir dans l'îlot forestier lequel se traduirait par des valeurs d'abondance relative totale et de consommation de nectar artificiel supérieures en bordure comparativement à l'intérieur de l'îlot. Je prévoyais détecter ces mêmes effets de bordure et de paysage pour l'abondance des mâles et des femelles. Toutefois, je m'attendais à ce que ces effets soient plus marqués chez les mâles puisque ces derniers semblent préférer les habitats ouverts où ils défendent activement les sources de nourriture, alors que les femelles sont plus dépendantes de la proportion de couvert forestier pour la nidification (Rousseu, 2010). Cette utilisation différentielle du paysage par les mâles et les femelles suggérait également l'hypothèse que l'abondance relative totale et la consommation de nectar soient supérieures dans les îlots de superficies intermédiaires. Je suspectais aussi un effet de la structure de la végétation de l'îlot forestier. En effet, la structure de la végétation peut d'abord influencer la quantité et la répartition de la ressource floristique en influençant le microclimat et la quantité de lumière atteignant le sol. Pour cette raison, je croyais possible de percevoir un effet de la structure de la végétation sur l'abondance relative totale et sur la consommation de nectar. Il demeure que la structure de la végétation peut également être un élément de 4^{e} ordre lors de la sélection d'habitat engendrant un effet potentiellement quantifiable sur l'abondance des femelles et des males. En effet, la structure de végétation interne d'un îlot forestier peut influencer la quantité et la distribution de ressource alimentaire (insectes et fleurs nectarifères) ou encore lors du choix du site de nidification (protection contre les prédateurs, régulation du microclimat).

Concernant les effets indirects, nous soupçonnons un effet de la structure du paysage sur les communautés de fleurs sur nos sites d'études. En effet, une influence du paysage sur la composition floristique peut se produire via les conséquences de la fragmentation causées par la perte d'habitat et/ou les changements de configuration de l'habitat (Fahrig, 2003).

Les caractéristiques du paysage à grande échelle, tels que le pourcentage de couvert forestier ou la superficie des îlots, sont souvent fortement inversement reliées au degré d'isolation des habitats ainsi qu'à la quantité disponible d'habitats adéquats. Ceci influencera particulièrement la capacité de colonisation (Forman, 1995) et le mouvement des individus , des graines ou du pollen entre les îlots d'habitat (Bélisle *et al.*, 2001), entre autres, en limitant l'action de certains pollinisateurs (Feldman, 2006; Wolf et Harrison, 2001). De plus, les effets de la fragmentation opérant à travers l'effet de bordure modifient la structure et la dynamique des communautés floristiques en affectant le microclimat, le régime hydrique du sol et les processus écologiques (Forman, 1995; Ries *et al.*, 2004). En plus de détecter un effet du paysage sur la communauté floristique, je m'attendais à percevoir un effet de cette communauté floristique sur l'abondance relative totale du colibri ainsi que sur sa consommation de nectar puisque qu'il est une espèce principalement nectarivore. À ce titre, je suspectais un effet plus prononcé sur l'abondance de mâles que sur celle des femelles, car ces derniers semblent investir beaucoup d'énergie à la monopolisation et à la défense des ressources alimentaires servant probablement à l'attraction des femelles (Robinson *et al.*, 1996; Rousseu, 2010).

Le second effet indirect évalué concerne la relation de commensalisme entre le colibri et le Pic maculé. En effet, la littérature suggère que les colibris se nourrissent de la sève issue des trous percés par le Pic maculé d'abord parce qu'elle contient des sucres, mais aussi afin de se nourrir des insectes s'y retrouvant et, ce, principalement en début de saison alors que le nectar et les insectes sont encore relativement rares dans le paysage (Freer et Murray, 1935; Kattan et Murcia, 1985; Kilham, 1953; Miller et Nero, 1983; Southwick et Southwick, 1980). Puisque la structure du paysage peut affecter les patrons d'occurrence et d'abondance du Pic maculé (Hobson et Bayne, 2000; Trzcinsky et al., 1999; Villard et al., 1999), il s'ensuit que celle-ci peut affecter le colibri par le biais du pic. Ainsi, je croyais retrouver une relation positive entre l'abondance relative totale du colibri et l'occurrence du Pic maculé de même que pour la consommation de nectar artificiel du colibri. Toutefois, je n'avais pas de raison claire de croire qu'il pourrait y avoir une différence d'effet de la présence du pic entre l'abondance des mâles et celle des femelles.

Cette étude est innovatrice puisqu’elle quantifie simultanément les répercussions directes et indirectes de la structure du paysage sur la sélection et l'utilisation d’habitat par le colibri, par opposition aux études qui évaluent l’impact de ces processus indépendamment. En outre, cette étude rapporte les premières observations non anecdotiques du Colibri à gorge rubis dans la partie nord de son aire de reproduction et est aussi la première à quantifier la relation entre une espèce de colibri et la configuration du paysage à grande échelle.

CHAPITRE 1: DIRECT AND INDIRECT EFFECTS OF LANDSCAPE STRUCTURE ON THE USE OF FOREST PATCHES BY RUBY-THROATED HUMMINGBIRDS (*ARCHILOCHUS COLUBRIS)*

MISE EN CONTEXTE DE L'ARTICLE

L'objectif de cette étude consiste à quantifier simultanément les effets directs de la composition et de la configuration du paysage et ceux indirects via des processus écologiques interagissant sur la sélection et l'utilisation de l'habitat par le Colibri à gorge rubis. Ces processus comprennent la disponibilité en ressources alimentaires (communauté floristique) ainsi que la co-occurrence d'une espèce potentiellement commensale, le Pic maculé.

Les auteurs de cette étude sont Claudie Desroches et Marc Bélisle. Quoique le projet soit le fruit d'un travail d'équipe entre les deux auteurs, Claudie Desroches a contribué le plus à l'achèvement de cette étude. Conjointement avec le second auteur, elle a développé le sujet d'étude et a participé à la conception du protocole d'échantillonnage. Elle a appliqué ce dernier sur le terrain, exécuté et interprété les analyses statistiques des données récoltées ainsi que rédigé une version préliminaire complète de cet article. Ce dernier est l'objet principal de ce mémoire et sera soumis à la revue scientifique *Landscape Ecology*.

ABSTRACT

The main goal of this study was to quantify the effects of landscape structure on the abundance of Ruby-throated Hummingbirds (*Archilochus colubris*) in forest patches and this, while accounting for its indirect effects on open flower community and the occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*), a potential commensal of hummingbirds. We sampled 40 forest patches (0.5 to >100 ha) where we had installed 2 nectar feeders (forest edge and 40 m within forest) during 2 breeding seasons (2006 and 2007). We visited forest patches weekly and recorded the number of hummingbirds detected within 10 m of feeders during 10 min. Mean daily artificial nectar consumption by hummingbirds, as well as their relative total abundance and the respective relative abundance of adult males and females, were all affected by forest cover. Except for the relative total abundance, this effect of forest cover depended upon the size of forest patches. Nectar consumption and abundance generally peaked in forest patches of intermediate size found in landscapes characterized by intermediate forest cover. Mean daily artificial nectar consumption and the relative total abundance, as well as that of males, were higher at feeders located on the forest edge compared to 40 m inside forest patches. Regarding indirect landscape effects, landscape structure influenced the structure of open flower communities surrounding feeders, which in turn, affected the relative total abundance of hummingbirds, as well as that of adult males. On the other hand, we failed to find strong evidence that landscape structure affected the occurrence of Yellow-bellied Sapsuckers or that the latter influenced Ruby-throated Hummingbird abundance patterns. These results support the idea that landscape structure may affect the abundance pattern of a species directly as well as through mechanisms which are themselves dependent upon the composition and configuration of landscapes.

Keywords: habitat fragmentation, habitat selection, Ruby-throated Hummingbird, *Archilochus colubris*, landscape structure, Yellow-bellied Sapsucker, *Sphyrapicus varius*, indirect effects, nectar consumption, spatial scale

INTRODUCTION

The influence of landscape structure on species patch occupancy or abundance patterns have so far been addressed within a conceptual framework primarily dictated by metapopulation theory (Hanski 1999). In that framework, occupancy is predicted to increase with patch size and to decrease with patch isolation. Compared to small patches, large patches are more likely to be occupied by numerous individuals and have greater chances of intercepting dispersing individuals, thereby increasing local population persistence and the likelihood of patch occupancy. Habitat patches close to other patches are also more likely to be occupied by persistent local populations as they have more chances of being colonized by dispersing individuals, especially if surrounded by numerous, large patches that are likely to provide immigrants. Another framework in which large scale, patch occupancy and abundance patterns have been addressed is habitat selection theory (Morris 1995). Landscape structure is here expected to directly affect species and individual distributions, mainly through travel costs and stochastic events involved when searching for and assessing habitat patches (e.g., Bernstein et al. 1991, Beauchamp et al. 1997, Miller and Coll 2010). Although the above processes operate at relatively large spatial scales, landscape composition and configuration may also directly constrain patch occupancy or abundance patterns of species through mechanisms that operate at finer scales. For instance, the shape and spatial disposition of habitat patches may limit the ability of individuals to use several patches in order to secure enough habitat or find every type of resources they need (e.g., food, mates, breeding sites) within a manageable territory or home range size, again largely because of the travel costs involved (Taylor et al. 1993, Huhta et al. 1999, Hinsley 2000, Pope et al. 2000, Norris and Stutchbury 2001).

Landscape structure may further affect, yet indirectly, species patch occupancy or abundance patterns (Fig. 1A). For instance, landscape structure may affect the nature and distribution of a species' food resources (e.g., Burke and Nol 1998), competitors (e.g., Kelly et al. 2003), predators (e.g., Andrén 1992) or parasites (e.g., Donovan et al. 1997), and thereby affect habitat quality (Mortelliti et al. 2010). Such indirect mechanisms may be particularly important, as in nest-web communities, where some bird species strongly depend on woodpeckers to provide nesting cavities (e.g., Daily et al. 1993, Saab et al. 2004). Although many studies have addressed the influence of either direct or indirect mechanisms by which landscape structure may affect a species' occupancy or abundance pattern, very few have attempted to address both types of mechanisms simultaneously (see Lima and Zollner 1996, Mortelliti et al. 2010).

In this paper, we quantify the effects of landscape structure on the abundance of Ruby-throated Hummingbirds (*Archilochus colubris*) in forest patches and this, while accounting for its indirect effects on flower abundance and the occurrence of a potential commensal of hummingbirds, the Yellow-bellied Sapsucker (*Sphyrapicus varius*, Fig. 1B). Ruby-throated Hummingbirds may be directly affected by the amount and spatial configuration of forest habitats as they influence, at least locally, the monopolization and defence of food sources (i.e., nectar; Rousseu 2010) and the foraging movements of these birds (Hadley and Betts 2009, Charette 2011), even after controlling for the number of competitors and the spatial distribution of food sources. Yet, landscape structure may also affect this nectar-dependent bird species indirectly by influencing the structure of plant communities through variation in the amount and spatial distribution of forest and agricultural habitats and edge effects (Gehlhausen et al. 2000, Murphy and Lovett-Doust 2004). Moreover, forest loss and fragmentation in agricultural landscapes are known to affect negatively the occurrence and abundance of the Yellow-bellied Sapsucker (Trzcinski et al. 1999, Villard et al. 1999, Hobson and Bayne 2000). Ruby-throated Hummingbirds may partly depend on this woodpecker species which drills and maintains holes in live trees in order to feed upon the sap exuding from these holes. Ruby-throated Hummingbirds have been observed to drink sap and catch insects at these holes (Robinson et al. 1996). It has even been suggested that the dates of spring arrival and the northern limit of Ruby-throated Hummingbirds' breeding distribution may be related to that of the Yellow-bellied Sapsucker, especially where nectar sources are scarce (Miller and Nero 1983). Addressing simultaneously some of the direct and indirect influences of landscape structure on the abundance of Ruby-throated Hummingbirds will help assess the (non-mutually exclusive) hypotheses stating that this bird is an area-insensitive, edge species (Miller and Miller 1971, Freemark and Collins 1992), is related to early-successional forests (Imbeau et al. 2003) or linked to forest gaps (Robinson et al. 1996). All three hypotheses are partly based on the facts that this bird likely needs both open areas for finding food (i.e., nectar producing plants) and forest cover area for effective nesting.

Because hummingbirds are very difficult to detect using conventional bird census methods (e.g., point counts) and are usually too small to carry radio-transmitters or their analog, there is a clear lack of empirical information regarding how these birds select the habitats they use and at what spatial scale(s) they perform this selection (Kotliar and Wiens 1990, Baum and Grant 2001). Hence, we first assessed the spatial scale at which Ruby-throated Hummingbirds responded most strongly to landscape structure. We then quantified the influence of landscape structure on the abundance of Ruby-throated Hummingbirds and their consumption of artificial nectar at this specific scale controlling for variations in the community structure of nectar-producing plants and in the occurrence of Yellow-bellied Sapsuckers. We expected Ruby-throated Hummingbird abundance and artificial nectar consumption to peak in landscapes characterized by intermediate levels of forest cover as these bear the highest amount of forest edges. We also expect these responses to be greater at the forest edge compared to 40 m inside forest. We further predicted that this edge effect should be more important for males as these are likely to prefer open habitats where they are more apt to monopolize and defend nectar sources which may serve to attract females (Robinson et al. 1996, Rousseu 2010). Finally, we expected a positive relationship between Ruby-throated Hummingbird abundance or artificial nectar consumption and the presence of Yellow-bellied Sapsuckers.

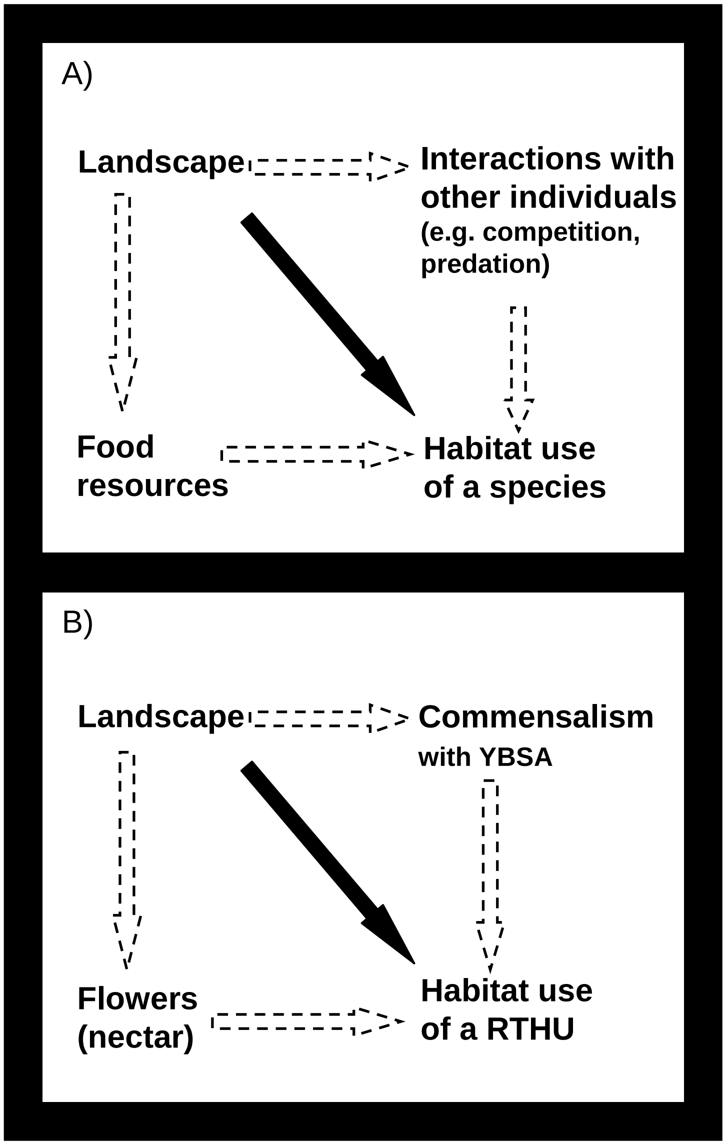

Fig 1: Influence of landscape structure on habitat use. A) Most studies have either quantified direct (solid arrows) or indirect (dashed arrows) influences of landscape structure on habitat use. B) This study attempts to simultaneously quantify direct and indirect influences of landscape structure on the habitat use of Ruby-throated Hummingbirds (RTHU; *Archilocus colubris*).

METHODS

STUDY AREA AND FEEDER SETUP

Field work was conducted from April to August in south-eastern Québec (Canada, Fig. 2) during two consecutive summers (2006-2007). The study area consisted in 5748-km^2 mosaic of deciduous and mixed-deciduous forests, dairy farmlands and intensive cultures of maize, soybean and other cereals (Bélanger et al. 1999, Jobin et al. 2005). Our study was based on a set of 40 forest patches chosen through a stratified random process to cover a wide range of patch sizes and isolation levels, defined by the amount of forest surrounding focal patches. Focal forest patch sizes varied from ≤ 0.5 to ≥ 100 ha and > 80% consisted of deciduous forest. Forest patch isolation was considered low if there was > 60% forest cover within 2.5 km of the focal patch and high if ≥ 70% of the land was covered by crops, hayfields and pastures. We first randomly chose 10 forest patches that covered the ≤ 0.5 to ≥100-ha range in a “forested” landscape and paired them based on patch size with 10 forest patches surrounded by an “agricultural” landscape. We then replicated this process to select a second set of forest patches. The first set of 20 patches was equipped with nectar feeders (2 feeders/patch) at the end of April whereas the second set received nectar feeders (2 feeders/patch) only at the end of June (see below). All forest patches were spaced by >5 km to minimize the likelihood of observing a given hummingbird or sapsucker in more than one forest patch.

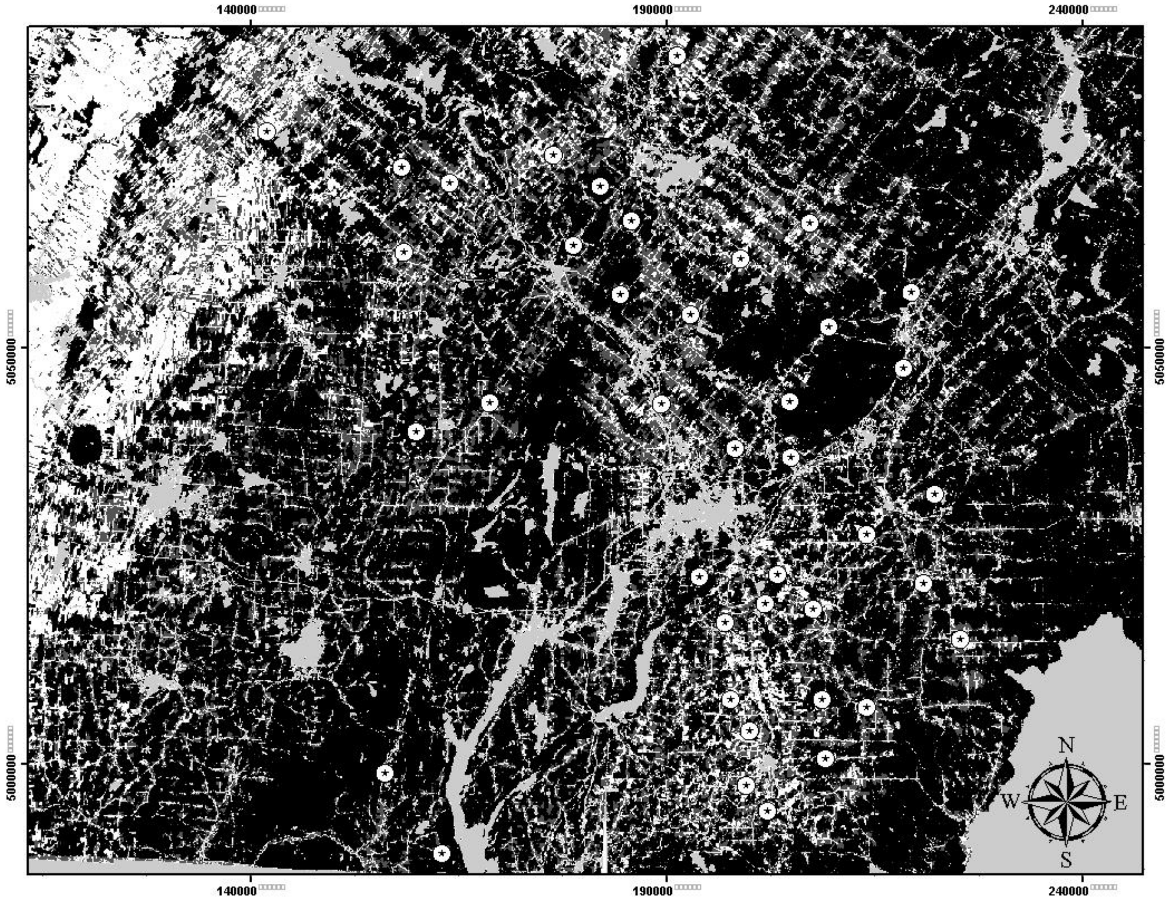

Fig. 2 Distribution of the 40 forest patches used to model habitat use of Ruby-throated hummingbird (*Archilochus colubris*) in south-eastern Quebec, Canada, in 2006 and 2007. Land cover types are based on a mosaic of classified LANDSAT-TM satellite images (Canadian Wildlife service 2004). Coordinates are in projected reference system of Canada national grid NAD 1983 MTM 7. Land cover types include forest (black), extensive agriculture (dark gray), intensive agriculture (white), water and urban (light gray).

We installed a first set of nectar feeders at 20 sites at the end of April, before the spring arrival of Ruby-throated Hummingbirds. We installed a second set of feeders at 20 sites at the end of June assuming that Ruby-throated Hummingbirds had established their territories by then, as determined by observations made at two local hummingbird banding sites (J. Turgeon and Y. Charette *pers. comm.*). We used this two-phase schedule of feeder installation to assess the potential bias that feeders may cause on habitat selection by hummingbirds. Whereas feeders installed before the hummingbirds' arrival could influence territory choice, feeders installed after territory establishment should have a much lower impact on habitat selection. We used nectar feeders in order to increase the likelihood of detecting Ruby-throated Hummingbirds when present at a site because these birds are small, cryptic and difficult to detect by ear at long distance. For the second summer, we kept the same forest patches and the same feeders' location, but the first set of 20 feeders installed in April in 2006 was set up in June in 2007, and vice-versa. This switch aimed to dissociate philopatry from habitat selection.

We assessed edge effects by installing one nectar feeder at the edge of the patch, in the first row of trees, and another one 40 m inside the patch. This distance was the maximum possible given the smallest patch size in this study. This distance should be sufficient to quantify edge effects (Matlack 1994, Matlack and Litvaitis 1999). All nectar feeders were filled with a 20% (w/v) sucrose solution, the usual concentration in the nectar of wild flowers visited by hummingbird (Baker 1975, Bolton et al. 1979, Chalcoff et al. 2008). Feeders consisted of reversed glass bottles supplying a red basin-style bottom with four holes each covered by a glued yellow flower (Yule Hide, model HB81, capacity: 455 ml). To minimize exposure to rain or sun, we fixed a green aluminium plate 60-cm in diameter above the feeder, which was hanging at about 1.75 m from the ground. We removed the perches allowing hummingbirds to feed while sitting in order to prevent other bird species to gain access to nectar. We did not have problems with ants, bees, wasps or black bears.

OBSERVATIONS AT FEEDERS

We visited each patch once a week between 30 April and 18 August in both 2006 and 2007. It took 5 to 6 days to visit all 40 sites. We scheduled visits to patches according to a random weekly and daytime order. To quantify patch use, a 10-min observation period was conducted simultaneously at both nectar feeders (edge and inside) where we recorded the number of Ruby-throated Hummingbirds (the only hummingbird in our study area) within 10 m of the feeder, the exact time at which they did so, as well as their sex and their age based on morphologic characteristics (Baltosser 1987). A 10-min observation period was judged sufficient to detect an individual because hummingbirds need to feed about every 10 min to maintain their high metabolic rates (Robinson et al. 1996) and because we assumed them to be territorial. We classified individuals into four groups: 1) adult male (ruby-throated), 2) adult or hatching year female (white-throated with white-tipped outer rectrices), 3) hatching year male (red-speckled throated with outer white-tipped rectrices), and 4) unclassified. We could not use a more precise classification using binoculars (Baltosser 1987). Simultaneous sampling and timed observations allowed us to increase the minimum number of individuals detected at a given study site. We also quantified patch use by measuring weekly the average daily consumption of artificial nectar ($g \cdot day^{-1}$). Artificial nectar was changed weekly to assure its quality and innocuousness. Lastly, we recorded the date (Julian day), hour and meteorological conditions during each visit (Table 1).

HUMMINGBIRDS CAPTURE-MARK-RECAPTURE

To improve our assessment of the number of Ruby-throated Hummingbirds that used nectar feeders, and to assess whether adult hummingbirds can be considered a closed population, we conducted a capture-mark-recapture (CMR) study between 19 June and 14 August 2007. Once a week, we made a 1-hour sampling effort at 12 of the 40 study sites. Hummingbirds were captured using a Hall trap (Russell and Russell 2001). Once a hummingbird was captured, we dye-marked its breast with a permanent non-toxic Marquette marker. We had 6 different colors which were assigned to individuals in the same order at all sites. It was impossible to use color combinations so each bird bore only one colour.

OPEN FLOWER ABUNDANCE

We monitored the abundance of open flowers every 2 weeks (i.e., 8 out of 16 weeks of sampling from early May to mid-August) at each site. We counted the number of open flowers by species within each 10-m stretch of an 80-m line transect that started in the open 20 m ahead of the edge feeder and ended 20 m behind the core feeder, inside the forest patch. We monitored all flower species even though many are not typically visited by hummingbirds because our study group often observed hummingbirds visiting non-nectariferous species (pers. observ. and Y. Charette *pers. comm.*). Non-nectariferous flowers may be important for acquiring insects, which are essential sources of proteins for hummingbirds (López-Calleja et al. 2003).

FOREST COMPOSITION AND STRUCTURE

Although we strove to select forest patches sharing the same vegetation composition and structure, there remained some variation among study sites. We thus quantified some aspects of forest composition and structure of each forest patch that are expected to affect habitat selection through resource defence and/or nest site selection in Ruby-throated Hummingbirds (Rousseu 2010). First, we set a central point 5 m of each feeder at an angle of 130^o where 0^o corresponded to a line perpendicular to the forest edge and pointing towards the open. Following Philibert (2005), we then assessed tree density (percent cover of basal area) within a 20 m-radius, the percent cover of ferns and shrubs within a 10-m radius, and the presence of canopy gaps (> 50 m^2) within 20 m. We also measured foliage density by counting the number of leaves touching a stick within different height classes from the ground to 20 m high. The foliage density was measured at the centered point and at two additional points located 5 m to the south and north and then we used the mean of these three counts for each height class. We characterized forest composition and structure only during the first of the two study years (i.e., from 29 August to 20 September 2006).

OCCURRENCE OF YELLOW-BELLIED SAPSUCKERS

We monitored the weekly occurrence of Yellow-bellied Sapsuckers at each forest patch between 29 May and 23 June 2006 and between 30 April and 8 June 2007. These dates encompass the periods during which Yellow-bellied Sapsuckers defend territories and raise their young (Walters et al. 2002), thereby maximizing the probability of detecting this species when present. To further improve sapsucker detectability, we broadcast four successions of 30 sec of calls (10 sec of drums, cat-like calls, and territorial calls; Elliot and Mack 1991) followed by 2 min of silent listening, for a total of 10 min each week, using a 20-W Pignose Lil’PA ® speaker. The observer stood half way between the two hummingbird feeders at a distance of 20 m from the edge. Note that calls were broadcast only after hummingbird abundance had been estimated at the nectar feeders. A forest patch was considered occupied only if a sapsucker was observed within the patch.

LANDSCAPE STRUCTURE

The landscape scale of analysis is very important for data interpretation because the scales at which a species integrates landscape information with respect to habitat selection decisions may vary (Kotliar and Wiens 1990). Although hummingbirds respond to temporal or spatial heterogeneity in nectar volume or quality at single flowers or patches of flowers, they are also expected to monitor and respond to regional floral availability (Bronstein 1995; see also Visscher and Seeley 1982, Carpenter 1987). Lacking any strong reference on which to base our choice of landscape scales, we chose an exploratory approach and compared the response of hummingbirds to landscape structure measured within a range of 20 different radii varying from 1 to 20 km.

We characterized landscape structure around each feeder by measuring the relative amount of forest and agricultural cover (%) and total amount of forest edge (km). Relative forest and agricultural covers were measured based on a mosaic of classified Landsat-7 satellite images (taken between August 1999 and May 2003; pixel size = 25 m X 25 m; Canadian Wildlife Service 2004). Pixel information was extracted with ArcInfo GIS (ESRI 2005) and fed to Fragstats 3.3 (McGarigal et al. 2002) for calculation of relative covers and amount of forest edge within each buffer. We found a strong negative correlation between the relative amount of forest and agricultural covers at each radius ($0.60 \leq r^2 \leq 0.97$). We therefore only used forest cover in regression models (see *Statistical analysis* section). We also found a strong quadratic relationship between the relative amount of forest cover and total amount of forest edge at most spatial scales (Fig. 3). The R^2 of quadratic polynomial regressions varied between 0.20 and 0.57 for landscape radii of 500 m to 16 km and from 0.16 to 0.09 for radii of 17 km to 20 km (Fig. 4). Because regression models including both the relative amount of forest cover and total amount of forest edge did not converge, we used the relative amount of forest cover squared as to account for the influence of the total amount of forest edge in further analyses.

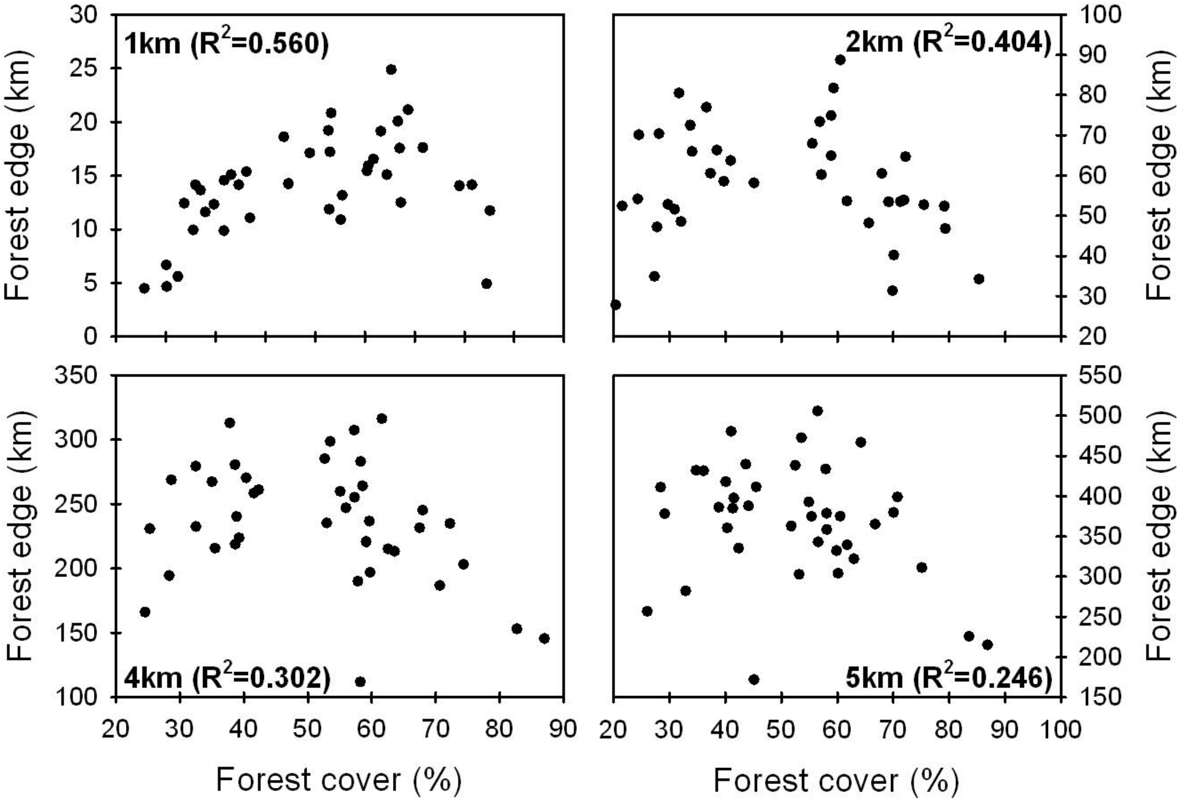

Fig. 3: Examples of quadratic relationships between landscape forest cover (%) and total amount of forest edge (km) measured around nectar feeders. Coefficients of determination (R^2) are given for quadratic polynomial regressions. Examples were chosen in accordance to the best spatial scale obtained for each of the four response variables (see Table 4, RTHU total relative abundance = 1 km, relative adult male RTHU abundance = 2 km, RTHU artificial nectar consumption = 4 km and relative adult female RTHU abundance = 5 km).

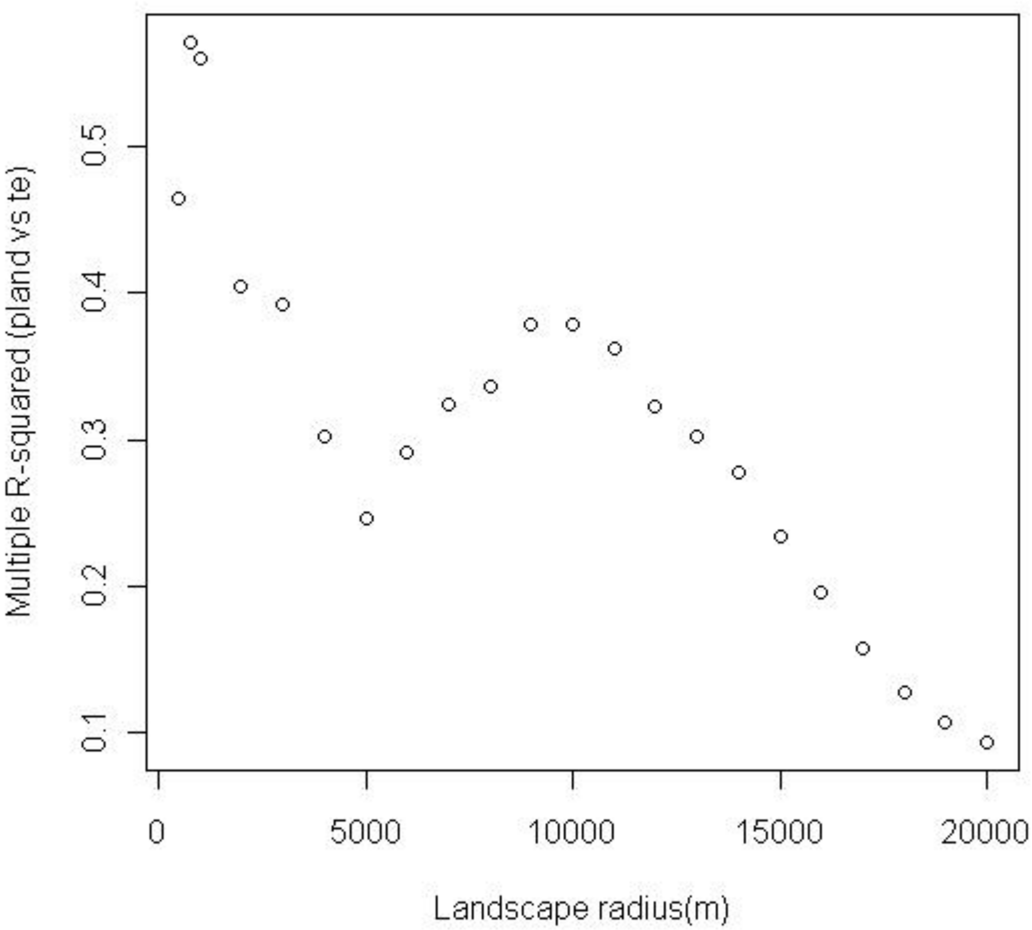

Fig 4: Coefficients of determination (R^2) of quadratic polynomial regressions between the relative amount of forest cover (%) and total amount of forest edge (km) assessed within radii varying from 500 m to 20 km around nectar feeders.

STATISTICAL ANALYSIS

HUMMINGBIRDS CAPTURE-MARK-RECAPTURE (CMR)

CMR data were primarily aimed to assess whether adult hummingbirds could be considered part of a closed population. Population closure is a critical assumption of Royle's N-mixture model (Royle 2004), which would have allowed us to model the influence of explanatory variables on adult hummingbird abundance while correcting for imperfect detectability. Unfortunately, as mentioned in the Results, we did not recapture enough individuals to support a closed-population, thereby preventing the use of Royle's N-mixture model (Royle 2004) or any other CMR analyses.

LOCAL VARIABLES

Flower Community Index

Open flower availability data were recorded into an abundance matrix where each row corresponded to a site and each column to a species. Because the flower selection behaviour of Ruby-throated Hummingbirds is poorly known, we used a flower community index that contrasts the different study sites with respect to their flower community in order to assess the influence of variation in open flower community structure on hummingbird abundance and artificial nectar consumption across study sites. The flower community index consisted in the site loadings of the first two principal component axes of a principal component analysis (PCA; Legendre and Legendre 1998) applied to Hellinger-transformed abundance data (Legendre and Gallagher 2001). The PCA performed on a covariance matrix and Hellinger transformation was applied using the functions rda() and decostand() (package vegan v.1.11-2) in R 2.6.2 (R Development Core Team 2008).

Forest Composition and Structure Index

In order to control for the influence that forest composition and structure may have on hummingbird abundance and artificial nectar consumption, we used an index analogous to the flower community index defined above. The forest composition and structure index consisted in the site coordinates along the first two principal axes of a principal coordinate analysis applied to Gower-transformed data (PCoA; Legendre and Legendre 1998). We used a PCoA, instead of a PCA, because the forest composition and structure variables were measured in different units. We performed the PCoA and Gower transformation using the cmdscale() (package stats v.2.6.2) and daisy() functions (package cluster v.1.11.9) in R 2.6.2 (R Development Core Team 2008).

INDIRECT EFFECTS OF LANDSCAPE STRUCTURE

Open Flower Community Structure

We quantified the influence of landscape structure on the structure of open flower communities using a redundancy analysis (RDA; Legendre and Legendre 1998) applied to Hellinger-transformed abundance data (Legendre and Gallagher 2001). The open flower abundance matrix was constrained by a matrix including landscape variables (% forest cover, [% forest cover]^2 and their interactions with patch size) and the forest composition and structure index. All analyses were run in R 2.6.2 (R Development Core Team 2008). We performed the Hellinger transformation, RDA and variance partitioning analyses using the decostand(), rda() and varpart() functions (package vegan v.1.11-2). We compared models and conducted inference tests (5000 permutations) with the anova() function (package stats v.2.6.2).

Occurrence of Yellow-bellied Sapsuckers

We assessed the influence of landscape structure on the occurrence of Yellow-bellied Sapsuckers while correcting for imperfect detectability using the single-species, single-season model of MacKenzie et al. (2002; see also MacKenzie et al. 2006). Models were fitted for each year (i.e., 2006 and 2007) in PRESENCE 2.2 (v. 2.2 <090306.1055>; Hines 2006) because we did not have enough visits in each year to sustain a multi-season model. We used the same landscape variables as when modelling the influence of landscape structure on Ruby-throated Hummingbird abundance and artificial nectar consumption (Table 1). These variables are in accordance with Yellow-bellied Sapsuckers' dependence upon forest habitats (Walters et al. 2002) and its negative response to forest loss and fragmentation (Trzcinsky et al. 1999, Villard et al. 1999, Hobson and Bayne 2000).

Because Yellow-bellied Sapsuckers show a habitat preference for mature to old deciduous and mixedwood forests (Paradis 1995, Savignac and Machtans 2006), we also considered variations in tree community among study sites when modelling their occurrence. To do so, we used the site loadings of the first two principal component axes of a principal component analysis (PCA; Legendre and Legendre 1998) applied to Hellinger-transformed tree abundance data (Legendre and Gallagher 2001). The PCA on a covariance matrix and Hellinger transformation was applied using the functions rda() and decostand() (package vegan v.1.11-2) in R 2.6.2 (R Development Core Team 2008). Finally, we used Julian date, time of day, Beaufort wind speed and the intensity of precipitation as covariates that could affect the likelihood of detecting sapsuckers.

Because no study had investigated the spatial scales at which Yellow-bellied Sapsuckers are more likely to respond to landscape structure, we compared 22 models that included all the explanatory variables mentioned above, but differed with respect to the spatial scale at which forest cover was measured. Model comparison was based on the second-order Akaike's information criterion (AIC_c or $QAIC_c$ if in presence of overdispersion; Burnham and Anderson 2002). Specifically, forest cover was measured within radii varying from 500 m to 20 km. We finally considered a model which included no explanatory variables that could affect the occurrence of sapsuckers (i.e., only the intercept) for a total of 23 models.

DIRECT EFFECTS OF LANDSCAPE STRUCTURE

We modelled the influence of explanatory variables (Table 1) on Ruby-throated Hummingbird abundance and mean daily artificial nectar consumption using generalized linear mixed-effect models (Zuur et al. 2009). We used mixed-effect models because our hierarchical sampling design involved repeated weekly observations at the same sites and two nectar feeders within each site. Feeders were accordingly nested within sites and site ID treated as a random factor. For simplicity, we only allowed the intercept to vary among sites. We used Poisson regressions for modelling relative total hummingbird abundance, adult male abundance and adult female abundance in terms of the minimum number of individuals observed at a feeder during a visit. Mean daily artificial nectar consumption

($g \cdot day^{-1}$) at one feeder was modelled with an identity link function and assuming gaussian errors. Note that coefficients and standard errors were estimated by maximum likelihood using a Laplacian approximation for Poisson regression and residual (restricted) maximum likelihood for linear models. Poisson regressions and linear models were fitted using respectively the lmer() (package lme4 v.0.99875-9) and lme functions (package nlme v. 3.1-86) within the R statistical environment (v. 2.6.2, R Development Core Team 2008).

In order to determine the spatial scale at which Ruby-throated Hummingbirds responded most strongly to landscape structure, we first created a set of “global models” incorporating all explanatory variables (Table 1), but where landscape variables were measured within a range of radii varying from 1-km step between 1 and 20 km. We also considered a model that did not include any explanatory variables (intercept). These 21 models were then compared based on the (marginal) Akaike’s information criterion with finite-sample correction (AIC_c) following Vaida and Blanchard (2005). The best model was used as the response scale in further analyses. This exploratory procedure was repeated for each of the three abundance variables and for the artificial nectar consumption.

Having determined the spatial scale at which Ruby-throated Hummingbirds responded most strongly to landscape structure, we defined a set of competing models which contrasted the importance of different groups of variables with respect to hummingbird relative abundance and artificial nectar consumption (Table 2). We then compared models based on the marginal AIC_c following Vaida and Blanchard (2005) and performed multimodel inference according to Burnham and Anderson's (2002) recommendations. We accordingly report model-averaged coefficients, unconditional standard errors and the resulting 95% confidence intervals.

Table 1 : Justification of explanatory variables used for modelling Ruby-throated Hummingbird (*Archilochus colubris*) abundance and artifical nectar consumption. We will henceforth refer to the group names of variables (filter, local, and landscape variables) when describing explanatory variables in models.

Justification of explanatory variables			
		Justification	
Variable	Definition (units)	Models for Nectar consumption	Models for RTHU abundance
Filter (variables found in all models)			
Year	2006 (0) 2007 (1)	Interannual variation	Idem
Temperature	Temperature based on hourly observation data archives (°C)	---	Temperature may affect the degree of activity of birds and so the probability of detection
Rain	Intensity of precipitation at the beginning of each visit: none (0) light (1) strong (2) storm (3)	---	The intensity of precipitation may affect the degree of activity of birds and so the probability of detection
Mean Individuals	Mean number of individuals seen during the visit and the visit before	To control for the increase in nectar consumption only due to the increase in number of individuals feeding	---
Treatment	Feeder's installation date end of April (0) end of June(1)	To control for the habitat selection bias that feeders may cause.	Idem
Year * Treatment		Switch-back experiment of feeders' hanging date to dissociate the homing effect from the habitat selection effect	Idem
Local variables			
Feeder location	edge (0) core (1) of patch	To quantify the importance of edge habitat	Idem
Structure Index	Loadings on the two first axes of the Principal coordinate analysis (PCoA)	Habitat structure of the patch may impact the visibility, accessibility and defendability of nectar resources and RTHU individuals	Idem

Table 1 (extended)

Landscape variables			
Patch area	log10 [area (ha)]	Habitat size is known to influence the habitat selection	Idem
Forest cover	Percentage of forest in the landscape	RTHU is considered to be a forest species	Idem
$(\text{Forest cover})^2$	Square of the percentage of forest in the landscape	There is a quadratic relation between forest cover et edge quantity in our dataset (R^2 = 10% to 57% depending on radius)	Idem
Patch area * Forest cover		RTHU may react differently to the amount of forest cover within surrounding landscape according to patch size	Idem
Patch area * $(\text{Forest cover})^2$		RTHU may react differently to the amount of total edge (assessed using squared forest cover) within surrounding landscape according to patch size	Idem
Food (RTHU's sources of food)			
Floristic index	Loadings on the two first axes of the Principal component analysis (PCA)	Flowers are RTHU's sources of food (nectar and insects). This index enables comparison of flower composition between patches	Idem
Sapsucker	absence (0) presence (1) of YBSA at the patch	RTHU may rely on sap when other nectar sources are scarce or unavailable	Idem

Table 2 : Explanatory variables used in each of the seven models compared using the second-order Akaike information criterion (AIC_c) for all of four response variables. See Table 1 for variable description.

Models in competition		
		1) Filter + Local + Landscape + Flowers + Sapsucker
Nectar consumption		2) Filter + Local + Landscape + Sapsucker
Relative abundance		3) Filter + Local + Landscape + Flowers
Male abundance	=	4) Filter + Local + Landscape
Female abundance		5) Filter + Local
		6) Filter + Landscape
		7) Filter + Flowers + Sapsucker

RESULTS

HUMMINGBIRDS CAPTURE-MARK-RECAPTURE

We marked 154 different individuals at 12 sites. We made 6 recaptures with Hall traps and 7 by resight that involved 5 and 4 different individuals, respectively. Such low recapture rate (9/154 or 7%) suggests that Ruby-throated Hummingbird local populations were opened or dense. We therefore did not satisfy the closed-population assumption crucial to the application of Royle's N-mixture model (Royle 2004) and thus had to model hummingbird abundance without correcting for an imperfect detection probability (i.e., use raw abundance data in further analyses).

LOCAL VARIABLES

Flower Community Index

The first two PCA axes represented 41.02% of the total variation found in the open flower abundance matrix. Most sites were distributed close to the ordination centre. This is not surprising given that we selected sites that were very similar in terms of forest composition and structure and since agricultural practices are not very diversified in our study area.

The PCA partitioned study sites mostly according to the abundance of a few flower species (Fig. 5). Quadrant I: *Trifolium repens* (sp.99), *Tr. pratense* (sp.98) and *Prunella vulgaris* (p.75). Quadrant II: *Solidago canadensis* (sp.89). Quadrant III: *Spiraea latifolia* (sp91). Quadrant IV: *Ranunculus acris* (sp.79); *Allium tricoccum* (sp.04) and *Maianthemum canadense* (sp.59) were also present but had a much lower importance due to their position near the ordination centre. Axis 2 seemed to correspond to a humidity gradient whereby "xeric" open habitat species were mostly found in quadrant I and II, "mesic" forest or open habitat species associated to the centre and quadrant III, while quadrant IV included species found in "xeric" to "mesic" open habitats. Axis 1 seemed to represent a disturbance gradient. Sites associated to *Solidago canadensis* (sp.89) typically consisted in forest patches adjacent to fallow fields with a history of severe and recurrent anthropogenic disturbances (Fig. 6). Sites characterized by *Trifolium* species (sp.98-99) usually corresponded to forest patches bordered by fodder or hayfield habitats while sites associated to *Spiraea latifolia* (sp91) comprised shrubby fallows or pastures (Fig. 6).

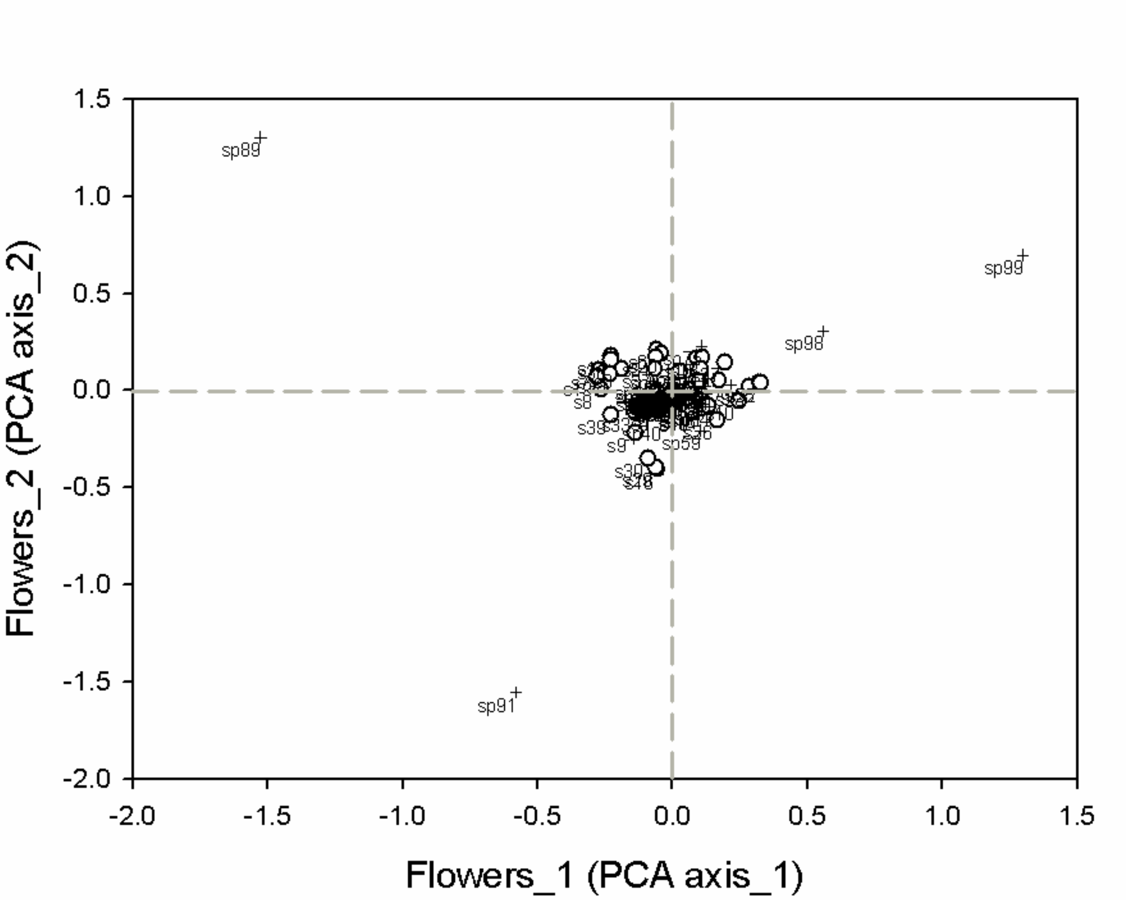

Fig. 5: Ordination biplot of open flower communities found in study sites. Crosses depict flower species and empty circles correspond to study sites. Species that weigh the most in this analysis are *Solidago canadensis* (sp.89), *Trifolium repens* (sp.99), *Tr. pratense* (sp.98), *Prunella vulgaris* (p.75), *Ranunculus acris* (sp.79), and *Spiraea latifolia* (sp91). *Allium tricoccum* (sp.04) and *Maianthemum canadense* (sp.59) are also influential but to a lower level given they are located near the graphic's centre.

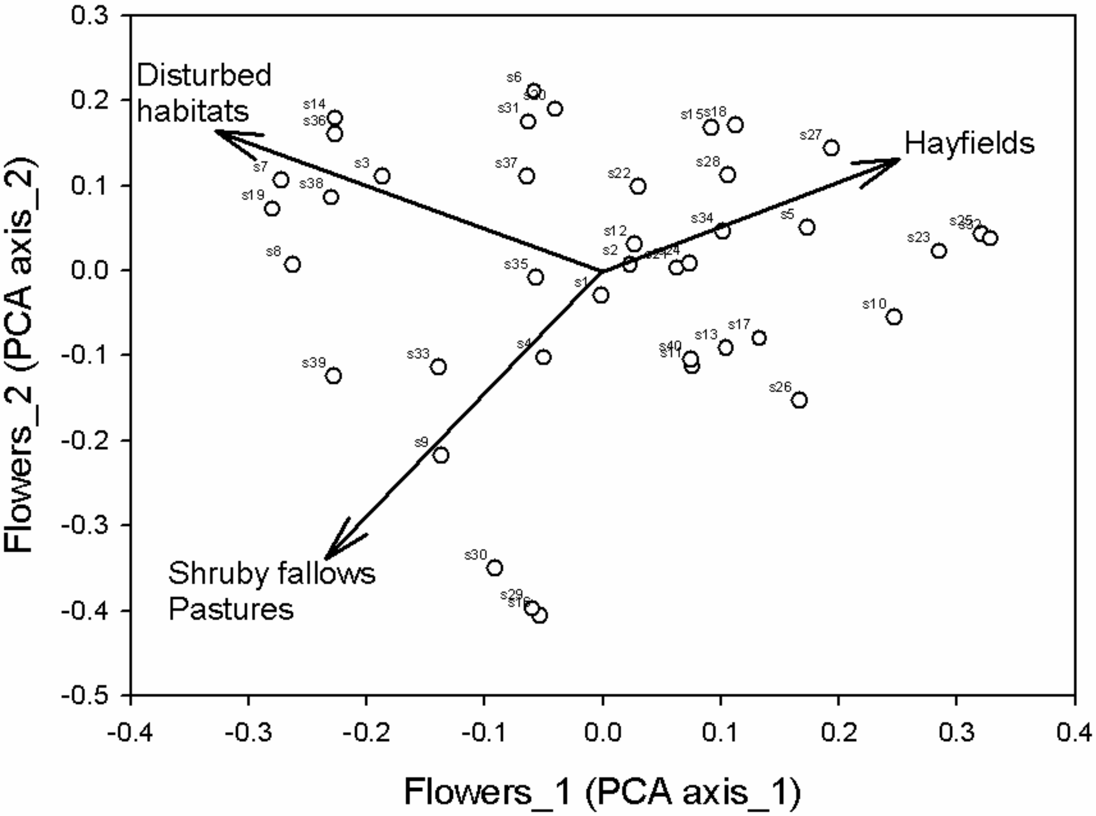

Fig. 6: Ordination biplot showing three major groups of study sites according to their similarity in habitat type. This plot is an enlargement of the cloud of points (sites) found in Fig. 5.

Forest Composition and Structure Index

The PCoA on forest composition and structure variables partitioned the nectar feeders into two relatively distinct groups (Fig. 7). Whereas feeders grouped on the left of the ordination diagram (A) were characterized by the absence of forest gaps (> 50 m^2) within 20 m, feeders grouped on the right of the diagram (B) were characterized by the presence of such gaps. Feeder group A was further defined by a tree (DBH ≥ 9 cm) density ≥ 80%, a mean leaf density that peaked between 10 and > 20 m from the ground, and a mean shrub cover of 35%. Feeder group B had a tree (DBH ≥ 9 cm) density varying between 40% and 80%, a mean leaf density that peaked between 0 and 10 m from the ground, and a 52% mean shrub cover. These results suggest that the first PCoA axis corresponds to a gradient of forest openness. Feeders on the left (A) were surrounded by high mature trees within closed-canopy forests with few or no understory vegetation, whereas feeders on the right (B) were located into early, seral open forests with a dense shrub layer.

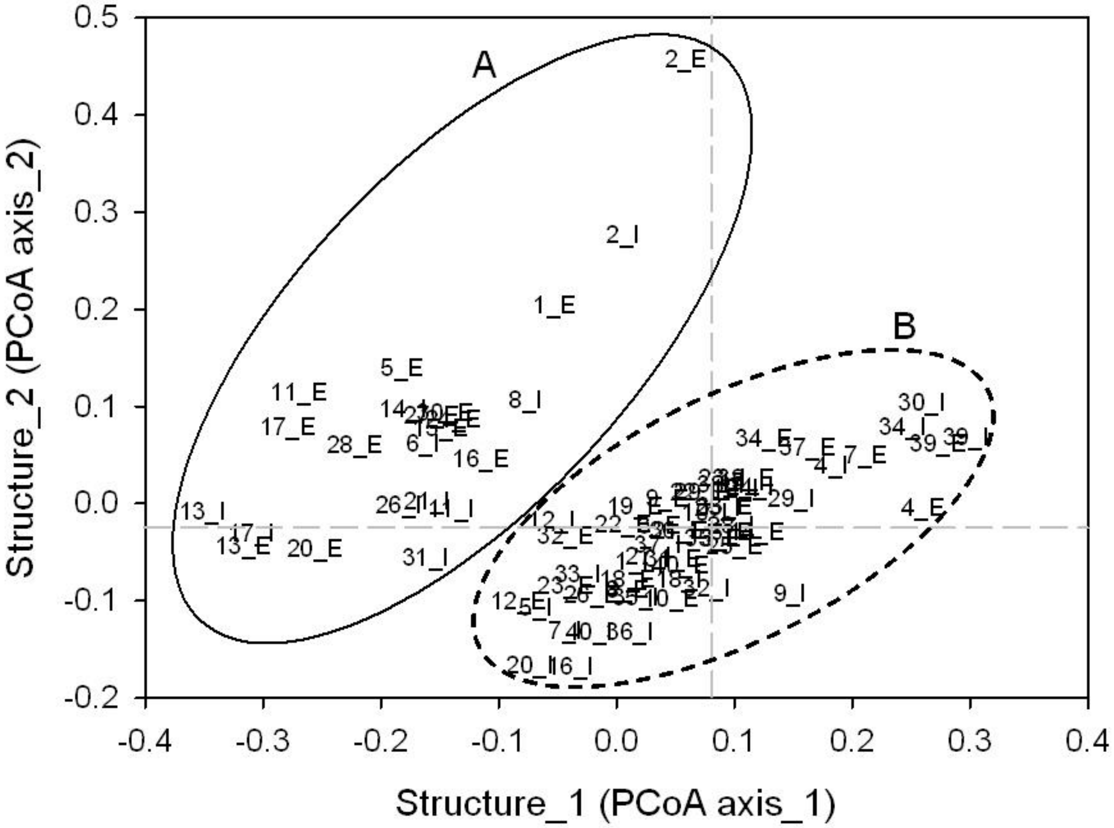

Fig.7: Feeder partitioning based on a principal coordinate analysis (PCoA) applied to forest composition and structure variables. Numbers indicate site ID and letters the location of the feeder (E= forest edge and I = forest interior).

INDIRECT EFFECTS OF LANDSCAPE STRUCTURE

Open Flower Community Structure

According to RDA, landscape structure had the greatest influence on open flower community structure when forest cover and forest patch size were measured within a 5-km radius. Landscape and local variables explained together 69.61% of total variance. After controlling for local variables, landscape variables explained 14.44% (P = 0.01) of the total variation in open flower community structure.

We found evidence based on AIC$_c$ that across-site variations in open flower community structure may affect mean daily artificial nectar consumption by Ruby-throated Hummingbirds, as well as their relative total and adult male abundances, when controlling for the effects of local and landscape variables (Table 5-7). On the other hand, no such evidence was found regarding the relative abundance of adult females (Table 8). Moreover, multimodel inference indicated that only the relative total and adult male abundances were affected by the structure of open flower communities. Indeed, decreases of 0.54 and 0.36 individual were found along the community gradient characterized by the second axis of the PCA fitted to the open flower abundance data for the relative total abundance (Table 6) and relative adult male abundance (Table 7), respectively.

Occurrence of Yellow-bellied Sapsuckers

We found no landscape variable affecting the occurrence of Yellow-bellied Sapsuckers, independently of spatial scale (Table 3). The intercept model clearly had the smallest AIC$_c$ in 2006 and QAIC$_c$ ($\hat{c}$ = 1.4) in 2007 with corresponding Akaike weights of 99.98% and 88.6%, respectively (Table 3). The probability of detecting (ρ) a Yellow-bellied Sapsucker when present on a given visit was estimated to be 0.59 ± 0.05 (SE) and 0.48 ± 0.04 in 2006 and 2007, respectively. After correcting for imperfect detectability, the probability (ψ) that Yellow-bellied Sapsuckers occupied a forest patch was estimated to 0.67 ± 0.08 and 0.64 ± 0.08 for 2006 and 2007, respectively. Naïve estimates of occurrence for the same years were 0.65 and 0.63, respectively. The small difference between naive and corrected probabilities of occurrence suggest that we had a very good chance of detecting Yellow-bellied Sapsuckers in a forest patch when present and this, across the repeated visits we made to a site on a given year. These results hence warrant our use of the raw Yellow-bellied Sapsucker occurrence data to assess the influence of the presence of this species on Ruby-throated Hummingbird abundance and artificial nectar consumption.

Table 3: Selection of models assessing the influence of landscape variables on the occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in forest patches where landscape structure has been characterized at one of 22 spatial scales ranging from 500 m to 20 km. Explanatory variables affecting occurrence included landscape variables (% forest cover, [% forest cover]^2, patch size and the interactions between forest cover variables and patch size; see Table 1) and the first two axes of a principal component analysis applied to tree abundance data (see Methods). Explanatory variables affecting detectability included Julian date, time of day, Beaufort wind speed and precipitation intensity. Models were fitted using PRESENCE (v. 2.2 <090306.1055>; Hines 2006) in order to correct for imperfect detectability. The level of overdispersion is given by $\hat{c}$.

Model 2006	AICc	delta i	ACIc weight	Model 2007	QAICc ($\hat{c}$ = 1.4)	delta i	QAICc weight
Intercept	**194.22**	**0.00**	**0.9998**	**Intercept**	**190.00**	**0.00**	**0.8860**
radius=10km	216.51	22.29	0.0000	radius=2km	198.66	8.66	0.0117
radius=9km	216.74	22.52	0.0000	radius=1km	199.21	9.21	0.0089
radius=12km	216.89	22.67	0.0000	radius=16km	199.42	9.43	0.0080
radius=11km	216.93	22.71	0.0000	radius=15km	199.53	9.53	0.0075
radius=18km	217.02	22.80	0.0000	radius=17km	199.60	9.60	0.0073
radius=13km	217.16	22.94	0.0000	radius=14km	199.74	9.75	0.0068
radius=14km	217.25	23.03	0.0000	radius=13km	199.88	9.88	0.0063
radius=15km	217.27	23.05	0.0000	radius=12km	199.94	9.95	0.0061
radius=16km	217.35	23.13	0.0000	radius=19km	199.99	10.00	0.0060
radius=8km	217.41	23.19	0.0000	radius=20km	200.14	10.14	0.0056
radius=500m	217.59	23.37	0.0000	radius=11km	200.34	10.35	0.0050
radius=17km	218.03	23.81	0.0000	radius=3km	200.50	10.50	0.0046
radius=2km	218.45	24.23	0.0000	radius=10km	200.64	10.64	0.0043
radius=7km	218.59	24.37	0.0000	radius=9km	201.02	11.03	0.0036
radius=750m	218.79	24.57	0.0000	radius=18km	201.14	11.15	0.0034
radius=19km	218.79	24.57	0.0000	radius=750m	201.26	11.27	0.0032
radius=20km	219.01	24.79	0.0000	radius=4km	201.35	11.35	0.0030
radius=6km	219.23	25.01	0.0000	radius=8km	201.38	11.38	0.0030
radius=5km	219.64	25.42	0.0000	radius=7km	201.69	11.69	0.0026
radius=3km	219.69	25.47	0.0000	radius=6km	201.70	11.70	0.0025
radius=1km	220.00	25.77	0.0000	radius=5km	201.71	11.72	0.0025
radius=4km	220.28	26.06	0.0000	radius=500m	202.03	12.03	0.0022

Contrary to our expectation, we found only weak evidence based on AIC_c that the occurrence of Yellow-bellied Sapsuckers influenced abundance of Ruby-throated Hummingbirds. Models suggesting an influence of sapsucker occurrence on the mean daily artificial nectar consumption, the relative total abundance or the relative adult male abundance, did so only after controlling for the effects of local and landscape variables (Table 5-7). No such evidence was found regarding relative adult female abundance (Table 8). Furthermore, multimodel inference did not reveal any influence of the occurrence of

Yellow-bellied Sapsuckers on the mean daily artificial nectar consumption or any of the relative abundance estimates (Table 5-8).

DIRECT EFFECTS OF LANDSCAPE STRUCTURE

Step 1: Identification of the Spatial Scale

Adult male Ruby-throated Hummingbirds responded most clearly to landscape structure in terms of abundance when forest cover and patch size were measured within 2 or 3 km from nectar feeders (Table 4). On the other hand, relative adult female abundance was most strongly related to landscape structure within radii of 4 or 5 km; the strongest relationship being at 5 km (Table 4). Regarding the relative total hummingbird abundance, which included adults and juveniles, the radii varied between 1 and 4 km; the lowest AIC_c was observed at 1 km (Table 4). Analogously, daily artificial nectar consumption was most strongly related to landscape structure within radii of 1, 4 and 5 km; the lowest AIC_c occurred at 4 km (Table 4). We used the spatial scale leading to the lowest AIC_c for each response variable in further analyses.

Table 4: Model selection used to identify the spatial scales at which Ruby-throated Hummingbirds (RTHU; *Archilochus colubris*) responded most strongly to landscape structure. Models contained the same explanatory variables (Table 1) with the exception that landscape variables have been measured at one of 20 spatial scales ranging from 1 to 20 km. Mean daily artificial nectar consumption was modelled using linear mixed-effect models and relative abundance with mixed-effect Poisson regressions (see Methods). *K* refers to the number of model parameters.

RTHU Consumption						RTHU Abundance					
Radius (m)	Deviance	K	AICc	delta i	AICc weight	Radius (m)	Deviance	K	AICc	delta i	AICc weight
4000	**437.42**	**19**	**475.62**	**0.00**	**0.39**	**1000**	**1049.96**	**20**	**1090.62**	**0.00**	**0.38**
5000	437.65	19	475.85	0.23	0.35	4000	1050.59	20	1091.25	0.63	0.28
1000	439.73	19	477.93	2.31	0.12	3000	1051.46	20	1092.13	1.50	0.18
6000	441.80	19	480.00	4.39	0.04	2000	1052.21	20	1092.87	2.25	0.12
2000	442.50	19	480.70	5.09	0.03	5000	1054.95	20	1095.62	5.00	0.03
3000	442.82	19	481.02	5.40	0.03	6000	1060.21	20	1100.88	10.26	0.00
7000	443.39	19	481.59	5.97	0.02	7000	1062.80	20	1103.47	12.85	0.00
8000	445.62	19	483.81	8.20	0.01	20000	1062.99	20	1103.66	13.03	0.00
9000	449.03	19	487.23	11.62	0.00	19000	1063.23	20	1103.90	13.27	0.00
10000	451.77	19	489.97	14.35	0.00	18000	1063.51	20	1104.17	13.55	0.00
11000	452.69	19	490.89	15.27	0.00	17000	1063.61	20	1104.27	13.65	0.00
12000	453.41	19	491.61	15.99	0.00	16000	1064.33	20	1105.00	14.38	0.00
13000	453.49	19	491.69	16.07	0.00	15000	1064.49	20	1105.15	14.53	0.00
17000	453.53	19	491.73	16.11	0.00	14000	1064.77	20	1105.44	14.81	0.00
14000	453.54	19	491.74	16.12	0.00	8000	1065.42	20	1106.09	15.46	0.00
18000	453.69	19	491.89	16.27	0.00	13000	1065.54	20	1106.21	15.58	0.00
15000	453.76	19	491.96	16.34	0.00	12000	1066.21	20	1106.87	16.25	0.00
16000	453.80	19	492.00	16.38	0.00	11000	1066.54	20	1107.21	16.59	0.00
19000	453.97	19	492.17	16.55	0.00	9000	1066.68	20	1107.35	16.72	0.00
20000	454.42	19	492.61	17.00	0.00	10000	1066.96	20	1107.63	17.00	0.00
intercept	778.87	4	786.88	311.26	0.00	intercept	1125.00	3	1131.02	40.40	0.00
RTHU Male abundance						**RTHU Female abundance**					
Radius (m)	**Deviance**	**K**	**AICc**	**delta i**	**AICc weight**	**Radius (m)**	**Deviance**	**K**	**AICc**	**delta i**	**AICc weight**
2000	**822.25**	**20**	**862.92**	**0.00**	**0.45**	**5000**	**891.41**	**20**	**932.07**	**0.00**	**0.59**
3000	822.26	20	862.92	0.01	0.45	4000	892.33	20	933.00	0.92	0.37
4000	826.30	20	866.97	4.06	0.06	3000	898.68	20	939.35	7.28	0.02
1000	828.15	20	868.82	5.90	0.02	6000	899.72	20	940.38	8.31	0.01
5000	831.55	20	872.22	9.30	0.00	2000	900.00	20	940.67	8.59	0.01
6000	833.53	20	874.19	11.28	0.00	intercept	937.95	3	943.97	11.89	0.00
10000	834.80	20	875.47	12.55	0.00	1000	903.77	20	944.44	12.37	0.00
11000	834.80	20	875.47	12.55	0.00	7000	903.89	20	944.56	12.48	0.00
7000	834.82	20	875.48	12.57	0.00	8000	908.75	20	949.42	17.34	0.00
15000	834.94	20	875.61	12.70	0.00	9000	912.06	20	952.73	20.65	0.00
14000	835.09	20	875.76	12.84	0.00	10000	913.99	20	954.66	22.59	0.00
9000	835.09	20	875.76	12.84	0.00	11000	914.56	20	955.23	23.16	0.00
12000	835.22	20	875.89	12.97	0.00	13000	914.76	20	955.43	23.35	0.00
16000	835.26	20	875.93	13.01	0.00	14000	914.91	20	955.58	23.51	0.00
13000	835.28	20	875.95	13.03	0.00	12000	914.93	20	955.59	23.52	0.00
17000	835.29	20	875.95	13.04	0.00	15000	915.35	20	956.02	23.94	0.00
18000	835.43	20	876.10	13.18	0.00	16000	915.56	20	956.23	24.16	0.00
19000	835.48	20	876.15	13.24	0.00	17000	915.61	20	956.28	24.20	0.00
8000	835.64	20	876.30	13.39	0.00	20000	915.72	20	956.39	24.32	0.00
20000	835.80	20	876.47	13.55	0.00	18000	915.85	20	956.52	24.45	0.00
intercept	919.98	3	926.00	63.09	0.00	19000	915.87	20	956.53	24.46	0.00

Step 2: Modelling hummingbird abundance and nectar consumption

Daily artificial nectar consumption

None of the mean daily artificial nectar consumption models clearly stood out as the best one based on AICc (Table 5), but the two that performed poorly (#5 and 7) did not include landscape variables. The strongest model (# 6, ω_i= 0.31) only included variables referring to landscape structure (Table 5).

The influence of the period at which nectar feeders were installed on the mean daily nectar consumption depended on year of study (Table 5). In 2006, nectar consumption averaged 17.16 $g\cdot day^{-1}$ at feeders installed in April and 8.63 $g\cdot day^{-1}$ at feeders installed in June. In 2007, nectar consumption was higher at feeders set up in June (15.53 $g\cdot day^{-1}$), which were the same feeders as those installed in April 2006, compared to feeders installed in April (12.47 $g\cdot day^{-1}$). We also observed that nectar consumption was 2.84 $g\cdot day^{-1}$ higher on average at feeders located at the edge of forest patches compared to feeders 40 m inside forest patches (Table 5). Furthermore, mean daily nectar consumption increased non-linearly with the number of hummingbirds detected at the feeder (Table 5). For instance, it varies from 11.1 to 52.5 $g\cdot day^{-1}$ where a difference between 0 and 1 detected hummingbird translated into an increase of 7.75 $g\cdot day^{-1}$, while passing from 1 to 2 and from 2 to 3 detected hummingbirds led to increases of 12.73 $g\cdot day^{-1}$ and 20.90 $g\cdot day^{-1}$, respectively.

Forest composition and structure did not influence mean daily nectar consumption (Table 5) which was, however, strongly influenced by landscape structure within 4 km of feeders (Table 5). In small forest patches (< 10 ha), mean daily nectar consumption increased with forest cover, peaked when it reached 55% to 60%, and decreased afterwards (Fig. 8). In forest patches between 10 and 15 ha, nectar consumption increased relatively linearly with the surrounding forest cover. Yet, in forest patches ≥ 20 ha, nectar consumption followed a pattern opposite to that of patch sizes < 10 ha. Nectar consumption decreased with forest cover up to a minimum between 50% and 55% cover after which it increased until the landscape was fully covered by forest. Nectar consumption thus increased with patch size in poorly or highly forested landscapes but the converse occurred in mildly forested landscapes (Fig. 8).

Table 5: Upper part: Model selection regarding mean daily artificial nectar consumption by Ruby-throated Hummingbirds (*Archilocus colubris*). Nectar consumption was modelled using linear mixed-effect models. Feeders were nested within sites and site ID treated as a random factor. See Table 1 for variable definition and Table 2 for model composition. Landscape variables were measured within a 4-km radius around nectar feeders. *K* refers to the number of model parameters. Lower part: Multimodel inference resulting from the above model selection. Variables in bold have 95% confidence intervals of regression slopes that exclude zero.

Models in competition by Akaike's information criterion for LOG$_{10}$(NECTAR CONSUMPTION) (4km)

Model	Deviance	K	AICc	Δ AICc	AICc weight (ωi)
6	**447.31**	**13**	**473.40**	**0.00**	**0.31**
4	**441.60**	**16**	**473.74**	**0.34**	**0.26**
3	**438.09**	**18**	**474.27**	**0.86**	**0.20**
2	**441.27**	**17**	**475.43**	**2.03**	**0.11**
1	**437.42**	**19**	**475.62**	**2.21**	**0.10**
5	458.89	11	480.96	7.55	0.01
7	465.81	11	487.88	14.48	0.00

Multimodel Inference for LOG$_{10}$(NECTAR CONSUMPTION) (4km)

Explanatory variables	MMI_coefficient	uncond_SE	lower_CI	upper_CI
Intercept	**1.3456**	**0.0763**	**1.1960**	**1.4951**
Year	**-0.1297**	**0.0601**	**-0.2476**	**-0.0118**
Feeder installation date	**-0.2755**	**0.0604**	**-0.3939**	**-0.1571**
Mean of individuals	**0.2154**	**0.0145**	**0.1869**	**0.2438**
Feeder location	**-0.0740**	**0.0365**	**-0.1456**	**-0.0024**
log10(patch area_ha)	**-0.1417**	**0.0504**	**-0.2405**	**-0.0430**
% Forest cover	0.4884	0.3986	-0.2930	1.2697
(% Forest cover)^2	**-6.5318**	**2.3195**	**-11.0780**	**-1.9855**
structure_axis 1	-0.0279	0.1767	-0.3743	0.3185
structure_axis 2	0.1995	0.2781	-0.3457	0.7446
Flowers_axis 1	0.3305	0.1995	-0.0606	0.7215
Flowers_axis 2	0.0896	0.1849	-0.2729	0.4521
Presence of YBSA	-0.0300	0.0327	-0.0942	0.0341
Year: Feeder installation date	**0.3644**	**0.1165**	**0.1362**	**0.5927**
log10(patch area_ha):% Forest cover	-0.1631	0.3460	-0.8414	0.5151
log10(patch area_ha):(% Forest cover)^2	**6.2933**	**2.3217**	**1.7427**	**10.8438**

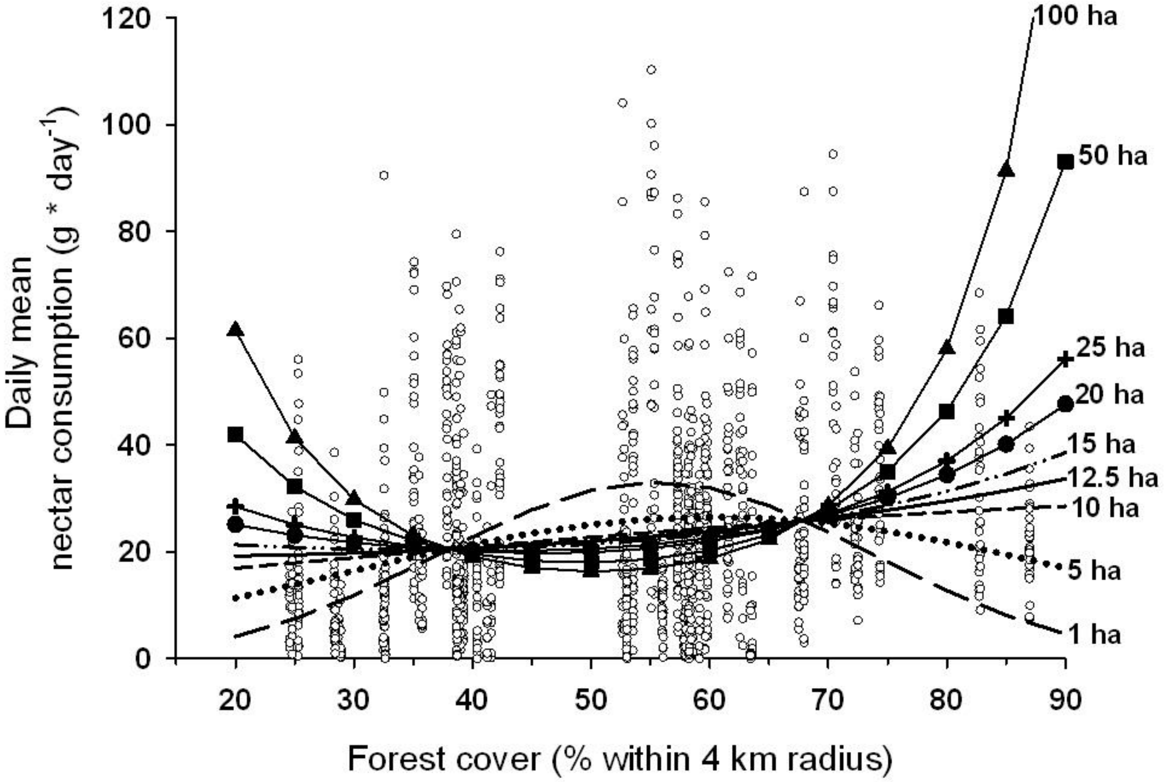

Fig. 8: Influence of landscape variables (forest cover and forest patch size) on the mean daily artificial nectar consumption by Ruby-throated Hummingbirds (*Archilocus colubris*). Effects were based on multimodel inference (Table 5). Categorical variables were fixed at 0 and thereby correspond to year 2006, feeder set up in April, no precipitation, feeder located at forest edge and no occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Quantitative variables (temperature and mean number of individuals detected) were fixed at their mean (i.e., 21.8°C and 0.82 ind., respectively).

Relative total abundance

The four models that performed best according to AIC$_c$ (# 3, 4, 2 and 1) suggest that Ruby-throated Hummingbird relative total abundance was influenced by both local and landscape variables (Table 6). Relative total abundance showed the same pattern as mean daily artificial nectar consumption with respect to the interaction between year and feeder installation date (Table 6). More individuals were detected on average at feeders installed in April 2006 (1.24 ind.) than in June 2006 (0.65 ind.). Conversely, total abundance was higher at feeders set up in June 2007 (1.14 ind.) than in April 2007 (0.94 ind.). Hence, feeders which were set up before the spring arrival of hummingbirds in 2006 attracted the highest number of hummingbirds in both years even though they were installed after the birds had established their territories in 2007. Whereas the amount of precipitation did not influence total abundance, a temperature increase of 1˚C resulted in a 1.76% decrease in the number of detected individuals at feeders (Table 6). Such a decrease corresponded to a differential of 0.7 individual across the temperature range (i.e., from 5˚C to 32˚C).

Local variables also influenced the relative total abundance of Ruby-throated Hummingbirds (Table 6). Relative total abundance was lower by 0.80 individual at feeders located 40 m inside forest patches compared to feeders set up on the forest edge. Across-site variations in forest composition and structure did not influence the number of detected hummingbirds, though. Landscape structure effects occurred only through a quadratic effect of forest cover measured within a 1-km radius and whereby relative total abundance peaked at intermediate levels of forest cover (Table 6). For instance, when setting forest patch size at its mean value (i.e., 72 ha), total abundance increased from 0.61 individual to 1.29 individuals between 5% and 50% forest cover before decreasing down to 0.99 individual at 75% forest cover (Fig. 9).

Table 6: Upper part: Model selection regarding the relative total abundance of Ruby-throated Hummingbirds (*Archilocus colubris*). Relative total abundance consisted in the number of juveniles and adults detected within 10 m from a nectar feeder during a 10-min period. Total abundance was modelled using mixed-effect Poisson regressions. Feeders were nested within sites and site ID treated as a random factor. See Table 1 for variable definition and Table 2 for model composition. Landscape variables were measured within a 1-km radius around nectar feeders. *K* refers to the number of model parameters. Lower part: Multimodel inference resulting from the above model selection. Bold variables have 95% confidence intervals of regression slopes that exclude zero.

Models in competition by Akaike's information criterion for RELATIVE ABUNDANCE (1km)

Model	Deviance	K	AICc	Δ AICc	AICc weight (ωi)
3	**1050.20**	**19**	**1088.80**	**0.00**	**0.32**
4	**1054.58**	**17**	**1089.07**	**0.27**	**0.28**
2	**1053.02**	**18**	**1089.56**	**0.76**	**0.22**
1	**1049.96**	**20**	**1090.62**	**1.82**	**0.13**
6	1064.02	14	1092.36	3.56	0.05
5	1078.52	12	1102.77	13.97	0.00
7	1086.59	12	1110.83	22.04	0.00

Multimodel Inference for RELATIVE ABUNDANCE (1km)

Explanatory variables	MMI_coefficient	uncond_SE	lower_CI	upper_CI
Intercept	0.4129	0.2236	-0.0253	0.8512
Year	**-0.2753**	**0.1226**	**-0.5157**	**-0.0349**
Feeder installation date	**-0.6537**	**0.1292**	**-0.9068**	**-0.4005**
temp	**-0.0178**	**0.0067**	**-0.0309**	**-0.0047**
Light rain	0.1468	0.1072	-0.0633	0.3569
Heavy rain	0.4172	0.3024	-0.1756	1.0100
Feeder location	**-0.1383**	**0.0624**	**-0.2606**	**-0.0161**
log10(patch area_ha)	0.1033	0.1138	-0.1197	0.3263
% Forest cover	**1.9392**	**0.5213**	**0.9175**	**2.9609**
(% Forest cover)^2	3.7849	3.0965	-2.2843	9.8541
structure_axis 1	0.5543	0.3070	-0.0474	1.1561
structure_axis 2	0.4631	0.4665	-0.4513	1.3774
Flowers_axis 1	-0.0739	0.3418	-0.7438	0.5959
Flowers_axis 2	**-0.6673**	**0.3241**	**-1.3026**	**-0.0321**
Presence of YBSA	-0.1011	0.1103	-0.3173	0.1152
Year: Feeder installation date	**0.8388**	**0.2205**	**0.4066**	**1.2710**
log10(patch area_ha):% Forest cover	-0.6132	0.5367	-1.6652	0.4388
log10(patch area_ha):(% Forest cover)^2	-4.1343	2.1455	-8.3395	0.0709

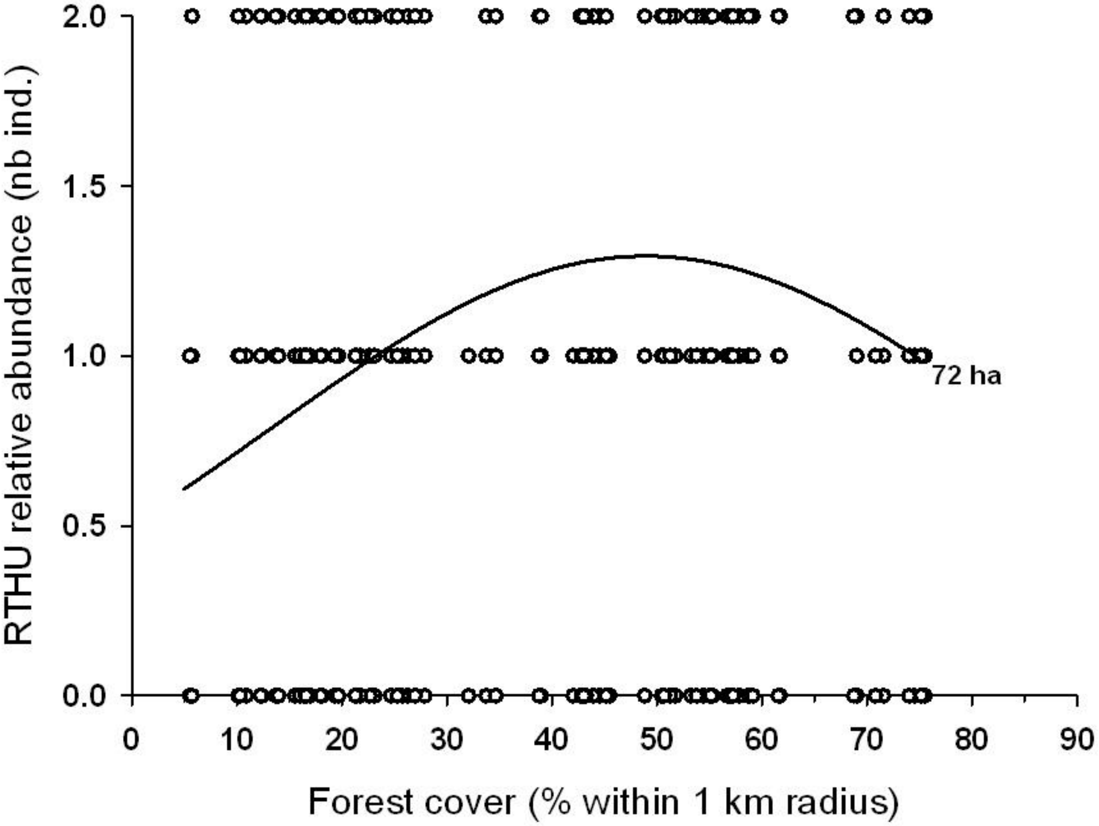

Fig. 9: Influence of forest cover on the relative total abundance of Ruby-throated Hummingbirds (*Archilocus colubris*). Effects were based on multimodel inference (Table 6). Categorical variables were fixed at 0 and thereby correspond to year 2006, feeder set up in April, no precipitation, feeder located at the forest edge and no occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Forest patch size and temperature were fixed at their mean (i.e., 72 ha and 21.8°C, respectively).

Relative abundance of adult males

We found evidence based on AIC_c that both local and landscape variables, in addition to variables associated to food resource availability, had to be taken into account when modelling the relative abundance of adult male Ruby-throated Hummingbirds (Table 7). Relative adult male abundance was on average higher at feeders installed in April 2006 and June 2007 (0.48 and 0.34 ind.) compared to those set up in June 2006 and April 2007 (0.15 and 0.32 ind.; Table 7), respectively. As for the mean daily artificial nectar consumption and relative total abundance, it was the same feeders that showed the greater relative abundances in 2006 and 2007. Precipitation did not influence the number of adult males detected at feeders (Table 7). Males were, however, slightly more abundant at low temperatures (a differential of 0.3 individuals across temperatures ranging from 5 to 32˚C; Table 7).

Local variables affected relative adult male abundance through both feeder location and forest composition and structure (Table 7). Feeders 40 m inside forest patches showed a decrease of 0.10 individual on average compared to edge feeders. Relative adult male abundance also increased by 0.40 individuals along the gradient associated to the first PCoA axis of the forest composition and structure index (Table 7). Regarding landscape variables, the influence of forest cover on relative adult male abundance varied according to forest patch size (Table 7). Depending on forest patch size, relative adult male abundance reached its lowest point between ca. 35% to 50% forest cover within a 2-km radius; the location of the lowest point increased with forest patch size (Fig. 10). Furthermore, relative adult male abundance increased with forest patch size at low forest cover but decreased in forest-dominated landscapes (Fig. 10).

Table 7: Upper part: Model selection regarding the relative abundance of adult male Ruby-throated Hummingbirds (*Archilocus colubris*). Relative abundance consisted in the number of adult males detected within 10 m from a nectar feeder during a 10-min period. Adult male abundance was modelled using mixed-effect Poisson regressions. Feeders were nested within sites and site ID treated as a random factor. See Table 1 for variable definition and Table 2 for model composition. Landscape variables were measured within a 1-km radius around nectar feeders. *K* refers to the number of model parameters. Lower part: Multimodel inference resulting from the above model selection. Bold variables have 95% confidence intervals of regression slopes that exclude zero.

Models in competition by Akaike's information criterion for MALES (2km)

Model	Deviance	K	AICc	Δ AICc	AICc weight (ωi)
3	**822.25**	**19**	**860.85**	**0.00**	**0.47**
4	**827.61**	**17**	**862.10**	**1.25**	**0.25**
1	**822.25**	**20**	**862.92**	**2.06**	**0.17**
2	**827.12**	**18**	**863.66**	**2.81**	**0.12**
5	847.42	12	871.67	10.82	0.00
6	847.86	14	876.19	15.34	0.00
7	864.00	12	888.24	27.39	0.00

Multimodel Inference for MALES (2km)

Explanatory variables	MMI_coefficient	uncond_SE	lower_CI	upper_CI
Intercept	-0.3346	0.3257	-0.9729	0.3037
Year	**-0.3984**	**0.1721**	**-0.7357**	**-0.0611**
Feeder installation date	**-1.1809**	**0.1948**	**-1.5628**	**-0.7990**
temp	**-0.0227**	**0.0097**	**-0.0418**	**-0.0036**
Light rain	0.1887	0.1500	-0.1052	0.4826
Heavy rain	-0.5907	0.7266	-2.0148	0.8334
Feeder location	**-0.3157**	**0.0932**	**-0.4984**	**-0.1331**
log10(patch area_ha)	0.0495	0.2108	-0.3637	0.4628
% Forest cover	**2.6559**	**0.7277**	**1.2295**	**4.0822**
(% Forest cover)^2	8.5846	5.2864	-1.7769	18.9460
structure_axis 1	**1.4741**	**0.4692**	**0.5545**	**2.3937**
structure_axis 2	0.3396	0.6661	-0.9659	1.6451
Flowers_axis 1	0.1501	0.5076	-0.8448	1.1449
Flowers_axis 2	**-1.0949**	**0.4575**	**-1.9917**	**-0.1982**
Presence of YBSA	-0.0451	0.1669	-0.3723	0.2821
Year: Feeder installation date	**1.2362**	**0.3208**	**0.6073**	**1.8650**
log10(patch area_ha):% Forest cover	**-1.6495**	**0.6385**	**-2.9009**	**-0.3981**
log10(patch area_ha):(% Forest cover)^2	-1.3795	5.2673	-11.7035	8.9445

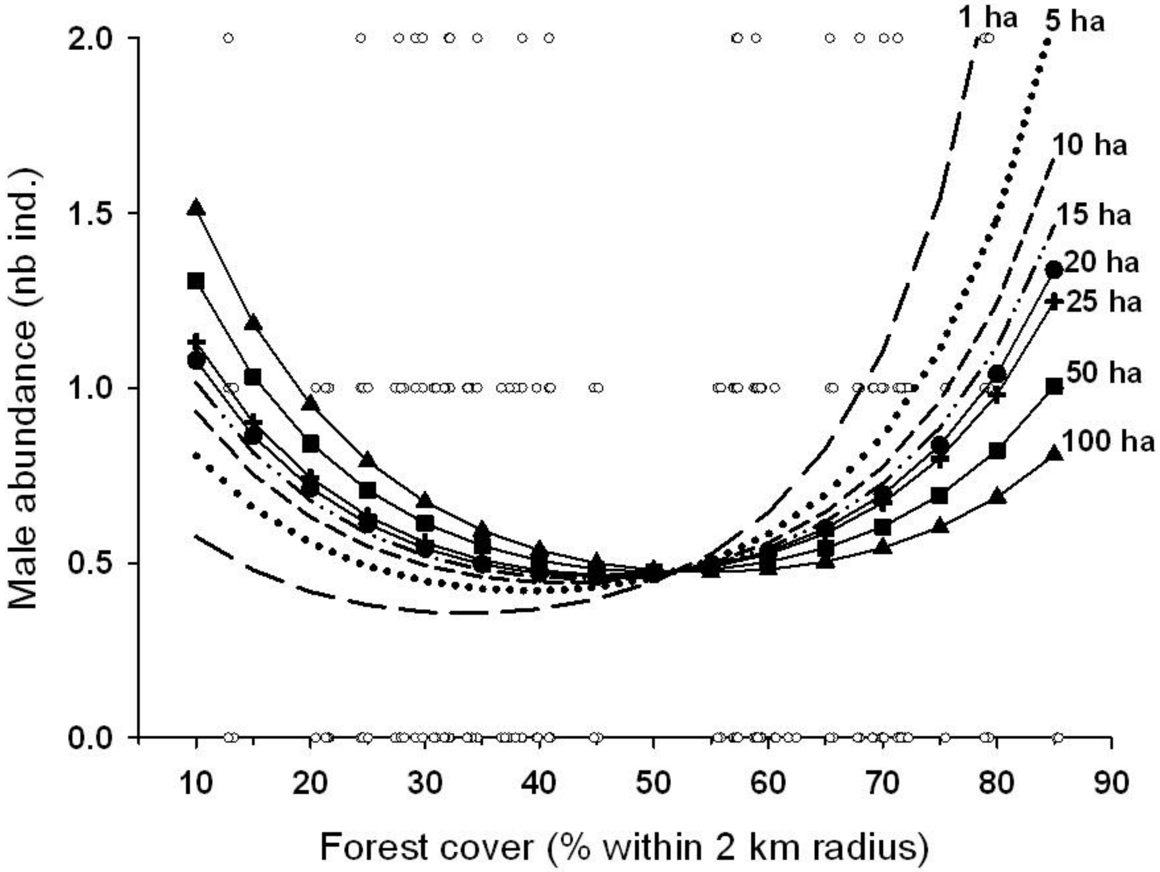

Fig. 10: Influence of landscape variables (forest cover and forest patch size) on the relative abundance of adult male Ruby-throated Hummingbirds (*Archilocus colubris*). Effects were based on multimodel inference (Table 7). Categorical variables were fixed at 0 and thereby correspond to year 2006, feeder set up in April, no precipitation, feeder located at the forest edge and no occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Temperature was fixed at its mean (21.8°C).

Relative abundance of adult females

In opposition to the three previous response variables, model selection based on AIC_c identified a single model (#6) that clearly outclassed others (Table 8). This model contained only landscape variables in addition to the covariates found in all models (i.e., filter variables, Table 1). Similarly to the three previously-examined response variables, relative adult female abundance was affected by an interaction between year and feeder installation date (Table 8). Adult female abundance was on average higher at feeders installed in April 2006 (0.26 ind.) compared to feeders set up in June 2006 (0.22 ind.). Conversely, mean adult female abundance was higher at feeders set up in June 2007 (0.29 ind.) than at those installed in April 2007 (0.19 ind.). Nevertheless, the highest abundance in both 2006 and 2007 were obtained at the same group of feeders. Although temperature did not affect the number of adult females detected, relative adult female abundance was on average higher under heavy rain by 0.36 individual compared to days with no or light rain (Table 8).

Neither the location of feeders with respect to the forest edge nor the composition and structure of forest habitat affected relative adult female abundance which was, however, influenced by landscape structure within a 5-km radius (Table 8). Forest cover effects on relative adult female abundance varied according to forest patch size (Table 8, Fig. 11) in the same way as for artificial nectar consumption (Fig. 8). In forest patches < 10 ha, relative adult female abundance peaked between 55% and 65% forest cover but decreased at an increasing rate if either lower or higher. In forest patches between 10 and 20 ha, relative adult female abundance increased more or less linearly with forest cover. In forest patches ≥ 20 ha, the number of adult females detected decreased at a decelerating rate with forest cover, reached a minimum between 45% and 50% forest cover, and increased at an increasing rate as forest cover increased further. Moreover, relative adult female abundance increased with forest patch size when forest cover varied between 40% and 65% but increased otherwise.

Table 8: Upper part: Model selection regarding the relative abundance of adult female Ruby-throated Hummingbirds (*Archilocus colubris*). Relative abundance consisted in the number of adult females detected within 10 m from a nectar feeder during a 10-min period. Adult female abundance was modelled using mixed-effect Poisson regressions. Feeders were nested within sites and site ID treated as a random factor. See Table 1 for variable definition and Table 2 for model composition. Landscape variables were measured within a 1-km radius around nectar feeders. *K* refers to the number of model parameters. Lower part: Multimodel inference resulting from the above model selection. Bold variables have 95% confidence intervals of regression slopes that exclude zero.

Models in competition by Akaike's information criterion for FEMALES (5km)

Model	Deviance	K	AICc	Δ AICc	AICc weight (ωi)
6	**897.12**	**14**	**925.45**	**0.00**	**0.76**
4	895.23	17	929.71	4.26	0.09
2	893.85	18	930.39	4.94	0.07
3	892.17	19	930.78	5.32	0.05
1	891.41	20	932.07	6.62	0.03
5	922.97	12	947.22	21.76	0.00
7	923.96	12	948.20	22.75	0.00

Multimodel Inference for FEMALES (5km)

Explanatory variables	MMI_coefficient	uncond_SE	lower_CI	upper_CI
Intercept	-0.1969	0.2857	-0.7570	0.3631
Year	-0.3101	0.1685	-0.6404	0.0201
Feeder installation date	-0.1738	0.1640	-0.4954	0.1477
temp	-0.0200	0.0107	-0.0409	0.0009
Light rain	0.2129	0.1715	-0.1232	0.5491
Heavy rain	**0.8704**	**0.3754**	**0.1346**	**1.6061**
Feeder location	0.0281	0.0995	-0.1669	0.2231
log10(patch area_ha)	**-0.3890**	**0.0990**	**-0.5830**	**-0.1950**
% Forest cover	1.0373	1.0889	-1.0969	3.1716
(% Forest cover)^2	**-27.7544**	**6.8468**	**-41.1740**	**-14.3347**
structure_axis 1	-0.4835	0.4217	-1.3101	0.3431
structure_axis 2	0.2928	0.6499	-0.9810	1.5666
Flowers_axis 1	0.5876	0.4577	-0.3095	1.4847
Flowers_axis 2	-0.3770	0.3921	-1.1455	0.3914
Presence of YBSA	-0.1466	0.1397	-0.4205	0.1273
Year: Feeder installation date	**0.6049**	**0.2645**	**0.0866**	**1.1233**
log10(patch area_ha):% Forest cover	0.3324	0.9504	-1.5304	2.1952
log10(patch area_ha):(% Forest cover)^2	**22.6737**	**5.8587**	**11.1906**	**34.1569**

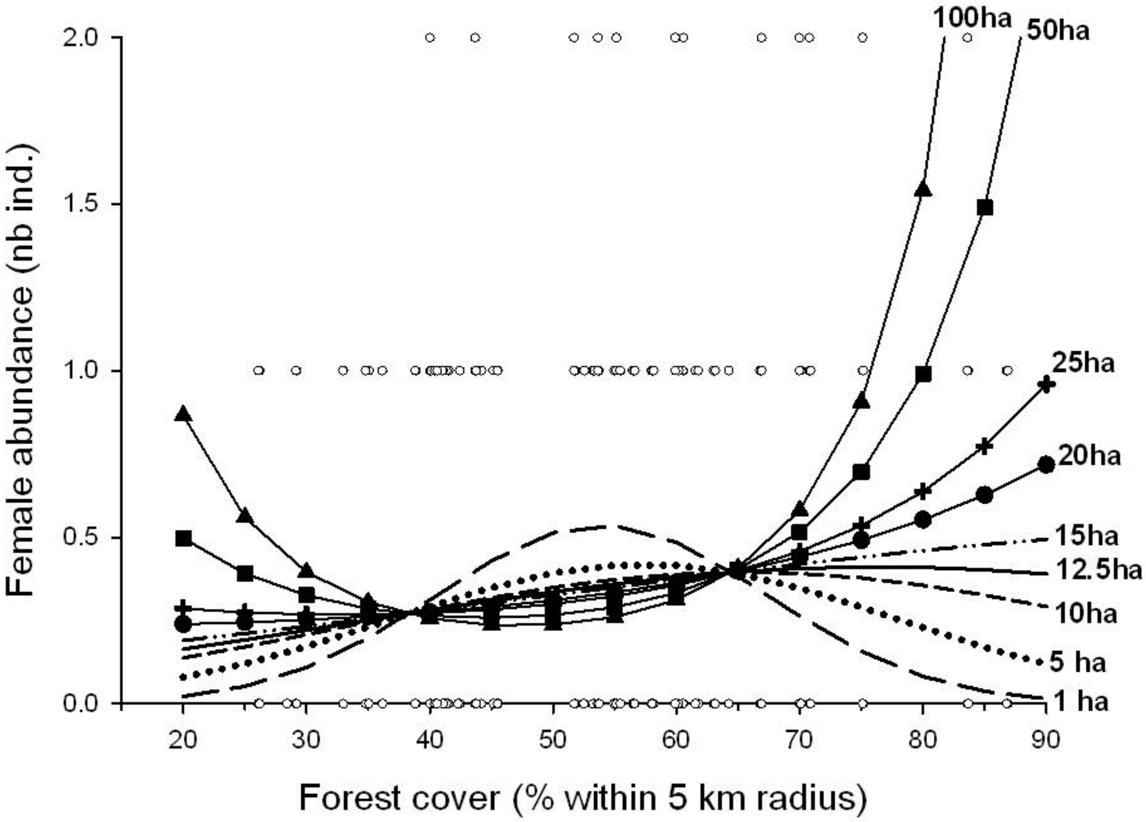

Fig. 11: Influence of landscape variables (forest cover and forest patch size) on the relative abundance of adult female Ruby-throated Hummingbirds (*Archilocus colubris*). Effects were based on multimodel inference (Table 8). Categorical variables were fixed at 0 and thereby correspond to year 2006, feeder set up in April, no precipitation, feeder located at the forest edge and no occurrence of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Temperature was fixed at its mean (21.8^{o}C).

DISCUSSION

The goal of this study was to quantify the effects of landscape structure on the abundance of Ruby-throated Hummingbirds in forest patches while accounting for its indirect effects through open flower community structure and the occurrence of Yellow-bellied Sapsuckers, a potential commensal of hummingbirds (Fig. 1B). We found evidence that landscape structure, specifically the amount of forest cover and the size of forest patches, directly affected our relative estimate of total hummingbird abundance, as well as that of adult male and adult female abundance. Local effects related to landscape structure also affected the abundance of hummingbirds as more individuals were usually detected at the edge of forest patches compared to 40 m within patches. Mean daily artificial nectar consumption generally support these results. Moreover, we found evidence that landscape structure indirectly affected the abundance of Ruby-throated Hummingbirds through variation in open flower community structure. Indeed, landscape structure affected the structure of open flower communities, which in turn, influenced both the relative total abundance of Ruby-throated Hummingbirds and that of adult males. Such an indirect effect of landscape structure was, however, not found with Yellow-bellied Sapsucker. Landscape structure did not influence the occurrence of this woodpecker and we only found some weak evidence that its occurrence affected the abundance or artificial nectar consumption of Ruby-throated Hummingbirds. Our study nevertheless emphasizes the importance of studying the interaction between ecological processes and landscape patterns as the former will be instrumental in determining the direct and indirect influences that landscape structure may have on species abundance patterns.

HUMMINGBIRDS CAPTURE-MARK-RECAPTURE

Population closure is defined by a demographic and a geographic component (Lancia 1996). The first refers to the absence of natality or mortality during a given period, and the second implies neither immigration nor emigration during the same period. Given that Ruby-throated Hummingbirds are assumed to strongly defend territories < 1 ha during the breeding period (Robinson et al. 1996), we expected high recapture rates suggesting a closed population, at least before the appearance of fledged young. The very low rate of resights and recaptures of marked individuals (7%) in spite of a high capture effort suggests, however, that the local populations of Ruby-throated Hummingbirds we studied were open or very abundant. We are aware of no other field-intensive assessment of abundance and population closeness of breeding Ruby-throated Hummingbirds under natural conditions (as opposed to gardens or backyards). Nevertheless, our CMR results question the idea that breeding Ruby-throated Hummingbirds defend small, stable territories (Robinson et al. 1996). Our results thus lend support to the conclusions of Rousseu (2010) and Charette (2011) who showed that Ruby-throated Hummingbirds vary strongly in their resource defence strategies and in the spatial scale and stability of their foraging movements, respectively.

INDIRECT EFFECTS

LANDSCAPE → OPEN FLOWER COMMUNITY → RUBY-THROATED HUMMINGBIRDS

Variations in the amount and spatial distribution of forest and agricultural habitats have been found to affect the structure of plant communities (Gehlhausen et al. 2000, Murphy and Lovett-Doust 2004). Our RDA results also showed such landscape effects on open flower community structure when forest cover and forest patch size were measured within a 5-km radius. In turn, we found that relative total abundance and adult male abundance of Ruby-throated Hummingbirds were affected by the open flower community index while controlling for the influence of landscape variables, thereby suggesting that landscape structure could indirectly affect hummingbird abundance patterns. However, no influence of open flower community structure was found with respect to relative adult female abundance or mean daily artificial nectar consumption. The fact that males seemed to be more influenced by open flower community structure than females may be linked to the fact that males of this polygynous (or polygynandrous) species are thought to defend nectar-rich territories to attract females and mate with them as males do not built nests or care for eggs or young (Robinson et al. 1996). It remains that in absence of studies on the use and selection of natural flowering plants by free-ranging Ruby-throated Hummingbirds or their close relatives, and this either for feeding upon nectar or insects, it is very difficult to interpret the relationship between hummingbird abundance or artificial nectar consumption and our open flower community index. Although we are aware of the difficulties involved in tracking wild hummingbirds, it is crucial that future studies address the determinants of natural flower use and selection by wild hummingbirds in a variety of habitats.

LANDSCAPE → YELLOW-BELLIED SAPSUCKER OCCURRENCE → RUBY-THROATED HUMMINGBIRDS

Although several studies have found that the occurrence and abundance of Yellow-bellied Sapsuckers are negatively affected by forest loss and fragmentation in agricultural landscapes (Trzcinsky et al. 1999, Villard et al. 1999, Hobson and Bayne 2000), we failed to find any indication that the amount of forest cover or forest patch size influenced the occurrence of this woodpecker within a wide range of spatial scales (0.5-20 km). This absence of relationship between the occurrence of Yellow-bellied Sapsuckers and landscape structure is surprising given that we sampled a wide range of forest patch sizes (0.5 to > 100 ha) in landscapes that varied strongly in forest cover (5-75%). On the other hand, we sampled forest patches whose habitat characteristics were optimal for Yellow-bellied Sapsuckers (Walter et al. 2002) in addition to being relatively similar in terms of forest composition and structure. Possibly, high habitat quality overruled the influence of landscape structure on the occurrence of Yellow-bellied Sapsuckers (see Mortelliti et al. 2010 and references therein). Modelling density instead of occurrence would likely not have led to a different interpretation as we rarely detected more than one individual of this highly territorial species (Walter et al. 2002) on a given visit.

We expected that the abundance of Ruby-throated Hummingbirds would be higher in sites occupied by Yellow-bellied Sapsuckers because this species may act as a commensal for hummingbirds by providing alternative sources of sap and insects (Freer et Murray 1935; Kilham 1953; Southwick et Southwick 1980; Miller et Nero 1983; Kattan et Murcia 1985). Yet, we did not find any strong evidence for such commensalism after controlling for the influence of landscape structure. Models of relative total abundance and adult male abundance that included the presence of sapsuckers along with landscape variables performed better according to AIC_c than those that did not, but multimodel inference failed to produce estimates with narrow confidence intervals or intervals that excluded zero. This may be due to the fact that Yellow-bellied Sapsuckers occupied a large portion of forest patches (i.e., 67% ± 8% (SE) and 64% ± 8% of sites in 2006 and 2007, respectively), leaving little room to detect an effect of sapsucker occurrence. Moreover, given that our results suggest that the abundance patterns of Ruby-throated Hummingbirds vary according to landscape structure at spatial scales ranging from 1 to 5 km, it may be important to assess the density of Yellow-bellied Sapsuckers at such scales rather than simply assess their occupancy at a local scale as we did. This would also be supported by the fact that some Ruby-throated Hummingbirds have recently been found to exploit food sources more than 1 km apart on a given day during the breeding season (Charette 2011).

Overall, we cannot conclude that landscape structure may indirectly affect the abundance of Ruby-throated Hummingbirds through the occurrence of Yellow-bellied Sapsuckers. Such an indirect effect of landscape structure may nevertheless be more easily detected at the northern fringe of the Ruby-throated Hummingbird's distribution range. Sap wells drilled by sapsuckers are indeed more likely to provide key alternative food sources under harsh environmental conditions, especially in early spring (Miller and Nero 1983).

DIRECT EFFECTS OF LANDSCAPE STRUCTURE

1) Daily mean artificial nectar consumption and Ruby-throated Hummingbirds total abundance

LOCAL VARIABLES

Habitat use and selection can be either assessed through species abundance or resource use in different habitats (MacKenzie 2006; MacKenzie et al. 2006). In our study, we quantified both options. First, we modelled the relative abundance of Ruby-throated Hummingbirds seen within 10 m of nectar feeders. Second, we modelled the mean daily consumption of artificial nectar at each feeder as a proxy of habitat use between each visit to a site. Variation in artificial nectar consumption can nevertheless originate from two different components: 1) the number of individuals using a feeder, and 2) the amount of nectar consumed by a given individual.

We partly controlled the effect of the number of individuals using a feeder by including the mean number detected in the previous and the current week when modelling the mean daily artificial nectar consumption. Nevertheless, we obtained a non-linear increase of nectar consumption with the two-week mean abundance of hummingbirds. Consumption values were a little higher than the individual nectar consumption reported in the literature which usually varies maximally between 5-6 g (Robinson et al. 1996). These results suggest that relative total abundance under-estimated the real abundance of Ruby-throated Hummingbirds within our forest patches. Such an underestimation agrees with our CMR results that suggest open or very abundant local populations. Another reason to think of an underestimation is that other Ruby-throated Hummingbird studies showed that females visit feeders less frequently than males, but spend as much time at feeders as males (Rousseu 2010, Charette 2011). Besides, despite the absence of perches on feeders, we cannot entirely exclude the possibility that other species used feeders. These potentially include the Baltimore Oriole (*Icterus galbula*), woodpeckers (*Picoides pubescens*, *P. villosus*, *Sphyrapicus varius*) or small forest songbirds (e.g., *Poecile atricapillus*) interested by the nectar or insects such as ants.

Mean daily artificial nectar consumption at feeders was not influenced by the forest composition and structure index nor the open flower community index. This suggests that variation in habitat did not strongly influence the consumption of artificial nectar by individual Ruby-throated Hummingbirds.

Negative effects of feeder location within forest patches

Models show that relative total abundance as well as mean daily artificial nectar consumption was lower at feeders located within forest patches. When controlling for all other variables, a decrease of 2.84g of nectar consumption was observed for core feeders compared to edge feeder. The same effect can be observed for the relative total abundance with a diminution of 0.8 individual at core feeders compared to edge feeders. These results are in accordance with our expectation that Ruby-throated Hummingbird are an edge (Miller and Miller 1971; Freemark and Collins 1992) or early-successional forest species (Imbeau et al. 2003), suggesting that this species is not associated to high, closed canopy forest. Edge effects often increase biodiversity at the boundaries of a forest patch (Fahrig 2003). An increase that could lead to more nectar-producing flowers along edges than in the core area of forest patches. Edge habitats could therefore be more suitable than pure forested ones for Ruby-throated Hummingbirds.

LANDSCAPE VARIABLES

The unimodal effect of forest cover on forest patch use measured via the mean daily artificial nectar consumption differed according to forest patch size (Fig.8). This suggests that these patches may not be considered as preferred habitat. Nevertheless, because this relationship was found in poorly forested landscapes (≤ 40% forest cover), these large patches of continuous forest (≥ 20 ha) have a greater nectar consumption than smaller forest patches probably because they reflect the only available habitat. On the other hand, the effect of forest patch size was weaker in landscapes with very low forest cover because almost all forest patches would be used since preferred habitat is rare.

When forest cover was intermediate, the daily mean nectar consumption was higher in small forest patches. These results may be associated to an “edge effect”. In fact, the smallest patches may be characterized by vegetation associated to deep light penetration. Indeed, vegetation composition of sites where a high amount of light reaches the ground is distinguished by important flowers availability and dense shrub layers offering a prime feeding habitat. Thus, although small, these forest patches were also surrounded by relatively large amount of contiguous forest cover. In highly forested landscapes (≥ 70% forest cover), mean daily artificial nectar consumption increased in large forest patches while it decreased in small ones. This may reflect the non suitability of such landscapes as open areas with high flower availability are too scarce. These results suggest that most used habitats are small patches from 1 ha up to 12.5 ha within extensive agricultural landscape were forest cover is between 40 and 65%.

Contrary to mean daily artificial nectar consumption, the effect of forest cover on relative total abundance of Ruby-throated Hummingbirds did not vary according to forest patch size (Fig.9). When we modelled for mean patch size, we still obtained a positive unimodal relationship where the optimum peaked at around 50% forest cover. In low forested landscapes, an increase of forest cover led to a greater relative total abundance, suggesting that they do not only need open habitats. Indeed, females require forest cover for nesting (Robinson et al. 1996). Conversely, in highly forested landscape, the relationship was negative since open habitats are likely insufficient for feeding requirements.

Models of relative total abundance and mean daily artificial nectar consumption suggest that Ruby-throated Hummingbirds prefer landscapes with intermediate amounts of forest cover, which are usually found in extensive agricultural landscape in our study area. When forest cover was scarce, Ruby-throated Hummingbirds appeared to compensate by using large contiguous forest patches. Highly forested landscapes seemed avoided since they do not include many small forest patches. In fact, these landscapes are mainly formed by large contiguous forest patches, and if hummingbirds are present then they would mainly rely on artificial nectar resources, since open habitat with nectar availability is scarce. Besides, even though hummingbirds are edge species and would be favoured by fragmented landscape, some species of hummingbirds seem to prefer forest cover or corridors-connected forest patches (Stouffer and Bierregaard 1995, Hadley and Betts 2009) which supports our interpretation of preferred habitat at intermediate level of forest cover.

2) Relative adult male and female abundances

Shifts in the effect of forest cover on Ruby-throated Hummingbird relative total abundance and mean daily artificial nectar consumption could result from sex-dependent habitat selection patterns. Indeed, male Ruby-throated Hummingbirds do not provide parental care and are assumed to defend flower-rich territories to attract females which breed in forest habitats, suggesting a different response to landscape variables because of differences in habitat requirements (Robinson et al. 1996).

Results on relative adult male and female abundances support the existence of such sex-dependent differences in habitat selection. The best models based on AIC_c for male abundance were #3, #4, #1 and #2 (Table 7) while for females only model #6 stood out as best (Table 8). Males were sensitive to local and landscape variables and also to the open flower community structure index. Females were only sensitive to landscape variables. This suggests that males are more tied up to small scale variations in habitat while females based their habitat selection mainly on broad scale landscape variables. Accordingly we found that relative adult male abundance responded most strongly to landscape structure when it was characterized within a 2-km radius compared to within a 5-km radius for females.

LOCAL VARIABLES

Relative adult male abundance was influenced by local habitat variables. First, adult male abundance was lower at feeders set up 40 m from the forest edge compared to on the edge. There was also an effect of the forest composition and structure index suggesting that males were more abundant in areas with younger open-canopy forests compared to areas of mature closed-canopy forests. Flower availability may be greater in habitat with higher light penetration (Tilman, 1993, Foster *et al.*, 2002), such as in younger open-canopy forests compared to in mature closed-canopy forests.

Regarding relative adult female abundance, we found no effect of feeder location, forest composition and structure index, or the open flower community index. Female habitat requirements may be less influenced by the amount or proximity of forest edges, compared to males, as they need forest habitat to raise their young and depend less on flowers but rather need large supplies of insects to build eggs and feed young (Robinson et al. 1996).

LANDSCAPE VARIABLES

The negative unimodal relationship between relative adult male abundance and forest cover found for all forest patch sizes (Fig.10) suggests that males avoid very low forested landscapes characterized by intensive agriculture; and when they use such landscapes, they prefer large forest patch sizes. This is true up to ca. 50% forest cover, because further increases in forest cover bring an increase in adult male abundance that is more pronounced in small forest patch sizes. Adult male Ruby-throated Hummingbirds thus look for habitats where they will find high amounts of ecotones between forest and agricultural fields.

Results concerning relative adult female abundance also indicate that they need high amounts of forest edges within a 5-km radius (Fig.11). In fact, landscapes in which forest patch sizes were small showed that relative adult female abundance increased with forest cover and, conversely, that it decreased with forest cover in landscapes composed of large forest patches. Contrary to males, when landscapes were highly forested (≥ 50-55%), females seemed to prefer larger forest patches.

The Ruby-throated Hummingbird is categorized as an “edge species”, but also as an “area-insensitive” species as likely to occur in small forests as in large ones (Freemark and Collins 1992). Such a classification may reflect he potential sex-dependent habitat segregation of Ruby-throated Hummingbirds. If such sex-dependent habitat selection truly exists, landscape modifications may strongly affect breeding parameters and thereby population structure and dynamics. Indeed, landscapes that do not fulfill habitat requirements of both sexes may create difficulties for finding mates or have reproductive success. According to our modelling results and assuming equal probability of using feeders for adults of both sexes, male and female abundances would be similar in forest patches area ranging from 25 to 35 ha, independently of the amount of forest cover. This area may present the best trade-off in terms of food resource and sexual partner availability as well as in terms of habitats suitable for courtship and nesting.

Interaction between year and nectar feeder installation date

For all four response variables, the interaction between year of sampling and nectar feeder installation date was significant. The first year of sampling (2006) we set up 20 nectar feeders in forest patches ranging from 0.5 to 100 ha before the spring arrival of Ruby-throated Hummingbirds. The second set of 20 nectar feeders was installed at the end of June when migration was over and Ruby-throated Hummingbirds are considered to have selected their territories. In 2007, we reversed the schedule of feeder installation. This treatment was in order to account for the possible bias that feeder might create in habitat selection. If individuals were observed at sites placed at the end of June, this means that their choice was based on habitat characteristics other than the presence of feeders. Moreover, it has been shown that nectar consumption at feeders decreases when flowers are abundant (Inouye et al. 1991, McCaffrey and Wethington 2008), suggesting that feeders do not lead to significant biases. Ruby-throated Hummingbirds showed higher mean daily artificial nectar consumption and relative abundances for the first set of feeders even on year 2007 when they have been installed in late June. This carry over effect is likely related to the high proportion of Ruby-throated Hummingbirds that return to breed at the same site between years (Charette et al. 2010 submitted). It can also be explained, as for many other bird species, by the fact that adult individuals often selecting habitats based on habitat characteristics that they experienced as juveniles (Brewer and Harrison 1975, Catchpole 1972, Hildén 1965, Löhrl 1959). Thus, if more juveniles were produced in habitats where feeders were installed in late April 2006, our results reflect the strong selection of these habitats the year after even if feeders were installed in late June (2007).

CONCLUSION

We found evidence that landscape structure can affect the abundance of Ruby-throated Hummingbirds through both direct and indirect effects. Indirect landscape effects occurred via variation in open flower community structure, and thus likely through variation in food resource availability. Contrary to our expectation, we did not find indirect effects of the occurrence of Yellow-bellied Sapsucker. We detected a complex unimodal influence of landscape variables on total relative abundance and mean daily nectar consumption as well as on the respective abundance of adult males and females. This effect was also dependent of forest patch size and, this, for mean daily artificial nectar consumption, as well as for relative adult male and female abundances. We also detected a small scale effects through nectar feeder location with respect to the forest edge and the composition and structure of forest habitat around feeders. In fact, mean daily artificial nectar consumption, relative total abundance and relative adult male abundance were all higher at edge feeders, but vegetation composition and structure only influenced adult male abundance. Adult female abundance was only influenced by broad-scale variables. These results strongly support the interpretation of a differential use of landscape according to sex, leading to a global habitat selection for landscape with intermediate levels of forest cover and patch size.

We were also able to quantify indirect effects of landscape since we detected a direct effect of landscape variables on our open flower community index, while this index influenced relative total abundance and adult male abundance. These results also suggest differential landscape use according to sex. Nevertheless, we could not detect an effect of landscape variables on the occurrence of Yellow-bellied Sapsuckers and we only found weak evidence that occurrence of this woodpecker affected the abundance patterns of Ruby-throated Hummingbirds.

There are no good estimates of Ruby-throated Hummingbird abundance, and therefore of its determinants, because of the difficulties to detect this species using traditional monitoring methods. Because hummingbirds play a key role as pollinators (Fenster and Dudash 2001), we have an interest in studying this species for conservation. However, we first need to understand the basic determinants of its habitat use and selection patterns over a range of spatial scales. Our project is a first step toward achieving this goal.

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CONCLUSION GÉNÉRALE

Ce projet a vu le jour dans un contexte exploratoire concernant l’influence de la structure du paysage sur une espèce très peu étudiée sous nos latitudes, soit le Colibri à gorge rubis. Il faisait partie d’une grande étude comportant un dispositif d'abreuvoirs à nectar à petite échelle (ca. 1 km^2; Charrette, 2011; Rousseu, 2010), ainsi qu'un dispositif à grande échelle (>3000 km^2; présente étude), tous deux visant à quantifier les multiples relations entre le Colibri à gorge rubis et différentes caractéristiques du paysage. Le présent projet visait à évaluer l’impact du paysage à une échelle régionale sur la sélection et l’utilisation de l’habitat par le Colibri à gorge rubis. La structure du paysage peut avoir un effet direct sur l’utilisation de l’habitat par le colibri, mais peut également agir indirectement à travers différents processus et patrons écologiques. Les résultats obtenus suggèrent fortement l’existence de tels effets directs et indirects.

LES EFFETS DIRECTS

La composition et la configuration du paysage affectent le colibri, mais à différentes échelles (rayons de 1 à 5 km) selon que l’on parle d’abondance spécifique à un sexe donné ou de consommation de nectar artificiel. Ces échelles concordent avec les observations faites sur le dispositif d’abreuvoirs à nectar à petite échelle mentionné ci-haut et où les colibris parcourent fréquemment des distances de l’ordre de 1,2 km entre des sources de nectar connues pour s’alimenter (Charette, 2011; Rousseu, 2010). Ces résultats additionnés au faible taux de recapture que j’ai obtenu lors de l’effort de capture-marquage-recapture (7%) m’amènent à remettre en question la forte territorialité sur une petite superficie souvent associée à cette espèce.

J’ai détecté un effet quadratique complexe du pourcentage de couvert forestier sur l’abondance relative totale et la consommation quotidienne moyenne de nectar artificiel, ainsi que sur l’abondance des mâles et de femelles. De plus, l’importance de l’effet du couvert forestier varie selon la superficie des îlots, sauf pour l’abondance relative totale.

Ainsi, pour toutes les variables mesurées, les valeurs maximales ont été observées à des niveaux intermédiaires de couvert forestier (40 à 60%) et à des tailles intermédiaires d'îlots autour de 10-15 ha. Toutefois, les mâles, quoique sans être désavantagés dans les îlots de tailles intermédiaires, semblent être plus abondants dans les îlots de petites tailles. Les femelles, quant à elles, ont une abondance maximale dans les conditions où le couvert forestier est élevé tant pour le pourcentage global que pour la taille des îlots.

J'ai également trouvé une influence du paysage à petite échelle à travers les variables locales telles que la position de l'abreuvoir dans l'îlot forestier ainsi que la structure de la végétation de l'îlot. L'abondance relative totale, la consommation de nectar artificiel et l'abondance relative des mâles étaient plus grande en bordure de la forêt comparativement à l'abreuvoir situé à 40 m à l'intérieur. Quant à la structure de la végétation, l'effet était significatif seulement pour l'abondance relative des mâles. Les femelles, pour leur part, ne semblaient pas répondre aux variables locales.

Les résultats de l'effet direct de la structure du paysage soutiennent globalement l'hypothèse d'une utilisation différentielle du paysage selon le sexe entraînant globalement chez cette espèce une sélection unimodale des habitats où les valeurs maximales sont situées à des niveaux intermédiaires de couvert forestier. D'ailleurs, quelques espèces sont reconnues pour avoir des patrons d'abondance suivant une relation quadratique avec différentes caractéristiques du paysage, surtout parmi les espèces généralistes comme la Corneille noire (*Corvus corone*; Andrén, 1992; Andrén, 1994; Andrén *et al.*, 1997) ou encore d'avoir une ségrégation sexuelle dans l'utilisation de l'habitat le Grand Corbeau (*Corvus corax*; Roth *et al*., 2004).

LES EFFETS INDIRECTS

J'ai pu quantifier les effets indirects du paysage à travers deux processus écologiques influençant le Colibri à gorge rubis. Tout d'abord, j'ai observé un effet indirect de la structure du paysage via la disponibilité de la ressource alimentaire. En effet, les résultats montrent une influence du paysage sur les communautés floristiques retrouvées sur nos sites d'études. Ces mêmes communautés floristiques influençaient, à leur tour, l'abondance relative totale et celle des mâles, mais n'affectaient pas la consommation moyenne quotidienne de nectar artificiel ni l'abondance relative des femelles. Ces résultats soulignent encore une fois la différence existant entre les mâles et les femelles quant aux facteurs ayant un effet sur leurs patrons d'abondance. L'abondance relative totale et celle des mâles étaient en effet corrélées négativement avec l'axe 2 de l'indice floristique induisant respectivement une diminution de 0,54 et 0,36 individu le long de cet axe. Le sens de cette relation est plutôt surprenant lorsque l'on regarde la distribution des espèces végétales le long de cet axe. Alors que l'on devrait s'attendre à une relation positive du fait que *Trifolium repens* et *pratense* sont des espèces nectarifères déjà connues pour être utilisées par le colibri. *Spiraea latifolia* ne produit pas du nectar. Je suggère deux interprétations possibles. (1) Premièrement, si l'on se base sur le fait que l'axe 2 représenterait un gradient de régime hydrique, on pourrait supposer que les sites associés à *Spiraea latifolia* ont un drainage modéré ou mauvais reflétant un milieu ayant une perturbation hydrique récurrente ou permanente et qui pourrait laisser croire à une diversité florale plus faible dans ce type de conditions environnementales. Ainsi, puisque ces sites pourraient être caractérisés par une faible abondance florale, les colibris qui y sont associés pourraient dépendre plus fortement des abreuvoirs augmentant ainsi le nombre total d'individus observés. Alors que les sites associés aux espèces *Trifolium sp* et *Solidago canadensis* seraient des sites à drainage élevé permettant ainsi une grande diversité d'espèces florales. Les colibris passeraient donc moins de temps aux abreuvoirs puisqu'ils peuvent retrouver dans le milieu naturel une grande diversité de sources alimentaires, ce qui engendrerait une abondance observée plus faible. D'ailleurs, d'autres études ont démontré que les colibris utilisent moins les sources de nectar artificiel durant le pic de la période de floraison (Inouye *et al*., 1991; McCaffrey et Wethington, 2008). Cependant, cette interprétation implique que la consommation de nectar artificiel sera supérieure aux abreuvoirs sur site à drainage modéré ou mauvais. Par contre, nos résultats n'ont pas détecté une telle relation entre la consommation moyenne quotidienne et l'indice de communauté floristique. Cela suggère donc que cette interprétation n'est peut-être pas la meilleure. (2) La seconde interprétation fait référence au regroupement des espèces de fleurs. En effet, si l'on se concentre sur la position des espèces de fleurs dans les graphiques (Figures 5 et 6), on peut y distinguer trois groupes principaux relatifs au type d'habitat : sites à perturbations anthropiques sévères et récurrentes (quadrant I), les champs de fourrage naturels et ceux semés avec *Trifolium sp.* (quadrant I et II) ainsi que les friches et pâturages (quadrant IV) qui correspondent à des habitats où l'on retrouve des perturbations naturelles et anthropiques récurrentes, mais d'une intensité plus faible. Ces derniers offrent aux colibris des conditions où ils peuvent retrouvés une grande diversité et disponibilité en ressources alimentaires tout au long de la saison estivale. D'ailleurs, parmi ces sites, il n'y avait qu'un seul avec des animaux en train de paître en permanence. Tous les autres pâturages ou friches n'étaient visités qu'une ou deux fois durant la saison par des animaux d'élevage. Concernant les champs de fourrage, malgré qu'ils offrent une diversité florale intéressante, ils sont principalement caractérisés par des plantes de très petite taille en termes de hauteur. Ce sont donc des sites probablement moins utilisés par les colibris puisque ces derniers sont connus pour avoir une préférence envers les sources de nourriture localisées à une hauteur élevée (Blem *et al.*, 1997). Quant aux sites à perturbations anthropiques sévères et récurrentes, ils ont tous simplement une diversité et une disponibilité d'espèces florales très restreintes. Ainsi, ces regroupements expliqueraient mieux la relation négative que l'on retrouve le l'on de l'axe 2 de l'indice de communauté floristique et, ce, tant pour l'abondance relative totale que celle des mâles. Ces explications restent toutefois spéculatives. Les prochaines études devraient éclaircir la relation entre le colibri et les espèces de fleurs visitées en nature comme sources de nourriture (nectar et insectes) en lien avec la structure du paysage. Il sera difficile d'aller plus loin dans l'étude de cette espèce si cet aspect n'est pas éclairci.

Le second effet indirect concerne l'impact de la structure du paysage via la relation interspécifique de commensalisme entre le Pic maculé et le Colibri à gorge rubis. Je n'ai pas détecté un effet significatif des caractéristiques du paysage sur la répartition du Pic maculé. Ces résultats sont probablement dus au fait que le pic était présent pratiquement à tous les sites et, ce, possiblement parce que les critères de sélection des îlots en terme de composition en essences forestières correspondaient aux caractéristiques préférentielles de cette espèce (Walters *et al*., 2002). Quant à la relation entre la présence du Pic maculé et l'abondance relative des colibris ou leur consommation quotidienne moyenne de nectar artificiel, aucun modèle n'a pu quantifier un effet significatif. En effet, le taux d'occupation des sites par le Pic maculé était si élevé qu'il était impossible de discriminer un effet significatif. Toutefois, lors de la sélection de modèles sur la base du critère d'information d'Akaike, les modèles incluant la présence du Pic maculé avaient un poids explicatif non négligeable et, ce, pour l'abondance relative totale et celle des mâles de même que la consommation quotidienne moyenne de nectar artificiel. Il semble que l'abondance des femelles ne soit pas influencée par la présence du Pic maculé, probablement parce que l'arrivée de femelles à nos latitudes survient un peu plus tard que celle des mâles, soit à partir de la mi-mai alors que la disponibilité en nectar et en insectes est peut-être suffisante. Afin de quantifier l'effet réel du Pic maculé, il faudrait refaire l'étude avec des sites ayant un taux d'occupation plus faible.

MOT DE FIN

En somme, les résultats obtenus avec notre approche montrent l'importance de considérer plusieurs effets directs et indirects de la structure du paysage pour comprendre l'influence de cette dernière sur les patrons de distribution résultant de la sélection d'habitat. D'ailleurs, plusieurs études dont celles de Leighton *et al*. (2008), Tavarnia et Reed (2010) ou Turgeon *et al*. (2010) montrent que cette tendance commence à être à la hausse depuis la parution l'article de Lima et Zollner (1996), article faisant état de la problématique d'exclusion entre les deux domaines d'études que forment l'écologie comportementale et l'écologie du paysage qui sont pourtant interdépendantes.

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