

**MONOPOLISATION DES RESSOURCES ALIMENTAIRES DANS UNE
POPULATION MARQUÉE DE COLIBRI À GORGE RUBIS (*Archilochus colubris*)**

par

François Rousseau

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 2010

SOMMAIRE

Les comportements de défense menant à la monopolisation des ressources sont souvent expliqués par l'abondance et la distribution spatiale et temporelle des ressources. Il est généralement prédit que les bénéfices nets associés aux comportements agressifs vont être maximisés lorsque les ressources sont moyennement abondantes, concentrées spatialement et prévisibles dans le temps. Plusieurs autres variables peuvent toutefois affecter la capacité des individus à défendre et à monopoliser les ressources. Par exemple, la compétition peut contribuer à augmenter le temps alloué à la défense alors qu'une augmentation dans la complexité structurelle d'un habitat peut contribuer à réduire la détection des compétiteurs, rendant ainsi la défense moins efficace. L'utilisation de l'espace par les individus, qui peut varier en fonction de caractéristiques individuelles ou d'éléments non reliés à la distribution des ressources, peut également affecter leur capacité à défendre et à monopoliser une ressource donnée. Étant donné que la plupart des études concernant la défense et la monopolisation des ressources ont été exécutées en milieu contrôlé, peu d'études se sont penchées sur la monopolisation des ressources avec des individus non contraints spatialement. La présente étude avait pour but d'évaluer les niveaux de défense et de monopolisation des ressources alimentaires dans une population marquée de Colibri à gorge rubis (*Archilochus colubris*) tout en quantifiant l'effet de l'utilisation de l'espace par les individus, de la compétition, et de la structure des habitats sur ceux-ci. Mon système d'étude, en fonction depuis 2007, consiste en un réseau de 45 abreuvoirs au sein duquel toutes les visites effectuées par des colibris marqués sont enregistrées grâce la technologie des transpondeurs passifs intégrés («PIT tags»). Plus spécifiquement, j'ai modélisé le nombre de visites par les compétiteurs à un abreuvoir et une date donnée en fonction des caractéristiques de l'abreuvoir (nombre de compétiteurs, visibilité autour de l'abreuvoir) et d'un individu focal fréquentant cet abreuvoir (concentration spatiale à cet abreuvoir, stabilité spatiale). Mes résultats indiquent premièrement que les abreuvoirs à l'intérieur de notre système sont défendus et monopolisés à

des degrés variables selon les individus et dans le temps et que les individus sont généralement concentrés à un ou deux abreuvoirs principaux. L'effet négatif de la concentration spatiale sur le nombre de visites par les compétiteurs, impliquant qu'il y a défense des abreuvoirs, montre que plus les individus sont concentrés à un abreuvoir, plus l'abreuvoir est utilisé de façon exclusive. Bien que cet effet négatif de la concentration spatiale soit d'autant plus important lorsque les individus sont stables dans l'utilisation des abreuvoirs de la grille, l'ampleur de cet effet est toutefois très variable entre les individus. Ces deux résultats pris ensemble suggèrent qu'il y a un gradient dans la stratégie des individus allant d'individus territoriaux défendant les abreuvoirs à des individus peu concentrés et stables spatialement qui peuvent correspondre soit à des individus errants (« floaters») ou à de faibles utilisateurs des abreuvoirs de la grille. Malgré que le nombre de compétiteurs diminue la monopolisation des abreuvoirs, l'effet négatif de la concentration spatiale ne diminue pas avec le nombre de compétiteurs suggérant que la capacité de défense des abreuvoirs n'est pas affectée par la compétition dans notre système. Finalement, une visibilité accrue en milieu fermé favorise la monopolisation des abreuvoirs, quoique la préférence pour les milieux ouverts par les mâles adultes et la difficulté de quantifier la visibilité en milieu ouvert rendent difficile l'évaluation du rôle que la visibilité peut jouer dans ces milieux. À ma connaissance, cette étude est parmi les premières à se pencher sur la défense et la monopolisation des ressources alimentaires dans un contexte où les individus sont marqués et ne sont pas contraints spatialement. À ce titre, mes résultats montrent qu'il est important de considérer ce dernier aspect pour comprendre l'utilisation conjointe des ressources par les individus. De plus, bien que les études expérimentales en milieu contrôlé permettent de mieux comprendre le rôle de certaines variables prises séparément, les études en milieu naturel considérant de multiples variables simultanément permettent de tenir compte de la complexité retrouvée en nature et c'est cette complexité qui ultimement détermine les patrons d'utilisation conjointe des ressources par les individus.

Mot clés : écologie spatiale, monopolisation des ressources, territorialité, structure des habitats, colibris

REMERCIEMENTS

Je tiens premièrement à remercier mon directeur de recherche, Marc Bélisle, qui m'a accepté comme étudiant de maîtrise et qui a toujours été présent pour répondre à mes questions et toujours prêt à se casser la tête sur des questions difficiles! Je tiens également à remercier mon collègue Yanick Charette, étudiant à la maîtrise, qui a développé la technique de suivi des colibris à l'aide des PIT tags et par le fait même rendu possible mon projet de maîtrise. Il a surtout été mon mentor « *colibriz* » pendant mes deux années de terrain et un compagnon de terrain et d'études incomparable. Je suis aussi reconnaissant envers les multiples assistants de terrain qui ont contribué à récolter nos données; Pamela Garcia-Cournoyer, Benoît Gendreau, Léonie Mercier, Guy-guy (Alexandre Anctil) pour son rire contagieux et Squidgy (Carol-Ann Émond). Merci également à Gilles Defoy pour l'utilisation de sa propriété comme aire d'étude, à Jacques Turgeon pour son aide dans la compilation des données et sa passion pour les colibris et à Dany Garant et Marco Festa-Bianchet, membres de mon comité, pour leurs commentaires sur mon projet. Finalement, merci aux membres du labo Bélisle, Arnaud, Audrey, Claudie, Geneviève, Louis, Ludovic, Marie-Claude, Stéphane et extensions comme Élise et Mélanie pour leur support et surtout pour leur camaraderie. Très finalement, merci à Aurélie pour son support et ses multiples rappelotrons pour me remettre dans le droit chemin! Ça n'a pas toujours marché, mais ce n'est pas parce que tu n'as pas essayé! Cette étude a été réalisée grâce au support financier de la Chaire de recherche du Canada en écologie spatiale et en écologie spatiale, du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), du Fonds québécois de recherche sur la nature et les technologies (FQRNT), de l'organisme Protection des oiseaux du Québec (POQ) et de l'Université de Sherbrooke.

TABLE DES MATIÈRES

SOMMAIRE	ii
REMERCIEMENTS.....	iv
LISTE DES TABLEAUX	vii
LISTE DES FIGURES.....	ix
INTRODUCTION	1
Autres facteurs influençant la défense et la monopolisation des ressources	2
<i>Compétition</i>	2
<i>Structure des habitats.</i>	3
<i>Utilisation de l'espace</i>	5
Projet.....	7
Organisation spatiale et territorialité chez les colibris.....	7
Espèce cible.....	10
Objectifs et hypothèses.....	11
CHAPITRE 1.....	13
Mise en contexte.....	13
Abstract.....	14
Introduction.....	15
Methods.....	20

<i>Study System</i>	20
<i>Capture and Marking</i>	22
<i>Space use and competitors</i>	23
<i>Visibility</i>	24
<i>Food quality</i>	25
<i>Sex and control variables</i>	25
<i>Statistical analyses and model selection</i>	26
Results	28
Discussion	40
<i>Measuring resource defense and monopolization in nature</i>	41
<i>Individual variation and space use</i>	42
<i>Competition</i>	43
<i>Habitat structure and visibility</i>	44
<i>Influence of natural food sources on our results</i>	45
<i>Purpose of food resource defense for breeding male Ruby-throated Hummingbirds</i>	46
Appendix 1	49
References	52
CONCLUSION	62
BIBLIOGRAPHIE	66

LISTE DES TABLEAUX

1. Number of adult Ruby-throated hummingbirds considered as focal individuals and number of bird-days for the four sex combinations (focal individual vs. competitors) used for modeling the number of visits by competitors at nectar feeders in Cleveland County, Quebec (Canada), 2007-2009. Only individuals followed for at least three days were considered as focal individuals..... 29
2. Model selection and explanatory variables composing the 10 models put in competition by AICc for modeling the number of visits by Ruby-throated Hummingbird competitors in Cleveland County, Quebec (Canada), 2007-2009. Variables included and omitted from a model are indicated by a cross and a circle, respectively. The same set of models was used for the four sex combinations (Table 2). Feeder rank is based on the sex of competitors. Akaike weights (w_i) represent the probability that a particular model best describes the data. The response variable was log-transformed and modeled with linear mixed-effect models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects..... 31
3. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult male Ruby-throated Hummingbirds competitors at feeders potentially defended by a male in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects..... 32

4. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult female Ruby-throated Hummingbirds competitors at feeders potentially defended by a female in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.....	49
5. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult female Ruby-throated Hummingbirds competitors at feeders potentially defended by a male in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.....	50
6. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult male Ruby-throated Hummingbirds competitors at feeders potentially defended by a female in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.....	51

LISTE DES FIGURES

1. Schematic view of habitats within the feeder grid providing a nectar sucrose solution for Ruby-throated Hummingbirds in Cleveland County, Quebec (Canada), 2007-2009..... 21
2. Boxplots showing number of visits and spatial concentration of adult Ruby-throated hummingbirds in Cleveland County, Quebec (Canada), 2007-2009. A) For a given feeder on a given day, every individual has been ranked according to its number of visits at the feeder, with rank 1 being the individual with the most visits to the feeder. This figure shows how the number of visits at feeders decreased with the rank of individuals. B) For a given individual on a given day, every feeder has been ranked according to the number of visits made by the individual, with rank 1 being the most visited feeder. This figure shows the decrease in spatial concentration of individuals in relation to feeder rank. Both graphics are for the male vs. males combination only..... 29
3. Predicted number of visits by competitors (NVC) against the spatial concentration of focal Ruby-throated Hummingbirds for the four sex combinations studied in Cleveland County, Quebec (Canada), 2007-2009. Predictions are derived from model-averaged, linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. Other numeric variables were fixed to their mean value and factors were fixed to their reference level..... 33

4. Model-averaged predictions for the number of visits made by female or male Ruby-throated Hummingbird competitors (NVC) in Cleveland County, Quebec (Canada), 2007-2009, in relation to the spatial concentration of focal female and the number of female or male competitors. Predictions are derived from linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. The response variable was log-transformed. Other numeric variables were fixed to their mean value and factors were fixed to their reference level..... 34
5. Predicted reductions in the number of visits made by adult male Ruby-throated Hummingbird competitors (NVC) when focal males' spatial concentration goes from 0.0 to 1.0 in Cleveland County, Quebec (Canada), 2007-2009. The X axis represents NVC when spatial concentration is 0.0. Values were obtained using the model-averaged BLUPs of the linear mixed models listed in Table 2 as individuals were treated as random effects for the intercept and the slope characterizing the effect of spatial concentration. Other numeric variables were fixed to their mean value and factors were fixed to their reference level..... 35
6. Model-averaged predictions for the number of visits made by male Ruby-throated Hummingbird competitors (NVC) in Cleveland County, Quebec (Canada), 2007-2009, in relation to the spatial concentration of the focal male and A) the total number of visits by the focal individual, B) the spatial stability of the focal individual, C) the number of competitors, and D) the lateral visibility (meters) and habitat openness (open; gray lines, closed; black lines). Predictions are derived from a linear mixed-model with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. The response variable was log-transformed. Other numeric variables were fixed to their mean value and factors were fixed to their reference level..... 37

7. Relation between spatial stability and the mean maximum daily spatial concentration of adult male Ruby-throated Hummingbirds in Cleveland County, Quebec (Canada), 2007-2009. The mean maximum daily spatial concentration represents the spatial concentration of the individual at the most visited feeder on a given day. For cases in which an individual was followed for more than one season, the mean was calculated across all season without distinction of the year. Lines correspond to the standard deviation for every individual..... 38
8. Number of visits made by adult male Ruby-throated Hummingbird competitors at feeders potentially defended by males when containing nectar with a low (20% W/V) or a high (35% W/V) sucrose concentration in Cleveland County, Quebec (Canada). Data shown are restricted to the period when sucrose concentration was manipulated (i.e., between June 10 and August 11, 2009)..... 39

INTRODUCTION

Les patrons d'utilisation de l'espace par les espèces animales varient fortement d'une espèce à l'autre, et parfois même au sein d'une même espèce. Ces patrons varient 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). Ces patrons sont généralement déterminés par l'abondance et la distribution spatiale et temporelle des ressources, en particulier les ressources alimentaires (Maher et Lott, 2000). Lorsque les ressources alimentaires sont très dispersées et peu abondantes, il peut être difficile pour un individu de défendre efficacement un espace assez grand pour subvenir à ses besoins alimentaires. À l'opposé, il n'est pas nécessairement avantageux de dépenser inutilement son énergie à défendre un territoire lorsque les ressources sont très abondantes (Grant 1993). Puisque la défense de zones de petites tailles est considérée comme étant moins coûteuse que la défense de zones de grandes tailles, il est généralement prévu que les comportements de défense ou de territorialité devraient également augmenter avec la concentration spatiale des ressources (Grant 1993, Grant et Guha 1993, Noël et al. 2005). Cependant, si les ressources sont trop concentrées, spatialement ou temporellement, la défense peut être impossible si la compétition pour cette ressource devient trop forte et dans ce cas, la compétition entre individus se fait principalement par exploitation. Les individus les plus compétitifs peuvent bénéficier d'un niveau de concentration des ressources qui rend la défense d'une ressource donnée possible et ainsi détenir un accès plus ou moins exclusif à cette ressource en excluant les autres individus (Grant et Guha 1993). Dans ce cas, la compétition entre les individus se fait surtout par interférence. On observe généralement des comportements de défense ou un comportement territorial, c'est-à-dire de défense d'une ressource ou d'un emplacement donné contre les congénères ou les individus d'autres espèces (Brown et Orians 1970, Maher et Lott 1995), lorsque les bénéfices obtenus par l'utilisation exclusive d'un endroit dépassent les coûts associés au maintien de cette exclusivité (Brown 1964, Grant 1993). À ce moment, on dit que

la défense d'une ressource est économiquement possible dans le sens où il y a des bénéfices nets associés à ce comportement. L'utilisation exclusive par certains individus entraîne la monopolisation des ressources, c'est-à-dire une répartition inégale des ressources entre les individus, ce qui peut influencer autant le régime d'appariement (Emlen et Oring 1977) que la dynamique des populations (Patterson 1980, Newton 1992, Sutherland 1996, Lopez-Sepulcre and Kokko 2005).

Autres facteurs influençant la défense et la monopolisation des ressources

Compétition

Le niveau de compétition pour une ressource donnée doit également être pris en compte pour l'évaluation des coûts et bénéfices associés à la défense de cette ressource ou aux comportements de territorialité (Grant 1993). Indépendamment de la distribution spatiotemporelle d'une ressource donnée, on considère généralement que plus la compétition pour une ressource est forte, plus les coûts de défense seront élevés, ce qui réduira autant l'efficacité à la défense que l'utilité des comportements agressifs (Grant 1993). Par conséquent, la capacité des individus à défendre et monopoliser les ressources dépend non seulement de la distribution spatiotemporelle, mais également du niveau de compétition pour cette ressource. Par exemple, on considère qu'une ressource très concentrée spatialement devrait être facilement défendable. Par contre, si cette concentration spatiale est associée à une relative rareté de la ressource en périphérie ou régionalement (Carpenter 1987), cela peut entraîner une compétition accrue au niveau des parcelles où la ressource est concentrée et ainsi rendre une défense efficace difficile. Il faut donc considérer l'interaction entre la distribution spatiotemporelle des ressources et la compétition dans l'évaluation des coûts et des bénéfices associés à la défense des ressources ou aux comportements de territorialité (Vahl et al. 2005). Tout comme dans le cas de l'abondance ou de la concentration spatiale des ressources, on

considère généralement que c'est à un niveau intermédiaire de compétition que les bénéfices nets associés aux comportements de défense sont maximisés (Grant 1993). C'est donc à ce niveau que les comportements agressifs entre individus devraient être les plus intenses. Lorsque les compétiteurs sont peu abondants, peu de ressources sont perdues aux mains des compétiteurs et la défense n'est donc pas essentielle, par contre, lorsqu'ils sont très nombreux, la défense devient rapidement très coûteuse, voire impossible. Bien que plusieurs études en milieu naturel se soient penchées sur les effets de la compétition sur la capacité des individus à défendre et à monopoliser des ressources, peu d'études ont couvert un gradient de compétition suffisant pour observer le point où les bénéfices associés aux comportements de défense sont maximisés en raison du niveau de compétition (Chapman et Kramer 1996). À ce titre, les études expérimentales ou en laboratoire demeurent la meilleure façon de couvrir un gradient de compétition important tout en contrôlant pour les effets liés à la distribution spatiotemporelle des ressources. En contrôlant expérimentalement le nombre de compétiteurs, ces études se sont penchées principalement sur les niveaux de monopolisation ou sur différentes mesures de l'agressivité dans les groupes (e.g., Chapman et Kramer 1996, Syarifuddin et Kramer 1996, Johnson et al. 2004, Kim et Grant 2007, Kaspersson et al. 2010). Par exemple, Chapman et Kramer (1996) ont montré en aquarium que la monopolisation des ressources alimentaires par des Danios géant (*Danio aequipinnatus*) diminuait de façon continue en faisant passer le nombre de Danio zébré (*Danio rerio*) compétiteurs de 1 à 20. De plus, le taux de poursuites atteignait un maximum à un nombre intermédiaire de compétiteurs, pour ensuite diminuer graduellement, suggérant ainsi une réduction des bénéfices associés aux comportements agressifs à haute densité.

Structure des habitats

Bien que la distribution spatiotemporelle des ressources et la compétition soient probablement les principaux facteurs influençant les patrons d'utilisation de l'espace par les espèces animales, d'autres éléments peuvent affecter ces patrons, notamment la structure des habitats.

Un nombre croissant d'études se penchent d'ailleurs sur les relations entre la structure des habitats et la défense ainsi que la monopolisation des ressources par les individus. L'hétérogénéité d'un habitat peut, par exemple, être liée à une obstruction visuelle accrue qui réduirait la capacité des occupants à défendre efficacement l'ensemble d'une zone donnée, déterminant ainsi les limites d'un territoire économiquement défendable. En ce sens, les discontinuités, que ce soit au niveau de la végétation ou du relief, peuvent agir comme des contraintes déterminant en partie les limites, la taille et la forme d'un territoire ou d'un domaine vital à un endroit donné (Reid et Weatherhead 1988, Eason 1992, Powell et Mitchell 1998, Rolando et al. 2000, Adams 2001). À titre d'exemple, dans une étude cherchant à déterminer s'il y avait une association entre les discontinuités naturelles créées par la végétation et les caractéristiques abiotiques et la délimitation des territoires de deux espèces de passereaux, St-Louis et al. (2004) ont observé un chevauchement significatif entre les limites des territoires et les bordures créées par ces discontinuités. Les discontinuités peuvent également favoriser la territorialité en fournissant des repères à partir desquels les animaux peuvent établir les limites de leur territoire (Maher et Lott 2000, St-Louis et al. 2004). L'utilisation de repères pour la délimitation des limites territoriales s'expliquerait par une réduction des coûts associés à la défense du territoire contre les congénères (Eason et al. 1999, LaManna et Eason 2003, Mesterton-Gibbons et Adams 2003). Cette réduction des coûts de défense, ainsi que les effets sur la taille des territoires, ont été montrés expérimentalement en fournissant des repères artificiels à des espèces territoriales et en observant les modifications des limites territoriales et des comportements de défense (Eason et al. 1999, LaManna et Eason 2003). Par exemple, en fournissant un repère visuel formé d'une ligne de roches plates n'entrant pas la visibilité, LaManna et Eason (2003) ont montré chez un cichlidé (*Steatocranus casuarius*) en aquarium une réduction des coûts de défense et de l'agressivité. De plus, ces auteurs ont aussi noté une division de l'espace plus équitable entre les individus en présence du repère visuel, montrant ainsi l'importance que peuvent jouer les repères dans la délimitation des territoires.

Un habitat présentant une complexité structurelle élevée peut également impliquer une visibilité réduite qui, sans nécessairement affecter les limites d'un territoire, peut entraîner une réduction dans l'efficacité de la défense et donc, du niveau de monopolisation d'une ressource ou d'un espace donné (Eason et Stamps 1992, 2001). En effet, un individu tentant de défendre une ressource aura vraisemblablement plus de difficultés à détecter un intrus dans un environnement où la visibilité est faible. Les compétiteurs ont donc probablement une plus grande facilité à atteindre une ressource défendue dans ce type d'environnement, ce qui peut limiter le niveau de monopolisation par un individu tentant de défendre une ressource. Plusieurs études se sont penchées sur l'influence de la complexité structurelle ou de la visibilité à l'intérieur des habitats sur différentes variables reliées à l'utilisation conjointe des ressources ou de l'espace par les individus. Par exemple, des effets positifs de la complexité structurelle ou de la visibilité réduite ont été montrés sur la densité d'individus (Venter et al. 2008), alors que des effets négatifs ont été observés sur la taille des territoires (Breau et Grant 2002, Imre et al. 2002, Venter et al. 2008), les niveaux d'agressivité (Basquill and Grant 1998, Corkum et Cronin 2004, Baird et al. 2006, Carfagnini et al. 2009, Cenni et al. 2010) et le taux de croissance des individus dominants (Höjesjö et al. 2004). Plus directement, Basquill et Grant (1998) ont montré qu'une augmentation de la complexité structurelle de l'habitat entraînait une diminution du niveau de monopolisation des ressources alimentaires chez le *Danio* zébré (*Danio rerio*) en aquarium. De plus, il a été observé que la relation positive entre l'agressivité des individus et leur niveau de monopolisation était moins prononcée dans les milieux où la complexité structurelle était élevée, ce qui suggère que l'agressivité et la compétition par interférence sont des stratégies moins rentables dans les environnements où la visibilité est réduite.

Utilisation de l'espace

La majorité des études se penchant sur les liens entre la complexité structurelle des habitats et la défense et la monopolisation des ressources ont été réalisées en milieu contrôlé où la

disponibilité des ressources était facilement quantifiable et où les individus étaient contraints spatialement. En milieu contrôlé, tel qu'en aquarium (e.g., Basquill et Grant 1998), les individus sont confinés et doivent nécessairement accéder à la source de nourriture fournie par les expérimentateurs pour s'alimenter. L'utilisation de l'espace par les individus dans ces milieux restreints n'est donc pas nécessairement représentative des patrons observés en milieu naturel. Or, la capacité des individus à monopoliser les ressources ou l'espace risque de dépendre fortement du temps devant être alloué aux différentes parties de leur domaine vital et à différentes activités comme la recherche de nourriture (Hamilton et Dill 2003) et la défense de zones alternatives d'alimentation (Steingrímsson et Grant 2008) ou encore, la recherche de partenaires sexuels (Sikkel 1998, Stutchbury 1998, Sikkel et Kramer 2006). Par exemple, chez les jeunes saumons de l'Atlantique (*Salmo salar*), Steingrímsson et Grant (2008) ont observé que les individus fréquentaient différentes zones d'alimentation d'où ils excluaient les intrus. L'utilisation de l'espace par les jeunes saumons est donc caractérisée par un comportement de territorialité où le territoire est composé de différentes zones défendues de façon temporaire. L'allocation du temps alloué aux différentes zones risque ainsi d'influencer le niveau d'exclusivité dans l'utilisation des ressources contenues dans le territoire. De plus, les patrons d'utilisation de l'espace à l'intérieur d'une même espèce peuvent varier en fonction de caractéristiques individuelles, comme le statut de dominance, l'expérience ou l'âge, ce qui peut faire la différence entre l'acquisition et la défense d'un territoire de qualité et l'errance associée aux individus non-territoriaux (Smith et Arcese 1989, Zack et Stutchbury 1992, Sergio et al. 2009). Bien que la distribution spatio-temporelle des ressources alimentaires soit un déterminant majeur des patrons d'utilisation et de défense de l'espace par les individus, ces patrons peuvent aussi être influencés par plusieurs autres facteurs indépendants des ressources alimentaires, comme la qualité individuelle, ce qui risque d'influencer la monopolisation des ressources et de l'espace. Il est donc essentiel de tenir compte des patrons d'utilisation de l'espace par les individus afin de mieux comprendre la monopolisation des ressources et de l'espace.

Projet

Mon projet de maîtrise tire avantage de l'utilisation de sources artificielles de nectar afin d'étudier l'organisation spatiale du Colibri à gorge rubis (*Archilochus colubris*). À ce titre, j'ai utilisé une grille de 45 abreuvoirs répartis systématiquement sur une superficie de 44 hectares et espacés de 100 mètres. Les colibris fréquentant la grille étaient marqués individuellement à l'aide de transpondeurs passifs intégrés (« passive integrated transponder devices; PIT tags ») et la durée, l'heure et la date de leurs visites aux abreuvoirs étaient enregistrées grâce à un système d'identification de radio-fréquences rattaché à l'abreuvoir. Ce système permettait donc d'obtenir un portrait complet de l'utilisation conjointe des abreuvoirs par les individus. De plus, la grille couvrait une diversité d'habitats incluant des champs de foin, une friche arbustive, une forêt de gaulis, ainsi qu'une forêt mature. Grâce à une distribution uniforme des abreuvoirs, il fut donc possible de découpler partiellement l'effet de la structure des habitats de celui de la distribution des ressources alimentaires. Le site d'étude était situé dans le comté de Cleveland à environ 40 km au nord de Sherbrooke, Québec (Canada) et la grille était en fonction depuis 2005. Cependant, des détecteurs étaient présents aux 45 abreuvoirs seulement depuis 2007. Par conséquent, seules les données récoltées depuis 2007 furent utilisées.

Organisation spatiale et territorialité chez les colibris

L'organisation sociale et le régime d'appariement chez les colibris seraient principalement déterminés par la distribution spatiale et temporelle des sources de nectars (Stiles et Wolf, 1979). Lorsque les sources de nectars sont très dispersées dans l'environnement, les systèmes d'appariement de type lek seraient favorisés et les mâles défendraient de petits territoires de parade généralement dépourvus de fleurs. Pour s'alimenter, ces individus doivent sortir de leur territoire de parade et parcourir des circuits (« traplines ») composés de plusieurs bosquets de fleurs à partir desquels ils obtiennent leur nectar. Ces circuits ne seraient généralement pas

défendus contre les intrus et la compétition entre les individus pour la nourriture se ferait surtout par exploitation. À l’opposé, lorsque les sources de nourriture sont très concentrées, les individus peuvent potentiellement défendre des territoires qui contiennent suffisamment de nectar pour subvenir à leur besoin alimentaire. Dans ce cas la compétition entre individus se ferait davantage par interférence. Contrairement aux cas des leks, ces territoires agiraient à la fois comme territoires d’alimentation et comme territoires de parades. Ces deux extrêmes formeraient un continuum à l’intérieur duquel tous les intermédiaires peuvent être observés selon la distribution des ressources. Ce continuum serait aussi variable entre les espèces et même à l’intérieur d’une même espèce (Stiles et Wolf, 1979).

Plusieurs études concernant la territorialité et les modes d’acquisition de nourriture ont été effectuées sur les espèces d’oiseaux nectarivores (Kodric-Brown et Brown 1978, Ewald et Bransfield 1987, Dearborn 1998), et particulièrement sur les colibris (Powers et McKee 1994), un groupe comportant une forte proportion d’espèces territoriales. Les colibris forment un groupe intéressant pour l’étude des facteurs influençant la territorialité en raison, entre autres, de leur propension à utiliser des sources artificielles de nourriture (Ewald et Carpenter 1978), de leur agressivité lors de la défense territoriale (Camfield 2006), de la relative facilité avec laquelle la disponibilité de leur nourriture peut être quantifiée (Dearborn 1998, Temeles et al. 2005) et de leur métabolisme élevé (Suarez et Gass 2002), lequel entraîne une réponse rapide suite à des changements dans la qualité de leur nourriture (Hixon et al. 1983, Marchesseault et Ewald 1991, Camfield 2006). La plupart des études sur la territorialité chez les colibris se sont penchées avec une approche économique sur les relations entre la taille du territoire, la quantité de nectar et la pression d’intrusion. Ces études ont été exécutées autant avec des ressources non manipulées en milieu naturel (Carpenter et al. 1983, Temeles et al. 2005) qu’avec une approche expérimentale (Kodric-Brown et Brown, 1978, Hixon et al. 1983, Marchesseault et Ewald 1991, Eberhard et Ewald 1994). D’autres se sont plutôt attardées sur les effets de la quantité ou de la qualité de la nourriture sur l’investissement dans la défense territoriale (Tamm 1985, Ewald et Bransfield 1987, Dearborn 1998, Temeles et al. 2004, Camfield 2006). Quant aux études effectuées sur les *trapliners*, elles se concentrent surtout sur

les patrons de visites à différentes sources de nectars isolées du circuit et sur l'effet des variations dans la quantité de nectar (simulant les variations naturelles et/ou la compétition) sur ces patrons de visitation, que ce soit avec des sources naturelles (Temeles et al. 2006) ou artificielles de nectar (Gill 1988, Garrison et Gass 1999, Gass et Garrison 1999, Henderson et al. 2006).

Cependant, la plupart de ces études ont basé leurs observations sur un faible nombre d'individus, souvent non marqués, et suivis pendant une période de temps généralement courte. Bien que l'influence de la distribution des ressources sur l'organisation sociale des colibris soit partiellement connue, peu d'études se sont véritablement penchées sur l'utilisation de l'espace par les individus et sur leur interaction dans l'espace en terme d'utilisation des ressources (e.g., Stiles et Wolf 1979). Malgré que les oiseaux nectarivores n'aient généralement pas un accès exclusif aux ressources de leur territoire, peu d'études concernant les colibris ont quantifié ce niveau d'exclusivité bien que cet aspect soit essentiel pour caractériser le comportement territorial (Pyke et al. 1996). De plus, le fait que les mouvements des colibris territoriaux ne sont vraisemblablement pas restreints aux territoires (Powers et McKee 1994, Temeles et al. 2005) et que les territoires subissent une certaine pression d'intrusion suggèrent que les individus territoriaux sortent occasionnellement de leur territoire ou qu'une certaine proportion de la population est formée d'individus non-territoriaux (« floaters »). Cette variabilité dans l'utilisation de l'espace par les individus est donc susceptible de se refléter dans les patrons de défense et de monopolisation des ressources.

Plusieurs études effectuées sur les colibris montrent que les individus peuvent défendre et s'approprier une source de nourriture localisée et abondante comme un abreuvoir d'eau sucrée et ce, même lorsque la quantité de nectar est illimitée (Powers et McKee 1994, Camfield 2006). Cependant, la plupart des études ayant fourni des sources artificielles de nectar ont été effectuées en captivité ou encore les dispositifs expérimentaux étaient limités à quelques abreuvoirs dispersés. Or, lorsque utilisés à plus grande échelle, les abreuvoirs offrent la

possibilité de quantifier les patrons d'utilisation de l'espace et les niveaux d'interaction entre les individus dans l'espace en terme d'utilisation des ressources alimentaires étant donné la forte propension des colibris à utiliser les abreuvoirs et de la relative facilité avec laquelle les visites peuvent être observées à ces sources ponctuelles de nectar. De plus, l'utilisation d'abreuvoirs permet de quantifier expérimentalement les changements dans l'organisation spatiale en réponse aux variations dans la qualité ou la distribution des ressources. Par exemple, il est possible de manipuler la concentration en sucre du nectar fourni et d'observer les modifications dans les patrons d'utilisation des abreuvoirs.

Espèce cible

Le Colibri à gorge rubis, tout comme la majorité des espèces de la famille des trochilidés, est une espèce présumée polygyne, et possiblement polygynandre, chez laquelle le mâle ne procure aucun soins parentaux (Robinson et al. 1996). Les deux partenaires ne se rencontrent que pour la cour et l'accouplement (Robinson et al. 1996) et le succès reproducteur des mâles seraient caractérisés par une très grande variance (Mulvihill et al. 1992). Il s'agit également d'une espèce chez laquelle les mâles seraient fortement territoriaux en période de reproduction (Robinson et al. 1996). Ceux-ci défendraient des territoires centrés sur des sources de nourriture et le territoire aurait secondairement une fonction liée à l'acquisition de partenaires sexuelles (Pitelka 1942). L'écologie des deux sexes différerait donc fortement, les femelles seraient dépendantes des ressources pour elles-mêmes et pour l'élevage des jeunes, alors que les mâles devraient s'assurer un accès à une source de nourriture tout en maximisant le nombre de femelles avec lesquelles ils s'accoupleraient. Ces différences sont donc susceptibles de se refléter dans les patrons d'utilisation de l'espace et de défense et de monopolisation des abreuvoirs par les individus. De plus, plusieurs observations suggèrent qu'il y aurait une ségrégation d'habitat entre les sexes chez les espèces de colibris nord-américaines (Armstrong 1987). Les femelles fréquenteraient les milieux boisés pour la nidification alors que les mâles seraient davantage retrouvés dans les milieux relativement

ouverts en bordure des boisés. Toutefois, cette ségrégation des sexes est surtout supportée par des observations ponctuelles et opportunistes réalisées sur le terrain et peu d'études ont tenté de la quantifier.

Objectifs et hypothèses

L'objectif général de mon projet est de caractériser l'organisation spatiale du Colibri à gorge rubis en quantifiant l'influence de la compétition, de l'utilisation de l'espace par les individus et de la structure de la végétation, par son biais sur la visibilité, sur la capacité des individus à défendre et à monopoliser les ressources alimentaires. Pour ce faire, je vais modéliser le nombre de visites par les compétiteurs à un abreuvoir donné en fonction des caractéristiques d'un individu focal, telle son utilisation de l'espace, et de différentes variables d'intérêt rattachées à l'abreuvoir, telles la visibilité et le nombre de compétiteurs détectés à l'abreuvoir. Bien que les taux d'intrusion aux abreuvoirs ne puissent être inférés à partir du nombre de visites par les compétiteurs, le nombre de visites peut être utilisé pour quantifier le niveau de monopolisation à un abreuvoir donné puisque qu'il mesure l'accès à la ressource par les compétiteurs par rapport à un individu focal. De plus, le niveau de réduction du nombre de visites par les compétiteurs par un individu focal peut être interprété comme une mesure de sa capacité ou de sa volonté à exclure les compétiteurs d'un abreuvoir donné. Cette réduction représente donc la défense des abreuvoirs. Par conséquent, il est possible de différencier entre la monopolisation et la défense des abreuvoirs en considérant respectivement le nombre de visites par les compétiteurs et sa réduction par l'individu focal. Spécifiquement, je cherche à tester les hypothèses suivantes : 1) le nombre de compétiteurs a un effet négatif sur la capacité des individus à défendre et à monopoliser les abreuvoirs, 2) la visibilité permet une meilleure défense des abreuvoirs, mais elle réduit la monopolisation en raison de préférences d'habitat, et 3) les individus plus concentrés et stables spatialement ont une plus grande exclusivité dans l'utilisation des abreuvoirs. En 2009, nous avons également effectué des manipulations de la

concentration en sucre du nectar artificiel fourni afin de vérifier l'hypothèse selon laquelle les abreuvoirs ayant une concentration plus élevée devraient être plus fortement défendus.

CHAPITRE 1

RESOURCE MONOPOLIZATION IN A MARKED POPULATION OF RUBY-THROATED HUMMINGBIRD (*Archilochus colubris*)

Mise en contexte

La présente étude porte sur les niveaux de défense et de monopolisation des ressources alimentaires dans une population marquée de Colibri à gorge rubis et sur les effets de la compétition, de la structure des habitats et de l'utilisation de l'espace par les individus sur l'utilisation conjointe de ces ressources. Les auteurs de cette étude sont François Rousseau et Marc Bélisle. François Rousseau est l'auteur ayant le plus contribué à cette étude, ayant participé à la récolte des données, l'élaboration de la problématique de recherche, l'exécution et l'interprétation des analyses statistiques et la rédaction de la première version de cet article. Marc Bélisle a supervisé le bon déroulement des travaux en fournissant son expertise sous forme d'idées et de conseils quant aux développements de la problématique et aux analyses statistiques et a révisé la version finale de cet article. Le présent article est l'objet principal de ce mémoire.

Abstract

Resource defense behaviors are often explained by the spatial and temporal distribution of resources. However, factors such as competition, habitat complexity and individual space use may also affect the capacity of individuals to defend and monopolize resources. Yet, studies frequently focused on one or two factors or were realized in laboratories, overlooking the complexity found in natural settings. Here, we addressed defense and monopolization of nectar feeders in a population of free-ranging Ruby-throated Hummingbirds marked with passive integrated transponder (PIT tags). Our study system consisted of a 44 ha systematic grid of 45 feeders equipped with PIT tag detectors recording every visit made at feeders. We modeled the number of visits by competitors at feeders in response to space use by a focal individual potentially defending a feeder, number of competitors, nectar sucrose concentration and habitat visibility. Individuals who were more concentrated at certain feeders and who were more stable in their use of the grid gained higher exclusivity in the use of feeders, especially for males competing against males. The level of spatial concentration at feeders and its negative effect on the numbers of visits by competitors was, however, highly variable among individuals, suggesting a continuum in resource defense strategies. Although the apparent capacity to defend feeders was not affected by competition or nectar sucrose concentration, the level of monopolization decreased with increasing number of competitors and higher nectar quality. Defense was enhanced by visibility near feeders, but only in forested habitats. The reverse effect of visibility in open habitats was more difficult to interpret as it was probably confounded by perch availability. Our study is among the first to quantify the joint use of food resource by overlapping individuals unconstrained in their use of space. Our results show the importance of accounting for an individual's space use as variability among individuals translated into varying levels of defense and monopolization of feeders independently of food resource distribution.

Introduction

Resource defense behaviors, such as territoriality and temporary defense of food patches, are often explained by the spatial and temporal distribution of food resources (Brown 1964, Grant 1993). When food abundance is low, the area needed to secure enough food may be too large to efficiently expel competitors, increasing the costs of defense for an aggressive individual. Conversely, when food is extremely abundant, an aggressive individual excluding others from a food source may waste energy that could be allocated to more profitable activities, such as feeding or resting, and may expose itself to higher predation risks (Carpenter 1987, Martel 1996, Diaz-Uriarte 1999, Kim et al. 2004, LaManna and Eason 2007). Theory predicts that resource defense will occur when the fitness benefits of exclusive use outweigh the costs of defense, that is, when defense is economical (Brown 1964). Hence, resource defense should usually peak at intermediate levels of abundance as well as of spatial clumping of resources (Grant 1993, Grant and Guha 1993, Grant et al. 2002, Noël et al. 2005). This leads to variable levels of resource monopolization in a population and can thereby affect mating systems (Emlen and Oring 1977) and population dynamics (Patterson 1980, Newton 1992, Sutherland 1996, Lopez-Sepulcre and Kokko 2005).

The ability of individuals to defend resources or space containing it can be influenced by many other factors (Maher and Lott 2000), notably the level of competition (Grant 1993). High levels of competition for a resource can result in high intrusion rates in a given territory or at a given food patch, leading to high defense costs, reduced benefits associated with aggressive behaviors and ultimately lower monopolization (Chapman and Kramer 1996, Syarifuddin and Kramer 1996). A growing number of studies suggests that habitat structure can also play an important role in the ability of individuals to efficiently defend food resources against competitors (Eason and Stamps 1992, Basquill and Grant 1998, Hamilton and Dill 2003). Most studies found a negative relationship between habitat complexity and monopolization. In habitats where structural complexity is high, visual detection of intruders is

likely more difficult because of a more obstructed field of view (Eason and Stamps 1992, Breau and Grant 2002) which leads to easier access to a defended resource for intruders. Studies that looked at the influence of habitat complexity or reduced visibility on resource defense and monopolization (Hamilton and Dill 2002, Hamilton and Dill 2003) or space use (Eason and Stamps 2001), also showed a positive effect on population density (Venter et al. 2008, Dolinsek et al. 2007) and a negative effect on territory size (Breau and Grant 2002, Imre et al. 2002, Venter et al. 2008), aggression level (Basquill and Grant 1998, Corkum and Cronin 2004, Baird et al. 2006, Carfagnini et al. 2009, Cenni et al. 2010) and in some cases the growth rates of dominant individuals (Höjesjö et al. 2004, Hasegawa and Yamamoto 2009).

Except for certain studies on fishes (Hamilton and Dill 2003), and particularly on salmonids (Imre et al. 2002, Venter et al. 2008, Hasegawa and Yamamoto 2009), few studies examined the effect of habitat complexity in natural settings, where resources are often difficult to quantify and where individuals are unconstrained in their use of space. How individuals use space likely affects their ability to monopolize a certain area or food patch depending on the amount of time they allocate to different part of their home ranges and to different activities, such as foraging (Hamilton et Dill 2003), feeding in other defended areas (Steingrímsson and Grant 2008) or seeking mating opportunities (Sikkel 1998, Stutchbury 1998, Sikkel and Kramer 2006). For example, by adding simulated vegetation around territories, Hamilton and Dill (2003) reduced the defendability of territories in western buffalo bream (*Kyphosus cornelii*), increasing kleptoparasitism toward other territorial individuals and intrusions rates on the focal individual's territories. Sikkel and Kramer (2006) showed in female yellowtail damselfish (*Microspathodon chrysurus*), which leave their territories to spawn, that the temporal patterns and total duration of their absence affected intrusions rates on their territories. Although individual space use can be viewed as a consequence of resource distribution and competition, it can also be influenced by individual characteristics such as age or dominance status, which may in turn affect the ability of individual to defend and monopolize resources. For example, subordinate individuals can become floaters if they are not able to acquire a territory (Sergio et al. 2009) and this will likely influence their use of

space. Thus, taking into account space use by individuals is essential to understand the factors influencing resource monopolization at both the individual and population level. Furthermore, despite numerous studies quantifying spatial overlap among conspecifics, and sometimes taking into account territory or home range internal structure (Millspaugh et al. 2004, Fieberg and Kochanny 2005), how spatial overlap results in resource sharing among neighboring individuals has rarely been explored, though it is ultimately what characterizes territorial behavior. Quantifying resource monopolization also allows us to characterize spatial organization as a continuum from completely undefended home ranges with extensive overlap between individuals to totally exclusive territories (Maher and Lott 1995, 2000, Tyre et al. 2007), which better represents reality than the simple home range/territory dichotomy (Maher and Lott 1995). This approach is also particularly useful for inferring territoriality in species lacking overt territorial behaviors or in species defending specific areas within extensively overlapping home ranges (Kerr and Bull 2006, Pierro et al. 2008).

In this paper, we took advantage of a new technique to mark Ruby-Throated Hummingbirds (*Archilochus colubris*, Charette et al. in prep.) to quantify how resource monopolization and the capacity of individuals to defend food resources are influenced by competition, habitat structure and the use of space by individuals. Our study system consists of a systematic grid of artificial feeders set up in the wild where feeders are equipped with radio-frequency identification detectors (RFID) and individuals are marked with passive integrated transponders (PIT tags). This system allows us to record every visit made on the grid and to monitor differential use of feeders by individuals, thus taking into account their use of space. The study system also provides a uniform distribution of feeders which standardizes food distribution across the grid, therefore eliminating the effect of food distribution on the ability of individuals to monopolize certain feeders. Differential use of feeders is thus ultimately determined by surrounding habitat features and interactions between individuals.

Nectarivorous birds, especially hummingbirds, have been the subject of many studies testing economic models of feeding territoriality (Carpenter et al. 1983) and investigating the links between territory size, food abundance and intrusion pressure (Gass et al. 1976, Kodric-Brown and Brown 1978, Norton et al. 1982, Hixon et al. 1983, Eberhard and Ewald 1994). Most studies found a negative effect of food abundance or intrusion pressure on territory size, whereas others tried to disentangle the complex interaction between these two variables (Eberhard and Ewald 1994). For example, Norton et al. (1992) experimentally manipulated intrusion pressure while maintaining food abundance constant and found a negative effect of intrusion pressure on territory size. Likewise, Marchesseault and Ewald (1991) showed that a reduction in food abundance decreased intrusion rates, indicating that food abundance could affect territory size through intrusion pressure. On another front, several studies showed that investment in territorial defense (as measured by proportion of intruding individuals chased or number of chases per unit time) is positively influenced by the quantity and/or quality of food sources (Tamm 1985, Ewald and Bransfield 1987, Dearborn 1998, Temeles et al. 2004, Camfield 2006) which could be a response to increased competition or to a higher incentive to defense due to the resource seen as more profitable or both (Camfield 2006).

The above studies clearly demonstrate that hummingbirds will aggressively defend food sources, including feeders providing *ad libitum* artificial nectar (Carpenter 1987, Ewald and Bransfield 1987, Powers and McKee 1994, Camfield 2006). Yet, defense and territorial behavior was often characterized in terms of territory size or investment in defense, but rarely in terms of resource monopolization. Indeed, few studies quantified the extent to which territorial hummingbirds have exclusive use of their defended area or food source, which is an essential component of territorial behaviour (Pyke et al. 1996), and what factors besides food distribution and abundance affected this exclusivity. Moreover, space use by territorial hummingbirds is likely not restricted to the area defended (Powers and McKee 1994, Temeles et al. 2005), and intrusion pressure indicates that either territorial birds occasionally leave their territories or that a certain proportion of the population is made of “floating” individuals. Such extra-territorial forays may be linked to foraging or food sampling (Armstrong 1987), other

temporarily defended areas or searching for mating opportunities. Because of the difficulty of marking and following individuals in the wild, the characterization of simultaneous space and resource use by hummingbirds, or by other organisms, has rarely been done.

The Ruby-Throated Hummingbird is known to aggressively defend natural and artificial food sources, especially in the case of adult males (Robinson et al. 1996). Males presumably defend territories centered on food sources that may also play a role in mate acquisition (Pitelka 1942). Like in most hummingbird species, males provide no parental care and their only role in reproduction is mating (Robinson et al. 1996). Therefore, competition between males for access to females is probably strong and space use by both sexes likely differs substantially. Anecdotal evidences suggest differential habitat selection by males and females of some North American hummingbird's species (Armstrong 1987). Females may be found more in forested habitats, which presumably provide better nesting cover, whereas males may be using more open habitats, adjacent to female habitats (Armstrong 1987), because it may offer better opportunities for detecting and displaying to females. High variability in male reproductive success (Mulvihill et al. 1992) could also imply different spatial strategies among males, possibly related to individual characteristics such as age, experience or dominance status. This variability could translate to varying levels of aggression and efficiency at defending food sources.

Here, we addressed monopolization and defense of feeders in Ruby-throated Hummingbirds by modeling the number of visits made by competitors (NVC) at a given feeder in response to the number of competitors, feeder visibility, and space use by a focal individual. Although intrusion pressure cannot be inferred from NVC, it measures competitor access to food and thus the level of exclusivity experienced by a focal individual at a given feeder. Furthermore, the extent by which a focal individual lowers the NVC can also be interpreted as a measure of its capacity or motivation to exclude competitors. Therefore, the monopolization and the capacity to defend feeders, which are not necessarily equivalent, can be differentiated. For

instance, if habitat preferences cause a disproportionate use of feeders in open habitats compared to feeders in forest habitats, a higher NVC, and thus lower feeder monopolization, would be observed in open habitats. Yet, the negative effect of a focal individual on NVC could be more pronounced in open habitats, indicating a better defense capacity, even though its monopolization level would be lower because of habitat preferences. We thus differentiate between monopolization and capacity to defend feeders to test three hypothesis: 1) the number of competitors reduces the capacity of individuals to defend feeders and increases NVC; 2) higher visibility improves capacity at defense, but also cause a higher NVC linked to habitat preferences; and 3) higher spatial concentration and stability of focal individuals in their use of feeders lead to a lower NVC. We also manipulated sugar concentration in feeders to assess the influence of resource quality on monopolization and defense of feeders. Specifically, we tested the hypothesis that high food quality leads to greater defense of feeders, but results in lower monopolization because of higher competition for high-quality feeders.

Methods

Study System

We conducted field work during the breeding seasons (20 May – 30 August) of 2007-2009 in Cleveland County, Quebec, Canada (45° , $40'$ N; 72° , $05'$ W). Our study system consisted of a grid of 45 feeders distributed systematically over 44 ha. Feeders were spaced 100 m apart and were set up in 2 rows of 12 feeders followed by 3 rows of 7 feeders (Figure 1). The grid covered a gradient of vegetation cover, going from hayfields and fallows to mature deciduous and mixed forests (8 feeders in hayfields, 6 in fallows and 31 in forests) (Figure1).

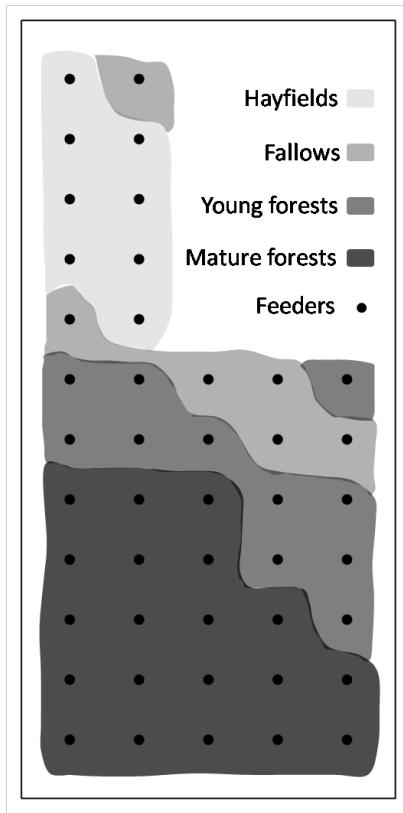


Figure 1. Schematic view of habitats within the feeder grid providing a nectar sucrose solution for Ruby-throated Hummingbirds in Cleveland County, Quebec (Canada), 2007-2009

Feeders (Yule Hide, model HB81, capacity: 455 ml) were red and included a single opening mimicking a yellow flower. Feeders were installed on metal poles at a height of 1.3-1.7 m and covered by an aluminum plate to prevent evaporation and excessive heating from direct sunlight. We changed feeders once a week by sterilized ones filled with a solution of 20% (W/V) of sucrose, a concentration similar to the nectar of natural flowers (Baker 1975, Bolten et al. 1979, Roberts 1996). Each feeder was equipped with an antenna hooked to a radio-frequency identification reader (Trovan Electronic Identification System, model LID650). The antenna consisted in a rectangular-shaped copper wire attached to the only perching site of the feeder. We removed three of the four original feeder openings (flowers), as well as the perches associated with those openings, in order to force individuals to drink through the opening that

bears the antenna. The antenna was set up vertically on the perch so that birds were forced to perch in the antenna while drinking, which enabled detection. The readers were programmed to scan for passive integrated transponders (PIT tags) every second. Hence we recorded every second (date and time of day) that a tagged individual spent in the antenna along with its tag ID. We transformed those readings in visits such that every visit by an individual was characterized by a start time and a duration. Because detectors occasionally skipped some readings, we considered that 2 consecutive readings by the same individual at a given feeder and <21 sec apart were part of the same visit. Two consecutive readings at a given feeder and >20 sec apart were thus considered to be part of different visits. Detectors were active on a 24h/day schedule.

Capture and Marking

We captured hummingbirds near or at feeders using mist-nets (36 mm or 28 mm mesh) or Hall traps (Russel and Russel 2001), respectively. Capture was usually done between 06h00 and 13h00 throughout the study period. Although capture efforts were oriented toward feeders where unmarked individuals were seen during standardized focal observations, we made sure that all feeders were subjected to a minimum capture effort within a 10 day period. We also increased capture efforts when unmarked individuals were seen and when hummingbird activity on the grid was high. We fitted individuals with an aluminum leg band and we glued the 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 (for details, see Charette et al., in prep). The leg band, the PIT tag and the glue represented 5% or less than the hummingbird's body mass, which is acceptable according to established standards (Kenward 1987, White and Garrot 1987).

Space use and competitors

We quantified space use by focal individuals using spatial concentration and stability. Spatial concentration was defined as the ratio between the number of visits by an individual to a given feeder on a given day and its total number of visits on the grid for the same day. This value thus reflects the daily level of concentration of an individual at a particular feeder. Stability was defined as the linear correlation between daily spatial concentration and seasonal spatial concentration. Seasonal spatial concentration consisted in the same measure as spatial concentration, but was calculated for the entire period during which an individual was followed. The correlation between these measures therefore represents the level to which the daily use patterns of the grid mimicked the seasonal pattern, which can be seen as an index of spatial stability or fidelity in the usage of the grid by an individual. It varies from 0 to 1, with 1 representing total stability. Because spatial stability requires at least three days to be evaluated, only individuals that were followed for more than two days were considered as focal individuals (mean \pm SD = 38.3 ± 22.2 days), though all adults were included in the calculation of the number of competitors (daily number of individuals detected at the feeder) and NVC.

Competitors should not be restricted in their access to a feeder unless it is defended. We thus expected that spatial concentration would have no effect on NVC if an individual did not defend feeders. On the other hand, we expected a negative effect of spatial concentration on NVC for an individual that aggressively defends feeders. Assuming that spatial concentration somehow reflects the importance of a feeder to an individual, the more a defending individual is concentrated at a given feeder, the greater indeed should be its negative impact on NVC at that feeder. The effect of spatial concentration on NVC thus reflects, at least partially, the ability and/or the will to defend of an individual and the strength of this effect represents the degree or the effectiveness of its defense. Therefore, looking at the effect of different variables on the ability of individuals to efficiently defend feeders required that we include interactions between spatial concentration and variables thought to affect this ability in our models (Table

2). For instance, if the ability of individuals to defend feeders is reduced by the number of competitors, the negative effect of spatial concentration on NVC should be weaker when the number of competitors is high. Similarly, an individual using the same feeders day after day probably indicates that those feeders have a greater importance for the individual; therefore, we also expected that the negative effect of spatial concentration on NVC should be stronger when spatial stability is high.

Visibility

We assessed visibility around feeders using two habitat variables. First, each feeder was categorized as being in an opening or not. An opening was defined as a $>50\text{ m}^2$ gap in the canopy. Fourteen of the 31 feeders located in forest habitat fell in the former category along with all of the 14 feeders situated in hayfields and fallows. Second, lateral visibility between 1 and 2 m was measured around each feeder at eye's height (~1.5m). It was defined as the maximum distance (m) at which 90% of a banner (width = 30 cm) located at the feeder was visible. This measure was evaluated by the same observer and averaged over the four cardinal directions. We assumed that feeders located in openings were in high visibility environments, independently of lateral visibility, while lateral visibility in closed environments was a better indicator of general visibility for a hummingbird at the feeder. This assumption was made because hummingbirds usually perch high in open habitats and thereby have an overview of feeders unobstructed by the shrubby vegetation that contributes to the low lateral visibility that may occur in these habitats. In order to model the influence of visibility on the relationship between spatial concentration and NVC, we thus had to include a three-way interaction among openness, lateral visibility and spatial concentration. Indeed, we expected the negative effect of spatial concentration on NVC to be independent of lateral visibility in open habitats, but to increase with lateral visibility in closed habitats.

Food quality

To assess the effect of food quality on resource defense and monopolization, we manipulated feeder quality in 2009 by increasing the sucrose concentration of some feeders from 20% to 35% (W/V of solution). Previous studies showed that hummingbirds preferred nectar of high sucrose concentration and that this preference peaked somewhere between 40% and 65% across studies (e.g., Tamm and Gass 1986, Roberts 1996, Blem et al. 2000). Although our measurement units may differ from other studies, our high concentration treatment fell within the range of preferred concentrations (Bolten et al. 1979). Moreover, Camfield (2006) found higher intrusion rates by Rufous (*Selasphorus rufus*) and Broad-tailed Hummingbirds (*S. platycercus*) at feeders filled with a 30% (W/V) sucrose nectar compared to feeders containing a 20% sucrose nectar. We are therefore confident that a 35% solution represents higher quality nectar compared to a 20% solution. Our manipulation was divided into 3 blocks of 3 weeks each, lasting from 10 June to 11 August. Each week, we randomly assigned the high concentration to 15 of the 45 feeders with the constraint that every feeder had to be of high concentration exactly once throughout a block, ensuring a complete coverage of feeders within 3 weeks. Because feeders were replaced once a week in the morning, we considered that the state of the feeders after their replacement represented their state for the whole day. As the low concentration treatment corresponded to the standard sucrose concentration found in the first two years, we decided to run our analyses using the three years of the study with year as an explanatory variable and the low concentration treatment assigned to all feeders in 2007 and 2008.

Sex and control variables

Because of the numerous interactions that could arise from the inclusion of sex as an explanatory variable, we chose to restrict our analyses to the four possible sex combinations of

focal individuals and competitors, that is, the effect of focal males on male or female competitors and the effect of focal females on male or female competitors. This approach allowed us to determine the extent of intra- and intersexual territoriality, while reducing model complexity. The total daily number of visits by the focal individual was included to account for the fact that a spatial concentration of 90% at a given feeder was unlikely to have the same impact on NVC if the individual made 10 visits on the grid compared to 100 visits. To control for variable meteorological conditions, such as temperature and precipitations, and availability of natural food sources that may affect the level of feeder use, we derived an index corresponding to the mean daily number of visits across hummingbirds that used the grid. To control for the fact that certain feeders may be more attractive to hummingbirds, we ranked feeders according to the number of different individuals detected at the feeder at least once throughout the season. Feeders were ranked in ascending order with the feeder with the highest number of individuals detected having the lowest value. Ranks were consistent across the three years of study with a high interannual correlation ($r = 0.89-0.95$, $n = 45$), suggesting that feeder attraction was maintained through time. We were not able to consider the age of individuals, which might affect territorial behavior or dominance (Ewald 1985, Carpenter et al. 1993), because aging beyond juvenile in Ruby-throated Hummingbirds is only possible by recapture of individuals initially captured as young of the year, which seldom occurred in our study system. From 67 individuals captured as young of the year, 14 were recaptured giving a ratio of 14/191 adults of known age.

Statistical analyses and model selection

We used boxplots to describe the populational pattern of individuals' concentration at feeders. For a given individual on a given day, we ranked every feeder visited according to the number of visits at the feeder, with rank 1 being the most visited feeder. Ties were given the same and lowest possible rank. To determine whether individuals were more concentrated at a certain feeder than what would be expected from a random use, we randomly assigned visits to every

feeder visited on a given day by a given individual and we calculated the mean spatial concentration at feeders of rank 1 for the whole population. This procedure was repeated 100 times. A higher observed value for the mean spatial concentration at feeders of rank 1 than the values generated randomly indicates that individuals are more concentrated at their “primary” feeder than expected by chance.

A similar procedure was used to describe the pattern of use of a single feeder on a given day by different individuals. Individuals were ranked according to the number of visits with rank 1 given to the individual with the most visits at the feeder. To determine whether individuals of rank 1 made a disproportionately higher number of visits than others, we randomly assigned every visit made at the feeder to individuals visiting it on that day. We then calculated the mean number of visits at feeders by individuals of rank 1 for the whole population and this procedure was repeated 100 times. A higher observed value for the mean number of visits by the individual of rank 1 than the values generated randomly shows that the “primary” individual usually made a disproportionately higher number of visits compared to other individual visiting the feeder. This indicates that feeder use is more exclusive than what would be expected by chance alone.

We used linear mixed models to quantify the influence of explanatory variables on the number of visits made by competitors (NVC), with feeder ID and focal individual ID as random effects. We also expected individuals to vary in their will and ability to defend feeders and thereby allowed the slope characterizing the effect of spatial concentration to vary as a random parameter across focal individuals. Competitors were defined in relation to a focal individual at a given feeder. Hence, every individual that visited a given feeder on a given day was in turn considered as a focal individual while others as its competitors. We log-transformed NVC to meet assumptions of normality and homoscedasticity. We restricted analyses to adults as juveniles were detected only at the beginning of August and most stayed on the grid only for a few days. Cases where only one individual was detected at a feeder on a given day were

excluded as there is no variation in NVC in such cases. The time spent at feeders by competitors was also used as a response variable and results were highly similar. Only analyses based on NVC are thus presented here. We selected models and performed multimodel inference based on the Akaike Information Criterion corrected for small sample sizes (AICc) following Burnham & Anderson (2002) and Vaida and Blanchard (2005). We used the same set of models and variables for the four sex combinations, except for feeder rank for which the calculation was restricted to the sex of competitors (see Table 2; Results section). Most models were built so that every interaction representing the effect of a variable on the capacity of individuals to defend feeders was sequentially left out. Another model (8) was built without any interaction to represent the possibility that there was nothing influencing the capacity of individuals to defend feeders. Two models (3, 9) tested whether habitat structure influenced the number of visits by competitors without affecting the capacity of individuals to defend feeders. Finally, all models included year, grid usage, nb of competitors, feeder rank and nectar sucrose concentration as these variables were mostly used as controls. AICc values were computed based on the models' maximum likelihood and model averaging performed on coefficients obtained by restricted maximum likelihood. Analyses were conducted in R 2.10.1 (R Development Core Team 2009) using the lmer function from the lme4 package (version 0.999375-32).

Results

Over the 3 breeding seasons, we followed at least 75 focal individuals in every sex combination, representing a minimum of 1539 bird-days for every combination (Table 1). Feeders were used with some degree of exclusivity, because individuals that made the most visits to a given feeder on a given day made a disproportionately higher number of visits than other individuals (Figure 2A) (mean number of visits by individual of rank 1 = 19.29 ; random values (mean \pm sd) = 7.88 ± 0.03 ; $p < 0.01$). Moreover, most if not all individuals made a disproportionately higher proportion of their visits at a single feeder (Figure 2B) (mean spatial

concentration at feeder of rank 1 = 0.631 ; random values (mean \pm sd) = 0.378 ± 0.002 ; $p < 0.01$). In spite of a strong variation among individuals, those results suggests that feeders are used more or less exclusively, that individuals are moderately to highly concentrated in space, and that in most cases, every individual can be linked to a “primary” feeder.

Table 1. Number of adult Ruby-throated hummingbirds considered as focal individuals and number of bird-days for the four sex combinations (focal individual vs. competitors) used for modeling the number of visits by competitors at nectar feeders in Cleveland County, Quebec (Canada), 2007-2009. Only individuals followed for at least three days were considered as focal individuals.

Combination	Nb of focal individuals	Nb of days-focal individuals
male vs males	88	3326
male vs females	86	2497
female vs females	75	1709
female vs males	75	1539

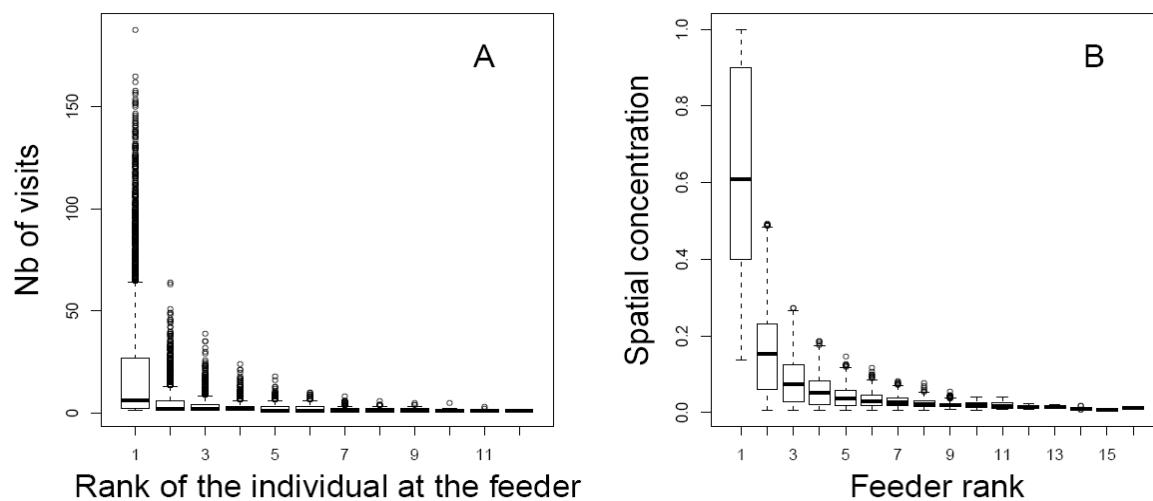


Figure 2. Boxplots showing number of visits and spatial concentration of adult Ruby-throated hummingbirds in Cleveland County, Quebec (Canada), 2007-2009. A) For a given feeder on a given day, every individual has been ranked according to its number of visits at the feeder,

with rank 1 being the individual with the most visits to the feeder. This figure shows how the number of visits at feeders decreased with the rank of individuals. B) For a given individual on a given day, every feeder has been ranked according to the number of visits made by the individual, with rank 1 being the most visited feeder. This figure shows the decrease in spatial concentration of individuals in relation to feeder rank. Both graphics are for the male vs. males combination only.

The set of variables influencing NVC varied among sex combinations (Table 2-3, Appendix 1), suggesting that resource defense dynamics strongly depend on the sex of both the defender and the competitors. Nevertheless, models that did not consider the spatial concentration of individuals, either as a main effect or in interactions, were the least supported by the data in all sex combinations (Table 2). There was also either a significant negative effect of spatial concentration or a significant interaction involving spatial concentration, except for the male vs. females combination (Table 3, Appendix 1). However, the negative effect was strong only in the case of the male vs. males combination (Figure 3). Indeed, when spatial concentration goes from 0.0 to 1.0, the reduction in the number of visits by competitors in the male vs. males combination is 53% compared to 25% and 24% for the female vs. females and female vs. males, respectively. This implies that food resource defense or territorial behavior is more pronounced among males, at least during the breeding season. Moreover, the only significant interaction for the female vs. females and female vs. males combinations was the interaction between number of competitors and spatial concentration (Appendix 1). Although significant and showing a positive influence of spatial concentration over 5 competitors, this effect is still relatively small (Figure 4). We will thus focus on male vs. males interactions in the remaining parts of this paper as the level of defense in other cases may not be strong enough to study the influence of factors other than spatial concentration on food resource defense and monopolization (see Appendix 1 for results regarding other sex combinations).

Table 2. Model selection and explanatory variables composing the 10 models put in competition by AICc for modeling the number of visits by Ruby-throated Hummingbird competitors in Cleveland County, Quebec (Canada), 2007-2009. Variables included and omitted from a model are indicated by a cross and a circle, respectively. The same set of models was used for the four sex combinations (Table 2). Feeder rank is based on the sex of competitors. Akaike weights (w_i) represent the probability that a particular model best describes the data. The response variable was log-transformed and modeled with linear mixed-effect models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.

Variables	1	2	3	4	5	6	7	8	9	10
year	x	x	x	x	x	x	x	x	x	x
grid usage	x	x	x	x	x	x	x	x	x	x
nb of competitors	x	x	x	x	x	x	x	x	x	x
feeder rank	x	x	x	x	x	x	x	x	x	x
nectar sucrose concentration	x	x	x	x	x	x	x	x	x	x
spatial concentration	x	x	x	x	x	x	x	x	o	o
daily nb of visits	x	x	x	x	x	o	x	x	o	o
spatial stability	x	x	x	x	x	x	o	x	o	o
openness	x	x	x	o	x	x	x	x	x	o
lateral visibility	x	x	x	o	x	x	x	x	x	o
spatial concentration:daily nb of visits	x	x	x	x	x	o	x	o	o	o
spatial concentration:nb of competitors	x	x	x	x	o	x	x	o	o	o
spatial concentration:spatial stability	x	x	x	x	x	x	o	o	o	o
spatial concentration:openness:lateral visibility	x	x	o	o	x	x	o	o	o	o
spatial concentration:feeder concentration	x	o	o	o	o	o	o	o	o	o
male vs. males	ΔAICc	2.15	0.24	26.87	39.58	0.00	34.47	2.01	77.68	901.67 911.79
	w_i	0.132	0.342	0.000	0.000	0.385	0.000	0.141	0.000	0.000 0.000
male vs. females	ΔAICc	5.13	3.31	0.00	3.07	2.34	13.37	1.15	5.44	50.92 53.96
	w_i	0.032	0.079	0.413	0.089	0.128	0.001	0.232	0.027	0.000 0.000
female vs. females	ΔAICc	0.00	0.75	0.44	8.18	5.00	0.80	6.71	9.00	253.05 263.46
	w_i	0.303	0.208	0.242	0.005	0.025	0.203	0.011	0.003	0.000 0.000
female vs. males	ΔAICc	4.85	3.20	0.00	3.69	6.86	9.66	3.92	11.34	41.08 45.36
	w_i	0.054	0.124	0.612	0.097	0.020	0.005	0.086	0.002	0.000 0.000

Table 3. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult male Ruby-throated Hummingbirds competitors at feeders potentially defended by a male in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.

variables	coef	se	lowerCI	upperCI
year2008	-0.09017	0.03778	-0.16423	-0.01612
year2009	-0.17854	0.04631	-0.26931	-0.08777
grid usage	0.01735	0.00090	0.01560	0.01911
nb of competitors	0.34542	0.00571	0.33423	0.35660
feeder rank for males	0.01531	0.00328	0.00889	0.02173
nectar sucrose concentration (high)	0.51430	0.03940	0.43708	0.59152
spatial concentration	-0.20918	0.21631	-0.63314	0.21479
daily nb of visits	-0.00028	0.00049	-0.00123	0.00067
spatial stability	0.15381	0.11210	-0.06591	0.37353
openness (open)	0.62874	0.20028	0.23620	1.02129
lateral visibility	0.00347	0.00395	-0.00427	0.01122
spatial concentration:daily nb of visits	-0.00587	0.00120	-0.00822	-0.00352
nb of competitors:spatial concentration	0.02693	0.01979	-0.01186	0.06572
spatial concentration:spatial stability	-0.81189	0.31734	-1.43387	-0.18991
spatial concentration:feeder concentration (high)	0.03809	0.13691	-0.23026	0.30644
spatial concentration:openness (close):lateral visibility	-0.04051	0.01601	-0.07189	-0.00914
spatial concentration:openness (open):lateral visibility	0.00744	0.00170	0.00411	0.01078

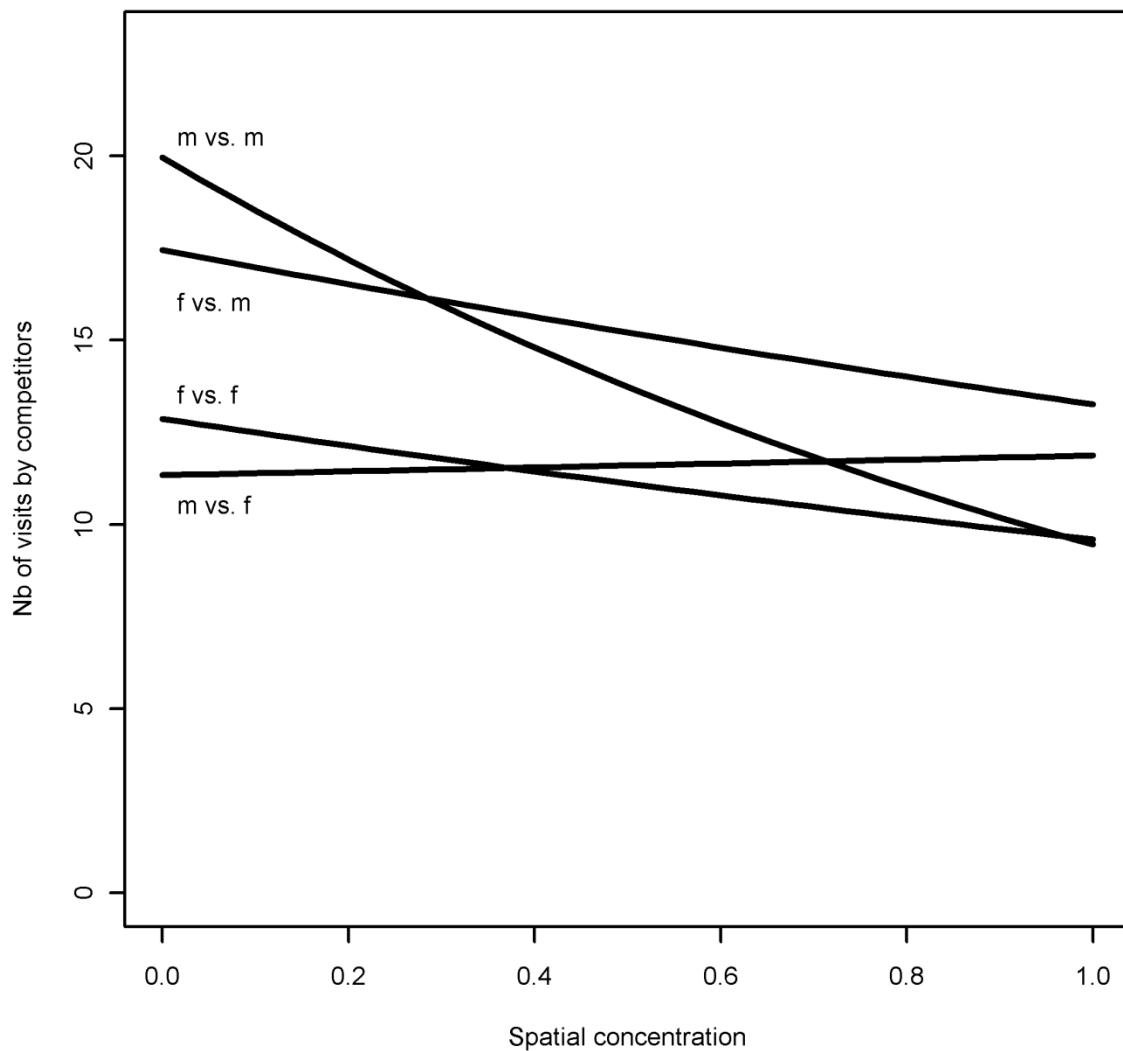


Figure 3. Predicted number of visits by competitors (NVC) against the spatial concentration of focal Ruby-throated Hummingbirds for the four sex combinations studied in Cleveland County, Quebec (Canada), 2007-2009. Predictions are derived from model-averaged, linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. Other numeric variables were fixed to their mean value and factors were fixed to their reference level.

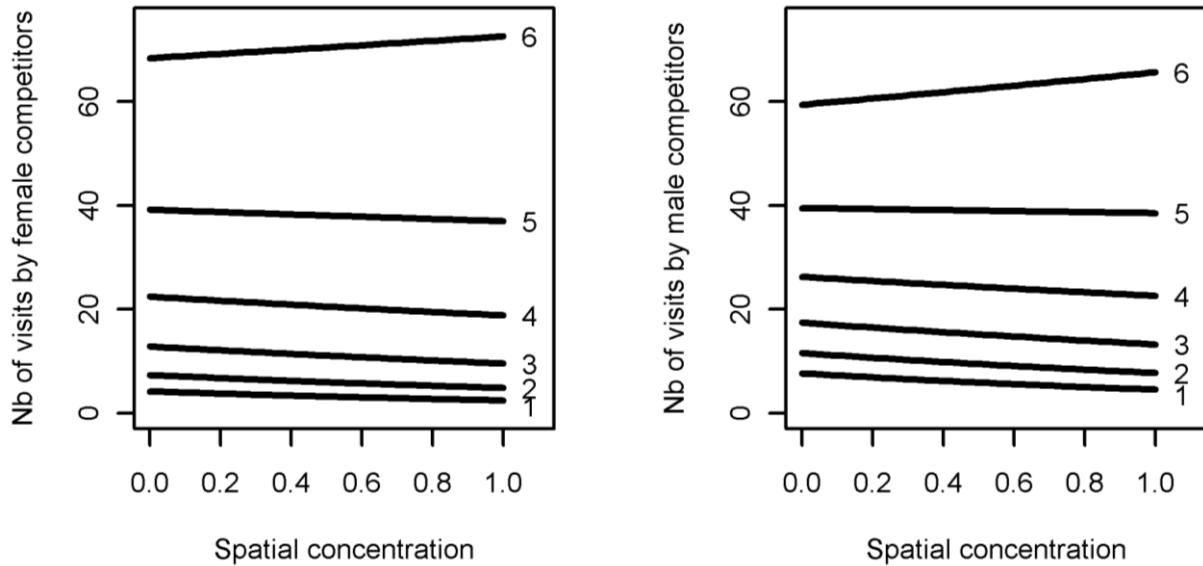


Figure 4. Model-averaged predictions for the number of visits made by female or male Ruby-throated Hummingbird competitors (NVC) in Cleveland County, Quebec (Canada), 2007-2009, in relation to the spatial concentration of focal female and the number of female or male competitors. Predictions are derived from linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. The response variable was log-transformed. Other numeric variables were fixed to their mean value and factors were fixed to their reference level.

Model selection based on AICc indicates that the influence of spatial concentration on the number of visits made by competitors (NVC) varied among individuals in all sex combinations. A comparison between full models with and without a random effect that allowed the slope of spatial concentration to vary among individuals indeed showed a clear differential support for treating this parameter as random (ΔAICc : male vs. males = 86.2; male vs. females = 46.7; female vs. females = 74.5; female vs. males = 13.4). Variability among focal males was particularly high, with some individuals showing no, or even a positive effect of spatial concentration, while others showed a strong negative effect (Figure 5). Thus, the level of defense by males seems to be characterized by a continuum from no apparent defense

to a strong defense level of feeders, although most individuals showed a moderate level of defense.

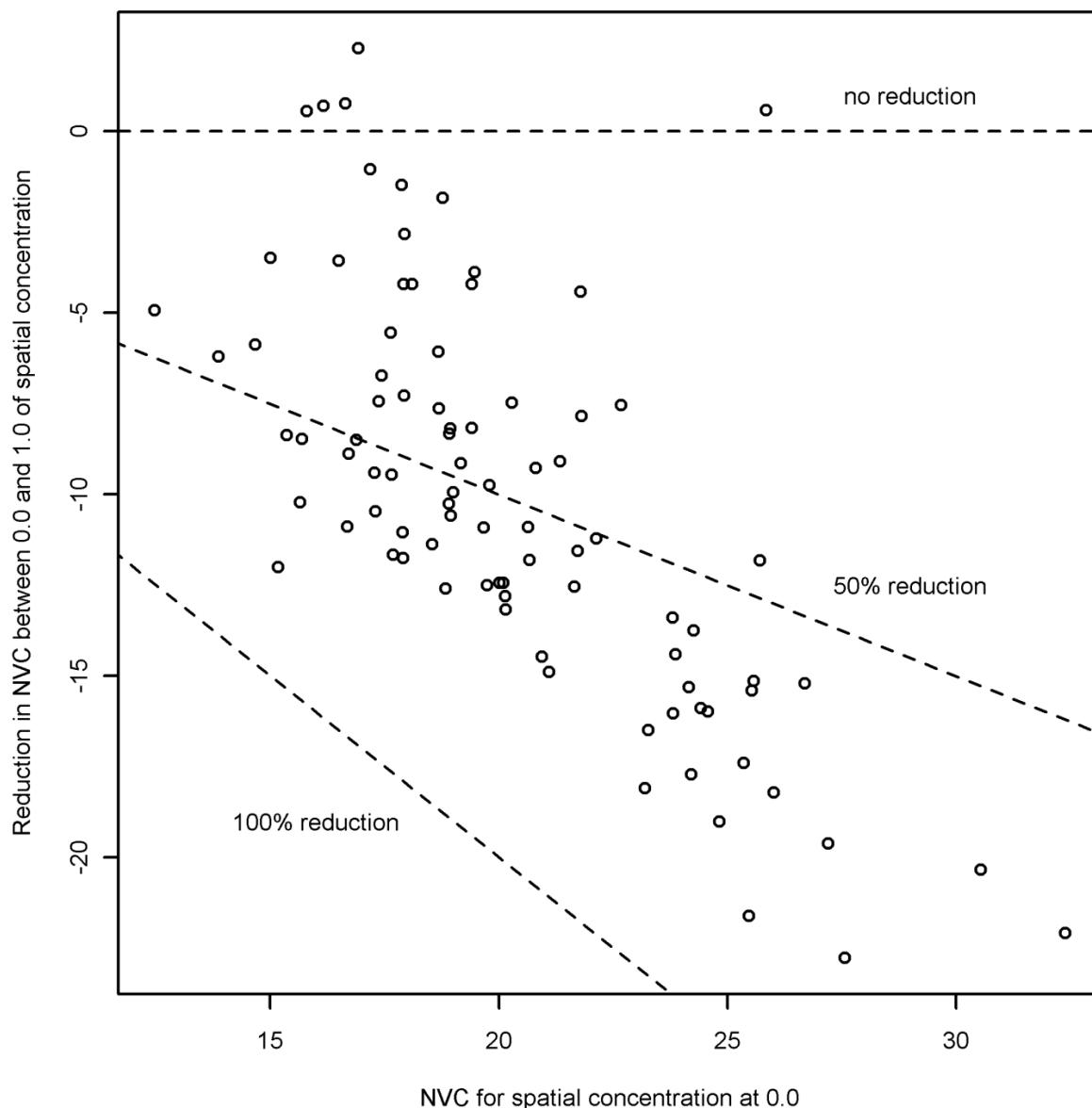


Figure 5. Predicted reductions in the number of visits made by adult male Ruby-throated Hummingbird competitors (NVC) when focal males' spatial concentration goes from 0.0 to 1.0 in Cleveland County, Quebec (Canada), 2007-2009. The X axis represents NVC when spatial concentration is 0.0. Values were obtained using the model-averaged BLUPs of the linear mixed models listed in Table 2 as individuals were treated as random effects for the

intercept and the slope characterizing the effect of spatial concentration. Other numeric variables were fixed to their mean value and factors were fixed to their reference level.

Among males, the negative effect of spatial concentration on NVC was more pronounced when the total number of visits by the focal individual was high, that is, when the focal individual made a greater use of the grid (Table 3, Figure 6A). This effect also became stronger with increasing spatial stability, indicating that individuals concentrated and stable in space gained higher exclusivity in the use of feeders (Table 3, Figure 6B). Moreover, there is a slight increase in the mean daily maximum spatial concentration of individuals with spatial stability, indicating that concentrated individuals also tend to be more stable in space, although this relation is characterized by high variability (Figure 7). Although NVC increased with the number of competitors, this increase did not depend on the level of spatial concentration, which suggests that an individual's capacity to defend feeders was not affected by the number of competitors (Table 3, Figure 6C). Finally, habitat structure influenced the capacity of individuals to defend and monopolize feeders. When feeders were in open habitat, the negative effect of spatial concentration decreased with lateral visibility contrary to our prediction (Table 3, Figure 6D). Regarding feeders in closed habitat, however, the interaction was reversed and the negative effect of spatial concentration increased with lateral visibility as we predicted. Although, these results suggest that capacity to defend feeders is influenced by visibility, a high capacity to exclude competitors from feeders does not necessarily imply a higher degree of monopolization. Indeed, NVC was much higher in open habitats than in closed ones, which may indicate a disproportionate use of feeders in open areas. To achieve the same degree of monopolization or NVC, an individual defending a feeder in the open would thus have to exclude more intruders than an individual defending a feeder in closed habitat, where intrusion rates are probably lower.

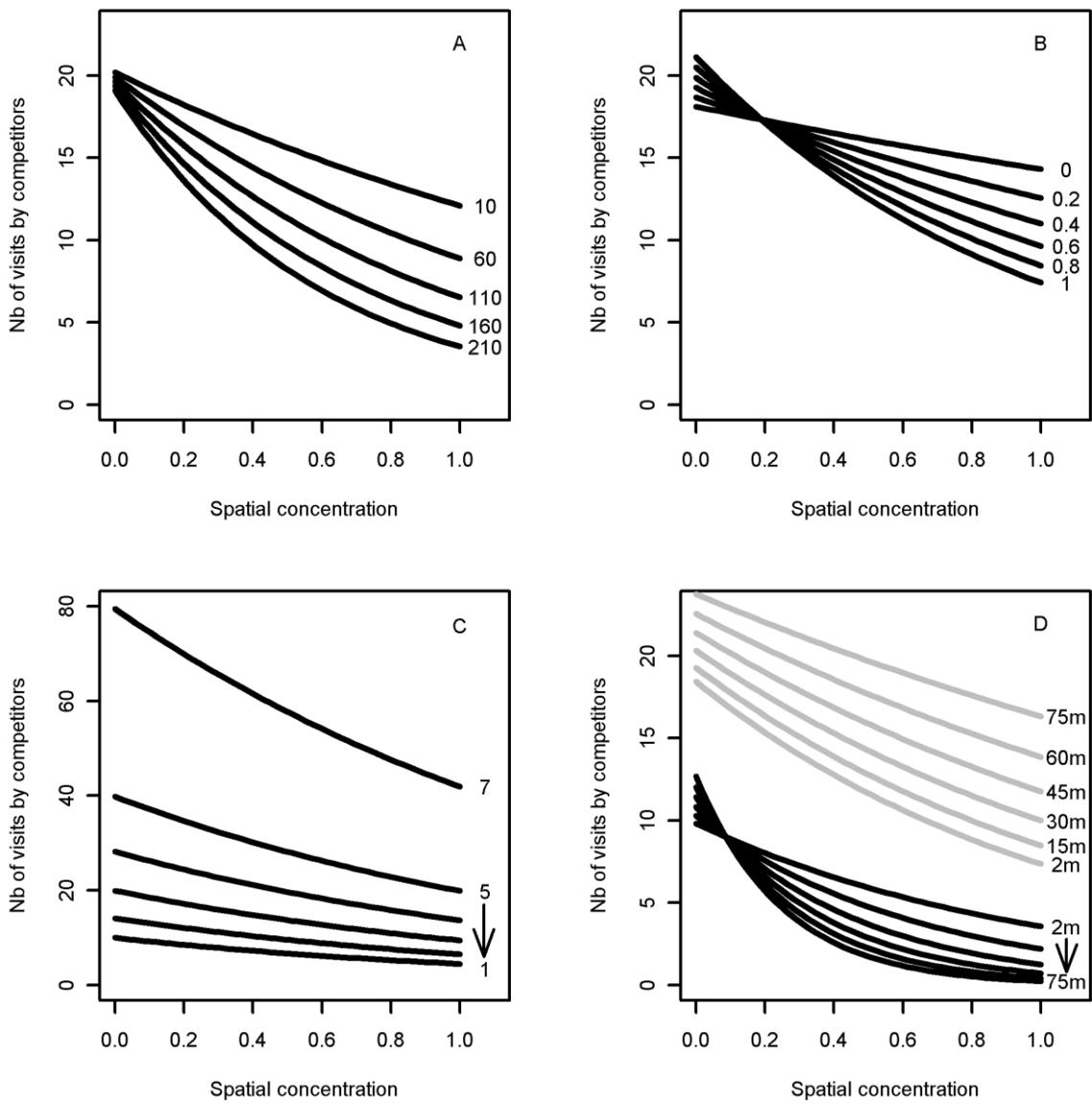


Figure 6. Model-averaged predictions for the number of visits made by male Ruby-throated Hummingbird competitors (NVC) in Cleveland County, Quebec (Canada), 2007-2009, in relation to the spatial concentration of the focal male and A) the total number of visits by the focal individual, B) the spatial stability of the focal individual, C) the number of competitors, and D) the lateral visibility (meters) and habitat openness (open; gray lines, closed; black lines). Predictions are derived from a linear mixed-model with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects. The response variable

was log-transformed. Other numeric variables were fixed to their mean value and factors were fixed to their reference level.

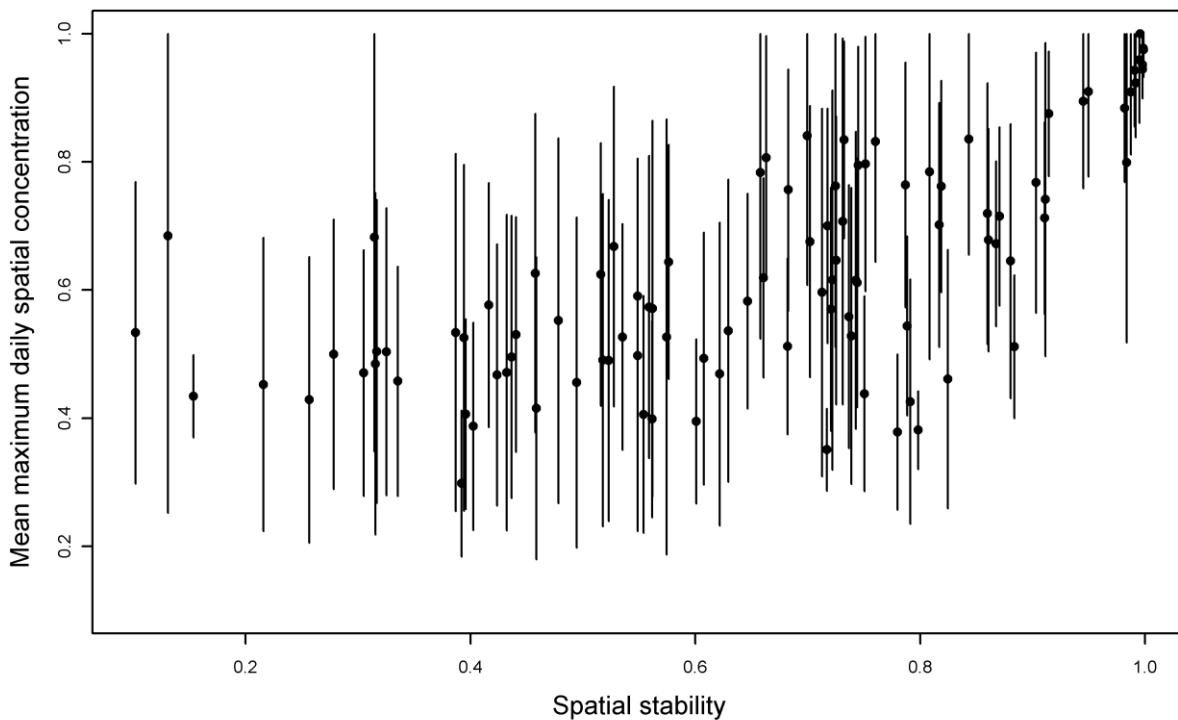


Figure 7. Relation between spatial stability and the mean maximum daily spatial concentration of adult male Ruby-throated Hummingbirds in Cleveland County, Quebec (Canada), 2007-2009. The mean maximum daily spatial concentration represents the spatial concentration of the individual at the most visited feeder on a given day. For cases in which an individual was followed for more than one season, the mean was calculated across all season without distinction of the year. Lines correspond to the standard deviation for every individual.

Increasing the sucrose concentration of the nectar contained in 15 of the 45 feeders modified the use of feeders by male hummingbirds. The daily number of visits by males was higher at 35% (W/V) feeders than at 20% (W/V) feeders (Figure 8). Moreover, compared to males that visited low concentration feeders, the ones that visited feeders with 35% sucrose nectar

experienced higher NVC, which lowered their resource monopolization at these feeders (Table 3). However, the negative effect of spatial concentration on NVC was not affected by nectar sucrose concentration, suggesting that feeder defense was not affected by higher nectar quality (Table 3).

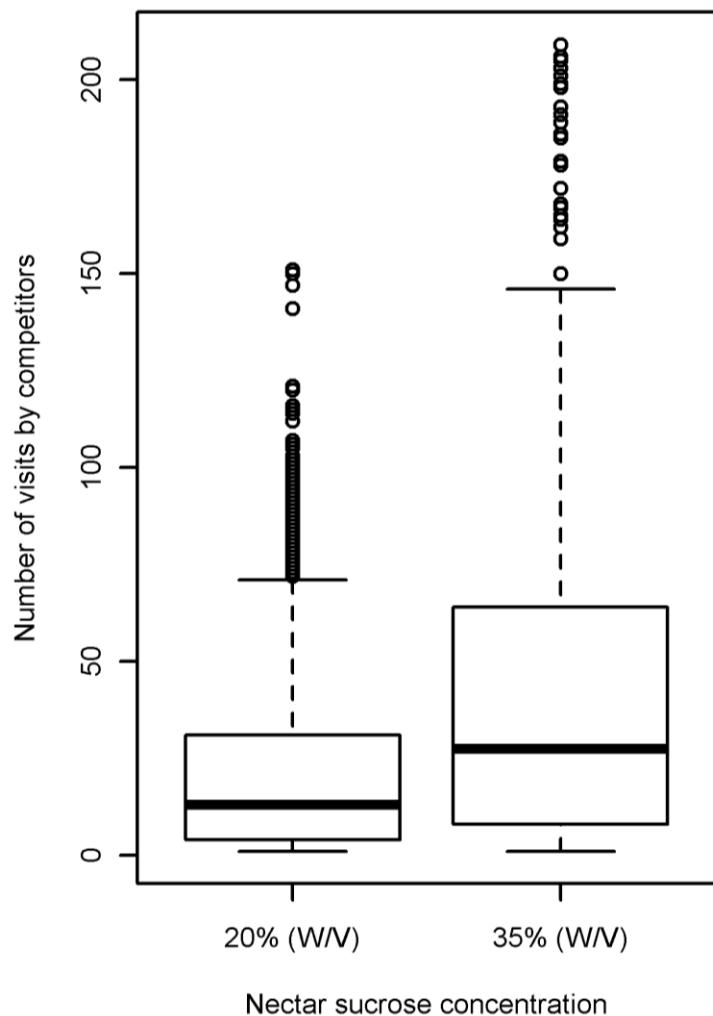


Figure 8. Number of visits made by adult male Ruby-throated Hummingbird competitors at feeders potentially defended by males when containing nectar with a low (20% W/V) or a high (35% W/V) sucrose concentration in Cleveland County, Quebec (Canada). Data shown are restricted to the period when sucrose concentration was manipulated (i.e., between June 10 and August 11, 2009).

Discussion

To our knowledge, our study is the first that quantify the defense and monopolization of food resources within a marked population of wild animals that range freely over a spatial scale that can encompass numerous territories. In spite of the fact that numerous studies quantified the degree of spatial overlap among individual home ranges or territories (Millspaugh et al. 2004, Fieberg and Kochanny 2005), few have linked this overlap with the joint use of food resources within more or less defended areas even though this is the ultimate result of defensive and territorial behavior that should lead to resource monopolization. By monitoring the access of individuals to available food sources (feeders), we were able to show that the relative spatial concentration and the stability in space use patterns of breeding male Ruby-throated Hummingbirds at specific sources of nectar increased their monopolization of those sources toward other males. Also, this relationship was influenced by habitat structure (in terms of feeder visibility). For instance, the negative effect of spatial concentration on the number of visits made by male competitors increased, as we expected, with the lateral visibility of feeders in forested (closed) habitat, but decreased in open habitat. The negative effect of spatial concentration on the number of visits by male competitors was however not affected by the number of competitors nor by the sucrose concentration of the nectar, albeit resource monopolization decreased with increases in both of those factors. Similar results were obtained when total time spent at feeders by competitors was used as the response variable instead of the number of visits by competitors. Those findings, along with the fact that we documented that food resource defense dynamics depends on both the sex of the defenders and the competitors and that individuals vary strongly in their level of food resource defense and monopolization, clearly support Maher and Lott's (2000) claim that one should address territoriality within a multivariate context.

The sharp decrease in the number of visits to a given feeder on a given day between the individual that made the most visits and the other individuals that visited the feeder suggests

that feeders were monopolized to some degree (Figure 2A). Although many individuals were able to clearly dominate in terms of visits to a given feeder, this situation was not the norm in our system. By providing *ad libitum* nectar, we may have relaxed the incentive for individuals to defend feeders. Reduced defense when food is overabundant or unlimited has been shown in other hummingbird studies, with lower investments in fights for the most productive feeders in Black-chinned Hummingbirds (*Archilochus alexandri*) (Ewald 1985) and a smaller percentage of interspecific competitors being chased by Blue-throated Hummingbirds (*Lampornis clemenciae*) when food was very abundant (Powers and McKee 1994). It remains that conspecifics were still being chased at a high rate in the latter study, which suggests that food defense in this species has other functions than energy acquisition, such as acquiring mates. The pattern of decrease in the number of visits with the rank of the individual at the feeder we observed could also be due to avoidance of conspecifics instead of active defense in which case our conclusions about the effects of explanatory variables on feeder defense would be erroneous. However, standardized 10 min focal observations we conducted weekly at feeders showed that pursuits and aggressive interactions (involving individuals of the same sex or not) were common (2459 visits were made at feeders compared to 415 pursuits), indicating that even if conspecific avoidance was present, there was an active defense of feeders as well. This defense of feeders seemed to be restricted to one or two feeders as illustrated by the sharp decrease in the proportion of visits made by an individual between the feeder it visited the most and the other feeders it visited (Figure 2B). Unfortunately, our analysis was not spatially and temporally explicit and we have yet to determine how individuals distributed their visits to feeders in space and time in order to assess, for instance, the overlap among individuals in both of those dimensions.

Measuring resource defense and monopolization in nature

Individuals are often constrained to feed from a single food patch in spatially confined, experimental laboratory set ups in order to facilitate tractability and the measurement of

resource defense and monopolization (e.g. Chapman and Kramer 1996, Basquill and Grant 1998). In natural settings, however, the competition among individuals of varying quality evolving within heterogeneous landscapes likely result in some individuals being forced to less favorable habitats where competitor pressure may be reduced. Resource monopolization in these poorer habitats can thus appear high, but it may be due to low competitive pressure rather than to resource defense. Therefore, the utilization level of the different habitats needs to be considered when quantifying resource monopolization in natural environments.

Assuming that natural nectar availability was negligible in our study system, nectar quality and abundance were likely uniform across the feeder grid in the first two years of study. The varying level of feeder use we observed was thus probably linked, at least partially, to habitat features bringing variation in mating opportunities or nesting cover availability. Being able to track visits to feeders through our use of PIT tags, we were able to circumvent the problems associated with variable habitat use by taking into account the relative spatial concentration of individuals at feeders. Indeed, this measure allowed us to quantify the baseline level of visits by competitors at feeders (i.e., when a focal individual's spatial concentration ~ 0), and thereby assess the reduction in the number of visits made by competitors caused by the focal individual, which allows to separate between feeder defense and monopolization.

Individual variation and space use

The variability among male Ruby-throated Hummingbirds in their spatial concentration and the negative effect of spatial concentration on the number of visits by male competitors show that space use must be taken into account to assess how individuals overlap in their use of resources and/or space. Furthermore, the high individual variation in spatial concentration and its effect and the interaction between spatial concentration and stability suggest that males adopt different strategies with respect to the defense of nectar sources (Figure 4, 6 and 7).

Indeed, highly uneven spatial concentration and high spatial stability in the use of feeders might be indicative of individuals adopting a territorial strategy while even concentration and low stability could be linked to sporadic use of feeders or to floating individuals. It remains that the individual variation we observed in our system probably reflects a continuum rather than two opposing strategies. Moreover, individuals showed low to strong daily variation in their daily spatial concentration at feeders, suggesting that individuals may vary their defense strategy from day to day. As aging adult Ruby-throated Hummingbirds based on plumage is impossible, we were not able to assess if age affected the space use and defense strategies adopted by individuals. Although we believe that one should also consider the morphological and physiological characteristics of individuals, along with their age, when addressing the determinants of resource defense strategies, as these may strongly depend on the state of the individuals (Kelly 2008), these proved difficult to measure on birds as small as hummingbirds.

Competition

The rapid increase in the number of visits by competitors with the number of competitors we have detected at feeders indicates lower resource monopolization with increased competition as observed in many studies, independently of taxa (e.g., Chapman and Kramer 1996, Syarifuddin and Kramer 1996). On the other hand, the lack of a significant interaction between spatial concentration and the number of competitors suggests that the effectiveness of defense was not overly affected by competition. This result may, however, be due to competition levels that were not sufficient for some individuals to cease defending feeders. Such a situation may be typical of what occurs on the breeding grounds compared to at migratory stopovers where tens of hummingbirds can often be observed feeding simultaneously at one feeder with barely any chasing among individuals. There was a slight decrease in the negative effect of spatial concentration with higher competition in the female vs. females or males competitors, which could indicate that females' capacity to defend feeders was more affected by competition, but it is unclear whether female actually defended feeders. Another possibility that could explain

the lack of interaction between spatial concentration and the number of competitors in males vs. males is that there may have been a link between the quality or the aggressiveness of individuals and their position on the feeder grid, with the most defensive individuals occurring more often in hotspots where competition was higher.

Habitat structure and visibility

As predicted, the negative effect of spatial concentration was stronger when lateral visibility was high in closed habitats. Yet, the inverse relationship we observed in open habitats was unexpected if we assume that overall visibility was likely better in these environments. One variable that may have confounded our results is the availability of perches around feeders. Indeed, prominent perches can be important in hummingbirds for detecting and displaying to females (Armstrong 1987), and thereby likely to provide standpoints that facilitate competitor detection. As feeders with high lateral visibility in open habitats are mostly found in hayfields, where perches are often located far from feeders in hedgerows bordering the fields, the reduced effect of spatial concentration with high lateral visibility in open habitats may therefore result from a low availability of good perches. Given that quantifying perch availability is bound to be highly subjective, one may have to design an experiment whereby the availability of artificial perches is manipulated to test this hypothesis.

An alternative explanation for the positive effect of habitat visibility on defense efficiency could be that open habitats may have represented a higher risk of predation for aggressive individuals and that few individuals were willing to take such a risk. Hamilton and Dill (2002) tested this hypothesis in Zebrafish (*Danio rerio*) and found that food monopolization increased in habitats perceived as riskier compared to in safer habitats of similar visibility. This predation-risk effect could thus play a role in addition to the increased detectability of competitors in high-visibility environments. However, this is unlikely given that

hummingbirds are presumed to experience low predation risks (Robinson et al. 1996). In support of this, males in our study area often used fully exposed perches and chased competitors high in the air and far from cover. Moreover, males made a disproportionate use of feeders in open habitats (table 3), suggesting that predation avoidance, if high-visibility environments are associated with high predation risk, is not the primary determinant of settlement decisions by males. It remains that low susceptibility to predation should not be equated with a lack of sensitivity to this risk (Lima 1991).

Influence of natural food sources on our results

Energetic considerations alone cannot explain the feeder use patterns we observed. The relative use of feeders showed high variability. Some feeders, mostly in forested areas, were almost never visited by males, while others were used daily and to a great extent (mean number of daily visits at feeders = 20.3 ± 14.2 , range = 1.7 – 51.2). As nectar sucrose concentration was maintained constant, at least in the first two years of the study, differential use of feeders is ultimately determined by surrounding habitat features. One variable that could be related to energetic considerations is the availability of natural food sources. Negative correlations between flower abundance and feeder use have been observed in other hummingbird species (Inouye et al. 1991, McCaffrey and Wethington 2008). Yet, the only plant species known to be important for Ruby-throated Hummingbirds and which occurred on our study site, namely *Impatiens capensis* (Bertin 1982), was in low abundance and present only for a short period of time at the end of the season. In addition of rarely observing pollen on the bill and forehead of individuals, except at the end of the season, we never observed Ruby-throated Hummingbirds feeding from sap-filled holes in trees maintained by Yellow-bellied Sapsuckers (*Sphyrapicus varius*, Southwick and Southwick 1980). Although we believe that natural sources of nectar did not bias our analyses, it remains that small insects were often caught in flight by Ruby-throated Hummingbirds and that the relative importance of nectar vs. insects in their diet should be addressed in future studies.

Purpose of food resource defense for breeding male Ruby-throated Hummingbirds

Although the primary function of territoriality in male Ruby-throated Hummingbirds is presumably related to food defense, little is known about the relative importance of mating acquisition in the defense of such food-related territories. High food quality territories may be linked to higher mating success for males, for instance. Accordingly, female and male Broad-tailed Hummingbird showed higher visitation and display rates at high sugar concentration feeders, respectively, suggesting that defending males might benefit from higher resource value through higher encounter rates with females (Camfield 2003). In Purple-throated Carib (*Eulampis jugularis*), males defending territories with greater standing crops of nectar also experienced higher mating success (Temeles 2010). In our study, we observed higher numbers of visits by both male and female (see Appendix 1) competitors at high sucrose concentration feeders and an apparent lack of defense of males toward females suggesting that males may benefit from defending high concentration feeders, although defense was not enhanced at those high concentration feeders.

The link between territory food quality and reproductive success does not seem to hold in all species of hummingbirds, though (Armstrong 1987, Powers 1987). Indeed, several species of hummingbirds form leks where males defend small territories solely for the purpose of mating. These territories are often devoid of food sources and males have to forage outside their territory boundary. Food distribution would be the greatest factor explaining spatial and mating systems in hummingbirds, with scarce and dispersed food leading to the defense of mating territories devoid of food source (lekking) and traplining (*sensu* Feinsinger and Colwell 1978), and more abundant and clumped food leading to the defense of feeding territories that possibly serve mating purposes as well (Stiles and Wolf 1979). Even within a single species, variability in food distribution can cause individuals to switch from defending strict mating territories to defending feeding territories (Feinsinger and Colwell 1978, Stiles 1973). Lekking in North American hummingbirds has been suggested in at least two species

(Armstrong 1987, Powers 1987). For instance, Armstrong (1987) showed that breeding season territoriality in male Calliope Hummingbirds (*Stellula calliope*) was not affected by seasonal variation in natural food abundance or by experimentally preventing access to two flowers inside male territories. He suggested that males preferentially choose sites with prominent perches near female habitats and that these considerations were more important than the benefits associated with the defense of nectar-rich areas. Experiments manipulating food abundance and quality thus appear necessary to evaluate the relative importance of energetic and reproductive considerations in the defense of territories by male hummingbirds (Temeles et al. 2004).

As feeder use patterns were studied without consideration of the daily temporal pattern of visits, it is possible that we have underestimated the degree of exclusivity in the use of feeders by breeding male Ruby-throated Hummingbirds. Indeed, the temporal nature of data in studies measuring the spatial overlap among defended areas is often neglected although it can provide significant insights regarding the joint use of space or resources by individuals (Minta 1992, Kernohan 2001). For example, it is unknown whether hummingbirds switch between feeders during the day or if intruders have access to a particular feeder only when the “owner” is away. By visiting or temporally defending several feeders, male Ruby-throated Hummingbirds may cover large areas and thereby gain greater access to females, though the relative importance of male and female mobility and territorial behavior for mating success is unknown. We believe that future studies addressing the determinants of resource defense and monopolization in free ranging Ruby-throated Hummingbirds should try to determine the importance of food resources in the defense of territories in natural and experimental set-ups as well as to establish the role of males’ individual characteristics and spatial strategies in their relative mating success.

Our study shows the importance of studying territorial and resource defense behaviors within a multivariate context as many variables will influence the level to which animals can

monopolize space or food resources. Moreover, our study highlights the importance of considering the space use of individuals as feeder monopolization by male hummingbirds was strongly influenced by their use of space in our system. Territoriality is often viewed as a static behavior where individuals do not leave their territories. However, studies show that territorial animals often show a more complex space use than what is assumed by a rigid view of territoriality, but this complexity is often neglected, partly because of the difficulty of following animals in the wild. For example, fishes will often leave their territories for foraging or defending other feeding areas (Hamilton and Dill 2003, Steingrímsson and Grant 2008) or for mating and/or spawning (Sikkel 1996, Sikkel and Kramer 2006). Although space use patterns and factors affecting them may differ across species, factors which may or may not be related to food resource distribution, these patterns will inevitably affect the extent to which an individual can monopolize a given area or a given resource. Following individuals in space thus appear crucial to gain a better understanding of why and how territorial animals can monopolize resources in the wild as well as providing greater insights into the costs and benefits of different spatial strategies, which ultimately impact fitness and population dynamics.

Appendix 1

Table 4. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult female Ruby-throated Hummingbirds competitors at feeders potentially defended by a female in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.

variables	coef	se	lowerCI	upperCI
year2008	-0.21603	0.04807	-0.31025	-0.12181
year2009	-0.47663	0.07031	-0.61445	-0.33882
grid usage	0.00714	0.00147	0.00426	0.01003
nb of competitors	0.55635	0.01597	0.52504	0.58766
feeder rank for males	-0.00821	0.00267	-0.01344	-0.00297
nectar sucrose concentration (high)	0.76434	0.11555	0.53785	0.99082
spatial concentration	-0.23988	0.33744	-0.90126	0.42150
daily nb of visits	0.00189	0.00094	0.00005	0.00372
spatial stability	-0.37015	0.16959	-0.70254	-0.03775
openness (open)	-0.55542	0.17047	-0.88954	-0.22130
lateral visibility	0.00004	0.00355	-0.00693	0.00700
spatial concentration:daily nb of visits	-0.00368	0.00247	-0.00852	0.00115
nb of competitors:spatial concentration	0.11757	0.04747	0.02453	0.21062
spatial concentration:spatial stability	-0.47474	0.50005	-1.45485	0.50536
spatial concentration:feeder concentration (high)	-0.44004	0.26707	-0.96350	0.08342
spatial concentration:openness (close):lateral visibility	0.02319	0.01212	-0.00056	0.04694
spatial concentration:openness (open):lateral visibility	0.00308	0.00343	-0.00364	0.00980

Table 5. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult female Ruby-throated Hummingbirds competitors at feeders potentially defended by a male in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.

variables	coef	se	lowerCI	upperCI
year2008	-0.01387	0.04091	-0.09406	0.06632
year2009	-0.10482	0.05091	-0.20461	-0.00503
grid usage	0.00930	0.00114	0.00706	0.01153
nb of competitors	0.64941	0.01322	0.62350	0.67531
feeder rank for females	-0.00266	0.00191	-0.00640	0.00108
nectar sucrose concentration (high)	0.31911	0.06423	0.19323	0.44500
spatial concentration	0.03194	0.20508	-0.37002	0.43389
daily nb of visits	-0.00108	0.00060	-0.00225	0.00010
spatial stability	0.13970	0.11458	-0.08488	0.36428
openness (open)	-0.42793	0.17317	-0.76734	-0.08851
lateral visibility	-0.00044	0.00350	-0.00729	0.00641
spatial concentration:daily nb of visits	-0.00265	0.00144	-0.00547	0.00017
nb of competitors:spatial concentration	0.04258	0.04048	-0.03677	0.12193
spatial concentration:spatial stability	0.02904	0.31582	-0.58998	0.64805
spatial concentration:feeder concentration (high)	-0.10513	0.24035	-0.57621	0.36595
spatial concentration:openness (close):lateral visibility	0.01095	0.01329	-0.01509	0.03699
spatial concentration:openness (open):lateral visibility	0.00001	0.00192	-0.00375	0.00377

Table 6. Model-averaged coefficients (coef), unconditional standard errors (se) and 95% confidence intervals (lowerCI and upperCI) for the explanatory variables used for modeling the number of visits made by adult male Ruby-throated Hummingbirds competitors at feeders potentially defended by a female in Cleveland County, Quebec (Canada), 2007-2009. The response variable was log-transformed and modeled using linear mixed-models with feeder ID and the intercept and slope of spatial concentration for focal individual ID as random effects.

variables	coef	se	lowerCI	upperCI
year2008	-0.17667	0.05680	-0.28800	-0.06535
year2009	-0.49535	0.08018	-0.65251	-0.33818
grid usage	0.01299	0.00186	0.00935	0.01664
nb of competitors	0.40796	0.01434	0.37985	0.43607
feeder rank for males	-0.00259	0.00519	-0.01276	0.00757
nectar sucrose concentration (high)	-0.02277	0.12597	-0.26966	0.22413
spatial concentration	-0.75438	0.38194	-1.50298	-0.00578
daily nb of visits	0.00021	0.00117	-0.00208	0.00250
spatial stability	-0.35625	0.19069	-0.73001	0.01751
openness (open)	0.46342	0.19119	0.08869	0.83816
lateral visibility	-0.00605	0.00364	-0.01318	0.00107
spatial concentration:daily nb of visits	-0.00921	0.00325	-0.01557	-0.00285
nb of competitors:spatial concentration	0.12489	0.04944	0.02799	0.22179
spatial concentration:spatial stability	0.96033	0.56992	-0.15672	2.07737
spatial concentration:feeder concentration (high)	0.28712	0.45861	-0.61176	1.18600
spatial concentration:openness (close):lateral visibility	-0.01200	0.01546	-0.04231	0.01831
spatial concentration:openness (open):lateral visibility	-0.00158	0.00373	-0.00889	0.00573

References

Armstrong, D. P. 1987. Economics of breeding territoriality in male Calliope hummingbirds. The Auk 104: 242-253

Baird, H. P., B. Patullo and D. L. MacMillan. 2006. Reducing aggression between freshwater crayfish (*Cherax destructor* Clark: Decapoda, Parastacidae) by increasing habitat complexity. Aquaculture Research 37: 1419-1428

Baker, H.G. 1975. Sugar concentrations in nectars from hummingbird flowers. Biotropica 7: 37-41

Basquill, S. P. and J. W. A. Grant. 1998. An increase in habitat complexity reduces aggression and monopolization of food by zebrafish (*Danio rerio*). Canadian Journal of Zoology 76: 770-772

Bertin, R. I. 1982. The Ruby-throated Hummingbird and its major food plants: ranges, flowering, phenology, and migration. Canadian Journal of Zoology 60: 210-219

Blem, C. R., L. B. Blem, J. Felix and J. van Gelder. 2000. Rufous hummingbird sucrose preference: precision of selection varies with concentration. The Condor 102: 235-238

Bolten, A. B., P. Feinsinger, H. G. Baker and I. Baker. 1979. On the calculation of sugar concentration in flower nectar. Oecologia 41: 301-304

Breau, C. and J. W. A. Grant. 2002. Manipulating territory size via vegetation structure: optimal size of area guarded by the convict cichlid (Pisces, Cichlidae). Canadian Journal of Zoology 80: 376-380

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. The Wilson Bulletin 76: 160-169

Burnham, K. P. and D. R. Anderson. 2002. Model selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Camfield, A. F. 2003. Quality of food source affects female visitation and display rates of male Broad-tailed Hummingbirds. *The Condor* 105: 603-606

Camfield, A. F. 2006. Resource value affects territorial defense by Broad-tailed and Rufous hummingbirds. *Journal of Field Ornithology* 77: 120-125

Carfagnini, A. G., F. H. Rodd, K. B. Jeffers and A. E. E. Bruce. 2009. The effects of habitat complexity on aggression and fecundity in zebrafish (*Danio rerio*). *Environmental Biology of Fishes* 86: 403-409

Carpenter, F. L. 1987. Food abundance and territoriality: To defend or not to defend? *American Zoologist* 27: 387-399

Carpenter, F. L., D. C. Paton and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proceedings of the National Academy of Sciences USA* 80: 7259-7263

Carpenter, F. L., M. A. Hixon, R. W. Russell, D. C. Paton and E. J. Temeles. 1993. Interference asymmetries among age-sex classes of rufous hummingbirds during migratory stopovers. *Behavioral Ecology and Sociobiology* 33: 297-304

Cenni, F., G. Parisi and F. Gherardi. 2010. Effects of habitat complexity on the aggressive behaviour of the American lobster (*Homarus americanus*) in captivity. *Applied Animal Behaviour Science* 122: 63-70

Chapman, M. R and D. L. Kramer. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* 52: 83-94

Charette, Y., F. Rousseau, M. J. Mazerolle and M. Bélisle. 2010. Tracking hummingbird foraging movements and patch-use in the wild with passive-integrated transponders. In prep.

Corkum, L. D. and D. J. Cronin. 2004. Habitat complexity reduces aggression and enhances consumption in crayfish. *Journal of Ethology* 22: 23-27

Dearborn, D. C. 1998. Interspecific territoriality by a Rufous-tailed Hummingbird (*Amazilia tzacatl*): effects of intruder size and resource value. *Biotropica* 30: 306-313

Diaz-Uriarte, R. 1999. Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proceedings of the Royal Society B* 266: 2457-2464

Dolinsek, I. J., J. W. A. Grant and P. M. Biron. 2007. The effect of habitat heterogeneity on the population density of juvenile Atlantic salmon *Salmo salar* L. *Journal of Fish Biology* 70: 206-214

Eason, P. K. and J. A. Stamps. 1992. The effect of visibility on territory size and shape. *Behavioral Ecology* 3: 166-172

Eason, P. K. and J. A. Stamps. 2001. The effect of visibility on space use by territorial Red-capped Cardinals. *Behaviour* 138: 19-30

Eberhard, J. R. and P. W. Ewald. 1994. Food availability, intrusion pressure and territory size: an experimental study of Anna's hummingbirds (*Calypte anna*). *Behavioral Ecology and Sociobiology* 34: 11-18

Ewald, P. W. 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behaviour* 33: 705-719

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223

Ewald, P. W. and R. J. Bransfield. 1987. Territory quality and territorial behaviour in two sympatric species of hummingbirds. *Behavioral Ecology Sociobiology* 20: 285-293

Feinsinger, P. and R. K. Colwell. 1978. Community organization among neotropical nectar-feeding birds. *American Zoologist* 18: 779-795

Fieberg, J. and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management* 69: 1346-1359

Gass, C. L., G. Angehr and J. Centa. 1976. Regulation of food supply by feeding territoriality in the Rufous Hummingbird. *Canadian Journal of Zoology* 54: 2046-2054

Grant, J. W. A. 1993. Whether or not to defend? The influence of resource distribution. *Marine and Freshwater Behaviour and Physiology* 23: 137-152

Grant, J. W. A., I. L. Girard, C. Breau and L. K. Weir. 2002. Influence of food abundance on competitive aggression in juvenile convict cichlids. *Animal Behaviour* 63: 323-330

Grant, J. W. A. and R. T. Guha. 1993. Spatial clumping of food increases its monopolization and defense by convict cichlids, *Cichlasoma nigrofasciatum*. *Behavioral Ecology* 4: 293-296

Hamilton, I. M. and L. M. Dill. 2002. Monopolization of food by zebrafish (*Danio rerio*) increases in risky habitats. *Canadian Journal of Zoology* 80: 2164-2169

Hamilton, I. M. and L. M. Dill. 2003. The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory defendability. *Behavioral Ecology* 14: 561-568

Hasegawa, K. and S. Yamamoto. 2009. Effects of competitor density and physical habitat structure on the competitive intensity of territorial white spotted charr *Salvelinus leucomaenis*. *Journal of Fish Biology* 74: 213-219

Hixon, M. A., F. L. Carpenter and D. C. Patton. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *American Naturalist* 122: 366-391

Höjesjö, J., J. Johnsson and T. Bohlin. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behavioral Ecology and Sociobiology* 56: 286-289

Imre, I., J. W. A. Grant and E. R. Keeley. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 59: 303-309

Inouye, D. W., W. A. Calder and N. M. Waser. 1991. The effect of floral abundance on feeder censuses of hummingbird populations. *The Condor* 93: 279-285

Kelly, C. D. 2008. The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: How much variation can we explain? *Behavioral Ecology and Sociobiology* 62: 855-871

Kenward, R. 1987. *Wildlife radio tagging*. Academic Press, New York, New York, USA.

Kernohan, B. J., R. A. Gitzen and J. J. Millspaugh. 2001. Analysis of animal space use and movements. In: Millspaugh, J. J. and J. M. Marzluff (eds) *Radio tracking and animal populations*. Academic Press, San Diego, California, pp. 125-166

Kerr, G. D. and C. M. Bull. 2006. Exclusive core areas in overlapping ranges of the sleepy lizard (*Tiliqua rugosa*). *Behavioral Ecology* 17: 380-391

Kim, J.-W., G. E. Brown and J. W. A. Grant. 2004. Interactions between patch size and predation risk affect competitive aggression and size variation in juvenile convict cichlids. *Animal Behaviour* 68: 1181-1187

Kodric-Brown, A. and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59: 285-296

LaManna, J. R. and P. K. Eason. 2007. Effects of predator presence on territory establishment. *Behaviour* 144: 985-1001

Lima, S. L. 1991. Energy, predators and the behaviour of feeding hummingbirds. *Evolutionary Ecology* 5: 220-230

Lopez-Sepulcre, A. and H. Kokko. 2005. Territorial defense, territory size and population regulation. *American Naturalist* 166: 317-329

Maher, C. R. and D. F. Lott. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* 49: 1581-1597

Maher, C. R. and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* 143: 1-29

Marchesseault, L. and P. W. Ewald. 1991. Effect of territory quality on intrusion rate in nonbreeding hummingbirds. *Behavioral Ecology Sociobiology* 28: 305-308

Martel, G. 1996. Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 53: 660-669

McCaffrey, R. E. and S. M. Wethington. 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: a case study from southern Arizona. *The Condor* 110: 786-791

Millspaugh, J. J., R. A. Gitzen, B. J. Kernohan, M. A. Larson and C. L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32: 148-157

Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. *Ecological Applications* 2: 178-188

Mulvihill, R. S., R. C. Leberman and D. S. Wood. 1992. A possible relation between reverse sexual size dimorphism and reduced male survivorship in the Ruby-Throated Hummingbird. *Condor* 94: 480-489

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biological Reviews* 67: 129-173

Noël, M. V., J. W. A. Grant and J. G. Carrigan. 2005. Effects of competitor-to-resource ratio on aggression and size variation within groups of convict cichlids. *Animal Behaviour* 69: 1157-1163

Norton, M. E., P. Arcese and P. W. Ewald. 1982. Effect of intrusion pressure on territory size in Black-chinned Hummingbirds (*Archilochus alexandri*). *The Auk* 99: 761-764

Patterson, I. J. 1980. Territorial behaviour and the limitation of population density. *Ardea* 68: 53-62

Pierro, E. D., A. Molinari, G. Tosi and L. A. Wauters. 2008. Exclusive core areas and intrasexual territoriality in Eurasian red squirrels (*Sciurus vulgaris*) revealed by incremental cluster polygon analysis. *Ecological Research* 23: 529-542

Pitelka, F. A. 1942. Territoriality and related problems in North American hummingbirds. *The Condor* 44: 189-204

Powers, D. R. 1987. Effects of variation in food quality on the breeding territoriality of the male Anna Hummingbird. *The Condor* 89: 103-111

Powers D. R. and T. McKee. 1994. The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. *The Condor* 96: 1064-1075

Pyke, G. H., M. Christy and R. E. Major. 1996. Territoriality in honeyeaters: reviewing the concept and evaluating available information. *Australian Journal of Zoology* 44: 297-317

R Development Core Team. 2009. R: A language and environment for statistical computing. Version 2.10.1 R Foundation for Statistical Computing, Vienna, Austria.

Roberts, W. M. 1996. Hummingbirds' nectar concentration preferences at low volume : the importance of time scale. *Animal Behaviour* 52: 361-370

Robinson, T. R., R. R. Sargent and M. B. Sargent. 1996. Ruby-throated Hummingbird. *Birds of North America* 204: 1-16

Russell, S. M., and R. O. Russell. 2001. The North American bander's manual for banding Hummingbirds. The North American Banding Council, Point Reyes Station, California, U.S.A.

Sergio, F., J. Blas and F. Hiraldo. 2009. Predictors of floater status in a long-lived bird : a cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology* 78: 109-118

Sikkel, P. C. 1998. Competitor intrusions and mate-search tactics in a territorial marine fish. *Behavioral Ecology* 9: 439-444

Sikkel, P. C. and D. L. Kramer. 2006. Territory revisits reduce intrusion during spawning trips by female yellowtail damselfish, *Microspathodon chrysurus*. *Animal Behaviour* 71: 71-78

Southwick, E. E. and A. K. Southwick. 1980. Energetics of feeding on tree sap by Ruby-throated Hummingbirds in Michigan. *The American Midland Naturalist* 104: 328-334

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.

Steingrímsson, S. Ó. And J. W. A. Grant. 2008. Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 77: 448-457

Stiles, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. *University of California Publication in Zoology* 97: 1-109

Stiles, F. G. and L. L. Wolf. 1979. Ecology and evolution of lek mating behaviour in the Long-tailed Hermit Hummingbird. *Ornithological Monograph* 27. American Ornithologists' Union, Washington, D.C., USA.

Stutchbury, B. J. M. 1998. Extra-pair mating effort of male hooded warblers, *Wilsonia citrina*. *Animal Behaviour* 55: 553-561

Syarifuddin, S. and D. L. Kramer. 1996. The effect of group size on space use and aggression at a concentrated food source in blue gouramis, *Trichogaster trichopterus* (Pisces: Belontiidae). *Environmental Biology of Fishes* 46: 289-296

Tamm, S. 1985. Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. *Behavioral Ecology and Sociobiology* 16: 203-207

Tamm, S. and C. L. Gass. 1986. Energy intake rates and nectar concentration preferences by hummingbirds. *Oecologia* 70: 20-23

Temeles, E. J., R. S. Goldman et A. U. Kudla. 2005. Foraging and territory economics of sexually dimorphic Purple-throated Caribs (*Eulampis jugularis*) on three Heliconia morphs. The Auk 122: 187-204

Temeles, E. J. and W. J. Kress. 2010. Mate choice and mate competition by a tropical hummingbird at a floral resource. Proceedings of the Royal Society B 277: 1607-1613

Temeles, E. J., A. B. Muir, E. B. Slutsky and M. N. Vitousek. 2004. Effect of food reductions on territorial behaviour of Purple-throated Caribs. The Condor 106: 691-695

Tyre, A., G. D. Kerr, B. Tenhumberg, C. M. Bull. 2007. Identifying mechanistic models of spatial behaviour using pattern-based modelling: An example from lizard home ranges. Ecological Modelling 208: 307-316

Vaida, F. and S. Blanchard. 2005. Conditional Akaike information for mixed-effects models. Biometrika 92: 351-370

Venter, O., J. W. A. Grant, M. V. Noël and J.-W. Kim. 2008. Mechanisms underlying the increase in young-of-the-year Atlantic salmon (*Salmo salar*) density with habitat complexity. Canadian Journal of Fisheries and Aquatic Sciences 65: 1956-1964

White, G. and R. Garrot. 1987. Analysis of wildlife radio tracking data. Academic Press, New York, New York, USA.

CONCLUSION

À ma connaissance, cette étude est parmi une des premières à se pencher sur la défense et la monopolisation des ressources alimentaires dans une population marquée en milieu naturel où les individus ne sont pas contraints spatialement et où l'utilisation de l'espace par les individus est prise en compte. Malgré le fait que plusieurs études aient quantifié le degré de chevauchement spatial entre conspécifiques, peu d'études ont pu relier ce chevauchement à l'utilisation conjointe des ressources alimentaires contenues dans les territoires bien qu'ultimement, c'est ce qui caractérise les comportements de défense et de territorialité menant à la monopolisation des ressources alimentaires. Grâce à une méthode innovatrice de marquage et de suivi des colibris (Chapitre 1), mon étude a permis de quantifier l'influence de différentes variables susceptibles d'affecter la capacité des individus à défendre et à monopoliser des ressources alimentaires au sein d'une population marquée de Colibri à gorge rubis.

Telles les nombreuses études concernant les comportements territoriaux chez les colibris, mes résultats suggèrent que certains individus défendent des sources de nectar. Cependant, bien que les patrons d'utilisation des abreuvoirs à nectar montrent que les colibris utilisaient les abreuvoirs avec un certain niveau d'exclusivité, particulièrement dans le cas des mâles envers les mâles, la monopolisation des abreuvoirs n'était certes pas totale. De plus, cette monopolisation variait grandement à la fois entre les abreuvoirs et entre les individus. On note premièrement une grande variabilité individuelle en termes de la proportion des visites consacrée aux différents abreuvoirs. Cette variabilité dans la concentration spatiale aux abreuvoirs se devait d'être prise en compte étant donné l'effet positif qu'avait la concentration spatiale sur la monopolisation des abreuvoirs. Un effet positif de la stabilité spatiale, laquelle quantifie la fidélité des individus dans l'utilisation des différents abreuvoirs, a aussi été noté

sur la monopolisation. Prises ensemble, ces deux variables suggèrent un gradient dans les stratégies individuelles d'utilisation des abreuvoirs. Ce gradient va d'une concentration et d'une stabilité spatiale élevée, caractérisant vraisemblablement des mâles davantage territoriaux, jusqu'à une utilisation moins concentrée et stable spatialement, probablement associée à des individus errants (*floaters*) ou à de faibles utilisateurs des abreuvoirs. Il est par contre difficile de relier cette variabilité aux caractéristiques individuelles du fait que les colibris sont trop petits pour faire des prélèvements physiologiques, fluctuent fortement en masse au sein d'une même journée et que peu d'adultes sont d'âge connu en raison de l'absence de critères associés au plumage qui permettraient d'âger les colibris adultes.

Par ailleurs, bien que la compétition diminuait la monopolisation des abreuvoirs, la capacité des individus à les défendre ne semblait pas affectée par le nombre de compétiteurs. Ceci s'explique probablement par des niveaux de compétition aux abreuvoirs qui n'étaient vraisemblablement pas assez élevés pour nuire à la défense des abreuvoirs. Les abreuvoirs étant disposés de façon systématique, mon système d'étude m'a également permis de découpler partiellement l'effet de la structure des habitats de celui de la distribution des ressources et ainsi mesurer l'effet de la visibilité sur les patrons d'utilisation conjointe des abreuvoirs par les individus. Mes résultats suggèrent qu'une visibilité accrue facilite la défense des abreuvoirs, du moins en milieux forestiers. Les résultats obtenus en milieux ouverts sont plus difficiles à interpréter du fait que le couvert arbustif peut biaiser fortement le niveau de visibilité que peut avoir un colibri d'un abreuvoir et ce, lorsqu'évalué à partir du sol par un chercheur. En effet le couvert arbustif peut ne pas nuire à la visibilité d'un abreuvoir pour un colibri perché en hauteur. Malheureusement, il est également très difficile de quantifier la disponibilité en perchoir à proximité des abreuvoirs, disponibilité qui est probablement corrélée négativement à l'ouverture de la végétation autour de l'abreuvoir. Pour ces raisons, une approche expérimentale permettant de manipuler la disponibilité en perchoirs au sein de milieux ayant différentes structure de végétation serait souhaitable.

Malgré que la défense des abreuvoirs par le Colibri à gorge rubis représente un comportement de défense des ressources alimentaires, et donc que ce comportement peut être interprété d'un point de vue énergétique, la défense accrue des mâles envers les mâles indiquent que ce comportement est probablement également lié à l'acquisition de partenaires sexuels, dû moins en période de reproduction. Par contre, l'importance relative de ces deux causes de la défense des abreuvoirs ne peut être déterminée à partir de nos données. Puisque les mâles de certaines espèces de colibris peuvent défendre des territoires dépourvus de sources de nectar et que les variations en quantité de nectar à l'intérieur des territoires peuvent parfois ne pas affecter le comportement territorial (Armstrong 1987, Powers 1987), il est donc possible que la défense des abreuvoirs sur mon site d'étude n'était qu'une conséquence de la défense de territoires de au sein d'un lek contenant les abreuvoirs. Cette explication est toutefois peu probable puisque les abreuvoirs représentent une source de nourriture localisée, et donc probablement facilement défendable, et ces sources de nourriture sont défendues par le Colibri à gorge rubis en dehors de la période de reproduction. Par conséquent, comme il est suggéré dans la littérature (Robinson et al. 1996), le rôle de la territorialité chez les mâles de cette espèce est probablement lié à la défense de sources de nourriture et secondairement à l'acquisition de partenaires sexuelles. Mon système d'étude ne me permet toutefois pas de relier la variabilité observée au niveau individuel en termes de concentration ou de stabilité spatiale et de propension à la défense au succès reproducteur des mâles. Ultimement, il serait intéressant de relier la stratégie spatiale des mâles à leur succès reproducteur étant donné que la territorialité chez les colibris a surtout été interprétée d'un point de vue énergétique et peu d'études ont tenté de quantifier l'importance que joue l'acquisition de partenaires sexuels dans la défense des ressources alimentaires (Temeles et Kress 2010).

Je me dois de noter que mon système d'étude ne me permet pas d'inférer sur la territorialité des Colibri à gorge rubis lorsque seules des sources naturelles de nourriture sont disponibles. La nature exacte, et donc la distribution spatio-temporelle des ressources alimentaires de cette espèce en milieu naturel, qui incluent des sources de nectar et des insectes, sont très peu connues. Il est par le fait même difficile de déterminer si ces sources sont économiquement

défendables ou si un individu peut défendre un même territoire sur une longue période de temps. Par conséquent, en assumant que les mâles Colibri à gorge rubis sont agressifs en milieu naturel, la position de cette espèce dans le gradient entre la défense de territoire de parades dépourvus de ressources alimentaires et la défense de territoires jouant également un rôle alimentaire est inconnu. Considérant que l'aire de répartition de cette espèce en période de nidification s'étend de l'Alberta à la Nouvelle-Écosse le long de la frontière sud du Canada et qu'elle couvre tout l'Est des USA, il est probable que plusieurs stratégies soient adoptées selon la distribution spatio-temporelle locale des ressources nectarifères.

La variabilité individuelle observée dans notre système en termes de stratégie spatiale montre l'importance d'effectuer des recherches en milieu naturel où les individus ne sont pas contraints spatialement. En effet, bien que les études expérimentales en milieu artificiel permettent en général de contrôler l'effet de multiples variables confondantes, elles ne peuvent rendre compte de la complexité retrouvée en milieu naturel. Il demeure que les comportements de défense et de territorialité sont déterminés par plusieurs variables, dont les effets peuvent aussi dépendre d'autres variables, et qu'une approche expérimentale semble nécessaire pour bien isoler leurs effets respectifs. Un des avantages de mon système d'étude est qu'il permet une standardisation de la distribution spatio-temporelle des ressources alimentaires. Ce système, couplé à ma technique de marquage et de suivi des colibris, offre de multiples opportunités pour pousser plus loin l'étude des déterminants de la défense et de la monopolisation des ressources alimentaires dans un contexte spatial explicité et ainsi départager les effets associés à la distribution spatio-temporelle des ressources alimentaires et à la structure des habitats et du paysage.

BIBLIOGRAPHIE

Adams, E. S. (2001). Approaches to the study of territory size and shape. Annual Review of Ecology and Systematics *32*, 277-303.

Armstrong, D. P. (1987). Economics of breeding territoriality in male Calliope Hummingbirds. The Auk *104*, 242-253.

Baird, H. P., Patullo, B. et MacMillan, D. L. (2006). Reducing aggression between freshwater crayfish (*Cherax destructor* Clark: Decapoda, Parastacidae) by increasing habitat complexity. Aquaculture Research *37*, 1419-1428.

Basquill, S. P. et Grant, J. W. A. (1998). An increase in habitat complexity reduces aggression and monopolization of food by zebrafish (*Danio rerio*). Canadian Journal of Zoology *76*, 770-772.

Breau, C. et Grant, J. W. A. (2002). Manipulating territory size via vegetation structure: optimal size of area guarded by the convict cichlid (Pisces, Cichlidae). Canadian Journal of Zoology *80*, 376-380.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. The Wilson Bulletin *76*, 160-169.

Brown, J. L. et Orians, G. H. (1970). Spacing patterns in mobile animals. Annual Review in Ecology and Systematics *1*, 239-262.

Camfield, A. F. (2006). Resource value affects territorial defense by Broad-tailed and Rufous Hummingbirds. Journal of Field Ornithology *77*, 120-125.

Carfagnini, A. G., Rodd, F. H., Jeffers, K. B. et Bruce, A. E. E. (2009). The effects of habitat complexity on aggression and fecundity in zebrafish (*Danio rerio*). Environmental Biology of Fish **86**, 403-409.

Carpenter, F. L. (1987). Food abundance and territoriality: To defend or not to defend? American Zoologist **27**, 387-399.

Carpenter, F. L., Paton, D. C. et Hixon, M. A. (1983). Weight gain and adjustment of feeding territory size in migrant Rufous hummingbirds. Proceedings of the National Academy of Sciences U.S.A. **80**, 7259-7263.

Cenni, F., Parisi, G. et Gherardi, F. (2010). Effects of habitat complexity on the aggressive behaviour of the American lobster (*Homarus americanus*) in captivity. Applied Animal Behaviour Science **122**, 63-70.

Chapman, M. R et Kramer, D. L. (1996). Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. Animal Behaviour **52**, 83-94.

Corkum, L. D. et Cronin, D. J. (2004). Habitat complexity reduces aggression and enhances consumption in crayfish. Journal of Ethology **22**, 23-27.

Dearborn, D. C. (1998). Interspecific territoriality by a rufous-tailed hummingbird (*Amazilia tzacatl*): effects of intruder size and resource value. Biotropica **30**, 306-313.

Dubois, F., Giraldeau, L.-A. et Grant, J. W. A. (2003). Resource defense in a group-foraging context. Behavioral Ecology **14**, 2-9.

Eason, P. K. (1992). Optimization of territory shape in heterogeneous habitats: a field study of the red-capped cardinal (*Paroaria gularis*). Journal of Animal Ecology **61**, 411-424.

Eason, P. K. et Stamps, J. A. (1992). The effect of visibility on territory size and shape. *Behavioral Ecology* **3**, 166-172.

Eason, P. K. et Stamps, J. A. (2001). The effect of visibility on space use by territorial Red-capped Cardinals. *Behaviour* **138**, 19-30.

Eason, P. K., Cobbs, G. A. et Trinca, K. G. (1999). The use of landmarks to define territorial boundaries. *Animal Behaviour* **58**, 85-91.

Eberhard, J. R. et Ewald, P. W. (1994). Food availability, intrusion pressure and territory size: an experimental study of Anna's hummingbirds (*Calypte anna*). *Behavioral Ecology and Sociobiology* **34**, 11-18.

Emlen, S. T. et Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215-223.

Ewald, P. W. et Bransfield, R. J. (1987). Territory quality and territorial behavior in 2 sympatric species of hummingbirds. *Behavioral Ecology and Sociobiology* **20**, 285-293.

Ewald, P. W. et Carpenter, F. L. (1978). Territorial responses to energy manipulations in the Anna Hummingbird. *Oecologia* **31**, 277-292.

Garrison, J. S. E. et Gass, C. L. (1999). Response of a traplining hummingbird to changes in nectar availability. *Behavioral Ecology* **10**, 714-725.

Gass, C. L. et Garrison, J. S. E. (1999). Energy regulation by traplining hummingbirds. *Functional Ecology* **13**, 483-492.

Gill, F. B. (1988). Trapline foraging by Hermit Hummingbirds – competition for an undefended, renewable resource. *Ecology* **69**, 1933-1942.

Goldberg, J. L., Grant, J. W. A. et Lefebvre, L. (2001). Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behavioral Ecology* **12**, 490-495.

Grant, J. W. A. (1993). Whether or not to defend? The influence of resource distribution. *Marine and Freshwater Behaviour and Physiology* **23**, 137-152.

Grant, J. W. A. et Guha, R. T. (1993). Spatial clumping of food increases its monopolization and defense by convict cichlids, *Cichlasoma nigrofasciatum*. *Behavioral Ecology* **4**, 293-296.

Grant, J. W. A., Gaboury, C. L. et Levitt, H. L. (2000). Competitor-to-resource ratio, a general formulation of operational sex ratio, as a predictor of competitive aggression in Japanese medaka (Pisces: Oryziidae). *Behavioral Ecology* **11**, 670-675.

Hamilton, I. M. et Dill, L. M. (2003). The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory defendability. *Behavioral Ecology* **14**, 561-568.

Henderson, J., Hurly, T. A., Bateson, M. et Healy, S. D. (2006). Timing in free-living Rufous Hummingbirds, *Selasphorus rufus*. *Current Biology* **16**, 512-515.

Hixon, M. A., Carpenter, F. L. et Patton, D. C. (1983). Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *American Naturalist* **122**, 366-391.

Höjesjö, J., Johnsson, J. et Bohlén, T. (2004). Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behavioral Ecology and Sociobiology* **56**, 286-289.

Imre, I., Grant, J. W. A. et Keeley, E. R. (2002). The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 303-309.

Kaspersson, R., Hojesjo, J. et Pedersen, S. (2010). Effects of density on foraging success and aggression in age-structured groups of brown trout. *Animal Behaviour* **79**, 709-715.

Kim, J-W et Grant, J. W. A. (2007). Effects of patch shape and group size on the effectiveness of defense by juvenile convict cichlids. *Animal Behaviour* **73**, 275-280.

Kodric-Brown, A. et Brown, J. H. (1978). Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* **59**, 285-296.

LaManna, J. R. et Eason, P. K. (2003). Effects of landmarks on territorial establishment. *Animal Behaviour* **65**, 471-478.

Lopez-Sepulcre, A. et Kokko, H. (2005). Territorial defense, territory size and population regulation. *American Naturalist* **166**, 317-329.

Maher, C. R. et Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* **49**, 1581-1597.

Maher, C. R. et Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* **143**, 1-29.

Marchesseault, L. et Ewald, P. W. (1991). Effects of territory quality on intrusion rate in nonbreeding hummingbirds. *Behavioral Ecology and Sociobiology* **28**, 305-308.

Mesterton-Gibbons, M. et Adams, E. S. (2003). Landmarks in territory partitioning: a strategically stable convention? *American Naturalist* (161), 685-697.

Mulvihill, R. S., Leberman, R. C. et Wood, D. S. (1992). A possible relation between reverse sexual size dimorphism and reduced male survivorship in the Ruby-Throated Hummingbird. *Condor* **94**, 480-489.

Newton, I. (1992). Experiments on the limitation of bird numbers by territorial behaviour. *Biological Reviews* **67**, 129-173.

Noël, M. V., Grant, J. W. A. et Carrigan, J. G. (2005). Effects of competitor-to-resource ratio on aggression and size variation within groups of convict cichlids. *Animal Behaviour* **69**, 1157-1163.

Patterson, I. J. (1980). Territorial behaviour and the limitation of population density. *Ardea* **68**, 53-62.

Pitelka, F. A. (1942). Territoriality and related problems in North American hummingbirds. *Condor* **44**, 189-204.

Powell, R. A. et Mitchell, M. S. (1998). Topographical constraints and home range quality. *Ecography* **21**, 337-341.

Powers, D. R. et McKee, T. (1994). The effect of food availability on time and energy expenditures of territorial and nonterritorial hummingbirds. *Condor* **96**, 1064-1075.

Pyke, G. H., Christy, M. et Major, R. E. (1996). Territoriality in honeyeaters: reviewing the concept and evaluating available information. *Australian Journal of Zoology* **44**, 297-317.

Reid, M. L. et Weatherhead, P. J. (1988). Topographical constraints on competition for territories. *Oikos* **51**, 115–117.

Robinson, T. R., Sargent, R. R. et Sargent, M. B. (1996). Ruby-throated Hummingbird. *Birds of North America* **204**, 1-16.

Rolando, A., Laiolo, P. et Conti, A. (2000). Do topographical constraints and space availability influence birds' ranging behaviour? The Alpine Chough (*Pyrrhocorax graculus*) as a study case. *Revue d'écologie – La terre et la vie* **55**, 383-394.

Sergio, F., J. Blas et Hiraldo, F. (2009). Predictors of floater status in a long-lived bird : a cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology* **78**, 109-118.

Sikkel, P. C. (1998). Competitor intrusions and mate-search tactics in a territorial marine fish. *Behavioral Ecology* **9**, 439-444.

Sikkel, P. C. et Kramer, D. L. (2006). Territory revisits reduce intrusion during spawning trips by female yellowtail damselfish, *Microspathodon chrysurus*. *Animal Behaviour* **71**, 71-78.

Sirot, E. (2000). An evolutionary stable strategy for aggressiveness in feeding groups. *Behavioral Ecology* **11**, 351-356.

Smith, J. N. M. et Arcese, P. (1989). How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. *The American Naturalist* **133**, 830-845.

Steingrímsson, S. Ó. et Grant, J. W. A. (2008). Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**, 448-457.

Stiles, F. G. et Wolf, L. L. (1979). Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. *Ornithological Monographs* **27**.

Stutchbury, B. J. M. (1998). Extra-pair mating effort of male hooded warblers, *Wilsonia citrina*. *Animal Behaviour* **55**, 553-561.

St-Louis, V., Fortin, M. J. et Desrochers, A. (2004). Spatial association between forest heterogeneity and breeding territory boundaries of two forest soundbirds. *Landscape Ecology* **19**, 591-601.

Suarez, R. K. et Gass, C. L. (2002). Hummingbird foraging and the relation between bioenergetics and behaviour. *Comparative Biochemistry and Physiology A-Molecular and Integrative Physiology* **133**, 335-343.

Sutherland, W. J. (1996). From individual behaviour to population ecology. Oxford University Press, Oxford.

Syarifuddin, S. et Kramer, D. L. (1996). The effect of group size on space use and aggression at a concentrated food source in blue gouramis, *Trichogaster trichopterus* (Pisces: Belontiidae). *Environmental Biology of Fishes* **46**, 289-296.

Tamm, S. (1985). Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. *Behavioral Ecology and Sociobiology* **16**, 203-207.

Temeles, E. J., Goldman, R. S. et Kudla, A. U. (2005). Foraging and territory economics of sexually dimorphic Purple-throated Caribs (*Eulampis jugularis*) on three Heliconia morphs. *Auk* **122**, 187-204.

Temeles, E. J., Muir, A. B. Slutsky, E. B. et Vitousek, M. N. (2004). Effect of food reductions on territorial behavior of Purple-throated Caribs. *Condor* **106**, 691-695.

Temeles, E. J., Shaw, K. C., Kudla, A. U. et Sander, S. E. (2006). Traplining by Purple-throated Carib Hummingbirds: behavioural responses to competition and nectar availability. *Behavioral Ecology and Sociobiology* **61**, 163-172.

Temeles, E. J., Kress, W. J. (2010). Mate choice and mate competition by a tropical hummingbird at a floral resource. *Proceedings of the Royal Society B* **277**, 1607-1613.

Vahl, W. K., Lok, T., van der Meer, J., Piersma, T. et Weissing, F. J. (2005). Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology* **16**, 834-844.

Venter, O., Grant, J. W. A., Noël, M. V. et Kim, J.-W. (2008). Mechanisms underlying the increase in young-of-the-year Atlantic salmon (*Salmo salar*) density with habitat complexity. *Canadian Journal Fisheries and Aquatic Sciences* **65**, 1956-1964.

Zack, S. et Stutchbury, B. J. (1992). Delayed breeding in avian social systems: the role of territory quality and floater tactics. *Behaviour* **123**, 194-219.