INFLUENCE DE LA STRUCTURE DU PAYSAGE SUR LES MOUVEMENTS ET LES STRATÉGIES DE QUÊTE ALIMENTAIRE DU COLIBRI À GORGE RUBIS

(*Archilochus colubris*)

par

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mémoire présenté au Département de biologie en vue
de l'obtention du grade de maître ès Sciences (M.Sc.)

FACULTÉ DES SCIENCES
UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, août 2011

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ISBN: 978-0-494-83738-2

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ISBN: 978-0-494-83738-2

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Le 18 août 2011

le jury a accepté le mémoire de Monsieur Yanick Charette
dans sa version finale.

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SOMMAIRE

Le *traplining* est une stratégie de quête alimentaire permettant aux animaux d'exploiter des points de ressources renouvelables dans le temps et distribués de façon inégale dans l'environnement et ce, dans un ordre fixe et répété de façon prévisible. Un exemple bien connu de ressources qui aurait avantage à être exploité par *traplining* est le nectar présent dans les fleurs. On distingue deux composantes principales au *traplining*. La première est temporelle du fait que l'animal doit exploiter la fleur du moment que la quantité de nectar générée est suffisante pour au moins combler les pertes énergétiques engendrées par les déplacements, mais sans trop de délais afin de minimiser les pertes occasionnées par les compétiteurs. La deuxième composante est spatiale. L'animal doit exploiter les parcelles de nourriture dans un ordre fixe, répété et prévisible. À ce jour, ce comportement fût généralement décrit de façon plutôt anecdotique en nature ou observé et étudié de façon plus formelle en captivité. De plus, la composante spatiale fût très souvent, sauf pour quelques exceptions, négligée. Cette négligence s'explique d'une part, parce que les nectarivores sont généralement très petits et d'autre part, parce qu'ils se déplacent très rapidement sur de grandes distances, ce qui rend le suivi de leur déplacements difficile. Dans cette étude, je développe un indice permettant de quantifier ce comportement au niveau spatial et modélise cet indice en fonction de variables écologiques afin de mieux comprendre les motivations d'un individu à adopter cette stratégie d'exploitation des ressources, et ce, en utilisant comme modèle d'étude le Colibri à gorge rubis *Archilochus colubris* et une technique innovatrice de suivi des déplacements de ces petits oiseaux. Mes résultats montrent qu'il existe une grande variabilité entre les individus, de même qu'entre les jours pour un individu donné, au niveau de la conformité des patrons de déplacements entre les sources de nectar et les patrons attendus si les individus adoptaient le *traplining*. De plus, mes résultats montrent que la structure du paysage, le niveau de concentration spatiale de l'individu, l'ampleur de ses déplacements et le nombre de sources de nectar fréquentées affectent tous le niveau de conformité de la quête alimentaire avec le *traplining.* Finalement, mon travail souligne l'importance de considérer simultanément les composantes spatiale et temporelles du *traplining* avant de conclure qu'une espèce ou un individu opte pour une telle stratégie de quête alimentaire.

REMERCIEMENTS

Je tiens à remercier mon directeur de recherche et ami, Marc Bélisle, pour la confiance qu'il m'a accordée durant ces dernières années. Ce fût un réel plaisir de travailler dans son laboratoire de recherche. Je lui suis grandement reconnaissant également pour m'avoir donné l'opportunité de travailler sur une des espèces animales des plus intéressantes et fascinantes que j'ai eu la chance de côtoyer, le Colibris à gorge rubis. Grâce à ce projet de recherche, j'ose espérer que nous serons en mesure de mieux comprendre les comportements en milieux naturels de cette espèce très méconnue.

Merci également à François (Poncho) Rousseu pour son aide sur le terrain, son expertise inestimable en statistiques et en programmation informatique. Je le remercie grandement pour les nombreuses discussions que nous avons tenues afin de me faire cheminer dans mon projet. Merci aussi à tous les étudiants du Laboratoire de recherche de Marc Bélisle : Claudie, Stéphane, Audrey, Geneviève, Ludo et Louis pour leur soutient et pour avoir su m'endurer durant ces 2 dernières années. Merci aussi à Alexandre, Benoit, Léonie et tous les stagiaires qui ont contribué à la collecte de données terrain; 9 000 000 de lignes de données, ça ne se ramasse pas tout seul.

Merci à Dany Garant et Marco Festa-Bianchet pour avoir partagé leur point de vue sur mon projet de maîtrise. Je retiens surtout un commentaire de Marco : « C'est compliqué ton affaire! » et c'est bien vrai. Merci à Sara Derivière pour son aide dans le développement de l'algorithme et merci à Alain Gervais pour ses commentaires et son aide.

Ce projet a été réalisé grâce au support financier de la Chaire de recherche du Canada en écologie spatiale et en écologie du paysage, la Fondation canadienne pour l'innovation, les Fonds québécois de la recherche sur la nature et les technologies, le Conseil de recherches en sciences naturelles et en génie du Canada, et l'Université de Sherbrooke.

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INTRODUCTION GÉNÉRALE

Les paysages consistent en des mosaïques dynamiques et composées de parcelles d'habitat organisées hiérarchiquement selon différentes échelles spatiales (Wiens 1985; Kozakiewicz 1995). Il s'ensuit que les espèces vivent dans des environnements hétérogènes composés de parcelles de différentes qualités et disposées de façon plus ou moins avantageuse. À ce titre, le mouvement devient une composante fondamentale des comportements associés à l'exploitation optimale des ressources dans l'espace et dans le temps (Kozakiewicz 1995; Turchin 1998). Comprendre comment la structure du paysage influence la recherche de nourriture et de partenaires, la sélection d'habitat, la dispersion et les mouvements dans les différents éléments du paysage revêt donc une importance cruciale en écologie (May et Southwood 1990; Ims 1995; Bélisle 2005), car ultimement cela pourrait avoir des répercussions au niveau de la structure et de la dynamique des populations (With et al. 1997; Turchin 1998).

Malgré le rôle clé des mouvements pour l'étude des phénomènes écologiques (Wiens et al. 1993; Ims 1995; Wiens 1995), les études portant sur les patrons de mouvements des animaux ont longtemps été descriptives et souvent basées sur des observations anecdotiques (revue par Turchin 1998). Le manque d'informations empiriques solides sur l'utilisation de l'espace par les animaux en relation avec la structure du paysage a d'ailleurs fait l'objet de nombreuses critiques dans le passé. (Ims 1995). Or le développement de nouvelles technologies permettant de suivre les déplacements des animaux sur de grandes échelles spatiales et temporelles avec précision, nous permettent aujourd'hui de s'attaquer à comprendre comment les individus se déplacent dans l'espace et utilisent cette dernière (e.g., Weimerskirch et al. 2007; Pinaud

2008). Ces percées technologiques ont également permis le développement d'un cadre de recherche intégré sur le mouvement (Nathan et al. 2008). Ce cadre met l'emphase sur l'importance de relier les quatre composantes sous-jacentes au mouvement des organismes : l'état interne (pourquoi se déplacer), la capacité à se mouvoir (comment se déplacer), la capacité de navigation (quand et où se déplacer) des individus et les facteurs externes affectant le mouvement (e.g., distribution des ressources; Nathan et al. 2008). L'étude du mouvement des animaux à travers l'écologie comportementale offre à ce titre une structure intéressante pour faire le lien entre ces composantes, notamment dans le cadre de la quête alimentaire d'individus au sein de paysages hétérogènes (Bélisle 2005).

En effet, l'étude du mouvement dans une perspective de la théorie de la quête alimentaire en écologie comportementale (Stephens et Krebs 1986) confère l'avantage que les comportements doivent être interprétés à l'intérieur d'un cadre évolutif définis par des contraintes et des règles de décisions spécifiques (Bélisle 2005). Le mouvement est d'ailleurs impliqué dans chacun des quatre types de choix que doivent faire les animaux pour optimiser leur quête alimentaire : 1) choix d'une proie, 2) choix d'une parcelle de ressources 3) choix du groupe d'alimentation et 4) choix d'une stratégie de recherche (Krebs et Cowie 1976). Les décisions prises dans chacun de ces types de choix vont avoir un impact crucial sur la survie et l'aptitude phénotypique des individus. Ainsi, les individus qui tendent à adopter des comportements alimentaires optimaux vont pouvoir investir plus de temps et d'énergie à d'autres activités de leur cycle vital, telles la migration, la reproduction, la défense d'un territoire et la protection contre les prédateurs (Anderson 1983; Hutto 1990). Bien que les comportements impliqués dans les trois premiers types de choix aient été très étudiés (Stephens et Krebs 1986, Giraldeau 2005), ceux rattachées aux stratégies de recherche et d'exploitation l'ont été beaucoup moins (e.g., Anderson 1983; Hadley et Betts 2009). Ce manque serait grandement relié aux difficultés à suivre des individus, ainsi qu'à mesurer la distribution et la qualité des ressources alimentaires, sur de grandes échelles spatiales et temporelles. Tel que mentionné plus haut, les avancées technologiques permettent de contourner en partie les difficultés rattachées au suivi des individus. Il reste donc à se pencher sur les stratégies de quête alimentaire d'organismes dont les ressources alimentaires sont circonscrites dans l'espace et relativement faciles à mesurer ou à manipuler. Les nectarivores rencontrent ces exigences. Mon projet de maîtrise portant sur l'influence de la structure du paysage sur les stratégies de quête alimentaire et les mouvements du Colibri à gorge rubis (Archilochus colubris), un oiseau nectarivore, je m'attarderai maintenant à synthétiser les connaissances actuelles sur la quête alimentaire des nectarivores et la distribution spatio-temporelle de leurs ressources alimentaires.

INTRODUCTION AUX NECTARIVORES

Une des composantes principales de la structure de l'habitat pour des nectarivores en quête alimentaire est la distribution spatiale des fleurs desquelles ils vont récolter le nectar (Cartar et al. 1997). Par la position statique des plantes, il est relativement facile d'évaluer la distribution spatiale de cette ressource, de la mesurer et ainsi de déterminer la quantité d'énergie qui pourrait être fournie aux pollinisateurs (Wolf et Hainsworth 1978). De plus, il est relativement facile d'observer le comportement alimentaire des nectarivores, de le quantifier et d'y relier une estimation du gain en aptitude phénotypique en termes d'énergie nette (Pyke 1978). Enfin, l'analyse du comportement alimentaire des nectarivores est d'intérêt non seulement fondamental par le biais de l'application de concepts théoriques (e.g., modèles de quête alimentaire optimal), mais également pratique pour le rendement des cultures dont la fertilisation est dépendante des pollinisateurs (Lefebvre et al. 2007). Pour toutes ces raisons, le groupe des nectarivores est un excellent modèle d'étude pour répondre à des questions écologiques associées à l'exploitation des ressources alimentaires.

On retrouve des nectarivores dans plusieurs ordres du règne animal. Plusieurs de ces groupes ont d'ailleurs fait l'objet d'études portant sur les stratégies de quête alimentaire optimale : insectes (May 1988; Pleasants 1989; Possingham 1992; Dreisig 1995; Goulson 2000; Hill et al. 2001; Lefebvre 2007), oiseaux (Krebs et Cowie 1976; Gill et Wolf 1977; Pyke 1978; Gass et Montgomerie 1981; Scoble et Clarke 2006; Temeles et al. 2006), reptiles (Eifler 1995) et mammifères (Garber 1988; Goldingay 1990; Fisher 1992; Horner et al. 1998). Malgré ce nombre important d'études, il demeure que nous avons très peu d'informations concernant l'exploitation des sources de nectar et les mouvements chez cette guilde alimentaire en milieu naturel (Anderson 1983). Encore une fois, ce manque d'informations résulterait de la petite taille des organismes, de leur grande vitesse de déplacement et du fait qu'ils exploitent des ressources distribuées de façon inégale dans leur environnement (e.g., Pleasants et Zimmerman 1979; Zimmerman 1981), rendant ainsi le suivi des mouvements entre chacune des sources de nectar très difficile.

Les nectarivores sont généralement caractérisés par un métabolisme élevé, lequel nécessite un apport important et constant en ressources alimentaires (Robinson et al. 1996; Rappole et al. 2003). Il s'ensuit que la recherche des ressources alimentaires est probablement à la base de la plupart des mouvements quotidiens et saisonniers des nectarivores. (Karr 1990; Fleming 1992). Jusqu'à présent, nous disposons de très peu d'informations concernant la réponse des pollinisateurs face aux changements spatio-temporels de leurs ressources alimentaires (Bronstein 1995). Cette réponse risque de dépendre de plusieurs facteurs, incluant les besoins énergétiques du nectarivore, l'apport énergétique des sources de nectar et la présence de compétiteurs, intraspécifiques ou non (Bronstein 1995; Zollner et Lima. 1999). De plus, nous ne disposons que de très peu d'information concernant les échelles spatiales et temporelles à l'intérieur desquelles les nectarivores sont capables de réagir face à des variations environnementales, en partie parce que nous ne connaissons pas les capacités de mouvement des nectarivores aux différentes échelles tant spatiales que temporelles (Bronstein 1995).

La structure du paysage est généralement considérée comme étant implicite au sein des modèles de quête alimentaire optimale (Ims 1995, Bélisle 2005). Ces modèles considèrent donc des paramètres décrivant simplement la distribution ou la valeur moyenne de certains attributs comme la taille et la qualité des parcelles de ressources et parfois, leur dispersion dans l'espace (Ims 1995; e.g., Cartar et al. 1997; Ohashi et al. 2005). Cependant, la taille, la forme et la qualité des parcelles de nourriture, ainsi que leur dispersion explicite dans l'espace, risque d'affecter les mouvements d'un animal en déterminant, par exemple, son temps de résidence dans une parcelle, son temps de recherche, de même que les différentes stratégies de recherche qu'il adoptera (Ims 1995). Bien que l'influence de la distribution des ressources sur l'organisation sociale de certaines espèces de nectarivores soit partiellement connue, peu d'études se sont véritablement penchées sur l'utilisation de l'espace par les individus en termes d'utilisation des ressources (e.g., Stiles et Wolf 1979). De plus, l'influence de la distribution spatiale explicite des ressources alimentaires n'a fait l'objet que de très peu d'études (Ims 1995). Durant la dernière décennie, quelques équipes de recherche ont néanmoins mesuré, via des simulations (Baum et Grant 2001; Ohashi et al. 2005) ou des expériences en captivités (Thompson et al. 1997; Gass and Garrison 1999; Ohashi et al. 2006; Makino et al. 2007; Ohashi et al. 2008), les déplacements de nectarivores au sein de parcelles de nourriture distribuées de différentes façons. Cependant, dans un environnement naturel, les pollinisateurs évoluent au sein d'un paysage déterminé, entre autres, par une combinaison des attributs des plantes (e.g., la durée et la synchronisation de floraison) et par les attributs des pollinisateurs, comme la capacité de se déplacer entre les parcelles de nourriture et leur flexibilité dans leur diète (Bronstein 1995). Compte tenu de l'importance de la disponibilité des ressources alimentaires pour les nectarivores (Possingham 1989), la prochaine section est dédiée aux mécanismes affectant sa distribution en termes de quantité et de qualité dans l'environnement.

DISTRIBUTION DES RESSOURCES ALIMENTAIRES POUR LES NECTARIVORES

Savoir si les ressources sont distribuées inégalement ou non dans l'espace et dans le temps est d'une importance cruciale pour construire les modèles de quête alimentaire optimale (Pleasants et Zimmerman 1979). À ce titre, les fleurs sont généralement réparties de façon inégale dans l'espace, et ce, à différentes échelles spatiales (Goulson 2000). Par exemple, les fleurs sont groupées dans des inflorescences, lesquelles peuvent également être groupées sur une même plante alors que les plantes elles-mêmes sont souvent réparties inégalement (Goulson 2000). De plus, le nectar disponible pour les nectarivores varie en quantité et en qualité dans l'espace et dans le temps (Scoble et Clarke 2006). Selon Gill et Wolf (1977), trois principaux facteurs contribuent à la variation en disponibilité du nectar. Premièrement, la qualité d'une parcelle peut augmenter à mesure qu'il y a de nouvelles fleurs produites ou diminuer à mesure que ces dernières vieillissent. De plus, les caractéristiques propres au nectar (composition et agencement des sucres tels que glucose, fructose et sucrose), lesquelles peuvent varier avec l'âge des fleurs, vont influencer sa valeur énergétique (May 1988). Deuxièmement, le renouvellement du nectar à l'intérieur d'une même fleur peut varier. Ceci est appuyé par les résultats de May (1988) qui montrent que la quantité de nectar produite est plus grande le matin, généralement peu de temps après l'ouverture des fleurs, et qu'elle décline à mesure que la journée avance. Troisièmement, le taux de consommation de nectar par les compétiteurs, de la même espèce ou non, causerait également une variabilité, tant spatiale que temporelle, de la disponibilité en nectar. En effet, plusieurs études ont montré que l'activité de quête alimentaire des nectarivores peut générer une distribution très inégale de cette ressource (Pleasants et Zimmerman 1979; Zimmerman 1981).

La distribution spatio-temporelle des fleurs est considérée un déterminant majeur de la quantité d'énergie dépensée par un nectarivore en quête alimentaire. Lorsque les fleurs sont densément regroupées, par exemple, il devrait en résulter une diminution du temps passé à voyager entre les fleurs et une augmentation du nombre de fleurs visitées par unité de temps. En effet, la distance parcourue et le temps pris pour effectuer les déplacements sont reconnus pour être des bons indicateurs de l'énergie dépensée par un nectarivore durant la recherche de nourriture (Hill et al. 2001). Ceci est d'autant plus important pour des espèces qui ont un gros coût énergétique relié au vol (May 1988). Par le fait que les ressources en nectar sont distribuées de façon inégale dans l'espace et dans le temps, et ce, à différentes échelles, et par le fait que la quantité d'énergie disponible est limitée, la majorité des nectarivores devraient adopter un comportement alimentaire qui maximise le taux net d'acquisition d'énergie en minimisant, par exemple, le temps passé à voler (Gass et Montgomerie 1981). Ainsi, les patrons de mouvements au sein de ces parcelles d'alimentation sont considérés comme des facteurs clés de l'aptitude phénotypique des nectarivores (Ohashi et al. 2005).

Les décisions qu'ont à prendre les pollinisateurs lors de la recherche de leur nourriture ont été généralement étudiées à l'échelle d'une seule fleur ou d'une seule parcelle de fleurs (e.g., Pyke 1978; Heinrich 1979; Pleasants 1989; Williams et al. 1998; Temeles et al. 2006). Cependant, aucune étude empirique n'a été effectuée pour évaluer la pertinence de ces échelles spatiales relativement à la façon dont les individus perçoivent les ressources en nectar dans leur environnement (Bronstein 1995). Il y a toutefois de bonnes évidences que certains pollinisateurs, tels les bourdons et les oiseaux, soient capables d'évaluer et de mémoriser la disponibilité des ressources en fleurs à une échelle «régionale» et d'incorporer cette information dans leurs décisions à l'échelle «locale» (Bronstein 1995; voir aussi Visscher et Seeley 1982; Carpenter 1987) De plus, les patrons d'utilisation de l'espace par ces nectarivores varient fortement d'une espèce à l'autre et même entre les individus, allant de la défense d'un territoire restreint et exclusif jusqu'à l'utilisation d'aires non-défendues fréquentées par plusieurs individus (Brown et Orians 1970; Powers et Mckee 1994). Ces patrons seraient déterminés par la distribution spatiale et temporelle des ressources, en particulier les ressources alimentaires (Grant 1993; Maher et Lott, 2000).

Enfin, les études antérieures n'ont considéré le paysage des nectarivores que du point de vue des ressources alimentaires (e.g., Cartar et al. 1997; Osborne et al. 1999; Kreyer et al. 2004). Par conséquent, la structure de la végétation (e.g., densité d'arbres et de feuilles, essences végétales, présence de trouées, etc.) n'a jamais été considérée par ces études. Il demeure que la structure de la végétation a le potentiel d'exercer une influence majeure sur les mouvements et l'exploitation des ressources en limitant, par exemple, les possibilités de défendre les sources de nectar (Basquill and Grant 1998), de trouver et découvrir les ressources alimentaire (Eason et Stamps 2001) et même de restreindre l'accès aux partenaires sexuels en limitant, par exemple, les activités de parades liées à la reproduction et à la défense du territoire (Eason et Stamps 2001).

STRATÉGIES DE QUÊTE ALIMENTAIRE DES NECTARIVORES

Dans une étude visant à évaluer l'efficacité de différentes stratégies de quêtes alimentaire des nectarivores, Ohashi et Thompson (2005) concluent que le *traplining* est, dans la grande majorité des conditions, le comportement de recherche de nourriture offrant le plus de bénéfices aux individus qui l'adoptent.

Le *traplining* est une stratégie de quête alimentaire qui implique des visites à des parcelles de nourriture renouvelables qui sont effectuées selon un ordre fixe (prévisible) et répété (Ohashi et Thompson 2005; Saleh et Chittka 2007). Le *traplining* serait une stratégie rentable lorsque les individus fréquentent relativement peu de sources de nectar, que le niveau de compétition pour le nectar est faible et que les bénéfices énergétiques sont suffisants pour compenser les coûts énergétiques engendrées par les déplacements entre les fleurs et les parcelles de fleurs (Gill et Wolf 1977). Des stratégies s'apparentant au *traplining* furent non seulement observées chez des insectes et des oiseaux (voir Janzen 1971; Gill et Wolf 1977; Davies et Houston 1981; Thomson et al. 1997; Temeles et al. 2006), mais également chez certains groupes de mammifères (Lemke 1984; Garber 1988; Reid et Reid 2005). Ces observations suggèrent que cette stratégie serait utilisée par des animaux non territoriaux qui exploitent des parcelles isolées de ressources renouvelables de nourriture en suivant un trajet régulier (Gill 1988). Le *traplining* est par conséquent souvent opposé à la territorialité du fait que la territorialité est une stratégie d'exploitation des ressources basée sur une défense active de cette dernière alors que le *traplining* est surtout basé sur une défense par exploitation de la ressource (Feinsinger et Chaplin 1975; Stiles 1975; Feinsinger et Colwell 1978; Gill 1988). Il est intéressant de noter que cette stratégie semble être utilisée par quelques espèces de colibris où certains individus adoptent une séquence régulière dans l'utilisation de leurs ressources alimentaires (i.e., une *trapline*; Wolf et Hainsworth 1971; Wolf et Wolf 1971; Temeles et al. 2004). Par conséquent, il se pourrait que le niveau de traplining utilisé par les individus ne varie pas qu'entre espèces, mais aussi entre les individus d'une même espèce (e.g., Stiles and Wolf 1979).

La rentabilité du *traplining* serait intimement liée aux capacités cognitives des nectarivores. En effet, plusieurs études ont suggéré que certains nectarivores utilisent leur mémoire spatiale lorsqu'ils cherchent leur nourriture (Sutterland et Gass 1995; Miller et al. 1984) et qu'ils apprennent et se souviennent de l'emplacement des sources de nourritures les plus profitables et les choisissent préférentiellement tant qu'elles sont profitables (Miller et al. 1984). Healy et Hurly (2003) ont d'ailleurs montré que des colibris étaient capables d'évaluer la qualité des parcelles de fleurs, de se remémorer leur position et de mesurer le taux de renouvellement du nectar au sein des parcelles de fleurs. Ainsi, la capacité des colibris à se remémorer des informations importantes concernant les parcelles de nourriture (position, qualité) est une composante majeure du succès de leur stratégie de quête alimentaire (Sutterland et Gass 1995). La sélection naturelle devrait donc favoriser les individus qui s'alimentent dans les fleurs les plus riches en nectar, tout en minimisant leurs déplacements, de façon à ce qu'ils augmentent leurs gains nets par rapport à ceux s'alimentant de façon aléatoire (Gill et Wolf 1977).

MODÈLE ET OBJECTIFS DE L'ÉTUDE

Bien que le *traplining* fût observé dans plusieurs groupes du règne animal, il demeure qu'en nature, nous ne savons pas vraiment si ces animaux adoptent effectivement un comportement de *traplining* et jusqu'à quel point ils utilisent cette stratégie de quête alimentaire. D'une part, parce que la ressource est distribuée inégalement dans l'espace (Pleasants et Zimmerman 1979; Zimmerman 1981), il est difficile de relier le mouvement des nectarivores avec les endroits exacts où ils s'alimentent, et dans les cas où nous connaissons la position des individus (e.g., via l'utilisation d'émetteurs radio VHF), nous ne savons pas ce qu'ils font (voir Hadley et Betts 2009). De plus, l'adoption d'un comportement de *traplining* est généralement inféré alors que nous n'avons aucune idée du trajet d'alimentation complet effectué par les individus suivis (e.g., Stiles et Wolf 1979; Garrison 1995; Temeles et al. 2006). Par conséquent, nous avons bien peu d'information sur l'existence de ce comportement en nature et sur l'influence de variables jugées clés sur le *traplining*, notamment, l'influence des compétiteurs (Gill 1988; Temeles et al. 2006; Ohashi et al. 2008), de la distribution spatiale et temporelle des ressources en nectar, du nombre de parcelles de fleurs fréquentées et surtout de l'influence de la structure du paysage sur les mouvements et les stratégies d'exploitation des ressources des nectarivores..

On constate également un manque flagrant d'études rattachées aux façons de quantifier les comportements de *traplining*. Or pouvoir quantifier le niveau de *traplining* est essentiel pour comparer le comportement de différents individus et estimer les effets de différentes variables sur la genèse et la persistance d'un tel comportement en nature. À ma connaissance, une seule étude s'est véritablement penchée sur la question (voir Thompson et al. 1997). Ces auteurs ont développé trois indices permettant de quantifier le *traplining*. Par contre chaque indice pris individuellement ne peut quantifier à lui seul le comportement et chacun d'eux explorent le *traplining* sous différents angles. Il demeure donc que la méthode pour arriver à ces indices reste à peaufiner. Effectivement, ces indices sont basés sur une série de déplacements qui exclue les transitions entre les sources de nectar qui ne sont observées que très peu de fois, favorisant par le fait même la détection d'individus adoptant le *traplining*. De plus, la nécessité de devoir combiner chaque indice en un seul pour réellement comprendre la genèse de ce comportement rend le calcul de ce genre d'indice assez laborieux, surtout s'il doit être réalisé sur un grand nombre d'individus suivis sur une longue période de temps.

Au Québec, le seul représentant des oiseaux nectarivores est le Colibris à gorge rubis (*Archilochus colubris*). Comme toutes les espèces de colibris, cet oiseau dépend fortement des ressources en nectar pour survivre (Rappole et Schuchmann 2003). À l'instar des autres espèces de colibris, voire des nectarivores en général, le Colibri à gorge rubis est très petit, se déplace rapidement et il est presqu'impossible de le localiser au chant. Il s'ensuit que nous disposons de très peu d'information sur les mouvements des colibris, d'autant plus qu'aucun mode de suivi n'a été développé pour suivre les déplacements de ces oiseaux. Les rares individus qui ont été suivis en nature l'ont été entre un nombre restreint de parcelles de fleurs sur une courte période de temps (e.g., Powers 1987). De plus, la grande majorité des suivis proviennent d'individus en captivité (e.g., Montgomerie et al. 1984; Wolf et Hainsworth 1991; Powers et McKee 1994). Les observations étant aussi restreintes à des parcelles de fleurs focales, voire une seule parcelle, nous n'avons aucune idée des déplacements effectués par les colibris entre les parcelles de fleurs et de l'utilisation des parcelles de fleurs en dehors de celles observées (voir Temeles et al. 2006). De plus, il y a un manque flagrant d'études, autant en milieu naturel qu'en captivité, qui intègrent à la fois les mouvements et l'utilisation des parcelles de nourriture en reliant la structure de l'habitat dans lequel les colibris évoluent, la présence de compétiteurs et la quantité et la qualité des ressources alimentaires. Enfin, les colibris sont généralement exclus des analyses de patrons d'occurrence ou d'abondance en relation avec la structure du paysage en raison de leur faible niveau de détection lors des inventaires (e.g., Villard et al. 1999; Robinson et Robinson 1999). Ceci a donc pour effet de limiter encore davantage les connaissances associées aux effets de différentes composantes ou modifications des paysages sur ces oiseaux.

En se basant sur une technique récente et innovatrice de suivi des déplacements des petits oiseaux nectarivores (Charette et al. 2010, *soumis*), l'objectif principal du présent mémoire est (1) de développer un indice permettant de quantifier, sur une base quotidienne, le niveau de *traplining* adopté par des Colibris à gorge rubis au sein d'un dispositif expérimental à grande échelle spatiale en milieu naturel et (2) de mesurer l'influence de plusieurs facteurs d'importance écologique sur le niveau de *traplining* démontré par les individus. Ces variables incluent le sexe de l'individu, l'utilisation de l'espace par l'individu en termes de concentration spatiale, la compétition par les autres colibris, la structure de la végétation et les conditions météorologiques. En évaluant le niveau de *traplining* adopté par les individus, ce projet permet également de quantifier l'utilisation d'autres stratégies d'exploitation des ressources (e.g., aléatoire, directionnelle, recherche en milieu restreint,) qui pourraient être associées, par exemple, à la disposition de base des ressources dans notre aire d'étude (voir Zollner and Lima 1999; Baum et al. 2001). Finalement, mon projet de maîtrise est une première en ce qui concerne l'étude des stratégies de quête alimentaire des nectarivores en milieu naturel dans une perspective d'écologie du paysage et permet de mesurer l'influence simultanée de plusieurs variables clés sur les mouvements de ces animaux.

CHAPITRE 1 : ECOLOGICAL DETERMINANTS OF TRAPLINING TENDENCY IN FREE-RANGING RUBY-THROATED HUMMINGBIRDS

(Archilochus colubris)

MISE EN CONTEXTE

Le présent chapitre consiste en une étude portant sur les mouvements et les stratégies de quête alimentaire des Colibri à gorge rubis en nature. Les auteurs de cette étude sont Yanick Charette, François Rousseu, Alain Gervais et Marc Bélisle. Yanick Charette, l'auteur principal, a développé la technique de suivi des mouvements des colibris et est celui qui a contribué le plus à la collecte de données sur le terrain. De plus, celui-ci a exécuté et interprété la majorité des analyses statistiques des données ainsi que rédigé une version préliminaire complète de cet article. François Rousseu a contribué de façon substantielle à la collecte des données terrain. De plus, son support fût essentiel pour la gestion de l'énorme base de données que nous avons amassées au fil des ans (i.e., > 9 000 000 de lignes de données) et à contribué énormément à la programmation informatique dans le logiciel de statistiques R. Le support d'Alain Gervais, bio-informaticien, fût également requis pour fins de programmations informatiques et sa contribution mérite d'être soulignée en le plaçant sur la liste des auteurs du présent article. Marc Bélisle est l'instigateur du projet et a offert un support à tous les niveaux. Le présent chapitre est l'objet principal de ce mémoire et sera soumis en tant qu'article à une revue qui reste encore à déterminer.

ABSTRACT

Traplining is a foraging strategy whereby an individual visits in a repeatable order, in both space and time, a series of food sources whose replenishment is predictable to some point. Trapliners sometimes derogate from their route in order, for instance, to skip food sources that have become unprofitable or to look for newer or better foraging opportunities. This study explores the influence of several ecological variables on the traplining tendency of 140 breeding adult Ruby-throated Hummingbirds (*Archilocus colubris*) fitted with passive integrated transponders and foraging freely within a 44-ha grid composed of 45 artificial nectar feeders in Cleveland County, Quebec, Canada (2007-2009). Although most (84.3%) individuals included potential traplines in their movement paths on some days there was a strong variation in the traplining tendency of individuals as well as among days within individuals. Moreover, individuals showed a low propensity to trapline without derogating from their route. Overall, females exhibited a greater traplining tendency than males based on the series of nectar feeders they visited, yet they visited feeders included in potential traplines with less temporal regularity than males. While traplining tendency increased at cold temperatures, it was not affected by precipitations. Landscape composition (tree and sapling density, occurrence of forest gaps) had a greater influence on the traplining tendency of males than of females, favoring traplining when resource defense efficiency was reduced. For females, traplining tendency appeared to decrease with increasing density of natural flowers. Flower density may have caused derogations to sample and exploit these alternative sources of nectar as well as modified the cost:benefit ratio of defending feeders. In spite of the apparent negative relationship between the tendency of individuals to trapline and to defend feeders, the number of visits made by competitors at feeders within potential traplines had no bearing on traplining tendency. Traplining tendency was affected by how individuals distributed their visits among feeders, the number of feeders included in potential traplines, and the minimum-

spanning tree linking all visited feeders. Our results support the hypothesis that hummingbirds tend to trapline when environmental conditions do not favor the defense of nectar sources.

INTRODUCTION

Traplining is a foraging strategy whereby an individual visits in a repeatable order, in both space and time, a series of food sources which replenish according to a schedule that is predictable to some point (Thomson et al. 1997). By adjusting its schedule of visits to exploit standing crops of food before their rate of replenishment decreases or to limit exploitation by competitors, a traplining individual can theoretically experience a greater and less variable gross rate of food intake than if it foraged randomly or adopted an area-restricted search strategy (Possingham 1989, Ohashi and Thomson 2005). Traplining also confers the theoretical advantage of reducing the mean standing crop of resources per patch and thereby creates a vacuum of resources that can discourage competitors (defense by exploitation; Possingham 1989, Ohashi and Thomson 2005). These benefits may be improved if the trapliner optimizes its route to reduce travel costs, such as in the traveling salesman problem (Ohashi and Thomson 2005, Ohashi et al. 2006). Trapliners, however, may sometimes modify their route to leave out food sources that have become unprofitable or seek newer or better foraging opportunities (Ohashi and Thomson 2005, Ohashi et al. 2008).

Foraging patterns compatible with the spatial or temporal component of traplining have been observed in herbivores (e.g., geese; Prins et al. 1980), frugivores (e.g., monkeys; Janson 1998), insectivores (e.g., wagtails; Davies and Houston 1981), and nectarivores (e.g., bumblebees; Saleh and Chittka 2007). Yet most quantitative accounts of traplining are anecdotal (e.g., Janzen 1971) or focus on the return times of a few marked individuals at one or a very limited sample of feeding locations (e.g., Gill 1988, Williams and Thomson 1998, Temeles et al. 2006). Only a few studies, mostly on bumblebees, recorded the foraging movements of either captive or free-ranging individuals among food sources to address ecological aspects of traplining, likely because of the difficulty of tracking individuals in space for long time periods (Thomson et al. 1982, 1987, Thomson 1996, Thomson et al. 1997, Comba 1999, Makino and Sakai 2004, 2005, Makino et al. 2007, Saleh and Chittka 2007, Ohashi et al. 2006, 2008). To our knowledge, no study has integrated both spatial and temporal information to quantify traplining and assess the influence of its ecological determinants. Despite this lack of data, species or individuals are routinely classified as trapliners or nontrapliners in the literature, especially for hummingbirds (e.g., Feinsinger 1976, Gill 1988, Garrison and Gass 1999, Temeles et al. 2006). In the near-absence of empirical evidence, the same literature on hummingbirds even suggests that traplining should be exhibited by nonterritorial individuals or species. In fact, there is no reason why territorial individuals should not trapline to some point within defended areas as shown by the Pied wagtail (*Motacilla alba*) study of Davies and Houston (1981).

To quantify traplining, one minimally requires spatial data on the foraging routes taken by an individual. Because we cannot expect foragers to use the exact same trapline over time leads to a statistical challenge (Thomson et al. 1997). For instance, hummingbirds are expected to modify their trapline as they learn the location and profitability of nectar sources, sample for better foraging opportunities, and optimize their route to reduce travel costs or loss to competitors (Thomson 1996, Ohashi et al. 2006, Saleh and Chittka 2007). Derogations could also originate from foraging preferentially at the periphery of the territory early in the day to decrease the standing crop of nectar and thereby discourage potential intruders (Paton and Carpenter 1984), from chasing competitors (Davies and Houston 1981), or from engaging in courtship and mating. Traplining may occur within a hierarchy of spatial scales (i.e., flowers, inflorescences, plants, and patches of plants) and nectar quality and availability may vary over space and time (Pleasants and Zimmerman 1979, Zimmerman 1981) further complicating the assessment of traplining. Given those potential sources of derogation, a quantitative measure of an individual's traplining tendency would be more informative than simply determining whether it traplines or not. Moreover, inferring whether an individual traplines or not is afflicted by several problems (Thomson et al. 1997). First, the rejection of a null hypothesis, such as "the forager moves randomly among food patches", does not provide any evidence that traplining is being used because the forager could adopt any other strategy. Second, since strict traplining is not realistic, using this movement pattern as a null hypothesis would still require us to establish a subjective, acceptable level of derogation. Third, the level of derogation that would need to be established may vary with environmental conditions. Lastly, the non rejection of such a null hypothesis would not guarantee either that traplining is being used.

Here we first build on a new method that identifies movement path recursion (Bar-David et al. 2009) to develop two indices of traplining tendency, one that does not allow derogation and one that does. Using the two indices, we then explore the influence of several ecological variables on the traplining tendency of breeding Ruby-throated Hummingbirds (*Archilochus colubris*) fitted with passive integrated transponders and foraging freely within a 44-ha grid composed of 45 artificial nectar feeders. Hummingbirds on the grid show a large variation in both the number of feeders that they visit on a given day and their relative use of the different feeders visited on a given day, even though feeders provide nectar *ad libitum* (Rousseu 2010). Some individuals concentrate their visits to a single feeder, others distribute their visits more or less evenly among several feeders (Rousseu 2010). These contrasting patterns suggest that some individuals may attempt to defend one feeder and others to trapline. Ecological determinants of traplining tendency in our study area may thus include variables affecting resource defense, as resource defense is a likely source of traplining derogations.

We examined how traplining tendency was affected by the proportion of visits made by a hummingbird to the feeder it visited most, as well as by variables that could affect the resource holding potential of individuals, such as age, sex and parasite load (Ewald 1985, Temeles and Kress 2010). Although competitors cannot cause a steep decline in the expected standing crop of nectar as feeders "replenish" instantly, hummingbirds may still detect competitors visually (Tamm 1985, Temeles et al. 2006). We thus considered the number of visits made by competitors to feeders included in traplines as an index of competition. We also considered the availability of natural flowers along traplines as it could modify resource defense economics on the feeder grid (Grant 1993) while providing additional foraging and mating opportunities (i.e., sources of derogations; Makino et al. 2007, Temeles and Kress 2010). We characterized the habitats along traplines because landscape structure can affect territory establishment and defense (LaManna and Eason 2003, Rousseu 2010) as well as the movement paths of hummingbirds (Hadley and Betts 2009). Moreover, landscape structure may affect mating opportunities and breeding site availability in Ruby-throated Hummingbirds, which are polygynous, and possibly polygynandrous, with only females providing parental care (Robinson et al. 1996). Lastly, we measured the influence of the number and spatial spread of feeders included in traplines on traplining tendency, as these spatial variables should affect route learning, travel costs and spatial overlap with competitors (Ohashi et al. 2006, 2008). We used the above variables to address the temporal component of traplining and assess their influence on the variation in time between consecutive visits at feeders included in traplines. Hummingbirds with a strong traplining tendency should demonstrate highly regular intervisit duration (Gill 1988, Williams and Thomson 1998, Garrison and Gass 1999, Temeles et al. 2006).

METHODS

Study area and sampling design

We monitored the foraging movements of Ruby-throated Hummingbirds fitted with passive integrated transponders (PIT-tags) between 20 May and 30 August 2007-2008 on a 44-ha grid with 45 artificial feeders located in Cleveland County, Quebec, Canada (45°, 40' N; 72°, 05' W; Fig. 1). The grid comprised different vegetation covers, including hayfields (8 feeders), fallows (6 feeders), as well as mature deciduous and mixed forests (31 feeders). Feeders (Yule Hide, model HB81, capacity 455 ml) were spaced by 100 m and mounted on a metal pole 1.5

m above ground. They were covered with an olive-painted, aluminum plate (diameter: 60 cm) to reduce direct sun exposure and prevent evaporation and variation in sucrose concentration. We cleaned and replaced feeders weekly (within a few hours on the same day) and filled them with a fresh solution of 20% (w/v) sucrose, to mimic the nectar found in flowers visited by wild hummingbirds (Baker 1975, Bolten et al. 1979, Chalcoff et al. 2008).

Feeders were red and originally contained four yellow 'flowers' from which hummingbirds could drink while hovering or sitting on a small perch. We removed three of the four flowers and perches to force hummingbirds to visit a single flower. Each feeder was equipped with a PIT-tag reader (Trovan Ltd., UK, model LID650, model ANT 614 OEM; see Charette et al. submitted for details). Readers were programmed to scan for PIT tags every second and record the PIT tag ID, date, and time (hour, min, sec) if detected using the LID650/LID665/LID1260 software (Trovan Ltd., UK, version 703). We transformed time series of detections into visits characterized by a visitor ID, a start time and a duration.

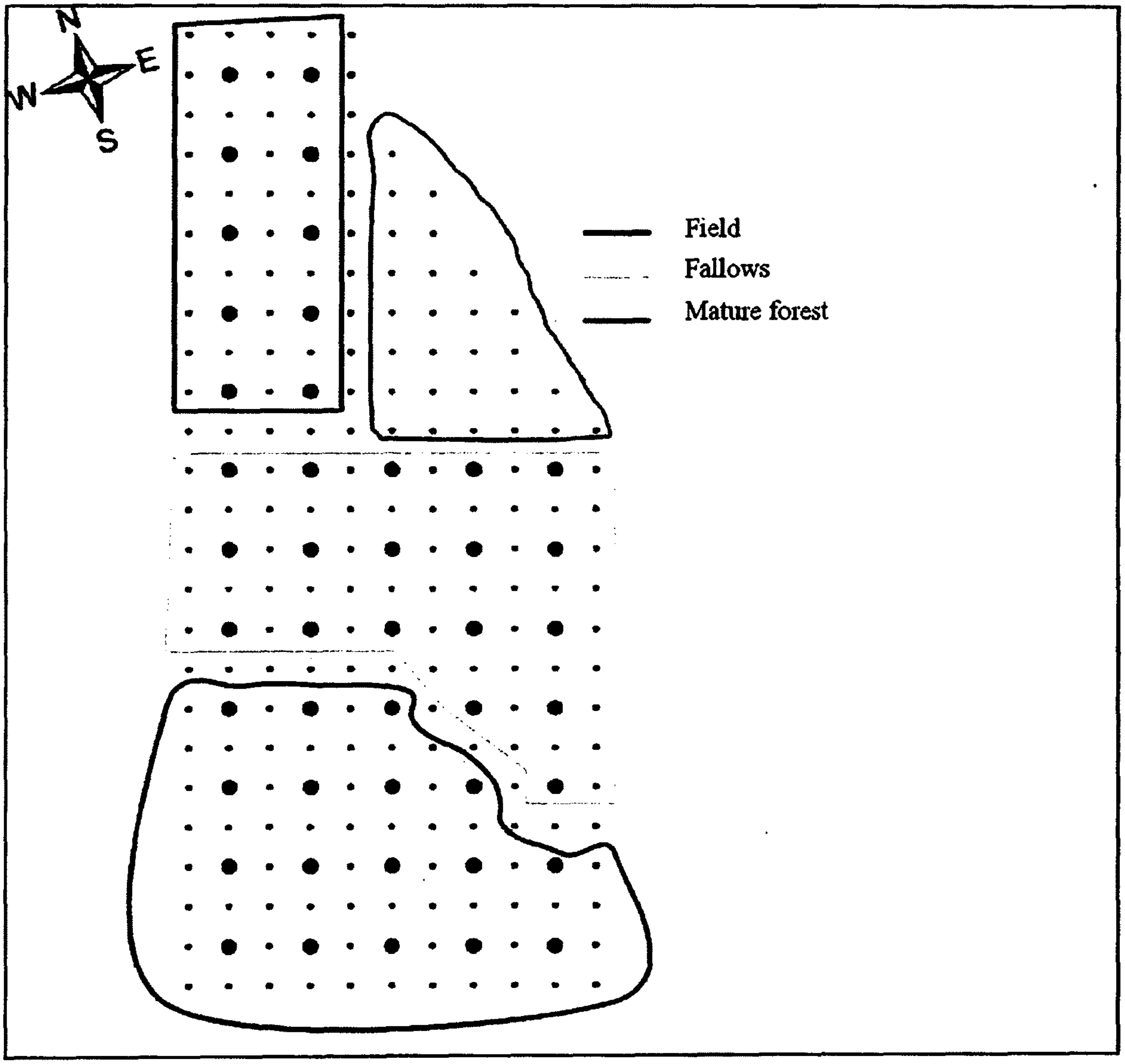


Fig. 1. Hummingbird study area consisting of a 44-ha grid composed of 45 artificial feeders, each equipped with a PIT-tag reader, and located in Cleveland County, Quebec, Canada. Feeders (large dots) were spaced by 100 m and vegetation sampling points (small dots) by 50 m.

Capturing and marking hummingbirds

We captured hummingbirds with mist nets and Hall traps (Russell and Russell 2001) between 06h00 and 13h00 (EST) throughout the study period. All feeders were subjected to a minimum capture effort every 10 day period. We oriented our capture efforts toward feeders where unmarked individuals were seen during weekly standardized focal observations. We also increased capture efforts when unmarked individuals were seen and when hummingbird activity on the grid was high. Captured individuals were fitted with an official, aluminum leg band (size X). We glued a PIT tag (Trovan Electronic Identification System, model ID100A; weight: 0.09 g; size: 2.12 x 11.50 mm) on the back feathers in the interscapular region (see Charette et al. submitted for details). We then noted the hummingbirds' body mass (± 0.1 g), wing chord (± 1 mm), exposed culmen length (± 1 mm), as well as sex and age following Pyle (1997). We also recorded the number of mallophaga hidden in the hummingbirds' throat feathers (likely *Trochiliphagus lineatus*; Price et al. 2003) as an index of parasite load. Finally, we colored the breast of hummingbirds with a non-toxic, permanent marker for visual identification (Russell and Russell 2001). Hummingbirds were allowed to drink nectar from an artificial feeder every 2-5 min throughout the manipulations.

Traplining: definitions and quantification

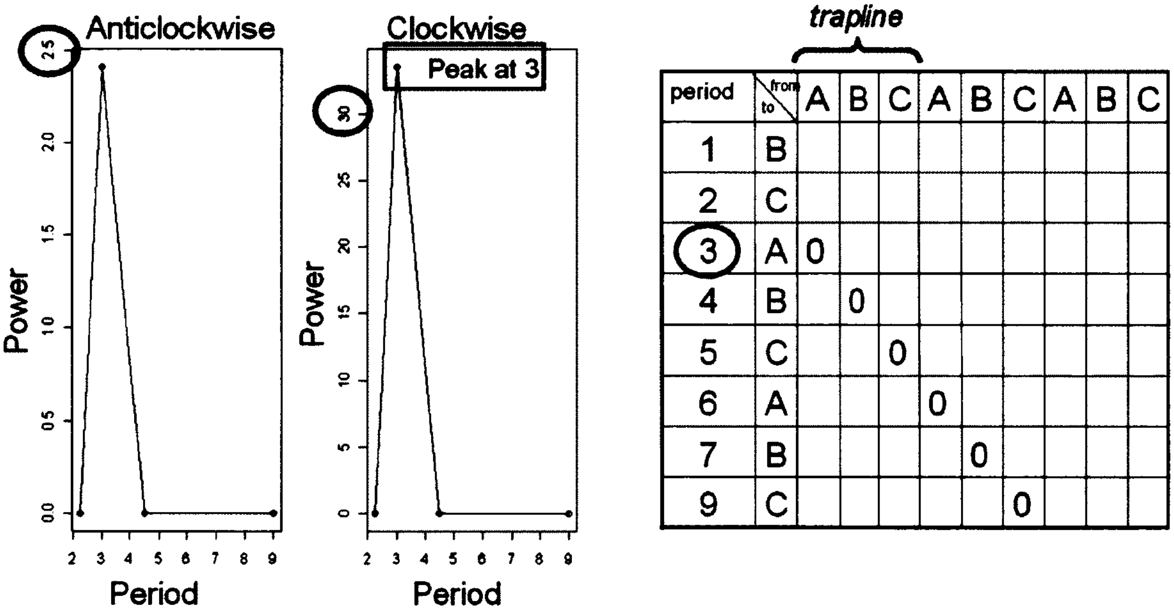
Traplining implies that visits made by an individual to food sources follow a repeatable order in both space and time. Quantifying the repeatability of foraging paths in both space and time is, however, challenging (Thomson et al. 1997). As a first spatially explicit exploration of traplining behavior, we used two traplining indices that measure repeatability of foraging paths in space and one that quantifies the variation in the duration between consecutive visits to a given food source. Each index was computed daily.

In the strictest acceptable scenario, a hummingbird could sample available food sources at the onset of the day and establish a trapline from which it will not derogate until the next morning. Our first index of spatial traplining tendency, ST for strict traplining, assesses how well individuals fit within this inflexible scenario, which matches basic traplining definitions (Thomson et al. 1997). Our second index of spatial traplining tendency, FT for flexible traplining, quantifies the propensity of individuals to trapline while being allowed to derogate from their trapline or to switch traplines during a day. Before presenting how we computed these two indices we first need to explain how we identified potential traplines.

Potential traplines were identified following Bar-David et al. (2009) to assess movement path recursions (repeated visits to a particular location). Beginning with the sequence of visits made to feeders by an individual on a given day, we built a recursion matrix which identified all closed paths as well as their length (i.e., number of feeders visited before returning to a given feeder) and locations (Fig. 2). Traplining, however, should also involve circular movement paths. Whether a recursion was part of a circular path was determined using two periodograms, for clockwise and counterclockwise cycles, based on the complex Fourier transform of the feeders' spatial coordinates (Fig. 2). Note that the conjugate of the complex Fourier transform identifies clockwise cycles instead of counterclockwise cycles (Bar-David et al. 2009). We thus identified all periods (i.e., number of feeders visited to complete a cycle) associated with peaks in both periodograms. A peak was defined as a period for which the power dropped on either side of it or on one side if the period was at the beginning or the end of the periodogram. These periods allowed us to identify which diagonals in the lower triangular recursion matrix contained recursions (denoted by zeros “0”) that were part of circular movement paths (Fig 2). If peaks were associated with non-integer period values, we considered the periods on either side of these values. Movement path segments along potential traplines corresponded to all sequences of contiguous recursions encountered on diagonals characterized by periods with peaks. Potential traplines of length *p* thus corresponded to the first *p* feeders of each sequence of contiguous recursions encountered on a diagonal characterized by a peak period of size *p*. Yet, if a recursion sequence on a given diagonal was smaller than the period associated with that diagonal, the trapline then equalled the recursion length. According to this definition, traplines may comprise food sources that are visited more frequently than others as this could occur if some food sources renew faster than others. Note that recursion "sequences" composed of only one feeder were rejected. Hence, if all recursion sequences were rejected for a given movement path, the movement data for that individual on that day were not considered in the analyses. Individuals with fewer than 15 visits to feeders on a given day were also omitted from the analyses. Recursion and circle analyses were performed in R v. 2.10.1 (R Development Core Team 2009) based on the MATLAB codes provided by Bar-David et al. (2009).

We computed the ST index of spatial traplining tendency using the diagonal (with a peak period) of the recursion matrix that contained the greatest number of contiguous recursions. Specifically, ST was obtained by dividing the length of the longest sequence of contiguous recursions on that diagonal by the length of the diagonal. If more than one diagonal or sequence were identified, the first ones were used.

Instead of focusing on a single recursion sequence, the FT index of spatial traplining tendency considered all potential traplines found in the recursion matrix. We computed FT according to an algorithm that first determined if a given visit to a feeder was part of the potential traplines. For instance, suppose that the sequence of feeders visited by an individual on a given day was {ABCABCRABBBDCAJBCAB} and that the potential trapline{ABC} was identified. The algorithm would sequentially search for A, B, C, A, B and so on until it reached the end of the feeder sequence. Feeder visits encountered according to the expected order of the {ABC} trapline would be marked as ones (1) and others as zeros (0), which would result in the occurrence vector {1111110110001101111}. The algorithm would then calculate FT as the sum of occurrences (1) divided by the length of the feeder sequence (i.e., 14/19 = 0.737). In this particular case, the FT index indicate that 73% of visits to feeders were along the {ABC} trapline. If more than one potential trapline was identified, we calculated an occurrence vector for each trapline. Feeder visits scored as (1) in at least one occurrence vector were then treated as (1) in a global occurrence vector and as zeros (0) otherwise. The FT index then indicated the proportion of visits made according to any of the potential traplines.



period	from / to	A	B	C	A	B	C	A	B	C
1	B									
2	C									
3	A	0								
4	B		0							
5	C			0						
6	A				0					
7	B					0				
9	C						0			

Fig. 2. Basic examples of a recursion matrix and periodograms used to identify potential traplines (see Methods for details). Let the sequence of feeders visited by an individual on a given day be {ABCABCABC}. That number of visits is too low to have been considered in the analyses, but this feeder sequence is used for simplicity. Both periodograms (for clockwise and anticlockwise cycles) would show a peak at a period of 3, indicating that it took 3 moves to complete a cycle. On the other hand, the lower triangle of the recursion matrix would contain zeros (0) on the diagonal of period 3. These zeros indicate recursions (i.e., repeated visits to a particular location). The fact that contiguous recursions are aligned on a diagonal with a period that peaked in at least one periodogram indicates that the recursions were part of a circular movement path. These results would identify a potential trapline {ABC}.

Traplining also requires that individuals synchronize their visit to food sources to maximize benefits from resource replenishment and to minimize losses to competitors (Gill and Wolf 1977, Gill 1988, Williams and Thomson 1998). Based on this rationale, traplining individuals should return to food sources at regular intervals (Williams and Thomson 1998). Traplining tendency should therefore be inversely proportional to variation in the time between consecutive visits to individual feeders in a trapline. We quantified this variation using the standard deviation of the intervisit durations (± 1 sec; SD.IVD) to each feeder in a trapline. Because some intervisit durations were very large (i.e., > 50 000 sec) and potentially caused by observers replacing feeders, we computed the standard deviation after trimming the first and last 5th percentiles of durations on each day. Note that SD.IVD was log-transformed prior to model fitting.

Potential determinants of traplining tendency

As mentioned in the Introduction, many variables may affect the traplining behavior of hummingbirds and lead to derogations from the spatio-temporal patterns expected from this foraging behavior (Table 1). How we measured these explanatory variables is detailed below.

Meteorological conditions

We measured daily precipitations (± 1 mm) at 6h00 (EST) using a pluviometer located in field habitat. Precipitations that may have affected traplining in a given day were thus measured the next day. We placed one Thermochron® iButton® (Embedded Data Systems, model DS1922L) in the center of each of the three main habitat types found in our study area: hayfields, fallows and forests, to record temperature (± 0.5 °C). We programmed iButtons to record temperature once per hour throughout the study. Since the three habitat types covered areas of similar sizes, we calculated the average temperature on a given day as the mean hourly temperatures from 21h00 on the previous day to 21h00 on the focal day across the three habitats. This period covered the time during which hummingbirds fasted at night then fed during the day of interest.

Landscape composition

We quantified landscape composition within a 10-m buffer zone on each side of potential traplines used by hummingbirds on a given day. We delimited buffer zones following the actual sequence of feeders visited by hummingbirds along traplines. Landscape composition variables (i.e., tree, sapling and flower densities as well as forest gap occurrence) were first measured on a systematic grid of 236 sampling points spaced by 50 m (Fig. 1) before estimating the value of each variable within 277.8-m^2 square pixels by kriging. We then computed the value of each landscape composition variable by averaging across pixels included in trapline buffers weighted by the number of times the hummingbird visited the pixel.

We estimated tree density using a basal area prism and "sapling" density by counting stems with 1-9-cm DBH in a 2.2-m radius centered on the sampling point. We considered that a forest gap (> 50 m^2) was present when found within 15 m from a sampling point. While these variables were measured once in June 2006, the number of flowers of herbaceous plants and fruit trees (e.g., *Amelanchier* spp., *Prunus* spp.) was counted in a 2.2-m radius centered on the sampling point every two weeks between early May and late August 2007 and 2008. We used flower densities measured on the date closest to that of traplines in the analyses.

We performed kriging in ArcGIS v. 9.2 (ESRI 2006) after having determined the correct semi-variance function to be used with a variogram computed with the package GeoR v. 1.6-25 in R

v. 2.10.1 (R Development Core Team 2009). The variogram analysis suggested a Gaussian model for kriging interpolation with all landscape composition variables, except for forest gap occurrence, which required a spherical model.

Competition

We assessed the influence of competition on traplining tendency (i.e., ST and FT) using the number of visits made by competitors to feeders comprised in an individual's traplines as a daily index of competition. When modeling SD.IVD, we used the daily number of visits made by competitors to the focal feeder. These estimates assume (1) that hummingbirds can assess competition from the foraging activity of competitors, because feeders provided nectar *ad libitum* (Tamm 1985); (2) that the amount of nectar taken by competitors is proportional to the number of visits made by competitors; and (3) that the number of visits made by competitors fitted with a PIT tag is proportional to those made by hummingbirds without a PIT tag. Although we cannot assess the validity of last two assumptions, we believe that our trapping effort kept the proportion of unmarked individuals very low and homogeneous across the study area, which lend support to the second assumption.

Space use

We used three variables that characterized the use of space by an individual hummingbird on a given day, namely the level of spatial concentration, the number of trapline feeders, and the minimum spanning tree (MST; Urban et al. 2009) linking all visited feeders. When modeling traplining tendency based on the ST and FT indices, spatial concentration consisted of the proportion of visits to the most visited feeder. On the other hand, we defined spatial concentration as the proportion of visits made to the feeder of interest when modeling SD.IVD. The number of trapline feeders was the total number of feeders included in potential traplines. We computed the minimum distance linking all visited feeders, independently of their occurrence in a potential trapline, as a MST using the packages ecodist v. 1.1.2 and vegan v. 1.17-0 in R v. 2.10.1 (R Development Core Team 2009).

Statistical analyses

We defined a set of nine models for each response variable that assessed traplining tendency of individual hummingbirds on a given day (i.e., ST, FT and SD.IVD; Table 2). These models contrasted plausible hypotheses regarding traplining tendency based on theory and empirical observations (Table 1). For ST and FT indices we used generalized linear mixed models with a logit link function and binomial errors (Gelman and Hill 2007) because these indices were proportions. Because individual hummingbirds were usually observed on several days, individual ID was treated as a random factor. In contrast, for the log-transformed SD.IVD index we used generalized linear models with an identity link function and Gaussian errors (Gelman and Hill 2007). Because the SD.IVD index was computed for each feeder included in potential traplines, we included both feeder and hummingbird IDs as random factors. All models were fitted using the lme4 v. 0.999375-32 package in R v. 2.10.1 (R Development Core Team 2009). We fitted models only for adult hummingbirds because we were not able to track the foraging movements of enough juvenile birds.

We compared the models of each set based on the second-order Akaike information criterion (AIC$_c$), and resulting Akaike weight (w_i), following Vaida and Blanchard (2005). Because no single model clearly outclassed others for the ST and SD.IVD indices (Table 2), we performed multimodel inference following Burnham and Anderson (2002) to assess the influence of explanatory variables on these traplining tendency indices. In all cases, we report unconditional standard errors computed according to equation 6.12 of Burnham and Anderson (2002) and resulting unconditional 95% confidence intervals. This form of unconditional standard error is advocated by Anderson (2008). We conducted model selection on models fitted by maximum likelihood using the Laplacian approximation and performed model averaging with parameter values obtained by restricted maximum likelihood.

RESULTS

We tracked the foraging movements of 65 adult males and 75 adult females in 2007-2008, for a total of 4,123 movement paths. Movement paths included an average (± SD) of 61.0 ± 31.2 visits at feeders. About half (52.8%) of the movement paths included potential traplines. Among movement paths that did not include traplines, 19.3% involved < 15 visits at feeders and 27.8% did not include at least 2 feeders or 2 recursions. These cases were thus often associated to individuals that did not make a strong use of feeders or that were spatially concentrated at a single feeder on a given day, respectively. Although most (84.3%) individuals included potential traplines in their movement paths on one day or another, there was a strong variation in the traplining tendency of individuals as well as among days within individuals, based on both the ST and FT indices (Fig. 3). However, the ST index was much lower than the FT index, suggesting that Ruby-throated Hummingbirds have a low propensity to trapline according to the strict definition of traplining typically found in the literature (Thomson et al. 1997).

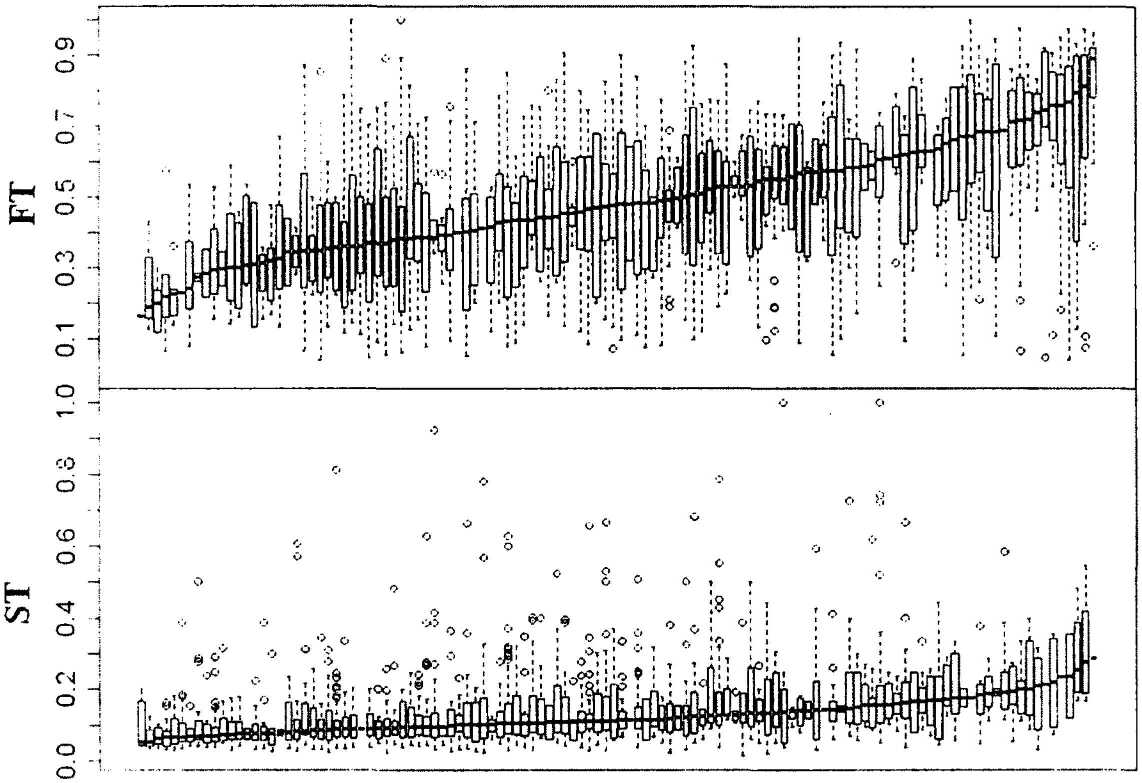


Fig. 3. Box-plots illustrating the distribution of the daily, spatial traplining tendency of 118 adult Ruby-throated Hummingbirds based on the strict (ST) and flexible (FT) definition of traplining tendency (see Methods; n = 2,178 movement paths; 1 path/day/individual). Individuals have been ranked according to median values.

Strict traplining (ST)

Of the 9 models, #1 and 2 accumulated 98.5% of Akaike weights (Table 2). Although both models included variables from each group of explanatory variables (Table 1), the model including two-way interactions between sex and landscape composition, sex and Julian date, and between temperature and rain (#1) was three times more likely than the other (#2). According to our predictions (Table 1), multimodel inference revealed that females showed a greater traplining tendency than males (Table 3). The sex difference remained constant over the breeding season, in contrast to our prediction that it should vary with breeding phenology. Body mass and parasite load did not influence ST, but traplining tendency according to this index increased with temperature independently of precipitation. Unexpectedly, however, the amount of precipitations had no effect on ST.

Among landscape composition variables (Table 1), only tree density and the occurrence of a forest gap affected ST (Table 3). As expected, ST increased with tree density for males and decreased slightly for females. Moreover, ST increased with the occurrence of forest gaps for males, but decreased for females. Although the level of competition did not seem to influence traplining tendency, ST increased unexpectedly with the spatial concentration of the focal hummingbird. Analogously, ST increased with the total number of feeders contained in potential traplines while we expected a decrease. Lastly, ST decreased as expected with the MST linking all feeders included in potential traplines.

Table 1. Potential determinants of traplining tendency for 118 adult Ruby-throated Hummingbirds in southern Quebec, Canada, 2007-2008. Spatial traplining tendency was measured according to a strict (ST) and a flexible (FT) definition. Temporal traplining tendency was assessed through the standard deviation of intervisit durations at feeders included in traplines identified using the FT index (SD.IVD; see Methods for details).

Group	Variable (units)	Justification	Effect on ST or FT	Effect on SD.IVD
date	Year (reference = 2007)	Partly controls for unmeasured environmental variations.	±	±
	Julian date	Traplining tendency may vary with breeding phenology due to its link with resource defense (1-3).	±	±
ind	Sex (reference = males)	Traplining should mainly be used by non-territorial individuals (1,3). Males are expected to defend territories or food sources to attract females (2).	+	-
	Body mass (g)	May reflect body condition and dominance status. These can in turn affect resource defense and monopolization (4,5).	±	±
	Parasite load (number of parasites)	See Body mass.	±	±
meteo	Temperature (°C)	May affect thermoregulation costs, insect availability and resource needs (6).	±	±
	Rain (mm)	See Temperature.	±	±
land	Tree density (number of trees)	Resource defense increases with visibility in forest habitat (7). Forest cover/gaps may affect movement (8).	+	-

	Sapling density (saplings/m^2)	See Tree density.	+	-
	Flower density (flowers/m^2)	Use of artificial feeders decreases with abundance of natural flowers (9,10) and may affect the value of feeders with respect to resource defense and monopolization (11).	-	+
	Forest gap (reference = occurrence)	Resource defense is lower in open habitat compared to forest (7). Forest cover/gaps may affect movement (8).	+	-
comp	Competition (number of visits made by competitors at trapline feeders [ST, FT] or at a focal trapline feeder [SD.IVD])	Traplining should occur under relatively strong competition for nectar (1,3). Resource monopolization decreases with the number of competitors (7). Territory size and chasing activity increases with intruder pressure in some hummingbird species (12,13).	+	-
space	Spatial concentration (proportion of visits made to a given feeder by a focal individual [SD.IVD] or to the most visited feeder of an individual's traplines [ST, FT])	Spatial concentration at a given feeder is negatively correlated with the number of visits made by competitors at that feeder (7). The proportion of visits made to the most visited feeder by an individual may thus reflect its resource defense strategy, if any, and thereby its traplining tendency.	-	+
	Number of feeders (within potential traplines)	Territorial individuals are expected to exploit a smaller number of food sources than traplining individuals (7,11,14). Yet more feeders increases the likelihood of derogations.	±	±
	MST (minimum spanning tree linking all visited feeders in m)	Territorial individuals are expected to exploit food sources that are more concentrated in space, as they are more defendable, than traplining individuals (7,11,14). Yet feeders spread in space increases the likelihood of derogations.	±	±
interactions	Sex × Julian date	Traplining may vary with breeding phenology, especially for	±	±

	females, as males do not provide any form of parental care (2,15).		
Temperature × Rain	Effects of cold temperatures may be exacerbated by rain (see Temperature).	±	±
Sex × Tree density	Habitat openness affects resource defense and may thereby have a preponderate influence on male resource exploitation strategies compared to females (2,7). Males and females are not found in the same habitats (16; see Appendix 1).	-	+
Sex × Sapling density	See Sex × Tree density.	-	+
Sex × Flower density	Males are expected to defend territories or food sources to attract females (2). Flower density, which may affect the value of feeders and thereby resource defense and monopolization (11-13), may thus have a preponderate influence on resource exploitation strategies of males compared to that of females (2,7).	±	±
Sex × Forest gap	See Sex × Tree density.	-	+
Sex × Competition	Competitor pressure affects resource defense and may thereby have a preponderate influence on male resource exploitation strategies compared to females (2,7,11-13).	-	+

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1. Gill (1988). 2. Robinson et al. (1996). 3. Temeles et al. (2006). 4. Carpenter et al. (1983). 5. Witter and Cuthill (1993). 6. Suarez and Gass (2002). 7. Rousseu (2010). 8. Hadley and Betts (2009). 9. Inouye et al. (1991). 10. McCaffrey and Wethington (2008). 11. Grant (1993). 12. Tamm (1985). 13. Eberhard and Ewald (1994). 14. Temeles et al. (2005). 15. Baltosser (1996). 16. Armstrong (1987).

Flexible traplining (FT)

The data supported only model #1 for the FT index (Table 2). Although this was also the best model for ST, the determinants of traplining tendency, as well as their effect sizes, varied between the two indices (Table 3). Again supporting our predictions (Table 1), females generally had a greater propensity to trapline than males. This effect of sex, however, varied with landscape composition along potential traplines (see below). Moreover, traplining tendency decreased slightly over the breeding season and more so for females than males. As for ST, parasite load did not affect FT. Yet, FT decreased marginally with body mass. Contrary to our predictions, neither temperature nor the amount of precipitations affected FT.

Table 2. Model selection for traplining tendency of 118 adult Ruby-throated Hummingbirds in southern Quebec, Canada, 2007-2008. Spatial traplining tendency was measured according to a strict (ST) and a flexible (FT) definition. Temporal traplining tendency was assessed through the standard deviation of intervisit durations at feeders included in traplines identified using the FT index (SD.IVD; see Methods). Meaning and rationale of explanatory variables or groups of variables can be found in Table 1. Models consisted in generalized linear mixed models and included individual ID as a random term for ST and FT, and individual ID and feeder ID for SD.IVD. SD.IVD has been log-transformed prior to model fitting. K, □AICc, and wi correspond to the number of model parameters, difference in second-order Akaike information criterion (AICc) values between model i and the model with lowest AICc, and Akaike weight of model i, respectively.

Model #	Index	Model	K	⊗AIC$_c$	w_i
1	ST	date + ind + meteo + land + comp + space + sex.Julian + temp.rain + sex.land	22	0.00	0.740
2		date + ind + meteo + land + comp + space	18	2.22	0.245
3		date + ind + meteo + comp + space + sex.Julian + temp.rain	14	7.77	0.015
4		date + ind + sex.Julian	7	804.38	0.000
5		date + sex + meteo + sex.Julian + temp.rain	7	755.30	0.000
6		date + sex + land + sex.Julian	8	759.01	0.000
7		date + sex + space^a + sex.Julian	6	303.75	0.000

8		date + sex + comp + sex.Julian	5	777.88	0.000
9		date + sex + sex.Julian	4	813.90	0.000
1	FT	date + ind + meteo + land + comp + space + sex.Julian + temp.rain + sex.land	22	0.00	1.000
2		date + ind + meteo + land + comp + space	18	168.12	0.000
3		date + ind + meteo + comp + space + sex.Julian + temp.rain	14	236.09	0.000
4		date + ind + sex.Julian	8	5343.40	0.000
5		date + sex + meteo + sex.Julian + temp.rain	7	5452.23	0.000
6		date + sex + land + sex.Julian	8	5320.46	0.000
7		date + sex + space + sex.Julian	7	276.56	0.000
8		date + sex + comp + sex.Julian	5	4934.81	0.000
9		date + sex + sex.Julian	4	5461.69	0.000
1	SD.IVD	date + ind + meteo + flower + comp + space + sex.Julian + temp.rain + sex.land + FT	19	1.01	0.353
2		date + ind + meteo + flower + comp + space + FT	15	4.49	0.062
3		date + ind + meteo + comp + space + sex.Julian + temp.rain + FT	16	0.00	0.585
4		date + ind + sex.Julian	8	1890.47	0.000
5		date + sex + meteo + sex.Julian + temp.rain	7	1877.17	0.000
6		date + sex + flower + sex.Julian	7	1895.51	0.000
7		date + sex + space + sex.Julian + FT	8	44.43	0.000
8		date + sex + comp + sex.Julian	5	1791.55	0.000
9		date + sex + sex.Julian	4	1904.25	0.000

[a] This model did not converged with MST as a descriptor of space use. This term was therefore dropped from the space variables (see Table 1).

All of the landscape composition variables (Table 1) influenced traplining tendency according to FT (Table 3). As for ST and supporting our predictions, FT increased with tree density for males and decreased slightly for females, leading to a difference in FT between sexes only at low tree densities (Fig. 4a). The same relationships occurred for sapling density. Yet, FT increased with the occurrence of forest gaps for males, but decreased for females, as we expected and observed for ST (Fig. 4b). Contrary to ST, FT decreased with natural flower density for females as expected, but remained relatively unaffected for males (Fig. 4c). As for ST, FT was not affected by the number of visits made by competitors at feeders within potential traplines despite a predicted increase. On the other hand, FT decreased as predicted with the level of spatial concentration of the focal hummingbird (Fig. 4d). The opposite was surprisingly observed for ST. Nevertheless, FT increased with the total number of feeders contained in potential traplines (Fig. 4e) as we observed for ST when predicting a decrease. Like ST, FT decreased as expected with the MST linking all feeders included in potential traplines (Fig. 4f).

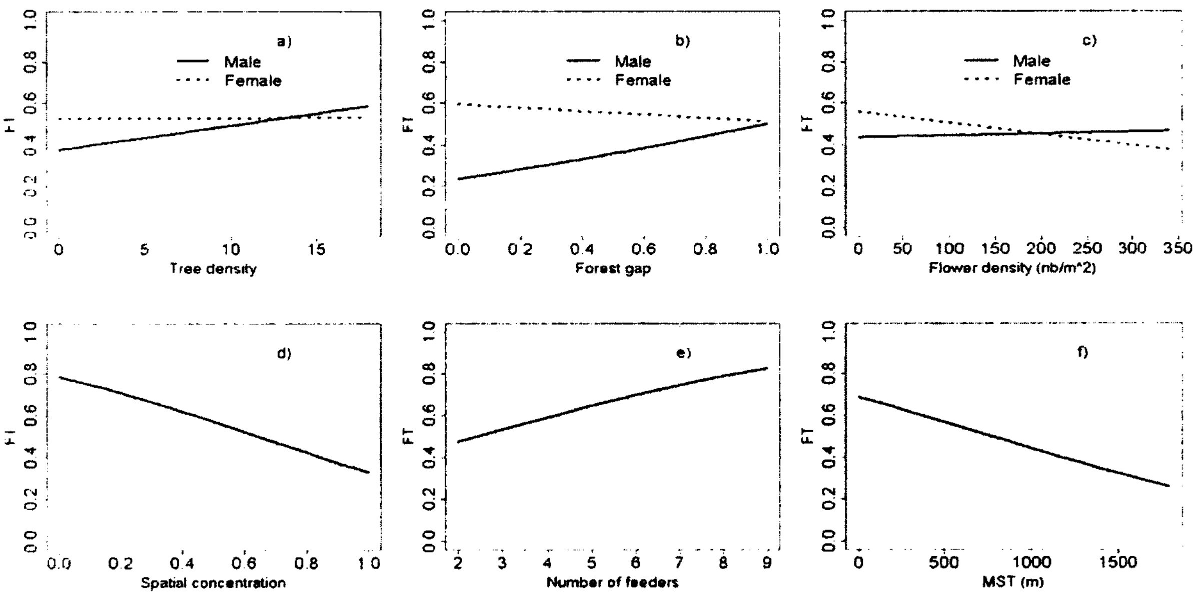

Fig. 4. Determinants of the daily, spatial traplining tendency of 118 adult Ruby-throated Hummingbirds in southern Quebec, Canada, 2007-2008. Traplining tendency was based on its flexible (FT) definition (see Methods; n = 2,178 movement paths; 1 path/day/individual). Meaning and rationale of explanatory variables can be found in Table 1. Predicted values result from multimodel inference using females and 2008 as reference categories (Table 3).

Predicted values are shown over the observed ranges of explanatory variables, while maintaining other explanatory variables at their mean values.

Table 3. Results of the multimodel inference regarding the spatial traplining tendency of 118 adult Ruby-throated Hummingbirds tracked in southern Quebec, Canada, 2007-2008. Traplining tendency was measured according to a strict (ST) and a flexible (FT) definition (see Methods). Meaning and rationale of explanatory variables can be found in Table 1. Models consisted in generalized linear mixed models and included individual ID as a random term. Multimodel inference was based on the model selection found in Table 2. Reference category for Year and Sex are 2007 and males, respectively.

	ST				FT			
Variable	Coef	SE	Lower 95% CI	Upper 95% CI	Coef	SE	Lower 95% CI	Upper 95% CI
Year (2008)	-0.098	0.033	-0.162	-0.034	0.131	0.028	0.076	0.186
Julian date	-0.001	0.001	-0.003	0.001	-0.002	0.001	-0.004	0.000
Sex (female)	1.049	0.356	0.351	1.747	2.507	0.279	1.960	3.054
Body mass	-0.100	0.073	-0.243	0.043	-0.349	0.066	-0.478	-0.220
Parasite load	0.003	0.005	-0.006	0.013	0.008	0.005	-0.002	0.018
Temperature	0.023	0.004	0.016	0.031	-0.002	0.003	-0.008	0.004
Rain	-0.013	0.012	-0.036	0.010	-0.007	0.007	-0.021	0.007
Tree density	0.026	0.010	0.007	0.045	0.047	0.007	0.033	0.061
Sapling density	0.002	0.004	-0.006	0.009	0.030	0.003	0.024	0.036
Flower density	0.000	0.000	-0.001	0.000	0.000	0.000	0.000	0.000
Forest gap (occurrence)	0.219	0.172	-0.119	0.556	1.160	0.126	0.913	1.407
Competition	0.000	0.000	-0.001	0.000	0.000	0.000	0.000	0.000
Spatial concentration	0.841	0.062	0.720	0.963	-2.003	0.043	-2.087	-1.919
Number of feeders	0.089	0.039	0.013	0.165	0.235	0.008	0.219	0.251
MST	-0.001	0.000	-0.001	0.000	-0.001	0.000	-0.001	-0.001
Sex × Julian date	-0.002	0.001	-0.004	0.006	-0.002	0.001	-0.004	0.000
Temperature × Rain	0.000	0.001	-0.001	-0.002	0.000	0.000	0.000	0.000
Sex × Tree density	-0.036	0.013	-0.061	-0.010	-0.046	0.010	-0.066	-0.026
Sex × Sapling density	-0.014	0.009	-0.032	0.004	-0.050	0.007	-0.064	-0.036

Sex × Flower density	0.000	0.001	-0.001	0.001	-0.003	0.000	-0.003	-0.003
Sex × Forest gap	-0.438	0.218	-0.865	-0.011	-1.503	0.158	-1.813	-1.193

Intervisit duration (SD.IVD)

In light of the above results, we computed SD.IVD only for feeders included in potential traplines identified through the FT index. Fewer explanatory variables influenced the ST index according to predictions, compared to FT. Moreover, FT seems more biologically acceptable than ST as it allows derogations along traplines as well as temporal variations in trapline structure. We thus calculated SD.IVD based on 132,923 visits made over 6,372 feeder·days by 118 adult Ruby-throated Hummingbirds.

The three same models selected when measuring spatial traplining tendency through the ST and FT indices were supported by the SD.IVD data (i.e., #1-3; Table 2). These models emphasized the importance of determinants found in all groups of explanatory variables as well as sex-specific effects of landscape composition (Table 1). Multimodel inference, however, indicated that many variables did not have biologically relevant effect sizes (Table 4). Contrary to our expectations (Table 1) and the fact that females showed a greater spatial traplining tendency than males (Table 3), females visited trapline feeders with less temporal regularity (Table 4). Analogously, SD.IVD decreased over the breeding season and more so for females than males (Fig 5a). Body mass and parasite load did not affect SD.IVD. While temperature had a positive influence on SD.IVD (Fig. 5b), and this independently of the amount of precipitations, the latter had no effect on SD.IVD.

Table 4. Results of the multimodel inference regarding the temporal traplining tendency of 118 adult Ruby-throated Hummingbirds tracked in southern Quebec, Canada, 2007-2008. Traplining tendency was measured as the standard deviation of intervisit durations at feeders included in traplines identified using the FT index (SD.IVD; see Methods). Meaning and rationale of explanatory variables can be found in Table 1. Models consisted in generalized linear mixed models applied to log-transformed SD.IVD values and included individual ID and feeder ID as random terms. Multimodel inference was based on the model selection found in Table 2. Reference category for Year and Sex are 2007 and males, respectively.

Variable	Coef	SE	Lower 95% CI	Upper 95% CI
Year (2008)	-0.042	0.036	-0.112	0.029
Julian date	-0.001	0.001	-0.002	0.001
Sex (female)	0.377	0.516	-0.634	1.388
Body mass	-0.058	0.078	-0.210	0.095
Parasite load	0.001	0.006	-0.010	0.012
Temperature	0.020	0.006	0.008	0.033
Rain	-0.004	0.021	-0.046	0.038
Flower density	0.000	0.000	0.000	0.001
Competition	0.001	0.000	0.000	0.001
Spatial concentration	-1.925	0.048	-2.019	-1.830
Number of feeders	0.011	0.010	-0.008	0.029
MST	0.000	0.000	0.000	0.000
Sex × Julian date	-0.003	0.001	-0.005	0.000
Temperature × Rain	0.001	0.001	0.000	0.002
Sex × Flower density	-0.001	0.000	-0.001	0.000
Sex × Competition	-0.001	0.001	-0.002	0.001
FT	0.332	0.062	0.211	0.453

In contrast to our predictions (Table 1), neither the density of natural flowers nor the number of visits made by competitors at trapline feeders influenced SD.IVD (Table 4). Yet, SD.IVD decreased with the level of spatial concentration of the focal hummingbird as we had predicted (Fig. 5c). Contrary to ST and FT, SD.IVD did not vary according to the total number of feeders contained in potential traplines nor with the MST linking these feeders. Although we predicted a negative correlation between FT and SD.IVD, we observed the contrary (Fig. 5d).

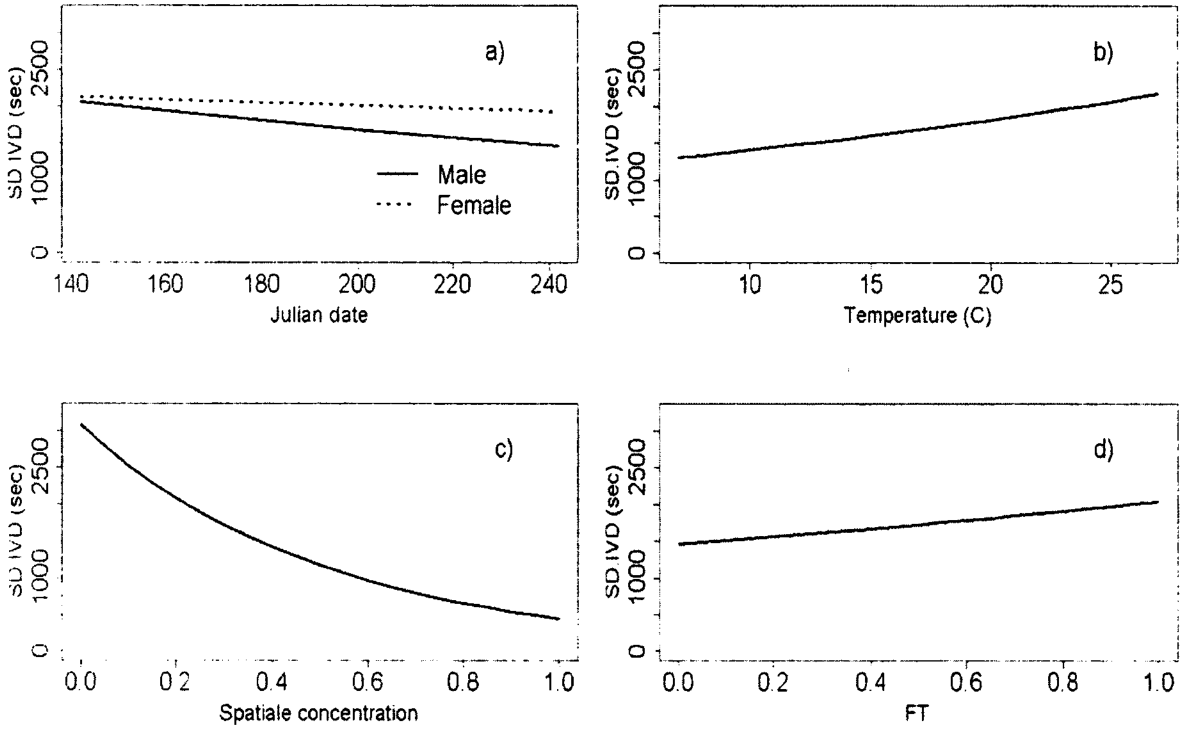

Fig. 5. Determinants of the daily, temporal traplining tendency of 118 adult Ruby-throated Hummingbirds tracked in southern Quebec, Canada, 2007-2008. Traplining tendency was measured as the standard deviation of intervisit durations at feeders included in traplines identified using the flexible, spatial traplining (FT) index (SD.IVD; see Methods; *n* = 132,923 visits). Meaning and rationale of explanatory variables can be found in Table 1. Predicted values (in sec) result from multimodel inference using females and 2008 as reference categories (Table 4). Predicted values are shown over the observed ranges of explanatory variables, while maintaining other explanatory variables at their mean values.

DISCUSSION

Our study innovates in many aspects. First, it is the first to track precisely, in both space and time, the large-scale foraging movements of free-ranging hummingbirds. Second, it builds on a new method that identifies path recursions (Bar-David et al. 2009) to propose two indices of the spatial traplining tendency of individuals. These two indices clearly reveal that Ruby-throated Hummingbirds are unlikely to trapline according to the typical definition of trapline foraging, which implies that food sources should be visited in a strict repeatable order (Thomson et al. 1997). Third, this study quantifies the influence of several variables on both the spatial and temporal components of trapline foraging. Our results suggest that variables known to influence resource defense and monopolization also affect the traplining tendency of individuals, as expected based on the hypothesis that traplining is more likely to be exhibited by nonterritorial individuals or species (e.g., Gill 1988, Temeles et al. 2006).

Traplining: definitions and quantification

We quantified traplining tendency by identifying path recursions, and thereby potential traplines, using objective, quantitative criteria (see Bar-David et al. 2009). This method allowed us to derive indices of traplining tendency from the entire series of visited food sources. This was a clear advantage compared to previous methods (Thomson et al. 1997), which subjectively deleted rare transitions among visited food sources and were thereby more likely to identify (long) traplines or to infer that individuals used traplining.

By using a spatial traplining tendency index (ST) that penalized derogations from the potential trapline associated with the greatest number of moves without derogations, we showed that breeding Ruby-throated Hummingbirds rarely visit food sources according to a strict repeatable order during a given day (Fig. 3). Moreover, we found that the time between subsequent visits to a given feeder within potential traplines (SD.IVD) was often highly variable (Fig. 5). These results must be interpreted according to the spatial and temporal scales of our study, as well as to the nature of food sources. We quantified traplining tendency over 1-day periods within a 44-ha habitat mosaic containing 45 very rich food sources systematically spaced by 100 m. First, one may expect "strict traplining" to occur at lower spatial and temporal scales, such as among flowers composing inflorescences (e.g., Feinsinger 1976, Stiles and Wolf 1979, Wolf and Hainsworth 1991, Garrison 1995, Temeles et al. 2006). Need for sampling and stochastic sources of derogations, such as interactions with competitors or mates, are necessarily less likely to interfere with "strict traplining" at small spatial and temporal scales. Second, the fact that nectar feeders did not deplete mimicked very rich food sources. Traplining being thought to occur under strong competition (Gill 1988, Temeles et al. 2006), our setup may not favor this foraging strategy in its most strict form. Our results, however, stress the importance of investigating traplining behavior within a hierarchy of spatial and temporal scales, as well as within a system allowing various, yet standardized or known, schedules or levels of food depletion. Although our indices of traplining tendency helped pushing the envelope further regarding our understanding of hummingbird foraging strategies, some efforts should be spent developing an index that integrates the traplining tendency of individuals in both space and time.

Potential determinants of traplining tendency

A large variation in spatial traplining tendency was observed both among individuals and among days within individuals (Fig. 3). Analogously, we found a large variation in temporal traplining tendency among individuals as well as among feeders included in potential traplines (results not shown). These results clearly indicate the existence of a gradient in traplining tendency among individual Ruby-throated Hummingbirds. Furthermore, these results suggest that Ruby-throated Hummingbirds can alter their traplining tendency according to environmental conditions.

Individual characteristics

Among individual characteristics, which included body mass, parasite load and sex, only sex was identified as a determinant of traplining tendency. Moreover, females exhibited a greater overall spatial traplining tendency than males, as expected based on the fact that males are hypothesized to defend resource patches to attract females (Robinson et al. 1996). Nevertheless, in opposition to this finding, females visited trapline feeders with less temporal regularity than males. This apparent contradiction may result from the fact that our traplining tendency indices were calculated over an entire day. At such a large temporal scale, it is possible that females showed less temporal regularity in their visits to feeders outside periods during which they used traplining. This greater variation of intervisit durations in females may be linked with the need to feed chicks in a nest. Male hummingbirds do not participate in parental care (Baltosser 1996, Robinson et al. 1996). This potential explanation is reinforced by the fact that female traplining tendency decreased (more than for males) as the season progressed based on the FT index while it increased (more than for males) based on SD.IVD.

Meteorological conditions

Temperature and humidity certainly constrains the ecophysiology of birds especially that of hummingbirds which have very high mass specific metabolic rate (Suarez and Gass 2002). Indeed, energy demands are likely to increase at low temperatures, especially when it rains

(Suarez and Gass 2002, Wilson et al. 2004). How individuals modify their activity budgets and foraging strategies in face of those constraints is nevertheless difficult to predict, partly because of the thermogenesis implied by physical activity (Suarez and Gass 2002, Welch and Suarez 2008). We observed an increase in temporal traplining tendency at cold temperatures, and this when mean daily temperatures ranged from 7 to 27 °C while controlling for Julian date (Fig. 5b). This result was however not backed up by a similar effect on spatial traplining tendency. Moreover, we found no evidence that precipitations influenced traplining tendency. The absence of a relationship between precipitations and traplining tendency may simply result from the fact that we measured precipitations once per day. At this temporal scale, we probably lacked the resolution necessary to link rain episodes with bouts of a specific foraging behavior. Quantifying the importance (i.e., correlation strength) of the various pathways by which temperature and precipitations determine the foraging strategies of hummingbirds will likely prove to be a challenge as meteorological conditions are known to affect the availability of both flower nectar and insects (Taylor 1963, Wilmer 1982), which may in turn influence the profitability of resource defense and monopolization (Powers and McKee 1994, Temeles et al. 2004, 2005, 2006).

Landscape composition

The increase in spatial traplining tendency with tree and sapling density observed for adult males (Fig. 4a) may result from the reduced efficiency of adult male Ruby-throated Hummingbirds at monopolizing resources in dense forest habitat (Rousseu 2010). Unprofitable conditions for resource defense and monopolization are indeed hypothesized to lead to a greater profitability and use of traplining (Gill 1988, Temeles et al. 2006). Analogously, spatial traplining tendency increased for males in presence of forest gaps (Fig. 4b), an habitat where feeder defense and monopolization are likely reduced because of a greater influx of male competitors and lack of perching sites nearby feeders (Rousseu 2010).

We have no clear explanation for the decrease in spatial traplining tendency of females in presence of forest gaps as this sex is thought to be much less territorial than males (Robinson et al. 2006, Rousseu 2010). One possibility is that females have a greater reluctance than males to fly in the open (Hadley and Betts 2009) and we indeed noted on our feeder grid that males mostly visited feeders in open habitats, whereas females concentrated their visits to feeders under forest cover, suggesting differential habitat preferences or displacement of one sex by another.

While spatial traplining tendency decreased with natural flower density for females and remained stable for males (Fig. 4c), temporal traplining tendency was not affected in either sex. The presence of flowers could explain the decrease in spatial traplining tendency of females as these alternative sources of nectar (Pleasants and Zimmerman 1979, Zimmerman 1981, Pleasants and Chaplin 1983) should lead to derogations associated with sampling or exploitation (Ohashi and Thomson 2005, Makino et al. 2007, Ohashi et al. 2008). Although this the same effect should also apply to males, the density of natural flowers may have modified the cost:benefit ratio of defending feeders and thereby masked its effect on male traplining tendency (Tamm 1985, Grant 1993, Eberhard and Ewald 1994). Overall, the sex-dependent influence of landscape composition on traplining tendency support the existence of a spatial segregation based on a sex-dependent use of habitat (Armstrong 1987, Desroches 2011). Nevertheless, whether such a spatial segregation, as observed on our study area (Appendix 1), result from a competitive exclusion of one sex by another or from sex-dependent ecological needs remains open to question.

Competition

Given the apparent inverse relationship between the tendency of adult Ruby-throated

Hummingbirds to trapline and to defend food sources (see above), it is surprising that we did not find a positive effect of the number of visits by competitors on the traplining tendency of individuals. Yet, although territorial hummingbirds react to intruder pressure, this reaction may be reduced if is not accompanied by resource depletion, which would not have occurred at feeders (Tamm 1985, Eberhard and Ewald 1994, Garrison and Gass 1999). Moreover, competition pressure measured only on feeders included in potential traplines may not reflect the range of food sources used by hummingbirds to assess competition when determining the foraging strategy to employ. Future studies should also address the possibility that male and female do not react similarly to competition pressure and that individuals distinguish between male and female competitors (Temeles and Kress 2010).

Space use

Because Ruby-throated Hummingbirds can defend and monopolize feeders to which they devote a large proportion of their visits (Rousseu 2010), it is not surprising that both spatial and temporal traplining tendency decreased with the level of spatial concentration, again reinforcing the link between resource defense and traplining. Although we predicted a decrease in traplining tendency with both the total number and spatial spread (MST) of trapline feeders, as individuals would have more opportunities to derogate from traplines (Ohashi et al. 2006, 2008), the expected relationship was only observed for spatial spread. The positive correlation between spatial traplining tendency and the number of feeders may on the other hand reflect that traplining individuals tend to use a greater number of feeders (yet close in space) in opposition to individuals which tend to defend feeders, especially given that feeders were spaced by 100 m and are thus increasingly difficult to defend as their number add up (Grant 1993, Robb and Grant 1998, Rousseu 2010).

CONCLUSION

Our results indicate that adult Ruby-throated Hummingbirds vary in traplining tendency based on their sex and environmental conditions, especially if those conditions affect the defense and monopolization of nectar sources. Moreover, we found that the traplining tendency of individuals may vary substantially among days. Our study suggests that traplining and resource defense are two foraging tactics which are used as part of a conditional strategy that determines the frequency at which each tactic must be used (*sensu* Gross 1996). Future research should attempt to quantify the fitness benefits associated with both foraging tactics under various environmental conditions. This may prove challenging, however, as foraging tactics may be linked with mating tactics if females are attracted to food-rich territories (Robinson et al. 1996, Temeles and Kress 2010).

ACKNOWLEDGMENTS

We are grateful to G. Defoy for giving us access to his land. Sincere thanks go to A. Anctil, M. Cusson, P. Garcia-Cournoyer, B. Gendreau, C. Girard, and L. Mercier for their help in the field. S. Derivière helped us with imaginary and complex numbers and J. Turgeon with database management. S. Bar-David kindly provided MATLAB code for the recursion and circle analyses. Financial support for this project came from the Canada Research Chair in Spatial and Landscape Ecology, the Canadian Foundation for Innovation, the Fonds québécois de la recherche sur la nature et les technologies, the Natural Sciences and Engineering Research Council of Canada, and the Université de Sherbrooke. This research was conducted under protocol MB02 approved by the Institutional Animal Care Committee of the Université de Sherbrooke.

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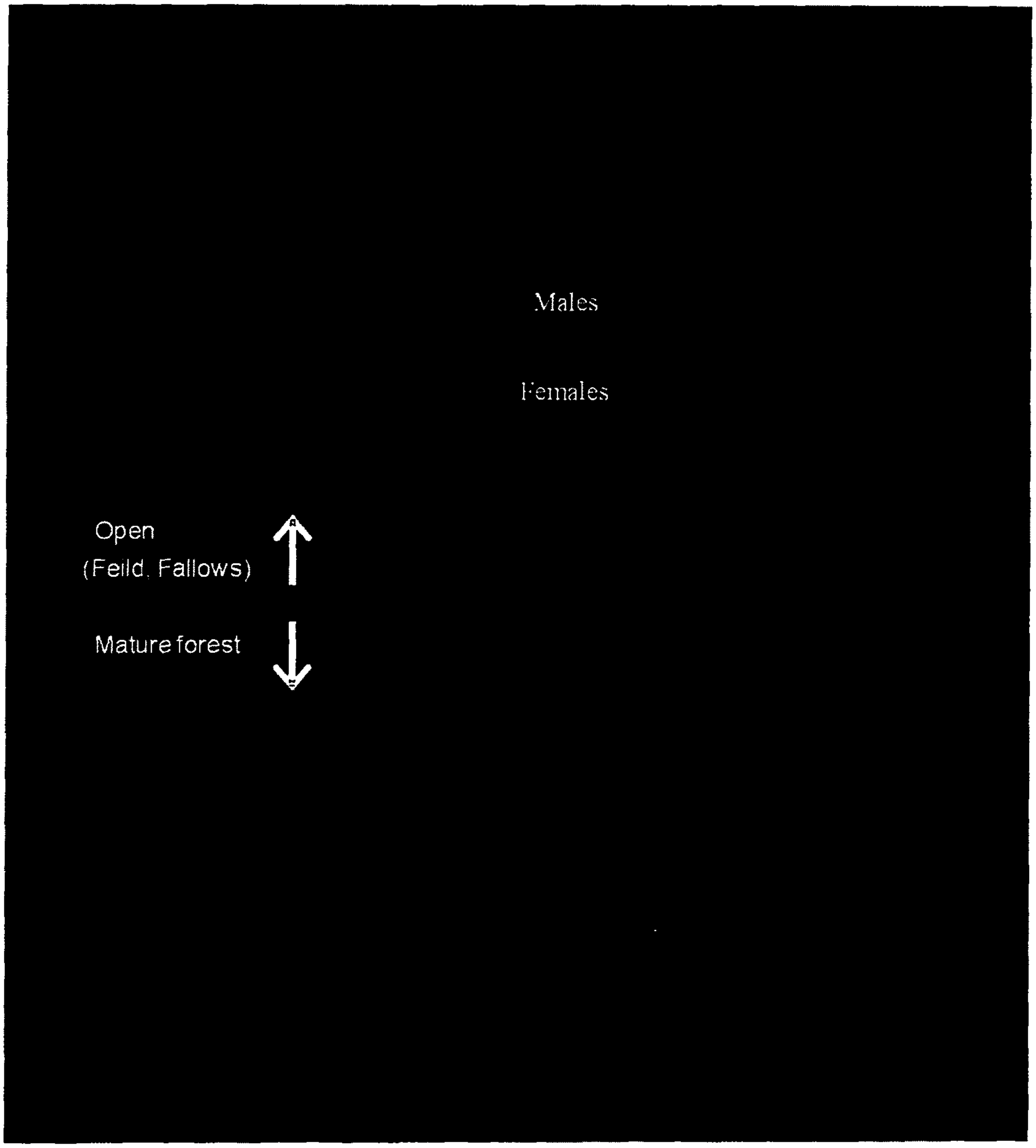
APPENDIX

Appendix 1. Spatial segregation of 191 adult Ruby-throated Hummingbirds based on the sex-dependent use of nectar feeders on the study area during the breeding seasons of 2007, 2008, and 2009. The study area located in Cleveland County, Quebec, Canada, consisted in a 44-ha grid composed of 45 artificial feeders, each equipped with a PIT-tag reader. Feeders (pie charts) were spaced by 100 m. Each pie chart depict the proportions of visits (n = 274,752) made by male (n = 95; blue) and female (n = 96; red) hummingbirds at a given feeder. The green line delimit open (fields and fallows) and closed (mature forest) habitats.



CONCLUSION GÉNÉRALE

L'écologie spatiale des nectarivores est un sujet de recherche peu développé du fait des difficultés à suivre les déplacements des individus en milieu naturel. Compte tenu que les nectarivores se nourrissent à partir de fleurs qui ont la capacité de régénérer le nectar consommé et que les sources de nectar sont distribuées de façon hétérogène dans l'espace et dans le temps, les écologistes comportementaux ont posé l'hypothèse que les nectarivores puissent quérir leur nourriture par *traplining*. Le *traplining* consiste en une stratégie où les individus visitent des parcelles de nourriture renouvelables qui sont effectuées selon un ordre fixe (prévisible) et répété (Ohashi et Thompson 2005; Saleh et Chittka 2007). Cette stratégie généralement décrite de façon anecdotique en réalisant des observations que sur une portion du circuit d'alimentation des individus, n'a jamais été formellement observée chez des nectarivores en milieu naturel. De plus, le *traplining* fût quasiment toujours étudié sur une base temporelle (i.e., sur les intervalles de temps séparant les visites aux sources de nectar) alors que ce comportement possède nécessairement une composante spatiale. Enfin, on note dans la littérature scientifique une absence quasi totale de méthodes permettant de quantifier ce comportement et ainsi de comparer la propension de différents individus à adopter cette stratégie d'exploitation des ressources alimentaires. Par conséquent, il était difficile, voire impossible, de modéliser le niveau d'utilisation de ce comportement en fonction de variables susceptibles de l'influencer.

La qualité des données récoltées dans le cadre de mon projet de maîtrise et la méthode développée pour quantifier l'utilisation de ce comportement en nature me permettent de combler en partie le manque de connaissances sur les stratégies de quête alimentaire des nectarivores et plus particulièrement, du Colibri à gorge rubis. En effet, l'algorithme et les indices que j'ai développés, selon des définitions biologiquement valables du *traplining*, m'ont permis de quantifier l'utilisation des différentes stratégies de quête alimentaire que pouvait adopter une espèce pourtant jugée territoriale et ce, même si la disponibilité des ressources était *ad libitum*. Mes résultats montrent clairement que le Colibri à gorge rubis peut moduler quotidiennement sa stratégie de quête alimentaire en optant pour une défense active d'une seule source de nectar, une utilisation de plusieurs sources qui semblent non défendues et ce, selon un patron conforme au *traplining*, ou encore pour une combinaison de ces extrêmes. La technique de suivi des déplacements que j'ai aussi développée (Charette et al., *soumis*) permet, pour la première fois, de connaître l'ensemble des parcelles d'alimentation fréquentée par des colibris et permet enfin de se pencher sur la composante spatiale du *traplining*. En modélisant cette composante spatiale à partir d'un nombre substantiel d'individus suivis sur une période de temps considérable, j'ai montré que plusieurs variables peuvent avoir un impact majeur sur la propension d'un individu à adopter le *traplining*. Par exemple, le fait de pouvoir utiliser la concentration spatiale comme variable explicative est une première dans ce genre d'étude et nous permet de constater les liens étroits entre cette variable décrivant la propension d'un individu à monopoliser et défendre des sources de nectar et le niveau de *traplining*. En effet, il semble que ces deux composantes soient fortement et inversement reliées entre elles, témoignant ainsi du choix d'un individu à adopter le *traplining* plutôt que la défense active d'une source de nourriture comme stratégie de quête alimentaire. Encore grâce à la méthode de suivi des déplacements que j'ai employée, j'ai pu caractériser l'ampleur des déplacements quotidiens des colibris au sein de mon dispositif expérimental. J'ai ainsi pu déterminer que le *traplining* se manifestait à une échelle assez locale, soit dans un rayon de moins de 1 km. Quoique je ne peux exclure la possibilité que les colibris aient pu fréquenter des sources de nectar externes à mon aire d'étude, je suis toutefois confiant que les colibris étudiés concentraient leur activités d'alimentation au sein de mon dispositif expérimental, entre autres parce que l'étude s'est déroulée durant la période de reproduction. De plus, j'ai montré que la structure du paysage dans lequel évolue les colibris peut avoir une influence sur leurs stratégies de quête alimentaire et que cette influence peut avoir un impact différent et plus ou moins marqué selon le sexe des individus. Finalement et contre toute attente, je n'ai détecté aucun effet de la pression de compétition sur le niveau de *traplining*. J'attribue cela principalement à la présence de ressource *ad libitum* sur l'aire d'étude.

Mes résultats concernant les effets des différentes variables sur la composante temporelle du *traplining* me permettent de conclure qu'à l'instar de la composante spatiale, la concentration spatiale des individus a un impact majeur sur le niveau de *traplining*. Toutefois, la régularité dans le temps séparant les visites était corrélée positivement à la concentration spatiale et n'allait donc aucunement dans le sens de mes prédictions basées sur la littérature. En effet, on assume que plus un individu à un comportement de *traplineurs* plus cette variabilité devrait diminuer (Thompson et al. 1997; Williams et al. 1998). Effectivement, ce dernier devra synchroniser ces visites aux parcelles d'intérêts avec le taux de renouvellement de la ressource à cette parcelle dans le but de maintenir la qualité de la parcelle à un niveau assez bas afin d'inciter les compétiteurs à délaisser cette parcelle (Paton and Carpenter 1984). Toujours pour la première fois, j'ai pu explorer le lien entre les composantes spatiales et temporelles du *traplining*. J'ai entre autres noté que plus un individu semblait utiliser le *traplining* d'un point de vue spatial, plus ses durées inter-visites étaient variables. Aussi, il est important de noter que ce ne sont pas le même ensemble de variables qui a un impact sur les composantes spatiale et temporelle du *traplining*. J'en conclue qu'il est important de considérer le *traplining* dans son ensemble avant de conclure qu'une espèce adopte le *traplining*. Néanmoins, je crois que la composante spatiale est la plus informative à l'égard de la stratégie de quête alimentaire adoptée par un individu puisque qu'elle reflète davantage les déplacements réellement effectués alors que la composante temporelle n'implique pas, de façon implicite, un mouvement d'une parcelle à une autre.

Bien que mon projet permette de mieux comprendre le *traplining* et certains facteurs influençant cette stratégie de quête alimentaire des colibris, il demeure que le dispositif expérimental mériterait d'être modifié afin d'imiter le plus fidèlement possible les variations spatio-temporelles en nectar que l'on trouve en milieu naturel. En effet, il me semble essentiel de modifier le mode de distribution du nectar aux abreuvoirs afin de contrôler le volume de nectar pouvant être exploité par les colibris, de même que le taux auquel se nectar se régénère. Ces modifications constituent, selon moi, des incontournables pour de futurs projets de recherche portant sur les stratégies de quête alimentaire. De plus, il serait intéressant de pousser plus loin notre compréhension des mouvements des colibris en manipulant, par exemple, la qualité des sources de nectar en modifiant, entre autres, la concentration en sucrose dans les abreuvoirs ou encore en manipulant la densité des abreuvoirs sur l'ensemble de l'aire d'étude ou seulement dans certaines sections de celle-ci. Finalement, afin de mieux cerner les effets de la structure du paysage sur les mouvements des colibris, il serait pertinent de modifier le paysage de notre aire d'étude en procédant à certains aménagements sylvicoles.

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