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DÉTERMINANTS DE LA SURVIE ET DE LA DISPERSION DE REPRODUCTION PAR UNE APPROCHE CAPTURE-MARQUAGE-RECAPTURE CHEZ L'HIRONDELLE BICOLORE AU QUÉBEC.

par

Paméla Lagrange

thèse en cotutelle présentée

au Département de biologie en vue
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UNIVERSITÉ DE MONTPELLIER 2

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THÈSE

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Présentée par **Paméla LAGRANGE**

Déterminants de la survie et de la dispersion de reproduction par une approche Capture-Marquage-Recapture chez l'Hirondelle bicolore au Québec.

Soutenue le 09/04/2015 devant le jury composé de

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UNIVERSITÉ MONTPELLIER 2 SCIENCES ET TECHNIQUES

SOMMAIRE

En Amérique du Nord, la superficie des monocultures utilisatrices d'intrants tels que des fertilisants et des pesticides couvre aujourd'hui 85 % des surfaces agricoles et autant de pâturages ont disparus en 50 ans afin de répondre aux besoins de l'Homme. Ces changements d'usage des terres ont profondément transformé le paysage et altéré la biodiversité des agro-écosystèmes. Parmi les espèces d'oiseaux champêtres, les insectivores aériens tels l'Hirondelle bicolore, *Tachycineta bicolor*, ici étudiée, présentent un fort taux de déclin des effectifs, reflétant probablement une dégradation des agro-écosystèmes. Les mécanismes biologiques à l'origine de ce déclin sont encore méconnus ainsi que les patrons de dispersion chez les passereaux migrateurs. Le présent travail vise à étudier les effets environnementaux sur les traits individuels (survie et succès reproducteur) et la dispersion de reproduction (probabilité de disperser et taux d'occupation des sites de reproduction) chez l'Hirondelle bicolore. Pour ce faire, 2200 reproducteurs et 8000 oisillons ont été bagués entre 2004 et 2013 et suivis en reproduction pendant 10 ans sur une aire d'étude au Sud du Québec, laquelle est composée de 40 sites et couvre une mosaïque de paysages agricoles hétérogènes. Le développement d'un nouveau modèle de capture-marquage-recapture, flexible d'utilisation, a permis de réduire les biais d'estimation des probabilités de survie et de dispersion de l'espèce. Cette approche a permis de tester l'effet de plusieurs variables en lien avec la qualité de l'habitat, l'information publique et les caractéristiques individuelles sur la variabilité des paramètres de dispersion, de survie et de succès reproducteur au niveau individuel. Les milieux cultivés intensivement associés à la présence du Moineau domestique, *Passer domesticus*, un compétiteur pour les cavités de reproduction, diminuaient au maximum de 19 % la survie des mâles. Les femelles étaient quant à elles affectées par le coût de la reproduction, qui était d'autant plus grand en milieu intensif qu'il y avait une présence de moineaux et une disponibilité moindre en ressources alimentaires. Pour autant, la décision de disperser n'était pas affectée par les conditions environnementales que ce soit par la présence de compétiteurs ou la qualité du

milieu, et ne dépassait pas les 4 % chez les mâles. Les femelles dispersant jusqu'à 14 fois plus s'appuyaient sur leur expérience personnelle pour décider de disperser. Un échec de reproduction augmentait jusqu'à 7 fois la probabilité de disperser et pour la première fois chez une espèce à courte durée de vie, nous avons montré que la probabilité de disperser était augmentée l'année suivant une première dispersion. Ces patrons de dispersion étaient stables dans le temps. La dispersionsemblait donc être un processus coûteux, comparé à la fidélité au site, qui apparaîssait comme un phénotype minoritaire dans la population. Elle répondait à des conditions défavorables de reproduction. Enfin, ce travail montre l'utilisation de l'information publique dans la décision de s'établir sur un site généralement fortement dense et productif en jeunes l'année précédente et ce, une fois que la décision de disperser est amorcée. La présence de moineaux et la forte proportion de cultures intensives dans un rayon proche participaient également à ll'évitement des sites lors de l'établissement. D'après ces résultats, le milieu intensif contribuerait au déclin de l'Hirondelle bicolore.

Mots-clés : congénères, dispersion de reproduction, Hirondelle bicolore, Moineau domestique, paysage agricole, sélection des nichoirs, succès reproducteur, survie.

ABSTRACT

In North America, monoculture areas using high inputs of fertilizers and pesticides cover 85 % of agricultural lands, and as many pastures disappeared in the past 20 years to satisfy human food needs. These land-use changes have deeply transformed landscapes and altered the biodiversity of agro-ecosystems. Among farmland birds, aerial insectivores such as Tree Swallow, *Tachycineta bicolor*, studied here show a high rate of decline in their abundance, partly reflecting the degradation of agro-ecosystems where they breed. Biological mechanisms leading to the decline and dispersal patterns in migratory passerines are still poorly known.

The present work quantifies the environmental effects on Tree Swallow individual traits (survival, reproductive success) and breeding dispersal (probability to disperse and occupation rates of breeding sites). Between 2004 and 2013, 2200 breeders and 8000 chicks were ringed and monitored during 10 breeding seasons on a study area composed of 40 sites and covering a mosaic of heterogeneous agricultural landscapes in southern Québec. The development of a new, flexible capture-mark-recapture model has reduced estimate bias of survival and dispersal probabilities of Tree Swallows. This approach allowed to assess the effect of several variables linked to habitat quality, public information and individual characteristics on dispersal, survival and reproductive success parameters of individuals. Within intensively cultivated landscapes associated to the presence of a nest site competitor, the House sparrow, *Passer domesticus*, male survival is up to 19 % lower. Females were affected by the cost of reproduction, especially in intensive landscapes where House sparrows and found and where food resources and nest site appear limited. Dispersal probability was not affected by environmental conditions either through the presence of House sparrows or habitat quality, and was restricted to 4 % in males. Females, which dispersed up to 14 times more than males, based their decision on their personal experience. Breeding failure increased up to 7 times the probability to disperse and for the first time in a short-lived species, I show that dispersal likelihood increased if the individual had dispersed in the previous year. These dispersal patterns were stable in time. Dispersal appeared as a costly process compared to site fidelity and was a minority phenotype in the population. It appeared an answer to unfavorable condition for reproduction. Finally, this work shows the use of public information (partners density, fledglings productivity the previous year) on the decision to settle on a site and this, after the dispersal decision had been initiated. The presence of House sparrows and the proportion of intensive areas near nest boxes were used as information to select a breeding site. Based on these findings, agricultural intensification likely plays a role in the decline of Tree swallow populations.

Key-words: agricultural landscape, breeding dispersal, conspecifics, nest boxes selection, House sparrow, reproductive success, survival, Tree Swallow.

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

1.1. Mise en contexte

1.1.1. Les traits d'histoire de vie dans l'évolution

Définition

Les traits d'histoire de vie sont définis comme étant un ensemble de caractères biologiques fonctionnels d'un individu permettant de décrire son cycle de vie. C'est en 1976 que Stearns introduit cette notion dans un contexte évolutif, en caractérisant cet ensemble de traits comme coadaptés, issus de la sélection naturelle, pour résoudre un problème écologique particulier (Stearns, 1976). D'après la théorie de l'évolution de ces traits, l'individu maximise sa valeur reproductive (ou fitness) – définie comme sa capacité à transmettre son génotype à sa descendance – en optimisant l'investissement de son énergie entre survie et reproduction (Roff, 1992 ; Stearns, 1992). Dans la nature, les individus sont donc contraints d'effectuer des compromis adaptatifs favorisant l'investissement dans un trait ou un autre selon les conditions environnementales (Williams *et al.,* 2002). Cette allocation différentielle résulte d'un ensemble de stratégies évolutives concernant des adaptations comportementales, physiologiques et anatomiques. Les traits ne sont donc pas une réponse directe des individus à des variables environnementales, ils expriment des adaptations résultant d'interactions longues avec l'environnement (Ricklefs, 1990).

Causes environnementales de la variabilité des traits d'histoire de vie

Si la valeur reproductive d'un individu contribue à la génération d'une descendance, l'interaction de cette descendance avec son environnement participe à la viabilité et à la transmission du génotype parental. Dans la nature, les conditions environnementales ne sont pas constantes – on parle de stochasticité – et la valeur reproductive de l'individu dépend de sa capacité à y répondre. La variabilité environnementale peut être définie comme l'ensemble des variations affectant l'environnement d'une population dans le temps et l'espace, et par conséquent, les ressources dont elle dépend. Elle se caractérise par son intensité, sa fréquence ou sa prévisibilité (Nevoux, 2008). De nombreuses variables environnementales affectent les traits d'histoire de vie. Elles peuvent être liées aux caractéristiques biotiques et abiotiques de l'écosystème, comme par exemple les conditions climatiques, la composition du paysage assurant l'abondance en ressources alimentaires, les caches contre les prédateurs ou la disponibilité en sites de reproduction (Betts *et al.,* 2008 ; Møller *et al.,* 2006). S'ajoutent également des variables relatives aux interactions trophiques comme la compétition, la prédation ou les relations sociales intraspécifiques.

Traits et cycles de vie

Prenons l'exemple d'espèces à longue durée de vie (longévives) et d'une espèce à courte durée de vie pour illustrer les stratégies d'allocation énergétique en fonction des conditions environnementales (Fig. 1). Les pétrels et les albatros sont des oiseaux pélagiques longévifs, soumis à des ressources alimentaires fluctuantes et peu prévisibles dans le milieu marin. Cette variabilité de la disponibilité alimentaire, ainsi que la distance à parcourir entre leurs aires d'alimentation et la colonie de reproduction, ont un coût non négligeable sur la survie des adultes lorsqu'ils recherchent leur nourriture. Par conséquent, on retrouve chez ces deux espèces des traits similaires, tels un faible effort reproducteur (un seul œuf pondu par année), une maturité sexuelle tardive, une longue période de développement des poussins et une longue espérance de vie. Aussi, ces espèces utilisent une stratégie dite de « bet-hedging » consistant en une réduction annuelle des performances reproductrices en faveur d'une augmentation de la survie des adultes face à des conditions environnementales fluctuantes

(Murphy, 1968 ; Nevoux, 2008 ; Orzack et Tuljapurkar, 2001). Au contraire, les mésanges dont l'espérance de vie n'excède pas 4 ans, ont une stratégie privilégiant les traits de la reproduction plutôt que ceux de la survie (De Heij *et al.,* 2006 ; Stjernman *et al.,* 2004). Elles sont ainsi capables de synchroniser leur reproduction sur la période où les ressources alimentaires sont les plus abondantes (Blondel *et al.,* 1993 ; Caro *et al.,* 2009). On retrouve par exemple chez ces espèces, comme chez beaucoup de passereaux, un fort effort reproducteur (jusqu'à 12 œufs par couvée), une ponte de substitution en cas d'échec de la première couvée et une maturité sexuelle atteinte dès le deuxième été. Un ensemble d'alternatives permet à ces espèces de se reproduire, quelles que soient les conditions extérieures. Pour conclure, moins un individu a de chances de survivre à la prochaine saison de reproduction, plus son effort actuel de reproduction augmentera (Williams, 1966).

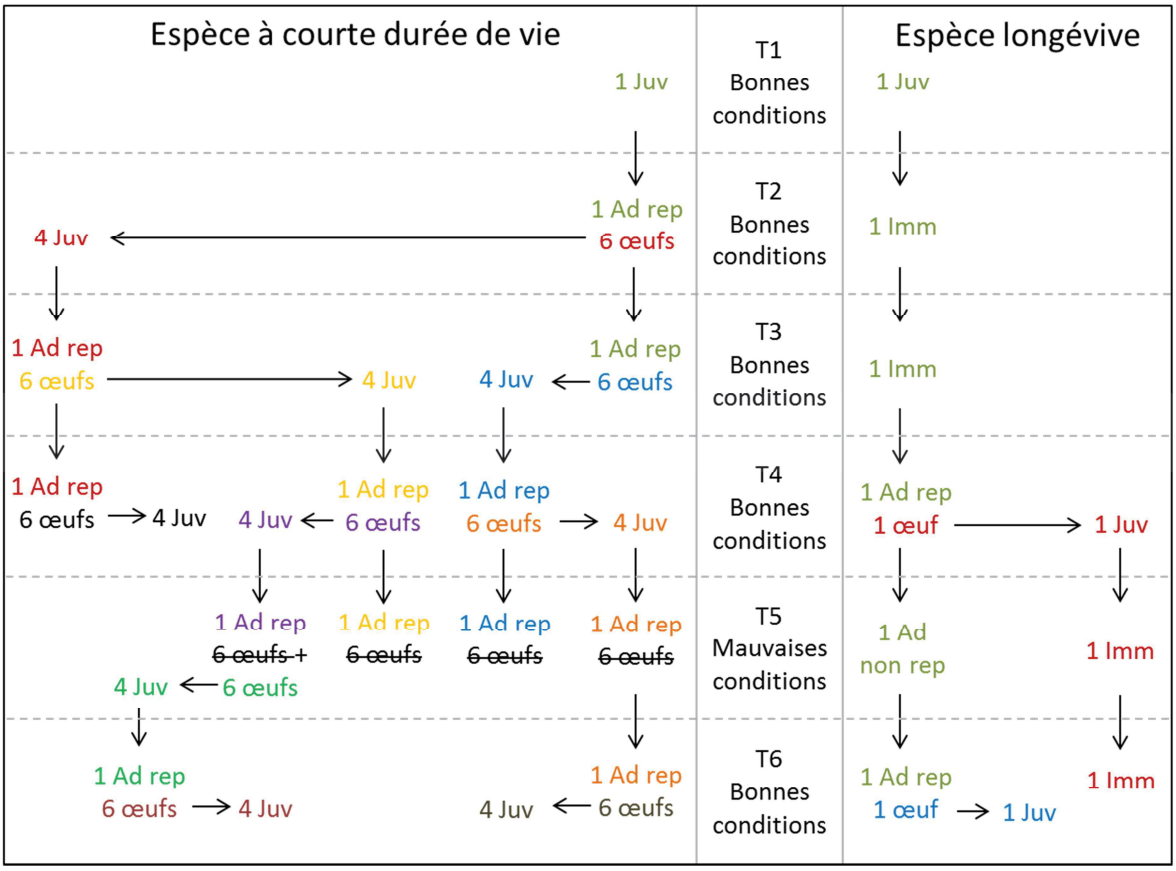


Figure 1 : Illustration de deux stratégies de vie chez une espèce à courte durée de vie *vs.* longévive. Chaque ligne correspond à une année (T1 à T6) caractérisée par des conditions environnementales. Une couleur représente un individu qui atteindra le stade adulte. Quatre stades

sont identifiables : juvénile (Juv), immature (Imm), Adulte non reproducteur (Ad non rep) et adulte reproducteur (Ad rep). Chaque flèche horizontale correspond au produit de la reproduction à la fin d'une saison (6 œufs donnent 4 juvéniles car 2 œufs n'éclosent pas) et chaque flèche verticale correspond à la survie annuelle (sur 4 juvéniles, un seul survit jusqu'à la 1ère reproduction, et les adultes ont une espérance de vie de 2 ans *vs.* 30 ans chez l'espèce longévive). Les échecs de reproduction ne produisant pas d'adulte sont barrés.

1.1.2. La dispersion comme réponse adaptative

Migration versus dispersion

Afin d'améliorer leur fitness, les organismes développent des comportements afin d'éviter des conditions défavorables. Par exemple lorsqu'ils sont doués de mobilité, les organismes changent d'habitat par des déplacements. On retrouve ainsi les comportements migratoires, déplacements entre les aires de reproduction et les aires d'hivernage pour déjouer la rudesse de l'hiver, ou encore le comportement de dispersion. La définition de la dispersion s'oppose à celle de la migration par le caractère permanent et souvent aléatoire du déplacement, alors qu'il est qualifié de cyclique avec un retour vers le lieu de départ dans la migration. La dispersion peut se décomposer en trois étapes : la décision de quitter un site appelée initiation, le déplacement en tant que mouvement ou transfert, et l'installation dans le nouveau site de reproduction (Clobert *et al.,* 2001 ; Ronce, 2007). Lorsque la dispersion s'effectue entre le site de naissance et le premier site de reproduction, on la nomme dispersion natale, alors que lorsqu'elle s'effectue entre deux sites de reproduction, on la nomme dispersion de reproduction (Greenwood et Harvey, 1982). Cette dernière s'oppose au comportement de fidélité au site qui s'opère entre deux évènements de reproduction. Deux grands types de fidélité sont répertoriés : la fidélité au site de reproduction, où le site de reproduction diffère du site natal et la philopatrie, qui est un caractère propre à l'espèce se caractérisant par une tendance à rester ou à revenir sur le site natal pour se reproduire.

Le « choix » de disperser

L'initiation de la dispersion et l'établissement impliquent une sélection des sites de reproduction. La sélection est un processus où l'organisme choisit les habitats favorisant sa fitness au détriment d'autres habitats (Hall *et al.,* 1997). Ce choix sous-entend l'acquisition d'informations sur les alternatives qui s'offrent à lui et la décision d'opter pour celles qui, compte tenu d'un certain nombre de paramètres, lui permettent de maximiser sa fitness (Boulinier et Danchin, 1997 ; Danchin *et al.,* 2004). Pour qu'il y ait un choix du site de reproduction, il faut qu'il y ait une variabilité perceptible par les individus de la qualité des sites disponibles et que cette variabilité soit prévisible dans le temps si l'utilisation du site est différé du moment de la prise d'information (Switzer, 1993). Les modèles théoriques développés par Boulinier et Danchin en 1997 ont montré les avantages de la prospection, ou recherche d'informations, dans la sélection du site de reproduction à deux étapes du cycle de vie. Lors du recrutement, la prospection avant l'établissement pour la reproduction est la meilleure stratégie pour maximiser le succès reproducteur de l'individu (SRi), en particulier dans un environnement prévisible avec peu de parcelles de bonne qualité. Après expérience de reproduction, le SRi est meilleur quand la sélection du site de reproduction s'effectue sur la base du succès reproducteur des congénères (SRc) sur le même patch de l'année précédente, plutôt que sur l'expérience de reproduction de l'individu. Dans la nature, il semblerait que le SRi et le SRc sur un même site soient pris en compte simultanément pour initier la décision à disperser (Danchin *et al.,* 1998). Récemment, il a aussi été montré que l'information collectée ne se limitait pas à l'acquisition de données chez les congénères, mais également chez des espèces voisines nichant sur un même site (Kivelä *et al.,* 2014).

Rôle de la prospection dans la dispersion

La dispersion est particulièrement intéressante à étudier chez les oiseaux coloniaux, où, même si la philopatrie est de mise, une variabilité individuelle existe. La collecte d'informations est facilitée par la concentration d'individus reproducteurs en un même lieu. Cette acquisition d'informations publiques se fait par les prospecteurs, visitant les sites de reproduction des congénères. Les prospecteurs sont généralement des individus ayant du temps à allouer à la

prospection, soit parce qu'ils ont échoué leur reproduction ou parce qu'ils sont non reproducteurs (individus flottants), plus susceptibles de disperser (Dittmann *et al.,* 2005 ; Ward, 2005).

La prospection repose sur l'acquisition d'informations sociales (comme le succès de la reproduction des congénères) ou non sociales (comme les qualités physiques d'un habitat) informant sur la qualité des sites d'alimentation et le plus souvent, des sites de reproduction (Pärt *et al.,* 2011). De nombreux travaux sur le Gobemouche à collier, *Ficedula albicollis,* ont apporté des éléments sur l'information collectée et son utilité. Afin de limiter le coût de la prospection, la collecte d'information s'effectue en parallèle de la recherche alimentaire pendant l'élevage des oisillons (Pärt et Doligez, 2003 ; Schjørring *et al.,* 1999) et la récolte d'indices de qualité des sites est multiple : quantité de jeunes élevés, condition des jeunes (Doligez *et al.,* 2002). Cependant, l'information collectée semble propre à chaque espèce bien qu'elle soit principalement liée aux indices du succès reproducteur sur un site « hypothèse de l'attraction par la performance » ou à la densité en congénères « hypothèse de l'attraction sociale » (Calabuig *et al.,* 2008). Chez la Paruline bleue, *Setophaga caerulescens,* la présence d'un reproducteur chantant en fin de période de reproduction marque l'attrait pour ce site l'année suivante (Betts *et al.,* 2008). Chez l'Hirondelle à front blanc, *Petrochelidon pyrrhonota,* la condition corporelle des reproducteurs et la densité en oisillons envolés augmentent la probabilité d'utilisation du site l'année suivante (Brown *et al.,* 2000). Ces informations accessibles à tous les individus sont qualifiées d'information publique (voir Wagner et Danchin, 2010 pour la sémantique).

Le stockage de l'information pour la sélection des sites

Les études portant sur l'information publique considèrent que l'acquisition d'information s'effectue à la saison de reproduction précédant la décision à dispersion et qu'il n'y a pas d'accumulation d'information au fil des ans. Très peu d'études laissent entrevoir une mémorisation des informations sur le long terme qui pourrait se répercuter sur le comportement de dispersion des années suivantes. Danchin *et al.* (1998) montrent ainsi une

forte autocorrélation de l'information publique qui diminue avec le temps chez la Mouette tridactyle. De plus, ils indiquent que les taux de recrutement et de dispersion sont fortement corrélés au succès reproducteur de la même année. Ces éléments montrent que dans leur cas d'étude, la mémorisation de l'information ou de l'expérience de reproduction sur une longue période n'influence pas forcément l'initiation des déplacements ou la sélection du site de reproduction. L'étude de la probabilité de dispersion ou de recrutement en lien avec des évènements antérieurs n'a donc pas été réalisée. Cependant, chez une autre espèce longévive, la Bernache du Canada, *Branta canadensis,* il a été montré que le comportement de dispersion de l'année précédente pouvait influencer la probabilité de disperser l'année suivante (Hestbeck *et al.,* 1991 ; Rouan *et al.,* 2009).

Une toute autre expérience sur les sites d'alimentation chez le Cassenoix d'Amérique, *Nucifraga columbiana*, a montré une mémoire à long terme de seulement 7 à 9 mois concernant la mémorisation des caches pour des réserves nutritives. Au-delà de cette période, la capacité à retrouver les caches diminuait (Balda et Kamil, 1992). On peut donc supposer que la mémoire à long terme est une capacité cognitive limitée chez les oiseaux et que les informations acquises l'année subséquente sont les seules retenues pour le choix du prochain site de reproduction. De fait, l'effet d'un comportement antérieur sur le comportement dispersif des années futures n'a que très peu été étudié.

Conséquences de la dispersion

La dispersion est une stratégie reposant sur un compromis adaptatif entre les coûts du déplacement et les gains que procure l'accès à une zone plus propice à la reproduction. Bonte *et al.* (2012) définissent plusieurs types de coûts, à répercussion immédiate ou subséquente, associés à la dispersion. Le coût énergétique dû au mouvement lui-même et au développement de l'organisme (ontogenèse) associé à la dispersion, assure par exemple l'augmentation de la masse musculaire ou la taille des ailes. Le coût temporel directement lié au temps investi dans la dispersion ne peut être consacré à une autre activité comme la reproduction (Dow et Fredga, 1983). La dispersion augmente aussi l'exposition aux risques associés à la mortalité

(prédation) ou différés, par accumulation de dommages, de blessures ou de changements physiologiques (Bonte *et al.,* 2012). Par exemple, après dispersion, l'immunodéficience augmente et l'organisme devient plus sensible aux dérèglements physiologiques, aux pathogènes et aux parasites. Enfin, la dispersion n'est pas toujours associée à une opportunité de sélection du « meilleur » habitat. En plus de pouvoir perdre un territoire qu'ils possèdent déjà, les dispersants abandonnent donc les avantages des résidents qui ont connaissance de leur environnement local.

Parce que la qualité des habitats varie dans le temps et l'espace, les individus capables de disperser ont un avantage à changer d'habitat quand celui-ci limite leur valeur reproductive afin d'augmenter le succès de leur reproduction (Badyaev *et al.,* 1996). Malgré les coûts engendrés, la dispersion apporte parfois des bénéfices compensatoires (Bélichon *et al.,* 1996 ; Johnson et Gaines, 1990). Elle permet d'un point de vue génétique de limiter le risque de consanguinité et d'augmenter le polymorphisme. Le changement de territoire diminue le risque d'accouplement avec un congénère de même génotype (Greenwood *et al.,* 1979) et est souvent accompagné d'un changement de partenaire (Baeyens, 1981). Il s'ensuit donc un brassage génétique entre les populations, occasionné par les déplacements des individus (Clobert *et al.,* 2001 ; Greenwood et Harvey, 1982). Dans ce cas, la compensation du coût ne s'exprime pas directement après l'action de disperser, elle se répercute au cours de la vie et à chaque occasion de reproduction future (Shields, 1987). A l'inverse, si la dispersion a pour but de minimiser la compétition pour des ressources, il n'y a pas toujours de compensation. Les parents, dans le cas d'itéroparité, ont alors avantage à forcer les juvéniles à disperser bien qu'il n'y ait pas de compensation pour le juvénile (Bélichon *et al.,* 1996 ; Comins *et al.,* 1980).

1.1.3. Des traits individuels à la dynamique des populations

Concepts démographiques

Les compromis adaptatifs des organismes se répercutent à l'échelle de la population à travers la variation des paramètres démographiques (natalité, mortalité, immigration et émigration).

C'est en 1954 que le concept de population en tant que « structure de reproduction » d'un groupe d'individus est défini, laissant apparaître les prémices de possibles connexions entre plusieurs groupes de populations locales (Andrewartha *et al.,* 1954 ; Hanski, 1999). Odum en 1983, définira la population comme un ensemble d'individus d'une même espèce susceptibles de se reproduire ensemble et vivant sur une même aire géographique. Lorsque les populations sont interconnectées par des flux d'individus peu fréquents, mais réguliers, le concept de métapopulation défini par Levins (1968) est alors mis en avant. Ces flux résultent du processus de dispersion. Alors que l'immigration et la natalité favorisent le gain d'individus, l'émigration et la mortalité favorisent la perte d'individus au sein d'une population. Lorsque la population possède un taux de mortalité supérieur au taux de natalité et qu'elle ne peut se maintenir sans l'apport d'immigrants, elle est alors considérée comme une population puit, vouée à disparaître si de plus, l'émigration est plus forte que l'immigration. Par opposition, lorsque la population possède un effectif stable, dont les jeunes produits peuvent disperser sans perturber cet équilibre, elle est considérée comme une population source (Watkinson et Sutherland, 1995).

Survie, fécondité et cycles de vie

Alors que la survie des adultes est un paramètre peu variable et clé pour la viabilité des populations des espèces longévives, la survie juvénile et la fécondité sont des paramètres primordiaux chez les espèces à courte durée de vie (Roff, 1992). En effet, lorsque le cycle de vie est court, la proportion de jeunes produits et survivants jusqu'à la première reproduction influence directement le taux de recrutement. Ce dernier représente la proportion de nouveaux entrants (primo reproducteurs et reproducteurs immigrants) dans la population pour se reproduire. Il a été montré au sein d'une population d'Hirondelle noire, *Progne subis*, par exemple, que la survie des jeunes entre l'envol et la migration était de 87 %, alors qu'elle n'était plus que de 32 % entre la migration et l'hivernage, pour finalement atteindre 27 % à la fin de la première année (Tarof *et al.,* 2011). Si cette forte mortalité est également associée à une dispersion natale à grande distance comme chez la plupart des passereaux, il devient alors difficile de suivre les juvéniles et d'en estimer les paramètres démographiques associés, car les

recaptures d'individus se font rares. Chez l'Hirondelle rustique, *Hirundo rustica*, par exemple, la probabilité de recapture des juvéniles est de 2 %, soit 20 fois plus faible que chez les adultes (Shields, 1984).

Paramètres de dispersion

C'est lors de l'émancipation, attribuée à la phase de dispersion natale, que la plupart des espèces parcourent les plus grandes distances pour se reproduire. Paradis *et al.* (1998) ont répertorié 69 espèces d'oiseaux, parmi lesquelles 61 effectuaient une distance plus grande pendant la dispersion natale que pendant la dispersion de reproduction. La dispersion de reproduction est quant à elle soumise à une diminution de la fréquence de dispersion avec l'augmentation de la distance de dispersion (Newton et Marquiss, 1982). Paradis (1998) a montré également que la fragmentation d'un habitat de bonne qualité induit une augmentation de la dispersion afin de contrer l'isolation des habitats entrainant la limitation des ressources et l'augmentation de la compétition. Cependant, elle implique une capacité à migrer sur de plus grandes distances. La dispersion à longue distance est donc essentielle aux populations pour les processus d'invasion, de colonisation et la structuration des populations (Shaw, 1995).

1.1.4. Estimation des paramètres démographiques par capture-marquage-recapture (CMR)

Rôle de la dynamique des populations

L'étude des paramètres démographiques a trouvé sa place dans la dynamique des populations qui est apparue dans les années 1930, pour estimer les effectifs de populations aussi bien animales que végétales. Plusieurs problématiques sont nées de la prise de conscience des modifications environnementales causées par l'Homme sur les milieux naturels. Il devient alors primordial de comprendre les mécanismes régissant le fonctionnement et les réponses des populations face à ces modifications environnementales (Coulson *et al.,* 2001 ; Reed *et al.,* 2010). L'étude de la dynamique des populations est aujourd'hui en plein essor pour répondre à

des problématiques écologiques de plusieurs types, comme le contrôle d'espèces invasives ou en expansion, la gestion d'espèces chassées, ou encore la conservation d'espèces en déclin.

Historique des modèles

Les premiers modèles estimant les effectifs des populations considéraient que chaque population était un tout, où les individus la composant comportaient des traits identiques et subissaient les mêmes contraintes. Le modèle de Verhulst par exemple, excluait les variations environnementales en considérant que l'abondance d'une population était limitée par deux facteurs : la disponibilité en ressources du milieu et la densité en individus en compétition pour cette dernière grâce à des relations logistiques où l'augmentation de la population est la conséquence directe d'une augmentation de la natalité ou d'une diminution de la mortalité.

Avec le temps, les modèles ont pris en compte la variabilité individuelle grâce au suivi d'individus marqués par la technique de capture-marquage-recapture (CMR) pour estimer les paramètres démographiques utilisés en dynamique des populations. Ces méthodes relativement flexibles ont permis d'estimer des taux de mortalité grâce aux marquages de milliers d'individus ensuite recapturés ou repris morts par la chasse ou la pêche. À cette époque, l'estimation de la dispersion se faisait à partir de données de recaptures et nécessitait qu'un individu soit capturé au moins deux fois pour estimer le taux de mortalité. Les individus non capturés comportaient à la fois les individus non détectés (présents, mais non capturés par échec) et les individus réellement absents (car émigrants). C'est avec le modèle CJS, du nom de ses développeurs (Cormack, Jolly et Seber, voir Lebreton *et al.,* 1992) que la probabilité de détection est incluse et corrige les estimations de survie en supposant des variations temporelles. Plusieurs illustrations portant sur l'estimation des taux de survie entre une méthode naïve (considérant une détection parfaite) et une méthode CMR ont été rapportées et montrent une sous-estimation des taux de survie lorsque la détection est considérée parfaite (Gimenez *et al.,* 2008 ; Martin *et al.,* 1995).

A partir de 1972, l'intégration de plusieurs sites de recaptures dans les modèles dits Arnason-Schwarz (Arnason, 1973 ; Schwarz *et al*., 1993), donne les prémices des modèles multisites, permettant d'estimer les déplacements d'individus entre plusieurs sites (Brownie *et al.,* 1993 ; Hestbeck *et al.,* 1991). La généralisation du multisite en multiétat a ensuite permis de remplacer l'intérêt pour la localisation géographique par le statut biologique de l'individu, incluant ainsi l'hétérogénéité individuelle dans la démographie (voir Lebreton *et al.,* 2009 pour une revue). Alors que le multisite estime le flux d'individus entre un point A et un point B, le multiétat estime la probabilité individuelle de passer d'un état A (par exemple reproducteur) à un état B (non reproducteur). Enfin récemment, l'incertitude liée à l'attribution de l'état d'un individu a été intégrée dans les modèles multiévènement (Pradel, 2005). Ces modèles considèrent que l'information perçue au moment de la capture (appelé évènement) diffère du statut biologique de l'individu (état) (Fig. 2).

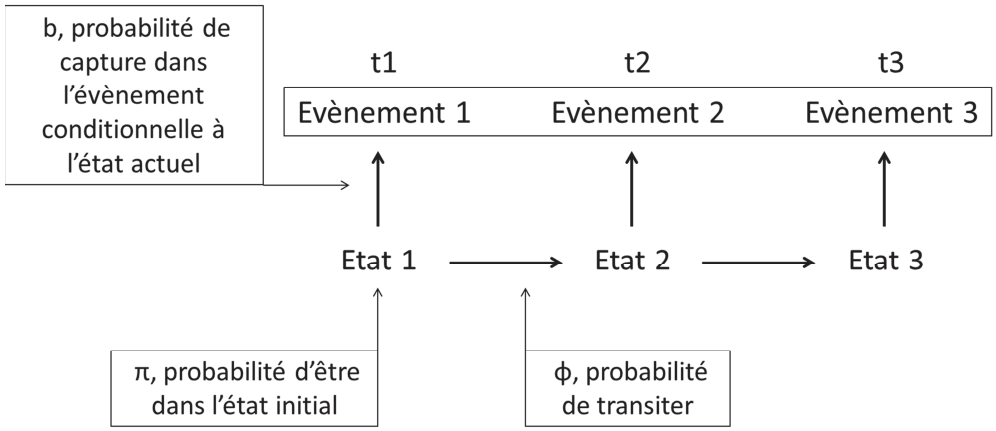


Figure 2 : Principe des modèles multiévènement (adapté de Pradel, 2009). L'histoire de capture d'un individu marqué (encadré) à trois occasions (temps) est faite à partir d'évènements et non d'états. Les états sont relatifs à l'observation de l'histoire de capture à travers la probabilité de génération d'évènements donnée par les états.

Limites des méthodes

L'une des contraintes des modèles CMR concerne la gestion des individus capturés une fois (nommés transients), ou à plusieurs sessions successives, puis non recapturés par la suite, alors que l'individu pourrait supposément être encore vivant. Ces individus passés au-delà de l'aire

d'étude peuvent biaiser les estimations de survie et de détection. Dans le cas d'individus transients, des méthodes distinguant la survie entre la première et la deuxième capture, des survies post-deuxième capture, permettent de corriger ce biais. Pour les autres cas, il faut donc distinguer la survie apparente estimée, qui peut être biaisée par les individus émigrés non recapturés, de la survie réelle (Lebreton *et al.,* 1992).

Actuellement, les méthodes CMR sont relativement limitées pour estimer les déplacements entre un grand nombre de sites entre deux occasions. Pour une aire d'étude comprenant N sites de recaptures, le modèle doit estimer les paramètres de transitions ϕ, soit $N * (N - 1)$ transitions entre les sites, ainsi que les paramètres concernant l'état initial π au nombre de $(N - 1)$, et les paramètres relatifs à l'association état/évènement b dont le nombre minimal est de N paramètres et variable suivant le nombre d'évènements considérés, (Fig. 2). Ainsi, en utilisant des données issues de 10 sites de recaptures, un modèle classique multisite doit estimer les probabilités de 90 transitions ϕ, 9 états initiaux π, et 10 recaptures b, soit 109 paramètres. Enfin, si l'intérêt porte sur l'estimation des déplacements entre les sites, les transitions peuvent être découpées en deux probabilités : une probabilité de survivre S sur chacun des sites et une probabilité de se déplacer D vers chacun des sites. L'inconvénient des modèles contenant un nombre élevé de paramètres réside dans l'incapacité à les estimer s'ils sont trop nombreux comparés à la quantité d'information extractible d'un jeu de données. Bien que la qualité des données récoltées dans le milieu naturel puisse être bonne (fiabilité, précision etc.), la quantité de données nécessaire à la modélisation est souvent limitée par le temps.

1.2. Application

1.2.1. L'érosion de la biodiversité aviaire au Canada

Au Canada, les populations d'oiseaux font l'objet d'un suivi depuis plusieurs dizaines d'années (Fig. 3). Même si la plupart des espèces sont globalement en déclin, certains groupes d'oiseaux, dont les oiseaux de proie, la sauvagine et les oiseaux de mer coloniaux, voient une augmentation de leurs effectifs. Ces améliorations sont en parties dues à la réduction de certains contaminants environnementaux (e.g., DDT), à la mise en place de programme de réintroduction (e.g., Faucon pèlerin, *Falco peregrinus*) et de gestion durable de la chasse (quota de chasse), ainsi qu'à la protection et la restauration de certaines zones humides (e.g., ZICO). Cependant, de nombreuses pressions anthropiques pèsent encore sur l'avifaune et causent le déclin de la majorité des espèces d'oiseaux de rivages, de prairies et des insectivores aériens. La destruction et détérioration des habitats, la surexploitation des ressources naturelles, la pollution, l'introduction d'espèces envahissantes et les changements climatiques figurent parmi les plus grandes menaces.

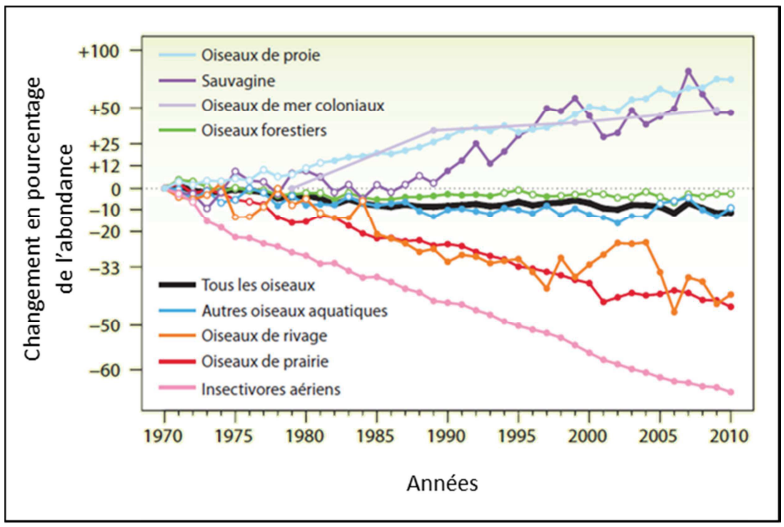


Figure 3 : Indicateurs de l'abondance des populations de toutes les espèces d'oiseaux indigènes observées au Canada appartenant à huit sous-groupes choisis (extrait du rapport d'Environnement Canada 2012).

Outre les intérêts récréatifs et économiques que procurent les oiseaux par les activités de chasse, d'observation ou de nourrissage chez les particuliers, l'intérêt écologique n'est pas moindre. Dans les écosystèmes, les oiseaux sont responsables de la régulation des ravageurs, de la dispersion de graines ou de la pollinisation (Howe, 1986 ; Wenny *et al.,* 2011). Certaines espèces comme les insectivores aériens sont donc étroitement liés à l'état de santé des milieux qu'ils fréquentent. Se nourrissant d'insectes chassés en vol, la plupart des espèces de ce groupe fréquente les milieux ouverts comme les prairies naturelles, les champs cultivés ou les marais. Ce groupe présente le taux de déclin le plus important depuis 40 ans avec une diminution de l'abondance des espèces de 60 % (Environnement Canada, 2012) suivant un gradient de déclin de plus en plus prononcé vers le Nord-Est de l'Amérique (Nebel *et al.,* 2010). Ce gradient a été corrélé positivement à la pollution environnementale présente dans le Nord-Est. Les principales causes du déclin évoquées sont la désynchronisation des dates d'arrivées des migrateurs de longues distances (majoritaires dans ce groupe) avec la période climatique propice à la reproduction, ainsi que la diminution de la disponibilité en proies due à l'utilisation de pesticides dans les zones d'hivernage tropicales et dans les zones de reproduction (Freemark et Kirk, 2001 ; Nebel *et al.,* 2010).

1.2.2. Les agroécosystèmes

Les agroécosystèmes sont des milieux ouverts fréquentés par plusieurs espèces d'insectivores aériens comme les hirondelles et certains moucherolles. Depuis la seconde moitié du XXème siècle, les agroécosystèmes sont soumis à une forte pression économique afin de répondre au besoin de l'Homme, notamment pour la production de céréales, de soja et de maïs. Les pratiques agricoles ont été modifiées par la mécanisation des cultures, l'utilisation de pesticides, l'augmentation de la fertilisation chimique, des surfaces irriguées et la sélection de nouveaux cultivars pour augmenter les rendements (Donald *et al.,* 2001). Les agroécosystèmes autrefois bocagers et divisés en de multiples parcelles tendent aujourd'hui à une homogénéisation et spécialisation des cultures sous forme de monoculture afin d'en augmenter le rendement (Benton *et al.,* 2002 ; Benton *et al.,* 2003). En Amérique du Nord, par exemple,

la superficie des monocultures couvre actuellement 85 % des surfaces cultivées et 85 % des pâturages ont disparu en 50 ans (Jobin *et al.,* 2005). Cette homogénéisation du paysage a réduit les zones extensives, les habitats semi-naturels des agroécosystèmes et fragmenté les habitats naturels (Freemark et Kirk, 2001). De ce fait, les changements d'usage des terres ont profondément altéré la qualité des habitats, engendrant une érosion de la biodiversité animale et végétale des agroécosystèmes, aussi bien en Amérique du Nord qu'en Europe (Chamberlain *et al.,* 2000 ; Newton, 2004 ; Norris, 2008).

1.2.3. Le modèle d'étude : l'Hirondelle bicolore

Un insectivore aérien en déclin

L'Hirondelle bicolore, *Tachycineta bicolor*, est un passereau occupant les milieux ouverts tels que les marais, les anciens brûlis de la forêt boréale, les prés et les zones agricoles pour s'alimenter d'insectes chassés en vol (Winkler *et al*., 2011). Cette particularité alimentaire fait de l'espèce un maillon intermédiaire des réseaux trophiques dans les agroécosystèmes. Bien que les effectifs de l'espèce soient en déclin dans le Sud du Québec (-4,2 % au Québec depuis 20 ans (Canadian Wildlife Service (CWS) 2012)), elle reste relativement abondante. Son aire de reproduction recoupe une bonne partie de l'Amérique du Nord, s'étendant de la limite nord de présence des arbres au centre des États-Unis. L'UICN la considère comme une espèce à préoccupation mineure (Canadian Wildlife Service (CWS) 2012). Pour toutes ces raisons, l'Hirondelle bicolore pourrait être considérée comme un bon bio-indicateur du milieu agricole, en particulier pour révéler la pollution environnementale (Jones, 2003 ; Landres *et al.,* 1988). De plus, l'espèce est facilement identifiable, capturable et est assez robuste pour supporter des manipulations pendant la période de reproduction. Elle n'est pas sujette à l'abandon des couvées lors des dérangements occasionnés par un suivi intensif de sa reproduction, ce qui en fait un modèle d'étude largement utilisé *in natura* par les chercheurs (Jones, 2003).

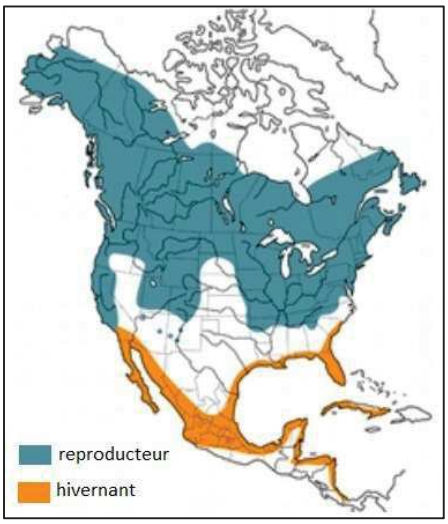


Figure 4 : Aire de répartition de l'Hirondelle bicolore pendant l'hivernage et la saison de reproduction (extraite de Winkler *et al.* 2011).

Reproduction et mode de vie

L'Hirondelle bicolore utilise des cavités secondaires, principalement des trous de Picidés pour nicher (Winkler, 2011). La destruction de ces habitats a favorisé la compétition pour cette ressource (Dobkin *et al.,* 1995). Plusieurs espèces comme le Merlebleu de l'Est, *Sialia sialis*, le Troglodyte familier, *Troglodytes aedon,* ou le Moineau domestique, *Passer domesticus*, concurrencent pour ces sites de reproduction, causant la désertion, la destruction des nichées et parfois la mort des hirondelles défendant leur territoire (Finch, 1990 ; Robillard *et al.,* 2013 ; Rustad, 1972). Bien qu'elle soit particulièrement territoriale, l'espèce explore les territoires voisins pour les copulations hors couple (Male *et al.,* 2006). En effet, l'espèce présente un des plus forts taux de copulation hors couple chez les oiseaux, avec jusqu'à 90 % des nichées comprenant au moins un jeune élevé par un mâle qui n'est pas le père génétique (Lessard *et al.,* 2014).

Dans le Sud du Québec, les couples commencent la construction du nid fin avril et pondent les premiers œufs vers la mi-mai. La taille de ponte varie de quatre à sept œufs et est généralement composée de cinq œufs (Ghilain et Bélisle, 2008 ; Paynter, 1954). L'incubation

commence dès que les conditions environnementales sont propices (ressources alimentaires, climat clément) et dure environ 13 jours (Zach, 1982). Fin mai, les premiers oisillons éclosent et peuvent quitter le nid dès 16 jours. Dans cette région, il n'y a pas de seconde ponte lorsque la première a mené les oisillons à l'envol. Jeunes et adultes se regroupent ensuite pour la migration. Son aire d'hivernage se situe sur le pourtour du Golfe du Mexique et du Golfe de Californie sur la côte Pacifique (Fig. 4).

Démographie

L'estimation des paramètres démographiques réalisée sur les données de recapture d'oiseaux bagués est fortement variable suivant les années et l'aire d'étude. Le taux de retour des oisillons sur le site natal a été évalué entre 0,8 % et 12 % (Butler, 1988). Shutler et Clark (2003) estiment la dispersion juvénile par analyses CMR à 18,4 % dans leur aire d'étude en Saskatchewan, Canada, où le milieu forestier contraint fortement les hirondelles à occuper les nichoirs artificiels, faute de site alternatifs. Une autre étude dans l'Est américain a associé le faible taux de retour à une forte mortalité juvénile (environ 79 %) plutôt qu'à de l'immigration, car seulement 2,7 % des recaptures ont été faites à plus de 100 km (Hosner et Winkler, 2007). Cependant, il est possible que la dispersion natale s'effectue au-delà de cette échelle, ce qui rend la recapture des individus limitée puisque la surface à couvrir augmente.

Chez les adultes, les plus récentes études s'accordent pour estimer une forte fidélité au site de reproduction (Shutler et Clark, 2003 ; Winkler *et al.,* 2004). Les femelles primo-reproductrices affichent un taux de dispersion de 14 % alors qu'il diminue jusqu'à 2 % avec l'âge (Shutler et Clark, 2003). Une plus forte fidélité et une moins grande distance de dispersion notées pour les mâles se retrouvent également dans les études plus anciennes, avec par exemple 66 % de mâles fidèles au site contre 33 % des femelles (Cohen, 1985). Bien que ces premiers chiffres donnent les grandes tendances du comportement de dispersion de l'espèce, ces estimations issues de l'analyse des distances de dispersion n'ont pas inclus la détection imparfaite des individus, et les modèles CMR ont utilisé des données ayant subi des modifications

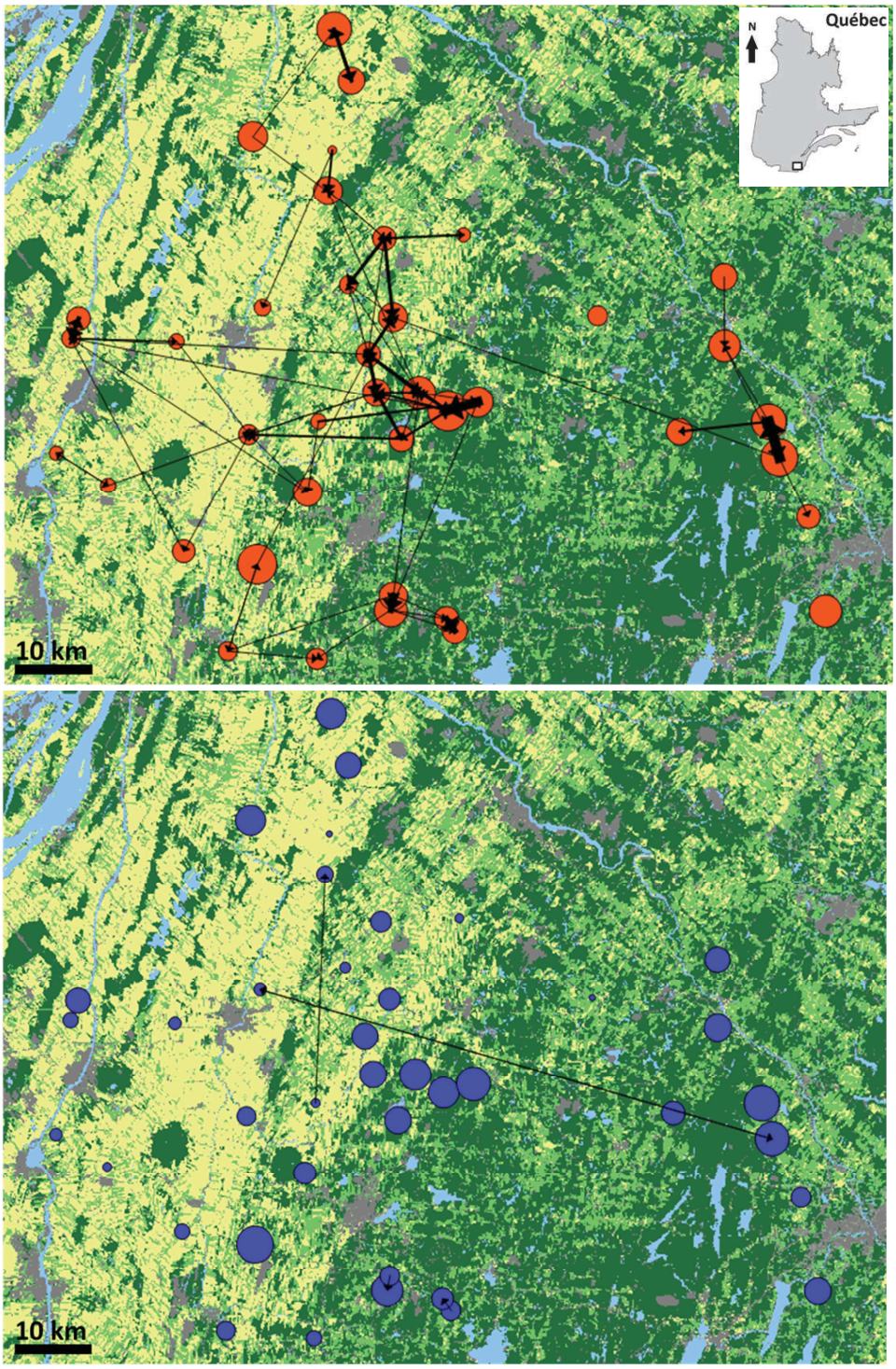
expérimentales (modification de la taille de couvée) pouvant altérer le comportement dispersif des individus. Il est donc fort possible que ces estimations soient biaisées.

L'espérance de vie maximale est de 8 à 12 ans, cependant dans la nature, l'âge moyen est de 2,7 ans (Butler, 1988). La survie apparente des adultes varie de 0,37 à 0,49 suivant la pollution des sites en biphényles polychlorés (BPC) ou en mercure (Custer *et al.,* 2007 ; Hallinger *et al.*, 2011). En milieux d'apparence non pollués, les taux de survie sont plus élevés et très proches entre les mâles et femelles (0,46 pour les mâles *vs.* 0,49 pour les femelles) (Hallinger *et al.,* 2011).

1.2.4. Le système d'étude

Située dans le Sud du Québec et recoupant la région de la Montérégie et de l'Estrie, l'aire d'étude couvre une superficie de 10 200 km² (Fig. 5). Elle est composée d'une mosaïque de paysages agroforestiers, composés majoritairement de cultures intensives (maïs, soja) le long du fleuve Saint Laurent et laissant progressivement place à des cultures de type extensif (pâturages, fourrages) au Sud-Est. La région centrale est composée d'un mélange équitablement distribué entre ces deux grands types de cultures. Au Sud-Est, la région forestière et vallonnée remplace les cultures intensives du Nord-Ouest. Sur l'aire d'étude sont implantés 400 nichoirs artificiels, à raison de 10 par exploitation agricole (ferme) afin de reconstituer les colonies recherchées par les hirondelles bicolores en milieux naturels (voir Ghilain et Bélisle, 2008 pour plus de détails sur le réseau de nichoirs). Actuellement, cette zone d'étude est la plus grande utilisée pour le suivi intensif de la reproduction d'un passereau migrateur. Les données de recaptures montrent une grande quantité de déplacements pour les femelles, en particulier à l'interface entre les cultures intensives, extensives et la zone forestière (zone centrale) où les fermes sont relativement proches les unes des autres (Fig. 5a).

(a)



(b)

Figure 5 : Recaptures des femelles (a) et des mâles (b) reproducteurs Hirondelle bicolore dans l'aire d'étude au sud du Québec. Chaque point représente la densité en individus recapturés au moins une fois sur l'exploitation agricole de baguage (de 2 à 40 recaptures sur le même site pour les

femelles, de 1 à 34 pour les mâles). Les flèches proportionnelles au nombre de flux, correspondent aux déplacements des reproducteurs entre deux sites (de 1 à 9 flux pour les femelles, seulement 1 flux pour les mâles). Assolement en fond de carte (jaune : milieu intensif correspondant aux cultures de soja, maïs, canola et céréales, vert clair : milieu extensif correspondant aux cultures biologiques, pâtures, fourrages, friches, vert foncé : forêt, bleu : eau, gris : urbain).

En revanche, des déplacements sur de plus grandes distances sont réalisés en Montérégie, alors que l'Estrie est moins connectée à la zone centrale et à l'Ouest. Les mâles sont quant à eux très peu mobiles, puisque malgré le grand nombre de recaptures, seulement cinq déplacements ont été observés sur dix années de suivi (Fig. 5b).

Initié en 2004, un suivi intensif de l'écologie de la reproduction des hirondelles bicolores nichant dans le Sud du Québec par des chercheurs de l'Université de Sherbrooke a permis de baguer jusqu'en 2013, 1459 femelles et 786 mâles reproducteurs et près de 8000 oisillons. Un suivi aux deux jours est effectué sur l'ensemble des nichoirs à partir du début mai pour documenter le taux d'occupation des nichoirs, l'évolution des couvées et la croissance de chaque oisillon. Pour chacun des nichoirs occupés par des hirondelles, la femelle est capturée pendant la phase d'incubation et le mâle pendant l'élevage des jeunes, ces derniers étant bagués à l'âge de 12 jours. La bague permet d'identifier les individus et de réaliser un suivi génétique, biométrique et parasitaire et éventuellement de faire l'assignation parentale, utile pour révéler le mâle génétique dans le cas de copulation hors couple. La richesse des données, incluant également plusieurs variables environnementales collectées sur chaque ferme aux deux jours (abondance et diversité d'insectes, pluviométrie et températures) ou à la fin de la reproduction (type d'assolement dans un rayon proximal de 500 m autour de chaque nichoir) permettent d'aborder l'étude de la survie et de la dispersion de l'Hirondelle bicolore avec une approche multidimensionnelle. De plus, avec un taux de recapture d'environ 30 % des individus bagués, le système est propice aux analyses de CMR.

1.2.5. Avantages de l'aire d'étude dans l'étude de la dispersion

Les aires d'étude des travaux antérieurs sur l'Hirondelle bicolore sont limitées de par leur superficie et la densité en nichoirs disponibles (e.g., Shutler et Clark, 2003 ; Winkler *et al*., 2004). Les nichoirs étant présents en grand nombre (72 nichoirs par km²) favorisent probablement la fidélité au site de par la grande disponibilité des sites de nidification, l'augmentation des interactions sociales, et un succès reproducteur relativement élevé et constant maintenu par le réseau artificiel de nichoirs. De fait, il est possible que les adultes se maintiennent à proximité des nichoirs occupés l'année précédente et que la fidélité au site soit surestimée. Dans notre système, la densité en nichoirs est jusqu'à sept fois moins importante que dans l'aire d'étude en Saskatchewan (Shutler et Clark, 2003). Les micro-colonies constituées au maximum de 10 couples, autorisent des dispersions de quelques kilomètres puisque les fermes sont espacées en moyenne de 7,28 ± 0,57 km de leur plus proche voisine. Cette répartition sur 40 fermes tend à reproduire d'une part des conditions moins artificielles, d'autre part à établir un éventuel gradient du succès reproducteur avec les variations paysagères (Ghilain et Bélisle, 2008), ce qui pourrait affecter la probabilité de disperser (Greenwood et Harvey, 1982 ; Johnson et Gaines, 1990).

La structure en micro-colonies est relativement avantageuse pour définir l'échelle de la dispersion. Dans notre cas, nous avons utilisé la ferme comme unité de fidélité au site. L'unité utilisée est justifiée du fait que la différence de probabilité de disperser s'effectue à l'échelle de la ferme, c'ets-à-dire moins d'un kilomètre autour du nichoir (Fig. 6).

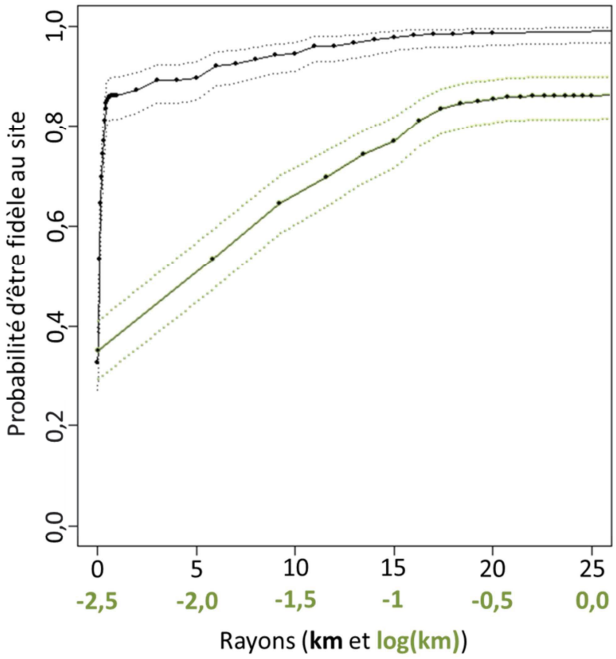


Figure 6 : Exploration du rayon de fidélité au site à considérer chez l'Hirondelle bicolore pour définir le seuil de la dispersion dans le système d'étude utilisé. Les probabilités de fidélité sont issues d'analyses CMR considérant le retour ou non dans un rayon donné autour du nichoir. L'échelle logarithmique rend compte du changement d'allure de la courbe à partir de 600 mètres, ce qui correspond au rayon définissant la superficie d'une micro-colonie (ferme regroupant 10 nichoirs).

Néanmoins, cette structure composée de 40 micro-colonies ponctuelles sur une aire d'étude aussi vaste permet des déplacements d'individus bagués d'une année à l'autre dans l'aire d'étude, mais à l'extérieur du réseau de nichoirs suivi. Cette supposition implique que des cavités naturelles ou des nichoirs chez des particuliers soient présents et fréquentés par les hirondelles bicolores. Une telle situation pourrait entrainer une surestimation de la mortalité ou une sous-estimation de la dispersion entre les fermes dans les modèles de capture-recapture. Les données opportunistes récoltées par les ornithologues et amassées sur le site internet eBird permettent de vérifier la présence de l'espèce et la quantité d'individus en dehors du réseau de nichoirs (Fig. 7).

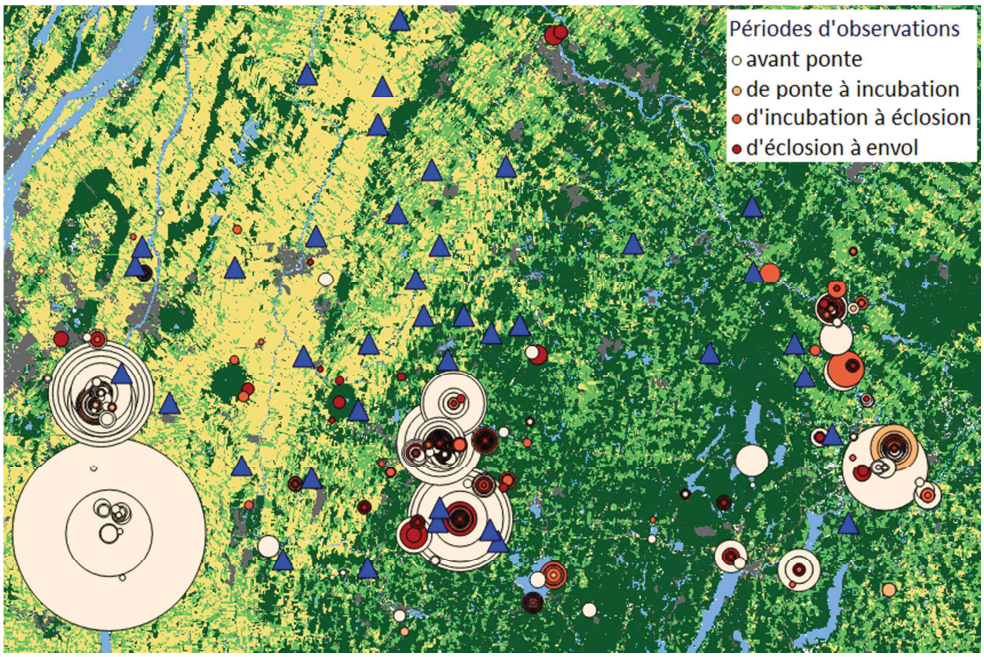


Figure 7 : Effectifs d'Hirondelle bicolore observés au Sud du Québec entre 2004 et 2013, pendant la période de reproduction (mai et juin) d'après les données eBird. Chaque triangle bleu localise une des exploitations agricoles appartenant au réseau de nichoir de l'Université de Sherbrooke. La surface des cercles est proportionnelle au nombre d'hirondelles bicolores observées (N de 1 à 1000) suivant la localisation et la période d'observations (basée sur les dates moyennes de ponte, d'incubation, d'éclosion et d'envol dans le réseau de nichoirs sur les dix années). Assolement en fond de carte (jaune : milieu intensif correspondant aux cultures de soja, maïs, canola et céréales, vert clair : milieu extensif correspondant aux cultures biologiques, pâtures, fourrages, friches, vert foncé : forêt, bleu : eau, gris : urbain).

Alors que chez les oiseaux nichant en cavité, le nombre de sites de reproduction en milieu naturel est souvent sous-estimé du fait de la difficulté à les détecter (voir Eadie et Gauthier, 1985 pour un exemple chez le genre *Bucephala*), le nombre de reproducteurs est probablement plus facilement estimable et détectable chez l'Hirondelle bicolore, du fait des déplacements aériens répétés des individus pour leur alimentation en milieu ouvert. Les observations rapportées sont principalement localisées près des cours et points d'eau, au sud de l'aire d'étude (milieu de cultures extensives) et en début de saison de reproduction. Entre le début (période du début mai à la date moyenne de ponte) et la fin de la reproduction (période de l'éclosion à la date d'envol des jeunes), le nombre d'observations diminue par deux alors que

les effectifs d'hirondelles observées diminuent d'un facteur dix. Cette forte diminution comparée au nombre d'observations peut traduire deux choses : un échec d'établissement pour la reproduction (les observations en début de saison représentent alors des individus non reproducteurs, en prospection de sites) ou un échec de reproduction au cours de la saison (menant à une désertion des sites avant la fin de la saison de nidification). Comparativement dans le réseau de nichoirs, le nombre de nichoirs occupés équivalent au nombre d'hirondelles en reproduction diminue de 1,6 entre ces deux périodes. Il est donc fort probable qu'en dehors du réseau de nichoirs, l'environnement soit moins favorable à la nidification de l'espèce, et par conséquent, que le nombre de reproducteurs hors réseau n'affecte pas drastiquement les estimations de dispersion et de survie.

1.2.6. Objectifs

Les objectifs du présent travail sont à la fois méthodologiques et écologiques. D'un point de vue méthodologique, nous avons vu que les méthodes de CMR ne sont pas encore adaptées pour les aires d'étude dont le nombre de sites de recapture est grand et d'autre part, que l'estimation de paramètres comme la survie ou la dispersion, dépendant de captures et de recaptures, ne peut s'étudier par une approche classique (analyse des distances par exemple) sans tenir compte de la détection imparfaite des individus dans le temps. Il a donc été question de développer un modèle CMR multi-évènement capable d'intégrer ce grand nombre de sites pour estimer les paramètres de survie et de dispersion de reproduction entre deux années consécutives chez l'Hirondelle bicolore. Ce modèle présenté dans le chapitre 2 est la base méthodologique des chapitres suivants.

D'un point de vue évolutif, les mécanismes de la dispersion chez les passereaux migrateurs sont encore peu connus, ni les mécanismes à l'origine du déclin des insectivores aériens, dont l'Hirondelle bicolore fait partie, et ce même si la perte d'habitat et la présence de polluants sont mis en cause. Pour y répondre, trois questions sont abordées au travers des chapitres 3 et 4.

1) Quelles variables environnementales affectent les composantes de la fitness (probabilité de survivre et succès reproducteur) des hirondelles et dans quelle mesure ?

2) Sachant que la dispersion de reproduction est une réponse adaptative à une diminution du succès reproducteur, quelle est la probabilité de disperser et qu'est-ce qui motive directement ce comportement ?

3) Enfin, suite à la dispersion, quels sont les sites de reproduction évités et les plus attractifs pour l'espèce ?

Le troisième chapitre vise à déterminer l'implication du succès reproducteur individuel (SRi) et du succès reproducteur des congénères (SRc) dans la décision à disperser. La contribution relative du SRi et du SRc dans la décision à disperser a été peu étudiée. Cette contribution relative n'a été quantifiée que chez le Gobemouche à collier, le Faucon crécerellette, *Falco naumanni*, et la Mouette tridactyle (Danchin *et al.,* 1998 ; Doligez *et al.,* 2004 ; Serrano *et al*., 2001). C'est dans un contexte CMR que j'ai abordé ce point, ce qui a permis de tenir compte du comportement dispersif de l'année précédente (effet mémoire) dans la décision à disperser l'année suivante. Cet aspect n'avait pas encore été étudié chez une espèce à courte durée de vie, où il n'est attendu ni une mémoire à long terme, ni la reproduction dans le temps d'un comportement dispersif décrit comme coûteux.

Enfin, un dernier chapitre aborde l'impact environnemental sur les traits individuels et le choix du site pour la reproduction. Puisque la dispersion est une réponse comportementale visant à améliorer la fitness, j'ai étudié l'effet de plusieurs variables environnementales sur la probabilité de survie, le SRi et la décision à disperser. Le choix du site d'établissement a été traité indirectement par le taux d'occupation de chaque ferme, en considérant que notre aire d'étude est représentative des divers milieux utilisés par l'Hirondelle bicolore dans les paysages agroforestiers Sud du Québec. Pour caractériser les divers milieux, trois types de variables ont été étudiés :

- L'environnement social, représenté par 3 variables à effet positif sur la fitness de l'individu : la densité en congénères sur une ferme, le nombre de partenaires disponibles pour les copulations hors couple et le SRc de l'année précédente.

- La disponibilité en ressources via le nombre de nichoirs disponibles, la présence du Moineau domestique comme compétiteur pour les nichoirs et la proportion de cultures intensives comme proxy de l'abondance alimentaire dans un rayon proximal (utilisé pour l'alimentation après l'éclosion) et distal (utilisé avant l'éclosion).
- Les caractéristiques individuelles comme le sexe, le SRi des femelles, ou le comportement dispersif de l'année antérieure.

Ce dernier chapitre apporte des éléments clés pour comprendre le fonctionnement de la dynamique de la population d'Hirondelle bicolore occupant l'environnement agricole hétérogène du Sud du Québec. C'est au travers de la discussion que j'aborderai l'aspect démographique et le rôle des agroécosystèmes pour la conservation de cette espèce.

CHAPITRE 2

ESTIMATING DISPERSAL AMONG NUMEROUS SITES USING CAPTURE–RECAPTURE DATA

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Modifié dans sa forme pour les besoins de la présente thèse

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Contribution des auteurs :
Paméla Lagrange, Marc Bélisle et Olivier Gimenez ont formulé la problématique, la mise en contexte et l'application du modèle.
Paméla Lagrange, Roger Pradel et Olivier Gimenez ont participé à la construction du modèle.
Paméla Lagrange a participé à la récolte des données pendant trois saisons de terrain et Marc Bélisle a assuré le soutien financier du programme.
Paméla Lagrange a rédigé la première version de l'article et tous les co-auteurs ont participé à la correction et l'amélioration de l'article.

Description de l'article :
Cet article présente une nouvelle méthode permettant d'analyser des données de recaptures dans une aire d'étude multi-site. Elle permet d'estimer les probabilités de disperser et de

survivre, qui sont des paramètres cruciaux pour l'évolution de la dynamique des populations. Jusqu'à présent, les méthodes utilisées en multi-site étaient contraintes par le nombre de sites de recaptures maximum à utiliser ou la nécessité de maîtriser des outils algorithmiques complexes. Le modèle ici développé est une alternative non limitée par le nombre de sites à considérer et capable d'être implémenté dans des logiciels faciles d'utilisation et fiables. En appliquant ce modèle au cas de l'Hirondelle bicolore, nous avons estimé les probabilités de disperser et de survivre avec précision, en révélant un effet jusqu'à présent peu mis en avant chez les espèces à courte durée de vie : l'effet du précédent comportement dispersif sur la décision à disperser. Ce chapitre est le support méthodologique des chapitres 3 et 4.

2.1. Abstract

Dispersal affects processes as diverse as habitat selection, population growth and gene flow. Inference about dispersal and its variation is thus crucial for assessing population and evolutionary dynamics. Two approaches are generally used to estimate dispersal in free-ranging animals. First, multisite capture-recapture models estimate movement rates among sites while accounting for survival and detection probabilities. This approach is however limited in the number of sites that can be considered. Second, diffusion models estimate movements within discrete habitat using a diffusion coefficient resulting in a continuous processing of space. However, this approach has been rarely used because of its mathematical and implementation complexity. Here, we develop a multievent capture-recapture approach that circumvents the issue of too many sites while being relatively simple to be implemented in existing software. Moreover, this new approach allows quantifying memory effects whereby the decision of dispersing or not on a given year impacts on the survival or dispersal likelihood of the following year. We illustrate our approach using a long-term dataset on the breeding ecology of a declining passerine in southern Québec, Canada, the Tree Swallow (*Tachycineta bicolor*).

Key-words: capture–recapture; dispersal; memory model; multi-event model; multisite model; site fidelity; southern Quebec, Canada; *Tachycineta bicolor*; Tree Swallow.

2.2. Introduction

Dispersal is a fundamental mechanism in ecology and evolution as well as a demographic process that affects the growth rate of populations and determines their spatial structure, particularly in fragmented habitats (Clobert et al. 2009). At the individual level, it reduces competition and provides opportunities to find new sites and ultimately to benefit from the best available habitats or mates while tracking favorable environmental conditions in a changing world (Ronce 2007). Regarding evolutionary dynamics, dispersal of individuals and the gene flow it can cause interact to constrain or facilitate adaptation (Garant et al. 2007). Assessing dispersal is thus a key step in conservation biology to understand extinction-colonization processes and population dynamics (Hanski 1999).

Fine scale abiotic and biotic features, such as habitat loss and fragmentation, individual productivity or conspecific and predator densities, can affect dispersal behavior and therefore genetic and demographic patterns of animal populations (Holderegger and Wagner 2008, Shanahan et al. 2011). Estimating dispersal within highly heterogeneous landscapes thus requires setting up a design with numerous monitoring sites to capture the influence of potentially important local features (Fernández et al. 2003).

Both indirect and direct methods exist to estimate dispersal in free-ranging populations. Indirect methods including techniques such as the measurement of isotope ratios incorporated in living tissues allow to determine the chronological suite of areas visited by an individual (Kendall and Nichols 2004). Analogously, the analysis of allele frequencies at different loci allows to assess the (relative) likelihood that an individual originates from a given population comprised within a set of putative sources (Rousset 2001). However, because these indirect methods make it possible to infer movements only among coarse regions or populations, they

prevent to quantify the influence of fine scale landscape heterogeneity on dispersal. Direct methods circumvent this drawback by marking individuals and "resighting" or recapturing them at known locations. These methods include the use of modern tracking devices, such as Argos-GPS platform transmitters, which can track individual movements with a high spatial resolution in real time but are financially expensive and generally too big or heavy to be fitted on small animals (Patterson et al. 2008). Another set of direct methods include the simple marking of individuals using bands or tags and are usually referred to as capture-recapture (CR) approaches (see Lebreton et al. 1992). Although the latter conveys much less information than the former, its cost affordability makes it the most widely used approach of both past and current animal population monitoring programs (Kendall and Nichols 2004). Here, we focus on CR methods that rely on banding programs to estimate dispersal while explicitly accounting for imperfect detection of individuals (Lebreton et al. 1992).

Two CR approaches are available to investigate dispersal in wild populations. In multisite CR models individuals can die, or survive and be recaptured as in standard CR models, but they can also move among sites according to probabilities of transition among geographical sites (Arnason 1973, Schwarz et al. 1993). However, this approach is computationally limited by the number of sites that can be considered since the number of transition parameters quickly increases with the number of sites (Lebreton and Pradel 2002). For example, with 2 sites, one would need to estimate 2 transition probabilities, 20 for 5 sites, 90 for 10 sites, etc. Alternatively a CR approach based on a diffusion model can be used to infer dispersal movements (Ovaskainen et al. 2008a, 2008b). However, biologists have rarely used this approach as it is mathematically complex (including the manipulation of differential equations) and requires a solid understanding of algorithmic tools for their practical implementation.

Here, we propose a new alternative to estimate breeding dispersal rate and site fidelity within a study area comprising many recapture sites. We develop a multievent CR approach (Pradel 2005) to circumvent the issue of too many transition probabilities in multisite CR models when the number of sites is large. More precisely, we categorize the state of an individual in a given year as being (1) in the same location as the year before or (2) in a different location. In

contrast with standard multisite CR models, a state here can correspond to several events, depending on whether an individual was seen in two consecutive years (or breeding events) in which case its state is known with certainty or in only one year in which case its state is uncertain. By doing so, dispersal and site fidelity can be estimated while accounting for mortality and imperfect detection as in multisite CR models, while coping with possibly numerous sites as in CR diffusion models. Moreover, the potential effect of behavior in a given year (i.e., staying *vs.* leaving a site) on survival or dispersal in the following year – a so-called memory effect – can also be investigated as with multisite CR models (Hestbeck et al. 1991, Brownie et al. 1993). Overall, our method relies on well-adopted CR models and is relatively simple to implement in existing software.

To illustrate our approach, we use a long-term data set on a migrating North American passerine, the Tree Swallow (*Tachycineta bicolor*). This secondary cavity nester is an aerial insectivore which typically occurs in open habitats near water (Winkler et al. 2011). As for most aerial insectivores, its population has been declining over a large part of its breeding range (Nebel et al. 2010, Shutler et al. 2012) and this, at alarming rates averaging 4.2 % per year between 1989 and 2009 in Québec, Canada (Shutler et al. 2012). Putative causes of this decline include a decrease in nesting site availability as well as the diminution of food resources and intoxication linked to agricultural intensification and widespread pesticide use. However, the exact mechanisms underlying the population decline of Tree Swallows and other aerial insectivores are still unknown (Nebel et al. 2010). Estimating dispersal among a large number of sites differing in habitat quality may help better understand this trend.

2.3. Materials and methods

2.3.1. A multievent Capture-Recapture model to estimate dispersal among numerous sites

Setting the scene with events and states

In multievent CR models, a distinction is made between events and states (Pradel 2005). An event is defined as the presence or absence of an observable character or symptom at each occasion in the encounter history of the individual. It is distinguished from the underlying, not necessarily observable state to which it is related by a probabilistic relationship (Pradel 2005, Gimenez et al. 2012).

Here, we consider seven states (Fig. 1) defined by combining the feature of interest, namely whether an individual occupies the same site as on the previous occasion (H for here) or not (E for elsewhere), with the information about whether it was captured or not on the previous and current occasions. The previous capture status is important because it partly determines the kind of events that are observable. Indeed, we are able to recognize if an individual moved or not only if it was observed on the previous occasion. The current capture also determines our ability to recognize whether the individual moved. Because in multievent models (and more generally in hidden Markov processes) only the information embedded in the state is carried over to the next occasion, the capture status at t - 1must be incorporated in the state to remain available at t where it is needed. For a similar problem and solution, see the treatment of trap-dependence by Pradel and Sanz-Aguilar (2012). We denote the composite states we are using by prefixing to the dispersal status (H or E) the previous capture status (+ if detected or o if not detected) and suffixing to it the current capture status (same notation). For instance, oH+ is for an individual in the same site at t and t - 1 (dispersal status H) that was not captured at t - 1 (prefix o) and captured at t (suffix +). When an individual is not captured at t, it does not matter whether it was captured at t - 1; in this case, we do not specify its capture status at t - 1. Thus, we retain the six composite states: Ho, oH+, +H+, Eo, oE+, +E+, to which we add the

state dead (D). Only four events appear in the capture histories. For individuals captured on both occasions, encode (1) if they occupied the same site on the two occasions and (2) if they occupied different sites; otherwise, encode (0) for individuals not captured at t and (3) for individuals captured at t but not at t - 1 (Fig. 1). Figure 2 provides an example of a capture history for an individual captured at several sites and the corresponding encoding of events and states.

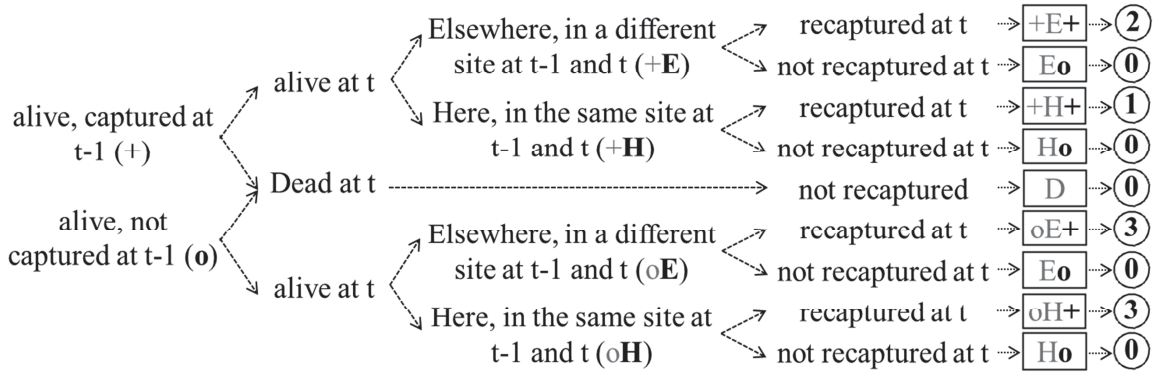

Figure 1: Transition steps of an individual from t - 1 to t and explanation of states associated with events. The diagram shows the steps leading to the observation (at t - 1 and t) of an individual: survival (alive or dead), fidelity (Here or Elsewhere) and recapture (recaptured or not). Each updated information appears in bold while the old one is grayed out. We end up in the last step with seven states (in boxes) that can generate four events (numbered rings). States are: Elsewhere and captured at t - 1 and t, Elsewhere and not captured at t (whatever the capture at t - 1), Here and captured at t - 1 and t, Here and not captured at t (whatever the capture at t - 1), Dead, Elsewhere and captured at t but not at t - 1, Here and captured at t but not at t - 1. Events are: not recaptured at t, recaptured at t and not recaptured at t - 1, recaptured at t in the same site as at t - 1, recaptured at t in another site as at t - 1.

Parameterization

We distinguish three successive transitions, that update in a stepwise fashion the information carried by the state taking place between times t - 1 and t: survival, fidelity and recapture. Survival comes first; then, site fidelity conditional on survival; and eventually, the recapture process at time t. For other examples of decomposition of transitions into several steps, see

Sanz-Aguilar et al. (2011) (skipping behavior) and Pradel and Sanz-Aguilar (2012) (trap-dependence).

When an individual is captured for the first time, its previous location, and thus its dispersal status, is unknown, but its previous and current capture statuses are known. Its state is either oE+ or oH+. With 1-π denoting the probability to be a disperser for a newly encountered individual, the probabilities of the initial states are as follows:

$$\textit{Initial states} = \begin{array}{c} \begin{array}{ccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{D} \end{array} \\ \begin{bmatrix} 0 & \pi & 0 & 0 & 1\text{-}\pi & 0 & 0 \end{bmatrix} \end{array} .$$

Later on, individuals will survive with a probability S (possibly dependent on their dispersal status). In the following matrix and afterwards, rows correspond to time t - 1, columns to time t, and the probabilities on the same row add up to 1. The departure state (in row) describes the situation at t - 1. Each time a status element is updated to its situation at time t, it becomes bold. At the end of the survival step, only the dead state is updated.

$$\textit{Survival} = \begin{array}{c} \\ \text{Ho} \\ \text{oH+} \\ \text{+H+} \\ \text{Eo} \\ \text{oE+} \\ \text{+E+} \\ \mathbf{D} \end{array} \begin{array}{c} \begin{array}{ccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \mathbf{D} \end{array} \\ \begin{pmatrix} S & 0 & 0 & 0 & 0 & 0 & 1\text{-}S \\ 0 & S & 0 & 0 & 0 & 0 & 1\text{-}S \\ 0 & 0 & S & 0 & 0 & 0 & 1\text{-}S \\ 0 & 0 & 0 & S & 0 & 0 & 1\text{-}S \\ 0 & 0 & 0 & 0 & S & 0 & 1\text{-}S \\ 0 & 0 & 0 & 0 & 0 & S & 1\text{-}S \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array} .$$

Survivors can go back to the same site (H) or move to another one (E). While in standard multisite CR, we would have as many transitions as pairs of sites, we opted for a more economical approach that considers the alternative: the individual did or did not change site; and expressed the probabilities of transition in terms of the probability of site fidelity F.

$$
\textit{Fidelity} = \begin{array}{c} \\ \text{Ho} \\ \text{oH+} \\ \text{+H+} \\ \text{Eo} \\ \text{oE+} \\ \text{+E+} \\ \text{D} \end{array}
\begin{array}{c}
\begin{array}{ccccccc} \mathbf{H}\text{o} & \text{o}\mathbf{H}\text{+} & \text{+}\mathbf{H}\text{+} & \mathbf{E}\text{o} & \text{o}\mathbf{E}\text{+} & \text{+}\mathbf{E}\text{+} & \text{D} \end{array} \\
\begin{pmatrix}
F & 0 & 0 & 1\text{-}F & 0 & 0 & 0 \\
0 & F & 0 & 0 & 1\text{-}F & 0 & 0 \\
0 & 0 & F & 0 & 0 & 1\text{-}F & 0 \\
F & 0 & 0 & 1\text{-}F & 0 & 0 & 0 \\
0 & F & 0 & 0 & 1\text{-}F & 0 & 0 \\
0 & 0 & F & 0 & 0 & 1\text{-}F & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\end{array} .
$$

For instance, a previously unobserved faithful individual at time t (state Ho, row 1) may remain faithful to its breeding site at time t (its dispersal status is then confirmed in bold in the first column Ho) or may change site (its dispersal status becomes Eo, column 4). Note that the fidelity probability can be made dependent on the dispersal status at time t thus allowing testing for a 'memory' effect in dispersal behaviour (F on the first three rows with dispersal status H distinct from F on the following three rows with dispersal status E).

Eventually survivors can be captured with a probability R at time t. In this last transition matrix, we introduce the capture status at time t as a suffix to the dispersal status and the capture status at time t - 1 (the suffix in the row state), if relevant, is now prefixed to the dispersal status.

$$
\textit{Recapture} = \begin{array}{c} \\ \mathbf{H}\text{o} \\ \text{o}\mathbf{H}\text{+} \\ \text{+}\mathbf{H}\text{+} \\ \mathbf{E}\text{o} \\ \text{o}\mathbf{E}\text{+} \\ \text{+}\mathbf{E}\text{+} \\ \text{D} \end{array}
\begin{array}{c}
\begin{array}{ccccccc} \text{H}\mathbf{o} & \mathbf{o}\text{H}\mathbf{+} & \mathbf{+}\text{H}\mathbf{+} & \text{E}\mathbf{o} & \mathbf{o}\text{E}\mathbf{+} & \mathbf{+}\text{E}\mathbf{+} & \text{D} \end{array} \\
\begin{pmatrix}
1\text{-}R & R & 0 & 0 & 0 & 0 & 0 \\
1\text{-}R & 0 & R & 0 & 0 & 0 & 0 \\
1\text{-}R & 0 & R & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1\text{-}R & R & 0 & 0 \\
0 & 0 & 0 & 1\text{-}R & 0 & R & 0 \\
0 & 0 & 0 & 1\text{-}R & 0 & R & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\end{array} .
$$

For instance, the individual that has remained faithful to its site but was not captured at time t - 1 (first row Ho), receives the state oH+ if it is captured at t (second column) because it was not captured at t - 1 (hence the prefix o), remained faithful at t to the site occupied at t - 1 (dispersal status H) and was just captured (suffix +). On the other hand, if the same individual

is not captured at t, it is uninformative whether it was captured at t - 1. It receives the state Ho (first column) meaning that it remained faithful (dispersal status H) and was not captured at t (suffix o).

The last step of multievent CR models links events to states. In our case, each state corresponds to only one possible event (but one event can correspond to several states) making the event probabilities trivial:

$$Event = \begin{array}{c} \\ Ho \\ oH+ \\ +H+ \\ Eo \\ oE+ \\ +E+ \\ D \end{array} \begin{array}{c} \begin{array}{cccc} \mathbf{0} & \mathbf{1} & \mathbf{2} & \mathbf{3} \end{array} \\ \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix} \end{array} .$$

Calculating the probability Pr of a capture history is straightforward. For instance, let us consider the first four occasions of the capture history illustrated in Figure 2 and composed of the following four events (i.e., 3120). For simplicity, let us also assume that all parameters are constant and that the animal did not die at the fourth occasion. As events 3 and 0 can be associated to different states, we have four scenarios to estimate Pr (3120): (oE+, +H+, +E+, Eo) or (oE+, +H+, +E+, Ho) or (oH+, +H+, +E+, Eo) or (oH+, +H+, +E+, Ho). The addition of these four probabilities gives: Pr (3120) $= [(1 - \pi)\ R^3.S^3.F(1 - F)^2.(1 - R)] + [(1 - \pi).R^3.S^3.F^2.(1 - F).(1 - R)] + [\pi.R^3.S^3.F.(1 - F)^2.(1 - R)] + [\pi.R^3.S^3.F^2.(1-F).(1-R)]$, which gives: $Pr(3120)=2.[S^3.R^3.(F-F^2).(1-R)]$.

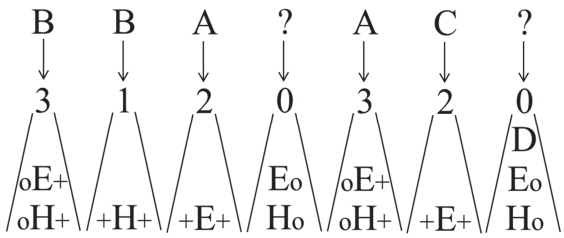

Figure 2: Example of a capture history. The top level lists the sites (letters) where individuals were captured; a question mark codes for "unknown" as the individual was not captured at this time step. The intermediate level provides the encoding of the capture history in terms of events. The bottom level displays the corresponding sequence of states.

Goodness of fit (GOF) and model selection

GOF tests are not yet developed for multievent models (Pradel et al. 2005). We therefore resorted to GOF tests for standard CR one-site models (Pradel et al. 2005) as implemented in program U-CARE (Choquet et al. 2009a). To do so, we simplified our dataset by using only recaptures (coded 1) or non-recaptures (coded 0) of individuals (Sanz-Aguilar et al. 2011). This approach is conservative because in doing so we test a coarser model than the one we will be able to fit. If some lack-of-fit occurs, inference tools (standard errors, confidence intervals and AIC values) can be adjusted by using a coefficient of overdispersion $\hat{c}$.

Models were built and fitted using maximum-likelihood methods in program E-SURGE (Choquet et al. 2009b). Details can be found in the Supplement Material (Appendix). Model selection was based on the Akaike information criterion corrected for small samples and overdispersion ($QAIC_c$; Burnham and Anderson 2002).

2.3.2. Application

Species and study sites

Breeding Tree Swallows are easily captured and manipulated, and tolerate high levels of nest disturbance, making them an exemplary model for studies in natura (Winkler et al. 2011). CR

data were collected as part of a long-term study assessing the influence of spatiotemporal environmental heterogeneity on the breeding ecology of Tree Swallows in southern Québec, Canada (Ghilain and Bélisle 2008). The study was initiated in 2004 and the CR data include recaptures until 2011, which represents 1999 individuals ringed and captured at least once as breeders of which 33 % were males. The study area covers approximately 10,200 km² and includes 40 farms (sites) separated by an average (± 1 SD) distance to the near farm of 7.28 ± 0.57 km and a pairwise distance of 42.21 ± 21.09 km within a gradient of agricultural intensification. Each farm bears a transect composed of 10 nest boxes spaced by 50 m for a total of 400 nest boxes. Aside from these nest boxes, there are very few alternative nesting sites (i.e. natural cavities or nest boxes) in the study area. Although Tree Swallows defend a territory of a few meters around the nest, foraging during the chick-rearing period extends over a radius of a few hundred meters (Dunn and Hannon 1992, Dunn and Whittingham 2005). We thus used a 500-m radius to define the spatial scale of "nest box colonies" located on the farms of the study area (Ghilain and Bélisle 2008). The farm thus determines the basic unit to define site fidelity (Here = captured on the same farm as the previous year), or otherwise dispersing to another site (Elsewhere = captured on a farm different from that of the previous year).

Effects on demographic parameters

We investigated the effect of time and sex on recapture (R) and survival (S) probabilities as well as that of memory on fidelity (F) probability through a sequential model selection procedure. R, S and F were assessed in turn, while holding the most general structure on the two other parameters. At each step, the best parameterization of the focal parameter expressed through the model with the lowest $QAIC_c$ was selected to proceed with the next parameter. Regarding R, capture effort was relatively constant between years for females but may have varied for males between years. Moreover, males are targeted and captured mostly during the chick-rearing period whereas females are captured throughout the breeding season according to our protocol. Similarly, we tested the effect of time and sex on S since males are expected to survive better than females in passerines (Siriwardena et al. 1998) or the opposite in

swallows (Siriwardena et al. 1998, Hallinger et al. 2011). Lastly, we focused on F for which we investigated a sex effect to verify empirical evidence of a higher dispersal propensity for females in passerines (Greenwood and Harvey 1982, Winkler et al. 2011). Besides, we considered a memory effect to assess the potential dependence of dispersal on the previous biological state (H or E). Additive effects and interactions were considered, hence resulting in a total of 13 candidate models (Table 1). To accommodate model selection uncertainty, we resorted to model averaging to calculate parameter estimates and their associated unconditional standard errors (SE) based on $QAIC_c$ weights (w_i) using models for which $w_i \geq 0.01$ (Burnham and Anderson 2002). Except where noted, estimates are presented with their standard error.

2.4. Results

We detected a lack of fit of the most complex model we fitted to the data (global test: $chi^2 = 47.06$, df = 31, P = 0.03). A closer inspection showed that this was due to a transience effect in females (component 3SR in Choquet et al. 2009a: $chi^2 = 27.81$, df = 6, $P < 0.001$), which was accounted for by using a coefficient of overdispersion ($\hat{c}$) of 1.52. Models with $w_i > 0.01$ suggested an effect of time on recapture probability, of memory and sex on fidelity, and of time and sex on survival, with some uncertainty on the type of effect (interaction or additive effect) on fidelity and survival (Table 1).

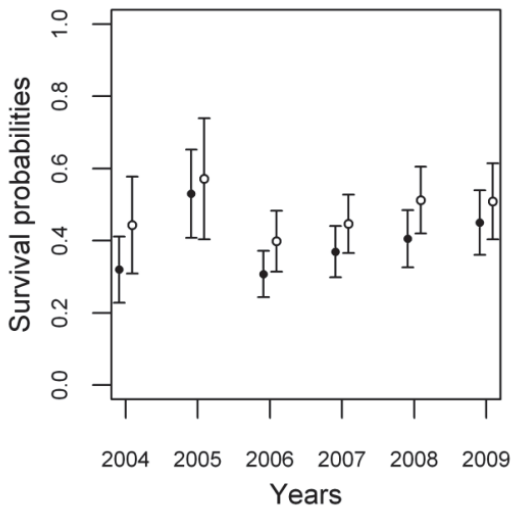

Figure 3: Model-averaged annual survival probability (± 1.96*unconditional SE) for female (filled circle) and male (circle) Tree Swallows breeding in southern Québec, Canada. Note that survival over the last time interval was not estimable.

As expected, males showed a stronger site fidelity than females. Indeed, fidelity was estimated at 0.94 ± 0.04 for males and 0.70 ± 0.10 for females when a dispersal event occurred the year before, and at 0.99 ± 0.01 for males and 0.94 ± 0.02 for females otherwise. Survival probability for females was lower than male survival and varied over time from 0.31 ± 0.03 to 0.53 ± 0.06 for females and from 0.40 ± 0.04 to 0.57 ± 0.09 for males (Fig. 3).

Recapture probabilities varied between 0.58 ± 0.07 and 0.86 ± 0.09. Finally, initial probabilities were estimated at 0.51 ± 0.23 in state Here, suggesting an equal proportion of individuals in each state at first capture. The high level of imprecision associated to this estimate is caused by the memory integrated in the state: when an individual enters in the population for the first time, it is impossible to define its state because the location of the previous year is unknown. This does not distort the other estimates as fidelity rates.

Table 1: Model selection examining the effect of sex, memory and time on demographic parameters of Tree Swallows breeding in southern Québec, Canada. Each model is defined by three parameters: survival probability (S), site fidelity probability (F) and recapture probability (R). The effects were tested alone, in addition (+) or in interaction (*) including the main effects. A constant parameter is represented by a dot. The number of parameters (k) and deviance were used to calculate the $QAIC_c$ (with a ĉ = 1.52) and weight (w_i) of each model. $\Delta QAIC_c$ gives the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest $QAIC_c$).

Models	*k*	Deviance	$QAIC_c$	Δ $QAIC_c$	w_i
S(sex+time) F(memory+sex) R(time)	19	4306.18	2871.28	0.00	0.37
S(sex+time) F(memory*sex) R(time)	20	4304.23	2871.73	0.45	0.30
S(sex*time) F(memory*sex) R(time)	24	4293.92	2873.36	2.08	0.13
S(sex*time) F(memory*sex) R(sex+time)	25	4292.10	2874.20	2.92	0.09
S(sex) F(memory*sex) R(time)	14	4328.10	2875.58	4.30	0.04
S(time) F(memory*sex) R(time)	18	4316.63	2876.12	4.84	0.03
S(sex*time) F(memory*sex) R(.)	19	4315.27	2877.25	5.97	0.02
S(sex*time) F(memory*sex) R(sex)	20	4314.86	2879.01	7.73	0.01
S(.) F(memory*sex) R(time)	13	4339.33	2880.95	9.67	0.00
S(sex*time) F(memory*sex) R(sex*time)	29	4339.33	2880.95	9.67	0.00
S(sex+time) F(sex) R(time)	17	4329.32	2882.45	11.17	0.00
S(sex+time) F(memory) R(time)	18	4344.97	2894.77	23.49	0.00
S(sex+time) F(.) R(time)	16	4374.83	2910.36	39.08	0.00

2.5. Discussion

We developed a multievent CR model to estimate site fidelity and dispersal within and among numerous recapture sites, thereby allowing to further quantify the influence of fine-scale spatiotemporal heterogeneity on these behaviors within landscapes of large extents. The widely used multisite CR modeling approach to estimate dispersal is limited in the number of sites that can be considered as it explicitly considers all possible transitions among all sites. As a consequence, these models are highly demanding in terms of data to accurately estimate the parameters (Lebreton and Pradel 2002), and even impossible to implement in practice if the number of sites is too high. For instance our case study would have implied >1500 transitions among the 40 farms. By considering only two states (Here and Elsewhere) depending on the

site occupied at t - 1 and t, this issue was circumvented therefore allowing the reliable and accurate estimation of site fidelity and dispersal among sites. Compared to the complex CR diffusion approach developed by Ovaskainen et al. (2008a, b), our proposal is a convenient and relatively easy method to implement in order to quantify dispersal in a large study area with numerous recapture sites.

Our case study with Tree Swallows illustrates well the benefits of using multievent CR methods to estimate survival and breeding dispersal rates among numerous sites. In our study area, adult males showed a higher mean survival rate than adult females in most years (0.40-0.57 *vs*. 0.31-0.53), a result that contrasts with apparent survival rate estimates reported in Saskatchewan (0.51 for both sexes; Shutler and Clark 2003), Massachusetts (0.40-0.48 for females; Custer et al. 2007), and Virginia (0.45-0.46 *vs.* 0.46-0.49; (Hallinger et al. 2011), where no sex difference or a slightly higher survival rate for adult females were found. This result warrants more attention as adult females in our study system have shown a significant decrease in body mass between 2005 and 2011 that may be indicative of the presence of an ecological stress that impacts females more strongly than males (Rioux-Paquette et al., unpublished manuscript). Despite also showing a greater inter-annual variability, which may result from a greater number of years, most of our yearly estimates fall within the 0.40-0.50 range reported elsewhere, at least for males. Regarding breeding dispersal, we found dispersal rates that were higher for females than for males as in previous studies on Tree Swallows (Shutler and Clark 2003, Winkler et al. 2004) and other species (Greenwood and Harvey 1982). If we ignore the memory effect, we obtain dispersal rates similar to those found in New York State (females *vs*. males: 0.15 *vs.* 0.02 and 0.14 *vs.* 0.04 in Québec and New York, respectively). Yet, the spatial configuration of nestbox networks varies considerably among studies and such comparisons should be made cautiously.

Our method also revealed individual heterogeneity suggesting that some phenotypes may be more predisposed to disperse than others. Although some evidence of phenotype-dependent dispersal propensity is starting to accumulate (Clobert et al. 2009), memory effects on dispersal have mostly been reported in long-lived bird species (Hestbeck et al. 1991). Our case

study provides the first evidence that such a phenomenon may occur in short-lived bird species. Being able to assess such individual heterogeneity in dispersal behavior is important given that it has the potential to strongly influence the dynamics of spatially-structured populations (Leimar and Norberg 1997, Clobert et al. 2009, Cote et al. 2010).

Our model can be extended to study dispersal into more details. For example, the decision to disperse between breeding seasons is often associated with breeding success (Greenwood and Harvey 1982). Such an influence of individual annual breeding success on the decision to stay or leave a breeding site could be assessed by, for instance, considering the following states: Here after successful reproduction, Here after failed reproduction, Elsewhere after successful reproduction, and Elsewhere after failed reproduction. Analogously, our model could be modified to assess if dispersal propensity is constrained by the structure of the landscape in which sites are embedded ("Here" to illustrate after breeding in a highly connected landscape, otherwise "Elsewhere"; Bélisle 2005). While this would imply amending the coding of events, these new models would allow estimating dispersal easily and precisely.

Although the case study dealt with birds, our approach can be used to investigate dispersal of any organisms amenable to CR monitoring protocols. For example, Casula (2006) addressed the determinants of fine-scale dispersal behavior of butterflies within a multisite CR framework but had to restrict his analyses to a subset of four sites, a constraint that could have been avoided with our approach. Another instance where our approach would be particularly relevant is the study of rodent movement behavior, which is usually conducted within trapping grids containing a large number (in the hundreds) of traps (sites), such as when addressing the infestation dynamics of a pathogen (Begon et al. 2003).

Despite the potential of our approach, it comes with some limitations. The first lies in the coding of the data that can be tedious since one needs to consider the previous capture to determine each event. This step can nevertheless be made less cumbersome via some programming (see the R script provided in Supplement). Second, in contrast with Ovaskainen's et al. approach, it cannot explicitly make use of the distance (Euclidean,

intervening landscape structure or functional connectivity) between recapture sites to improve dispersal estimates. As a consequence, the fact that dispersal between two close or connected sites is more likely to happen than between two distant or "disconnected" sites is informative in estimating dispersal (Bélisle 2005) but cannot be used in our approach. It remains that dispersal distance is constrained by the position of recapture sites. Indeed, dispersal rates are likely to be overestimated when recapture sites are too close, and underestimated if too distant as individuals are forced to remain on their site. For this reason, we emphasize that our model should be used only when the extent of the study area and the distance among recapture sites are greater and inferior than the mean dispersal distance of the species of interest, respectively. Moreover, the spatial scale defining sites, and thus dispersal events, must be clearly specified and taken into account when comparing dispersal rates among studies in order to avoid biases resulting from mismatched spatial scales. Third, the way we have defined the states puts an emphasis on behavior (staying *vs.* leaving) rather than explicitly using the site of departure or arrival. This is particularly problematic for models incorporating a memory effect in which we cannot discriminate if an individual dispersed between the two same sites from t - 1 to t + 1 or moved to a new site at each time step (i.e., visited three different sites). Biologically, the former behavior would suggest fidelity with occasional movements caused by unavailable breeding sites, while the latter would characterize the phenotype of a disperser likely to play a role in extinction-colonization processes among local populations. The solution would be to build a model distinguishing sites already visited from first capture to t from those new at t + 1. In conclusion, we developed a CR model to estimate fidelity and dispersal in finely spatially described landscape. The main feature of our method relies on well-adopted CR models and is relatively simple to implement in existing software. We hope this new approach will provide new insights in the mechanisms underlying dispersal in free-ranging populations.

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CHAPITRE 3

RELATIVE CONTRIBUTION OF PERSONAL AND SOCIAL INFORMATION IN DRIVING BREEDING DISPERSAL OF FEMALE TREE SWALLOWS: A CAPTURE-RECAPTURE APPROACH

Mise en page pour une première soumission dans *The American Naturalist*

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<u>Contribution des auteurs :</u>

Paméla Lagrange, Marc Bélisle et Olivier Gimenez ont formulé la problématique, la mise en contexte et l'application du modèle.

Paméla Lagrange, Roger Pradel et Olivier Gimenez ont participé à l'ajustement du modèle.

Paméla Lagrange a participé à la récolte des données pendant trois saisons de terrain et Marc Bélisle, Dany Garant et Fanie Pelletier ont assuré le soutien financier du programme.
Blandine Doligez, Dany Garant et Fanie Pelletier ont contribué à l'orientation du travail à l'enrichissement de la discussion.
Paméla Lagrange a rédigé la première version de l'article et tous les co-auteurs ont/auront participé à la correction et l'amélioration de l'article.

Description de l'article :
Il est communément admis que l'échec de reproduction d'un individu motive la dispersion vers un autre site à la prochaine reproduction. Cependant, peu d'études ont porté sur la contribution relative du succès reproducteur individuel et de celui des congénères dans la décision à disperser. L'article ci-dessous porte sur ce point en utilisant le modèle de capture-recapture décrit dans le chapitre 2. Nous avons montré que l'information portée par les congénères concernant leur productivité en jeunes à l'envol, n'a pas d'effet sur la décision à disperser. Ces résultats vont à l'encontre des patrons de dispersion chez d'autres espèces d'oiseaux. Nous discutons ces résultats en explorant plusieurs pistes à la fois biologiques et méthodologiques.

1.1. Abstract

Breeding dispersal is a key process of population structure and dynamics and is often triggered by an individual's breeding failure. In colonial and territorial birds, reproductive success of conspecifics (RSc) can also lead individuals to change breeding sites after a global failure on a site. Yet, few studies have investigated the relative contribution of individual reproductive success (RSi) and of RSc on dispersal decision. Here, we develop a framework to disentangle the effects of RSi and RSc on demographic parameters, while accounting for imperfect individual detection and other confounding factors such as age or dispersal behavior in the previous year. Using a 10-year dataset composed of 1595 banded tree swallows, Tachycineta bicolor, we assessed the effects of non-manipulated RSi and RSc on female breeding dispersal

in this semi-colonial passerine. Dispersal was strongly driven by RSi, but not by RSc. Unsuccessful females were 9.5 to 2.5 times more likely to disperse than successful ones, depending if they had dispersed or not in the previous year, respectively. Unsuccessful females were also three times less likely to be detected than successful ones. Because detection of individuals was driven by RSi, which was positively correlated to RSc, assuming a perfect detection as in previous studies may have lead us to conclude that RSc affected dispersal patterns. Our approach corrected for this bias and shown that dispersal decision is driven by RSi and dispersal behavior of the previous year.

Key-words: capture-recapture data, dispersal, multievent model, reproductive success, social information, Tree Swallow.

1.2. Introduction

Dispersal is a key process underlying movement between populations or sites and thereby, plays a key role in population structure and dynamics as well as evolution (Clobert et al. 2001). This behavior is inherent to habitat selection and thus strongly determines the survival and reproductive success of individuals (Bowler and Benton 2005). Such habitat choice implies a varying quality among breeding sites and that individuals can perceive and collect reliable information about their quality (Switzer 1993; Doligez et al. 2004a). Information about sites quality can be obtained from environmental attributes, such as food availability (Ward 2005) or predator density (Clobert et al. 2001; Ward 2005), as well as from social factors, such as density (Stamps 1988; Betts et al. 2008), body condition or reproductive success of conspecifics (Brown et al. 2000; Dall et al. 2005; Wagner and Danchin 2010). To be adaptive, site choice also implies that breeding site quality be predictable over some time (Switzer 1993; Doligez et al. 2003). Several cues must be collected through some form of prospection during the previous breeding occasion (year) or just before the onset of reproduction to decide whether or not to disperse (Clobert et al. 2001; Doligez et al. 2004a). Prospection is particularly well developed in non-breeders or unsuccessful breeders, which

tend to prospect neighboring sites more than successful breeders (Boulinier and Danchin 1997; Dittmann et al. 2005; Ward 2005).

Individuals can select breeding sites based on their own experience, such as their individual reproductive success (RSi) (i.e., personal information; Switzer 1997; Danchin and Cam 2002), or rely on inadvertent social information that consists of cues about the performance of others like the reproductive success of conspecifics (RSc) (i.e., public information, Boulinier and Danchin 1997; Danchin et al. 2004). In birds, the number and condition of offspring, typically fledglings, are likely the most important cues because they represent the best proxy of the reproductive success obtained by individuals at a given site (Doligez et al. 2003). Many empirical studies have shown the importance of RSi on the decision to disperse or to remain in the same site for successive breeding seasons: individuals with a higher RSi tend to be more philopatric (Greenwood and Harvey 1982; Johnson and Gaines 1990; Hoover 2003). Like RSi, RSc can affect the decision rules driving dispersal. Indeed, in some colonial seabirds, raptors and certain territorial passerines, individuals were more likely to disperse with a decreasing RSc (Serrano et al. 2001; Doligez et al. 2002; Parejo et al. 2007). Birds were also more likely to settle or settled at a higher rate on sites that presented a high RSc in the previous year than on sites that then showed a low RSc (Doligez et al. 2004b; Ward 2005; Calabuig et al. 2008). However, few empirical studies on birds have jointly assessed the relative importance of RSi and RSc on dispersal decisions (Boulinier and Danchin 1997; Danchin et al. 1998). The most comprehensive assessment of RSi and RSc effects on dispersal decisions was conducted by Danchin et al. (1998) on black-legged kittiwakes, *Rissa tridactyla*, a colonial, cliff-nesting seabird. This study showed that individual breeding performance did not affect the probability of changing cliffs for birds breeding on cliffs showing a high RSc, but that an individual's breeding failure increased the probability to disperse when breeding on cliffs showing a poor RSc. Because the recapture probability was close to 1 between breeders and non-breeders in the above study system (Cam and Monnat 2000), the conclusions reached by Danchin et al. (1998) using logistic regressions, while assuming a perfect detection of individuals between years, are likely to hold. Nevertheless, none of the other studies that addressed the role of RSc

on dispersal decisions have considered the potential biases on dispersal probability estimates that may result from an imperfect detection of marked individuals (Gimenez et al. 2008).

In this study, we assess the relative importance of RSi and RSc on the breeding dispersal decision of female tree swallow, *Tachycineta bicolor*. Like most studies that addressed the role of RSi on dispersal in birds, a previous analysis about tree swallows dispersal found that females were more likely to disperse (28 % *vs.* 5 %) when they failed to fledge at least one young (Winkler et al. 2004). Yet, as most other bird dispersal studies, that analysis assumed perfect detection and may thus subject to provide biased dispersal probability estimates. Moreover, the effect of RSi on tree swallows dispersal decisions may have been confounded by that of RSc, which has never been investigated in this species despite its semi-colonial breeding habits. We thus adapted a multi-event Capture-Recapture model (Lagrange et al. 2014) to quantify the relative effects of RSi and RSc on the decision to disperse in female tree swallows while accounting for imperfect detection. Our approach allowed us to test the prediction that the likelihood of dispersal increases as RSi decreases, especially at low RSc, and thereby to assess the potential of RSc to override the effect of RSi on dispersal decisions as observed in Danchin et al. (1998).

1.3. Materials and methods

1.3.1. Model species

The tree swallow is a passerine that feeds upon flying insects on the wing and which form loose colonies during the breeding season (Dunn and Hannon 1991; Winkler et al. 2011). Both sexes, but particularly males, are territorial and defend an area up to about 30 m from their nest (Muldal et al. 1985; Robertson and Rendell 1990). Males arrive first on the breeding grounds to secure a nest site (i.e., a natural tree cavity or nest box) and most (94 – 99 %) are faithful to their previous breeding site (Winkler et al. 2011). Females show a lower fidelity

probability to their nest site (70 % – 94 %; Lagrange et al. 2014). Extra-pair young are found in up to 90 % of nests, and compose on average about half of the young produced, despite social monogamy (Dunn et al. 1994, Lessard et al. 2014). Neighboring resident males generally sire less than 70 % of extra-pair young and females have been found to obtain copulations from males nesting up to 15 km from their own nest (Dunn et al. 1994; Kempenaers et al. 2001; Lessard et al. 2014). In our study area, females lay commonly 4 to 7 eggs and 65 % of nests produce at least one fledgling with an average (± SD) of 4.0 ± 1.5 fledglings per successful nest (Ghilain and Bélisle 2008). Once fledged, young of the year may explore nest sites for breeding in the following year (Chapman 1935). There is little information about adults prospecting in tree swallow but it is assumed that subadult female floaters gather information at the end of the breeding season (Stutchbury and Robertson 1987). During prospection, individuals can assess the density of both cavities and conspecifics as well as the level of breeding success experienced by conspecifics through the presence of nest material, eggs, young, feces, or dead nestlings in cavities (Nocera et al. 2006). Supporting evidence for the use of such information by tree swallows was found by Ghilain and Bélisle (2008) as well as by Robillard et al. (2013). Indeed, the likelihood that a nest box be occupied in a given year increased with the fledging success that occurred in that box in the previous breeding season. Moreover, this result could not be explained by the philopatry of the previous occupants alone.

1.3.2. Study area

We studied the dispersal of tree swallow within a network of 40 farms (hereafter sites) distributed within a 10,200-km² gradient of agricultural intensification in southern Québec, Canada (see Ghilain and Bélisle 2008 for additional details on the study system; Fig. 1). Each site was separated from the nearest one by an average distance (± SD) of 7.28 ± 0.57 km. The high levels of parental assignments obtained in our study area which presents very high rates of extra-pair copulations suggests that very few natural cavities or nest boxes offered alternative nesting sites outside of the nest boxes we provided (Lessard et al. 2014). We have

been monitoring closely the breeding activities of tree swallows on the 40 sites since 2004, banded 1595 breeding females by 2012 and included in this paper birds recaptured until 2013 through our intensive marking campaign. Each site comprised 10 nest boxes aligned along a single field margin and spaced by 50 m to prevent territorial competition. The first and last nest boxes were thus separated by 450 m, the distance up to which tree swallows are assumed to forage during the chick-rearing period (McCarty and Winkler 1999). Given this, we considered each cluster of 10 nest boxes (i.e., the farm) as the spatial unit for studying site fidelity. Between 2004 and 2013, an average of 2.25 ± 2.49 sites per year were not occupied by tree swallows.

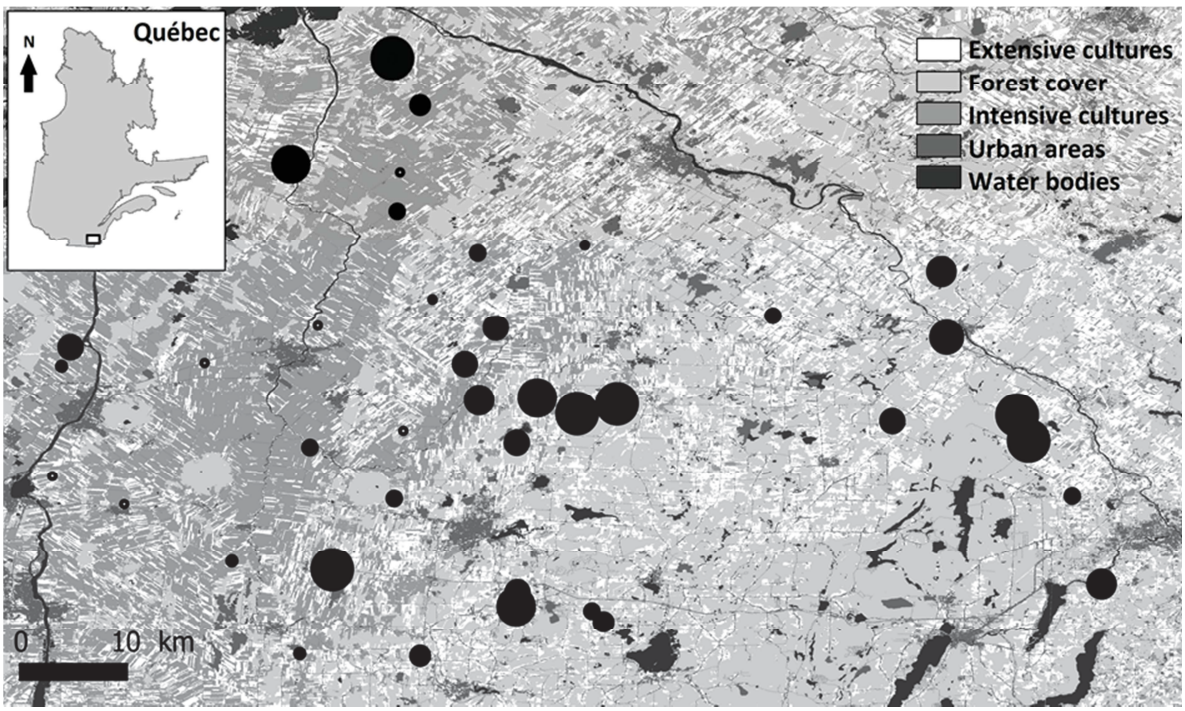

Figure 1: Study area of the 40 farms monitored in Québec for the reproduction of tree swallows, with the total number of fledglings since 2004 on each farm (number of fledglings in a black disk proportional from 59 to 313 fledglings, and fixed size below 58 fledglings). Land cover types were based on a mosaic of classified Landsat-TM satellite images (Canadian Wildlife Service 2004) by pooling cultures detailed in the Base de données des cultures assurées 'BDCA' et généralisées 'BDCG' (Financière agricole du Québec).

1.3.3. Definition of RSi, RSc and other variables

Previous empirical studies used either the number of fledglings produced by a female as a proxy of RSi (Beletsky and Orians 1987; Part and Gustafsson 1989; Schaub and Von Hirschheydt 2009), or simply discretized that number into at least one fledgling (good RSi) or no fledgling (bad RSi) (Doligez et al. 1999; Naves et al. 2006). In our study area, females either failed to fledge any young (42.59 % ± 14.01 % of females annually) or produced an average of 4.23 ± 1.41 fledglings per year between 2004 and 2013 (Fig. A1). Given this bimodal frequency distribution of the annual number of fledglings produced per female, we opted for the latter option inasmuch as our Capture-Recapture approach requires that reproductive success be coded as a qualitative variable defining reproductive state. To eliminate potential bias of intra-annual dispersal on the estimate of inter annual dispersal and the assessing of RSi, we excluded second nesting attempt of our analyses (10 % of clutch).

We first assessed the RSc of a given site as the number of nest boxes that produced at least one fledgling within that site on a given year. A site was then categorized as being bad if its RSc was lower or equal to the median RSc calculated across all sites occupied by tree swallows on a given year. Alternatively, it was categorized as good if its RSc was greater than the population median. Between 2004 and 2013, an average (± SD) of 4.61 ± 0.78 nest boxes per site produced at least one fledgling on a yearly basis, and between 38 % and 53 % of sites were characterized as showing a bad RSc depending on year. The RSc must be predictable from year to year to be used by individuals as an index of a site's reproductive quality (Danchin et al. 1998). We therefore estimated the level of temporal autocorrelation in RSc across years based on the working correlation matrix of generalized estimating equations (GEEs; Agresti 2002). Specifically, the annual RSc of sites (good/bad) was modeled as a constant in GEEs with a logit link function and binomial error structure. Given that RSc measures were spatially structured and longitudinal, the site acted as a clustering variable and the working correlation matrix was autoregressive. The GEEs were fitted in R 3.0.2 (R Development Core Team 2013) using the package geepack 1.1.6 (Halekoh et al. 2006).

To limit biases when estimating the effects of RSi and RSc on dispersal probabilities, we took into account the influence of the age and previous dispersal behavior of an individual on its likelihood to disperse using Capture Recapture analyses. As the age of individuals is linked with reproductive success and has been found to affect dispersal in various bird species, including tree swallows (Steven 1978; Bouwhuis et al. 2012), we distinguished females in their first reproduction (i.e., second year birds or SY) from more experienced ones (i.e., after second year birds or ASY) based on plumage (Hussell 1983). We also considered a "memory" effect (sensu Hestbeck et al. 1991) whereby individuals dispersing in the previous year may show a higher dispersal probability than faithful individuals at t - 1, as previously shown to occur in tree swallows from this system (Lagrange et al. 2014).

1.3.4. CR analyses

Definition of the multievent model

We used a multievent Capture Recapture model (Pradel 2005) to study dispersal among numerous sites as developed in Lagrange et al. (2014). Our model comprised 25 states that conveyed information about the location of each individual (whether it occupied the same site as on the previous breeding/capture occasion or not) as well as information about whether the individual was captured or not on the previous and current breeding occasions (Fig. B1). The capture status at $t - 1$ was required in the state because it partially conditions the event at t (see e.g. events 1 and 9 in Figure B1) and, by construction of multievent CR models, only information present in the state at t may be used to predict the event at t. In turn, it is important to distinguish whether the capture status at $t - 1$ is known because then the dispersal status may be known (i.e. event 1). We also added to the state information about RSi and RSc at t to evaluate their impact on future dispersal. We denoted the composite states by prefixing the dispersal status ('H' for here, occupying the same site or 'E' for elsewhere, occupying a different site) with the previous capture status ('+' if detected or 'o' if not detected at t -1) and suffixing it with the RSc ('b' if the site showed a bad RSc at t or 'g' a good one), the RSi ('b' if the individual had a bad reproduction at t or 'g' a good one) and the current capture status

(‘+’ if detected or ‘o’ if not detected at *t*). For instance, oHgb+ is for an individual that bred in the same site at $t - 1$ and t (dispersal status ‘H’), that was not captured at $t - 1$ (prefix ‘o’), experienced a good RSc at t (first lower-case letter ‘g’), had a bad RSi at t (second lower-case letter ‘b’) and was captured at t (suffix ‘+’). When an individual was not captured at t, it did not matter whether it was captured at $t - 1$; in such case, we did not specify a capture status at $t - 1$ for that individual. Thus, we retained the following 24 composite states: +Egg+, oEgg+, Eggo, +Egb+, oEgb+, Egbo, +Ebg+, oEbg+, Ebgo, +Ebb+, oEbb+, Ebbo, +Hgg+, oHgg+, Hggo, +Hgb+, oHgb+, Hgbo, +Hbg+, oHbg+, Hbgo, +Hbb+, oHbb+, Hbbo, to which we added the state dead (D). A total of 13 events corresponding to the deducible field observations appeared in capture histories (Fig. B1). We assigned (0) to individuals not captured at t. For individuals captured on both occasions and that occupied different sites between the two occasions, we assigned (1) if individuals had a good RSc and RSi, (2) if they had a good RSc and a bad RSi, (3) if they had a bad RSc and a good RSi, (4) if they had a bad RSc and RSi. For individuals captured on both occasions and occupying the same site on the two occasions, we assigned (5) if individuals had a good RSc and RSi, (6) if they had a good RSc and a bad RSi, (7) if they had a bad RSc and a good RSi, (8) if they had a bad RSc and RSi. For individuals captured at t but not at $t - 1$, we assigned (9) if individuals had a good RSc and RSi, (10) if they had a good RSc and a bad RSi, (11) if they had a bad RSc and a good RSi, and (12) if they had a bad RSc and RSi.

Parameterization steps

Transitions between t and $t + 1$ involved five steps that gradually updated the information carried by the state. These steps allowed to estimate parameters about apparent survival (S), fidelity (F), transition between RSc (C), transition between RSi (I) and recapture (R). The matrix for each type of parameters is detailed in the appendix B2. When first captured, the dispersal status of an individual cannot be known, but its RSi, RSc and current capture status are. Parameter π denotes the probability that an individual was captured for the first time in each of these initial states: oEgg+, oEgb+, oEbg+, oEbb+, oHgg+, oHgb+, oHbg+ or oHbb+. From its initial state, an individual can survive with probability (S), or die with probability

(1 – S). When an individual survives at *t*, it can return at *t* + 1 to the same site it occupied at *t* with probability (F), or disperse to another site with probability (1 – F). The model then estimates the probability (C) that an individual experiences different RSc between *t* and *t* + 1, or the same RSc between these two breeding occasions (1 – C). Note that C is independent of F because an individual can be faithful to a given site between two consecutive years while the RSc of that site can change. Similarly, the model goes on to estimate the probability (I) that an individual obtain a different RSi between *t* and *t* + 1, or the same RSi between the two breeding occasions (1 – I). In the last step of the transition between *t* and *t* + 1, the probability to be captured (R) or not (1 – R) at *t* (corresponding to the suffix of the dispersal status) in each state is estimated. In the last matrix of our multievent model, we linked events and states. Note that one event could correspond to several states, but that each state could only correspond to a single event (Fig. B1). Consequently, the probability of an event giving the state is 1 or 0.

Model selection and tested variables

We used goodness-of-fit (GOF) tests to assess transience and trap dependence. Because GOF tests are not yet developed for multievent models (Pradel et al. 2005), we had to rely on those intended for standard CR unisite models and implemented in program U-CARE (Choquet et al. 2009a). This implied that we had to simplify events by using only recaptures (coded 1) or non-recaptures (coded 0) of individuals (Sanz-Aguilar et al. 2011). Standard errors, confidence intervals and AIC values were adjusted for overdispersion, whenever detected, using the coefficient of overdispersion $\hat{c}$ following Burnham and Anderson (2002).

Given the numerous potential model structures resulting from the large number of parameters, and of states and variables potentially influencing those parameters, we used a model selection procedure that established a model structure one step at a time in order to reduce model selection uncertainty. Because no study examined the movement of tree swallows in a CR context before, we opted to establish model structures starting with the parameterization step having the least to the one having the most relevance regarding the questions addressed by our

study, namely R, C, I, S, and F. We defined a list of competing models for each step where parameters may vary with the effects of memory, RSi, RSc, or a combination of those as main effects or interactions, as well as the effects of time or age as main effects (Appendix C). For instance, starting with parameters in step R, we compared competing models whose structure varied in line with specific predictions (see Table 1), while keeping the other parameters (i.e., those included in steps C, I, S, and F) constant. The "best" model from this initial list was identified as the one showing the lowest Akaike information criterion corrected for small samples and overdispersion ($QAIC_c$; Burnham and Anderson 2002). The initial list of models was then augmented by adding time or age effects to the best model from that list (Appendix C, Table C1). The "best" model structure from the extended list of competing models was finally retained for R before repeating the same procedure with the next step of interest, here C. When the best model structure had been found for all parameterization steps, we conducted a second round of model selection whereby the evidence relative to the hypotheses concerning parameters included in step S, and then I, was reassessed (Table 1), but this time with the model structures for the other types of parameters identified in the previous round of model selection (Table C2). This second round allowed calculating the Akaike weight for each model i (w_i) having a structure already determined for all parameters (i.e., all models of the second round and models of step F of the first round; Table 2). In this way, w_i were not affected by the constant structure of a non-defined step in the first round of model selection. We display model-averaged parameter estimates and their unconditional standard errors (noted ± SE) based on the $QAIC_c$ and w_i (Burnham and Anderson 2002). All models were implemented in program E-SURGE (Choquet et al. 2009b).

Table 1: List of the predicted effects tested on parameter of recapture (R), transition between a good/bad conspecifics reproductive success (C), transition between a good/bad individual reproductive success (I), survival (S), fidelity (F) for the model selection and parameterization of each parameter.

Parameters	Effects	Predictions
R	i	No element affects the recapture probability.
	'RSi'	Recapture is higher if a female is successful at producing fledglings because there are more occasions to capture her.
	t	Recapture success varies over the time.
C	i	Probability of females transiting from bad to good RSc is constraint to be equal to probability to transit from good to bad RSc.
	'RSc'	Females transit from bad to good RSc differs from transit in the opposite direction.
	t	Females transit irregularly over time at the same rate both ways.
I	i	Probability of females transiting from bad to good RSi is constraint to be equal to probability to transit from good to bad RSi..
	'RSi'	Females have a variable RSi from one year to another.
	'RSc'*'RSi '	Females with a bad RSi at t are more likely to have a good RSi at t + 1 when RSc is good than when it is bad.
	'memory'*'RSi'	1) Assuming that dispersal responds to a bad RSi, dispersers should improve their RSi compared to faithful females.
		2) Assuming that dispersal is costly, dispersers with a good RSi have more chance to have a bad RSi than the faithful females.
	t	Females transit irregularly over time at the same rate both ways
	age	Young females without experience have more chance to transit from a bad to a good RSi than females ASY.
S	i	No element affects the survival probability.
	'memory'	Females dispersing have a smaller probability to survive than faithful individuals because they are exposed to more unknown risks.
	'RSi'	1) RSi is a proxy of the individual condition and we supposed females with a good RSi survive more than females with a bad RSi.
		2) RSi is a cost and female with a good RSi survive less than females with a bad RSi.
	t	Survival varies over the time.
	age	SY females should have a lower survival than ASY females because cost of reproduction is higher for SY than for ASY.
F	i	No element affects fidelity probability.
	'memory'	Dispersal behavior is reproducible: females dispersing at t - 1 disperse more than the faithfuls at t - 1.
	'RSi'	Females with a good RSi is more faithful than females with a bad RSi.
	'RSc'	Females on a farm with a bad RSc disperse more than females on a farm with a good RSc.
	t	Fidelity varies over the time.
	age	Young females SY disperse more than females ASY.

1.4. Results

RSc was strongly and positively autocorrelated across years (r = 0.70 ± 0.06). This result supports the assumption that RSc was predictable in space and time, and thus could potentially act as a determinant of dispersal decisions in our system.

1.4.1. Goodness-Of-Fit

Goodness-of-fit tests indicated a lack of fit of the general model to the data (χ^2 = 68.22, df = 35, $p < 0.001$). Although no trap-dependence was detected, a transience effect was found, especially for SY females (χ^2 = 30.04, df = 6, $p < 0.001$). Because survival was lower for SY than for ASY females (χ^2 =21.19, df = 7, p = 0.03), SY females were less likely to be recaptured than ASY ones. This lack of fit was accounted for by an age effect in our models. We corrected for the overall remaining lack of fit by using a variance inflation factor $\hat{c}$ = 1.94.

1.4.2. Model selection

The basic parameter structure obtained through the first selection indicated an effect of RSi on R, S, and F, an effect of RSc on I, a memory effect on F, and no time or age effects (Appendix C1). Results of the "nuisance" parameters (R and C) from the first selection are as follow.

First round: estimates of C, R

Recapture (R): The model including an RSi effect ($model_{14}$) showed a $QAIC_c$ 52.7 points lower than the constant model ($model_{11}$). As expected, a female with a good RSi was recaptured with a higher probability (0.99 ± 0.00) than a female with a bad RSi (0.32 ± 0.06). These probabilities appeared constant across years ($\Delta QAIC_c$ for $model_{18}$ *vs*. $model_{14}$ = 4.68).

Transition between RSc (C): The probability of breeding two consecutive years on a site exhibiting a good RSc (0.81 ± 0.03) was nearly twice as high as that of breeding two consecutive years on a site with a bad RSc (0.44 ± 0.06). Time had no effect on this parameter ($\Delta QAIC_c$ for $model_{22}$ *vs*. $model_{20}$ = 12.26).

Second round: estimates of I, S, F

The second round of model selection (Appendix C2) was initiated based on the "best" model identified in the first round of selection, namely $model_{55}$ ($QAIC_c$ = 4265.80). None of the models considered in that second round performed better than $model_{55}$ (w_{55} = 0.36), thereby lending support to the parameter structure obtained for F in the first round. Few models obtained an empirical support equivalent (i.e., $w_i > 0.05$) to that of $model_{55}$ (Table 2).

Table 2: Selected models for the model averaging (w_i ≥0.01) examining the effect of RSi, RSc, memory, age and time on the main demographic parameters (S, F, I) of tree swallows.

Models	*k*	Δ $QAIC_c$	w_i	#
S(RSi) F(RSi*memory) I(RSi*RSc) C(RSc) R(RSi)	22	0.00	0.36	55
S(RSi*memory) F(RSi*memory) I(RSi*RSc) C(RSc) R(RSi)	24	0.91	0.23	S44
S(RSi*age) F(RSi*memory) I(RSi*RSc) C(RSc) R(RSi)	24	1.95	0.14	S49
S(RSi) F(RSi*memory*age) I(RSi*RSc) C(RSc) R(RSi)	24	2.48	0.10	63
S(RSi) F(RSi*memory+t) I(RSi*RSc) C(RSc) R(RSi)	30	3.02	0.08	61
S(RSi) F(RSi*memory) I(RSi*RSc*memory) C(RSc) R(RSi)	26	3.83	0.05	I30
S(RSi+t) F(RSi*memory) I(RSi*RSc) C(RSc) R(RSi)	30	5.84	0.02	S47
S(RSi) F(RSi*RSc*memory) I(RSi*RSc) C(RSc) R(RSi)	26	7.22	0.01	58
S(RSi) F(RSi) I(RSi*RSc) C(RSc) R(RSi)	18	7.47	0.01	53

Notes: Other parameters conserved the basic structure with an effect of RSi on R, and no effect on C (as in #55, table C1). On S, F, I, the effects were tested alone, in addition (+) or in interaction (*) including the main effects. *k* is the number of parameters of each model used to calculate weight (w_i) and the $\Delta QAIC_c$ ($\hat{c}$ = 1.94) giving the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest: $Model_{55}$, $QAIC_c$ = 4265.80, deviance = 8227.94). # is the number of the model.

Transition between RSi (I): The likelihood that females kept the same RSi in two consecutive years varied with the RSc experienced in the first of these two breeding events, as indicated by all of the models that were retained after the second round of model selection (Table 2).

Dispersal behavior in the previous year was, however, not a clear determinant of I (w_{I30} = 0.05; Table 2). After breeding on a site characterized by a good RSc, females were less likely to keep a bad RSi in the second of two consecutive years (0.44 ± 0.10) than those that bred on a site with a bad RSc (0.82 ± 0.08; Fig. 2). Conversely, females had a higher probability of keeping a good RSi after breeding on a site that showed a good RSc (0.62 ± 0.05) than after breeding on a site with a bad RSc (0.34 ± 0.07).

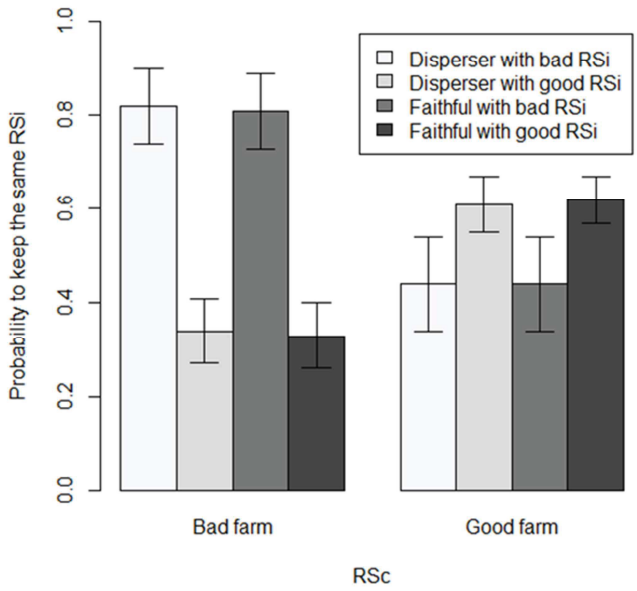

Figure 2: Probability to keep the same individual reproductive success (RSi) between two years according to the conspecifics reproductive success (RSc) on the farm, the previously dispersal behavior of the female and the RSi. Estimates come from averaged model (± SE) of the CR analysis.

Survival (S): Females obtaining a good RSi were more than twice as likely to survive to the next breeding season than females with a bad RSi (Fig. 3). Although the influence of RSi on apparent survival probability may depend on the age of females (w_{S49} = 0.14; Table 2), this dependency was marginal and SY females showed a survival probability only 0.01 lower than ASY females (Fig. 3). However, the dispersal behavior exhibited by females in the previous year modulated the influence of RSi on survival probabilities (w_{S44} = 0.23; Table 2). Indeed,

females that obtained a good RSi after dispersing in the previous year were less likely to survive to the next breeding season than faithful ones (SY: 0.50 ± 0.06 *vs.* 0.54 ± 0.06; ASY: 0.51 ± 0.05 *vs.* 0.54 ± 0.05), while when they had a bad RSi, they survived equally well (albeit at a much lower probability) whether they had dispersed in the previous year or not (SY: 0.22 ± 0.04 *vs.* 0.21 ± 0.04; ASY: 0.23 ± 0.04 *vs.* 0.22 ± 0.03). Although a time effect was included in a model selected for model averaging (i.e., w_{S47} =0.02; Table 2), apparent survival probability estimates barely varied across years.

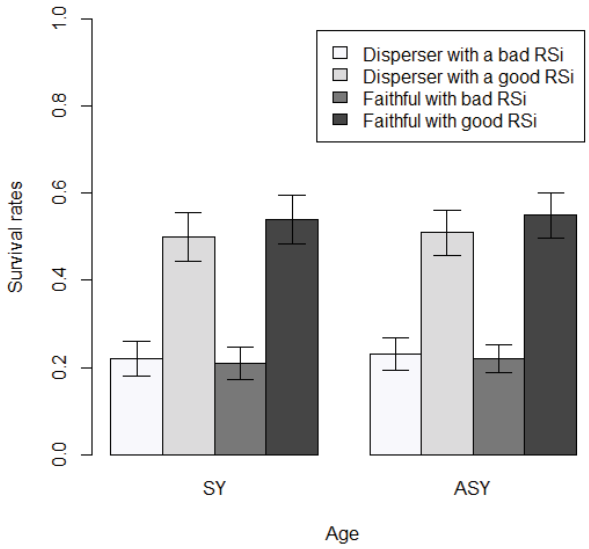

Figure 3: Probability to survive (apparent survival) at t according to the age (two classes: second year (SY) or after second year (ASY)), the previous dispersal behavior and individual reproductive success. Estimates come from averaged model (± SE) of the CR analysis.

Fidelity (F) and Dispersal: All but one of the models (i.e., $model_{53}$) implied in the multimodel inference provided support for the hypothesis that dispersal probabilities are affected by RSi and that this effect depends upon the dispersal behavior of the female in the previous year (Table 2). In contrast, only one model suggested that RSc could affect dispersal probabilities (w_{58} = 0.01; Table 2). Age and time effects were only contained in models that received moderate support from the data (age: w_{63} = 0.10 and time: w_{61} = 0.08; Table 2). According to model-averaged parameters, females that experienced a bad RSi after having dispersed in the

previous year were thirty times more likely to disperse than faithful females that obtained a good RSi (0.61 ± 0.13 *vs.* 0.02 ± 0.02; Fig. 4). Females with a bad RSi that did not disperse in the previous year and females with a good RSi that dispersed in the previous year showed similar and intermediate dispersal probabilities (0.19 ± 0.12 *vs.* 0.24 ± 0.05). Dispersal probabilities were relatively constant across years and age did not affect the probability of dispersal (Fig. 4).

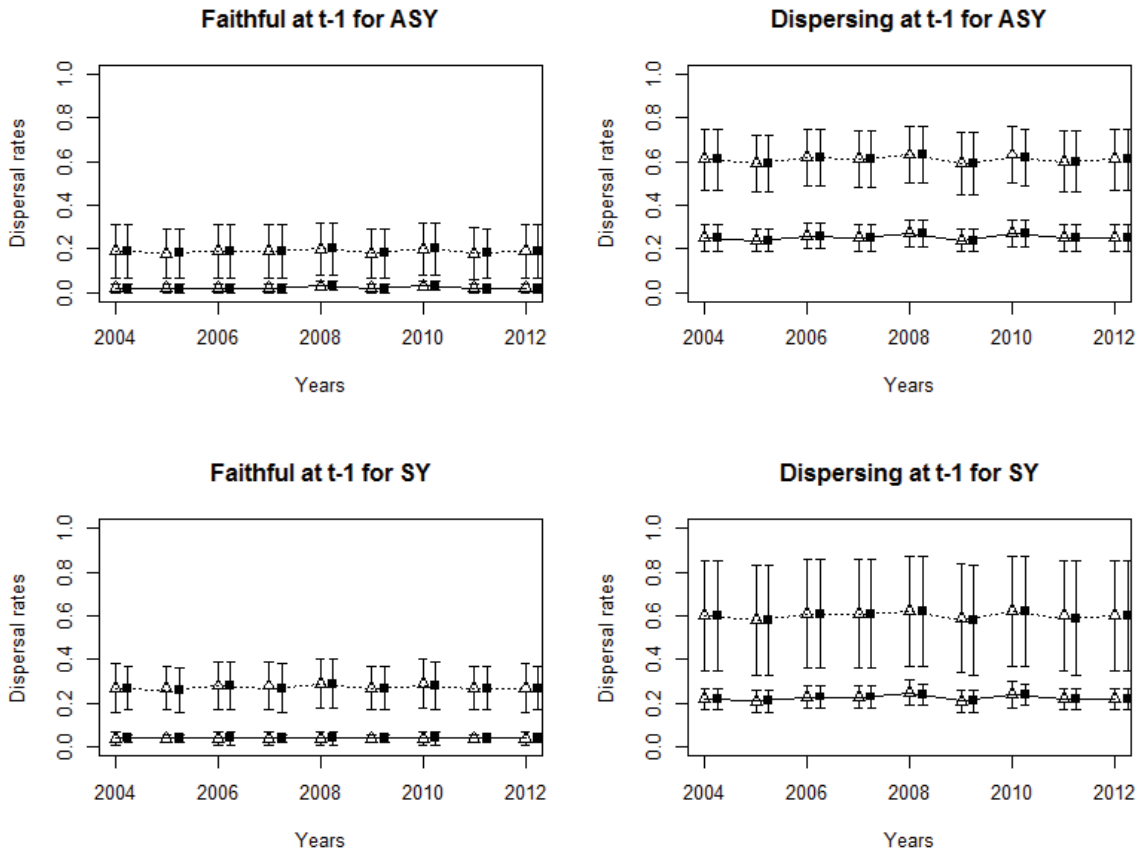

Figure 4: Dispersal probabilities of tree swallows from 2004 to 2012 in Québec according to individual reproductive success (RSi), conspecifics reproductive success (RSc), the age (second year (SY) or after second year (ASY)) and the previous dispersal behavior (faithful or dispersing) with the CR analysis. Estimates come from averaged model (± SE) of the CR analysis. RSi appears in lines (continuous for good RSi, dotted for bad RSi), RSc in the form of point (empty triangles for good RSc, black squares for bad RSc).

1.5. Discussion

Our results agree with the plethora of empirical studies suggesting that female birds are more likely to disperse after experiencing a breeding failure, a behavior expected to improve the odds of finding a better mate or breeding site for the next breeding event (Greenwood and Harvey 1982; Johnson and Gaines 1990; Hoover 2003). On the other hand, we found no evidence to suggest that female birds modulate their decision to disperse on the basis of the breeding success of surrounding conspecifics (RSc). Yet theoretical and empirical work suggested that reproductive failure of conspecifics should promote dispersal, especially when individuals experience a breeding failure themselves and (site-specific) RSc is temporally autocorrelated (Boulinier and Danchin 1997; Danchin et al. 1998). Given that our study system met this latter condition and that we used a Capture-recapture approach that limits potential biases when estimating dispersal probabilities (unlike previous studies that assessed RSc effects on dispersal; e.g., Doligez et al. 1999; Serrano et al. 2001), our results suggest that the value and use of RSc as public information to guide dispersal decisions are likely dictated by multiple ecological determinants if this cue is indeed used.

Female tree swallow that failed to fledge at least one young were 2.5 to 9.5 more likely to disperse than females that succeeded at fledging at least one young whether they dispersed or not in the previous year, respectively. Our results contrast with those of Shutler and Clark (2003) showing that tree swallows breeding dispersal among 115 nest boxes separated between 30 m and 3.8 km from one another (< 1 km between nest box clusters) was not driven by RSi (defined as the number of fledglings). Such a discrepancy may result from the fact that these authors considered dispersal as a change of nest boxes between two consecutive breeding events, implying that dispersal could occur at a much smaller spatial scale than within our multisite system. Moreover, Shutler and Clark (2003) manipulated RSi either by increasing or decreasing the clutch size of females and may thereby have affected the perception of reproductive success by females. On the other hand, our results agree with those of Winkler et al. (2004) who worked in a multisite context within an heterogeneous landscape,

but of a much smaller spatial extent than our study system (6 main sites of 22-131 nest boxes each and < 25 km apart; neighboring boxes spaced by 20 m). They observed that females failing to fledge any young dispersed more often than those which bred successfully (i.e., 28 % *vs.* 5 %). The methodological and conclusion discrepancies among studies about tree swallow dispersal emphasize the importance of landscape structure and extent when defining what constitutes a dispersal event and thus, when determining at which spatial scale it occurs and how it is affected by RSi.

Our study also provides an opportunity to shed some light on how tree swallows may perceive or use its RSi when making decisions about dispersal. As a first assessment, we removed RSc from the CR analysis, which allowed us to consider RSi into three classes: no fledgling (null RSi), number of fledglings inferior to the yearly median of brood with at least one fledglings (medium RSi), and number of fledglings superior or equal to the yearly median of brood with at least one fledglings (high RSi) as in (Schaub and Von Hirschheydt 2009) and Bötsch et al. (2012). Dispersal probability did not vary between the medium and high RSi classes (Fig. D1) and Capture-Recapture models performed better based on $QAIC_c$ values when the medium and high RSi classes were merged together (Appendix C3). Tree swallows thus appear to respond to a crude estimate (complete failure *vs.* ≥ 1 fledgling) of their reproductive success when basing their dispersal decisions unlike Barn Swallows, *Hirundo rustica,* nevertheless appear capable of gauging with more precision their breeding success and use this information to decide when dispersing as they show intermediate dispersal probabilities when experiencing a medium RSi (Schaub and Von Hirschheydt 2009). One avenue to explore for explaining variations in the perception or use of RSi to base dispersal decisions in closely related species may be to compare their life history traits such as clutch size or being single or multiple brooded as in tree and barn swallows, respectively.

The lack of effect of RSc on dispersal we observed contrasts with the influence that this variable has on the breeding dispersal probability of another passerine, the Collared Flycatcher, *Ficedula albicollis*, which is a second-order cavity nester just like the tree swallow. Indeed, low RSc promote dispersal defined as a change of woodland between

successive breeding events in females of this forest bird (Doligez et al. 1999). Although both species are migratory and defend territories restricted to the immediate surroundings of their nest sites, tree swallows differ from collared flycatchers by being semi-colonial (Robertson et al. 1986; Winkler et al. 2011). This latter aspect however likely cannot be used to explain the difference between our results and those of Doligez et al. (1999) as the other studies that found an effect of RSc on dispersal involved the colonial black-legged Kittiwakes (Danchin et al. 1998) and Lesser Kestrels, *Falco naumanni* (Serrano et al. 2001). The lack of RSc effect on dispersal we observed is also surprising given that the different breeding sites (farms) varied (substantially) in relative quality and that site quality was predictable to some point across breeding events, two conditions that must be met for RSc to influence dispersal (Danchin et al. 1998; Doligez et al. 1999). Yet, the quality of the best breeding sites was more predictable than that of poor ones (Fig. A2). Although such variation in predictability among sites differing in quality much likely reduces the value of RSc as public information (Switzer 1993, 1997), how much variation in predictability, whether sites differ in quality or not, is needed to impair decision making with respect to dispersal remains to be explored (Doligez et al. 2003; Lecomte et al. 2008).

We defined RSc based on the number of nest boxes that produced at least one fledgling within a given site (farm) on a given year, a measure that turned out to be associated with the density of breeders on the site ($r = 0.80$). This definition can be an indicator of expected number of potential sexual partners and reproductive success, inasmuch as dominant or healthy individuals should tend to gather in good sites, but also provide information about expected levels of competition or other detrimental effects such as parasitism (Brown and Brown 1986; Doligez et al. 1999). Whether such opposite density-dependent effects may have biased our results on female breeding dispersal is unclear. Indeed, although high breeder density has been found to promote dispersal in males and site fidelity in females of some species (e.g., Doligez et al. 1999), no clear general trend of density-dependent dispersal has been found for birds (Matthysen 2005). Yet, nest box occupancy in our study system (61 % ± 15) was such that intraspecific nest-site competition is unlikely to have played a significant role, as it was exceptional that all nest boxes of a given site were occupied on any given year (Robillard et al.

2013). Also, defining the RSc based on the proportion of nest boxes that produced at least one fledging (good site = proportion higher or equal to the yearly median) instead of on the number of nest boxes that fledged at least one young did not affect the decision of tree swallows to disperse or not (see model selection in Appendix C4). This being said, it appears clear that more studies focusing on the potential cues used by individuals to base their dispersal decisions are needed, especially given that these cues and effects may vary according to the species, sex and condition of individuals as well as in a nonlinear fashion with breeder density (Doligez et al. 2003).

The influence that RSc can have on dispersal decision making is likely modulated by movement constraints that could restrict site prospection. Indeed, travel costs, and thereby distance among resource patches, have the potential to impede movements, and in turn disrupt habitat sampling and selection (Bernstein et al. 1988; Beauchamp et al. 1997; Bélisle 2005). In our system, sites (farms) were distant from one another by 42.2 ± 21.1 km on average (pairwise mean distance ± SD), and the distance to the nearest site averaged 7.3 ± 3.5 km, with probably few alternative, natural or artificial breeding sites beside those provided by our nest box network. Under such conditions, tree swallows may not have had the opportunity to compare the quality of their breeding site with that of several other sites, especially given that they initiate their southward migration rapidly after fledging their young (Burke 2014). Although tree swallows are vagile early in the breeding period (Dunn and Whittingham 2005; Lessard et al. 2014), distance and time constraints could explain why the site-specific proportion of nest boxes producing at least one fledgling did not affect their dispersal decision. Studies showing the adaptive advantage of prospection and public information use as means to improve breeding success through dispersal are accumulating (Badyaev et al. 1996; Schjørring et al. 1999; Pärt and Doligez 2003; Dittmann et al. 2005; Pärt et al. 2011). Albeit, how landscape structure (i.e., the spatial distribution of potential breeding sites and the composition and configuration of intervening habitats) and the travel costs it may impose on individuals affect dispersal decisions is a research area still in its infancy (Stamps et al. 2005; Zollner and Lima 2005).

Although RSc did not affect the decision to disperse, it probably influenced the settlement decision of female tree swallows. Indeed, 69 % of the females were initially captured on a good site (based on RSc). Moreover, the probability that a female moved from a good site to a bad one in subsequent years was lower than the probability it stayed in a good site (0.19 *vs.* 0.81). Analogously, the probability that a female transited from a bad site to a good one was higher than the probability that it stayed in a bad site (0.56 *vs.* 0.44). Also, females that settled on a site where conspecifics experienced a good success were two times more likely to have a good RSi than females that settled on a bad site. Such settlement patterns toward the sites that produce the greater numbers of fledglings have been observed in other passerines (Brown et al. 2000; Doligez et al. 2002) and provide evidence that they result from an adaptive response of individuals to improve their fitness (Bowler and Benton 2005).

Using a simpler model, Lagrange et al. (2014) showed the presence of individual heterogeneity in dispersal propensity within the same tree swallow population. Yet, our results not only showed that some individuals appeared to have a greater dispersal propensity than others, they also showed that this tendency was modulated by their breeding experience. Indeed, the likelihood that a female dispersed after having dispersed in the previous year was 0.19 and 0.61 depending if she experienced a good or a bad RSi, respectively, and 0.02 and 0.24 if she was site faithful in the previous year. Moreover, our results suggested that this individual variation in dispersal propensity likely increase with age as females that showed site fidelity after breeding in their second year became more faithful in following years (+1.8 % to +8.5 % between SY and ASY), whereas females that dispersed after breeding in their second year were more inclined to disperse later on in life (+0.8 % to +2.7 % between SY and ASY). These patterns support the hypothesis that dispersal propensity may not only depend on individual experience, but also on phenotype; a condition that can have important implications for the dynamics of spatially-structured populations (Leimar and Norberg 1997; Clobert et al. 2009; Cote et al. 2010). Given the ever-increasing habitat loss and fragmentation of natural habitats, the study of individual heterogeneity in dispersal-related traits should certainly receive more attention.

Dispersal may involve a variety of costs including time, energy, predation risk and opportunity losses that can be incurred prior, during or after it occurred (Yoder et al. 2004; reviewed in Bonte et al. 2011). Our results suggest that tree swallows are not exempt from such costs. For instance, SY and ASY females that experienced a good RSi after having dispersed in the previous year had a survival reduction of 4 % compared to females that did not change location. The fact that this pattern was however not observed in females that experienced a bad RSi (and thus did not fledge any young and thereby probably invested less in reproduction) points toward a combined effect of dispersal and raising a brood on survival. Still, our results did not indicate that dispersal influenced the RSi of females. Yet, our RSi index may have been defined too crudely for detecting an effect of dispersal on subsequent reproductive output. Pursuing the development of Capture-Recapture models so to allow the incorporation of nominal ordinal or continuous "covariates", such as site isolation or reproductive success, is certainly warranted, especially given the importance of dispersal costs on the evolution and form of this behavior (Johnson and Gaines 1990).

Previous studies that found an effect of RSc on dispersal probabilities assumed a perfect detection of individuals. Applying a similar approach to our data (Appendix E1), models that included RSc and its interaction with RSi were found to be the most parsimonious (Appendix E2) even though the effect of RSc was non-significant (Appendix E3). Globally, dispersal probabilities estimated with GLMMs depicted the same trends as those found with Capture-Recapture models (Appendix E4). Yet, how dispersal was defined affected the estimates obtained with GLMMs. When the dataset was composed of individuals captured two consecutive years, dispersal probabilities were underestimated compared to those obtained by Capture-Recapture models, but were overestimated when the dataset included individuals captured at least twice but not necessarily in two consecutive years. Assuming a perfect detection thus appear more likely to bias dispersal estimates and the effect of covariates on those estimates than multievent Capture-Recapture models, which can include "nuisance parameters" to avoid confounding effects. The Capture-Recapture approach used in this paper partitioned the effects of variables through a series of matrices for each nuisance parameter: recapture (R) was conditional on RSi, and fidelity (F) was affected by RSi, and transitions

between good/bad RSi (I) were linked to RSc. With a GLMM approach, "nuisance parameters" (e.g., R or I) are absent and variables affecting them have the potential to act directly on F. This shortcut has the potential to bias conclusions and therefore advocates the systematic consideration of detection probabilities in future dispersal studies.

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CHAPITRE 4

EFFECTS OF AGRICULTURAL LANDSCAPE ON FITNESS AND DISPERSAL IN A DECLINING AERIAL INSECTIVORE

Mise en page pour une première soumission dans *Journal of Animal Ecology*

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Contribution des auteurs :

Paméla Lagrange, Marc Bélisle ont formulé la problématique et la mise en contexte des questions biologiques.

Paméla Lagrange a réalisé les analyses statistiques concernant les modèles CMR et l'analyse GLMM, et Olivier Gimenez a contribué aux analyses statistiques bayésiennes pour le SRi.

Paméla Lagrange a participé à la récolte des données pendant trois saisons de terrain et Marc Bélisle, Dany Garant et Fanie Pelletier ont assuré le soutien financier du programme.

Les co-auteurs ont contribué à l'orientation du travail et à l'enrichissement de la discussion.

Paméla Lagrange a rédigé la première version de l'article et tous les co-auteurs ont/auront participé à la correction et l'amélioration de l'article.

Description de l'article :

Cet article vise à éclairer les causes du déclin de l'Hirondelle bicolore. Au travers de ce travail, nous avons exploré diverses variables environnementales, principalement liées à l'intensification agricole et la compétition intra et inter-spécifique, afin d'identifier leur répercussion sur la survie, le succès reproducteur et la dispersion de l'espèce. Aussi, en déterminant les habitats les plus fréquentés par les reproducteurs, nous avons mis en évidence que le milieu intensif affecte négativement la fitness des hirondelles, directement en diminuant la survie et le succès reproducteur, indirectement en augmentant la compétition. Pour autant, la probabilité de disperser n'est pas plus élevée dans cet habitat. Elle dépend de l'expérience personnelle (échec de reproduction, comportement dispersif de l'année précédente). Ces résultats suggèrent que le milieu intensif est un « piège écologique », cause du déclin de l'espèce et plus globalement.

4.1. Abstract

1. In declining species, it is essential to understand what and how environmental variables affect survival, reproductive success and dispersal behavior, because variation of these demographic parameters modifies population size. In particular, nest-site selection affects fitness and conducts to evict sites withunfavorable conditions, decreasing fitness in birds.
2. The aim of the study was to identify what environmental characteristics impact these parameters and site occupation for the reproduction of Tree swallows.
3. We considered the presence of House sparrow as a nest-site competitor, sexual partner density for extra-pair copulation, availability of nest boxes, and agricultural landscape at local (foraging range during rearing) and regional scales (foraging range before incubation) as proxy of food availability. We used a network of nest boxes sparsely implanted on 40 farms in a study area with a mosaic of agricultural landscapes along a gradient of intensification from hedge field pastures to monocultures. Capture-recapture analyses were used to assess environmental effects on survival and fidelity probabilities

while accounting for imperfect detection, and generalized linear models to assess the environmental effects on site occupation and reproductive success.

4. Survival of males decreased by 13 % in regional intensive landscape and from 7 to 19 % in presence of House sparrow, but increased with increasing local density of conspecifics. Females were responsive only to the presence of House sparrow, with a 24 % decrease in survival when they were reproductively successful and a 40 % increase otherwise. This positive effect was likely due to the negative effect of sparrow on reproductive success that caused early nest abandonment and thereby decreased reproductive costs. Reproductive success was also reduced by the percentage of local intensive cultures and positively affected by sites with high density of conspecifics. Dispersal decision depended only on individual criteria, namely reproductive success and dispersal behavior the previous year, and not on environmental variables. This being said, individuals selected breeding sites without competitor in which the number of produced fledglings the previous year was higher, and in a regional environment populated with conspecifics.
5. Our results suggest that agricultural intensification negatively affects Tree swallow fitness, directly through mortality and indirectly by increasing competition. Despite this, dispersal probabilities from intensive sites were not higher than from extensive sites, which suggest that unfavorable habitats could lead farmland birds to an ecological trap hence explaining their decline.

Key-words: agricultural landscape, breeding dispersal, competition, habitat selection, House sparrow, individual reproductive success, survival, Tree swallow.

4.2. Introduction

Habitat selection is a set of behavioral responses based on the distinction of the environmental components resulting in the disproportional use of habitats (Block & Brennan 1993). Several theories have been proposed to explain the distribution of individuals in space. Fretwell and Lucas (1969) described an ideal free distribution where individuals have the same ability to

choose their optimal breeding site knowing the inherent quality of resources in a patch. But in nature, these conditions are rarely met because environment is stochastic and individuals are not free and omniscient (Lessells 1995). For example, a patch without any individual is not necessarily of poor quality, but might simply be the result of a partial knowledge of space (Jones 2001). Commonly, individuals can be subject to density effect, to availability and contrasted quality of sites when they select their breeding site, that leads animals to a preemptive distribution in their habitat (Fretwell 1972; Sutherland & Parker 1985; Pulliam & Danielson 1991; Citta & Lindberg 2007). This distribution is often driven by dominant individuals (particularly in territorial species) forcing subordinates to use poorer habitats following an ideal despotic distribution (Rendon-Martos *et al.* 2001; Citta & Lindberg 2007). Faced to these environmental pressures , individuals can quickly respond to and modify their distribution in real time (Beerens *et al.* 2011). If they cannot adapt their distribution when environmental conditions become unfavorable, fitness is affected. To cope with bad conditions, individuals move to select beneficial habitat to maintain or increase their survival and reproductive success (Block & Brennan 1993; Holmes, Marra & Sherry 1996; Jones 2001).

Because individuals cannot assess all the environmental components affecting their fitness, they use cues or a subset of physical factors correlated to their fitness to infer habitat quality (Block & Brennan 1993; Pärt & Doligez 2003). The main factors involved in habitat selection are linked to the habitat structure and to density of individuals via predation or competition for resources (accessibility and availability of food, breeding site and refuges). One method to study habitat selection is by studying fitness variations according to environmental characteristics. For migratory birds, consequences of habitat selection on fitness are particularly difficult to explain, because individuals use multiple habitats during an annual cycle (wintering, breeding, staging areas) in which cumulative events can impact fitness by nonlethal residual effects (Norris & Marra 2007). Unfavorable conditions such as food scarcity, for example in wintering areas, can hamper reproduction (Nagy & Holmes 2005; Brown & Sherry 2006). Generally, we expect that nest site choice maximizes fitness (increase

survival or reproductive success) when habitat is favorable and increases dispersal probability and reproductive costs when habitat is unfavorable.

Here we study nest-site selection in Tree swallow, a migratory passerine. Over the last decades, Tree swallow and more generally farmland birds decline while agricultural intensification increase, which cause the loss of biodiversity by decreasing food abundance and nest sites in North America (Freemark & Kirk 2001). The loss of their nesting habitat led Tree Swallows to easily nest in artificial nest boxes implanted in multiple habitats with varying resource quality. Thanks to a network of nest boxes scattered in a heterogeneous agricultural landscape, we assessed the repercussions of habitat quality on fitness through variation in demographic parameters, namely individual reproductive success, survival, dispersal and settlement decisions. We expected a positive effect on fitness and nest-site choice in habitat sufficient in resources (with availability of food, breeding sites and partners) and a negative effect on dispersal decision. Dispersal initiation was expected in females which are less faithful to their breeding site than males (Winkler *et al.* 2004; Lagrange *et al.* 2014). Survival and dispersal being parameters estimated between two breeding seasons, we used a capture-recapture approach to handle with the risk of imperfect detection of individuals over time and generalized linear models to study in detail the selected sites. We considered environmental variables related to 1) availability in breeding sites, partners and food directly linked to habitat perception 2) social cues of habitat quality with conspecifics density and number of fledglings. We assumed that social cues and nest boxes density favored survival, reproductive success, site fidelity and settlement decision on these sites, whereas the presence of competitor (House sparrow, *Passer domesticus*) and intensive landscape as a proxy of food availability, favored mortality, dispersal initiation and avoidance of these sites.

4.3. Materials and methods

4.3.1. The Tree swallow system

Study area

The study area covered 10,200 km² in Southern Québec (Canada, Fig. 1). In the North and West, habitats were composed of intensive monocultures of corn, soy and other cereals whereas in the South and East, habitats were more diversified with small marshes, woodlots and extensive agricultural landscapes including pastures and fodder fields (Jobin *et al.* 2010). The area was composed of 40 sites (farms), each including 10 nest boxes distant of 50 m to respect territorial behavior (Muldal et al. 1985; Robertson and Rendell 1990) and to allow the possible occupation of all the nest boxes (see Ghilain & Bélisle 2008 for more details on the study area).

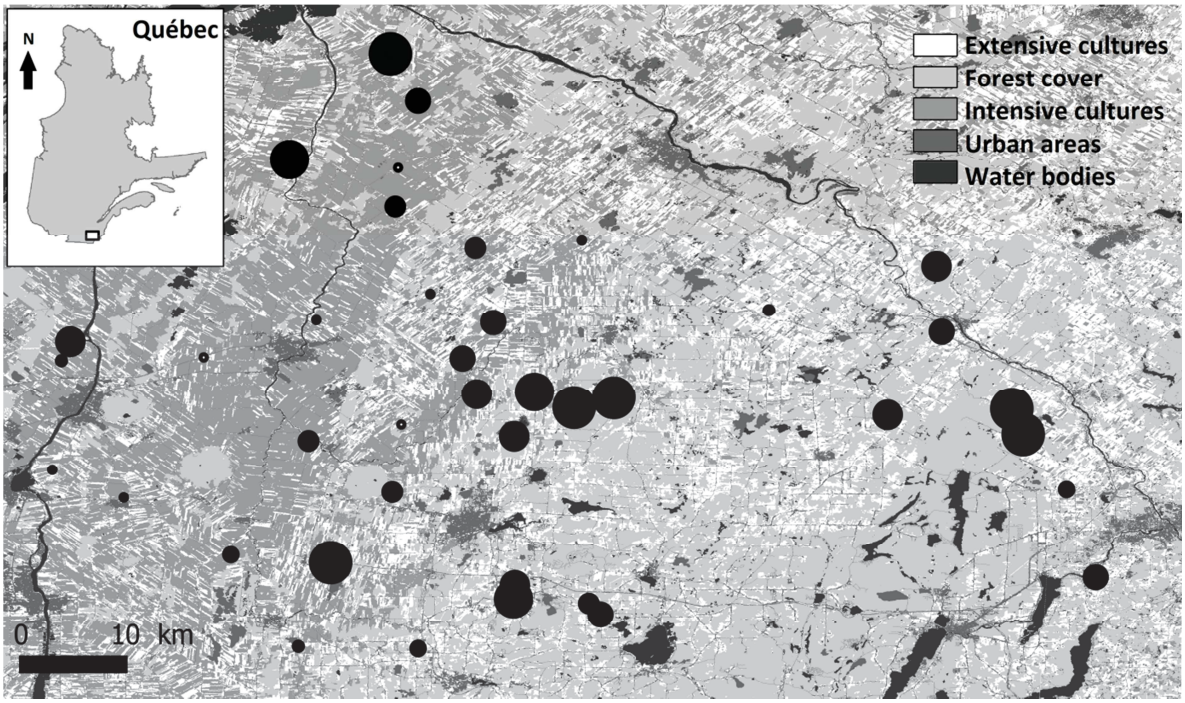

Figure 1: Study area of the 40 farms monitored in Québec for the reproduction of Tree swallows, with the density of nest boxes occupied since 2004 on each farm (number of occupied nest boxes in a black disk proportional from 35 to 162 occupations, and fixed size below 34

occupations). Land cover types were based on a mosaic of classified Landsat-TM satellite images (Canadian Wildlife Service 2004) by pooling cultures detailed in the Base de données des cultures assurées 'BDCA' et généralisées 'BDCG' (Financière agricole du Québec).

Species

The Tree swallow is a North American migratory passerine, living in open landscape such as marshes and agricultural areas. This secondary cavity-nester tolerates many types of habitat but its breeding area is limited by the number of cavities (Winkler *et al.* 2011). The density of nest boxes increases the number of nesting pairs on the short term and studies showed a return to the deserted areas after the installation of nest boxes (Holt & Martin 1997; Ghilain & Bélisle 2008). Several species like Eastern bluebird *Sialia sialis*, House wren *Troglodytes aedon* or House sparrow also compete for nest boxes, causing desertion, eggs and nestling destruction and sometimes the death of swallows (Rustad 1972; Finch 1990; Robillard, Garant & Bélisle 2013). Tree Swallows are territorial and defend additional breeding sites, which increases indirectly fitness by reducing usurpation of cavity, providing a second cavity in case of failure of the first, or by increasing occasion of bigamy for males (Robertson, Gibbs & Stutchbury 1986). In all studied population of Tree swallow, a minimum of 50 % of the young resulted from extra-pair copulations (Lifjeld *et al.* 1993; Dunn *et al.* 1994; Kempenaers *et al.* 2001), a figure which increased with high density and lower quality of habitats as intensive landscapes (Lessard *et al.* 2014). In these agricultural habitats, the use of chemicals contaminated the environment which affected the abundance of invertebrates composing the swallow diet and indirectly the survival and breeding performances of aerial insectivores (Donald, Green & Heath 2001; Benton *et al.* 2002; Boatman *et al.* 2004; Gentes *et al.* 2006; Custer *et al.* 2007). In this context, dispersal appears as a solution to avoid negative environmental effect. In female Tree Swallows, breeding performances affect the decision to disperse (Lagrange *et al. unpublished manuscript*) but the contribution of environment to dispersal decision is unknown. After a reproductive failure, 19 to 61 % of individuals disperse to another farm whereas after a success of reproduction only 2 up to 24 % disperse. Males are more faithful with a dispersal rate from 1 to 6 % according to whether individuals dispersed or not in the previous year.

Field methods

Tree swallows were captured since 2004 for females, during the incubation and since 2005 for males, during the nestling period. Nest box occupation and species reproduction were monitored for each nest box every second days, from the date of the first constructed nest to the last fledgling in the system. We built a capture-recapture dataset for survival and dispersal analyses containing all breeders banded until 2012 and recaptured until 2013, including 1459 females and 786 males. Second clutches represent 10 % of clutches, and we excluded them from analyses to limit the bias due to intra year dispersal. Females were aged following the plumage coloration to distinguish second year (first breeders, SY) from after second year (experienced breeders, ASY) that could have a better reproductive success (Robertson & Rendell 1990). Individual reproductive success (RSi) was studied only in females laying at least one egg and was defined by the number of fledglings, categorized in two classes (good if individual have at least one fledgling, otherwise bad) as in Naves et al. (2006) and Doligez et al. (1999). Reproductive success analyses covered 2728 events of reproduction over 10 years, among which 38 % produced no fledglings. Because environmental variables were similar for all the nest boxes on a farm, we used the number of nest boxes occupied on a site from 2005 to 2013 as a response variable for the settlement decision. We excluded the first year as the number of fledglings of the previous year was not available.

4.3.2. Explanatory variables

Landscape at regional and local scales

We considered landscape composition as a proxy of habitat quality since intensive cultures reduce food abundance (Benton *et al.* 2002; Paquette *et al.* 2013), food quality through chemical contamination (Lopez-Antia *et al.* 2015), density of potential sexual partners (Freemark & Kirk 2001), natural nest-site availability and increase nest-site competition (Robillard *et al.* 2013). At the beginning of the reproduction, Tree Swallows forage over several kilometers and reduce their foraging radius to several hundred meters during the rearing period (Dunn & Whittingham 2005). For this reason, we used two scales for defining

landscape: 300 m (local scale, ‘I300’) and 4 km (regional scale, ‘I4’) around the nest. These scales corresponded to the radii at which intensive cultures impacted most strongly swallow density and their number of fledglings (Appendix A.1). Due to constraints in the number of states we could incorporate in the capture-recapture analyses, we discretized landscape variable in two classes: intensive habitat when the intensive area on a farm was larger than the annual median of the system and extensive habitat otherwise. We predicted a lower reproductive success, higher mortality and an avoidance of nest boxes in intensive landscape because the accessibility of resources was limited. As RSi is a dispersal driver, we also predicted a higher dispersal rates from intensive landscape (Table 1).

Competition for nest boxes: availability of nest boxes and presence of House sparrow

Agricultural habitats are favorable to the presence of House sparrow, the main nest-site competitor of Tree swallow in our study system (Robillard *et al.* 2013). Because sparrows are resident during the winter and aggressive against other species during the reproduction (Gowaty 1984), Tree swallows are limited in the selection of nest boxes when they come back in spring. The proportion of nest boxes occupied by sparrows in the study area increased from 6.0 % in 2004 to stabilize around 24 % in 2010. As a result, a decrease in the occupation rate of Tree Swallows in nest boxes occurred when house sparrows were present on the farm, particularly close to buildings (Robillard *et al.* 2013). We assumed that the presence of sparrows (‘HOSP’) on a farm reduced reproductive success, survival, and settlement likelihood of Tree swallow and increased dispersal probability.

To account for the fact that competition leads to dispersal when breeding site had available nest boxes nearby, we used the density of nest boxes (‘NB’) implanted in a radius of 15 km around the breeding site as an index of the availability of breeding sites. This radius likely corresponds to the maximal distance of movements for females before the laying: foraging was effected within a 10 km-radius (Dunn & Whittingham 2005) and extra-pair copulations showed a better assignation of juvenile paternity at 15 km (Lessard *et al.* 2014). We assumed

that Tree Swallows choose farms with a high density of nest boxes within 15 km and disperse more when nest boxes were close (Hosner & Winkler 2007) and numerous.

Conspecifics density for extra-pair copulation and cue of good habitat quality

Tree swallow has the highest rate of extra-pair paternity in a passerine (Winkler *et al.* 2011) and we assumed that availability of sexual partners affected nest-site selection. Moreover, high density favors interactions and extra-pair copulation (Westneat & Sherman 1997). Depending of the year in our system, 78 up to 90 % of the nests had extra-pair young (Lessard *et al.* 2014). Although local density did not seem to affect extra-pair copulation in Tree swallow (Kempenaers *et al.* 1999), the genetic father was captured in a regional radius of 15 km around the nest box of the female in our system (Lessard *et al.* 2014). Therefore, within this radius, we defined the regional density ('DR') and assumed that denser breeding sites the previous year encouraged the settlement and site fidelity the following year in both sexes.

High local density increases advantages such as interactions between individuals to drive off predators or to detect foraging sites (Winkler 1994); its disadvantages are competition over resources and parasitism (Muldal, Gibbs & Robertson 1985; Brown & Brown 1986). In our system, on average 6 out of 10 nest boxes were occupied on each farm and nest boxes were spaced so that competition for nest boxes was limited. Despite density having no effect on reproductive success (Male, Jones & Robertson 2006), a higher local density ('LD') could be used as a cue of the good habitat quality (Beauchamp, Bélisle & Giraldeau 1997 for selection of foraging sites; Doligez *et al.* 2003 for selection of nestling sites). We assumed that sites with high density were more attractive for settlement, improved survival and reduced the likelihood of dispersal.

Table 1: Explanatory variables used to quantify the influence of environment on reproductive success (RSi), survival rates (S), decision of site fidelity (F, the opposite of dispersal decision) and settlement decision (SD) of Tree swallows in Southern Québec, Canada. In the first column, abbreviations of each variable are indicated between parentheses.

Explanatory variables	Affected parameters	Predicted effects	Description of the variables
Local habitat type (I300)	SD, RSi	-	Percentage of intensive cultures in a radius of 300 m centered on the nest box at t.
	F, S	-	Intensive/extensive cultures defined by the threshold such as the annual median of percentage of intensive culture around the nest boxes occupied by swallows at t.
Regional habitat type (I4)	SD, RSi	-	Percentage of intensive cultures in a disc of radius of 4 km centered on the nest box at t.
	F, S	-	Intensive/extensive cultures defined by the threshold such as the annual median of percentage of intensive culture around the nest boxes occupied by swallows at t.
Presence of House sparrow (HOSP)	S, F, SD, RSi	-	Presence or absence of House sparrow on a farm at t.
Availability of nest boxes (NB)	SD	+	Number of farms with nest boxes implanted in a radius of 15 km around the breeding site at t.
	F	-	High/Low availability of nest boxes defined by the threshold such as the median of density of nest boxes at t.
Local density (LD)	SD, RSi	+	Number of occupied nest boxes on a farm at t for I, at t - 1 for SD.
	S, F	+	High/Low breeders density defined by the threshold such as the annual median of the number of nest boxes used by a swallow at t.
Regional density (RD)	SD, RSi	+	Number of occupied nest boxes in a radius of 15 km around the nest box at t for I, at t - 1 for SD.
	S, F	+	High/Low breeders density defined by the threshold such as the annual median of the number of nest boxes used by a swallow at t.
RSc (RSc)	SD	+	Number of fledglings on a farm at t - 1.
Laying date (LAY)	RSi	-	Date in Julian day of the first laid egg at t, known to interfer on I (Ghilain & Bélisle 2008).

4.3.3. Statistical analyses

Parameterization of the capture-recapture model for estimating dispersal and survival

We used capture-recapture multievent models (Pradel 2005) to study the effects of habitat on survival and dispersal. In our case, multievent models were used to estimate between t and $t + 1$, the probability to be faithful (to return on the same farm two consecutive years) or to

have dispersed (to change of farm between two breeding seasons) even though an individual was not captured two consecutive years. We relied on a model developed by Lagrange *et al.* (2014) for study area with numerous sites (see Appendix B.1 for more details). States (real status of individuals) and events (observations linked to the capture of individuals) carried information on the capture of the individual at t and $t - 1$, on the location at t relative to the previous location at $t - 1$, on the individual reproductive success at t ('RSi'), and on one environmental variable at t (I300, I4, RD, LD, NB or HOSP). Integrated information on location at $t - 1$ and t could test the memory effect (if an individual disperse or not between $t - 1$ and t) as variable possibly affecting survival or dispersal probability from t to $t + 1$.

In Tree swallow, dispersal patterns differ between sexes (Lagrange *et al.* 2014), which led us to analyze males and females separately, and to integrate RSi (0 fledgling *vs*. 1 fledgling and more) only for female analyses because RSi for males was difficult to estimate with extra-pair copulation. The probability for a female to survive and disperse depends on confounding effects such as: the probability at $t + 1$ to be recaptured or not, to keep the same individual reproductive success or not, and to stay in the same environmental quality or to change. The probability to stay in the same environment quality two consecutive years informed on the type of occupied habitat. While these parameters of no direct ecological interest allowed correcting for potential bias in survival and dispersal estimates, having to deal with them limited the number of states in the model. We therefore discretized all variables in two categories, based on the presence/absence of the variable based on the low/high farm value of the environmental variable, the threshold being the annual median value of the system (class 1: inferior or equal to the median, class 2: strictly superior to the median) (Table 1).

Goodness-Of-Fit test and model selection in capture-recapture analyses

To assess the fit of models to the male and female datasets, we used goodness-of-fit tests (GOF). GOF tests are not yet developed for multievent models (Pradel, Gimenez & Lebreton 2005), therefore we used tests for standard capture-recapture models implemented in the software U-CARE (Choquet *et al.* 2009a) by reducing the numbers of events to captured or

not (e.g., Sanz-Aguilar *et al.* 2011). In case we detected a lack of fit, a coefficient of overdispersion $\hat{c}$ was used to adjust standard errors, confidence intervals and AIC values, the latter being corrected for small samples size too ($QAIC_{c;}$ Burnham and Anderson 2002).

The effect of environment was tested by including the variables one at a time with no interaction. Consequently, we performed one model selection by sex and by environmental variable. In a first selection, we defined the basal structure that we would use for each of the parameters. Building on a previous study (Lagrange et al. 2014, *unpublished manuscript*), we used a stepwise approach from a null model where all parameters were constant to parameterize models. Parameterization targeted one parameter at a time and started from the nuisance parameters to the relevant parameters (see details in Appendix B.2). Time effect for both sexes and age of females were also tested on all parameters.

We then performed a second selection with the model structure for each parameter identified above to calculate the Akaike weight (w) for each model i in each selection s. In this way, weight $w_{s.i}$ was not affected by the constant structure of a non-defined step in the first round of model selection. For each step of the model selection, we displayed model-averaged parameter estimates and their unconditional standard errors (± SE) based on the $QAIC_c$ and $w_{s.i}$ (Burnham & Anderson 2002). Models were implemented in the program E-SURGE (Choquet, Rouan & Pradel 2009b).

Zero-inflated generalized linear models for analyses of reproductive success (RSi)

Reproductive success was defined as the number of fledglings per nest. The dataset was composed of 2728 nest boxes of Tree Swallow with at least one laid egg, without females being necessarily captured. Consequently, we considered all reproductive attempts. The distribution of the number of fledglings by female displayed a peak of females with no fledgling due to two reproductive processes: failure because broods did not hatch and failure after hatching because their young died respectively (Appendix A.2). To model the mean number of fledglings, we used Zero-inflated Poisson regression (ZIP) (Zuur *et al.* 2009). ZIP

models 2 parameters: the probability p that an observation is generated through a Binomial distribution explaining if the failure is due to mortality before fledging or not (failure before hatching), and the mean number of fledglings λ of a Poisson distribution. We tested the effect of environmental variables (RD, LD, HOSP and I300) on the RSi, excluding I4 which was highly correlated to I300 and adding the laying date which was known to affect the RSi (Ghilain & Bélisle 2008). Farm identity and the capture year were considered as random effects. Following Martin et al. (2005), we used a Bayesian framework with Markov chain Monte Carlo to fit ZIP models. We used non-informative priors, 2 chains that we run for 20,000 iterations after 5,000 iterations as burn-in. We used program JAGS (Plummer 2011) that we called from R (R Development Core Team 2013) using package R2jags (Su & Yajima 2012). We modeled all the combination of variables on p then on λ and selected models using the technique described by Kuo & Mallick (1998) (see also Ntzoufras 2002)) based on posterior model probabilities. In a second step, we used the best parameterization for p and λ and fit the corresponding model to estimate the effect size of variables.

Statistical analyses of the settlement of the site

We modeled farm occupancy using generalized linear mixed models following a Gaussian distribution with the density of nest boxes occupied by Tree Swallows as response variable, farm and year as random effects. We built models using all combinations of variables weakly correlated ($|r| \leq 0.60$) in a same model (Appendix A.3). We included interaction effects between fixed effects relating to landscape and reproductive success variables (Ghilain & Bélisle 2008) or between landscape variables and House sparrow presence or between landscape variables and conspecific density (Robillard *et al.* 2013). Models were fitted in R using the lmer function with the maximum log-likelihood (package lme4, Bates *et al.* 2014)) and compared with AIC_c. Multimodel inference was performed with the AICcmodavg package (Mazerolles 2013) to calculate model weight (w_i) and the MuMIn package (Bartoń 2014) to estimate coefficient and their unconditional standard errors.

4.4. Results

4.4.1. Capture-recapture analyses for survival probabilities and dispersal decision

Goodness-of-fit tests

The goodness-of-fit tests for males indicated a good fit of the general model to the data (χ^2 = 23.21, df = 22, p = 0.39). We detected a slight trap-happiness (χ^2 = 10.73, df = 6, p = 0.02) probably due to the high philopatry to the nest box for males. We corrected for this lack of fit by using a variance inflation factor $\hat{c}$ = 1.05 for males.

The goodness-of-fit tests for females indicated a lack of fit of the general model to the data (χ^2 = 75.33, df = 39, p < 0.01). We detected a trap-happiness effect after the second year (χ^2 = 18.01, df = 7, p < 0.01) as for males, due to the high philopatry to the breeding site, but not for the second year (χ^2 = 2.07, df = 5, p = 0.84). Transience tests detected for the two age classes a transient effect particularly for second year due to a lower survival than for older females (SY: χ^2 = 30.16, df = 7, p < 0.01 and ASY: χ^2 = 22.69, df = 8, p < 0.01). These differences between age classes were probably due to the small sample size of second year comparing to after second year rather than a biological difference (N_{SY} = 333, N_{ASY} = 1459). We corrected for the overall lack of fit by using a variance inflation factor $\hat{c}$ = 1.93 for females.

Detection

Recapture probabilities depended on RSi for females with a value of 0.98 ± 0.01 for females in good RSi and 0.33 ± 0.05 for females in bad RSi. Males were recaptured less often than females because they could only be captured during the nestling period and one clutch in three failed earlier than this stage. The low recapture rate of 0.56 ± 0.10 in the first year of male capture was due to an unefficient capture protocol. The method was corrected the following years, increasing the recapture probabilities up to 0.80 ± 0.03. Since 2011, the addition of a

new manipulation has reduced the capture period, and consequently capture occasions, decreasing the recapture rate to 0.66 ± 0.06.

Survival

For males, we identified 3 main environmental factors affecting survival probabilities: local density ($w_{LD.18}$ = 0.22, Appendix D.3) had a positive influence whereas regional intensive landscape ($w_{I4.15}$ = 0.25, Appendix D.6) and the presence of House sparrow ($w_{HOSP.15}$ = 0.31, Appendix D.2) had negative impacts. On average, survival probability was close to 0.42 ± 0.03 for males previously disperser and 0.51 ± 0.02 for males previously faithful. Model selection showed that all models with a memory effect were retained. Survival probabilities increased of 0.05 between the less dense farms and populated farms and did not exceed 0.52 (Fig. 2). As expected, density at regional scale had no effect on survival ($\text{Model}_{\text{RD.24 and RD.22}}$, Appendix D.4). By contrast, males nesting in intensive landscapes at large scale had lower survival than individuals nesting in extensive landscapes. There was a link with the previous location since males previously dispersing had a survival of 0.46 ± 0.04 in extensive landscape, decreasing by 0.06 in intensive landscape at 4 km whereas males previously faithful in extensive landscape had a survival of 0.51 ± 0.03, decreasing by 0.03 in intensive landscape ($\text{Model}_{\text{I4.15}}$, Appendix D.6). The variable intensive landscape at 300 m exhibited the same trend, although this model had not the lowest QAIC_c ($\text{Model}_{\text{I300.24}}$, Appendix D.5). The last variable negatively affecting male survival was the presence of House sparrow. Survival probabilities for previously disperser decreased from 0.48 ± 0.04 to 0.39 ± 0.04 in presence of sparrow, and from 0.52 ± 0.03 to 0.48 ± 0.03 for previously faithful individuals.

Females survival increased with reproductive success (0.22 ± 0.03 for females in failure compared to females in success), and successful females had a lower survival probability when they had previously dispersed (0.44 ± 0.06) than females previously faithful (0.57 ± 0.05). Time and age had very little effect on survival: probabilities vary from 0.01 over time and second year females had the same mortality. Intensive landscape and conspecifics density had no effect on survival ($w_{I300.s48}$, $w_{I4.S44}$, $w_{LD.49}$, $w_{RD.48}$ all ≤ 0.07, Appendix C1 to C6). Only

the presence of House sparrow affected significantly survival, negatively when females were in success and positively when females were in failure of reproduction ($w_{HOSP.41}$ = 0.14, Appendix C.2). Survival probabilities for females in success previously disperser decreased from 0.58 ± 0.04 to 0.44 ± 0.05 in presence of sparrow, and from 0.57 ± 0.04 to 0.44 ± 0.05 for previously faithful. Survival probability for females in failure increased by 40 % in presence of sparrow (0.18 ± 0.03 *vs.* 0.30 ± 0.05).

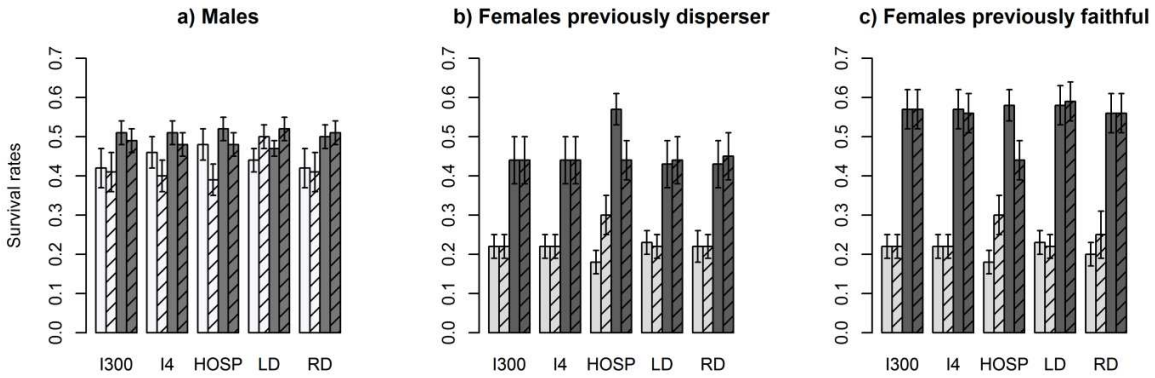

Figure 2: Annual survival probabilities following the environmental variables for males Tree swallows (a) after second year females previously dispersing (b) and previously faithful (c) in reproduction in Québec. Empty bars correspond to farms with the lower class and shaded bars to the higher class of environmental variable (I300, I4, HOSP, LD, RD, see Table 1 for details). For males, white bars represent individuals previously disperser, and grey bars are for individuals previously faithful. Females in light grey are in breeding failure, while unsuccessful females are in dark grey.

Dispersal decision

Males were highly faithful (0.96 ± 0.02), with a slight trend to disperse more when they had previously dispersed ($\text{Model}_{\text{NB.15}}$, Appendix D.1). Environmental variables and time did not affect dispersal decision (Fig. 3a and Appendix D.1). For females, dispersal probabilities were up to 14 times higher than in males and depended on both the memory effect and reproductive success (Fig. 3b). None of the 6 environmental variables seemed to influence the decision to disperse over two consecutive years for females (Appendices C.1 to C.6). Females in breeding

failure dispersed at 0.55 ± 0.12 and 0.25 ± 0.13 following if they previously dispersed or not, and females in success dispersed at 0.29 ± 0.06 and 0.04 ± 0.02 ($Model_{I300.36}$, Appendix C.5).

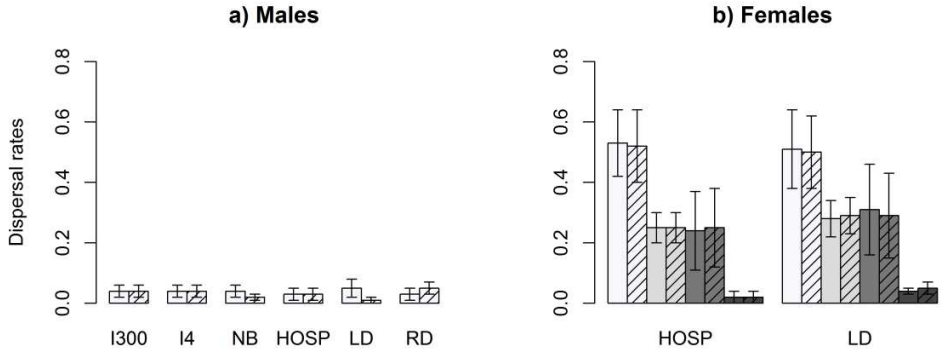

Figure 3: Dispersal probabilities between two breeding seasons according to environmental variables for males (a) and females (b). Empty bars for males and females correspond to farms with the lower class and shaded bars to the higher class of the environmental variable (I300, I4, NB, HOSP, LD, RD, see Table 1 for details). Probabilities for females depend on memory effect and individual reproductive success (white: previously disperser in failure, light grey: previously disperser in success, dark grey: previously faithful in failure, dark: previously faithful in success).

4.4.2. Linear regressions

Individual reproductive success (RSi)

Model selection retained two interactive variables affecting the probability to be in failure before hatching (on *p*) (Appendix E.2). In presence of House sparrow on a farm the number of failure before hatching decreased with the local density in conspecifics on a farm, but in absence of sparrow, local density did not affect the probability to fail before hatching (Fig. 4). We explained this interaction by the fact that local density in conspecific was negatively correlated to the number of sparrow on a farm (r = -0.57). The mean number of fledglings produced by each female was impacted only negatively by the intensive landscape at local scale (w_{17} = 0.95, Appendix E.1) (Fig. 4). Local density and House sparrow had no effect on λ

(w_{21} = 0.02, Appendix E.1). Variables at large geographical scales did not affect I. The laying date had no effect on parameters p and λ (selected in models with $w_i \leq 0.10$).

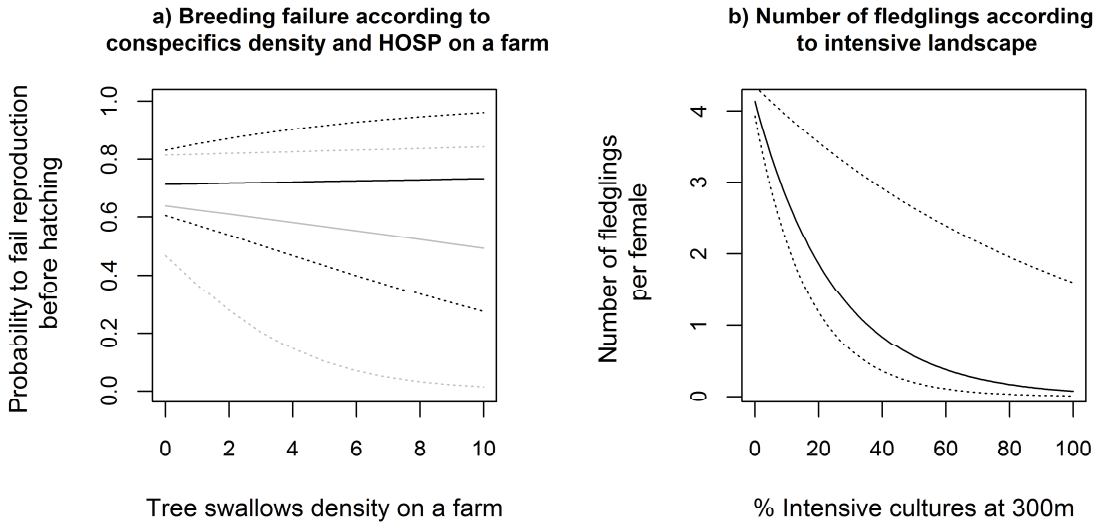

Figure 4: Environmental causes of breeding failure in Tree swallow. The probability p to fail reproduction before hatching is affected by the presence (gray line ± confidence interval in dotted lines) or the absence (dark line ± confidence interval in dotted lines) of House sparrow on a farm (a). Parameter λ is the mean number of fledglings per females (b).

Settlement decision

On average, occupation rate on each farm was 0.61 ± 0.15. The two variables presence of House sparrow and number of fledglings at $t - 1$ were retained in all models with a weight ≥ 0.01 (Appendix F.1). The presence of House sparrow decreased from 12 to 34 % the number of nest boxes occupied depending on the quality of the farm (measured by the number of fledglings the previous year) (Fig. 5). A farm with no fledgling at $t - 1$ was twice as less occupied as a farm with 50 fledglings the previous year (coef = 0.09 ± 0.01, Appendix F.2). Two other variables were retained: the regional density of conspecifics the previous year (correlated to 0.39 to the local density, Appendix A.3) increased the occupation rate on a farm, and intensive landscape at local scale decreased the occupation rate (respectively 0.02 and -

0.01, Appendix F.2.). Nest boxes density, local density of conspecifics and intensive landscape at regional scale had no effect on the occupation rate of the farms.

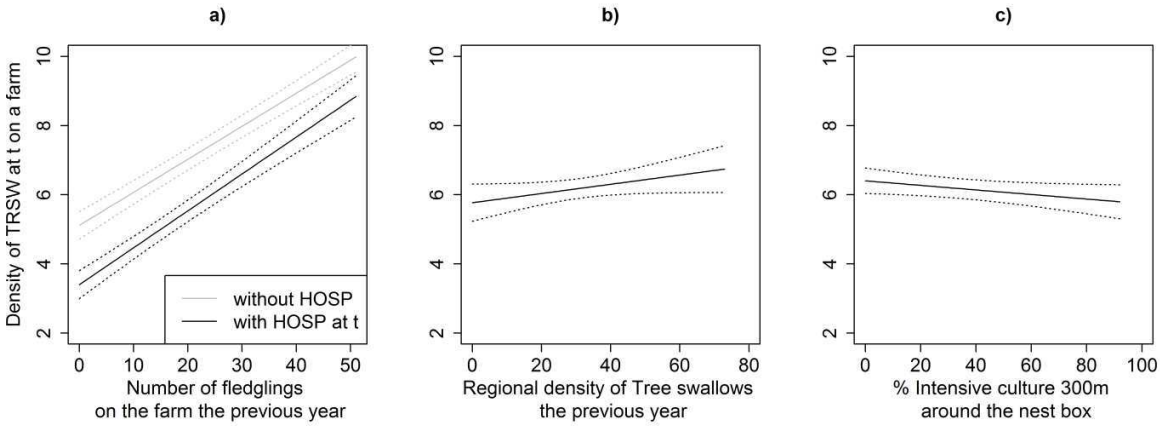

Figure 5: Density of Tree swallows on a farm as a function of environmental variables: the productivity of fledglings on the farm following the presence of House sparrow the previous year, the regional density of conspecifics the previous year, and the proportion of intensive culture 300 meters around nest boxes. The dotted lines delimit the 95 % confidence interval.

4.5. Discussion

4.5.1. Importance of competition and intensive landscapes on fitness

Survival of both sexes and reproductive success of females were particularly affected by some environmental variables while the dispersal decision was not. Survival of females was affected only by the presence of House sparrow, with a different relationship depending on whether they were in success or in failure of reproduction. In success, females reacted like males by a diminution of survival in presence of sparrow on the breeding site. But in reproductive failure, the presence of House sparrow increased female survival. Two reasons might explain this pattern. First, reproduction is a costly but non-lethal event, affecting more frail individuals (De Steven 1980; Wheelwright, Leary & Fitzgerald 1991; Paquette *et al.* 2014). The presence of House sparrow usually lead to breeding failure early in the season, which could decrease the

female investment in the reproduction and consequently increased survival of frail individuals. This early abandonment before incubation could not be detected in capture-recapture analyses because females were captured later on; however, during the incubation, reproductive success analyses support this hypothesis. In presence of House sparrows, the number of conspecifics decreased with increasing numbers of sparrows, which increased the probability to fail before hatching. In addition the reproductive status can appear as a cue of individual condition: females in failure are in a worse condition than successful females (Reznick, Nunney & Tessier 2000). Because we could not distinguish a failure caused by the presence of sparrows *vs*. a failure caused by a female in poor condition, it might be that females in failure in presence of sparrow would probably have been in success in their absence.

Other environmental variables like landscape and density of conspecifics did not affect survival of females, whereas male survival was positively affected by local density of conspecifics and extensive landscape. This sex-differential in sensitivity to environmental variables might be the result of higher costs of reproduction for females than for males (Wheelwright *et al.* 1991, Pellerin *et al.* unpublished manuscript) which might have masked environmental effects. Indeed, for males, local density is a cue of good habitat quality in our system rather than a source of competitive interaction with conspecifics as suggested in several studies on density-dependence effect (Rosenzweig 1991; Morris 2003); this is because competition for nest boxes is probably low since 39 % of nest boxes are not occupied and available for settlement by Tree Swallows. Moreover, these results corroborate the theory whereby conspecifics density is particularly attractive for habitat selection in a context of landscape fragmentation (Stamps 2001; Fletcher 2006). Our nest boxes network is implanted in an relatively homogeneous agricultural landscape where monocultures replaced habitat patches suitable for reproduction. With a decrease from 3 to 6 % of male survival in a regional intensive landscape, we suggest that current agricultural practices and/or landscape modifications induce indirectly several sources of mortality in aerial insectivores. For example, the use of phyto-sanitary products to fight against pests or enrich soils (Robinson & Sutherland 2002) can lead to invertebrate contamination and the occurrence of monocultures increases the abundance of House sparrows, the main nest-site competitors in our system. As

males were particularly faithful to their breeding site from one year to another contrary to females, they may more accumulate these negative effects in a regional intensive landscape. At a local scale, we did not find relevant effect of intensification because the landscape at 300 meters is more heterogeneous, the crop type varies between years to use less chemical input.

Our results show that the percentage of intensive landscape strongly decreased the number of fledglings in a nest. This is the direct consequence of a decrease in clutch size in intensive landscapes where females lay on average one less egg than in extensive landscapes (Ghilain & Bélisle 2008). Intensive landscape had no direct effect on the probability to fail before fledging, but indirectly through the presence of House sparrow negatively affecting RSi. The cost of reproduction in intensive landscape came later because females could compensate the poorer habitat quality by a higher investment in parental care (Lamoureux 2010). For example, parents were previously shown to spend less time in nest boxes in intensive landscapes than in extensive landscape (Lamoureux 2010) because they spent more time foraging where arthropods were less abundant (Bellavance 2014). Despite this, chicks grew slowly.

4.5.2. Movements and nest-site choice

While environmental variables affected fitness, none of them clearly influenced the dispersal decision between two breeding seasons. This is easily understood in males as only 4 % of them at most chose to disperse in contrast with females which dispersed up to 55 %. This low dispersal probability for males, combined with the high impact of environment on survival, should lead sites of bad quality to be deficient in males in our system. However, a strong immigration did compensate for this high level of mortality: 63 % of males (non-banded) immigrate from outside the network to our system each year. This high rate of immigration suggests whether a higher breeding dispersal probability outside our network or a higher natal dispersal. The recent decrease in natural nest-site availability in secondary cavity nesters (Winkler *et al.* 2011; Robillard *et al.* 2013) can support the hypothesis of a higher breeding dispersal from outside. . In our system, we assigned on average the father of 79 % of young

(Lessard *et al.* 2014) that also suggest a few number of breeders in natural cavity in the study area. Finally, immigration can be the result of individuals in natal dispersal. In passerines, it is commonly known that natal dispersal rates are higher than breeding dispersal rates (Greenwood & Harvey 1982).

Decision to disperse in females was only linked to the personal reproductive performance and to the dispersal behavior of the previous year (Lagrange *et al.* unpublished manuscript). Females dispersed more after a reproductive failure as shown repeatedly (see, e.g., the review by Greenwood & Harvey 1982) and none environmental variables affected the dispersal decision despite they affected fitness. Absence of effect of density in males and females and food availability were also documented in the yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Ward 2005). Although site fidelity was high, nest sites were strongly selected according to environmental variables, which suggest an oriented emigration. Individuals settled preferentially in sites without House sparrow in which the number of fledglings the previous year was higher, and in a regional environment populated with conspecifics.

Our results are in agreement with previous studies on passerine species showing that individuals search for the more attractive breeding sites with the higher densities of breeders (Stamps 1988; Fletcher 2006), the most productive sites in fledglings the previous year (Pärt & Doligez 2003) and avoid competitors impacting directly on their survival (Rustad 1972; Robertson *et al.* 1986; Finch 1990). Nevertheless, swallows did not avoid systematically intensive cultures for settlement since we detected a local but no regional effect of landscape. The two main resources required for succeeding in reproduction were – in appearance – present in intensive habitats: the nest site accessibility, artificially assured by our nest boxes, and food availability. A recent study on the abundance and diversity of aerial insects concluded that depending on the year, abundance can be better in the intensive habitat than in extensive even if globally, prey abundances are higher in the extensive habitat (Paquette *et al.* 2013). Besides, the difference of abundance of insects between the two habitats is maximal in June, during the rearing phase, later than the period where the nest site is selected. Since food availability seems to be equal between intensive and extensive cultures at the beginning of the

reproduction and because the implantation of nest boxes allows the recolonization of deserted habitats (Holt & Martin 1997), Tree swallows did not use the regional landscape as a criterion for selection.

To conclude, the environmental variables we considered did not affect variation in dispersal decision which was instead driven by individual criteria. Survival and reproductive success of both sexes were affected by competition, whereas conspecifics density and intensive landscape affected only males. Modifications of the agricultural landscape linked to intensification negatively affected survival without encouraging dispersal to better quality sites. Intensive breeding sites seemed to lead to a decline of local populations and it will be interesting to study these environmental effects on the population size. Although breeding sites are selected based on density and productivity of conspecifics on a site, the limited number of cavities might push the species to pick low quality habitats. Our network of nest boxes appears to be attractive for migrants colonizing our system (because annually around 65% of individuals were not ringed) probably the year following natal dispersal, bearing in mind that intensive and extensive landscapes did not differ in prey quality at the beginning of the breeding season. For all these reasons, the implantation of nest boxes in low quality habitats could lead to an ecological trap for Tree Swallows and it would be judicious to rethink the nest boxes implantation in a goal of species conservation.

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DISCUSSION GENERALE

ET CONCLUSION

Cette discussion fait le point sur les intérêts du présent travail en récapitulant les contributions biologiques portant sur 1) les patrons de dispersion de l'Hirondelle bicolore, un passereau migrateur, dans une aire d'étude composée de nichoirs artificiels implantés dans le Sud du Québec, 2) l'influence du paysage intensif sur la fitness des hirondelles bicolores et enfin 3) le rôle des congénères dans la sélection des sites de reproduction de cet insectivore aérien en déclin. Une autre partie présente la contribution méthodologique dans l'estimation des paramètres démographiques, en discutant des avantages et limites du modèle CMR construit. Enfin, les paramètres précédemment estimés dans les trois articles ont été inclus dans un contexte démographique afin de caractériser la dynamique de la population d'Hirondelle bicolore occupant le réseau de nichoir. Ce travail ouvre des perspectives de recherche en Biologie de la conservation.

1. Contribution biologique

1.1. La dispersion de reproduction, un processus adaptatif couteux

Les patrons de la dispersion de reproduction chez l'Hirondelle bicolore se sont avérés stables dans le temps. Chez les mâles, la probabilité de disperser d'une année à l'autre est de $0{,}04 \pm 0{,}02$ alors qu'elle peut être jusqu'à 14 fois plus élevée chez les femelles. Cette différence sexuelle est largement soutenue par la littérature, en particulier chez les passereaux (Clarke *et al.,* 1997 ; Winkler *et al.,* 2004). Cette fidélité au site de reproduction est probablement générée par la forte territorialité des mâles envers leur site qu'ils sélectionnent

et défendent d'une reproduction à l'autre (Arlt et Pärt, 2008a). La décision de disperser a donc été principalement étudiée chez les femelles dans notre système d'étude.

Les résultats montrent que la décision de disperser n'est pas affectée directement par les conditions environnementales : ni la présence de compétiteurs, ni la disponibilité en ressources ou les informations portées par les congénères n'ont influencé la probabilité de disperser. Les seuls motifs mis en évidence étaient liés à l'expérience personnelle. En effet, l'échec de reproduction de l'individu favorisait l'augmentation de la probabilité de disperser de deux à sept fois, ainsi que le fait d'avoir dispersé ou non l'année précédente.

1.1.1. Influence du succès reproducteur (SRi)

L'implication du succès reproducteur individuel dans la dispersion de reproduction est abondamment documentée chez les oiseaux (Beletsky et Orians, 1987 ; Bötsch *et al.,* 2012 ; Dow et Fredga, 1983 ; Forero *et al.,* 1999 ; Newton et Marquiss, 1982 ; Schaub et Von Hirschheydt, 2009 ; Schieck et Hannon, 1989). L'intégration de cette variable était donc indispensable pour quantifier la dispersion mais nécessitait une variable discrète pour limiter le nombre de paramètres pour les analyses CMR. Dans notre cas, le succès reproducteur individuel a été défini par deux classes : les femelles avec au moins un oisillon envolé (succès) et les femelles sans production d'oisillon envolé (échec). En distinguant le succès en deux classes (nombre d'envols < à la médiane annuelle *vs.* ≥ à la médiane annuelle), nous avons affiné la définition du SRi et estimé la probabilité de dispersion pour chacune de ces classes. Chez l'Hirondelle bicolore contrairement à l'Hirondelle rustique, *Hirundo rustica*, peu importe le nombre d'oisillons envolés car dès qu'une femelle a mené un oisillon à l'envol, la probabilité de disperser est stable contrairement à (Schaub et Van Hirschheydt, 2009). Parce que les cycles de vie diffèrent entre les espèces, notamment par le nombre de couvées annuellement produites, l'information issue du succès reproducteur individuel est possiblement propre à chacune de ces deux espèces. La présence d'une deuxième couvée chez *H. rustica* augmente l'investissement parental potentiel compte tenu du nombre d'oisillons

pouvant être élevés, alors que chez *T. bicolor*, la variation du nombre de jeunes produits (en moyenne 4 ± 1) est moindre et donc possiblement moins décisive dans l'initiation de la dispersion. Bien que 25 % des femelles en reproduction n'atteignent pas le stade d'éclosion des œufs dans notre système et que 12 % des femelles dont les œufs ont éclos ont perdu la totalité de leur nichée, ces individus ont été considérés dans la même classe « échec ». Pourtant, l'investissement de la femelle depuis l'incubation jusqu'à l'envol en passant par la phase d'élevage est inégalement réparti. La décision de disperser pourrait donc être inhérente à l'avancement de la reproduction, plutôt qu'au nombre de jeunes produits.

1.1.2. Influence du comportement dispersif

Le comportement dispersif antérieur a très peu été étudié dans la décision à disperser des passereaux et plus généralement chez les oiseaux. Chez l'Hirondelle bicolore, les individus précédemment dispersants ont une probabilité de disperser deux à six fois plus élevée que les individus fidèles suivant leur SRi. Dans un contexte CMR, le comportement antérieur, techniquement appelé « effet mémoire », a été étudié uniquement chez la Bernache du Canada, *Branta canadensis*, dans un cadre de dispersion (Brownie *et al.,* 1993 ; Hestbeck *et al.,* 1991 ; Rouan *et al.,* 2009) et chez d'autres espèces longévives dans le cadre de l'étude de la survie ou du succès reproducteur (Péron *et al.,* 2010 ; Barbraud et Weimerskirch, 2012).

Pour une espèce à courte durée de vie comme l'Hirondelle bicolore, la stratégie de dispersion a clairement été identifiée comme coûteuse comparée à la stratégie de fidélité au site de reproduction, puisque la probabilité de survivre des individus dispersants est diminuée de 0,13. Notons ici que la survie estimée est la survie apparente, c'est-à-dire que les individus dispersants à l'extérieur de la zone d'étude et n'y revenant pas sont considérés comme morts. Cependant, depuis le début du suivi dans l'aire d'étude, près de 10 000 hirondelles ont été baguées et seulement 14 ont été recapturées à l'extérieur du système (dont 10 dans l'aire d'étude, mais en dehors des nichoirs, 3 à moins de 50 km de l'aire d'étude et 1 dans le Vermont, USA), ce qui va dans le sens d'une faible proportion d'émigrants hors système.

Néanmoins, l'effort de capture en dehors du réseau de nichoir est relativement faible. La survie apparente estimée doit probablement être peu biaisée par ces émigrants et donc proche de la survie réelle. L'augmentation de la mortalité chez les dispersants semble, d'après la littérature, principalement associée à la recherche d'un nouveau site de reproduction et à l'établissement sur un nouveau site, période durant laquelle les individus s'exposent à davantage de risques : prospection, prédation, compétition etc. (Bonte *et al.,* 2012 ; Bowler et Benton, 2005).

Le maintien de ce comportement dispersif coûteux d'une année à l'autre laisse suggérer que ce caractère est propre à l'individu. Ces dernières années, il a été montré que les individus dispersants ont des adaptations physiologiques, morphologiques ou encore des prédispositions comportementales initiant le comportement de dispersion (Cote *et al.,* 2010). Physiologiquement, les dispersants ont une activité hormonale (corticostérone, testostérone, sérotonine) plus élevée que les résidents (Belthoff et Dufty, 1998 ; Clobert *et al.,* 2009). Morphologiquement, des adaptations aux déplacements ont été mises en avant. Chez les passereaux, la forme des ailes s'est effilée au cours du temps avec la nécessité de disperser et l'augmentation des déplacements entraînée par la fragmentation des habitats (Desrochers, 2010). Ces adaptations morphologiques découlant de la nécessité de se déplacer ont été acquises sur un siècle, ce qui montre l'héritabilité de ces adaptations à la dispersion. Cette héritabilité a été mise en évidence dans d'autres travaux comme chez la Rousserolle turdoïde, *Acrocephalus arundinaceus* (Hansson *et al.,* 2003) ou la Mésange charbonnière, *Parus major* (Greenwood *et al.,* 1979). Récemment, la personnalité apparait comme une autre composante intrinsèque à l'individu dans la décision à disperser. Il a été montré que les individus dispersants, par opposition aux individus résidents, présentaient des traits communs entre eux. Globalement, les dispersants sont généralement plus hardis, explorateurs, actifs et agressifs (Cote *et al.,* 2010 ; Réale *et al.,* 2007). Cette hétérogénéité individuelle joue un rôle important dans la structuration spatiale d'une population et sa dynamique, entre autre pour l'initiation des processus de colonisation de nouveaux habitats (Leimar et Norberg, 1997). De plus, l'agressivité des dispersants permet ainsi aux individus de s'imposer dans un nouvel habitat face à des compétiteurs (Duckworth, 2008 ; Duckworth et Badyaev, 2007). Par ailleurs, en

décomposant les effectifs des phénotypes des femelles Hirondelle bicolore recapturées deux années consécutives dans le Sud du Québec suivant leur succès reproducteur et leur comportement dispersif de l'année précédente, seulement 5 % des reproductrices représentent la portion d'individus fortement dispersants (probabilité de disperser de 0,55) et 80 % des reproductrices représentent la portion d'individus fortement fidèles (probabilité de disperser de 0,96) (Fig. 1). Le phénotype dispersant est donc minoritaire dans la population comparativement à la proportion des individus fidèles à leur site de reproduction. La dispersion apparait donc comme un processus coûteux, répondant à un échec de reproduction et visant à l'améliorer par un changement de site à la prochaine occasion de reproduction.

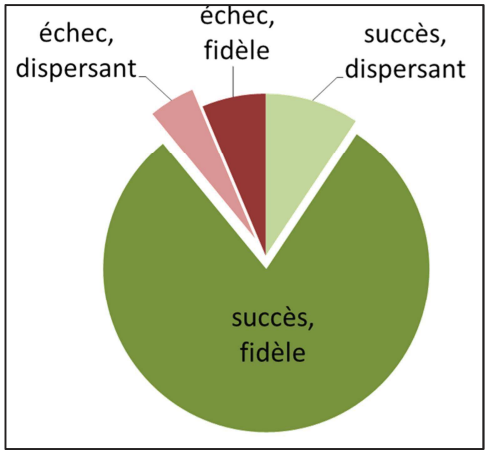

Figure 1 : Proportion des 4 phénotypes liés à la probabilité de disperser des femelles Hirondelle bicolore capturées deux années consécutives suivant leur succès reproducteur (succès ou échec) et leur comportement dispersif antérieur (fidèle au site ou dispersive), dans le Sud du Québec.

1.2. Quand le paysage intensif affecte la fitness

Nous venons de voir que la décision de disperser entre deux saisons de reproduction chez l'Hirondelle bicolore n'est pas directement liée aux conditions environnementales, mais serait affectée par le succès reproducteur individuel. Pourtant, survie et succès reproducteur sont directement affectés par l'environnement. En explorant deux échelles spatiales, une échelle proximale autour du nichoir (rayon de 300 m) et une échelle régionale (rayon de 4 km), nous

avons montré que la proportion de cultures intensives (soja, maïs, céréales) proche des nichoirs affecte le succès reproducteur et la densité en hirondelles sur les fermes, alors qu'à l'échelle régionale, celle-ci influence faiblement la probabilité de survivre.

1.2.1. Effets directs du paysage intensif

Bien que la composition du paysage en cultures intensives n'ait pas significativement diminué la probabilité de survivre, le paysage intensif a drastiquement diminué le nombre d'oisillons envolés par femelle. Dans un paysage sans culture intensive, le nombre moyen d'envols par femelle par année est de 4, alors qu'il chute à 1 lorsque la proportion de cultures intensives est supérieure à 30 %. Alors que le nombre d'envols est fortement corrélé au nombre d'œufs pondus, il a déjà été montré dans notre système que la taille de couvée était diminuée d'un œuf en milieu intensif comparé au milieu extensif (Ghilain et Bélisle, 2008), mais cela n'explique pas entièrement la diminution des envols en milieu intensif. Cette diminution peut avoir différentes causes, incluant une diminution des performances reproductrices des parents ou une mortalité des oisillons d'origine environnementale. Récemment, de nouvelles études ont montré la nocivité liée à l'utilisation de produits phytosanitaires dans l'agriculture intensive sur la survie et l'investissement reproducteur des oiseaux (Gibbons *et al.,* 2014 ; Hallmann *et al.,* 2014). Les pesticides systémiques diffusent dans toutes les parties de la plante dont le nectar et le pollen, et sont accumulés dans les invertébrés. Le transfert de ces produits se fait à travers le temps via la rémanence de la molécule chimique dans le sol et sa circulation dans le réseau trophique (Smits *et al.,* 2005). Dans notre aire d'étude, 38 substances phytosanitaires ont été retrouvées dans la diète alimentaire de l'Hirondelle bicolore, maillon intermédiaire de la chaine alimentaire (Haroune *et al.,* soumis). Certains pesticides, comme le DDT (Bishop *et al.,* 2000 ; Nocera *et al.,* 2012) ou le BTi utilisé dans la lutte biologique des insectes piqueurs (Poulin *et al.,* 2010), favorisent la mortalité des insectes, ce qui affecte indirectement les insectivores aériens en diminuant les ressources alimentaires. D'autres granivores subissent directement l'effet létal à forte dose des néonicotinoïdes (Goulson, 2013). Chez la Perdrix rouge, *Alectoris rufa,* les capacités reproductrices des parents sont diminuées à la fois par la

réduction de la taille de couvée, le retard de la date de ponte, et la survie des oisillons dont la réponse immunitaire est diminuée en présence de néonicotinoïdes (Lopez-Antia *et al.,* 2015). Indirectement, les soins parentaux sont également diminués en paysage intensif où le temps de quête alimentaire est augmenté pour faire face à une ressource en diptères moins abondante (Lamoureux, 2010). L'ensemble de ces résultats montre donc une grande diversité d'effets directs et indirects diminuant le succès reproducteur et la survie des oiseaux champêtres en milieu intensif.

1.2.2. Effets indirects par la présence du Moineau domestique

L'augmentation des surfaces agricoles et la construction de bâtiments de stockage de grains ont également favorisé l'installation d'espèces généralistes étroitement liées et adaptées au milieu agricole urbanisé tel le paysage intensif. Parmi celle-ci, le Moineau domestique est un des compétiteurs de l'Hirondelle bicolore pour l'appropriation des cavités de nidification (Robillard *et al.,* 2013). Nos résultats ont montré que la présence du Moineau domestique sur un site augmentait les abandons précoces de reproduction des femelles hirondelles lorsque la ferme était peu abondante en hirondelles. Néanmoins, suivant le statut reproducteur des femelles, la présence de moineaux n'avait pas le même effet sur les abandons plus tardifs. En échec de reproduction, la survie des femelles augmentait de 40 % en présence de moineaux par rapport aux femelles sur des sites sans moineau. En supposant que le succès reproducteur soit un proxy de la condition de la femelle (Reznick *et al.,* 2000 ; Pellerin, 2012), on peut alors mettre en relation le succès reproducteur, la survie, la condition de la femelle et l'influence du moineau. L'effet positif d'un compétiteur sur la survie des femelles en échec pourrait être dû à un abandon précoce bénéfique pour ces femelles en moins bonne condition, pour lesquelles le coût de la reproduction aurait pu diminuer leur chance de survivre. En revanche, pour les femelles ayant pu mener à terme leur reproduction, considérées comme des femelles en bonne condition, la mortalité est de 24 % plus élevée en présence de moineaux qu'en absence. Ce même effet du compétiteur a aussi été montré chez les hirondelles mâles avec une mortalité de 7 à 19 %. Cette influence négative des moineaux serait directement liée au coût de la défense

du territoire par les hirondelles, où les moineaux s'imposent fortement dans les zones les plus proches des bâtiments de ferme et globalement en milieu intensif (Robillard *et al.,* 2013).

Les paysages cultivés intensivement étant défavorables au maintien de la fitness, il est peu surprenant que la densité en hirondelles y soit moins élevée. Cependant, l'évitement de ce milieu n'est pas total et le taux d'occupation des nichoirs est de 5,4 ± 2,3 sur les fermes de milieu intensif contre 6,8 ± 1,9 dans les fermes de milieu extensif (catégories définies sur le seuil de la médiane annuelle de la proportion de cultures intensives sur chaque ferme). Il a également été montré que l'installation de nichoirs dans des zones précédemment désertées favorisait la recolonisation, ce qui pourrait expliquer la faible différence d'occupation des nichoirs entre agroécosystèmes intensifs et extensifs (Holt et Martin, 1997). De plus, en début de saison de reproduction et suivant les années, le milieu intensif peut s'avérer aussi abondant en ressources alimentaires que le milieu extensif (Rioux-Paquette *et al.,* 2012). Ce n'est que pendant la période d'élevage des jeunes que les diptères se retrouvent moins abondants en milieu intensif, piégeant ainsi les hirondelles qui s'établissent dans des zones de moins bonne qualité.

1.3. Attractivité des congénères

1.3.1. Succès reproducteur des congénères (SRc)

Contrairement aux prédictions, le succès reproducteur des congénères (SRc) ne s'est pas avéré être pris en compte dans la décision à disperser. Plusieurs hypothèses peuvent être avancées pour expliquer ce résultat, mais l'une des principales limites à l'utilisation de cette information reste l'incertitude quant à la date de prospection des sites par les reproducteurs. La pose récente de géo-localisateurs sur des hirondelles bicolores nichant en Nouvelle-Écosse indique que les individus initient leur migration automnale dans un intervalle de temps très court après l'envol puisque la majorité des individus équipés étaient rendus aux USA dès la mi-juillet (Burke, 2014). Dans cette optique, il est difficile de penser que les hirondelles aient le temps

de prospecter suite à leur reproduction si elle a été menée à terme. Il s'ensuit que le nombre d'oisillons à l'envol peut donc difficilement être une information prise en compte par l'Hirondelle bicolore, bien qu'elle le soit chez le Gobemouche à collier, *Ficedula albicollis,* un passereau proche de l'hirondelle de par son comportement territorial et l'attraction des mâles pour les sites de reproduction les plus denses en congénères (Doligez *et al.,* 1999). Néanmoins, les hirondelles bicolores pourraient se fier à d'autres informations témoignant d'échec de reproduction (e.g., nombre d'œufs non éclos, d'oisillons morts au nichoir, etc.) ou encore de l'occupation de la cavité, voire du succès de reproduction (e.g., présence de nid, de fèces dans le nichoir) (Ghilain et Bélisle, 2008). Une autre hypothèse qui peut être avancée pour expliquer le non effet des congénères dans la décision à disperser est l'éloignement entre les fermes du système. En effet, si les micro-colonies sont trop espacées, il se peut que le coût de la prospection soit plus élevé que le coût gagné dans l'acquisition d'information pour la sélection du site chez cette espèce déjà peu dispersante. Si tel est le cas, les individus ne peuvent percevoir l'information publique sur d'autres micro-colonies que la leur. Par conséquent, les données sur le SRc du site de reproduction ne pourraient pas être comparées à l'information sur un autre site, ce qui serait donc peu informatif pour initier la décision à disperser des hirondelles.

Néanmoins, les sites les plus productifs en oisillons envolés sont également les plus occupés l'année suivante pour l'Hirondelle bicolore tout comme chez de nombreux passereaux (Brown *et al.,* 2000 ; Pärt et Doligez, 2003 ; Stamps, 1988). Ce résultat suppose que les individus utilisent cette information pour s'établir une fois la décision de disperser initiée, et/ou simplement que le succès reproducteur des congénères est fortement corrélé au succès reproducteur individuel. Dans notre système, le SRi est lié modérément au SRc (V de Cramer = 0,58), mais la répartition des hirondelles est biaisée en faveur des fermes les plus productives en envols, puisque 69 % des établissements se font sur les sites à fort SRc. De plus, le SRi est deux fois meilleur sur une ferme avec un bon SRc que sur une ferme avec un mauvais SRc, ce qui témoigne d'un lien entre les deux variables. La dépendance de ces deux variables ne permet pas d'exclure que l'information portée par le SRc soit prise en compte dans la sélection des sites de reproduction.

1.3.2. Densité locale et régionale en congénères

La densité en congénères sur une ferme (densité locale) semble être un indice de la bonne qualité du milieu (Beauchamp *et al.*, 1997 ; Doligez *et al.,* 2003) plus efficace que le SRc, puisque cette variable a été retenue dans les modèles de survie et de succès reproducteur individuel (alors que le SRc n'a été retenu que sur le SRi). Fletcher (2006) a montré que les zones de reproduction les plus denses en congénères sont également celles où la survie et le succès reproducteur des individus sont les meilleures. Chez les espèces où le taux de copulation hors couple est élevé, il est donc supposé que l'occupation des sites denses en partenaires facilite les copulations hors couple (Lessard *et al.,* 2014 ; Westneat et Sherman, 1997). Cependant, l'avantage des sites denses en hirondelles n'est pas clairement identifié. Dans notre système, la densité ne semble pas avoir d'effet négatif sur la fitness ou la sélection des sites puisqu'il ne semble pas y avoir une forte compétition pour les sites de reproduction. De fait, seulement 61 ± 15 % des nichoirs sont occupés dans le réseau, lequel n'est donc pas saturé. La densité en congénères à une échelle régionale (rayon de 15 km autour du nichoir) serait un indice de la qualité du milieu de reproduction, puisque les régions les plus denses seraient les plus attractives.

1.4. Bilan

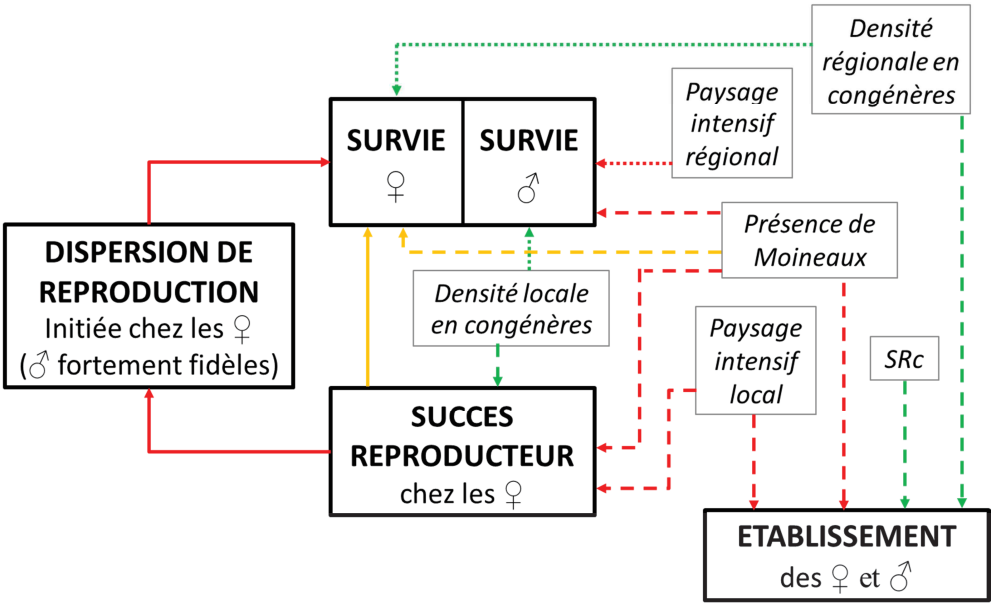

Figure 2 : Récapitulatif des variables environnementales affectant les paramètres démographiques de survie, dispersion et succès reproducteur selon le sexe des individus chez l'Hirondelle bicolore. Le SRi des mâles n'a pas été étudié puisque la présence de copulation hors couple complexifie la définition de ce paramètre et que leur probabilité de disperser est très faible.. Chacun des paramètres étudiés apparait en majuscule. Les variables environnementales étudiées apparaissent en italique. Les flèches rouges montrent un effet négatif, les vertes un effet positif et les oranges des effets mitigés. Flèches pleines : interactions entre les paramètres démographiques. Flèches en tirets : effet fort d'une variable environnementale sur un paramètre démographique. Flèches en pointillés : effet faible (tendance) d'une variable environnementale sur un paramètre démographique.

2. Contribution méthodologique

2.1. Avantages et limites du modèle CMR

2.1.1. Délimitation d'un seuil minimal de dispersion

Comme dans toutes les analyses CMR, l'estimation de la probabilité de disperser nécessite la définition d'un seuil de dispersion. Là où les analyses multisite permettent de calculer les déplacements entre un nombre limité de sites de recapture, la dispersion est souvent associée au changement de sites de recaptures. Dans notre aire d'étude, la structure en micro-colonies permet de définir aisément le seuil de la dispersion (retour sur une ferme deux années consécutives = fidélité, changement de ferme = dispersion), mais il n'en est pas de même pour toutes les aires d'étude où lorsqu'une grande surface est couverte par plusieurs sites de recaptures, un découpage en « régions » est de mise. La définition de ce seuil est donc propre à l'espèce et relative à la structure de l'aire d'étude et l'une des manières de le définir est d'étudier les distances de dispersion (Barlow *et al.,* 2013). L'une des précautions pour l'utilisation de ce modèle, consiste à utiliser une aire d'étude étendue où la distance entre les sites de recaptures est plus petite que la distance moyenne de dispersion de l'espèce étudiée (Koenig *et al.,* 1996), ce qui s'applique parfaitement à l'aire étudiée pour l'Hirondelle bicolore (Fig. 3).

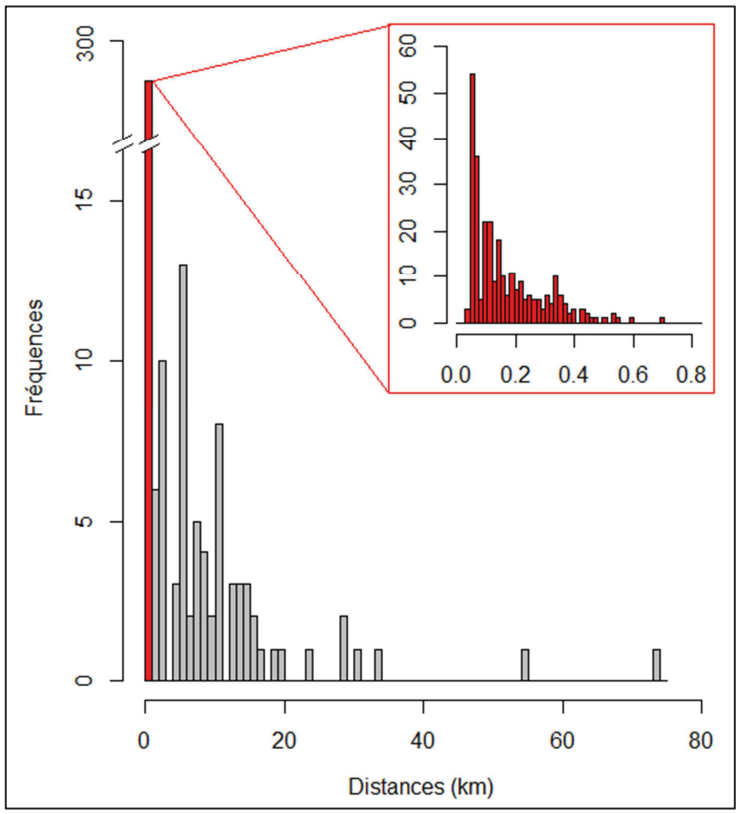

Figure 3 : Distances parcourues entre deux recaptures de femelles Hirondelle bicolore dans le Sud du Québec entre 2004 et 2012. Les recaptures ont lieu pendant la saison de reproduction entre deux années, consécutives ou non.

2.1.2. Exclusion de la connectivité et des distances

Contrairement à l'analyse des distances de dispersion (Hosner et Winkler, 2007 ; Winkler *et al.,* 2004), les analyses CMR n'intègrent pas les distances entre les sites de recaptures, elles reposent sur la détermination d'un seuil de retour au site *vs.* non-retour au site et omettent la matrice liant les sites de recaptures. L'utilisation d'une vaste aire d'étude contenant des sites relativement éloignés les uns des autres, rappelle la perte d'information concernant la matrice. Plusieurs études ont montré que la dispersion, et plus globalement les déplacements individuels, sont limités par la physionomie du paysage et sa composition. Par exemple, la probabilité de disperser diminue avec l'espacement entre les sites (Dunning *et al.,* 1992).

Cependant, la notion de connectivité entre les sites a remis en cause la contrainte de l'éloignement entre les sites dans un habitat fragmenté (Taylor *et al.,* 1993). En effet, la dispersion est dans ce cas non pas aléatoire, mais orientée suivant des « corridors » afin de minimiser les coûts du transfert entre deux sites (Bélisle, 2005 ; Conradt *et al*., 2003). Notre aire d'étude en milieu agricole est un très bon exemple d'habitat fragmenté, puisque l'action de l'homme depuis des décennies n'a cessé de diviser les parcelles forestières et d'homogénéiser les parcelles cultivées en monocultures (Bélanger et Grenier, 2002 ; Jobin *et al.,* 2003). Pour une espèce de milieux ouverts comme l'Hirondelle bicolore, on pourrait donc supposer que les déplacements seraient peu ou pas limités spatialement par le milieu agricole. Néanmoins, l'arrivée en début de migration par la voie fluviale du Saint Laurent et ses affluents, de même que l'installation sur les fermes les plus à l'ouest du système (Porlier *et al.,* 2009), laissent supposer que les hirondelles utilisent des corridors de milieux ouverts pour se déplacer, probablement pour s'alimenter d'insecte en vol en même temps qu'elles se déplacent pour sélectionner un site de reproduction. Pour autant, aucune trajectoire de dispersion n'a été observée dans notre aire d'étude (Fig. 4). Bien que l'arrivée de la migration puisse s'effectuer d'ouest en est, il est possible que la sélection des sites soit orientée suivant des indices biologiques recueillis pendant une phase de prospection pré-reproduction (e.g., milieux ouverts, densité en partenaires, abondance des proies).

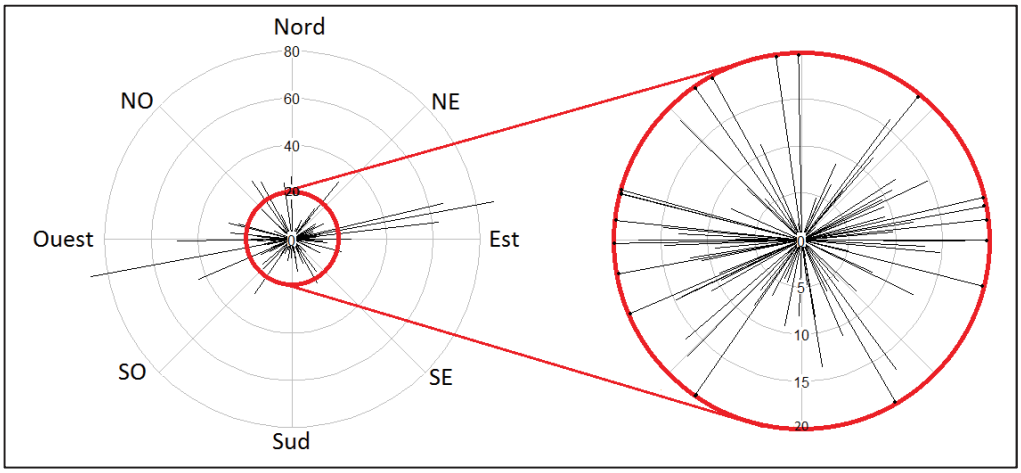

Figure 4 : Orientations et distances des déplacements des hirondelles bicolores dispersantes entre deux sites de recaptures inter-annuelles. Distances minimales-maximales parcourues en kilomètre = 1,73 km - 87,07 km.

2.1.3. Inclusion des paramètres de « nuisance »

Le développement d'un modèle de CMR a permis d'estimer les paramètres démographiques de survie et de dispersion de reproduction dans un contexte multisite. Ce modèle s'est affranchi du nombre limitant de sites de recaptures dans une aire d'étude de grande superficie. Relativement flexible, il permet d'inclure des paramètres de nuisance (i.e., pouvant donner lieu à des effets confondants) pour corriger les estimations des paramètres d'intérêt avec plus de précision. Le chapitre 2 met ainsi en lumière le contraste entre les résultats de la sélection de modèles de deux types couramment utilisés : les modèles CMR et les modèles linéaires généralisés « GLM » (Fig. 5). Dans la figure ci-dessous, la comparaison des deux modélisations montre combien l'introduction de paramètres de nuisance complexifie les relations entre les paramètres d'un modèle CMR. On y distingue des relations directes et indirectes, mettant ainsi en évidence l'effet direct de la probabilité de recapture et du SRi sur la survie ou la dispersion, alors que le SRc n'a qu'un effet indirect via sa relation directe avec le SRi. En revanche dans un contexte de GLM, les paramètres de nuisance sont absents, ce qui entraîne le remplacement des effets indirects entre les paramètres d'intérêt par une relation directe entre le SRc et la survie ou la dispersion. L'omission des relations indirectes par les GLM permet de sélectionner le SRc comme variable affectant la dispersion alors que la CMR l'exclue rapidement de la sélection de modèles. De faux effets peuvent ainsi être révélés par des modèles simples, au nombre de paramètres restreint.

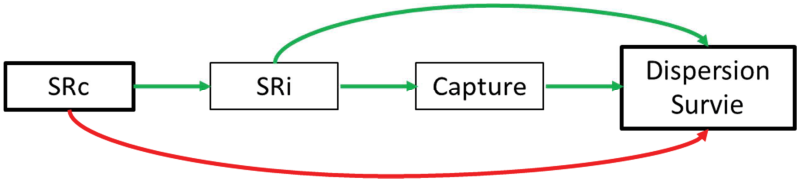

Figure 5 : Résultats de la sélection de modèles comparant les relations entre paramètres issus d'un modèle de Capture-Marquage-Recapture (CMR en vert) et d'un Modèle Linéaire Généralisé (GLM en rouge). Les paramètres estimés sont encadrés (trait fin pour les paramètres de nuisance, trait épais pour les paramètres d'intérêt). Les flèches représentent les relations montrées entre chaque paramètre suivant le type de modèle utilisé.

2.2. Pourquoi inclure la probabilité de détection?

2.2.1. Moins l'hirondelle s'investit dans la reproduction, moins elle est détectée

Bien que les probabilités de recapture soient désormais relativement élevées dans notre système, une forte hétérogénéité de détection a été notée chez les femelles. Ces dernières sont recapturées avec une probabilité de $0{,}98 \pm 0{,}01$ lorsqu'en succès de reproduction. En revanche, lorsqu'elles sont en échec, la probabilité de recapture tombe à $0{,}33 \pm 0{,}05$. Cette faible probabilité de détection des femelles en échec est en partie due au fait que les occasions de capture sont limitées en cas d'échec. Afin d'éviter un abandon précoce de la reproduction, notre protocole de capture de femelles au nid débute après un minimum de quatre jours d'incubation et peut se poursuivre tous les deux jours et ce, jusqu'au 12ème jour après la naissance des oisillons. La probabilité de détection est donc étroitement liée à l'avancement de la reproduction et au temps passé en reproduction (Choquet *et al.,* 2014). De fait, les femelles en échec avant l'incubation n'ont aucune chance d'être détectées et les femelles en échec après l'incubation sont d'autant moins détectées qu'elles abandonnent tôt leur reproduction.

Afin de remédier à ce biais de détection qui peut surestimer la mortalité et la dispersion de reproduction, ou encore le succès reproducteur, il serait envisageable de renforcer le protocole pour capturer les femelles avant les quatre jours d'incubation afin de détecter ces femelles en échec. Cependant, il faudrait alors proscrire les captures au nid pour éviter un dérangement trop intense avant l'installation définitive de la femelle au nichoir. À ce titre, nous pourrions envisager la pose de filets japonais à proximité des nichoirs pendant la phase de construction des nids, afin de capturer et baguer *ad libitum* les individus sur les sites. Envisager des captures en début de saison de reproduction permettrait probablement d'intercepter les mâles flottants (sans nichoir) ou prospecteurs. Cette proportion inconnue de mâles peut contribuer aux copulations hors couple et leur capture permettrait d'augmenter le taux d'assignation parental des jeunes qui fluctue actuellement autour de 80 % (Lessard *et al.,* 2014).

2.2.2. Un protocole hétérogène pour la capture des mâles

Quant à la probabilité de détection des mâles, elle a fluctué de 2005 à 2013 suivant les modifications apportées au protocole de capture. La première année de recapture, où les trappes masquant l'ouverture du nichoir n'étaient pas encore fonctionnelles, s'est soldée par une faible probabilité de recapture (0,56 ± 0,10). L'installation des trappes a permis d'améliorer la probabilité de recapture des mâles jusqu'à 0,80 ± 0,03. Néanmoins, depuis 2011 la probabilité de recapture a diminué pour atteindre 0,66 ± 0,06. Cette diminution peut traduire 1) une augmentation de la dispersion en dehors du système des mâles bagués ou 2) un apprentissage des mâles afin d'éviter les pièges de la capture ou encore 3) une modification du protocole de capture. Le fait que la probabilité de disperser soit constante dans le temps exclut la première hypothèse pour expliquer la diminution de la détection. S'il y avait apprentissage des mâles, les tests d'ajustements réalisés pour les analyses CMR auraient montré une « trap-shyness », c'est-à-dire une diminution des recaptures au cours de l'histoire de captures des individus. Or ces tests ont révélé un phénomène contraire : une légère trap-dépendance, traduisant probablement une forte fidélité des mâles à leur nichoir. La deuxième hypothèse est donc également exclue. Cependant, l'ajout d'une nouvelle manipulation sur les nichées a induit une diminution des occasions de captures des mâles, ce qui conforte son impact négatif sur la détection des mâles. En revanche, le protocole a été modifié depuis 2014 pour réduire l'impact de cette manipulation et ainsi augmenter la détection des mâles.

Globalement, la probabilité de recapture des mâles est plus faible que celle des femelles. Ceci découle probablement du fait qu'elle dépend du succès de reproduction de ces dernières. En effet, la capture des mâles débute une fois l'élevage des oisillons amorcé, soit quatre jours après la première éclosion. Puisque le succès reproducteur n'a pas été pris en compte dans la probabilité de détection des mâles et qu'une nichée sur trois n'atteint pas le stade d'élevage des oisillons, il est fort probable qu'une partie non négligeable des mâles reproducteurs en échec ne soit pas détectée et ainsi affecter l'estimation des effectifs des reproducteurs annuels dans le système.

3. Dynamique de la population dans le réseau artificiel de nichoirs

3.1. Perspectives

Le présent travail est une des premières études à long terme concernant la reproduction d'un passereau migrateur dont les paramètres démographiques ont été estimés avec fiabilité. L'aire d'étude couvrant une vaste surface aux habitats hétérogènes peut être qualifiée de semi naturel, c'est-à-dire composé de sites de reproduction « artificiels » afin de faciliter le suivi de l'espèce, mais dans un environnement où l'espèce est ou était naturellement présente. Dans le contexte du déclin généralisé des insectivores aériens (Nebel *et al.,* 2010), cette contribution est significative du fait que les paramètres démographiques estimés pourraient éventuellement être mis en scène dans un modèle démographique caractérisant la dynamique de la population d'Hirondelle bicolore occupant le réseau de nichoirs. L'intérêt d'un tel exercice résiderait, entre autres, dans la projection des effectifs de la population sur le long terme afin de déterminer l'impact de l'intensification agricole sur le taux de croissance de l'espèce dans le Sud du Québec. À ce titre, des scénarios se déroulant au sein d'un paysage agricole intensif ou extensif, ainsi qu'en présence ou en l'absence d'un compétiteur pour les cavités de nidification comme le Moineau domestique, permettraient de contraster le taux de croissance de populations d'Hirondelle bicolore dans quatre types d'habitats utilisés par cette espèce. Un exercice analogue a été réalisé avec le Traquet motteux, *Oenanthe oenanthe*, dans des paysages agroforestiers de la Suède (Arlt et Pärt, 2008b). Il fut trouvé que les traquets nichant dans des pâturages (associés aux milieux agricoles extensifs) présentaient un taux de croissance de population annuel de 8 %, alors que ceux nichant dans des parcelles de céréales d'automne (associées aux milieux agricoles intensifs) présentaient un taux de déclin annuel de 35 %, une différence principalement attribuable à une survie différentielle entre les deux habitats. Couplé à une analyse d'élasticité, un tel exercice permettrait donc d'identifier les paramètres démographiques sur lesquels les efforts de conservation devraient porter. La prochaine section présente des points qui devront être pris en compte lors de l'élaboration

éventuelle d'un modèle démographique pour la population d'Hirondelle bicolore nichant dans le Sud du Québec.

3.2. Fonctionnement du réseau de nichoirs

3.2.1. Oisillons produits

Entre la mise en fonction du réseau en 2004 et 2013, 7951 oisillons y ont été bagués avant l'envol (12 jours) et seulement 1,56 % de ces oisillons y ont été recapturés une fois adultes. Notons également que 11 oisillons bagués ont été recapturés en dehors du réseau, mais toujours en Estrie ou en Montérégie. Ces faibles taux de recapture suggèrent une forte mortalité des oisillons durant leur première année, possiblement lors de la migration, comme le suggéraient Hosner et Winkler (2007).

Par ailleurs, en se concentrant sur les femelles du fait qu'elles sont responsables de la descendance en alimentant les effectifs de la population, on remarque que seulement 15,59 % des oisillons de ce sexe et recapturés une fois adulte (i.e., 1,98 % de 3240 oisillons) étaient philopatriques (i.e., retrouvés adultes sur leur ferme de naissance). Cette faible proportion d'individus philopatriques laisse penser que le faible taux de recapture n'est pas uniquement la conséquence de la mortalité juvénile, mais également celle d'une dispersion natale s'effectuant probablement en dehors du réseau de nichoirs. Malheureusement, les rares recaptures d'oisillons rendent la quantification de cette dispersion inestimable avec les outils actuels.

3.2.2. Hétérogénéité des adultes

Alors que très peu d'oisillons du réseau de nichoirs sont recapturés, la présence de femelles primo reproductrices (SY, second year) dans le réseau représente tout de même 20 % des effectifs annuels de reproductrices (constitués en moyenne de 237 ± 49 femelles capturées).

Ces SY résultent d'un fort taux d'immigration (94 %) découlant de la dispersion natale. Chez les femelles plus expérimentées (ASY), le taux d'immigration avoisine les 59 %. En représentant le cycle de vie d'une hirondelle dans le réseau de nichoirs, deux systèmes doivent alors être pris en compte : le réseau artificiel et le milieu naturel (ou milieu extérieur aux nichoirs) afin d'intégrer l'immigration (Fig. 6). L'effectif de SY est dépendant de la productivité (R) des SY et des ASY du réseau, incluant la survie des jeunes produits jusqu'à la saison suivante et leur philopatrie au système, ainsi que de la proportion d'immigrants SY issus de l'extérieur du réseau. L'effectif d'ASY est quant à lui dépendant de la survie (S) des SY et des ASY du réseau incluant leur fidélité au réseau, ainsi que de la proportion d'immigrants ASY. Au sein de chaque système, le changement de site de reproduction peut s'opérer par de la dispersion.

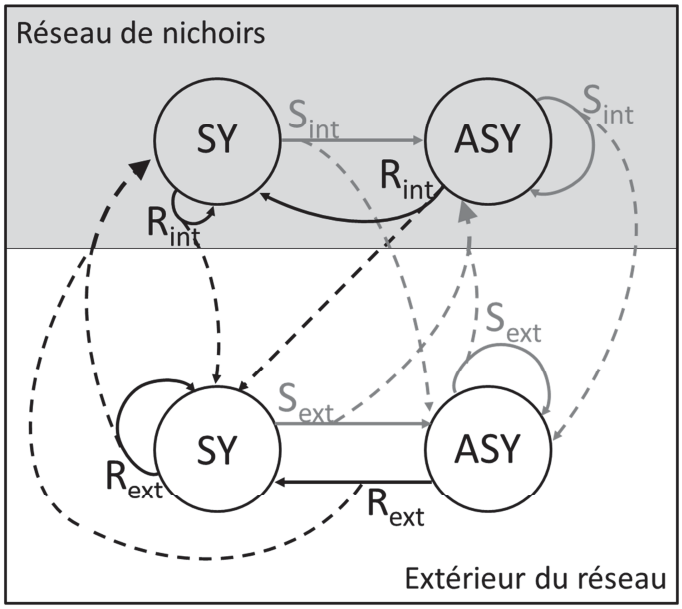

Figure 6 : Fonctionnement de la population d'Hirondelle bicolore dans le réseau de nichoirs et échangeant avec le milieu extérieur. Les reproductrices sont divisées en deux classes d'âge (SY : second year et ASY : after second year), suivant deux milieux (réseau de nichoirs « int » ou extérieur « ext »). La production d'ASY dépend de la survie (S, traits gris) des SY et des ASY entre deux années de reproduction, où S inclue la survie et la fidélité au système. La production de SY est issue de la reproduction (R, traits noirs), où R inclut le nombre de jeunes produits par individu et la survie des jeunes produits entre deux années. Les flèches pleines représentent des transitions intra-système entre deux années, alors que les flèches pointillées représentent les transitions extra-système.

Certaines transitions partant de l'extérieur du réseau se regroupent vers le réseau de nichoirs pour former un seul paramètre connu (flèches plus larges), correspondant à l'immigration des SY et ASY.

Dans les chapitres précédents, la dispersion estimée incluait à la fois la dispersion d'une ferme à une autre au sein du réseau, mais également la dispersion vers l'extérieur du système. Une adaptation du modèle décrit dans le chapitre 2 permettrait d'obtenir la fidélité au réseau et par conséquent la probabilité de disperser vers l'extérieur. L'immigration hors réseau pourrait également être prise en compte par modélisation intégrée (Abadi *et al.,* 2010 ; Schaub *et al.,* 2010).

Les résultats tirés des précédents chapitres ont révélé une forte hétérogénéité des individus nichant dans le réseau de nichoirs. Survie et fidélité au site étaient fortement dépendantes de caractéristiques intrinsèques à l'individu dont le comportement de dispersion de l'année précédente et le succès reproducteur. Alors que les modèles démographiques classiques définissent l'hétérogénéité des individus d'une population sur les différentes classes d'âge (Clark et Martin, 2007 ; Leslie, 1945), peu de modèles tiennent compte des différences comportementales qui modifient les paramètres démographiques (Pelletier et Garant, 2012). Il serait donc novateur de mettre en scène l'hétérogénéité de la survie, de la dispersion et du succès reproducteur suivant des classes d'individus aux caractéristiques communes. Dans le cas de l'Hirondelle bicolore, un modèle en quatre classes caractériserait les individus de quatre types :

- A : précédemment dispersant en échec de reproduction, avec une survie S_A, une fidélité F_A et un succès reproducteur $R_A = 0$
- B : précédemment fidèle en échec de reproduction, avec une survie S_B, une fidélité F_B et un succès reproducteur $R_B = 0$
- C : précédemment dispersant en succès de reproduction, avec une survie S_C, une fidélité F_C et un succès reproducteur R_C
- D : précédemment fidèle en succès de reproduction, avec une survie S_D, une fidélité F_D et un succès reproducteur R_D

Dans un tel modèle, l'effectif N de la population globale au temps t + 1 suivrait l'équation :

$$N(t + 1) = N(t)_A * S_A * F_A + N(t)_B * S_B * F_B + N(t)_C * S_C * F_C + N(t)_D * S_D * F_D + R_C + R_D,$$

où R inclut le nombre de jeunes produits par femelle, ayant survécu jusqu'à la première reproduction et étant revenus dans le système.

3.2.3. Contribution pour la biologie de la conservation

Si l'installation de nichoirs permet d'améliorer le suivi d'une population pour les projets de recherche (e.g., captures des reproducteurs, suivis des nids et manipulations expérimentales facilités (Jones, 2003 ; Lambrechts *et al.,* 2010), elle joue également un rôle dans la conservation des espèces en assurant la disponibilité des sites de reproduction (Bolton *et al*., 2004 ; Katzner *et al*., 2005). Cependant, de nombreux biais ou effets négatifs peuvent s'ajouter à la pose de sites de reproduction artificiels : augmentation du parasitisme au nid (Wesolowski et Stańska, 2001) ou mauvais emplacement des nichoirs (Lambrechts *et al.,* 2010). Alors que les nichoirs favorisent la réinstallation de reproducteurs dans des zones précédemment désertées (Holt et Martin, 1997), leur implantation dans des zones de moindre qualité pourrait aussi mener à accélérer le déclin de ses effectifs illustré dans la notion de piège écologique (Gates et Gysel, 1978). Cette attraction d'individus dans des habitats de moindre qualité (diminuant la survie ou le succès reproducteur) résulte de l'altération d'origine anthropique des indices autrefois fortement corrélés à la qualité de l'habitat (Bock et Jones, 2004 ; Schlaepfer *et al.,* 2002). L'identification de milieux limitant la croissance de la population permettrait donc de définir les zones propices à l'installation des nichoirs pour favoriser la croissance de la population.

ANNEXES

Annexes Chapitre 2

Appendix: Implementation of the new dispersal model in E-SURGE.

Here, we provide details and instructions to implement the new multievent capture-recapture model to estimate dispersal in program E-SURGE 1.8.5, which can be freely downloaded at http://www.cefe.cnrs.fr/en/biostatistics-and-biology-of-populations/software.
The first step is to define the number of states, events and other elements that are not used in our study (covariate, age classes etc…). Here, we have:
The states:

- Ho, to be in the same site at t and t - 1 but not observed at t and t - 1. Noted (1) in the matrix.
- oH+, to be in the same site at t and t - 1 but seen only at t. Noted (2) in the matrix.
- +H+, to be in the same site at t and t - 1 and seen at t and t - 1. Noted (3) in the matrix.
- Eo, to be in a different site at t and t - 1 but not observed at t and t - 1. Noted (4) in the matrix.
- oE+, to be in a different site at t and t - 1 but seen only at t. Noted (5) in the matrix.
- +E+, to be in a different site at t and t - 1 and seen at t and t - 1. Noted (6) in the matrix.
- D, to be dead. Noted (7) in the matrix.

The events:

- 0: individuals no recaptured at t. Noted (1) in the matrix.
- 1: individuals recaptured in the same site as the previous year. Noted (2) in the matrix.
- 2: individuals recaptured in a different site than the previous year. Noted (3) in the matrix.
- 3: individuals recaptured at t but not recaptured at t - 1. Noted (4) in the matrix.

We will be using the following parameters:

- p: initial state probability
- S: survival probability
- F: fidelity probability
- R: recapture probability
- D: detection probability, fixed to 1.

Second, one needs to provide the structure of the transition matrices using the GEPAT interface. The symbol '*' indicates the complement of the sum of a row while the symbol '-' indicates inactive cells associated to a probability of 0. Note that the same letter in two cells does not imply equality in parameter values. Lastly, it is important to remember that in the vector of initial state probabilities, the state 'dead' does not appear in GEPAT by default. We have:
Vector of Initial State:

	1	2	3	4	5	6
1	-	p	-	-	*	-

Matrices of Transition between states:

Step 1: Survival

	1	2	3	4	5	6	7
1	S	-	-	-	-	-	*
2	-	S	-	-	-	-	*
3	-	-	S	-	-	-	*
4	-	-	-	S	-	-	*
5	-	-	-	-	S	-	*
6	-	-	-	-	-	S	*
7	-	-	-	-	-	-	*

Step 2: Fidelity

	1	2	3	4	5	6	7
1	F	-	-	*	-	-	-
2	-	F	-	-	*	-	-
3	-	-	F	-	-	*	-
4	F	-	-	*	-	-	-
5	-	F	-	-	*	-	-
6	-	-	F	-	-	*	-
7	-	-	-	-	-	-	*

Step 3: Recapture

	1	2	3	4	5	6	7
1	*	R	-	-	-	-	-
2	*	-	R	-	-	-	-
3	*	-	R	-	-	-	-
4	-	-	-	*	R	-	-
5	-	-	-	*	-	R	-
6	-	-	-	*	-	R	-
7	-	-	-	-	-	-	*

Matrix of Event (detection): states in lines, events in columns.

	1	2	3	4
1	*	-	-	-
2	-	-	-	*
3	-	*	-	-
4	*	-	-	-
5	-	-	-	*
6	-	-	*	-
7	*	-	-	-

Third, the GEMACO interface allows to specify effects of interest for each parameter. Shortcuts can be used to indicate if the relation is time-dependent, state-specific or any other effect.

For example, in the fidelity matrix, one can estimate a fidelity probability (the complementary probability of the probability to disperse), by specifying f(1:6) where ‘f’ is the shortcut for ‘from’ (distinguishing each parameter by rows in the matrix) and ‘:’ for equality, meaning that all F parameters are equal in the matrix. Alternatively, one can add a memory effect by using the syntax f(1:3,4:6) to estimate one fidelity probability for individuals previously faithful (1:3) and for individuals previously dispersing (4:6), where ‘,’ is used to separate the 2 probabilities.

Fourth, one needs to go through the IVFV interface to define initial values or set parameters to some specific values. Here, we use the initial values provided by E-SURGE by default.

We refer to the E-SURGE manual: Choquet and Nogué 2011 and Choquet et al. 2009 for more details.

LITERATURE CITED :

Choquet, R., and E. Nogué. 2011. E-SURGE 1-8 user’s manual. cefe , UMR 5175, Montpellier, France. http://www.cefe.cnrs.fr/images/stories/DPTEEvolution/biostatistiques/LOGICIELS/E-SURGE-MANUAL.pdf

Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting multievent models. Pages 845–865 Modeling demographic processes in marked populations. Springer.

Supplement: R code to build the dataset for analyses in E-SURGE.

```
### Read in data
setwd('C:/Documents and Settings/lagrange/Bureau/Soumission Finale')
data<-read.table("metadata_Lagrangeetal.txt",head=T)
head(data)

### Build capture-recapture dataset
id<-unique(data$ring)
nbligne<-length(id)
dataoccaz<-matrix(NA,nrow=nbligne,ncol=11)
colnames(dataoccaz)<-
c('ring','2004','2005','2006','2007','2008','2009','2010','2011','F','M')
dataoccaz[,'ring']<-id

data04 <- subset(data,data[,'year']==2004)
data05 <- subset(data,data[,'year']==2005)
data06 <- subset(data,data[,'year']==2006)
data07 <- subset(data,data[,'year']==2007)
data08 <- subset(data,data[,'year']==2008)
data09 <- subset(data,data[,'year']==2009)
data10 <- subset(data,data[,'year']==2010)
data11 <- subset(data,data[,'year']==2011)

for (i in 1:nrow(dataoccaz)){
      id<-dataoccaz[i,'ring']
      mask<-(data[,'ring']==id) #seek the 'dataoccaz' ring in the data frame
'data'
      dataoccaz[i,2]<-
ifelse(sum(data[mask,'year']==2004),data04[data04[,'ring']==id,'farm'],0)
      dataoccaz[i,3]<-
ifelse(sum(data[mask,'year']==2005),data05[data05[,'ring']==id,'farm'],0)
      dataoccaz[i,4]<-
ifelse(sum(data[mask,'year']==2006),data06[data06[,'ring']==id,'farm'],0)
      dataoccaz[i,5]<-
ifelse(sum(data[mask,'year']==2007),data07[data07[,'ring']==id,'farm'],0)
      dataoccaz[i,6]<-
ifelse(sum(data[mask,'year']==2008),data08[data08[,'ring']==id,'farm'],0)
      dataoccaz[i,7]<-
ifelse(sum(data[mask,'year']==2009),data09[data09[,'ring']==id,'farm'],0)
      dataoccaz[i,8]<-
ifelse(sum(data[mask,'year']==2010),data10[data10[,'ring']==id,'farm'],0)
      dataoccaz[i,9]<-
ifelse(sum(data[mask,'year']==2011),data11[data11[,'ring']==id,'farm'],0)
#put in each year columns the farm number when individual was captured, and
0 when no capture
      dataoccaz[i,10]<-ifelse(sum(data[mask,'sex']=='F'),1,0)
      dataoccaz[i,11]<-ifelse(sum(data[mask,'sex']=='M'),1,0)
# add the sex for .inp format
}
head(dataoccaz)
```

```
### Build the capture-recapture dataset for the multievent approach:
site<-matrix(NA,nrow=nbligne,ncol=11)
colnames(site)<-
c('ring','2004','2005','2006','2007','2008','2009','2010','2011','F','M')
site[,'ring']<-dataoccaz[,'ring']

transformdata<-function(dataoccaz){
      for (i in 1:nrow(dataoccaz)){
            site[i,10]<-dataoccaz[i,'F']
            site[i,11]<-dataoccaz[i,'M']
#split the gender factor: one column by class for E-SURGE
            for (j in 2:(ncol(dataoccaz)-2)){
                  if (dataoccaz[i,j]!=0)
                  { #assign events
                        if (dataoccaz[i,j-1]==0)
                        {
                              site[i,j]<-3;
                        }
                        else if (dataoccaz[i,j-1]==dataoccaz[i,j])
                        {
                              site[i,j]<-1;
                        }
                        else
                        {
                              site[i,j]<-2;
                        }
                  }
                  else
                  {
                        site[i,j]<-0
                  }
            }
            site[i,2]<-ifelse(dataoccaz[i,'2004']!=0,3,0) # assign event for
the first year
      }
      site
}
result<-transformdata(dataoccaz)
head(result)

### To write the data in a 'inp' dataset ready to be used in E-SURGE
mat<-matrix(NA,nrow=nrow(result),ncol=2)
mat[,1]<-
paste(result[,'2004'],result[,'2005'],result[,'2006'],result[,'2007'],resul
t[,'2008'],result[,'2009'],result[,'2010'],result[,'2011'],sep='')
mat[,2]<-paste(result[,'F'],result[,'M'],sep=' ')
write.table(mat,file='dataset.inp',sep='
',eol=';\n',row.names=F,col.names=F,quote=F)
```

Annexes Chapitre 3

Appendices A: Description of the RSi and RSc in our system.

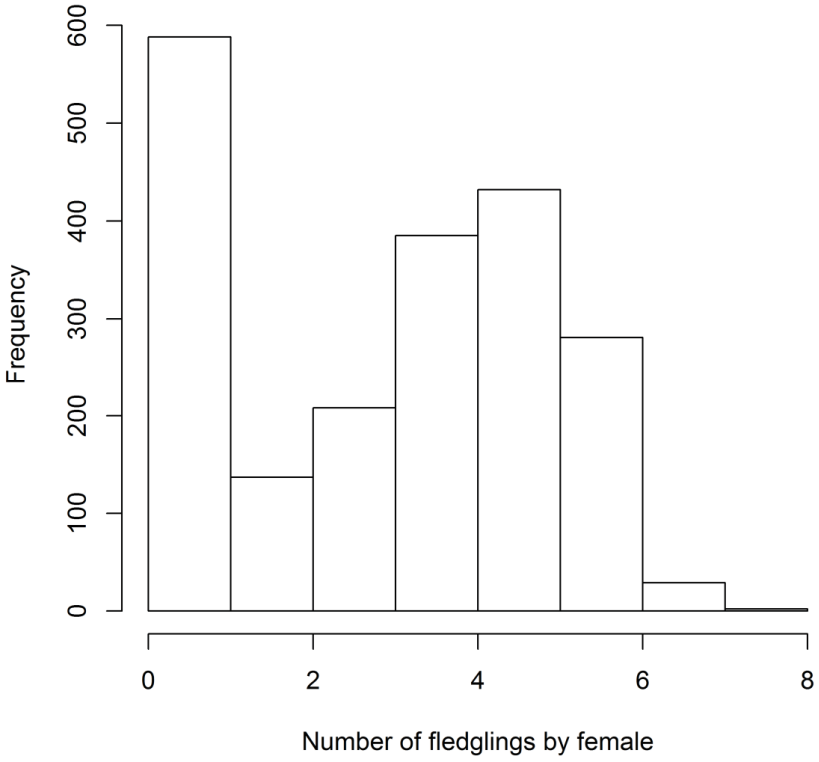

Figure A1: Distribution of the number of fledglings (RSi) by females Tree swallow in Southern Québec, Canada, since 2004 to 2013.

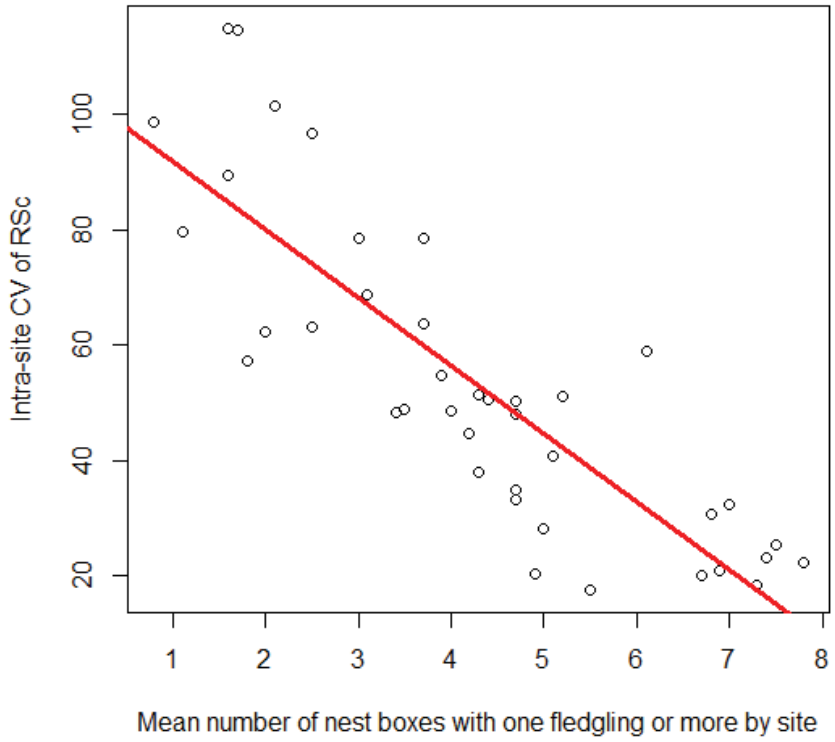

Figure A2: Coefficient of variation of the conspecifics reproductive success (RSc) through the year for each farm according to the mean number of nest boxes in success (with one fledgling or more) by farm.

Appendices B: CR method

Figure B1: Transition steps of an individual from t - 1 to t and explanation of states associated with events. The diagram shows the steps leading to the observation (at t - 1 and t) of an individual: survival (alive or dead), fidelity (Here or Elsewhere), RSc (good or bad), RSi (good or bad) and recapture (recaptured or not). Each updated information appears in bold while the old one is grayed out. We end up in the last step with 25 states (in boxes) that can generate 13 events (numbered rings).

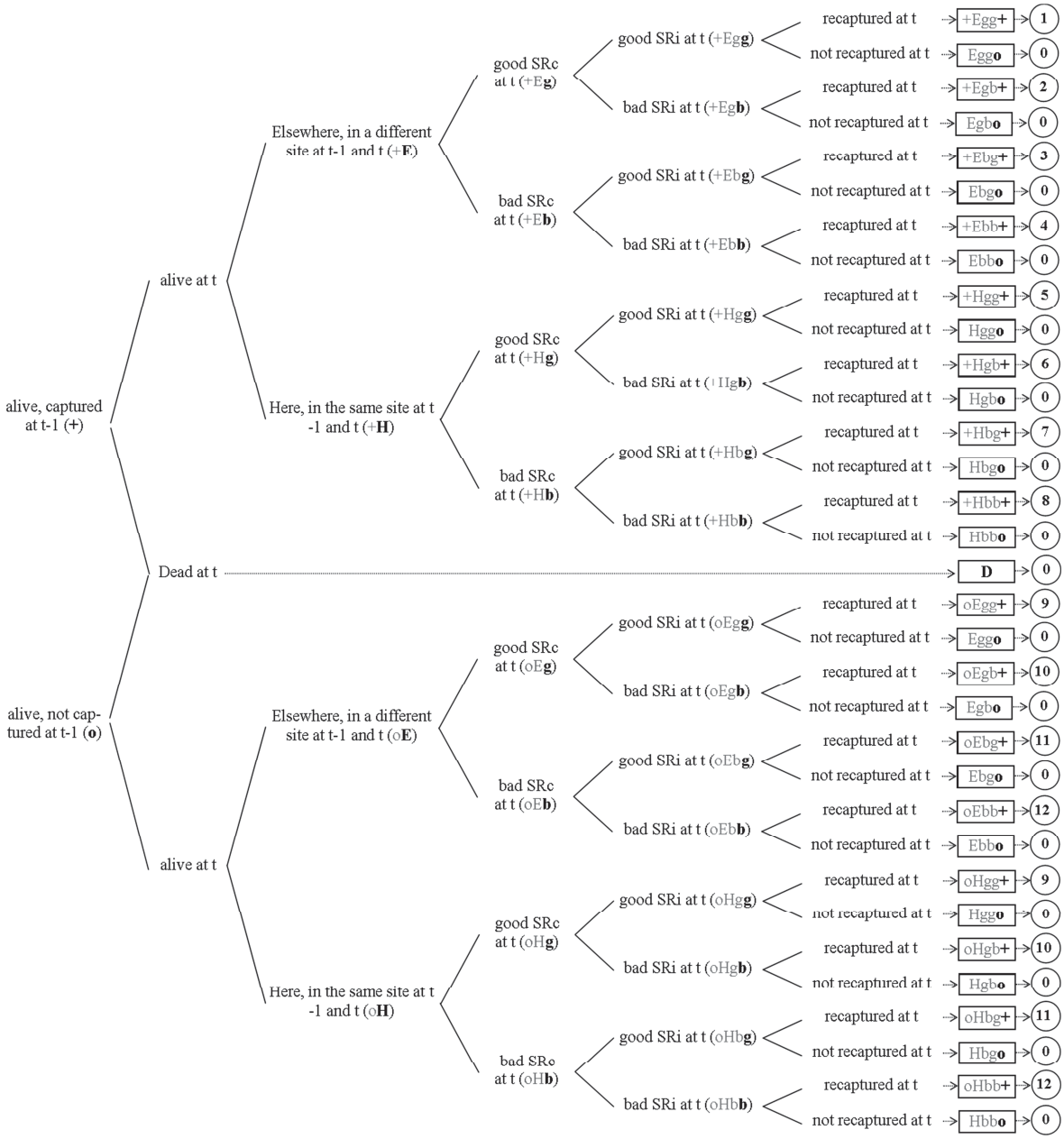

Figure B2: Matrices implemented in E-SURGE to estimate the probability to be in each state initially (π), to survive at t (S), to move or not between t and t + 1 (F), to keep or not the same RSi (I) and RSc (C) between t and t + 1, to be captured (R) at t + 1 and to be detected in the last step to link events and states. All unknown information appears in grey and for each step (or new matrix) information is actualized in black bold. Known and not concerned information on the matrix appear in black.

Initial states =

	+Egg+	+Egb+	+Ebg+	+Ebb+	oEgg+	oEgb+	oEbg+	oEbb+	Eggo	Egbo	Ebgo	Ebbo	+Hgg+	+Hgb+	+Hbg+	+Hbb+	oHgg+	oHgb+	oHbg+	oHbb+	Hggo	Hgbo	Hbgo	Hbbo
					π	π	π	π									π	π	π	1-π				

Survival =

	Egg+	Egb+	Ebg+	Ebb+	Eggo	Egbo	Ebgo	Ebbo	Hgg+	Hgb+	Hbg+	Hbb+	Hggo	Hgbo	Hbgo	Hbbo	**D**
+Egg+	S																1-S
+Egb+		S															1-S
+Ebg+			S														1-S
+Ebb+				S													1-S
oEgg+	S																1-S
oEgb+		S															1-S
oEbg+			S														1-S
oEbb+				S													1-S
Eggo					S												1-S
Egbo						S											1-S
Ebgo							S										1-S
Ebbo								S									1-S
+Hgg+									S								1-S
+Hgb+										S							1-S
+Hbg+											S						1-S
+Hbb+												S					1-S
oHgg+									S								1-S
oHgb+										S							1-S
oHbg+											S						1-S
oHbb+												S					1-S
Hggo													S				1-S
Hgbo														S			1-S
Hbgo															S		1-S
Hbbo																S	1-S
D																	1

Fidelity =

	Egg+	**E**gb+	**E**bg+	**E**bb+	**E**ggo	**E**gbo	**E**bgo	**E**bbo	**H**gg+	**H**gb+	**H**bg+	**H**bb+	**H**ggo	**H**gbo	**H**bgo	**H**bbo	D
Egg+	1-F								F								
Egb+		1-F								F							
Ebg+			1-F								F						
Ebb+				1-F								F					
Eggo					1-F								F				
Egbo						1-F								F			
Ebgo							1-F								F		
Ebbo								1-F								F	
Hgg+	1-F								F								
Hgb+		1-F								F							
Hbg+			1-F								F						
Hbb+				1-F								F					
Hggo					1-F								F				
Hgbo						1-F								F			
Hbgo							1-F								F		
Hbbo								1-F								F	
D																	1

1

$$RSc = \begin{array}{c|cccccccccccccccc|c}
 & Egg+ & Egb+ & Ebg+ & Ebb+ & Eggo & Egbo & Ebgo & Ebbo & Hgg+ & Hgb+ & Hbg+ & Hbb+ & Hggo & Hgbo & Hbgo & Hbbo & D \\
\hline
Egg+ & 1-C & & C & & & & & & & & & & & & & & \\
Egb+ & & 1-C & & C & & & & & & & & & & & & & \\
Ebg+ & C & & 1-C & & & & & & & & & & & & & & \\
Ebb+ & & C & & 1-C & & & & & & & & & & & & & \\
Eggo & & & & & 1-C & & C & & & & & & & & & & \\
Egbo & & & & & & 1-C & & C & & & & & & & & & \\
Ebgo & & & & & C & & 1-C & & & & & & & & & & \\
Ebbo & & & & & & C & & 1-C & & & & & & & & & \\
Hgg+ & & & & & & & & & 1-C & & C & & & & & & \\
Hgb+ & & & & & & & & & & 1-C & & C & & & & & \\
Hbg+ & & & & & & & & & C & & 1-C & & & & & & \\
Hbb+ & & & & & & & & & & C & & 1-C & & & & & \\
Hggo & & & & & & & & & & & & & 1-C & & C & & \\
Hgbo & & & & & & & & & & & & & & 1-C & & C & \\
Hbgo & & & & & & & & & & & & & C & & 1-C & & \\
Hbbo & & & & & & & & & & & & & & C & & 1-C & \\
\hline
D & & & & & & & & & & & & & & & & & 1
\end{array}.$$

2

$$RSi = \begin{array}{c|cccccccccccccccc|c}
 & Egg+ & Egb+ & Ebg+ & Ebb+ & Eggo & Egbo & Ebgo & Ebbo & Hgg+ & Hgb+ & Hbg+ & Hbb+ & Hggo & Hgbo & Hbgo & Hbbo & D \\
\hline
Egg+ & 1-I & I & & & & & & & & & & & & & & & \\
Egb+ & I & 1-I & & & & & & & & & & & & & & & \\
Ebg+ & & & 1-I & I & & & & & & & & & & & & & \\
Ebb+ & & & I & 1-I & & & & & & & & & & & & & \\
Eggo & & & & & 1-I & I & & & & & & & & & & & \\
Egbo & & & & & I & 1-I & & & & & & & & & & & \\
Ebgo & & & & & & & 1-I & I & & & & & & & & & \\
Ebbo & & & & & & & I & 1-I & & & & & & & & & \\
Hgg+ & & & & & & & & & 1-I & I & & & & & & & \\
Hgb+ & & & & & & & & & I & 1-I & & & & & & & \\
Hbg+ & & & & & & & & & & & 1-I & I & & & & & \\
Hbb+ & & & & & & & & & & & I & 1-I & & & & & \\
Hggo & & & & & & & & & & & & & 1-I & I & & & \\
Hgbo & & & & & & & & & & & & & I & 1-I & & & \\
Hbgo & & & & & & & & & & & & & & & 1-I & I & \\
Hbbo & & & & & & & & & & & & & & & I & 1-I & \\
\hline
D & & & & & & & & & & & & & & & & & 1
\end{array}.$$

$$Recapture = \begin{array}{c|cccccccccccccccccccccccc|c}
 & +Egg+ & +Egb+ & +Ebg+ & +Ebb+ & oEgg+ & oEgb+ & oEbg+ & oEbb+ & Eggo & Egbo & Ebgo & Ebbo & +Hgg+ & +Hgb+ & +Hbg+ & +Hbb+ & oHgg+ & oHgb+ & oHbg+ & oHbb+ & Hggo & Hgbo & Hbgo & Hbbo & D \\
\hline
Egg+ & R & & & & & & & & 1-R & & & & & & & & & & & & & & & & \\
Egb+ & & R & & & & & & & & 1-R & & & & & & & & & & & & & & & \\
Ebg+ & & & R & & & & & & & & 1-R & & & & & & & & & & & & & & \\
Ebb+ & & & & R & & & & & & & & 1-R & & & & & & & & & & & & & \\
Eggo & & & & & R & & & & 1-R & & & & & & & & & & & & & & & & \\
Egbo & & & & & & R & & & & 1-R & & & & & & & & & & & & & & & \\
Ebgo & & & & & & & R & & & & 1-R & & & & & & & & & & & & & & \\
Ebbo & & & & & & & & R & & & & 1-R & & & & & & & & & & & & & \\
Hgg+ & & & & & & & & & & & & & R & & & & & & & & 1-R & & & & \\
Hgb+ & & & & & & & & & & & & & & R & & & & & & & & 1-R & & & \\
Hbg+ & & & & & & & & & & & & & & & R & & & & & & & & 1-R & & \\
Hbb+ & & & & & & & & & & & & & & & & R & & & & & & & & 1-R \\
Hggo & & & & & & & & & & & & & & & & & R & & & & 1-R & & & & \\
Hgbo & & & & & & & & & & & & & & & & & & R & & & & 1-R & & & \\
Hbgo & & & & & & & & & & & & & & & & & & & R & & & & 1-R & & \\
Hbbo & & & & & & & & & & & & & & & & & & & & R & & & & 1-R \\
\hline
D & & & & & & & & & & & & & & & & & & & & & & & & & 1
\end{array}.$$

$$
Detection = \begin{array}{c}
\\ +Egg+ \\ +Egb+ \\ +Ebg+ \\ +Ebb+ \\ oEgg+ \\ oEgb+ \\ oEbg+ \\ oEbb+ \\ Eggo \\ Egbo \\ Ebgo \\ Ebbo \\ +Hgg+ \\ +Hgb+ \\ +Hbg+ \\ +Hbb+ \\ oHgg+ \\ oHgb+ \\ oHbg+ \\ oHbb+ \\ Hggo \\ Hgbo \\ Hbgo \\ Hbbo \\ D
\end{array}
\begin{array}{c}
\begin{array}{ccccccccccccc}
\mathbf{0} & \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} & \mathbf{6} & \mathbf{7} & \mathbf{8} & \mathbf{9} & \mathbf{10} & \mathbf{11} & \mathbf{12}
\end{array} \\
\begin{pmatrix}
 & 1 & & & & & & & & & & & \\
 & & 1 & & & & & & & & & & \\
 & & & 1 & & & & & & & & & \\
 & & & & 1 & & & & & & & & \\
 & & & & & & & & & 1 & & & \\
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1 & & & & & & & & & & & & \\
1 & & & & & & & & & & & &
\end{pmatrix}
\end{array}
$$

Appendices C: Model selections with CR analyses

Table C1: Forward model selection with Capture-Recapture analysis to determine the basic structure of demographic parameters in tree swallow. Each model is defined by five parameters: S, F, I, C and R. The effects were tested alone, in addition (+) or in interaction (*) including the main effects. A constant parameter is represented by 'i'. *k* is the number of parameters of each model and $\Delta QAIC_c$ ($\hat{c}$ = 1.94) gives the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest: $Model_{55}$, $QAIC_c$ = 4265.80, deviance = 8227.94). # is the number of the model. The best models for each parameter are in bold and the null model is #11.
The best structure of effects attained is retained when moving to the next type of parameter.

Parameters	Effects	*k*	Δ QAICc	#
Recapture (R)	i	11	176.96	11
	RSi	**12**	**124.22**	**14**
	t	19	191.67	17
	RSi+t	20	128.90	18
	RSi*t	28	140.82	19
Transition between a good/bad RSc (C)	**RSc**	**13**	**81.96**	**20**
	t	20	135.78	21
	RSc+t	21	94.22	22
	RSc*t	29	105.27	23
Transition between a good/bad RSi (I)	RSi	14	83.91	24
	RSc	14	80.14	25
	memory	14	79.69	26
	RSi*RSc	**16**	**67.80**	**27**
	RSc*memory	16	74.77	28
	RSi*memory	16	82.98	29
	RSi*RSc*memory	20	68.57	30
	t	21	90.19	31
	age	14	83.99	32
	RSi*RSc+t	24	76.99	33
	RSi*RSc*t	48	100.95	34
	RSi*RSc*age	20	72.94	35
Survival (S)	memory	19	66.35	38
	RSi	**17**	**25.17**	**39**
	RSi*memory	21	30.52	44
	t	24	68.19	45
	age	17	67.20	46
	RSi+t	25	30.86	47

	RSi*t	33	42.07	48
	RSi*age	19	27.05	49
Fidelity (F)	memory	20	10.94	52
	RSi	18	7.46	53
	RSc	18	22.19	54
	RSi*memory	**22**	**0**	**55**
	RSc*memory	22	11.859	56
	RSi*RSc	20	9.0016	57
	RSi*RSc*memory	26	7.2234	58
	t	25	30.393	59
	age	18	27.001	60
	RSi*memory+t	30	3.0204	61
	RSi*memory*t	52	36.487	62
	RSi*memory*age	24	2.4797	63

Table C2: Second forward model selection with Capture-Recapture analysis to evaluate the effects of variables on survival and individual reproductive success. R, C and F conserved the basic structure from the selection 1 (as in #55, table C1) and we retested the effect of the variables memory, RSi, age and time alone, in addition (+) or in interaction (*) on S and I. A constant parameter is represented by 'i'. *k* is the number of parameters of each model used to calculate the $\Delta QAIC_c$ ($\hat{c}$ = 1.94) giving the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest: $Model_{55}$, $QAIC_c$ = 4265.80, deviance = 8227.94). # is the number of the model. The best model for each parameter is in bold.

Parameters	Effects	*k*	Δ QAICc	#
Survival (S)	i	21	42.66	S11
	memory	22	36.88	S38
	RSi	**22**	**0.00**	**55**
	RSi*memory	24	0.91	S44
	t	29	43.16	S12
	Age	22	42.08	S13
	RSi+t	30	5.84	S47
	RSi*t	38	17.17	S48
	(RSi)*age	24	1.95	S49
Transition between a good/bad RSi (I)	i	19	14.55	I20
	RSi	20	16.59	I24
	RSc	20	12.22	I25
	memory	20	16.51	I26
	RSi*RSc	**22**	**0.00**	**55**
	RSc*memory	22	9.24	I28
	RSi*memory	22	19.32	I29
	RSi*RSc*memory	26	3.83	I30
	t	27	25.02	I31
	Age	20	16.42	I32
	RSi*RSc+t	34	11.93	I33
	RSi*RSc*t	90	81.27	I34
	RSi*RSc*age	34	17.09	I35

Table C3: Model selection with 3 classes of individual reproductive success (n: null RSi, m: medium RSi, h: high RSi). Each model is defined by four parameters: S, F, I and R. The effects of RSi, previous dispersal behavior (memory) and age were tested alone, in addition (+) or in interaction (*) including the main effects. A constant parameter is represented by 'i'. "RSi 2 classes" pools medium and high categories in the same class *vs.* null class. "RSi 2 reversed classes" pools null and medium categories in the same class *vs.* high class. *k* is the number of parameters used to calculate the weight (w_i) of each model and $\Delta QAIC_c$ ($\hat{c}$ = 1.94) gives the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest: $Model_{56}$, $QAIC_c$ = 3928.37, deviance = 7589.96). # is the number of the model. The best model for each parameter is in bold and the null model is #12.

Parameters	Effects	*k*	Δ QAICc	w_i	#
Recapture (R)	i	6	101.54	0.00	12
	RSi 2 classes	**7**	**87.03**	**0.00**	**13**
	memory	6	101.54	0.00	14
	RSi*memory	8	88.17	0.00	15
	t	14	115.61	0.00	16
	RSi 2 classes+t	15	97.88	0.00	17
	RSi 2 classes*t	15	97.88	0.00	18
	RSi 2 classes*age	9	87.74	0.00	19
	RSi 2 classes*t*age	39	128.01	0.00	20
	RSi 2 classes+t*age	17	97.28	0.00	21
Transition between a good/bad RSi (I)	i	7	87.03	0.00	13
	RSi 2 classes	8	86.59	0.00	24
	RSi 2 reversed classes	8	78.18	0.00	25
	RSi 3 classes	**12**	**67.62**	**0.00**	**27**
	memory	8	86.89	0.00	28
	RSi 3 classes*memory	18	73.88	0.00	29
	t	15	99.20	0.00	30
	Age	8	89.00	0.00	31
	RSi 3 classes+t	20	81.26	0.00	32
	RSi 3 classes*t	60	122.56	0.00	33
	RSi 3 classes*age	18	77.27	0.00	34
Survival (S)	i	12	67.62	0.00	27
	memory	13	88.76	0.00	38
	RSi 3 classes	**14**	**23.12**	**0.00**	**39**
	RSi 2 classes	13	23.78	0.00	40
	RSi 2 reversed classes	13	43.18	0.00	41
	RSi 3 classes*memory	17	27.37	0.00	42
	t	20	67.70	0.00	44

	Age	12	86.74	0.00	45
	RSi 3 classes+t	22	28.12	0.00	46
	RSi 3 classes*t	38	53.21	0.00	47
	RSi 3 classes*age	17	27.03	0.00	48
Fidelity (F)	i	14	23.12	0.00	51
	memory	15	10.25	0.00	52
	RSi 3 classes	16	7.38	0.02	53
	RSi 2 classes	15	5.50	0.04	54
	RSi 2 reversed classes	15	18.72	0.00	55
	RSi 2 classes	**17**	**0.00**	**0.70**	**56**
	t	22	28.35	0.00	57
	Age	15	24.96	0.00	58
	RSi 2 classes+t	25	4.07	0.09	59
	RSi 2 classes*t	48	39.99	0.00	60
	RSi 2 classes*age	20	3.13	0.15	61

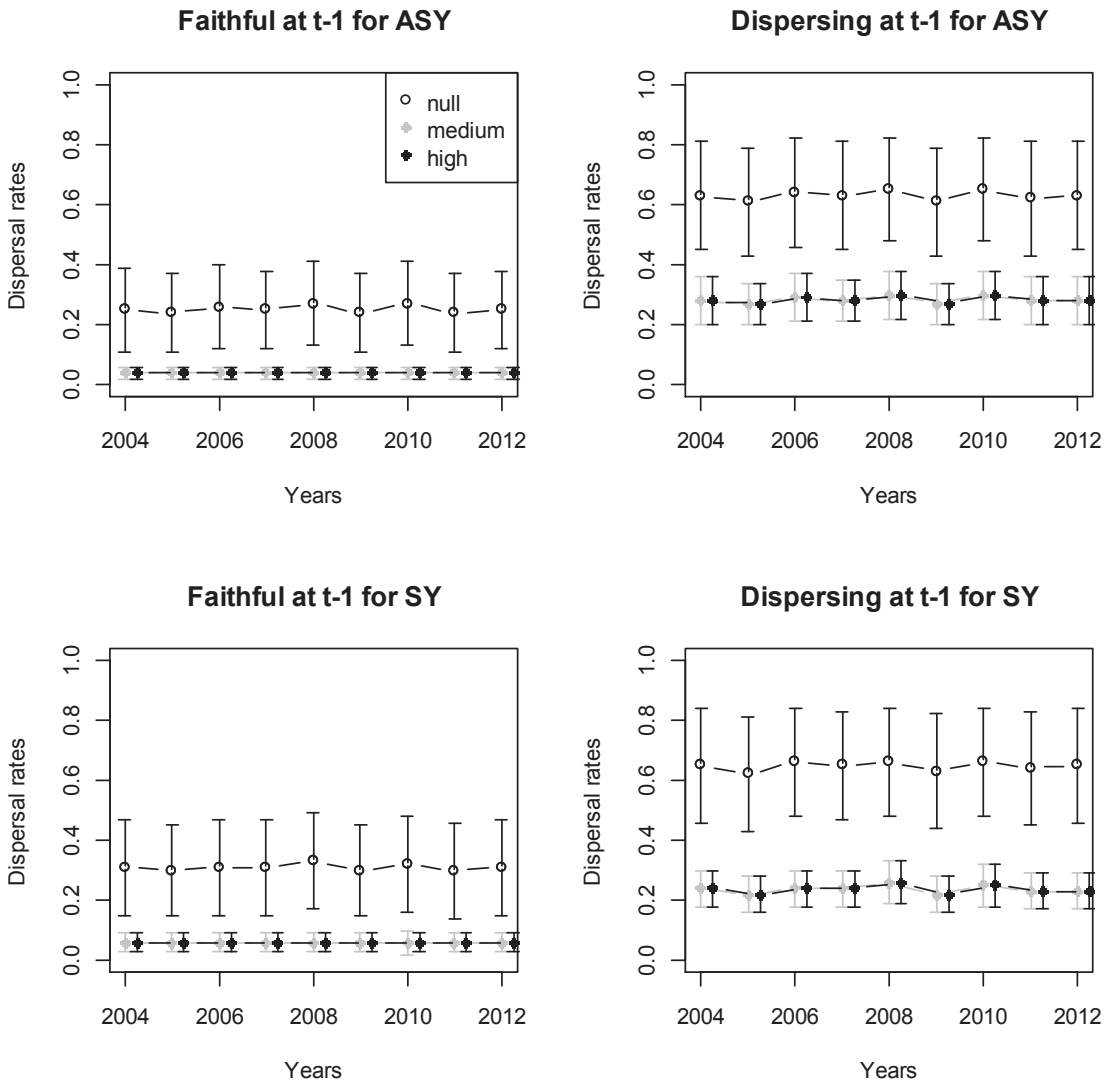
Table C4: Model selection with Capture-Recapture analysis to determine the basic structure of demographic parameters in tree swallows using RSc **disregarding the density**. RSc was defined on the threshold of the annual median of the ratio: number of nest boxes by farm with at least one fledglings on the density of nest boxes occupied by tree swallows. Each model is defined by four parameters: S, F, I, Cand R. The effects of RSi, RSc, previous dispersal behavior (memory) and age were tested alone, in addition (+) or in interaction (*) including the main effects as in the table C1. A constant parameter is represented by 'i'. *k* is the number of parameters used to calculate the weight (w_i) of each model and $\Delta QAIC_c$ ($\hat{c}$ = 1.94) gives the difference between the $QAIC_c$ value of the model and that of the best model (i.e., with lowest: $Model_{55}$, $QAIC_c$ = 4491.71, deviance = 8668.27). # is the number of the model. The best model for each parameter is in bold and the null model is #11.

Parameters	Effects	*k*	Δ QAICc	w_i	#
Recapture (R)	i	11	152.69	0.00	11
	RSi	**12**	**99.94**	**0.00**	**14**
	t	19	167.39	0.00	17
	RSi+t	20	104.63	0.00	18
	RSi*t	28	116.55	0.00	19
Transition between a good/bad RSc (C)	i	12	99.94	0.00	14
	RSc	**13**	**85.97**	**0.00**	**20**
	t	20	101.82	0.00	21
	RSc+t	21	90.25	0.00	22
	RSc*t	29	88.70	0.00	23
Transition between a good/bad RSi (I)	i	13	85.97	0.00	20
	RSi	14	87.91	0.00	24
	RSc	14	82.99	0.00	25
	memory	14	83.69	0.00	26
	RSi*RSc	**16**	**69.44**	**0.00**	**27**
	RSc*memory	16	78.30	0.00	28
	RSi*memory	16	86.98	0.00	29
	RSi*RSc*memory	20	71.60	0.00	30
	t	21	94.19	0.00	31
	age	14	87.99	0.00	32
	RSi*RSc+t	24	76.74	0.00	33
	RSi*RSc*t	48	102.13	0.00	34
	RSi*RSc*age	20	73.59	0.00	35
Survival (S)	i	16	69.44	0.00	27
	memory	19	60.35	0.00	38
	RSi	**17**	**26.11**	**0.00**	**39**
	RSi*memory	21	29.99	0.00	44
	t	24	69.62	0.00	45

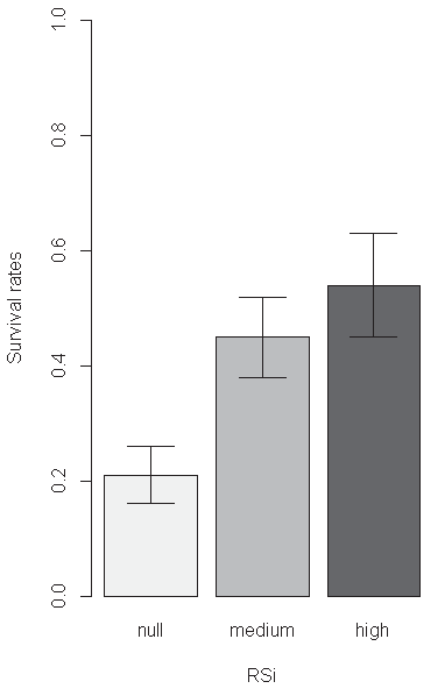
	age	17	68.67	0.00	46
	RSi+t	25	31.61	0.00	47
	RSi*t	33	42.84	0.00	48
	RSi*age	19	27.85	0.00	49
Fidelity (F)	i	17	26.11	0.00	39
	memory	20	9.01	0.01	52
	RSi	18	8.40	0.01	53
	RSc	18	21.78	0.00	54
	RSi*memory	**22**	**0.00**	**0.66**	**55**
	RSc*memory	22	8.55	0.01	56
	RSi*RSc	20	9.27	0.01	57
	RSi*RSc*memory	26	5.18	0.05	58
	t	25	31.33	0.00	59
	age	18	27.94	0.00	60
	RSi*memory+t	30	3.55	0.11	61
	RSi*memory*t	53	40.16	0.00	62
	RSi*memory*age	24	3.16	0.14	63

Appendices D: Estimated parameters for RSi in 3 classes with Capture-Recapture analyses

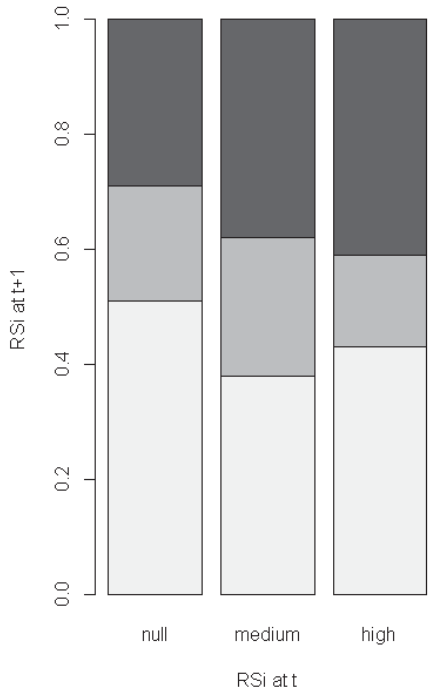
Figure D1: Results of the Capture-Recapture analysis presenting (A) dispersal probabilities according to individual reproductive success in 3 classes (no fledglings, number of fledglings < median, number of fledglings > median, the age (second year (SY) or after second year (ASY)) and the previous dispersal behavior (faithful or dispersing) during the time (B) the survival probabilities according to the RSi and (C) the probability to keep the same individual reproductive success. Estimates come from averaged model (± SE). Grey scale in (B) and (C) represent from the palest to the darkest, the RSi from low to high.



A)


Survival rates
0.0
0.2
0.4
0.6
0.8
1.0
null
medium
high
RSi

B)


RSi at t+1
0.0
0.2
0.4
0.6
0.8
1.0
null
medium
high
RSi at t

C)

Appendices E: Standard approach assuming perfect detection

We compared the results (dispersal probabilities and the effects of variables) of CR analyses with those obtained by generalized linear mixed models (GLMMs with logit link function and binomial error structure) considering a perfect detection (see (Gimenez et al. 2008) for a similar exercise). The GLMMs had whether individuals dispersed or not as response variable and RSi (good or bad), RSc (good or bad), age (ASY or SY), memory (disperser or faithful at t - 1), and the interactions between RSi and memory, as well as between RSi and RSc, as explanatory variables. The year of capture were considered as random effects. We used two datasets to assess the sensitivity of results with respect to case selection. The first dataset (dataset 1) was limited to 632 individuals captured two consecutive years and included 14% of dispersers based on 632 events of recapture. In this dataset, dispersal cannot be confounded with lack of survival but individuals not recaptured at $t + 1$ because they dispersed outside the study area or simply went undetected can still bias (likely underestimate) dispersal probabilities. The second dataset (dataset 2) included individuals captured at least twice but not necessarily in two consecutive years. With this dataset, we could assume that individuals not recaptured two consecutive years were dispersers. The dataset thereby included 667 individuals of which 23% were dispersers. This dataset has the advantage over the former of potentially alleviating the bias resulting from birds dispersing outside the study area but can also lead to overestimated dispersal probabilities via individuals that went undetected but did not disperse.

A list of models tested all combination of variables and, as for multievent analyses, we used multimodel inference based on AIC_c to estimate model-averaged regression coefficients using package MuMIn 1.9.13 in R 3.0.2 (R Development Core Team 2013).

Table E2: Model selection with traditional approach examining the effect of RSi, RSc, memory and age on dispersal for the two datasets (dispersal coded 1, faithful coded 0). All models include the capture year in random effects and fixed effects appear column 1. # is the name of the model. "Dataset 1" corresponds to dataset with individuals captured two consecutive years and "Dataset 2" to individuals captured at least two times but not two consecutive years. All combinations of the variables are tested. The number of parameters (k) and deviance were used to calculate the AIC_c and weight (w_i) of each model. ΔAIC_c gives the difference between the AIC_c value of the model and the AIC_c of the best model (i.e., with lowest AIC_c). Best model for dataset 1: m13 AIC_c = 447.0, deviance = 434.90. For dataset 2: m13 AIC_c = 579.40, deviance = 567.32.

Models	#	k	Dataset 1 (N=632)		Dataset 2 (N=667)	
			Δ AIC_c	w_i	Δ AIC_c	w_i
RSi+RSc+memory	m13	6	0.00	0.25	0.00	0.20
RSi+RSc+memory+RSi*RSc	m3	7	0.39	0.20	0.34	0.17
RSi+memory	m18	5	0.80	0.16	0.86	0.13
RSi+RSc+memory+age	m12	7	1.91	0.09	2.04	0.07
RSi+RSc+memory+age+RSi*RSc	m2	8	2.25	0.08	2.39	0.06
RSi+memory+age	m15	6	2.75	0.06	2.89	0.05
RSi+RSc+memory+RSi*RSc+RSi*memory	m11	9	3.85	0.04	1.53	0.09
RSi+RSc+memory+RSi*memory	m7	8	3.42	0.04	1.38	0.10
RSi+memory+RSi*memory	m9	7	4.13	0.03	2.45	0.06
RSi+RSc+memory+age+RSi*memory	m6	9	5.34	0.02	3.43	0.04
RSi+RSc+memory+age+RSi*RSc+RSi*memory	m10	10	5.72	0.01	3.58	0.03
RSi+memory+age+RSi*memory	m8	8	6.08	0.01	4.50	0.02
null	m1	1	65.10	0.00	60.22	0.00
RSi+RSc+age	m14	5	26.63	0.00	17.24	0.00
RSc+memory+age	m16	6	31.18	0.00	37.64	0.00
RSi+RSc	m17	4	25.10	0.00	16.07	0.00
RSi+age	m19	4	28.60	0.00	19.35	0.00
RSc+memory	m20	5	29.22	0.00	35.63	0.00
RSc+age	m21	4	56.42	0.00	54.17	0.00
memory+age	m22	5	35.60	0.00	43.22	0.00
RSi	m23	3	27.22	0.00	18.39	0.00
RSc	m24	3	55.00	0.00	53.28	0.00
memory	m25	4	33.63	0.00	41.23	0.00
age	m26	3	63.45	0.00	62.62	0.00
RSi+RSc+age+RSi*RSc	m4	6	27.89	0.00	18.41	0.00
RSi+RSc+RSi*RSc	m5	5	26.32	0.00	17.15	0.00

Table E3: Estimates of the variables and intercept coming from averaged model of the GLMM approach for the dataset 1 (a) (N = 632) and the dataset 2 (b) (N = 667). Unconditional Standard Error (SE) and the limits of the confidence intervals are presented for each variable and the intercept.

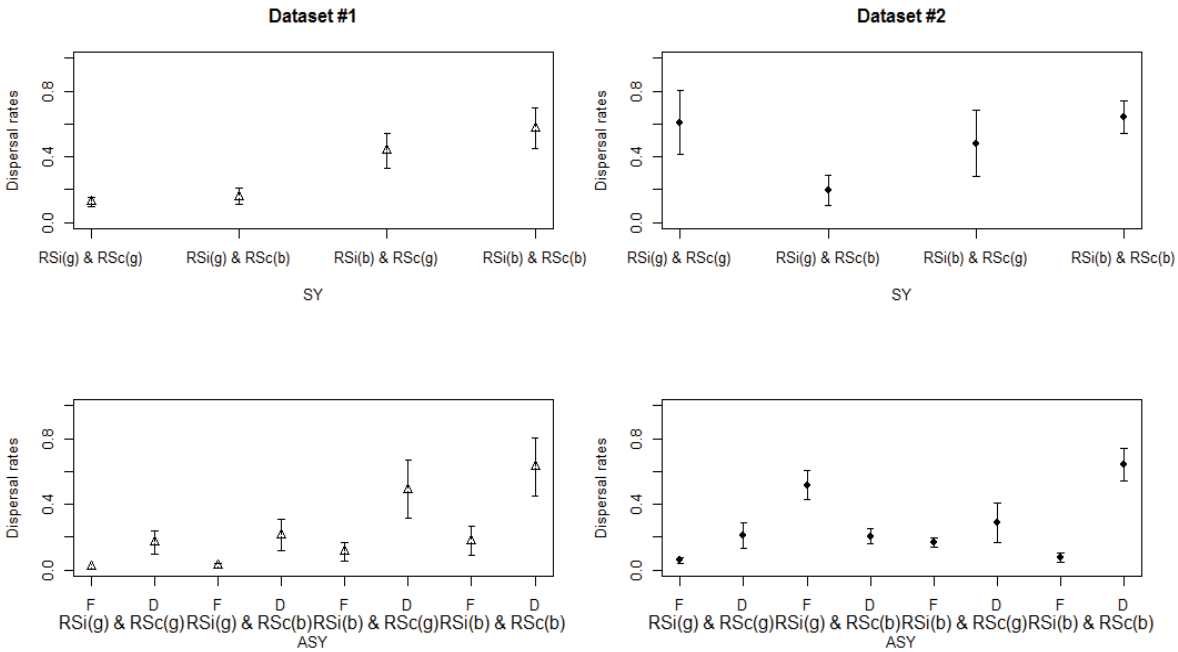
a)

Variables	Estimates	SE	CI (-)	CI (+)
(Intercept)	0.52	0.75	-0.95	1.99
RSi	-1.84	0.68	-3.18	-0.51
RSc	-0.76	0.53	-1.80	0.28
memory(faithful)	-2.05	0.79	-3.59	-0.51
RSc*RSi	0.84	0.66	-0.45	2.14
ageSY	-0.14	0.36	-0.85	0.58
memory(faithful)*RSi	-1.11	1.37	-3.79	1.57

b)

Variables	Estimates	SE	CI (-)	CI (+)
(Intercept)	0.44	0.82	-1.17	2.05
RSi	-1.51	0.86	-3.20	0.17
RSc	-0.69	0.48	-1.63	0.25
memory(faithful)	-1.35	0.79	-2.90	0.20
RSc*RSi	0.76	0.58	-0.38	1.90
memory(faithful)*RSi	-0.30	1.26	-2.79	2.18
ageSY	0.00	0.31	-0.60	0.60

Figure E4: Dispersal probabilities of tree swallow from 2004 to 2012 in Québec according to good/bad individual reproductive success (RSi(g)/RSi(b)), good/bad conspecifics reproductive success (RSc(g)/RSc(b)), age (second year (SY) or after second year (ASY) and previous dispersal status (faithful or dispersing). Estimations come from averaged model of the classical approach (GLMM) of the dataset #1 with females captured two consecutive years (empty triangles) and of the dataset #2 with females captured not necessarily two consecutive years (black circles). For each combination of reproductive status, we indicate in abscissa the dispersal status for the previous reproduction (D if females disperse the previous year, F, if females are faithful). The dispersal status is unknown for SY.



Annexes Chapitre 4

Appendices A: Information on the selection of environmental variables.

Figure A.1: Impact of intensive landscape at different scales on the reproductive success (number of fledglings in black) and the density of breeders (in grey). The coefficients come from the regression of the reproductive success on a farm or density according to the percentage of intensive cultures in one radius, considering the id of the breeding site, the year and the id of the brood as random effect.

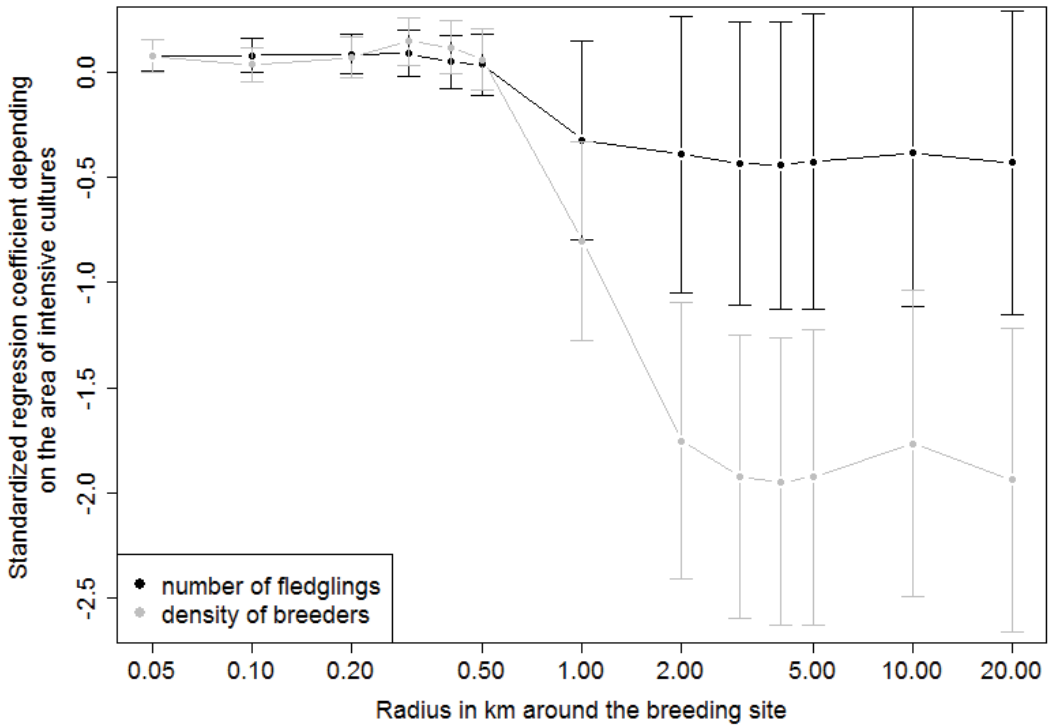


Figure A.2: Distribution of the number of fledglings (SRi) per female in our system from 2004 to 2013.

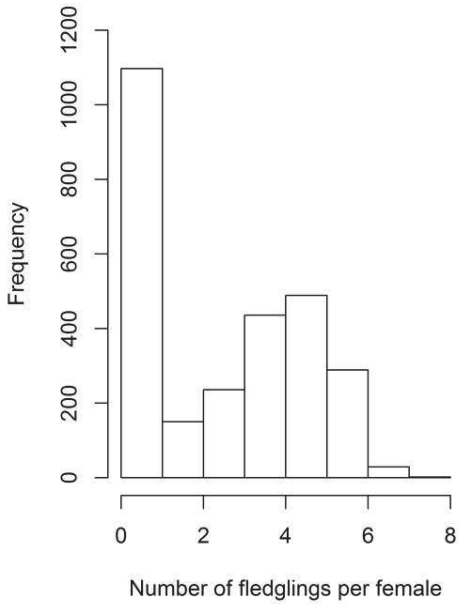
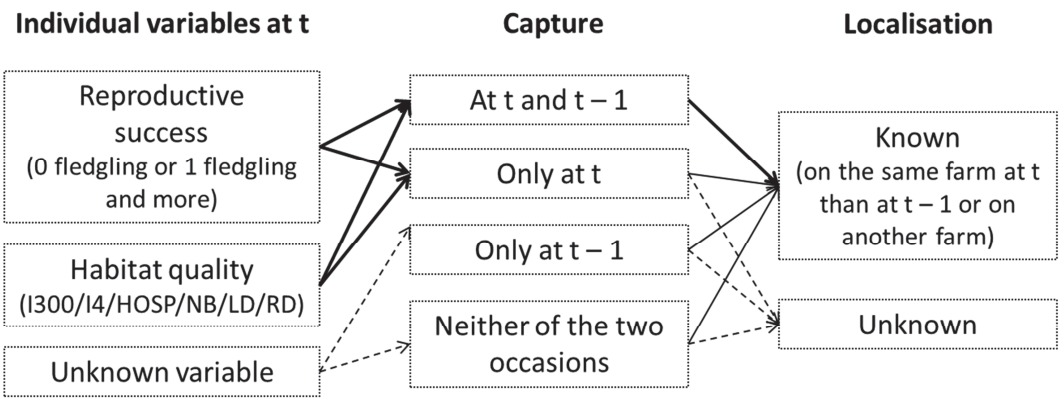


Table A.3: Correlations between variables used for modeling the settlement decision. Spearman (resp. Pearson) coefficients are on the lower (resp. upper) diagonal. NS is for non-significant at the 5 % significance level (see article, table 1 for the details of variables).

Spearman \ Pearson	HOSP	NB	$LD_{(t-1)}$	$RD_{(t-1)}$	$RSc_{(t-1)}$	I4	I300
HOSP	**1.00**	0.02 ^{NS}	-0.61	-0.16	-0.53	0.44	0.33
NB	0.05^{NS}	**1.00**	0.11	0.86	0.09 ^{NS}	0.16	0.25
$LD_{(t-1)}$	-0.57	0.11	**1.00**	0.39	0.80	-0.33	-0.28
$RD_{(t-1)}$	-0.17	0.83	0.39	**1.00**	0.34	-0.13	-0.03
$RSc_{(t-1)}$	-0.53	0.11	0.82	0.36	**1.00**	-0.36	-0.32
I4	0.47	0.18	-0.27	-0.11	-0.33	**1.00**	0.71
I300	0.41	0.17	-0.27	-0.10 ^{NS}	-0.31	0.68	**1.00**

Appendices B: Description of the capture-recapture model.

Figure B.1: Information carried by events and states (only by events with dotted arrows, only by states with thin arrows, by events and states with thick arrows).



Text B.2: The parameterization steps

The probability for a female to transit from a state one year to another the next year was the product of five steps: the probability to survive (S) or die (1 – S), the probability to return the following year to the same farm (F) or to disperse (1 – F), the probability to keep a good/bad individual reproductive success (I) or to change (1 - I), the probability to stay in the same habitat quality (EV) or to change (1 – EV) and lastly, the probability to be recaptured (R) or not (1 – R). For males, the probability to transit from a state one year to another state the next year depended on (S), (F), (EV), (R), not (I) and their relative complement. S and F were the two parameters of interest, while EV, R and I were used as control factors.

The effect of environmental variables was independently (= one dataset and one model selection by environmental variable) tested on I, S and F and no interaction between them. Consequently, we conducted one model selection by sex and by environmental variable. To parameterize models, we used a stepwise approach. First, we defined a null model for males and females where all parameters were constant. Building on our previous analyses of the data (Lagrange et al. 2014, unpublished manuscript), parameterization targeted one parameter at a time and focused first on the nuisance parameters to proceed then with the relevant parameters: R, EV, I, S, F in that order for females and R, EV, S, F for males. Starting with R, we compared models including effects below with the Akaike information criterion corrected for small samples and overdispersion ($QAIC_c$; Burnham & Anderson 2002) and kept other parameters constant. For females, we tested on R the effect of reproductive success, additive effect of time and interaction between the two, then on EV the effect of time or age and if the transition probability between inferior/superior class depend on the environmental variable, on I the same effects plus environmental effect, age and interaction between age and reproductive

success, on S and F the same effects as on I plus a memory effect, a combination between reproductive success and the memory effect, and their interaction and additive effect with age or time. When the structure of a parameter was determined (for example on EV), the following parameter (in this case I) undergo the same procedure keeping the previous retained structure of parameters (R) and the parameters not yet studied (S and F) constant. The same models were tested for males excluding those with age and reproductive success.

Before performing the selection on the last parameter F, we carried out the downward selection from F to EV but this time with the model structures for each parameter identified in the previous model selection in order to calculate the Akaike weight (w) for each model i in each selection s. In this way, the calculation of the weight $w_{s.i}$ was not affected by the constant structure of a non-defined step in the first round of our model selection.

Appendices C: Selected models for females from the model averaging (w_i ≥0.01) considering the effect of environmental variables on survival (S), fidelity (F), transition between good/bad individual reproductive success (RSi) and transition between inferior/superior class of the environmental variable (EV).

The effects were tested alone, in addition (+) or in interaction (*) including the main effects. *k* is the number of parameters of each model *i* used to calculate weight ($w_{s.i}$) and the $QAIC_c$ ($\hat{c}$ = 1.93) for a sample size of 1459 individuals (see article, table 1 for the details of variables).

Table C.1: Examination of the environmental variable 'density (low or high) of nest boxes into a radius of 15km around the breeding site' denoted NB.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
28	(memory on good RSi)	(RSi*memory)	i	(NB)*t	22	4211.80	0.22
45	(memory on good RSi)+a	(RSi*memory)	i	(NB)*t	23	4212.42	0.16
39	(RSi, memory)	(RSi*memory)	i	(NB)*t	23	4212.73	0.14
37	(RSi)	(RSi*memory)	i	(NB)*t	21	4212.81	0.13
48	(memory on good RSi)	(RSi*memory)	a	(NB)*t	23	4213.79	0.08
36	(memory on good RSi)	(RSi*memory)+a	i	(NB)*t	23	4213.84	0.08
46	(memory on good RSi)	(RSi*memory)	(RSi)	(NB)*t	23	4213.85	0.08
34	(memory on good RSi)	(RSi*memory)+t	i	(NB)*t	30	4214.58	0.05
44	(memory on good RSi)*a	(RSi*memory)	i	(NB)*t	25	4215.75	0.03
35	(memory on good RSi)	(RSi*memory)*a	i	(NB)*t	25	4216.39	0.02
43	(memory on good RSi)+t	(RSi*memory)	i	(NB)*t	30	4217.87	0.01
30	(memory on good RSi)	(RSi* memory*NB)	i	(NB)*t	26	4219.00	0.01

Table C.2: Examination of the environmental variable 'presence of House sparrow on the farm containing the breeder in nest boxes' denoted HOSP.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
41	(RSi* HOSP)	(RSi* memory)	(HOSP)	(HOSP)+t	23	4531.61	0.14
67	(RSi* HOSP)	(RSi* memory)	a	(HOSP)+t	23	4531.83	0.12
63	(RSi* HOSP)	(RSi* memory)	(RSi)	(HOSP)+t	23	4531.94	0.12
62	(RSi* HOSP)+a	(RSi* memory)	(HOSP)	(HOSP)+t	24	4531.94	0.12
s41	(RSi* HOSP)	(Hg vs others)	(HOSP)	(HOSP)+t	21	4532.84	0.07
65	(RSi* HOSP)	(RSi* memory)	(RSi on no HOSP)	(HOSP)+t	24	4533.39	0.06
71	(RSi* HOSP)	(RSi* memory)	(HOSP)+a	(HOSP)+t	24	4533.55	0.05
49	(RSi* HOSP)	(RSi* memory)+a	(HOSP)	(HOSP)+t	24	4533.61	0.05
75	(RSi* HOSP)	(RSi* memory)	(HOSP)	(HOSP)*t	31	4533.89	0.04
47	(RSi* HOSP)	(RSi* memory)+t	(HOSP)	(HOSP)+t	31	4534.77	0.03
48	(RSi* HOSP)	(RSi* memory)*a	(HOSP)	(HOSP)+t	26	4535.01	0.03
53	(RSi* memory)	(RSi* memory)	(HOSP)	(HOSP)+t	23	4535.17	0.02
70	(RSi* HOSP)	(RSi* memory)	(HOSP)*a	(HOSP)+t	25	4535.40	0.02
64	(RSi* HOSP)	(RSi* memory)	(RSi* HOSP)	(HOSP)+t	25	4535.42	0.02
55	(RSi* memory*HOSP)	(RSi* memory)	(HOSP)	(HOSP)+t	27	4535.60	0.02
43	(RSi* HOSP)	(RSi* memory*HOSP)	(HOSP)	(HOSP)+t	27	4535.67	0.02
50	(RSi)	(RSi* memory)	(HOSP)	(HOSP)+t	21	4535.99	0.02
72	(RSi* HOSP)	(RSi* memory)	(HOSP)	(HOSP)	15	4536.55	0.01
61	(RSi* HOSP)*a	(RSi* memory)	(HOSP)	(HOSP)+t	27	4536.87	0.01
60	(RSi* HOSP)+t	(RSi* memory)	(HOSP)	(HOSP)+t	31	4536.97	0.01
77	(RSi* HOSP)	(RSi* memory)	(HOSP)	(HOSP)+a	16	4537.12	0.01
73	(RSi* HOSP)	(RSi* memory)	(HOSP)	t	22	4537.85	0.01

Table C.3: Examination of the environmental variable 'density of conspecifics on the farm containing the breeder (local density)' denoted DL. We sometimes applied constraints on one.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
s37	(memory on good RSi)	(Eb, Hg, Eg Hb)	i	(DL)*t	28	4397.25	0.17
58	(memory on good RSi)+a	(Eb, Hg, Eg Hb)+a	i	(DL)*t	29	4397.86	0.13
60	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	(DL)	(DL)*t	29	4397.88	0.13
62	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	(DL on bad)	(DL)*t	30	4399.14	0.07
64	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	a	(DL)*t	29	4399.23	0.06
59	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	(RSi)	(DL)*t	29	4399.30	0.06
45	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	i	(DL)*t	29	4399.30	0.06
46	(RSi)	(Eb, Hg, Eg Hb)+a	i	(DL)*t	29	4399.30	0.06
37	(memory on good RSi)	(RSi, memory)	i	(DL)*t	29	4399.54	0.05
49	(RSi, DL)	(Eb, Hg, Eg Hb)+a	i	(DL)*t	30	4399.86	0.05
43	(memory on good RSi)	(Eb, Hg, Eg Hb)+t	i	(DL)*t	36	4400.37	0.04
61	(memory on good RSi)	(Eb, Hg, Eg Hb)+a	(RSi, DL)	(DL)*t	31	4400.72	0.03
57	(memory on good RSi)*a	(Eb, Hg, Eg Hb)+a	i	(DL)*t	31	4401.20	0.02
50	(RSi, memory)	(Eb, Hg, Eg Hb)+a	i	(DL)*t	30	4401.34	0.02
52	(RSi, memory,DL)	(Eb, Hg, Eg Hb)+a	i	(DL)*t	34	4401.61	0.02
44	(memory on good RSi)	(Eb, Hg, Eg Hb)*a	i	(DL)*t	31	4401.76	0.02
56	(memory on good RSi)+t	(Eb, Hg, Eg Hb)+a	i	(DL)*t	36	4403.30	0.01

Table C.4. Examination of the environmental variable 'regional density of conspecifics into a radius of 15km around the breeder in nest boxes' denoted DR.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
45	(RSi)	(RSi, memory)	i	t	19	4388.46	0.16
49	(RSi, memory)	(RSi, memory)	i	t	21	4388.47	0.15
36	(memory on good RSi)	(RSi, memory)	i	t	21	4388.66	0.14
38	(memory on good RSi)	(RSi, memory,DR)	i	t	25	4389.48	0.09
57	(memory on good RSi)+a	(RSi, memory)	i	t	22	4389.51	0.09
48	(RSi, DR)	(RSi, memory)	i	t	21	4390.03	0.07
51	(RSi, memory,DR)	(RSi, memory)	i	t	25	4390.16	0.07
58	(memory on good RSi)	(RSi, memory)	(RSi)	t	22	4390.64	0.05
59	(memory on good RSi)	(RSi, memory)	(DR)	t	22	4390.71	0.05
44	(memory on good RSi)	(RSi, memory)+a	i	t	22	4390.72	0.05
42	(memory on good RSi)	(RSi, memory)+t	i	t	29	4391.60	0.03
43	(memory on good RSi)	(RSi, memory)*a	i	t	24	4393.19	0.01
55	(memory on good RSi)+t	(RSi, memory)	i	t	29	4394.20	0.01
56	(memory on good RSi)*a	(RSi, memory)	i	t	25	4395.03	0.01

Table C.5. Examination of the environmental variable 'intensification level into a local radius of 300m around the breeder in nest boxes' denoted I300.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
36	(memory on good RSi)	(RSi, memory)	(I300)	i	13	4426.21	0.15
57	(memory on good RSi)+a	(RSi, memory)	(I300)	i	14	4426.78	0.12
45	(RSi)	(RSi, memory)	(I300)	i	12	4427.16	0.10
68	(memory on good RSi)	(RSi, memory)	(I300)	a	14	4427.81	0.07
49	(RSi, memory)	(RSi, memory)	(I300)	i	14	4427.83	0.07
59	(memory on good RSi)	(RSi, memory)	(RSi, I300)	i	15	4428.10	0.06
66	(memory on good RSi)	(RSi, memory)	(I300)	(I300)	14	4428.18	0.06
65	(memory on good RSi)	(RSi, memory)	(I300)+a	i	14	4428.20	0.06
44	(memory on good RSi)	(RSi, memory)+a	(I300)	i	14	4428.20	0.06
s48	(I300 on good RSi)	(RSi, memory)	(I300)	i	13	4428.54	0.05
61	(memory on good RSi)	(RSi, memory)	a	i	13	4428.82	0.04
58	(memory on good RSi)	(RSi, memory)	(RSi)	i	13	4428.88	0.04
42	(memory on good RSi)	(RSi, memory)+t	(I300)	i	21	4429.29	0.03
56	(memory on good RSi)*a	(RSi, memory)	(I300)	i	16	4430.07	0.02
64	(memory on good RSi)	(RSi, memory)	(I300)*a	i	15	4430.20	0.02
48	(RSi, I300)	(RSi, memory)	(I300)	i	14	4430.56	0.02
43	(memory on good RSi)	(RSi, memory)*a	(I300)	i	16	4430.93	0.01
55	(memory on good RSi)+t	(RSi, memory)	(I300)	i	21	4432.15	0.01

Table C.6. Examination of the environmental variable 'intensification level into a regional radius of 4km around the breeder in nest boxes' denoted I4.

i	Survival	Fidelity	RSi	EV	*k*	$QAIC_c$	w_i
32	(memory on good RSi)	(RSi, memory)	i	i	12	4208.87	0.15
59	(memory on good RSi)	(RSi, memory)	i	(I4)	13	4209.44	0.11
53	(memory on good RSi)+a	(RSi, memory)	i	i	13	4209.47	0.11
41	(RSi)	(RSi, memory)	i	i	11	4209.92	0.09
55	(memory on good RSi)	(RSi, memory)	(I4)	i	13	4210.33	0.07
s44	(I4 on good RSi)	(RSi, memory)	i	i	12	4210.33	0.07
61	(memory on good RSi)	(RSi, memory)	i	a	13	4210.43	0.07
45	(RSi, memory)	(RSi, memory)	i	i	13	4210.59	0.06
40	(memory on good RSi)	(RSi, memory)+a	i	i	13	4210.85	0.06
54	(memory on good RSi)	(RSi, memory)	(RSi)	i	13	4210.90	0.05
38	(memory on good RSi)	(RSi, memory)+t	i	i	20	4211.93	0.03
44	(RSi, I4)	(RSi, memory)	i	i	13	4212.14	0.03
52	(memory on good RSi)*a	(RSi, memory)	i	i	15	4212.75	0.02
60	(memory on good RSi)	(RSi, memory)	i	t	20	4212.79	0.02
39	(memory on good RSi)	(RSi, memory)*a	i	i	15	4213.03	0.02
56	(memory on good RSi)	(RSi, memory)	(RSi, I4)	i	15	4214.31	0.01
51	(memory on good RSi)+t	(RSi, memory)	i	i	20	4214.74	0.01

Appendices D: Selected models for males from the model averaging ($w_i \geq 0.01$) considering the effect of environmental variables on survival (S), fidelity (F) and transition between inferior/superior class of the environmental variable (EV).
The effects were tested alone, in addition (+) or in interaction (*) including the main effects. *k* is the number of parameters of each model *i* used to calculate weight ($w_{s.i}$) and the $QAIC_c$ ($\hat{c}$ = 1.05) for a sample size of 786 individuals(see article, table 1 for the details of variables).

Table D.1: Examination of the environmental variable 'density (low or high) of nest boxes into a radius of 15km around the breeding site' denoted NB.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
15	(memory)	(NB on disp memory)	(NB)*t	11	2980.04	0.57
12	(memory)	(memory)	(NB)*t	11	2981.64	0.26
14	(memory)	(memory, NB)	(NB)*t	13	2984.12	0.07
18	(memory)	(NB on disp memory)+t	(NB)*t	19	2985.46	0.04
13	(memory)	(NB)	(NB)*t	11	2986.08	0.03
16	(memory)	t	(NB)*t	17	2986.92	0.02
21	(memory)+t	(NB on disp memory)	(NB)*t	18	2988.76	0.01

Table D.2: Examination of the environmental variable 'presence of House sparrow on the farm containing the breeder in nest boxes' denoted HOSP.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
15	(memory on presence of HOSP)	(memory)	(HOSP)+t	18	3526.35	0.31
22	(HOSP)	(memory)	(HOSP)+t	17	3527.10	0.21
21	(memory)	(memory)	(HOSP)+t	17	3527.70	0.16
23	(memory, HOSP)	(memory)	(HOSP)+t	19	3528.38	0.11
29	(memory on presence of HOSP)	(memory)	(HOSP)*t	25	3529.12	0.08
20	(memory on presence of HOSP)	(memory)+t	(HOSP)+t	25	3530.01	0.05
17	(memory on presence of HOSP)	(memory, HOSP)	(HOSP)+t	20	3530.44	0.04
16	(memory on presence of HOSP)	(HOSP)	(HOSP)+t	18	3531.52	0.02
18	(memory on presence of HOSP)	t	(HOSP)+t	24	3531.79	0.02

Table D.3: Examination of the environmental variable 'density of conspecifics on the farm containing the breeder (local density)' denoted DL.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
18	(DL)	(DL on disp memory)	(DL)*t	25	3245.65	0.22
24	(DL on faithful memory)	(DL on disp memory)	(DL)*t	26	3245.73	0.21
15	(DL)	(memory)	(DL)*t	24	3245.75	0.21
21	(DL)	(DL on disp memory)+t	(DL)*t	32	3247.70	0.08
17	(DL)	(memory, DL)	(DL)*t	26	3247.73	0.08
23	(memory, DL)	(DL on disp memory)	(DL)*t	27	3247.82	0.07
22	(memory)	(DL on disp memory)	(DL)*t	25	3247.86	0.07
16	(DL)	(DL)	(DL)*t	24	3249.19	0.04
19	(DL)	t	(DL)*t	30	3251.02	0.02

Table D.4: Examination of the environmental variable 'regional density of conspecifics into a radius of 15km around the breeder in nest boxes' denoted DR.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
15	(memory)	(memory)	(DR)*t	24	3300.23	0.23
18	(memory)	(DR on disp memory)	(DR)*t	25	3300.57	0.19
28	(memory)	(memory)	(DR)	10	3301.65	0.11
24	(high DR on memory)	(memory)	(DR)*t	25	3302.15	0.09
22	(DR)	(memory)	(DR)*t	24	3302.21	0.08
30	(memory)	(memory)	(DR)+t	17	3302.50	0.07
17	(memory)	(memory, DR)	(DR)*t	26	3302.65	0.07
29	(memory)	(memory)	t	16	3303.39	0.05
23	(memory, DR)	(memory)	(DR)*t	26	3303.63	0.04
21	(memory)	(memory)+t	(DR)*t	31	3304.14	0.03
16	(memory)	(DR)	(DR)*t	24	3304.58	0.03
19	(memory)	t	(DR)*t	30	3307.55	0.01

Table D.5: Examination of the environmental variable 'intensification level into a local radius of 300m around the breeder in nest boxes' denoted I300.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
15	(memory)	(memory)	t	16	3303.64	0.23
24	(I300 on faithful memory)	(memory)	t	17	3304.13	0.18
22	(I300)	(memory)	t	16	3304.22	0.17
30	(memory)	(memory)	(I300)+t	17	3304.32	0.16
18	(memory)	(I300 on disp memory)	t	17	3305.55	0.09
23	(memory, I300)	(memory)	t	18	3306.11	0.07
21	(memory)	(memory)+t	t	23	3307.44	0.03
17	(memory)	(memory, I300)	t	18	3307.61	0.03
16	(memory)	(I300)	t	16	3309.62	0.01
19	(memory)	t	t	22	3310.54	0.01
29	(memory)	(memory)	(I300)*t	24	3310.76	0.01
28	(memory)	(memory)	(I300)	10	3310.98	0.01

Table D.6: Examination of the environmental variable 'intensification level into a regional radius of 4km around the breeder in nest boxes' denoted I4.

i	Survival	Fidelity	EV	*k*	$QAIC_c$	w_i
15	(I4)	(memory)	(I4)*t	17	3139.90	0.25
22	(memory)	(memory)	(I4)*t	17	3140.18	0.21
23	(memory, I4)	(memory)	(I4)*t	19	3140.28	0.20
24	(I4 on faithful memory)	(memory)	(I4)*t	18	3140.90	0.15
18	(I4)	(I4 on disp memory)	(I4)*t	18	3141.93	0.09
21	(I4)	(memory)+t	(I4)*t	24	3143.69	0.04
17	(I4)	(memory, I4)	(I4)*t	19	3143.99	0.03
16	(I4)	(I4)	(I4)*t	17	3145.64	0.01
19	(I4)	t	(I4)*t	23	3146.44	0.01

Appendices E: Analysis of the variation if individual reproductive success using ZIP models

Table E.1: Model selection examining environmental effects on the individual reproductive success. All models include the farm identifier and the capture year as random effects. Fixed effects appear in column "Models" for each model with a weight ≥ 0.01. *i* is the name of the model. Model performance was assessed using the posterior model probability p_i.

Selection	Models	*i*	p_i
p	LD+HOSP+LD*prscHOSP	35	0.47
	null	6	0.35
	LD+lay	39	0.10
	LD+HOSP+I300+LD*HOSP	31	0.02
	RD+HOSP+lay	45	0.01
	RD+lay	49	0.01
	LD+RD	7	0.01
	LD+HOSP+I300+LD*HOSP+I300*HOSP	32	0.01
	RD+I300+lay	48	0.01
	LD+HOSP+I300+annee*I300+lay+LD*HOSP+I300*HOSP	69	0.01
λ	I300	17	0.95
	LD+HOSP+I300	21	0.02
	LD+lay	25	0.02
	LD+I300	18	0.01

Table E.2: Parameter estimates of the best ZIP model explaining variation in the individual reproductive success of Tree Swallows. The probability *p* that an observation is generated through a Binomial distribution corresponding to failures before fledglings, and the mean number of fledglings λ of a Poisson distribution. Both parameters include the farm identifier and the capture year as random effects. Posterior means are displayed along with standard deviation (SD) and 95 % credible intervals (CI). Variables with confidence intervals excluding zero are in bold (see article, table 1 for the details of variables).

Parameter	Variable	Estimate	SD	Lower CI	Upper CI
p	(intercept)	**0.66**	0.16	0.36	0.97
	(1|farm)	**0.10**	0.05	0.03	0.20
	(1|year)	**0.15**	0.12	0.04	0.43
	LD	0.01	0.08	-0.14	0.16
	HOSP	**-0.34**	0.12	-0.56	-0.12
	LD*HOSP	-0.07	0.10	-0.27	0.14
λ	(intercept)	**1.42**	0.02	1.37	1.47
	(1|farm)	**0.00**	0.00	0.00	0.01
	(1|year)	**0.00**	0.01	0.00	0.01
	I300	**-0.04**	0.01	-0.06	-0.01

Appendices F : GLMM analysis of the variation in settlement decision

Table F.1: Model selection examining environmental effects on the settlement decision on a farm. All models include the farm identifier and the capture year as random effects. Fixed effects appear in column 1 for each model with a weight ≥ 0.01. *i* is the name of the model. The number of parameters (*k*) and deviance were used to calculate the AIC_c and weight (w_i) of each model. ΔAIC_c gives the difference between the AIC_c value of the model and the AIC_c of the best model (i.e., with lowest AIC_c of $Model_7$ = 1367.45, deviance of $Model_7$ = 1351.04 for N = 360) (see article, table 1 for the details of variables).

Models	*k*	Δ AIC_c	w_i	*i*
$RD_{(t-1)}$+HOSP+I300+$RSc_{(t-1)}$	8	0.00	0.19	7
$RD_{(t-1)}$+HOSP+$RSc_{(t-1)}$+HOSP*$RSc_{(t-1)}$	8	0.62	0.14	33
HOSP+I300+$RSc_{(t-1)}$+NB	8	1.39	0.10	15
$RD_{(t-1)}$+HOSP+I300+$RSc_{(t-1)}$+I300*$RSc_{(t-1)}$	9	1.55	0.09	9
HOSP+$RSc_{(t-1)}$+I300+HOSP*$RSc_{(t-1)}$	8	2.27	0.06	52
$RD_{(t-1)}$+HOSP+$RSc_{(t-1)}$	7	2.39	0.06	32
HOSP+$RSc_{(t-1)}$+NB+HOSP*$RSc_{(t-1)}$	8	2.74	0.05	46
HOSP+I300+$RSc_{(t-1)}$+NB+I300*$RSc_{(t-1)}$	9	2.84	0.05	17
$RD_{(t-1)}$+HOSP+I4+$RSc_{(t-1)}$	8	3.21	0.04	6
HOSP+$RSc_{(t-1)}$+HOSP*$RSc_{(t-1)}$	7	3.49	0.03	63
HOSP+$RSc_{(t-1)}$+I300	7	3.64	0.03	50
HOSP+$RSc_{(t-1)}$+I300+$RSc_{(t-1)}$*I300+HOSP*$RSc_{(t-1)}$	9	4.14	0.02	56
HOSP+$RSc_{(t-1)}$+I300+$RSc_{(t-1)}$*I300*HOSP	8	4.28	0.02	58
HOSP+$RSc_{(t-1)}$+I4+HOSP*$RSc_{(t-1)}$	8	4.71	0.02	51
HOSP+$RSc_{(t-1)}$+I300+$RSc_{(t-1)}$*I300	8	4.99	0.02	54
HOSP+I4+$RSc_{(t-1)}$+NB+I4*$RSc_{(t-1)}$	8	5.02	0.02	14
HOSP+$RSc_{(t-1)}$+NB+HOSP*$RSc_{(t-1)}$	7	5.22	0.01	45
$RD_{(t-1)}$+HOSP+I4+$RSc_{(t-1)}$+I4*$RSc_{(t-1)}$	9	5.31	0.01	8
HOSP+$RSc_{(t-1)}$	6	6.08	0.01	62
HOSP+$RSc_{(t-1)}$+I4+$RSc_{(t-1)}$*I4+HOSP*$RSc_{(t-1)}$	9	6.59	0.01	55
HOSP+$RSc_{(t-1)}$+I4	7	6.59	0.01	49
HOSP+I4+$RSc_{(t-1)}$+NB+I4*$RSc_{(t-1)}$	9	7.09	0.01	16

Table F.2: Parameter estimates corresponding to the variables influencing farm occupancy by Tree Swallows in agricultural landscapes. Estimates are model-averaged and displayed along with their unconditional standard error (uncond. SE) and 95 % confidence intervals (CI). Variables with confidence intervals excluding zero are in bold (see article, table 1 for the details of variables).

Variables	Estimates	Uncond. SE	Lower CI	Upper CI
(Intercept)	**4.84**	0.62	3.62	6.07
HOSP	**-1.72**	0.47	-2.63	-0.80
$RSc_{(t-1)}$	**0.09**	0.01	0.07	0.12
$LD_{(t-1)}$	**0.45**	0.05	0.35	0.56
I300	-0.01	0.01	-0.02	0.00
$RD_{(t-1)}$	0.02	0.01	0.00	0.05
$RSc_{(t-1)}$*HOSP	0.03	0.02	0.00	0.06
NB	0.19	0.10	0.00	0.38
I300*$RSc_{(t-1)}$	<0.01	0.00	0.00	0.00
I4	-0.01	0.01	-0.02	0.01
I300*$RSc_{(t-1)}$*HOSP	<0.01	0.00	0.00	0.00
I4*$RSc_{(t-1)}$	<0.01	0.00	0.00	0.00
I4*$RSc_{(t-1)}$*HOSP	<0.01	0.00	0.00	0.00
$LD_{(t-1)}$*NB	<0.01	0.02	-0.04	0.04

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