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Étude des déterminants du départ d'un site halte migratoire: modélisation et implications pour la gestion

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Avant-propos

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Le manuscrit est composé de 6 parties principales : une introduction générale, 4 articles et une discussion générale. Les annexes contiennent des informations supplémentaires sur les différents chapitres ainsi qu'un chapitre de livre auquel j'ai participé durant cette thèse.

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Résumé

Chaque année des dizaines de millions d'oiseaux migrants voyagent entre leurs aires de reproduction et leurs aires d'hivernage. Ce voyage de plusieurs milliers de kilomètres implique des contraintes météorologiques et énergétiques qui conduisent les oiseaux à effectuer des haltes migratoires. Les contraintes énergétiques forcent alors les oiseaux à refaire leurs réserves d'énergie durant ces haltes pour pouvoir effectuer de nouveau un vol de plusieurs centaines de kilomètres. En conséquence de cela, plus de 80% du temps total de migration est passé sur les sites de halte. Mieux comprendre les déterminants du départ d'un site de halte migratoire est donc crucial pour mieux appréhender le phénomène de la migration dans sa globalité ainsi que les variations de fitness d'une espèce. C'est pourquoi cette thèse, à l'interface entre modélisation et écologie de la migration, vise à obtenir une meilleure compréhension des décisions d'oiseaux migrants lors de leurs haltes à partir de données de capture-marquage-recapture récoltées parfois depuis des dizaines d'années et sur différents sites. En plus de cela, les potentielles implications en termes de gestion d'un site de halte seront abordées. La thèse s'articule sous la forme de 4 parties principales.

La première vise à mesurer la part relative des conditions environnementales et du temps depuis l'arrivée dans la décision de départ d'un passereau migrant. Elle a démontré que le temps depuis l'arrivée était alors plus important que les conditions environnementales pour un passereau migrant transsaharien quand il s'agissait de décider de partir d'un site de halte.

La seconde consiste à évaluer comment différents trajets de migration influencent les décisions de départ sur différents sites de halte d'une même espèce de limicole. Elle a de son côté démontré que la durée moyenne de halte était plus longue pour les oiseaux se préparant à un vol au-dessus de l'océan mais que les conditions environnementales choisies pour le départ convergeaient entre les deux sites.

La troisième a pour but le développement d'un modèle multi-espèces pour explorer la synchronie dans la décision de départ d'un site de halte entre plusieurs espèces de passereaux migrants transsahariens. Elle a révélé que les variations quotidiennes de probabilités de départ étaient fortement synchrones entre les différentes espèces et que ce résultat était répliable entre différents sites. De plus, dans la continuité de la partie 1, elle a révélé que le temps depuis l'arrivée était l'élément qui tendait à synchroniser les variations de probabilités de départ entre les espèces.

La quatrième porte sur le pourquoi et comment utiliser la durée de halte estimée par les modèles de capture-recapture comme un outil de gestion des zones de halte migratoire. Elle passe en revue les différents aspects utiles de cette métrique pour des problématiques de gestion et de conservation des oiseaux migrants.

Dans l'ensemble, ces travaux permettent d'affiner nos connaissances sur les décisions de départ d'un site de halte migratoire et des outils d'analyses associés pouvant à la fois être utiles pour découvrir de nouvelles facettes de la migration ainsi que pour la gestion et la conservation des oiseaux migrants et de leurs zones de halte.

Summary

Every year tens of millions of migratory birds travel between their breeding and wintering grounds. This journey of several thousand kilometres involves meteorological and energy constraints that lead the birds to make stopovers. The energy constraints force the birds to replenish their energy reserves during these stopovers in order to be able to make another flight of several hundred kilometres. As a result, more than 80% of the total migration time is spent at stopover sites. A better understanding of the drivers of the departure from a migratory stopover site is therefore crucial to better bird migration as well as the variations in fitness of a species. This is why this thesis, at the interface between modelling and migration ecology, aims to obtain a better understanding of the decisions made by migratory birds during their stopovers based on capture-marking-recapture data collected sometimes for decades and on different sites. In addition to this, the potential management implications of a stopover site will be addressed. The thesis is thus divided into 4 main parts.

The first aims to measure the relative importance of environmental conditions and time since arrival in the decision to depart from a stopover site. It showed that the time since arrival was then more important than the environmental conditions for a trans-saharan migratory passerine when deciding to leave a stopover site.

The second aims to assess how different migration routes influence the departure decisions at different stopover sites of the same shorebird species. It showed that the average duration of stopover was longer for birds preparing for a flight over the ocean, but that the environmental conditions chosen for departure converged between the two sites.

The third aims to develop a multi-species model to explore the synchrony in the decision to leave a stopover site between several species of trans-Saharan migratory passerines. It revealed that the daily variations in departure probabilities were thus highly synchronous between the different species and that this result was replicable between different sites. Moreover, in the continuity of part 1, it revealed that the time since arrival was the element that synchronises the variations in departure probabilities between species.

The fourth part deals with the why and how to use the estimated stopover time as a management tool for migratory stopover areas. It reviews the various useful aspects of this metric for migratory bird management and conservation issues.

Overall, this work will enable us to refine our knowledge of decisions to leave a migratory stopover site and the associated analysis tools that can be useful both for discovering new aspects of migration and for the management and conservation of migratory birds and their stopover areas.

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1 Contexte général

1.1 La halte migratoire chez les oiseaux

1.1.1 Le phénomène de la migration

La migration des oiseaux fascine depuis de nombreux siècles et un des premiers écrits la mentionnant est tiré d'Aristote il y a presque 2000 ans maintenant. Il y mentionnait environ 140 espèces différentes. Plus récemment Linné distingue environ 500 espèces différentes dans son ouvrage *Migrationes Avium* en 1757 mais soutient et propage encore l'idée que les hirondelles s'enterrent au fond des lacs pour y passer l'hiver. De nos jours, de nombreuses avancées concernant l'ornithologie et plus particulièrement la migration des oiseaux ont été réalisées. On compte à l'heure actuelle pas moins de 9,900 espèces d'oiseaux à travers le monde (Birdlife International 2008) et environ 20% d'entre elles sont considérées comme migratrices (Alerstam 1990, Kirby et al. 2008). Mais pourquoi les oiseaux migrant-ils ? La première explication, basique et surprenante de premier abord, est que la planète terre est inclinée de 23.5°. Cette inclinaison implique des différences de températures et d'ensoleillement au cours de l'année à travers différents endroits de la Terre, et ainsi de la saisonnalité (Alerstam 1990, Salewski and Bruderer 2007). Ces différences climatiques, modifiant la productivité en nourriture des habitats au cours de l'année est la principale raison aux mouvements migratoires des oiseaux (Alerstam 1990). La migration des oiseaux est un phénomène observable sur la majeure partie du globe (Alerstam 1990) et « s'organise » selon des voies de migration à l'échelle des continents (Figure 1).

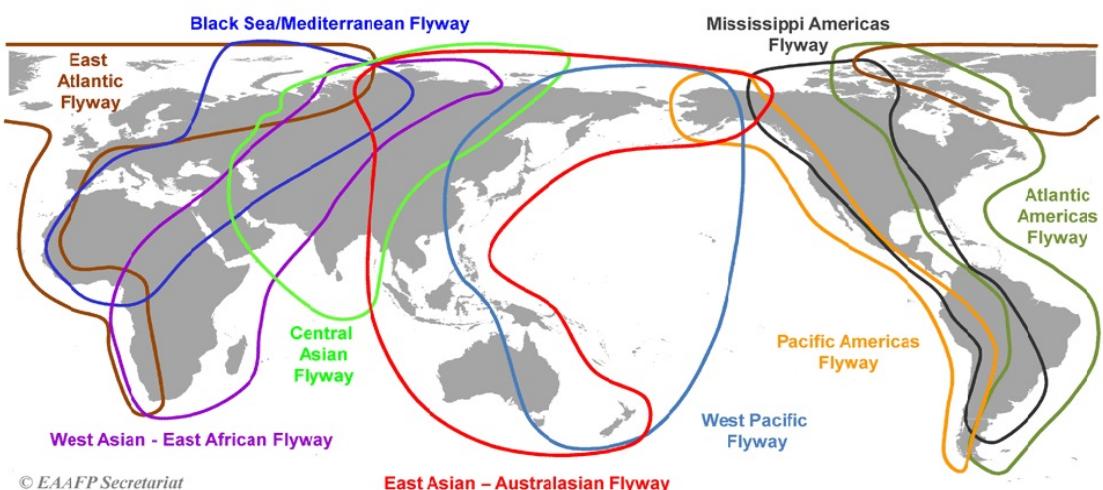


Figure 1 : Principales voies de migration (flyways) des oiseaux à l'échelle de la Terre.

Pour approfondir la question du « pourquoi la migration », de nombreuses études se sont attachées à comprendre les déterminants de la distribution des oiseaux migrateurs (Somveille et al. 2015, 2018, 2019) et à élucider ce que ce phénomène apportait aux individus, étant donné qu'il implique un coût énergétique important, et est associé à des risques de mortalité (Wikelski et al. 2003, Lok et al. 2015, Loonstra et al. 2019). Des études ont mis en avant une meilleure survie des populations migratrices d'une même espèce dans le cas d'une espèce migratrice partielle (Pulido 2011, Zúñiga et al. 2017). Cependant, les déterminants expliquant la répartition des oiseaux migrateurs et expliquant « pourquoi » ces oiseaux migrent semblent se situer dans un compromis entre la distance de migration (et la disponibilité de sites de haltes pour effectuer le voyage : connectivité) et l'abondance de ressources (Somveille et al. 2015, 2019). Les oiseaux migrateurs préféreraient des aires de reproduction avec hivers rigoureux et une forte production de ressource alimentaires durant l'été pour limiter la compétition (Somveille et al. 2015, 2018). Ces conclusions nous ramènent principalement aux impacts de la saisonnalité sur les ressources alimentaires comme le déterminant principal de la migration (Alerstam 1990, Dalby et al. 2014, Somveille et al. 2018).

1.1.2 Les différentes étapes d'un trajet migratoire

Étant donné que cette thèse se penche uniquement sur des jeux de données récoltés durant la migration postnuptiale, ce sera le sens dans lequel le voyage sera considéré dans la description ci-après (un trajet depuis les zones de reproduction vers les zones d'hivernage). Le trajet migratoire des espèces strictement migratrices se décompose de la façon suivante. Après s'être reproduits sur leurs quartiers d'été et pour anticiper la baisse de quantité de nourriture disponible, les oiseaux migrateurs commencent à entamer leur trajet vers leurs quartiers d'hivernage où la nourriture sera *a priori* plus abondante (Alerstam 1990). Étant donné les contraintes physiques et énergétiques propres au vol, la plupart des espèces ne peuvent pas réaliser un seul et unique vol de plusieurs milliers de kilomètres entre leurs quartiers de reproduction et ceux d'hivernage. Ainsi de nombreuses haltes, ayant différents objectifs (détaillés ci-après), sont réalisées au cours du trajet migratoire. Il en résulte que plus de 75% du temps total de la migration est passé sur les sites de halte migratoire (Alerstam 1990, Hedenstrom and Alerstam 1997, Schmaljohann et al. 2012, Schmaljohann 2018), ce qui confère au phénomène de halte une importance cruciale (Alerstam 1990, Alerstam and Lindström 1990, Kirby et al. 2008, Moore 2018). En effet, les différents choix réalisés au cours du trajet migratoire peuvent avoir d'importantes conséquences sur la fitness des individus (Ktitorov et al. 2010, Alves et al. 2013, Zúñiga et al. 2017). De manière générale, pour

maximiser leur fitness et minimiser les coûts associés à la migration, les individus cherchent à optimiser leur migration. Cette théorie de l'optimisation de la migration a été explicitement formulée par Alerstam et Lindström (1990). Les oiseaux chercheraient à optimiser leur migration suivant deux stratégies principales associées à des comportements et choix différents lors du trajet migratoire, ayant chacune des conséquences sur la fitness (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Dänhardt and Lindström 2001, Schmaljohann 2018). La première stratégie vise à minimiser le temps passé en migration : time-minimizing strategy. Cette stratégie s'appliquerait plutôt à la migration prénuptiale, quand les individus ont intérêt à arriver le plus rapidement possible sur leurs lieux de reproduction pour minimiser leurs interactions avec des compétiteurs, voire acquérir un statut dominant sur un territoire avant l'arrivée des congénères (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Alerstam 2011). La seconde stratégie vise, à minimiser la quantité d'énergie dépensée durant le voyage : energy-minimizing strategy. Cette stratégie s'appliquerait plutôt à la migration postnuptiale pendant laquelle les individus n'ont pas, à première vue, de fort avantage à arriver en premier sur les sites d'hivernage étant donné qu'il n'y a pas de compétition pour les sites et que la nourriture est abondante (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Alerstam 2011). Étape après étape, les individus font alors des choix (distance de vol entre deux sites de halte, durée de halte, choix du site de halte) dans le but d'économiser un maximum d'énergie.

Ces deux façons d'optimiser la migration sont associées à des adaptations différentes selon les espèces, individus, et sens de migration. Elles se traduisent par des comportements différents vis-à-vis de l'accumulation d'énergie sur un site de halte, la quantité d'énergie dépensée durant un vol de migration ou même de la sélection de l'habitat durant une halte migratoire. La théorie de la migration proposée par Alerstam et Lindström (1990) utilise un raisonnement basé sur l'optimisation et est explicitement ancrée dans le cadre contextuel de la sélection naturelle. Elle fait l'hypothèse que le comportement de l'oiseau durant sa halte migratoire joue un rôle crucial déterminant sa capacité à survivre et à se reproduire.

Nous n'abordons pas ici en détail une troisième stratégie qui consiste à minimiser le risque de prédation durant le trajet migratoire (Alerstam and Lindström 1990, Lank et al. 2003, Schmaljohann and Dierschke 2005). Bien que cette composante semble importante pour certaines espèces (Lank et al. 2003, Ydenberg et al. 2007), elle semble secondaire comparée aux composantes énergétiques liées à la migration (Schmaljohann and Dierschke 2005, Alerstam 2011, Schmaljohann 2018).

De nombreuses études visant à tester les prédictions de cette théorie dans différents cas de figure ont mis en évidence que ces stratégies pouvaient coexister au sein d'un même trajet migratoire et être aussi modulées en fonction de conditions environnementales (Wikelski et al. 2003, Schmaljohann et al. 2017, Anderson et al. 2019). Récemment, Anderson et al. (2019) ont montré que ces deux stratégies peuvent exister au sein de la même période de migration et qu'elles dépendent en partie de la distance totale de migration que l'espèce ou l'individu doit parcourir pour rejoindre ses sites d'hivernage. De la même manière, les conditions environnementales peuvent amener les individus à moduler leur stratégie en poussant les oiseaux à optimiser leur trajet et leur halte migratoire en fonction de la météo. Par exemple, les oiseaux peuvent fuir une tempête en raccourcissant leur halte migratoire pour diminuer les risques et les coûts engendrés par du mauvais temps (Wikelski et al. 2003). Enfin, la manifestation (ou l'existence-même) de deux stratégies utilisées selon le sens de la migration semble dépendre de la taille corporelle des espèces concernées (Zhao et al. 2017). Il est donc important de noter que ces stratégies constituent des bases théoriques pour étudier la migration mais que s'affranchir de ces bases peut permettre de découvrir de nouveaux aspects de la migration, qui peuvent ensuite éventuellement se révéler cohérents avec le cadre d'optimisation de la migration.

1.1.3 Déroulement d'une halte migratoire

La théorie de la migration optimale fait l'hypothèse que les décisions de rester ou de partir d'un site de halte sont fortement liées à la quantité d'énergie réassimilée (réserves) ainsi qu'à la vitesse à laquelle l'oiseau refait ses réserves sur un site de halte (Alerstam and Lindström 1990, Weber et al. 1999, Alerstam et al. 2003). Comme nous nous intéressons plus particulièrement aux décisions de départ d'un site de halte migratoire, il est important de détailler comment peut se dérouler cette halte dans le cadre des deux stratégies énoncées précédemment.

Sous l'angle d'une stratégie de « time-minimization », l'oiseau s'arrêtant sur un site de halte se nourrit intensément pour maximiser son taux d'engraissement et pouvoir repartir en migration le plus rapidement possible, afin de minimiser son temps total de migration (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). De ce fait, les décisions prises par les individus sont en majeure partie conditionnées par la quantité de graisse accumulée. Cependant, ce taux d'engraissement dépend de la disponibilité des ressources sur le site de halte et est donc fortement lié à la qualité de l'habitat et/ou aux conditions météorologiques du moment (Jenni and Schaub 2003, Cohen et al. 2012, Smith and McWilliams 2014). En effet, une météo particulièrement

mauvaise (pluie, vent contraire), peut non seulement bloquer les individus sur le site de halte pendant cet épisode météorologique mais également pendant plusieurs jours après la fin de cet épisode car les individus en halte n'ont pas pu se nourrir auparavant (Jenni and Schaub 2003, Schmaljohann and Eikenaar 2017).

Sous l'angle de la stratégie « energy minimization », les oiseaux cherchent aussi à refaire leurs réserves mais leurs décisions de repartir d'un site de halte ne sont pas conditionnées au taux d'engraissement (dans la mesure où il reste positif).

Si l'on résume brièvement les deux cas de figures théoriques suivant la stratégie employée, il est possible d'avoir **SOIT** des individus qui se posent sur un site de halte, refont leurs réserves le plus vite possible et repartent si les conditions météorologiques ne sont pas trop mauvaises (Hedenstrom and Alerstam 1997, Weber et al. 1999, Schaub et al. 2008), **SOIT** des individus qui se posent sur un site de halte, refont leurs réserves à une vitesse moins importante, restent donc plus longtemps sur les sites de halte et potentiellement choisissent des conditions minimisant la dépense d'énergie pour repartir (vent de dos; Arizaga et al. 2011a, Ma et al. 2011, Woodworth et al. 2015, Dossman et al. 2016).

Les prédictions théoriques de Alerstam et Lindström (1990) constituent le cadre théorique de beaucoup d'études sur les décisions des oiseaux lors des haltes migratoires, mais elles ne semblent cependant pas toujours être corroborées ou sont parfois combinées au sein d'un même trajet migratoire (Anderson et al. 2019). Les oiseaux migrants pourraient trouver un compromis entre minimisation du temps total de migration et énergie dépensée (Prop et al. 2003, Alerstam 2011).

1.1.4 Pourquoi s'intéresser plus particulièrement au phénomène de halte

Les décisions prises par les oiseaux migrants lors de leurs haltes conditionnent la réussite de leur migration et en conséquence, contribuent à déterminer leur fitness. Le phénomène de halte est donc central dans la biologie de la migration. Dans le but d'améliorer notre connaissance globale du phénomène de la migration il est crucial de connaître finement comment les oiseaux migrants prennent leurs décisions lors de ces haltes et de s'assurer de la généralité de nos conclusions en travaillant sur des échantillons à différentes échelles temporelles et spatiales. En 2003, Jenni et Schaub dressent, grâce à des études réalisées *in natura* et en laboratoire, une première revue des facteurs pouvant influencer les décisions des oiseaux lors de leur halte migratoire (Figure 2; Jenni and Schaub 2003). Les facteurs sont ainsi nombreux (compétition, préation, météo locale, la

météo en aval, la topographie du site, le poids de l'oiseau, la quantité de nourriture disponible), mais *a priori* ils influencent plus ou moins indirectement le taux d'engraissement de l'oiseau, qui à son tour contribue à déterminer la décision de départ du site et donc la durée de halte.

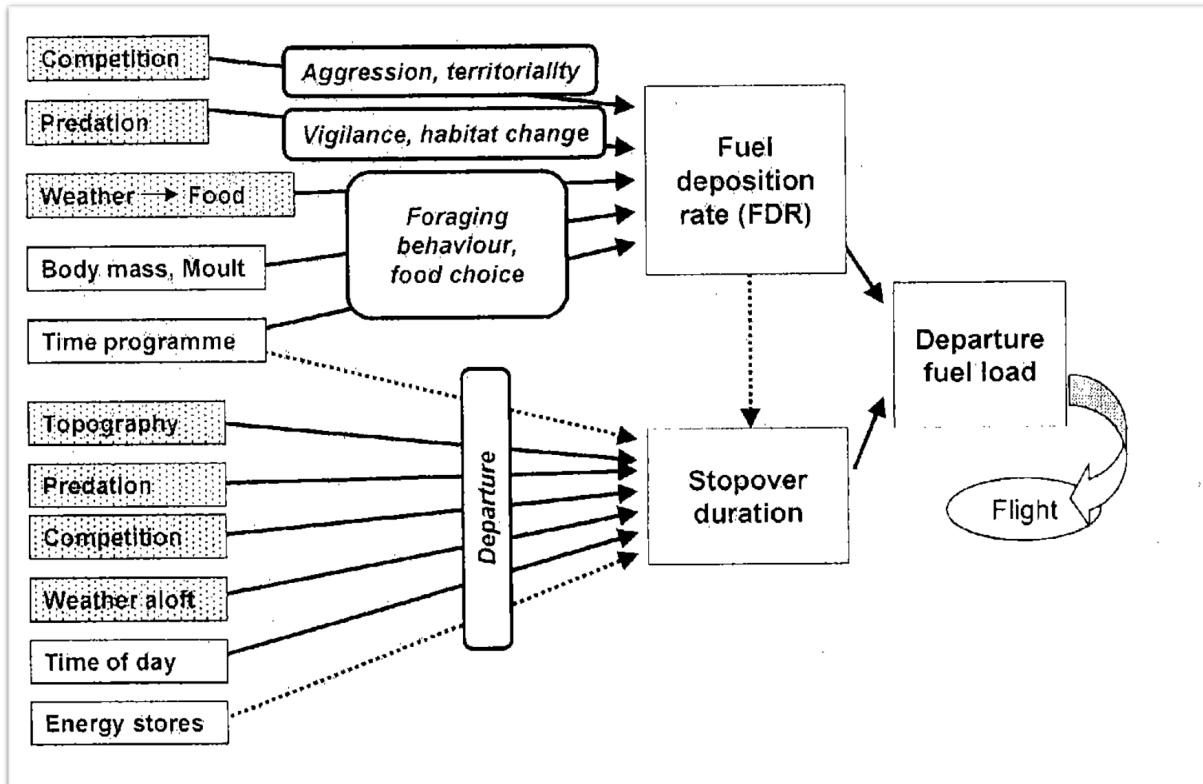


Figure 2 : Facteurs influençant le comportement des oiseaux sur un site de halte migratoire. Figure tirée de Jenni et Schaub (2003).

Plus récemment, en 2017, Schmaljohann et Eikenaar, réalisent une revue sur l'effet des réserves d'énergie sur les décisions des oiseaux migrants (Schmaljohann and Eikenaar 2017). Ils concluent que pour mieux comprendre les relations entre quantité d'énergie et décision de départ, de nombreux problèmes méthodologiques doivent être traités. Parmi les problèmes énoncés on trouve notamment le fait que la plupart des études sur les décisions des oiseaux migrants sont réalisées sans prendre en compte la probabilité de détection des oiseaux sur leur site de halte, et que ces études considèrent que le premier jour où l'oiseau est vu (ou capturé) correspond à son arrivée sur le site. De la même manière, elles font l'hypothèse que le dernier jour où l'oiseau est vu (ou capturé) correspond à son jour de départ et que, plus généralement, la durée de halte peut être calculée en comptant le nombre de jours écoulés entre la première et la dernière capture. Si, sur le terrain, il n'échappe à aucun observateur que ces hypothèses sont difficiles à accepter, ces études font néanmoins l'hypothèse que peut-être, (i) le biais lié à la détectabilité imparfaite des individus

est faible, (ii) qu'il n'est pas particulièrement plus grand en début qu'en fin de séjour (ou inversement), (iii) que ce biais est constant quelles que soient les conditions environnementales ou la condition intrinsèque des individus, et (iv) qu'il pourrait ne varier ni entre études, ni entre espèces, ou de manière systématique toujours dans le même sens (auquel cas des comparaisons entre études resteraient possibles). La conséquence très probable de ces hypothèses est la sous-estimation de la durée de séjour des individus, ce qui a notamment motivé la formalisation de cette thèse en 2016. Cependant, alors que Schmaljohann et Eikenaar préconisent d'utiliser des outils de radio-tracking pour appréhender plus finement les décisions individuelles lors des haltes migratoires, nous pensons que des centaines voire des milliers de jeux de données de baguage disponibles peuvent également nous aider à approfondir ces questions si on les analyse avec les outils statistiques appropriés. C'est pourquoi l'un des fondements méthodologiques de cette thèse réside dans la prise compte du problème de « détectabilité » des individus soulevé par Schmaljohann et Eikenaar, grâce à de nouveaux outils statistiques (voir section Analyse de données). Notre décision repose aussi sur le fait que nous sommes convaincus que certaines bases de données existantes, renfermant des milliers de données sur la migration parfois sur de très longues périodes et de grands effectifs, n'ont pas encore été suffisamment exploitées pour livrer tous leurs secrets. Enfin, sans ignorer des avancées rendues possibles par l'électronique embarquée, un autre avantage de ce type d'études est son coût limité comparé aux outils de géolocalisation ou de radio-tracking, qui coûtent parfois plusieurs centaines d'euros pour équiper un seul et unique individu, quand la même somme permet de baguer des centaines voire des milliers d'individus avec une simple bague (voir détails section: Récolte des données). Outre le coût des études, c'est surtout la taille des échantillons et la durée des séries temporelles qu'il est possible de documenter, qui confèrent au simple baguage une valeur indéniable.

Les différents facteurs affectant le départ d'un site de halte peuvent être grossièrement classés en deux catégories. D'un côté les facteurs internes (poids, condition corporelle, état de forme), de l'autre les facteurs externes ou autrement dit les conditions environnementales (vent, humidité, pression atmosphérique etc). Cette dichotomie a pu être parfois évitée en considérant que l'ensemble de ces facteurs constituent un « état » intégrateur de l'individu au temps t (e.g. Clark and Butler 1999), mais dans ce type d'approche la dynamique de cet état restait gouvernée par les deux types de facteurs. Ces facteurs ont été largement étudiés mais peu d'études l'ont fait en prenant en compte la probabilité de détection. Si les résultats concernant les facteurs environnementaux semblent clairs, ceux concernant les facteurs internes semblent plus hétérogènes. En effet, certaines

études avancent des effets du poids et de la condition corporelle sur la décision de départ (Schaub et al. 2008, Goymann et al. 2010, Cohen et al. 2012, Eikenaar and Schläfke 2013, Dossman et al. 2016, 2018, Schmaljohann and Eikenaar 2017, Klinner et al. 2020), alors que d'autres ne distinguent pas d'influence de la condition interne sur cette décision (Dänhardt and Lindström 2001, Tsvey et al. 2007, Ktitorov et al. 2010, Schmaljohann and Eikenaar 2017). Cependant, encore une fois beaucoup de ces études ne prennent pas en compte la probabilité de détection et considèrent la condition interne de l'oiseau lors du départ comme sa condition mesurée à la dernière capture.

Les facteurs déterminants le départ d'un site de halte conditionnent la durée de halte sur le site de migration, et la durée de halte elle-même conditionne le temps total de migration de l'oiseau (Schmaljohann 2018). Ce dernier est crucial pour la réussite du voyage et la survie de l'individu. Les décisions de départ d'un site de halte sont donc centrales quand on considère la migration dans son ensemble et certaines questions restent encore en suspens. Parmi ces questions, nous avons choisi d'en traiter trois principales qui sont : (i) « quelles sont les parts relatives des facteurs internes et externes dans la décision de départ d'un site de halte migratoire ? » (ce qui fut l'un des points de départ de cette thèse); (ii) « les différentes voies de migration empruntées conditionnent-elles la décision de départ chez une même espèce ? », et enfin (iii) « différentes espèces synchronisent-elles leur départ d'un site de halte migratoire ? ». Connaître plus finement les facteurs influençant le comportement des oiseaux sur un site de halte et la généralité de ces comportements entre sites et espèces permettra aussi de travailler à la gestion d'un site de halte migratoire.

1.1.5 Les espèces étudiées

Les quatre espèces étudiées appartiennent à deux ordres. D'un côté, nous avons trois espèces appartenant à l'ordre des passeriformes et de l'autre une espèce appartenant à l'ordre des charadriiformes. Les espèces de passereaux étudiées pendant cette thèse correspondent toutes à des migrants nocturnes inféodés aux milieux denses en végétation et n'ayant donc pas une morphologie adaptée à des vols rapides (Nafi et al. 2020). Ces trois espèces, pesant en moyenne moins de 20g, n'ont pas de ressources énergétiques très importantes pour réaliser de très longs vols (Alerstam 1990). D'un autre côté, nous avons un limicole, le Bécasseau semipalmé (*Calidris Pusilla*), qui a lui une morphologie plus adaptée aux vols longue-distance, parfois même aux dessus des océans, avec une vitesse plus importante (Nafi et al. 2020). Ces quatre espèces sont présentées ci-dessous dans des « encadrés espèces ».

Le phragmite des joncs

Le phragmite des joncs (*Acrocephalus schoenobaenus*) est un petit passereau migrateur transsharien de la famille des Acrocephalidae (fauvettes aquatiques) pesant entre 8 et 20g. Cet oiseau présente un plumage brun chamois avec un long sourcil blanc sale ou beige ainsi qu'un dos rayé de noir et de beige. Cette espèce principalement insectivore (Bibby and Green 1981) est, durant la période de reproduction, inféodée aux régions tempérées entre 40° et 70° de latitude Nord et se retrouve de l'Espagne à la Norvège, et de l'Irlande de l'Ouest jusqu'aux confins de la Sibérie Centrale (Shirihai and Svensson 2018). L'espèce se reproduit principalement proche de zones humides dans des zones présentant des roseaux, massettes ou buissons proches de marais ou eaux stagnantes. Les zones d'hivernage de l'espèce se situent au sud du Sahara sur une aire assez large atteignant quasiment le sud de l'Afrique. Durant sa migration vers ses quartiers d'hivernage l'espèce peut traverser un grand nombre d'habitats mais se focalise principalement sur les zones de roselières (Figure 4 ci-dessous). L'espèce se rencontre en migration, en France, principalement durant le mois d'Août où plus de 80% des individus migrants de l'espèce traversent le territoire Français (Dehorter and CRBPO 2015). Chaque année en France, environ 20 000 individus, sont capturés et bagués durant la migration postnuptiale. Elle est l'une des espèces migratrices les plus capturées à l'échelle du territoire.



Figure 3 : Phragmite des joncs (*Acrocephalus schoenobaenus*)

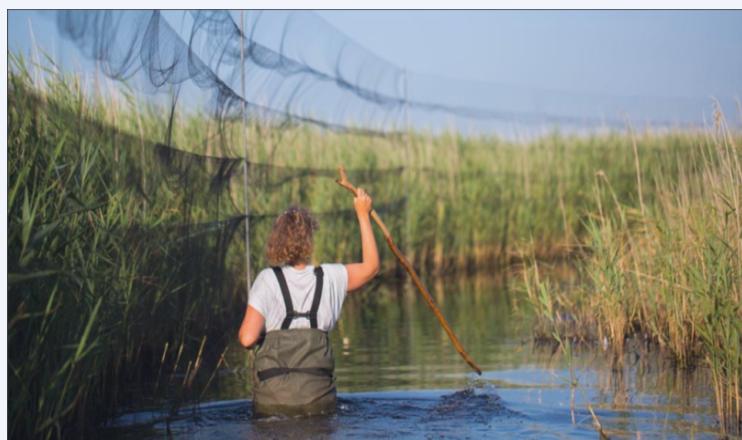


Figure 4 : Station de baguage de Trunvel. Habitat du phragmite des joncs en halte migratoire

La rousserolle effarvatte

La rousserolle effarvatte (*Acrocephalus scirpaceus*) est un petit passereau migrateur transsharien de la famille des Acrocephalidae (fauvettes aquatiques) pesant entre 9 et 16g. Cet oiseau présente un plumage dôté d'un dos brun uni avec des parties inférieures plutôt beiges blanchâtres (Figure 5). Le sourcil est vague et plutôt pâle (Figure 5). Cette espèce principalement insectivore (Bibby and Green 1981, Bibby and Thomas 1985) est, durant la période de reproduction, inféodée aux régions tempérées entre 40° et 60° de latitude Nord et se retrouve du nord de l'Afrique au sud de péninsule scandinave, et du sud de la Grande Bretagne jusqu'à l'ouest de l'Asie mineure (Shirihai and Svensson 2018). L'espèce se reproduit principalement dans les roselières, en eau ou à sec, mais peut aussi être plus rarement rencontrée dans d'autres végétations des marais.



Figure 5 : Rousserolle effarvatte (*Acrocephalus scirpaceus*)

Les zones d'hivernage de l'espèce se situent en Afrique tropicale, au sud du Sahara. Durant sa migration vers ses quartiers d'hivernages l'espèce peut traverser un grand nombre d'habitats mais se focalise, comme la plupart des *Acrocephalus*, principalement sur les zones de roselière (Figure 6 ci-dessous). L'espèce se rencontre en migration, en France, principalement durant le mois d'Août où plus de 75% des individus migrants de l'espèce traversent le territoire Français (Dehorter and CRBPO 2015). Chaque année en France, environ 20 000 individus, sont capturés et bagués durant la migration postnuptiale (Dehorter and CRBPO 2015). Elle est l'espèce migratrice la plus capturée à l'échelle du territoire.



Figure 6 : Habitat de halte et de reproduction de la Rousserolle effarvatte)

La gorgebleue à miroir

La gorgebleue à miroir (*Luscinia svecica*) est un petit passereau migrateur de la famille des Muscicapidae pesant entre 14 et 25g. Le plumage nuptial du mâle comporte un plastron d'un bleu vif bordé d'une ligne noire et blanche (Figure 7). Elle est ainsi nommée à cause d'une tâche rousse ou blanche (suivant la sous-espèce) au centre de ce plastron. Cette espèce principalement insectivore (Fontanilles et al. 2019) est présente, durant la période de reproduction, au centre de l'Espagne, dans l'Ouest et le Nord de la France, sur l'ensemble de la Scandinavie et sur une grande partie Est de l'Europe (Shirihai and Svensson 2018). L'espèce se reproduit principalement dans les zones humides. Elle affectionne les marais littoraux, les rives et bras de cours d'eau, ainsi que



Figure 7 : Gorgebleue à miroir (*Luscinia svecica*)

les marais et étangs intérieurs. Les zones d'hivernage de l'espèce sont très diverses (Afrique, Proche et Moyen-Orient, péninsule Ibérique et pourtour méditerranéen). Cependant, l'espèce comporte plusieurs sous-espèces (Shirihai and Svensson 2018), qui seraient en partie ségrégées sur les zones d'hivernage (Arizaga et al. 2011b, 2016, Shirihai and Svensson 2018).

Durant son voyage vers ses aires d'hivernage l'espèce se fait très discrète et fait halte principalement dans des zones de roselières où la capture d'oiseaux au filet a pu mettre en évidence des passages parfois importants. L'espèce se rencontre ainsi en migration, en France, principalement durant le mois d'Août et de Septembre. N'étant pas strictement transsaharienne, notamment pour les oiseaux nichant en Europe Occidentale, des individus peuvent être notés en migration jusqu'au mois de novembre (Dehorter and CRBPO 2015). Chaque année en France, environ 1200 individus, sont capturés et bagués durant la migration postnuptiale. Cette espèce est l'une des plus baguées en France.

Le bécasseau semipalmé

La bécasseau semipalmé (*Calidris Pusilla*) est un petit limicole migrateur de la famille des Scolopacidae pesant environ 30g. Cette espèce comporte en plumage nuptial un plumage moins contrasté que les autres espèces de bécasseau. Il possède un dos gris-brun sans contraste important. La poitrine comporte quelques stries grisâtres et le ventre ainsi que le bas-ventre sont clairs (Figure 8). Le bec est lui peu arqué et de longueur moyenne pour ce genre d'espèce. Cette espèce, comme beaucoup de bécasseaux, se nourrit principalement de petits invertébrés comme des mollusques, petits arthropodes, vers mais aussi, et notamment durant la migration, d'œufs de crabe (Macdonald et al. 2012). L'espèce se reproduit principalement en Arctique et couvre une distribution allant de l'ouest du Groenland, de l'arctique canadien à l'Alaska (Andres et al. 2012). Son habitat de nidification est la toundra arctique rase où le nid, plutôt sommaire, est confectionné à même le sol. Ils sont généralement proches de lacs, marais ou côtes. Ses quartiers d'hivernage se situent eux bien plus au sud, couvrant une importante partie de l'Amérique centrale et du nord de l'Amérique du

sud (Gratto-Trevor et al. 2012, Brown et al. 2017). Ses habitats de halte et d'hivernage sont généralement des berges de lacs ou des zones côtières intertidales où la nourriture est abondante (Lank 1983, Gratto-Trevor et al. 2012). Cette espèce est principalement observée en migration au nord des États-



Figure 8 : Bécasseau semipalmé (*Calidris pusilla*) marqué

Unis et sur la côte sud Canadienne durant les mois d'Août, Septembre et Octobre. Elle est particulièrement abondante sur les sites de halte et d'hivernage qui regroupent parfois plusieurs milliers d'individus. Cette espèce étant abondante et effectuant chaque année une migration de 5000 à 7500km entre ses zones de reproduction et d'hivernage, elle a fait l'objet de nombreuses campagnes de marquage (voir photo ci-dessus) pour étudier sa migration.

1.2 Comment étudier la halte migratoire

1.2.1 Récolte des données

Depuis plusieurs décennies de nombreuses études ont utilisé divers outils pour étudier et quantifier la migration des oiseaux. Nous présentons ici les principaux outils de marquage, suivi et quantification de la migration et plus précisément de la halte migratoire.

1.2.1.1 Marquage individuel (*bague, gps, gls*)

Dans le but de quantifier les mouvements des passereaux migrants nocturnes faisant halte dans des habitats fermés tels que des roselières, scirpaies et autres milieux humides à forte densité végétale appréciée des passereaux migrants, les biologistes ont mis en place des captures d'oiseaux à l'aide de filets à mailles fines disposés à l'intérieur même de ces habitats. Cette technique permet de mettre en évidence la grande quantité d'individus et d'espèces fréquentant un milieu que l'on ne peut détecter par observation directe. Ensuite, pour étudier plus précisément les trajets des oiseaux migrants, ces derniers ont été marqués, le plus souvent à l'aide d'une bague métal comportant un identifiant unique propre à chaque individu (ex Fig. 9).



Figure 9 : Bague Museum National d'Histoire Naturelle sur une Rousserolle effarvatte

Ceci a permis et permet encore aujourd’hui d’en apprendre un peu plus sur les trajets migratoires des espèces. Cependant, ce marquage individuel permet aussi d’étudier la halte migratoire à l’échelle d’un site. On peut par exemple quantifier le nombre d’individus différents capturés chaque jour et étudier la phénologie du séjour d’une espèce mais aussi, si des individus sont recapturés pendant plusieurs jours, leur attribuer un temps minimal de halte entre première et dernière capture. Cette technique fait l’objet de nombreux suivis à travers le monde. En France, ces suivis sont coordonnés par la Centre de Recherche pour la Biologie des Populations d’Oiseaux (CRBPO).

Grâce aux avancées technologiques de ces dernières décennies il est désormais possible d’équiper les oiseaux de radio-émetteurs (Figure 10; Fiedler 2009, Dossman et al. 2016) et même de dispositifs de géolocalisation (Fiedler 2009). Ce dernier n’est pas encore assez miniaturisé pour équiper des oiseaux très légers. Équiper les oiseaux de radio-émetteurs peut permettre d’étudier plus finement le comportement durant une halte migratoire, mais cette technique est plus invasive qu’une simple bague (Sharpe et al. 2009, Chivers et al. 2016) et pour des raisons de coûts, ne permet pas d’avoir des échantillons de plusieurs milliers d’oiseaux. Ce genre d’études est donc difficilement réalisable à long terme et sur de nombreux sites mais est, grâce à sa précision, fortement complémentaire du baguage (Bächler and Schaub 2007, Robinson et al. 2010, Schofield et al. 2018).



Figure 10 : Exemple d’un phragmite aquatique avec un radio émetteur

1.2.1.2 Études radars

Depuis quelques décennies, les ornithologues ont commencé à transposer des technologies radars utilisées à la base pour la météorologie et l'aviation afin d'étudier la migration des oiseaux (Richardson and Gunn 1971, Gauthreaux Jr. 1972, Liechti et al. 1995). Ces technologies très coûteuses ne permettent malheureusement pas dans la plupart des cas d'identifier une espèce. Cependant, ces outils peuvent être utilisés pour quantifier un passage migratoire et parallèlement tenter d'évaluer l'intensité des départs d'un site de halte de migratoire. En ce qui concerne précisément l'étude de la halte migratoire, ces techniques sont encore très peu utilisées mais cela semble être amené à évoluer dans le futur avec les avancées analytiques permettant d'être de plus en plus précis dans l'identification d'espèces ou de groupes d'espèces, notamment grâce à la fréquence de battements d'ailes (Schmaljohann et al. 2008, Nilsson et al. 2018, Liechti et al. 2019, Schmid et al. 2019)

1.2.1.3 Les données utilisées durant cette thèse

Cette thèse repose sur deux jeux de données principaux. Le premier est extrait de la base de données du CRBPO concernant le baguage des oiseaux palustres en France et le second d'une étude sur le bécasseau semipalmé réalisé par David B. Lank (Simon Fraser University) à la fin des années 70.

Concernant le premier jeu de données, le CRBPO est l'organisme français gérant la quasi-totalité des programmes de baguage à l'échelle du territoire français en mettant en place différents protocoles de capture adaptés aux questions biologiques sous-jacentes. Ainsi, nous exploitons ici les données issues du programme SEJOUR (anciennement appelé HALTE et THEME 10). Le protocole SEJOUR consiste à « collecter des données de baguage qui permettent de quantifier ces stratégies de halte (probabilité d'arrivée et de départ, temps de séjour, taux d'engraissement, nombre d'oiseaux en transit) et ce sur un réseau de sites déployés sur tout le territoire national, et dans les principaux habitats accueillant des concentrations de passereaux migrants » (Henry & CRBPO 2019). Ce programme centralise un nombre très important de données à l'échelle du territoire français pour les espèces étudiées ici. Le nombre total de captures pour le Phragmite des joncs est de 277 211, de 313 489 pour la Rousserolle effarvatte et de 29 255 pour la Gorgebleue à miroir sur une période allant de 1986 à 2018 (Dehorter & CRBPO 2018).

Le second jeu de données a été récolté en 1977 et 1978 par David Berel Lank et consiste en la capture et le marquage de bécasseau semipalmé sur deux sites de halte différents que sont Kent Island (île littorale à la frontière entre les Etats-Unis et le Canada) et Sibley Lake (lac dans les terres au nord des Etats-Unis). Les individus étaient ensuite recapturés visuellement grâce à un code lisible à distance sur la bague ou alors grâce à une capture au filet. Ce jeu de données avait déjà fait l'objet d'analyses (Lank 1983) détaillées dans l'Article 2.



Figure 11: Séance de capture au filet de bécasseau semipalmé (données de l'étude)

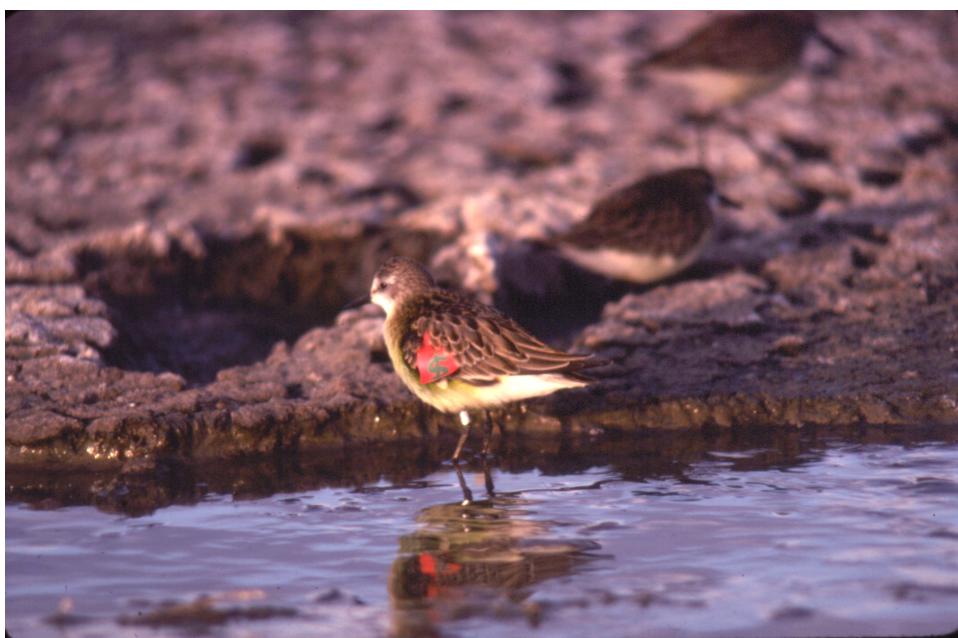


Figure 12 : Bécasseau semipalmé avec marquage alaire individuel

1.2.2 Analyse de données : Les modèles de capture-marquage-recapture

1.2.2.1 Introduction sur les modèles de CMR

Dans l'idéal, un échantillonnage exhaustif de tous les individus présents sur le site de halte pourrait fournir les éléments essentiels à l'étude de la halte migratoire chez les oiseaux. Cependant, un suivi sans faille du jour d'arrivée sur le site de halte jusqu'au jour de départ est quasiment impossible. Les questions sous-jacentes sont donc : (i) quand un individu n'est pas détecté, est-il déjà parti ? (ii) l'individu capturé ce jour-ci vient-il d'arriver sur son site de halte ?

Pour pallier ces difficultés de détection, les chercheurs ont mis en place des suivis individuels via des protocoles de capture-marquage-recapture (CMR; Lebreton, Burnham, Clobert, & Anderson, 1992). Ensuite, l'analyse statistique de ces données avec des modèles de CMR permet l'estimation de la probabilité de l'oiseau de rester sur le site tout en prenant en compte le processus de détection sur le terrain. Ces modèles ont vu en premier le jour dans le but d'étudier la survie des individus communément notée (ϕ). En pratique, les données CMR ne permettent pas d'estimer un paramètre par individu et les modèles s'appuient donc sur diverses contraintes d'homogénéité entre individus (Encadré 1). Si les modèles CMR d'origine considèrent tous les individus d'une population comme homogènes pour les probabilités de survie et de détection (Cormack 1964, Jolly 1965, Seber 1965), des extensions ont depuis permis de prendre en compte différentes sources d'hétérogénéité individuelle dans les paramètres démographiques tels que l'âge, le sexe ou l'expérience (Lebreton et al. 1992, 2009)

Un exemple du modèle de référence en CMR

A chaque intervalle de temps, ou occasion de capture, les individus capturés pour la première fois sont marqués puis relâchés, les données concernant les individus déjà marqués sont enregistrées. Les données CMR collectées se présentent sous la forme d'une suite de « 1 » et de « 0 » (le vecteur $h_{i,t}$), représentant respectivement la détection / non détection de l'individu i à chaque occasion de capture t , formant alors une histoire de capture individuelle. Le jeu de données créé représente l'ensemble des histoires de capture individuelle.

Le modèle de référence dit CJS (Lebreton et al. 1992) fait l'hypothèse d'une variation temporelle des probabilités de survie et de détection. Plus récemment ce modèle a été formulé sous forme d'un modèle à espace d'états pour faciliter son implémentation en Bayésien (Gimenez et al. 2007,

Royle 2008). Cette formulation permet de distinguer facilement le processus dit d'état du processus d'observation. Faisons l'hypothèse que nous avons capturé et marqué un individu au temps t . Il peut maintenant survivre jusqu'au temps $t+1$ avec une probabilité ϕ_t . D'une façon plus imagée, un tirage s'effectue entre chaque pas de temps avec deux probabilités possibles : la probabilité de survivre (ϕ_t) et la probabilité de mourir ($1-\phi_t$). Si l'individu est vivant au temps $t+1$, il pourrait survivre jusqu'au temps $t+2$ avec une probabilité (ϕ_{t+1}). Cela continue jusqu'à ce que l'individu meure ou que la période d'étude soit finie. Ceci est le processus d'état. Si l'on pouvait observer l'état de l'individu à chaque occasion de capture, le calcul de la survie en découlerait simplement. Cependant, la plupart du temps nous n'avons pas l'information complète. Ainsi, un individu marqué peut être recapturé ou revu avec une probabilité p_t . Encore une fois, nous pouvons imager cela avec un tirage durant lequel on aurait d'un côté la probabilité de détection/capture (p_t) et de l'autre la probabilité de ne pas détecter/recaptaurer l'oiseau ($1-p_t$). Quand l'individu est mort la probabilité de détecter l'individu est forcément de 0. Ceci correspond au processus d'observation et il est conditionnel au processus d'état. Cette représentation est une représentation hiérarchique du modèle de CJS. Pour analyser ces données comprenant toutes les histoires de capture ($h_{i,t}$), nous définissons une variable latente $z_{i,t}$ qui prend la valeur de 1 quand l'individu est vivant et 0 quand l'individu est mort. $z_{i,t}$ correspond alors aux réels états (non parfaitement observables) de l'individu. Ce modèle est aussi conditionné à la première capture : nous définissons un vecteur f_i qui informe sur l'occasion lors de laquelle l'individu a été capturé pour la première fois. Les états générés résultent de réalisations d'une variable de Bernoulli. Conditionné au fait qu'il était vivant à l'occasion t , l'individu i peut survivre avec une probabilité $\phi_{i,t}$ jusqu'à l'occasion $t+1$. Ce processus est défini par les équations suivantes :

$$z_{i,f_i} = 1$$

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}(z_{i,t-1} \phi_{i,t})$$

Ensuite, sachant qu'un individu i est vivant au temps t , le processus d'observation est aussi une réalisation d'une variable de Bernoulli :

$$h_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t})$$

De ces trois équations et à l'aide d'une méthode Markov Chain Monte Carlo (Gamerman and Lopes 2006) l'estimation des paramètres peut être faite dans le cadre Bayésien (Gimenez et al. 2007, Royle 2008, Kéry and Schaub 2011)

Cependant, l'analogie entre vivant ou mort d'un côté et présent ou pas sur le site de halte migratoire de l'autre, n'a été faite que tardivement et l'utilisation de ces modèles pour mieux comprendre le comportement des oiseaux sur un site de halte migratoire n'a commencé que dans les années 2000 (Schaub et al. 2001).

1.2.2.2 Les modèles de CMR pour étudier la halte migratoire

L'analogie entre la survie ($\phi_{i,t}$) présentée précédemment et la probabilité de rester sur un site de halte (que l'on nommera aussi $\phi_{i,t}$ pour la suite) permet d'utiliser les jeux de données de baguage présents à différentes échelles spatiales et temporelles (présentés précédemment) pour étudier le départ d'un site de halte migratoire (la probabilité de départ étant l'analogie de la probabilité de mourir, donc $1-\phi_i$). Cependant, l'un des problèmes principaux du modèle présenté précédemment ($1-\phi_i$) est qu'il est conditionné à la première capture, autrement dit on ne s'occupe pas de ce que l'individu peut faire avant son marquage car il n'est pas identifiable individuellement. Si l'on veut s'intéresser à la halte migratoire et plus précisément aux déterminants du départ d'un site de halte migratoire, il est nécessaire de prendre en compte le fait que l'oiseau ait pu arriver sur le site avant sa première capture et donc son marquage. Pour remédier à cela dans d'autres cas d'études que la migration, Crosbie & Manly (1985) ainsi que Schwarz & Arnason (1996) développent une formulation du modèle de Jolly-Seber (Jolly 1965, Seber 1965) appropriée (Lyons et al. 2016, Lok et al. 2019). Cette formulation modélise explicitement le processus d'arrivée des individus dans une population. Ceci peut être utilisé pour modéliser les arrivées d'oiseaux migrants sur un site de halte. Ainsi, si l'on veut construire un modèle de base pour l'étude de la halte migratoire, les trois paramètres principaux utilisés seront les suivants :

- ϕ_t la probabilité de rester sur le site de halte entre les occasions de capture t et $t+1$ sachant que l'individu est déjà arrivé sur le site.
- p_t la probabilité d'être détecté à l'occasion t
- η_t la probabilité d'entrer sur le site de halte à l'occasion t

De la même manière que dans l'exemple précédent (le modèle CJS), nous utilisons la formulation hiérarchique à espace d'états du modèle pour permettre une implémentation plus aisée dans le cadre Bayésien. Cette formulation repose donc d'un côté sur le processus d'état, résultant en un vecteur $z_{i,t}$ qui représente l'état de l'individu i au temps t ($z_{i,t} = 1$ si l'individu est présent sur le site de halte et $z_{i,t} = 0$ si l'individu n'est pas présent), et d'un autre côté le processus d'observation résultant en un vecteur $h_{i,t}$ qui correspond à l'histoire de capture de l'individu i au temps t ($h_{i,t} = 1$ si l'individu a été vu sur le site de halte et $h_{i,t} = 0$ si l'individu n'a pas été vu sur le site de halte). Le processus d'observation est ainsi conditionnel au processus d'état et lui est lié à travers le tirage d'une variable de Bernoulli :

$$h_{i,t}|z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_t)$$

Cela signifie que si l'individu n'est pas encore arrivé sur le site ou qu'il est déjà parti, $h_{i,t} = 0$ avec une probabilité de 1. A l'inverse, si l'oiseau est présent sur le site $h_{i,t} = 1$ avec une probabilité p_t .

Dans le cas de ce modèle le processus d'état correspond toujours à un tirage de Bernoulli mais n'est pas uniquement constitué du produit entre le vecteur $z_{i,t}$ et la probabilité de rester $\Phi_{i,t}$. Il est défini par l'équation suivante :

$$z_{i,t}|z_{i,t-1} \sim \text{Bernoulli}\left(\phi_{t-1} z_{i,t-1} + \eta_t \prod_{j=1}^{t-1} (1 - z_{i,j})\right)$$

Le terme $\prod_{j=1}^{t-1} (1 - z_{i,j})$ représente ici la disponibilité de l'individu pour entrer sur le site de halte. Il est égal à 1 si l'individu n'est pas encore arrivé sur le site de halte et à zéro s'il est présent ou a quitté le site de halte. Il sert à ce qu'uniquement ϕ_{t-1} soit appliqué si l'individu est présent sur le site de halte ou qu'uniquement η_t soit appliqué si l'oiseau n'est pas encore arrivé sur le site de halte.

Cette formulation avec les vrais états de l'individu enregistrés dans le vecteur $z_{i,t}$, permet aussi de calculer des paramètres dérivés liés à la présence ou non de l'individu sur le site. C'est le cas du temps de halte de l'individu, qui peut simplement se calculer ici en sommant les valeurs du vecteur $z_{i,t}$ à chaque occasion (ce vecteur représente la présence ou non de l'individu i au temps t). Ainsi, si on veut obtenir la durée moyenne de halte estimée de notre population d'étude (μ_{halte}), il faut utiliser l'équation suivante :

$$\mu_{halte} = \frac{\sum_i \sum_t z_{i,t}}{n}$$

En conséquence, si l'écart entre deux occasions de capture est d'une journée, μ_{halte} représente la durée de halte moyenne estimée en jours de notre population d'étude.

1.2.2.3 *Implémentation et optimisation*

Dans le cadre des modèles utilisés dans cette thèse (voir section précédente et les quatre chapitres), le temps de calcul peut être très long, et avoisine par moment un mois sur un serveur dédié. Ce temps de calcul semblait d'autant plus augmenter que le nombre d'occasions de captures, plutôt que le nombre d'individus, augmentait. Cela a considérablement ralenti et limité les différents scénarios que nous avons pu tester pendant ces trois ans de travail. L'implémentation des modèles de capture-recapture dans le cadre Bayésien est connue pour être à la fois plus flexible dans les possibilités de paramétrisation mais aussi beaucoup plus coûteuse en temps de calcul que leurs homologues fréquentistes (Kéry and Schaub 2011). D'autant plus, comme dans notre cas, quand la variable latente modélisant la présence ou non de l'individu sur le site de halte ($z_{i,t}$) est d'importance majeure pour l'estimation de nombreux paramètres dérivés comme la durée de halte ou le temps depuis l'arrivée. Cette augmentation de temps de calcul est fortement liée à l'utilisation de l'algorithme « Markov Chain Monte Carlo » (MCMC) qui permet de calculer la distribution *a posteriori* de la valeur estimée des paramètres dans nos modèles. L'avantage du cadre Bayésien est aussi l'utilisation du langage BUGS (Gilks et al. 1994, Kéry and Schaub 2011), qui est, grâce à sa flexibilité et sa facilité d'implémentation, plus abordable pour les écologues.

Les deux premiers chapitres de la thèse ont fait l'objet de l'utilisation du logiciel JAGS (Hornik et al. 2003), pour implémenter nos modèles dans le cadre Bayésien. Ce dernier, comme ses confrères WinBUGS, OpenBUGS et Nimble, utilise le language BUGS pour l'écriture des modèles. Cependant, le temps de calcul étant très conséquent avec l'utilisation de JAGS, une partie de cette thèse a consisté à tenter d'optimiser le temps de calcul à travers l'utilisation de Nimble qui possède deux avantages majeurs (de Valpine et al. 2017). Le premier est qu'il utilise une version compilée en C++ du modèle, ce qui améliore grandement la vitesse de calcul. Le second réside dans la flexibilité de la paramétrisation de l'algorithme d'échantillonnage des valeurs de paramètres dans la distribution *a posteriori*. En effet, on peut utiliser différents algorithmes d'échantillonnage déjà prédefinis dans la librairie nimble pour s'adapter aux différents cas de figure. Un exemple peut être le cas de valeurs de paramètres qui sont corrélées, dans ce cas on pourra tenter d'utiliser l'option

de « block sampling » qui consiste à ce que ces valeurs des paramètres soient échantillonnés ensemble dans l'algorithme de MCMC. Cela conduit souvent à des temps de calculs plus rapides et à une meilleure convergence. La flexibilité de Nimble, réside aussi dans le fait que l'on peut soi-même créer ses propres algorithmes d'échantillonnage. L'utilisation de Nimble nous alors permis de gagner jusqu'à 80% de temps de calcul en comparaison de JAGS (ce qui a grandement facilité la mise en place des modèles de l'Article 3).

1.3 Les sites de halte migratoire : importance et conservation

Les sites de halte migratoire sont d'une importance cruciale non seulement pour le succès du voyage migratoire, mais aussi pour la reproduction et la survie des individus, et éventuellement la viabilité des populations et de manière ultime, des espèces. Les oiseaux migrants ne dépendent pas seulement des sites de reproduction et d'hivernage mais aussi d'une multitude de sites positionnés sur leur trajet de migration. C'est pour cela que la conservation de chaque espèce migratrice doit être considérée à l'échelle de sa voie de migration (Davidson et al. 1998, Kirby et al. 2008). Il est important de maintenir une qualité d'habitat sur l'ensemble de la voie de migration. Les actions de conservation alors entreprises pour améliorer ou stabiliser l'état de conservation d'une espèce peuvent aussi bien être réalisées sur les sites de reproduction ou d'hivernage que sur des sites de halte migratoire. Il a été démontré que les baisses de l'effectif de certaines populations d'oiseaux sont dues à la baisse de qualité ou à la disparition de l'habitat de halte (Zöckler et al. 2010, Piersma et al. 2016). Cependant, la plupart de ces études font ce constat principalement après l'étude préalable de l'espèce sur les aires de reproduction, et ce pour une raison majeure : le signal indiquant une variation de la fitness dans une population d'oiseaux est plus aisément obtenu en étudiant directement les individus sur leurs zones de reproduction (accès au statut reproducteur des individus, fidélité au site de reproduction, détection plus importante grâce aux comportements territoriaux). Si l'idée de conservation d'une espèce à l'échelle de sa voie de migration est largement appliquée pour les oiseaux d'eau et les rapaces, comme par exemple pour le Bécasseau semipalmé étudié durant cette thèse (Gratto-Trevor et al. 2012, Brown et al. 2017), c'est moins le cas pour les passereaux (Kirby et al. 2008). Ceci s'explique par la forte concentration de certaines espèces d'oiseaux d'eau sur peu de sites de haltes, et par les distances de migration couvertes par ces espèces entre deux sites de halte durant leur migration. Il est alors plus aisément de regarder la connectivité entre ces sites et de protéger les zones humides d'importances majeures plutôt que de réaliser le même

travail pour les passereaux qui sont dépendants de beaucoup plus de sites de haltes (Gardner and Davidson 2011).

La vocation de cette thèse n'est pas de fournir des préconisations de conservation ou de gestion mais plutôt de mettre en lumière comment les études et outils statistiques permettant d'approfondir nos connaissances sur les décisions lors d'une halte peuvent être utiles dans le cadre de la gestion ou de la conservation de certains sites de halte migratoire.

1.4 Les objectifs de la thèse

Cette thèse se veut tout d'abord à l'interface entre écologie de la migration et modélisation. Ainsi, les objectifs de cette thèse peuvent être regroupés en deux parties à la fois liées et distinctes. La première (nécessaire pour pouvoir mettre en œuvre la seconde) est d'utiliser et d'adapter les outils récents de modélisation en capture-marquage-recapture (CMR) à l'étude de la halte migratoire. Cette partie était donc l'une des bases nécessaires à la réalisation des quatre articles présentés dans cette thèse. La seconde partie vise, elle, à étudier les déterminants du départ d'un site de halte en utilisant des données de CMR à différentes échelles : un site et une espèce sur 20 ans (Article 1), une saison et deux sites correspondant à des voies de migrations différentes (Article 2), et plusieurs sites et plusieurs espèces pour étudier la synchronie du départ d'un site de halte (Article 3). De plus, notamment dans l'Article 1, cette thèse vise à préciser la part relative des conditions météorologiques *versus* l'état interne de l'individu dans la décision de départ d'un site de halte. Grâce au développement de ces modèles dans le cadre Bayésien, nous avons pu créer et intégrer un prédicteur du départ d'un site de halte migratoire qui a joué un rôle central tout au long de nos travaux : le temps depuis l'arrivée (nommé Time Since Arrival (TSA) dans les trois premiers articles). Enfin, nous avons travaillé sur la manière d'utiliser ces modèles CMR, et plus particulièrement la métrique « temps de halte estimé », comme outils pour la gestion des sites de halte accueillant un nombre important d'oiseaux migrants (Article 4).

Cette thèse vise donc à explorer les déterminants du départ d'un site de halte migratoire à travers l'utilisation et le développement d'outils de modélisation récents, à valoriser des jeux de données de CMR déjà existants, et à préciser les implications de nos résultats et nos développements méthodologiques pour la gestion des zones de halte migratoire.

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2 Article 1 : Importance relative du temps depuis l'arrivée et des conditions environnementales dans la décision de départ d'un site de halte migratoire.

Statut de l'article : Soumis à Oecologia

2.1 When to depart from a migration stopover site ? Time since arrival matters more than weather conditions

When to depart from a stopover site? Time since arrival matters more than weather conditions

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Abstract

On the journey to wintering sites, migratory birds usually alternate between flights and stopovers where they rest and refuel. Migration strategies are assumed to differ according to season: a time-minimization pre-breeding migration strategy towards breeding locations, and an energy-minimization post-breeding migration strategy to wintering ones. The duration of flights and stopovers determines the energy requirements and the total duration of the journey. Since migrating birds actually spend most of the time at stopovers, selection to minimize the amount of energy or time spent on migration is very likely to operate on the effectiveness of stopover rest and refueling. Here we address the relative contribution of factors to departure decisions from stopover sites during the post-breeding migration in a long-distance migratory songbird. When capture probability is low it is impossible to assess the variation in body condition over the entire duration of the stopover. To get around this, we use Time Since Arrival (TSA) as a proxy for the changes in the state of individuals during the stopover. We propose that TSA is an integrative proxy for resting, feeding and fattening efficiency. We develop a capture-recapture model to address the relationship between departure probability, estimated TSA, and weather conditions. Using a 20-year dataset from sedge warblers, we show that TSA has a larger effect on departure probability than weather conditions. Low humidity and an increase in atmospheric pressure in the days preceding departure are associated with higher departure probability, but these effects are smaller than that of TSA.

Keywords: Stopover, Time Since Arrival, Capture-Recapture, Sedge warbler, Bayesian inference

Introduction

Each year migratory birds species commute between breeding and wintering areas (Alerstam 1990, Somveille et al. 2015). Most species cannot go from breeding to wintering grounds in a single flight of thousands of kilometers. They must stop to rest, feed and refill energy stores regularly (Alerstam 1990, Åkesson & Hedenström 2007, Schmaljohann & Eikenaar 2017, Schmaljohann 2018). The duration of migratory flights and stopovers determines the energy requirements and also the total duration of the journey. To maximize survival, individuals must optimize their journey to match with seasonal variation in food availability (and their energy requirements) at stopover sites and to arrive at wintering areas when resource availability is sufficient (Alerstam 1990, Somveille et al. 2015, 2018, 2019, Zúñiga et al. 2017, Schmaljohann 2018). Birds spend much more time at stopover sites than in migratory flight, with almost 85% of the journey spent on stopover (Hedenström & Alerstam 1997, Green et al. 2002, Schmaljohann et al. 2012, Schmaljohann 2018). Consequently, selection to minimize the amount of energy spent (energy minimization) or the total time spent on migration (time minimization) likely operates mainly on the effectiveness of stopover rest and refueling (Hedenström & Alerstam 1997, Schmaljohann 2018).

Deciding to leave the stopover site normally means a new flight of hundreds of kilometers. This movement itself, and its termination, are highly constrained by the maximal flight capacity (given the size of energy reserves and body size) and atmospheric conditions (Alerstam, 1990; Jenni & Schaub, 2003; Schmaljohann & Eikenaar, 2017; Wikelski et al., 2003). Once settled at a stopover site, the probability of departing (and the duration of the stay) depends on fuel store, resting state, food availability, weather conditions and migratory experience (Jenni & Schaub 2003, Schmaljohann & Eikenaar 2017). Recent studies have tried to disentangle the environmental factors driving departure decision (Schaub et al. 2008, Ktitorov et al. 2010, Arizaga et al. 2011, Deppe et al. 2015, Dossman et al. 2016, Schmaljohann & Eikenaar 2017). Weather conditions are usually considered through the constraint they impose on flight. Departure decision depends on wind speed and direction : tailwind assistance reduces the cost of flight but strong headwinds force the birds to stay at the stopover site (Tsvey et al. 2007, Arizaga et al. 2011, Ma et al. 2011, Dossman et al. 2016). This decision also depends on rainfall or humidity which usually force birds to stay at the stopover site (Tsvey et al. 2007, Arizaga et al. 2011, Deppe et al. 2015, Dossman et al. 2016). Last, cloud cover influences departure decision by decreasing visibility and the ability of birds to navigate

(Zehnder et al. 2001, Åkesson & Hedenstrom 2007). Even if weather factors influencing departure decisions seem to be clear, their relative contributions are less well known.

But the internal state of the individual (resting state, fuel store, migratory experience) also largely influences departure decision: birds need to rest and reach a sufficient level of fuel store to perform the next migratory flight (Alerstam 1990, Hedenstrom & Alerstam 1997, Schaub et al. 2008, Goymann et al. 2010, Schmaljohann et al. 2012, Dossman et al. 2016, Moore et al. 2017, Schmaljohann & Eikenaar 2017, Anderson et al. 2019). Apart from resting to recover from extreme physical exercise and sleeping to recover from sleep deprivation during migratory flight (Schwilch et al. 2002), birds at stopover allocate most of their time and energy to foraging (Hedenstrom & Alerstam 1997, Cohen et al. 2014, Smith & McWilliams 2014). They are assumed to refill their energy stores as fast as possible, and to continue their migratory journey if their energy stores and weather conditions are favorable (Schmaljohann 2018). In addition, the ability to refuel and rest may depend on age or experience, which can lead individuals migrating for the first time (juveniles) and those that already traveled to wintering areas in the past (adults) to depart from stopover sites after stays of different durations or under different weather conditions (Deppe et al. 2015, Dossman et al. 2016, Schmaljohann et al. 2018).

To our knowledge, the relative importance of individual internal state (resting state, fuel store) and weather conditions at determining departure probability has never been assessed within a single modelling framework. The different results of previous studies concerning the relationship between fuel store and departure probability could be due to different local constraints or to the migration strategy (time or energy-minimizing; Hedenstrom and Alerstam 1997; Schmaljohann 2018; Anderson et al. 2019). But more importantly, it could be due to the fact that fuel store can only be measured when individuals are captured (i.e., not necessarily at the very beginning and end of their stay). The lack of an effect of fuel store on departure probability could also arise because the method to jointly incorporate internal individual state and environmental covariates in the same capture-recapture (CR) framework was not available (Jenni & Schaub 2003, Schmaljohann & Eikenaar 2017). Here we define and estimate a variable that cannot be measured without using electronic devices: the time the individual has spent at the stopover site since its arrival: Time Since Arrival (Pledger et al. 2008). Our goal is to assess the influence of TSA on departure probability using a long-term dataset created when electronic devices were not available, and to include a large number of individuals and years in the analysis. Despite limitations of retrospective analyses of

long-term datasets (modern electronic techniques were not available), such datasets offer interesting opportunities: (i) large sample sizes to draw inference about departure probability using statistical approaches, and (ii) long time series of observations to characterize long-term patterns and yearly deviations from deep-rooted trends. Birds need to rest after a long distant migratory flight and fattening increases with the duration of the stay at stopover (Alerstam 1990, Schwilch & Jenni 2001, Jenni & Schaub 2003, Schaub et al. 2008, Schmaljohann & Eikenaar 2017). We propose that Time Since Arrival (TSA) is an integrative proxy for the overall change in the internal state of stopovering birds. If this assumption is true, then departure probability should decrease as the TSA increases, and TSA should be a major determinant of departure probability. Importantly, TSA must be estimated using an analytical technique accounting for the daily capture probability of marked individuals (i.e., the probability of capturing an individual that is alive and present in the site). This is a methodological challenge because investigators know neither the day when a bird arrives nor the day when it departs from the site. Many capture-recapture stopover studies have relied on the assumption that birds are captured for the first and last time on the exact days of arrival and departure from the site (Schmaljohann & Eikenaar 2017). This assumption is unrealistic: the probability that a bird is captured in a given day usually lies between 0.1 and 0.2 (Schaub & Jenni 1999, Schaub et al. 2001, Moore et al. 2017), and the resulting “minimal stopover duration” (duration between first and last captures) strongly underestimates the actual stopover duration (by a factor that may be as large as 3; Schaub, Pradel, Jenni, & Lebreton, 2001). Estimating TSA requires the development of a statistical model accounting of imperfect detection probability.

Here we evaluate the contribution of estimated TSA and weather conditions to departure probability. We develop a capture-recapture model and analyse a long-term CR dataset from a long-distance migrant songbird at a stopover site. Since refueling seems to be the primary biological function of stopover (Schmaljohann & Eikenaar 2017, Schmaljohann 2018, Klinner et al. 2020), we hypothesize that TSA is be the main driver of departure probability in this long-distant migrant and that wind, humidity, cloud cover and atmospheric pressure have a secondary, but significant effect on the departure probability. Estimated TSA should be closer to the genuine duration of the individual's stay than the time elapsed between the first and the last physical captures of the individual. If TSA integrates the overall changes in the individual internal state, this should help us detect the effect of stay duration on departure probability, if any. Moreover, we hypothesize that stopover duration differs according to migratory experience, as documented in other studies (Deppe et al. 2015) and test for differences between juveniles and adults.

Material and methods

Study area, sampling and dataset

The study site is the Trunvel ringing station (Tréogat, Brittany, France; 47.8964859, -4.3698274). Data from marked individuals have been collected using a standardized mist-netting protocol (including tape-luring; B. Bargain, C. Vansteenwegen, & J. Henry, 2002). Each captured bird was identified, ringed and aged. We used data collected from 1990 to 2014, from the 1st to the 30th of August because 90% of the captures occur in this month. The years when the number of recaptures was too low were not used in analyses (less than 10 birds recaptured only once). The sedge warbler (*Acrocephalus schoenobaenus*) is the most abundant species that stopovers at this site during its journey to winter quarters in sub-Saharan Africa. This 12-g songbird strictly depends on reedbeds where it essentially forages on one aphid species (*Hyalopterus prunii*) to refill energy stores (Bibby and Green 1981).

Between 1990 and 2014, 79,700 individuals have been marked (Dehorter and CRBPO 2015). Among all migrant songbirds that use this site, only a small fraction stays several days to rest and refuel (i.e. actual stopover; Warnock, 2010). The majority either continues migration by the following night, or moves to another stopover place (i.e., transients; Bächler & Schaub, 2007; Schaub et al., 2008). As we aim to study the departure probability of birds that stayed over at the site, we analyzed only capture-recapture data from birds that were caught at least twice during a season (including recaptures during the same day). Hence, the estimated stopover duration applies only to the part of the population passing by the site and that stays for at least some hours or days. The sample we used included data from 683 adults and 4927 juveniles; their latest recapture occurred at the site on average 3.4 ± 3.6 (SD) days after their first capture. The mean mass gain between first and last capture on individuals was $0.48g \pm 1.48$ (SD).

Weather conditions

Weather variables expected to influence daily departure probability (between day t-1 and t) were: (i) wind (on day t-1), (iii) relative humidity (on day t-1), (iii) cloud cover during the night [i.e. between day t-1 and t; scale from 0 (no cloud) to 8 (complete sky cover)] (iv) atmospheric pressure; as birds likely perceive changes in pressure rather than pressure itself, we used the change in atmospheric pressure between day t and day t-1 as a covariate (denoted as $\Delta Pressure$ in hPa). Depending on its direction, wind can either facilitate flight (tailwind) or increase the cost of flight

(headwind). To integrate both wind effects, we computed the wind covariate as in (Arizaga et al. 2011):

$$\text{wind} = V \cos[\alpha_T - (180^\circ + \alpha_W)],$$

where V is wind speed (in $m.s^{-1}$), α_T is the assumed departure direction (120° according to recovery data; note that birds don't cross the Bay of Biscay, Dehorter and CRBPO 2015, so 120° is almost the coast direction), and α_W is the direction the wind (Åkesson et al. 2002). Since birds depart on migration at the end of the day (Müller et al. 2018), we used wind speed and direction observed during a period of time starting 2 hours before sunset on day $t-1$ and ending in the middle of the night on day t . All weather covariates were scaled prior to the analyses. The weather data were provided by the Penmarch meteorological station ($47.797537, -4.374768$).

Modelling & statistical analyses

We used a formulation of the Jolly-Seber (JS) model (Jolly 1965; Seber 1965) parameterized with entry probability in the sampling area (Crosbie and Manly 1985; Schwarz and Arnason 1996). This allows modeling the arrival of birds at the stopover site and estimating stopover duration (Lyons et al. 2016; Lok et al. 2019). The parameters of the model are:

ϕ_t Probability of staying in the sampling area from day t to $t+1$,

η_t Probability of arriving at the stopover area on day t given that the individual was not present in the site before,

p_t Probability of capturing the individual on day t given that the individual has arrived and has not yet left the site.

We used the Bayesian, state-space formulation of the JS model (Gimenez et al. 2007; Royle 2008). This model contains a submodel for the state process: true, partially unobservable states are “not yet arrived”, “present in the study area”, and “departed”. The model also includes a submodel for the observations (conditional on true state) directly encoded in the individual capture histories. For each individual capture history h_i , the true state history is accounted for by the vector z_i . This vector of binary state variables describes if an individual i is present in the stopover area on day t , $z_{i,t} = 1$, or not, $z_{i,t} = 0$.

The state process is defined as:

$$z_{i,t}|z_{i,t-1} \sim Bernoulli\left(\phi_{t-1}z_{i,t-1} + \eta_t \prod_{j=1}^{t-1}(1 - z_{i,j})\right)$$

The term $\prod_{j=1}^{t-1}(1 - z_{i,j})$ accounts for the availability of the individual to enter the stopover area and is equal to 1 when the individual has not yet entered the stopover area, and 0 when it has already entered.

As the binary observations are conditionally independent Bernoulli random variables, the link between the state and observation processes is given by the following equation:

$$h_{i,t}|z_{i,t} \sim Bernoulli(z_{i,t}, p_t)$$

This means that if individual i has not yet entered the stopover area or has left ($z_{i,t} = 0$), then $h_{i,t} = 0$ with probability equal to 1. If $z_{i,t} = 1$, then the capture history $h_{i,t}$ is a Bernoulli trial with probability p_t , which is the probability of capturing the individual on day t . This formulation allows us to estimate TSA for each individual. The TSA covariate is a partially- or non-observable variable computed using the sum of true states $z_{i,t}$. TSA accounts for the time individual i has already spent in the stopover area on day t :

$$TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s}$$

The state vector z_i also allows us to use a new formulation of the stopover duration described in Lyons et al. (2016). We computed the mean stopover duration (in days) as follows:

$$SOD = \frac{\sum_i \sum_t z_{i,t}}{n}$$

where n is the number of individuals and z the true state variable (whether individual i was present or not at the stopover site on day t).

To account for heterogeneity in detection probability among capture occasions and limit the number of parameters to estimate, we modeled detection probability as a random effect. Hence, we modeled p as:

$$\text{logit}(p) \sim \text{Norm}(\text{logit } (\mu_p), \sigma_p),$$

where μ_p is the mean recapture probability and σ_p the standard deviation of the random effect.

We expressed the probability of remaining at the site as a function of the previously defined weather covariates and TSA. We considered effects as ‘statistically significant’ when the estimated slope corresponding to these covariates had a 95% credible interval excluding 0 (Kéry and Schaub 2011). We analyzed the 20 years of data simultaneously, but accounted for potential differences among years (Péron et al. 2007) by means of a random year effect, where y is the number of the year:

$$Year_y \sim Norm(\mu_{year}, \sigma_{year})$$

To account for the effect of the experience on an individual’s departure probability from the stopover site, we used age-dependent random effects with 2 age classes (Adult and Juvenile), where a is the age class:

$$Age_a \sim Norm(\mu_{Age}, \sigma_{Age})$$

Using a logit link, the probability of staying at the stopover area between $t - 1$ and t was formulated as:

$$\begin{aligned} Logit(\phi_{i,t-1}) = & \alpha + \beta_1 * TSA_{i,t-1} + \beta_2 * wind_{t-1} + \beta_3 * temperature_{t-1} + \beta_4 \\ & * cloudcover_{t-1} + \beta_5 * humidity_{t-1} + \beta_6 * \Delta Pressure + Year_y + Age_a \end{aligned}$$

Here we included all the covariates in the model despite a non-null collinearity between most of the environmental covariates (see online Supplementary material for details). However, this collinearity appeared sufficiently small to allow the inclusion of all effects in a same model (Hair et al. 2006). Also, because TSA is computed at each occasion for each individual, TSA cannot be standardized prior to analyses. To compare the effect of TSA on departure probability to that of weather covariates, we calculated the effect of a standardized TSA by multiplying the estimated values of the TSA slopes (β_1) by the standard deviation of all estimated TSA values.

We performed analyses with JAGS (with the package R2jags, Hornik et al. 2003; Su et al. 2015) using R version 3.6.1 (R Development Core Team 3.0.1. 2013). We used 60 000 iterations with a burnin of 30 000, and we checked chain mixing and convergence (Kéry and Schaub 2011). The JAGS code is available in the online Supplementary material.

Results

The mean estimated stopover duration for the whole study period is 12.5 ± 2.2 days CI [12.2; 12.8], with unstructured variation among years (Fig. 1). Adults (experienced birds) stay on average 1.6 days more than juveniles (naive birds) (13.8 ± 2.2 for adults, and 12.2 ± 2.1 days for juveniles; this age difference is robust through years; Fig. 1). However, the 95% credible intervals and standard deviation of estimated stopover duration for juveniles and adults overlap (Fig. 1) and therefore age accounts for a very limited part of the variation in stopover duration between individuals. This suggests that factors other than migratory experience and covariates accounted for in this study also determine departure probability.

Departure probability from the stopover site between two days ($1-\phi_t$, i.e. the complement of the probability of staying at the stopover site) is positively related to TSA (Table 1 and Fig. 2). In other words, the longer a bird has already stayed at the site, the higher its probability of resuming migration flight by the following night. TSA is the most important predictor of departure probability compared to other variables, based on effect sizes (Table 1). TSA effect is also the effect that is estimated with the largest precision, which suggests a small variability of the TSA effect among individuals (see CI in Table 1).

Both humidity and $\Delta\text{Pressure}$ have an effect on the departure probability from the stopover site (Table 1). Departure probability increases with drier conditions and large changes in pressure ($\Delta\text{pressure}$). We did not find evidence of an effect of wind on departure probability (Table 1). We found slight evidence of a negative effect of cloud cover on the departure probability from the stopover site (Table 1), but the robustness of this result is weak because one boundary of the CI overlaps 0. Estimates of TSA and humidity effects on departure probability (Fig 2a) or of $\Delta\text{pressure}$ (Fig. 2b) show that departure probability primarily depends on TSA, and that weather covariates have a smaller influence on this probability.

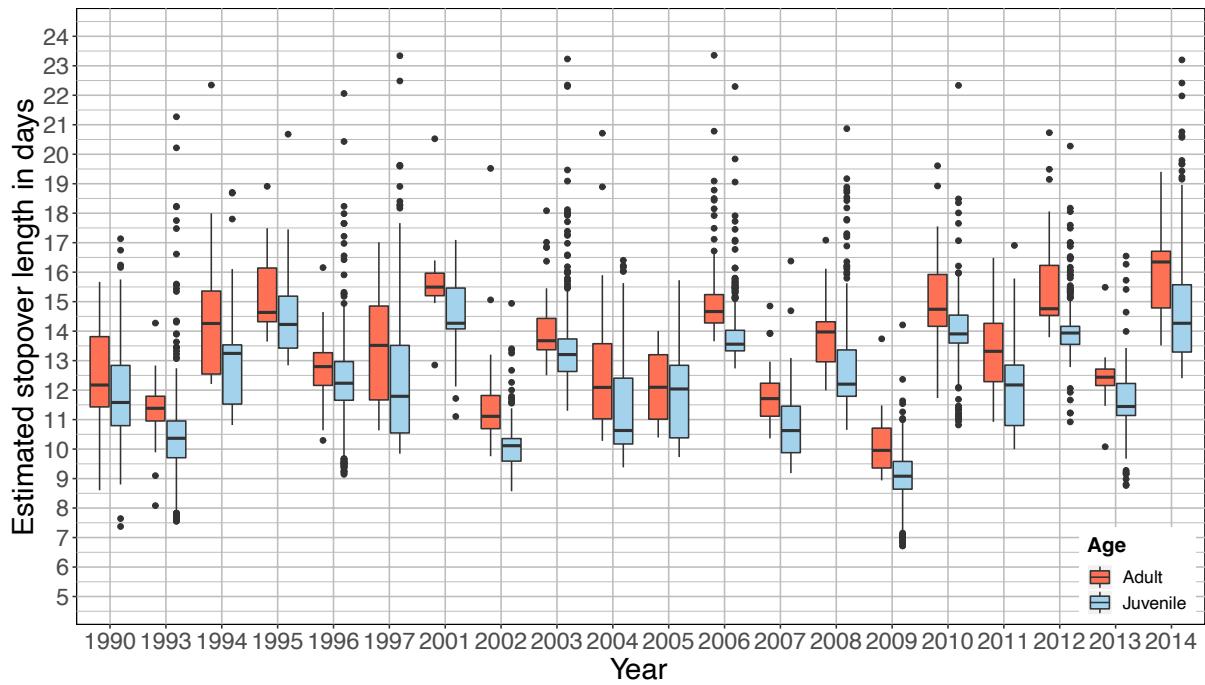


Figure 1: Between-year variation in individual stopover duration estimates (in days) per age category for the sedge warbler (*Acrocephalus schoenobaenus*).

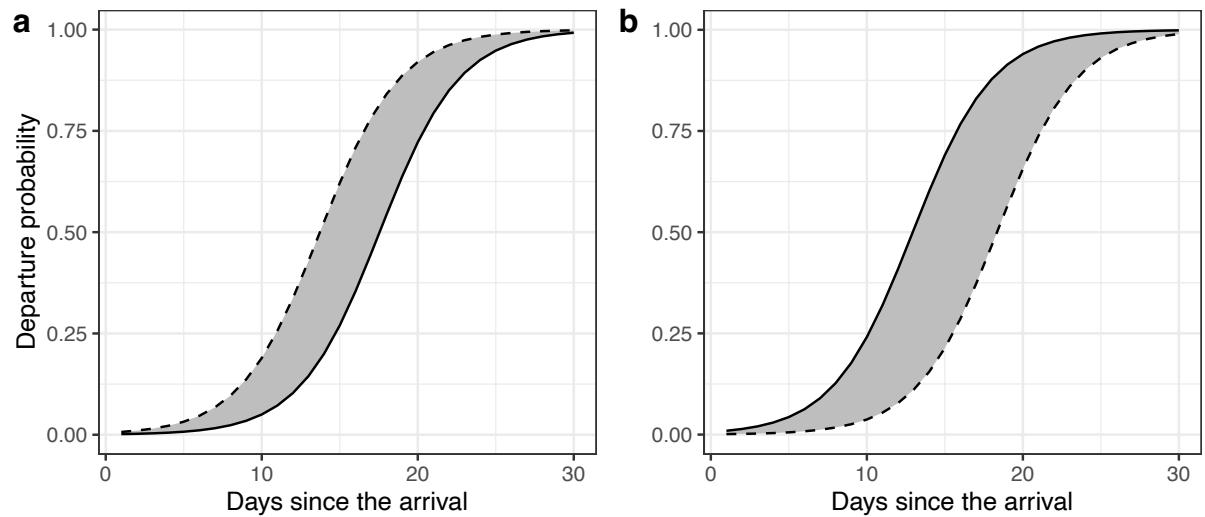


Figure 2: Departure probability as a function of the number of days since the bird arrived. (a) For different humidity conditions, dashed line: low humidity conditions (~70%); plain: high humidity conditions (~90%). (b) For different Δ Pressure conditions, dashed line: a substantial decrease of atmospheric pressure (-5Hpa); plain: a substantial increase of atmospheric pressure (+5Hpa). The grey area represents departure probability values for humidity between 70 and 90% (a) and Δ Pressure between -5Hpa and +5Hpa.

Table 1: Mean value, standard deviation and credible intervals (CI) for each covariate effect on the probability of staying at the stopover area. Bold: significant effects.

	<i>Mean</i>	<i>Sd</i>	<i>CI</i>
<i>(α) Intercept</i>	6.159	0.175	5.843, 6.578
(β_1) Time Since Arrival	-1.538	0.039	-1.652, -1.432
(β_2) Wind	0.116	0.1	-0.121, 0.196
(β_3) Temperature	-0.207	0.89	-0.387, 0.03
(β_4) Cloud cover	0.142	0.101	-0.052, 0.207
(β_5) Humidity	0.497	0.121	0.261, 0.735
(β_6) Δ Pressure	-0.702	0.23	-1.176, -0.196

Discussion

Effect of the Time Since Arrival on departure probability

Our statistical framework to address covariates influencing the probability of leaving a stopover site allowed us to provide evidence that TSA is the major determinant of this probability in sedge warblers in Trunvel. TSA is a reliable indicator of the propensity of an individual to leave the stopover site. We acknowledge that TSA is only a proxy of all the changes in the individual ‘state’ (*sensu* Clark and Mangel 2000) during the stopover, but it is reasonable to think that TSA reflects the progressive change in the individual internal state. On the first day after arrival, birds are supposed to be exhausted, starving and to lack fuel stores. The longer they stay, the more opportunities they have to rest, feed and fatten (Schmaljohann and Eikenaar 2017).

TSA encompasses different functions of the stopover behavior: (i) resting after a migratory flight (McWilliams et al. 2004; Skrip et al. 2015), and (ii) reaching a sufficient level of fuel load to perform the following migratory flight (Schmaljohann and Eikenaar 2017). TSA also reflects (iii) the

refueling rate, which depends on environmental conditions and physiological processes involved in refueling (Jenni and Schaub 2003; Schmaljohann and Eikenaar 2017). Here, TSA has a positive effect on departure probability: birds need to stay a sufficient number of days before leaving. For birds that do fatten, the fattening (or fuel deposition) increases through time: the longer individuals stopover, the larger their last measured body mass or fuel load (mean mass gain of 0.48g in this study; T. Alerstam, 1990; Schmaljohann & Eikenaar, 2017) and the larger the daily mass gain (Péron et al. 2007). Consequently, it is reasonable to think that birds need to rebuild a sufficient level of fuel store to perform another migratory flight (Alerstam 1990). Moreover, the resting time after a long migratory flight is apparently brief and confined to the first hours or days of the stopover (Fuchs et al. 2006, 2009; Németh 2009). This suggests that resting is not the physiological process that requires a 12-day stopover. Rather, most of the time spent in stopover is allocated to foraging in order to refill energy reserves; the latter is a long and progressive process. Hence, for the fraction of birds that stopover at this place, we believe that TSA reflects the time required by the physiological processes involved in refueling. Determining the relationship between TSA and fuel store will be an important area of future research in stopover ecology and more specifically for the application of the present modelling framework.

Traditional measures of fuel store such as size-scaled body mass or fat score have some limitations (extensively discussed in Schmaljohann & Eikenaar, 2017; Schwilch & Jenni, 2001), of which we want to highlight two. (i) In many long-term migration monitoring programs of marked birds, especially in old datasets, body mass was not systematically recorded at each recapture event. This drastically reduces the sample size available for long term analyses where we need a body mass measurement at each recapture. In the French dataset for sedge warblers, in the twentieth century, individuals were weighed on only 60% of the capture events (Dehorter and CRBPO 2015). Nowadays (2000-2016 period), individuals are weighed on nearly all the capture events (90%). (ii) Since the probability of being captured in a given day can be low in routine trapping protocols (0.161 [0.058, 0.376] in this study; Schaub et al. 2001, Schmaljohann and Eikenaar 2017), the body mass measured at the latest capture is unlikely to be representative of the body mass that actually triggers departure. Imperfect detection probability is a common situation where modeling the individual history before the first capture is required to estimate arrival date. This imprecision in the assessment of the body mass change through time can mask the effect of body mass on departure probability in datasets where daily capture probability is low. Overall, the proposed analytical method, relying on TSA, allows analyzing individual variations in stopover duration over

long time series, even in absence of biometric data, and even when body mass or fat score informations are too sparse to reliably document the progress through time of the energetic state of each monitored individual.

Using TSA as a proxy for the internal state of the bird just before departure make some critical assumptions. When birds stay only few days, they may not improve condition with time spent at the stopover site because they may first continue to degrade upon arrival waiting for their digestive system to redevelop to refuel after a long-distant migratory flight (McWilliams et al. 2004). The relevance of TSA may also be limited when birds relocate in the vicinity of the study site (Bächler and Schaub 2007): in this case the departure from the study site does not mean that individuals are resuming a long-distance migratory flight. Birds relocating a few kilometers away from the study site do not need to wait until their internal state improves before leaving the site. To get around these problems, birds captured only once are usually removed from capture-recapture datasets. This removes most of the transient individuals (Mills et al. 2011; Taylor et al. 2011; Sjöberg et al. 2015). Including both estimated TSA and fuel store data (body mass, fat score) into a model would be an interesting avenue to revisit previous analyses. This will help understand the contrasted results of previous studies about fuel store effects on departure probability (Tsvey et al. 2007; Schaub et al. 2008; Arizaga et al. 2011; Smith and McWilliams 2014; Schmaljohann and Eikenaar 2017). Also, other limitations, more related to modelling and data, appear when we use this type of model. It requires a large amount of recapture to test for more precise effects of the various determinants of departure probability. Interactions between TSA and date or TSA and age could have been tested. However, to correctly estimate the interaction, it is possible that it would have been necessary to drastically reduce the dataset to keep individuals captured at least three times, which does not exist for some years of our dataset. This would be interesting avenues to test on a dataset with a higher detection probability, for example with a capture-mark-resight shorebirds dataset (Lok et al. 2019).

Effect of weather conditions on departure probability

In relatively humid days, birds tend to postpone departure. Birds wait for dryer conditions to resume their migratory flight. Humidity can be high even in absence of precipitation in Western Brittany. The negative effect of high humidity can reflect not only the inhibitory effect of rain, but also the increased flight cost when the air is very humid (Åkesson et al. 2001, Deppe et al. 2015). The probability of departing from the stopover site increases when atmospheric pressure increases

between the day before the night of departure and two days before. When birds perceive an increase in pressure (indicative of improving, anticyclonic conditions), this could encourage them to resume migration flight by the following night. Unexpectedly, departure probability does not depend on wind, probably because wind was too rare and weak in the study area in August to be influential (mean wind force during the study period was 5 m.s⁻¹, see Supporting Information S1 for a summary of the weather covariates). Wind is usually one of the most important meteorological aspects for birds departure decisions in areas exposed to substantial air movement during the migration of the studied species (Åkesson et al. 2001, Zehnder et al. 2001, Schaub et al. 2004, Tsvey et al. 2007, Arizaga et al. 2011, Deppe et al. 2015, Sjöberg et al. 2015, Dossman et al. 2016).

Effect of migratory experience on departure probability

Juveniles (birds migrating for the first time) stay on average 1.6 days (11.6%) less than the older, more experienced birds at the stopover area. Even though there is no consensus about the age effect on stopover strategy (Hake et al. 2003; Moore et al. 2017), this result is consistent with former studies that have shown that juvenile and experienced birds behave differently regarding departure probability from stopover sites: juveniles make shorter and more frequent stopovers than adults (Reilly and Reilly 2009; McKinnon et al. 2014; Vansteelant et al. 2017). However, other studies reached opposite conclusions: telemetry studies of departure decisions in songbirds in the Gulf of Mexico did not find any effect of age on the decision to cross the Gulf of Mexico, or of weather conditions (McKinnon et al. 2014; Deppe et al. 2015). Again, it is legitimate to ask whether imperfect detection probability is involved in inconsistencies among studies concerning the relationship between age and departure probability from stopover sites, because capture probability can vary with age (Rguibi-Idrissi et al. 2003; Pardo et al. 2013; Sanz–Aguilar et al. 2019).

Respective effects of TSA and weather conditions on departure probability

In this study, we show that the contribution of TSA to departure probability in a long-distant migrant is larger than that of weather conditions. This suggests that even when weather conditions are favorable to departure, birds need to stay before departing. To our knowledge, this is the first time that the contributions of these factors were estimated with a capture-recapture model. Nevertheless, our result is consistent with numerous studies that have highlighted the key role of

the improvement of the individual internal state (fuel store, fuel deposition rate, body condition, body mass, resting) on departure decisions from a stopover site (see Schmaljohann and Eikenaar 2017 for a review and Anderson et al. (2019) for a recent study with telemetry tools).

The improvement of the internal state during a stopover could be indirectly related to environmental conditions. Indeed, harsh weather can decrease the ability of individuals to feed and food abundance in the stopover area. This likely leads to a decrease in the rate at which birds accumulate energy (Jenni and Schaub 2003). If this holds, weather conditions can affect TSA and stopover duration. Interestingly, here we found slight evidence of an effect of weather conditions on departure probability while TSA was taken into account in the analysis. The relationship between TSA and weather conditions during the stopover should be addressed in future work to better understand the processes involved in departure decisions from a stopover site.

Recent studies also highlighted that migration distance affects the stopover strategy of birds (Anderson et al. 2019) and that birds also behave differently between stopover sites along their journey (Schmaljohann et al. 2017). Concerning the sedge warbler at our studied site, we have no clues from a specific origin (controls indicate birds from Great Britain, Scandinavia, Eastern Europe; Dehorter and CRBPO 2015) or a final destination. However, as we only study one species which is strictly trans-saharian, the variability of stopover strategy induced by migration distance may be limited.

Conclusions

We incorporated TSA, a partially hidden individual state, and weather conditions in the same capture-recapture modeling framework to disentangle the factors playing a part in the decision to depart from a stopover site. Using a long-term dataset, we showed that TSA is the main driver of departure probability (and of stopover duration) in a long-distant migrant songbird. This approach will allow investigating the determinants of stopover duration and departure probability (not only weather variables but also some hidden physiological processes accounted for by TSA) in hundreds of existing long-term datasets, where there is no, or scattered information about mass or fat score. We demonstrated the feasibility and relevance of this analytical approach using data from one site, one species and over a large period of time. Our modeling approach will have to be used with data from several species, at several sites, to assess the robustness and generality of our conclusion about the major influence of TSA on the time when individuals decide to leave stopover sites.

TSA also has broader implications outside migration ecology in situations where the time individuals spend on sites is a partially observable variable. For example, in behavioral ecology and foraging ecology, the probability of an individual changing foraging site could also depend on the time spent in a site, the number of competitors, or food availability. TSA opens large perspectives when behavior depends on the time spent in a site, in a specific state, and when detection probability is imperfect at the time scale relevant to the research topic addressed.

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3 Article 2: Décisions de départ du bécasseau semipalmé (*Calidris pusilla*) sur deux sites aux conditions météorologiques contrastées et concernant des voies migratoires différentes.

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3.1 More Than Just Refuelling: Lengthy Stopover and Selection of Departure Weather by Sandpipers Prior to Transoceanic and Transcontinental Flights

Running title: Migratory sandpiper behaviour at stopover sites

More Than Just Refuelling: Lengthy Stopover and Selection of Departure Weather by Sandpipers Prior to Transoceanic and Transcontinental Flights

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Author contributions: SR helped to conceive the idea, did the analyses and drafted the manuscript. DBL conceived and designed the study, carried out the field work and critically revised the manuscript. RP and EC helped to conceive the idea and revised the manuscript. All authors gave final approval for publication.

Abstract

The evolutionary and behavioural ecology of migratory birds has received much theoretical and empirical attention. We contribute to this field by contrasting the weather at departure and stopover durations of a long-distance migratory sandpiper prior to initiating lengthy transoceanic versus transcontinental flights of potentially variable duration. Transoceanic flights provide few if any stopover options. We predicted that transoceanic migrants should therefore be more selective of energetically favourable weather at departure and have longer stopover durations prior to departing, using time as a surrogate for cumulative fuel acquisition, than transcontinental migrants. We used recent advances in capture-recapture modelling to quantify how weather conditions, length of stay, including estimated residence time prior to capture, and age class correlated with daily departure probabilities of Semipalmated Sandpipers (*Calidris pusilla*) at a coastal and an inland stopover site at comparable latitude. As expected, departure probabilities from both sites were higher with increasing strength of tailwinds, and the strength of this effect was larger for birds facing transoceanic versus transcontinental flights. Cloud cover and temperature conditions at departure converged between sites at intermediate values from different background distributions. Stopover durations at both sites were substantially longer than needed if the birds were pursuing a simple tactic of arrive-fatten-leave at the stopover site. We infer that both sites provided high levels of both food and safety relative to other stages in the birds' annual cycle, which favoured lengthy stopovers and subsequent use of lengthy flights from both sites. Our study shows that recent advances of capture-recapture models can provide additional resolution to studies of the migration strategies of birds and refine our perspective on global patterns of migration routes and stopover decisions.

Keywords: stopover decisions, migration, capture-recapture, Bayesian analysis, barrier effect

Introduction

Migratory birds make their biannual movements between breeding and non-breeding areas in a series of flights. Selection will favour flight strategies that include ‘hops skips or jumps’, and variable stopover durations between flights (Schaub *et al.* 2008, Warnock 2010, Anderson *et al.* 2019) that optimize fitness (Alerstam & Lindström 1990). Thus, birds’ internal conditions and external situations when initiating flights should provide information about the nature of selection during the subsequent migratory flight. As an extreme example, Bar-tailed Godwits (*Limosa lapponica baueri*) departing on spectacular 6–9 day non-stop trans-Pacific Ocean flights from Alaska to New Zealand carry fuel stores approximately equal to their airframe body mass and do so when stronger tailwinds are available (Gill *et al.* 2009). Ecologically, sufficiently food-rich and safe staging sites must be available to permit selection favouring the evolution of such flights (Lank *et al.* 2003, Ydenberg *et al.* 2007). But generally, theory shows that the costs of transporting excess fuel trades off against flight distance (Alerstam & Lindström 1990). Thus, most migration routes consist of multiple stopover sites where migrants prepare for successive stages of their journeys. Different migration strategies occur among species, among populations traversing different routes, between age classes and sexes, at different sites in a sequential journey, and even among individuals within these groups (McKinnon *et al.* 2014, Deppe *et al.* 2015, Hua *et al.* 2017, Vansteelant *et al.* 2017).

The decision whether to depart from a stopover site at a particular time is understood to be an evolved strategic decision rule conditioned proximately on internal state variables, principally potential food acquisition rate and current fuel stores, and environmental factors, especially weather conditions. Fuel stores can limit maximum flight ranges, and departure decisions are therefore often related to them (e.g. Schaub *et al.* 2008, Arizaga *et al.* 2011, Schmaljohann & Eikenaar 2017). Assessing an individual’s fuel and refuelling status usually requires its physical capture and recapture, but changes in state following a captured bird’s release are in most cases unmeasured (but see e.g. Schmaljohann *et al.* 2013). Fueling rates will vary largely as function of food abundance, predation danger, and seasonal time constraints of the individual (e.g., Ydenberg and Hope 2019). A potentially useful alternative behavioural metric that might index a bird’s fuel status is the time the individual has spent at a stopover site, hereafter “Time Since Arrival” (TSA) (Pledger *et al.* 2008, Roques *et al.* 2020). For migrants following a classic model of stopover behaviour of ‘arrive-fatten-depart’, TSA could provide a useful index of an individual’s cumulative fuel acquisition and storage, and therefore be predictive of its likelihood of departing from a site.

With respect to weather, wind strength and direction are strong general predictors of migratory flight initiation (Richardson 1978, 1990, Ma *et al.* 2011, Gill *et al.* 2014). Stronger tailwinds enable birds to fly further and/or arrive at subsequent sites with larger energy stores, while stronger headwinds have the opposite effect and thus are expected to delay departures from stopover sites (Butler *et al.* 1997, Åkesson & Hedenstrom 2000, Weber & Hedenstrom 2000, Grönroos *et al.* 2012). In addition, departure decisions have evolved with respect to probable consequences further along the migration route and their potential carryover effects on fitness consequences later in the birds' annual cycle (Alerstam & Lindström 1990, Bednekoff & Houston 1994, Weber *et al.* 1998, Lank *et al.* 2003). For many northward migrants, intraspecific competition for nesting sites and/or mates means that fitness declines with arrival dates; southward migrants are generally thought to be under less time pressure (e.g. Yohannes *et al.* 2009), but may still face deadlines in subsequent parts of their annual cycle, including the timing of post-migratory flight feather moult, when birds are more vulnerable to depredation (Lank *et al.* 2003, Ydenberg & Hope 2019). These broader strategic considerations may be invoked to account for otherwise enigmatic observations of shorter or longer times spent at migration stopovers.

In this study, we compared and contrasted the stopover departure decisions of southward migrating Semipalmated Sandpipers (*Calidris pusilla*) prior to initiating flights to non-breeding sites in South America via either a transoceanic flight from a coastal stopover site or an overland flight from an inland site (Fig. 1, Lank 1979, 1983, Gratto-Trevor *et al.* 2012, Brown *et al.* 2017). Since using a successful transoceanic route requires a lengthy flight, we expected *a priori* that migrants facing a transoceanic flight should (1) have stopover durations long enough to obtain large fuel stores and (2) be highly selective about leaving in wind conditions that would aid flight in the migratory direction. But what would inland birds do? Since birds leaving the inland site have shorter flight range stopover options, they might leave after shorter stopover durations with lower fuel stores and be somewhat less selective about the weather. Alerstam (2001) proposed that "barrier effects" such as oceans should increase overall energetic cost and danger relative to routes with stopover availabilities. In this case, all else being equal, inland birds should adopt a lower energy and safer strategy, departing after shorter stopovers and possibly being less selective about departure weather.

Alternatively, despite the potential availability of additional stopover sites *en route*, making a lengthy flight might be the selected strategy from the perspective of the full annual cycle, contingent on

the relative refuelling rates and safety of alternative sites. In the context of classical optimal migration theory (Alerstam & Lindström 1990), we ask whether birds following the transcontinental route behave more like energy or time minimizers, compared with coastal birds. Energy minimizers avoid the energetic cost of carrying excess fuel by departing with lighter fuel loads after shorter stopover durations. Time minimizers achieve faster overall migration speeds by carrying heavier fuel loads, despite higher energy requirements overall. Our interpretation of the patterns seen also considers tradeoffs with predation danger at stopover sites, a third dimension that interacts with and can alter predictions from simpler time-versus-energy tradeoffs (e.g. Ydenberg & Hope 2019 and references therein).

Adults and juvenile sandpipers were captured, marked, and resighted at a coastal and an inland migratory stopover location. The age classes differ in that adults migrate about a month ahead of juveniles and will undergo a post migratory wing moult, while juveniles will not. Previous analyses of these data using simpler recapture models showed that birds remained at both stopover sites for lengthy periods of time, declining at the end of the season (Lank 1983, Hope 2011). Here, we estimated individual's Time Since Arrival using a capture-recapture analytical approach that incorporates probabilities of entry prior to first capture and marking (Pledger *et al.* 2008, Lyons *et al.* 2016, Roques *et al.* 2020). TSA was used as a potential index of cumulative fuel storage, under the classic assumption that stopover activity consists of arrival, fuel storage at a given rate, and departure (Schmaljohann & Eikenaar 2017, Roques *et al.* 2020). Daily probabilities of leaving were then modelled with respect to TSA and daily weather conditions. We interpret the stopover and departure patterns found in the context of the flight options available and apparently utilized at each site, and in the context of the migrants' annual cycle.

Methods

Study system

The study system consisted of one coastal and one inland migratory stopover area for Semipalmated Sandpipers at comparable latitudes during southward migration (Fig. 1, Lank 1983). The coastal site was Kent Island, New Brunswick, Canada ($44^{\circ}35'N$, $60^{\circ}27'W$), in the mouth of the strongly tidal Bay of Fundy. The inland site was the area around Sibley Lake, North Dakota, United States of America ($46^{\circ}57'N$, $99^{\circ}43'W$), which includes a mosaic of shallow seasonal saline lakes. Both sites are intermediate stopovers situated between Arctic breeding areas and South

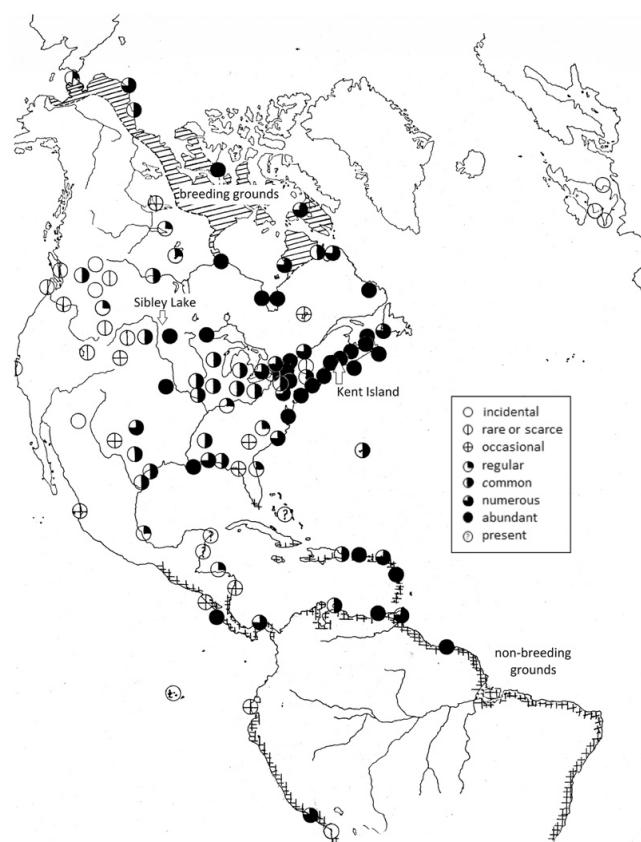
American wintering areas. Based on morphometrics, banding returns, and subsequent tracking studies, birds at Kent Island likely originated at breeding grounds in the central and eastern Canadian Arctic, may have previously staged along the shoreline of James Bay, and were preparing for a transoceanic flight to northeastern South America (Lank 1979, 1983, Richardson 1979, Harrington and Morrison 1979, Morrison 1984, Gratto-Trevor *et al.* 2012, Brown *et al.* 2017). Those at Sibley Lake were likely arriving from breeding grounds in Alaska or the western Canadian Arctic, and departed heading towards the Caribbean and northcentral or northwestern South America (Richardson and Gunn 1971, Lank 1979, 1983, Gratto-Trevor *et al.* 2012). Adults pass through both areas in July and early August, and moult flight feathers shortly after arrival on non-breeding grounds, while juveniles arrive through August and into early September (Lank 1983, Lank *et al.* 2003). At both sites, birds acquire substantial fuel for their next flight. A lean Semipalmated Sandpiper weighs ca. 20–22 g, but many individuals at both sites nearly double this mass prior to departing on the next leg of their journey (Lank 1983, Dunn *et al.* 1988).

Kent Island was monitored from 11 July–23 September 1977, and Sibley Lake from 13 July–27 September 1978. At each site, Semipalmated Sandpipers were captured almost daily using mist-nets, and/or walk-in traps at Sibley Lake, individually marked with conspicuous individually-coded wing-tags (Lank 1979) and released. Marked birds were subsequently recaptured or resighted during daily surveys of the local areas. Kent Island resightings were made exclusively on the intertidal mudflats surrounding the island; Sibley Lake resightings occurred along the shore of saline Sibley Lake and adjacent wetlands. Further details on capture, marking, and resighting effort are given in Lank (1979, 1983).

Birds initially landing at a site may not remain present to rest and refuel (i.e. actual ‘stopover’; Warnock, 2010). Inclusion of ‘transients’ will usually bias low estimates of ‘migratory’ emigration rates (Bächler & Schaub 2007, Schaub *et al.* 2008). At Kent Island, 26% of birds marked were never reencountered, nor were 36% of those marked at Sibley Lake (Lank 1983). A initial analyses of this dataset in a methodological paper, showed that daily survivorship estimates distinguishing first versus later captures of individuals provided better model fits than ignoring a possible capture/transient effect (Brownie & Robson 1983). Local population size may also have affected transience probability (Lank 1983). Since our interest was on the effects of meteorology and length of stay on departure decisions, we analysed only capture histories of individuals that were subsequently reencountered. The numbers of capture histories included were: 928 at Kent Island,

with 759 adults and 169 juveniles, resighted 4.5 times, on average; and 1073 at Sibley Lake, with 520 adults and 553 juveniles, resighted 5.3 times on average.

A



B

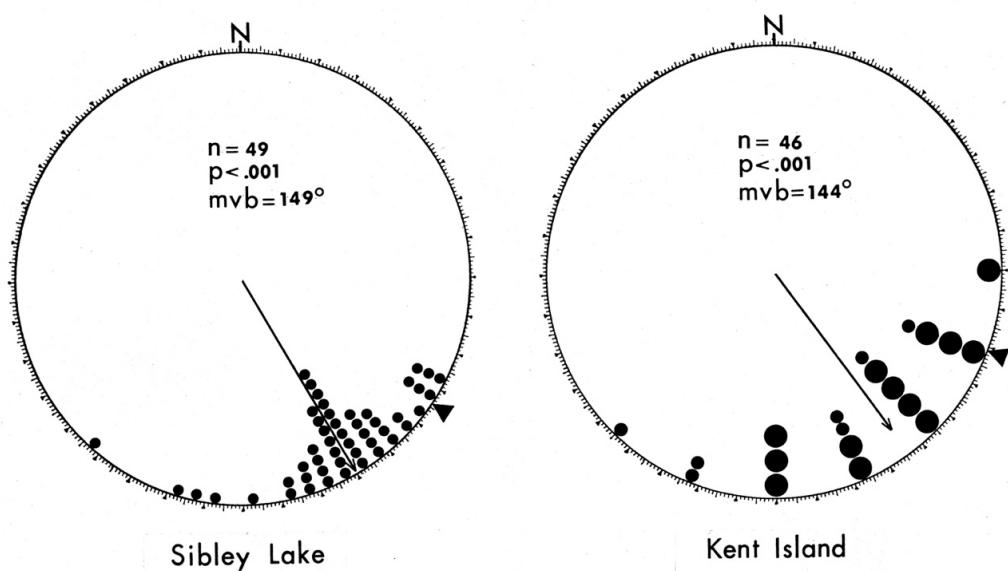


Figure 1: A. Breeding (diagonal hatching) and nonbreeding grounds (crosshatching) of Semipalmated Sandpipers, study site locations, and relative abundances of migrant Semipalmated Sandpipers reported during southward migration. Abundance classes at migration sites were compiled from regional accounts in literature prior to 1980. B. The directional distribution of presumed migratory departures of Semipalmated Sandpipers from Sibley Lake and Kent Island. Flocks leaving each study site were followed optically until they disappeared from view (details in Lank 1983, 1989). Vanishing bearings were assigned to one of 16 compass points at Kent Island, or to the nearest compass degree at Sibley Lake. Mean vector bearings (mvb) and statistical significance (p) were calculated using Baschelet (1981). The black triangle on the outside of each circle shows the mean direction towards which surface winds were blowing at the time of the departures. Both figures adapted from Lank (1983), which provides references to the migration site accounts used in A.

Weather variables

To describe how meteorological conditions relate to the departure decisions of sandpipers, we chose four weather covariates, measured daily at sunset, when most migratory departures occurred (Richardson & Gunn 1971, Richardson 1977, Lank 1989). Based on earlier analyses of this data set and other information on the timing of migratory departures (Lank 1983, 1989), our metric for wind was the 24-hour-trend in the strength of the tailwind-headwind component of wind direction (hereafter ‘wind’), which was the wind metric most predictive of departure decision. Radar studies and direct observations show that at that season shorebird migration in both regions occurs in along a northwest towards southeast axis (Fig. 1, Richardson & Gunn 1971, Lank 1979, Richardson 1979, Lank 1983), which we therefore defined as the expected migratory direction. The wind effect value at sunset was calculated as follows:

$$Wind = V * \cos(\alpha - 45)$$

where V is wind speed (in m/s) and α the direction where the wind comes from, in $^\circ$. Subtracting 45° from the wind direction creates a vector with positive values for tailwinds blowing from the northwest towards the southeast, the migratory direction. The 24-hour-trend in wind was calculated as the vector’s value each day minus that of the previous day. Thus positive values indicated that tailwinds were getting stronger, and negative values that they were becoming weaker.

Additional meteorological variables modeled were: temperature ($^{\circ}\text{C}$), percent cloud cover and relative humidity, measured at sunset.

Collinearity between weather covariates can lead to erroneous conclusions about the effect of particular focal weather covariates. We tested for collinearity between the weather covariates and found some significantly correlated, but not with high correlation coefficients (Lank 1983). Nonetheless, to characterize the weather patterns with respect to synoptically covarying meteorological conditions, we ran a Principal Component Analysis on the 4 meteorological variables pooled across both sites, which clearly distinguished two axes explaining 80% of the variation (Fig. 2, see Table S3 for details). We modelled departure probability with respect to both individual variables and the first two PCs.

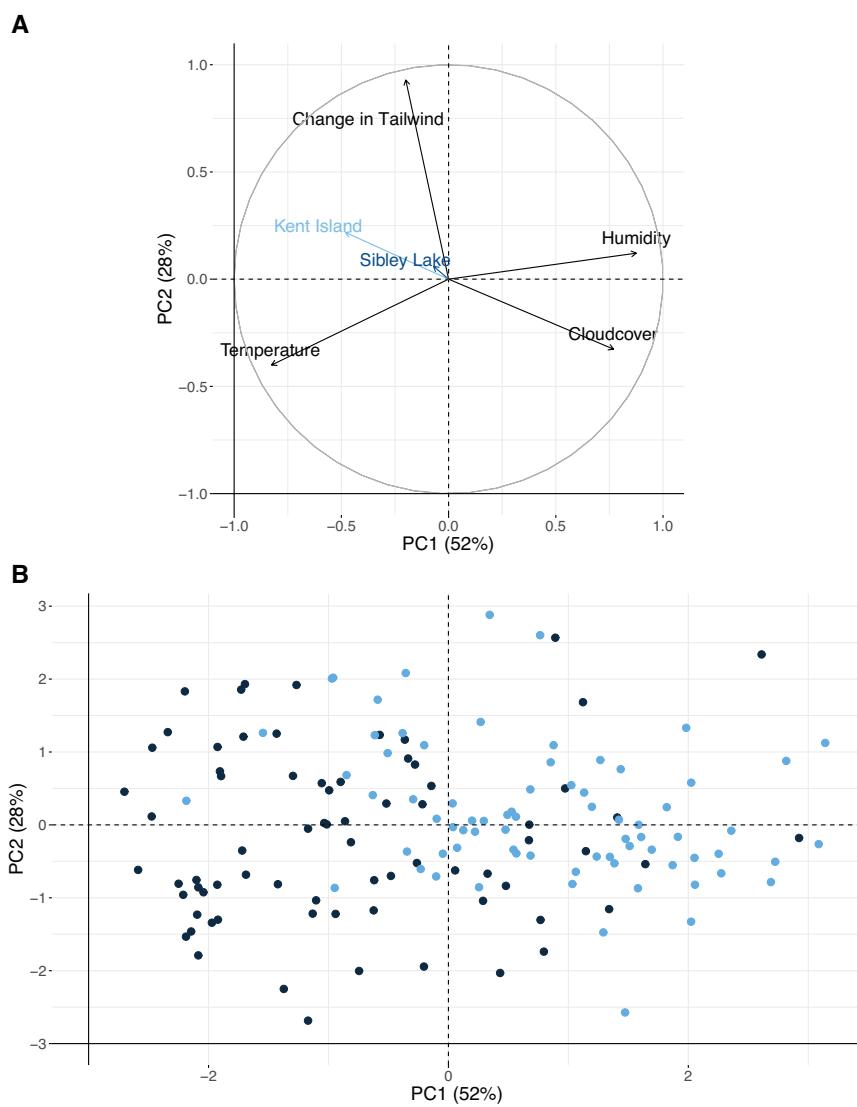


Figure 2. Principal component analysis of the four weather variables. A) Length and direction of vectors shows the relative weightings of the 4 weather variables along the two first axes of the PC (black arrows). PC1 largely captures covariation in temperature, humidity and cloud cover, while PC2 primarily captures the independent variation in wind direction. Vectors representing the conditions favouring departure of Semipalmated Sandpipers are plotted for Kent Island and Sibley Lake with light and dark blue arrows, respectively (Table 2). B) Scatterplot of daily local weather observations with respect to PC1 and PC2 scores (light blue: Kent Island, dark blue: Sibley Lake).

Statistical analyses of mark-recapture data

We used a Bayesian, state-space formulation of an open population capture-recapture model that incorporates entry probabilities to a sampling area (Pledger *et al.* 2009, Lyons *et al.* 2016). This formulation allows modelling both birds' arrival at and departure from the stopover site. The parameters of the model are:

ϕ_t Probability of departure from sampling area between the sampling occasions t and $t+1$

η_t Probability of arriving at the stopover area at sampling occasion t given that the individual was not there before

p_t Probability of physical capture at the sampling occasion t given the individual has arrived but not yet departed

$psight_t$ Probability of visual recapture (encounter) at the sampling occasion t given the individual has been captured and marked (wing-tagged) but has not yet departed

This formulation contains one submodel for the state process (states are “not yet arrived”, “present in the stopover site”, “departed”), and one submodel for the observations encoded in the individual capture histories. The observation process is conditional on the current state. For each individual capture history h_i , there is a true state history accounted for by the vector z_i . This vector of binary state variables describes if an individual i is present, $z_{i,t} = 1$, or not, $z_{i,t} = 0$, in the stopover area on day t . In our study, individuals can be physically captured or simply visually resighted, thus we separated the physical capture probability from the resighting probability, noted respectively as p and $psight$. Birds can also be captured and resighted during the same sampling occasion. To deal with this, we used a multi-state formulation of the observation process. Consequently, in an individual capture history, we distinguished four potential events (Pradel 2005) denoted as 0: not

seen, 1: physically captured, 2: resighted, 3: physically captured and resighted during the same occasion. This resulted in the following observation matrix $\theta_{i,t}$ that applies to an individual present:

$$\begin{bmatrix} 1 - p_t - psight_t + (p_t * psight_t) \\ p_t * (1 - psight_t) \\ psight_t * (1 - p_t) \\ p_t * psight_t \end{bmatrix}$$

For an individual i that has not yet entered the stopover area or has left it ($z_{i,t} = 0$), $h_{i,t} = 0$ with probability equal to 1. This formulation allows us to estimate the time since arrival (TSA) for each individual. This covariate is a non-observable variable that can be computed with the sum of the true states $z_{i,t}$ up to time t , and represents the time of presence of the individual i at time t in the stopover area:

$$TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s} \quad (1)$$

The state vector z_i also allows us to use a new formulation of the stopover duration described in Lyons et al. (2016). We computed the mean stopover duration (in days) as follows:

$$SOD = \frac{\sum_i \sum_t z_{i,t}}{n} \quad (2)$$

where n is the number of individuals and $z_{i,t}$ the true state variable (which defines if an individual i was present or not at the stopover area on day t). Juvenile individuals arrive later in the season at the stopover area. Thus, the entry probability (η_t) was modelled as age and time-dependent.

The probability of departure from the site between two days was written as a function of all previously defined weather covariates and TSA, with a slope to be estimated for each covariate. When the slope for an effect had a 95% confidence interval that did not include 0, the effect was considered statistically significant (Kéry & Schaub 2011).

Using the logit link, the probability of departure from the stopover area between t and $t + 1$ was formulated as:

$$Logit(\phi_t) = a + \beta_{age} * TSA_t + \beta * Cov_t \quad (3)$$

Where α is the intercept, β_{age} the age specific TSA effect to estimate, Cov_t is the weather covariate and β the associated slope to estimate.

To incorporate potential effects of meteorological variables, we first ran one model for each site with the two PC axes as covariates as follows:

$$Logit(\phi_t) = \alpha + \beta_{age} * TSA_t + \beta_1 * PC1_t + \beta_2 * PC2_t \quad (4)$$

Then, to test effects of each weather covariate, we ran one model for each weather covariate for each site according to formula (3) to avoid collinearity problem (Harrison *et al.* 2018). This resulted into 8 different slope values for each weather covariate for each site (Table 2).

Analyses were performed with JAGS (Hornik *et al.* 2003) using R version 3.6.1 (R Development Core Team 3.0.1. 2013). Models were run with 120,000 iterations with non-informative priors, and we checked chain mixing and the convergence (Kéry & Schaub 2011). The JAGS code is available in Appendix S2.

Results

Stopover duration, time since arrival, and recapture probability

The mean stopover duration estimates were 9–10 days longer at Kent Island than at Sibley Lake, being 42.0 versus 33.7 days, respectively, but the CIs are wide for both estimates (Table 1 and Fig. 3). At Kent Island, the stopover durations of adults appear shorter than that of juveniles, being 40.0 versus 51.2 respectively, again with large CIs, but quite similar at Sibley Lake, averaging 32.8 versus 34.5 days (Table 1 and Fig. 3).

The probability of departure increased for all classes of individuals as their residency times increased. The coefficients of the TSA effects were significant and estimated with a high precision at both sites (see the 95% CI Table 2). The strongest TSA estimated effect was for adults at Kent Island, with a 0.13 estimated slope on the logit scale. Kent Island juveniles had estimates, of 0.09, close to values at Sibley Lake of 0.08 for adults and 0.09 for juveniles, with overlapping 95% CIs (Table 2). Controlling for weather covariates, departure probabilities remained below ca. 0.1 for over 30 days since initial arrival (Figures 4C and 4D).

The physical recapture probability p was similar between the two sites (Kent Island: 0.03, Sibley Lake: 0.04), but the resighting probability $psight$ was lower at Kent Island than at Sibley Lake (0.14 and 0.22, respectively, Table 1).

Table 1. Mean and credible intervals (CI) of the resighting probability ($psight$), the capture probability (p) and stopover duration by age of southward migrating Semipalmated Sandpipers estimated from the models following equation 4. Estimates from Kent Island derived from 4178 encounters in capture histories from 759 adults and 169 juveniles; those from Sibley Lake derived from 5613 encounters in capture histories from 520 adults and 553 juveniles.

	Kent Island	Sibley Lake		
	Mean	CI	Mean	CI
Resighting probability ($psight$)	0.14	0.02, 0.30	0.22	0.11, 0.39
Capture probability (p)	0.03	0.01, 0.08	0.04	0.01, 0.10
Mean stopover duration (days)	42.07	21.65, 60.21	33.67	12.21, 55.52
Adult stopover duration (days)	40.04	19.30, 53.60	32.76	11.03, 59.32
Juvenile stopover duration (days)	51.19	37.46, 63.54	34.52	12.13, 50.44

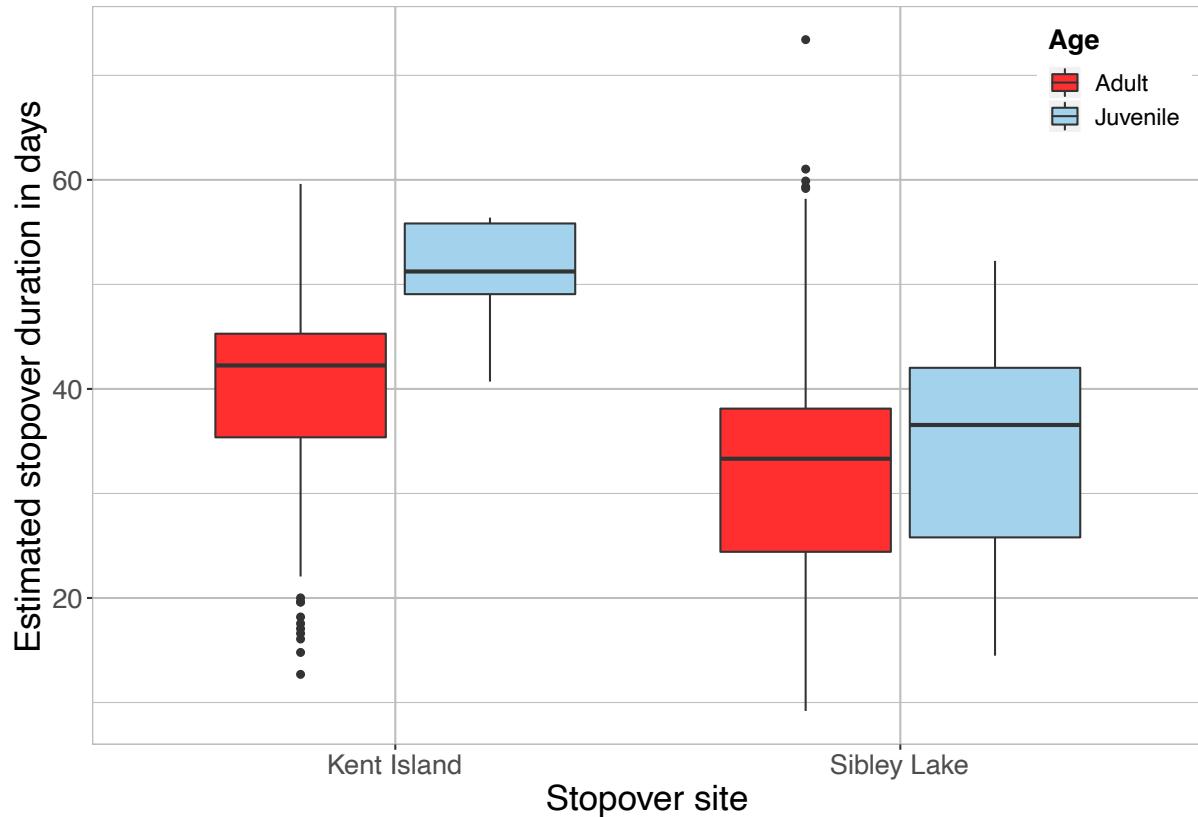


Figure 3. Estimated stopover duration by age classes at Kent Island and Sibley Lake. Adults: red, Juveniles: blue. Box plots show: median (thick line), first and third quartiles boundaries, lines extend to 1.5 times the box boundaries, and black dots show outliers.

Weather Covariate Effects

The first two principle component dimensions accounted for 52% and 29%, respectively, of the total variances of the four meteorological variables (Table S3). PC1 captured covariation in temperature, humidity and cloud cover (Fig. 2A, Table S3), patterns of which clearly differed between sites (Fig. 2B, Table S1). Mean values of PC1 were -0.8 ± 1.3 at Kent Island and 0.8 ± 1.1 at Sibley Lake (Table S3). Kent Island had the cooler, more humid and cloudier conditions expected from a marine site, contrasting with warmer and drier inland conditions at Sibley Lake (Fig. 2B). PC2 largely captured the independent variation in 24-hour wind trend (Fig. 2A), which ranged similarly between favourable and unfavourable conditions at both sites (Fig. 2B). Mean values of PC2 were -0.2 ± 1.2 and 0.2 ± 0.9 at Kent Island, and Sibley Lake, respectively.

In univariate models of each weather covariate at each site, the coefficient for 24-hour trend in headwind effect was positive at both sites (Table 2). Strengthening winds from the northwest,

defined as tailwinds, increased the probability of leaving the stopover area between t and $t+1$. The magnitude of the effect was 0.77 at Kent Island, larger than 0.39 at Sibley Lake, with marginally overlapping 95% CIs. Each of the other weather covariates tested also had significant univariate relationships with the probability of departing from the stopover site. At both sites, lower humidity, was associated with higher departure probabilities. However, the relationships with temperature and cloud cover differed in direction between sites. At Kent Island, where the weather was generally cooler and cloudier (Fig 2B), birds were more likely to leave under warmer and clearer skies. In contrast, at Sibley Lake, where warmer and clearer conditions prevailed, birds were more likely to leave in colder and cloudier local weather. These opposite trends produce some convergence of temperature and cloud cover conditions at intermediate values from both sites.

Table 2. Mean, standard deviation (Sd) and credible intervals (CI) of the estimated effects of covariates on departure probability. The first part of the table shows the results from the equation 4 with TSA (β_{1age}) and PCA axes covariates. The second part of the table shows the results from the equation 3, which included TSA (β_{1age}) and coefficients for weather covariates effects ($\beta_2, \beta_3, \beta_4, \beta_5$). Estimated values of intercept and TSA effects for each univariate models are not shown in this table as they are mostly similar to the ones of equation 4.

	Kent Island			Sibley Lake		
	Mean	Sd	CI	Mean	Sd	CI
Intercept	-8.85	0.55	-9.17, -7.94	-9.44	0.68	-10.87, -8.20
(β_{1adult}) TSA	0.13	0.01	0.11, 0.14	0.08	0.01	0.07, 0.10
($\beta_{1juvenile}$) TSA	0.09	0.01	0.06, 0.10	0.09	0.01	0.07, 0.10
PCA Axis 1	-0.48	0.15	-0.80, -0.20	-0.08	0.12	-0.30, 0.15
PCA Axis 2	0.22	0.19	-0.16, 0.58	0.06	0.11	-0.18, 0.26
(β_2) Wind	0.77	0.13	0.52, 1.01	0.39	0.08	0.23, 0.54

(β_3) Temperature	0.84	0.16	0.52, 1.15	-0.19	0.05	-0.30, -0.09
(β_4) Humidity	-0.58	0.18	-0.95, -0.23	-1.06	0.17	-1.43, -0.73
(β_5) Cloudcover	-0.33	0.16	-0.66, -0.02	0.42	0.11	0.20, 0.65

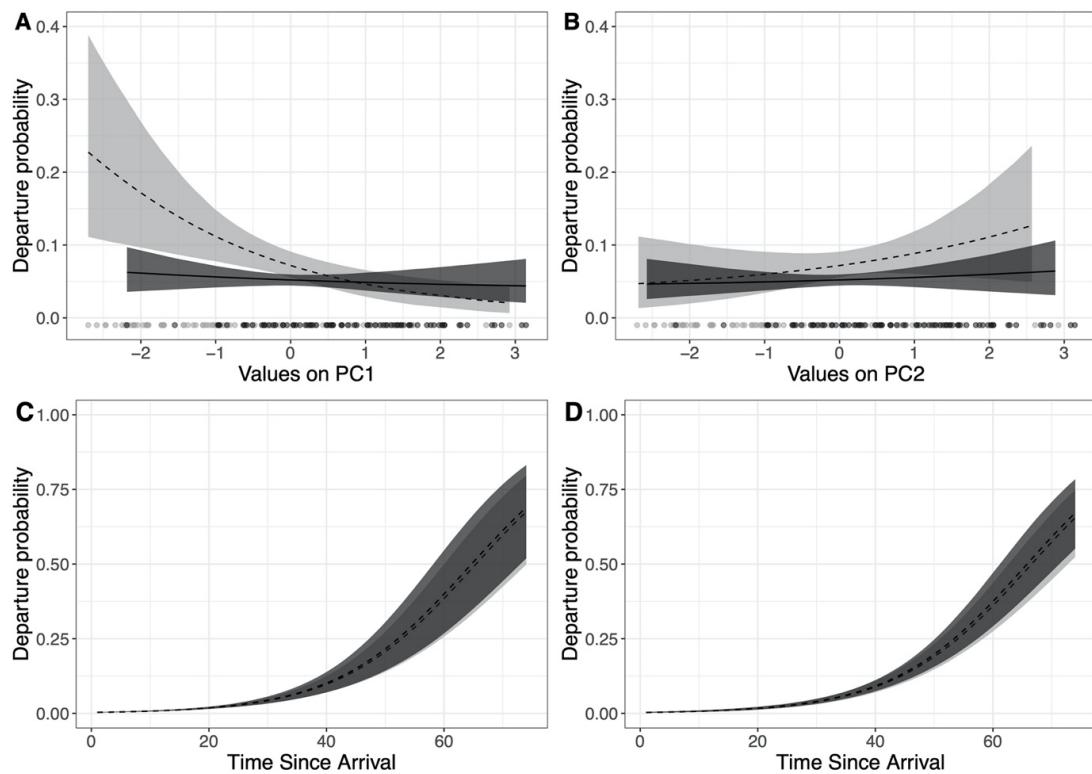


Figure 4. Predicted effects of: A,B) the first and the second PC axes (respectively A and B) on the departure probability of Semipalmated Sandpipers at both sites given birds are at their mean stopover duration (Kent Island : light grey, Sibley Lake : dark grey). In figures A and B, the light and dark grey points show the values encountered respectively at Kent Island and Sibley Lake. C,D) the TSA on departure probability given weather values are at their mean values at both sites (C: Kent Island, D: Sibley Lake) for both ages (Dark grey: Adults, Light grey: Juveniles). For all figures the dashed lines represent the mean values, and grey areas represent the 95% credible intervals.

PC1, primarily capturing variation in temperature, humidity and cloud cover (Fig. 1A), had a

significant negative effect on departure probability at Kent Island, but not at Sibley Lake (Table 2, Fig. 4A). Negative values on PC1 represent strengthening tailwinds, since the correlation between PC1 and wind is -0.20 (Table S3). The effect of PC1 appears larger at Kent Island than at Sibley Lake; the CIs overlap, but that at Kent Island does not overlap zero. PC2, associated strongly with the independent variation in 24 hour wind (Fig. 2, Fig 4B, Table S3), had no significant effect at either site, thus most of the variation responsible for the univariate relationship with wind must have been represented through covariation in PC1. The environmental conditions correlating with departure are the ones that maximize the component $\beta_1 \cdot \text{PC1} + \beta_2 \cdot \text{PC2}$, corresponding to the direction (β_1, β_2) on plane 1,2 of the PCA. The intensity of their effects are reflected by the length of the site-specific vectors shown in Fig. 2A for each site.

Discussion

We estimated the stopover durations, effects of Time Since Arrival and meteorological conditions on the daily departure probabilities of Semipalmated Sandpipers from stopover sites during southeastward migratory journeys. Birds at Kent Island, New Brunswick were preparing for a lengthy transoceanic flight, while those at Sibley Lake, North Dakota, were preparing for overland flights of unknown lengths. We proposed that contrasting the stopover durations and departure behaviour of migrants from the sites would provide information about the migratory strategies of comparable sandpiper populations when the migratory routes did or did not provide access to intermediate downstream stopover sites. At both sites, birds departed with favourable winds, and had lengthy stopover durations for most of the season, suggesting preparation for lengthy migratory flights even when intermediate sites were available. However, birds at both sites stayed substantially longer than necessary to simply refuel and continue migratory journeys, suggesting that in the context of the birds' annual cycles, being at each of these locations at those seasons had high fitness value. There were, however, quantitative differences between migrants' behaviour at the two sites. Birds at Kent Island had somewhat greater selectivity with respect to wind conditions at departure, and adults at that site had longer stays than juveniles or birds at Sibley Island. Below, we interpret the patterns found as adjustment of migratory strategy related to the differences in the downstream stopover options of each migratory route, within the context of the birds' annual cycles.

Weather effects

At both sites, birds had higher probabilities of initiating migratory flight after tailwinds had been strengthening for the past 24 hours. Departure with stronger tailwinds is expected on first principles and from previous studies (Table 1, Richardson & Gunn 1971, Richardson 1978, 1979, 1990, Alerstam 1990, Weber *et al.* 1998, Åkesson & Hedenström 2000, Loonstra *et al.* 2019). Surface winds assisting southeastwardly flight were blowing when migratory departures were directly observed (Fig 1B). From a synoptic weather point of view, as expected, sandpipers from both sites thus do depart on days with tailwinds, reducing cost of flight per kilometre travelled (Tsvey *et al.* 2007, Arizaga *et al.* 2011, Ma *et al.* 2011, Grönroos *et al.* 2012, Dossman *et al.* 2016).

We predicted that birds facing transoceanic flight would show greater selectivity in departure conditions than those facing transcontinental flight, and indeed, the effect size of change in headwind component was stronger at Kent Island than at Sibley Lake. Kent Island birds also showed stronger relationships with the integrated measures of meteorological covariation than the birds at Sibley Lake. Although the background weather regimes differed with respect to temperature, cloud cover and humidity, they were similarly variable in terms of the general distributions of favourable winds (Fig. 2). In the current study, favourable weather for migration occurred at fairly regular 4–5 day intervals at both sites throughout the migration season, with regular passage of cyclonic and anticyclonic weather systems, and the patterns in the specific years studied were typical of longer term weather regimes (Lank 1983). Thus, systematic differences in meteorological migration opportunities do not account for differences in selectivity between sites. Greater selectivity for wind assistance can trade-off against speed of migration; McCabe *et al.* (2018), argued that in general, time minimizers might be less selective because of fitness decreases associated with waiting for favourable weather conditions. In our cases, however the lengthy stopover durations shown by both of our migratory populations indicate that neither were time minimizers during much of the season (see below), and both populations selected tailwinds for departure.

Despite lower values of humidity in general at Sibley Lake (Fig. 2), the relationship between relative humidity and departure probability was negative at both sites. This is sensible in a synoptic sense, since northwesterly winds at both sites would likely bring in drier air. This effect may reflect a direct effect of rain, but also the fact that more humid air increases the cost of flight and decreases visibility (Åkesson *et al.* 2001). Similar effects have been found in other situations (Åkesson *et al.*

2001, Deppe *et al.* 2015, Roques *et al.* 2020), such as passerines selecting nights with lower humidity to cross the Gulf of Mexico (Deppe *et al.* 2015).

The direction of temperature and cloud cover effects were opposite at the two sites. Sandpipers were more likely to leave Kent Island with higher than average temperatures and less cloud cover for that site, while those at Sibley Lake left with lower than average temperatures and greater cloud cover for the site. Since Kent was generally cooler and cloudier than Sibley Lake (Fig. 2), this pattern produces a convergence of departure conditions between sites under intermediate conditions of both variables. Greater cloud cover decreases the visibility of the sky, and since migratory birds use the stars for the orientation (Wiltschko & Wiltschko 1988), including Semipalmated Sandpipers (Lank 1973), dense cloud cover could present initial navigational difficulties. Low cloud cover in particular may have a strong negative impact on the probability of departing from a stopover area, while high altitude clouds will have little effect (Martin 1990, Koistinen 2000).

PC1, which was strongly and approximately evenly weighted by humidity, cloud cover, and temperature, captured most of the covariation in departure probability from both stopover sites. Despite being heavily weighted by tailwind trend, PC2 was not strongly related to departure probability, although it may have been more so at Kent Island than at Sibley Lake. This means that most of the univariate relationship between departure probability and wind trend had been captured by PC1 through covariation between wind and the other variables (Table S2).

Modelling Considerations

The stopover durations estimated in this study incorporate estimates of entry probabilities to a sampling area prior to first capture. They are thus longer than the minimum lengths of stay (marking to last sighting) presented by Lank (1983), the conditional residence times estimated from Lank's data by Hope *et al.* (2011), and the minimum lengths of stay found in a separate study on the coast of Maine (Dunn *et al.* 1988). Including time prior to capture should make the values estimated in the current study more realistic.

Lank (1983, unpublished analyses) tested for relationships between daily emigration rates and prevailing daily weather conditions, using emigration rates estimated using a simpler capture-recapture model (Brownie & Robson 1983). The emigration rate-meteorology relationships in that study were weaker than those shown here (Table 2), suggesting that the approach taken in the

current study provided more useful estimates. Lank (1983) speculated that permanent local dispersal may have partially obscured relationships between the emigration rates and actual migratory departure probability, which also applies to our current analysis (Bächler & Schaub 2007, Schmaljohann & Eikenaar 2017). Our study provided some perspective on the local dispersal issue by distinguishing between physical and visual recapture events in the modelling process. The sites had similar physical recapture rates, but visual reencounter rate was lower at Kent Island than at Sibley Lake (Table 2). Regular surveys at Kent Island were restricted to birds visible from the island itself; small numbers of ad hoc sightings of wing tagged birds by local bird watchers at nearby sites were not included in the capture history. In contrast, regular surveys were made at additional waterbodies near Sibley Lake when these sites were used by birds as a function of changing rainfall conditions. The higher visual reencounter rate at Sibley Lake likely reflects the observers' greater ability to track local movements of birds at that stopover site. Separate parameterization of physical and visual reencounters thus added precision and highlighted sampling patterns between sites and data sources. We conclude from this that the potential effects of local dispersal would have weakened relationships with meteorological variables more at Kent Island than at Sibley Lake. If so, our conclusion of greater selectivity in departure weather at Kent Island is conservative.

Lengthy Stopover Durations

As argued in the introduction, preparing for a non-stop transoceanic flight rather than an overland flight should favour the acquisition of larger fuel stores, since the latter provides opportunities for shorter flights from the stopover sites. Consistent with our prediction, estimated stopover durations were ca. 10–15 days longer prior to transoceanic relative to transcontinental flights for adults and juveniles, respectively (Table 1, Fig.3). Further, the samples of birds captured and tagged at Kent Island averaged 3.4 g. heavier than those caught at Sibley Lake (33.0 versus 29.6 g, Lank (1983)).

We motivated this study in part by suggesting that stopover duration might be a useful index of cumulative refuelling that could be estimated without recapturing marked individuals, assuming a classical model of stopover behaviour as 'arrive-fatten-depart'. As expected under this model, the effects of estimated Time Since Arrival were positive and predictive of departure probabilities. Rapid refuelling often has been found at stopover sites, and the TSA approach used here should work best in analyses of such situations, namely for time-minimizing migrants whose stopover behaviour fits (Alerstam & Lindström 1990).

Despite the utility of TSA as a predictor of departures in our study, the stopover durations of most sandpipers at both sites are substantially longer than those expected if the stopover behaviour of these migrants was a good fit with the classical model. The model coefficients for TSA were small and quite similar at both sites (Table 2). Also, the departure probability curves as a function of TSA are low and nearly flat for the first 30 days (Fig. 4C and 4D). Lank (1983) provided information on the arrival mass, fattening rate, and departure masses at each site, inferred by comparing the masses of the daily samples of sandpipers caught throughout the season, and on successive days when weather was or was not favourable for southeastward migration. Lank estimated that departure masses from Sibley Lake were only about 2 g less than those from Kent Island (e.g. 16 vs. 18 g on birds with lean masses of 20–22 g). Thus, despite the availability of stopover opportunities *en route*, the transcontinental migrants were also preparing for lengthy flights.

At Kent Island, Lank (1983) estimated that adults arrived with an average of 5–6 g of fuel. Some, identified by colour-dyed breasts, had previously staged further north along the east coast of James Bay. Juveniles arrived at Kent Island lighter than adults. At Sibley Lake, many birds of both ages arrived with little or no fuel stores, potentially having flown directly from western Nearctic breeding grounds. Lank estimated fattening rates of up to 2.5 g/day at Kent Island and 1.5 g/day at Sibley Lake. The rate for Kent Island is high relative to those estimated for shorebirds at other sites (Alerstam & Lindström 1990, Anderson *et al.* 2019). But even at a lower rate, birds arriving completely lean at both sites could have added the 20–24 g of fuel needed to support maximal transoceanic or trans-continental flights in ca. 15 days, far fewer than their estimated mean stopover durations of 40.0 and 51.2 d for adults and juveniles at Kent Island, respectively, and 33.7 and 32.8 d at Sibley Lake (Table 1). If birds fit the classic model, we would expect clear inverse relationships between mass at capture and subsequent length of stay, as has indeed been found in many other situations (e.g. Schaub *et al.* 2008). No such relationship occurred at either Kent Island or Sibley Lake (Lank 1983), or at Dunn *et al.*'s (1988) coastal site. Since favourable departure weather occurs at regular 4–5 day intervals (Lank 1983, see above), waiting for favourable departure conditions (e.g. McCabe *et al.* 2018) would not add more than a few days to stopover durations. None of the sandpipers captured at these sites in our study was moulting, which can explain lengthy stays at stopover sites (Jehl 1990). We conclude that for most of the season the sandpipers at both sites were not in a hurry to undertake their next, lengthy, migratory flight. At James Bay, a major stopover site for central and eastern migrants further north, the relationship between length of stay and fuel loads at capture for Semipalmated Sandpipers and other shorebirds was actually positive

early in the season, but did become negative towards the end (Anderson *et al.* 2019). This finding also points towards a relatively leisurely southward migration schedule.

Life History Perspectives

Why were stopover durations so long at both sites, despite the apparent availability of food resources and favourable weather for departures at regular intervals? Answering this question requires taking a life history perspective, including migrants' age and prospects at subsequent stages of their annual cycles (Bednekoff & Houston 1994, Weber *et al.* 1998, Houston 1998, Weber *et al.* 1999).

Adults had shorter stopover durations than juveniles (Fig. 3). If we assume that at both age classes were preparing for similar migratory flights, the shorter duration for adults could indicate that their refuelling rate was higher, and/or reflect their arrival at Kent Island with higher fat stores, which did occur. Lank (1983) concluded that adults and juveniles present concurrently at Kent Island had similar daily mass increases. In addition, at Kent Island, adults may have been more likely than juveniles to be preparing for a direct transoceanic flight. In both Lank's (1983) and Dunn *et al.* (1988)'s studies, fewer juveniles than would be expected demographically utilized the coastal stopover sites. There is evidence that juvenile Semipalmated Sandpipers generally make shorter transoceanic flights by leaving from sites further south, possibly after first moving southwesterly down the Atlantic coast (Harrington & Morrison 1979, Anderson *et al.* 2019: their supplementary Fig. 3). Thus, adults had shorter lengths of stay despite being more likely to be preparing for a longer journey. In conclusion, as argued above, since none of these birds were fattening as rapidly as possible, stopover duration and fuel levels were to a considerable extent decoupled for these birds. Thus, we will look for alternative explanations for lengthy stopovers.

Lank *et al.* (2003) argued that the evolution of migratory routes involving lengthy migratory flights depends not only on the existence of staging sites with sufficient food to fuel flights, but also, critically, low predation danger at such sites, since birds become quite vulnerable when carrying stores needed to fuel such flights. Schedules of migrating falcons may thus influence both the timing and routes of migration, including Semipalmated Sandpipers in particular (Lank *et al.* 2003, Ydenberg *et al.* 2007). Models of migration's role within annual cycles stress the importance of date in the season, usually with fitness penalties for late arrivals (e.g. Weber *et al.* 1998). For southward migrating Semipalmated Sandpipers, Lank *et al.* (2003) argued that adults face stronger seasonal

deadlines than juveniles to arrive at their non-breeding grounds by a given date, in order to mitigate the increased vulnerability they experience during post-migratory wing moult to later-migrating avian predators. Since juveniles do not replace their feathers immediately on arrival, adults should put a higher priority on earlier arrivals on moulting sites further south, and thus have shorter stopover durations particularly later in the season. Hope *et al.* (2011) showed that conditional residency times calculated from this dataset were truncated at the end of the season, coinciding with the approach of migrant Peregrine Falcons (*Falco peregrinus*) towards the stopover sites.

When the observations reported here were made in the late 1970s, falcon populations were in fact relatively low, due to residual effects from the extensive use of DDT, and during the migratory seasons both sites were quite safe with respect to avian predators (Ydenberg *et al.* 2017). No attacks from falcons were observed at Kent Island. At Sibley Lake, only a few observations of Prairie Falcons (*Falco mexicanus*) and resident Short-eared Owls (*Asio flammeus*) attacking sandpipers were made (Lank 1979). Although proximate disturbance and danger was lacking, from an evolutionary sense, the predictable seasonal pattern of increasing danger may indeed have influenced birds' departure decisions towards the end of the season (Lank *et al.* 2003, Hope *et al.* 2011, Ydenberg & Hope 2019), but for much of the time there was little direct threat.

We infer that during most of the season, both these sites provided quite favourable habitat for Semipalmated Sandpipers, making these ideal places to stage on migration (Pomeroy *et al.* 2008), or indeed to allocate time to, broadly considered in the context of the full annual cycle.

Conclusions

Migratory populations of the same species of sandpipers traversing different migration routes had different relationships between departure probabilities with respect to time present at the site and meteorological variables. The open population capture-recapture model we used incorporates entry probabilities to a sampling area and provided novel estimates of stopover durations and departure probabilities. As expected, strong tailwinds favoured migratory departures, somewhat more strongly along a route where birds were initiating a non-stop transoceanic flight compared with a transcontinental flight that allowed for stopovers at shorter distances. However, stopover durations were lengthy at both sites studied, suggesting that birds were not simply arriving, refuelling, and leaving as quickly as possible. Time since arrival was nonetheless predictive of departure, despite likely violations in this case of seasonal homogeneity in departure probability, an underlying

assumption of the modelling approach. We recommend the further application of this approach, particularly for time minimizing migrants, combined with counts if available (Lyons *et al.* 2016, Lok *et al.* 2019) towards the analysis of migratory stopover and departure probabilities.

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Data availability statement

All data used here is available on the personal correspondence author github account.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details about environmental covariates and Principal Component Analysis

Appendix S2. JAGS code of the statistical model used in our study

Table S1. Mean and standard deviation of the weather variables at both sites

Table S2. Pearson correlation coefficients of weather variables at Kent Island (Upper part of the table) and Sibley Lake (lower part of the table).

Table S3. Correlations between weather covariates and dimensions. Eigenvalues and % of variance of dimensions are also displayed.

4 Article 3: Les variations quotidiennes de probabilités de départ sont-elles synchrones entre différentes espèces de passereaux paludicoles?

Statut: Corrections finales, à soumettre d'ici fin 2020.

4.1 Synchrony in departure decisions from stopover sites with a multi-species capture-recapture model

Synchrony in departure decisions from stopover sites with a multi-species capture-recapture model

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Abstract

1-During migration, migratory bird species often co-exist at the same stopover site because these sites are located on the same migratory route or because of the high level of food availability. Stopover decisions at the multi-species level have received little attention in migration studies; decisions are generally studied separately in each species.

2-Thanks to the recent development of capture-recapture modelling, we propose a multi-species capture-recapture model that allows quantifying synchrony in departure probability from stopover sites, and to identify covariates synchronizing departure probabilities among species. We applied this model to three migratory songbirds encountered in high numbers at French stopover sites.

3- These species synchronize their departure from stopover sites; this holds indifferent sites and years. Time Since Arrival is a highly synchronizing agent and weather conditions are secondary. This is also consistent among sites and years.

4-High synchrony in departure probability induced waves of departure among migrants. Even if this phenomenon has already been documented, it has rarely been quantified through synchrony indexes on elusive nocturnal reed songbirds.

5-Our model is flexible and can easily be extended to test different hypotheses like spatial synchrony in departure decisions. It is a good starting point to address hypotheses that also need to be tested at the individual level with recent miniaturized technologies such as GPS or radio transmitters.

Introduction

Each year, billions of migrating birds travel thousands of kilometres between breeding wintering areas. Long-distance travels require a large amount of energy and most species cannot perform this journey in a single flight. They need to stop at places where they can replenish their reserves (Alerstam, 1990; Hedenstrom & Alerstam, 1997). Stopover sites are critical in the travel of each bird species. The time spent stopovering represents more than 2/3 of the overall migration time and is critical for the success of the journey (Alerstam, 1990). Some species are restricted to a specific habitat during stopover (e.g reed habitats) but others may use the same habitat because food is abundant there. Thus, tens of different species can co-occur at the same favourable stopover site.

Species co-occurring at stopover areas should be considered as a community (Alerstam, 1990; Jenni & Schaub, 2003). These species are subject to the same environmental conditions (weather conditions, food availability, predators) and may interact with one another (e.g. compete for food). This may imply similar reactions between species to their environment during their stopover (e.g. refuelling, departures, staying at the site). If species shared the same reactions, a general pattern of how this group of species behave during their stopover may truly help to design management and conservation actions for them (Kirby *et al.* 2008). But, stopover behaviour at the multi-species level has received little attention. Yet, our understanding of migration ecology will benefit from approaches accounting for the fact that stopovering species co-occur in the same place: drivers of departure decisions can be common to several species. Peaks of arrivals and departures have already been documented by field ornithologists. Using radio-transmitters, Deppe *et al* (2015) showed that the factors affecting the decision of songbirds to cross the Gulf of Mexico during fall migration is likely common to different species. These factors are the amount of fat reserves, low humidity levels and favourable wind conditions (Deppe *et al.* 2015). Similarly, using the same technology Anderson *et al.* (2019) highlighted that different species of waders seem to take stopover decisions based on the remaining travel distance and body condition (Anderson *et al.* 2019). These studies showed that species can react in a same way to several factors, and rose the hypothesis that the decisions are synchronous among individuals and species.

Synchrony in departure from a stopover site can be analysed at two main different levels: the local level (synchrony in departure of species) or the spatial one (synchrony in departure from different stopover sites located in the study area). Here we focus on local synchrony in daily departure probability among three migratory songbirds: the Sedge warbler (*Acrocephalus schoenobaenus*), the

Reed warbler (*Acrocephalus scirpaceus*) and the Bluethroat (*Luscinia svecica*). These species have fairly similar ecological requirements during stopover (Bibby & Green 1981, Bibby & Thomas 1985, Fontanilles *et al.* 2019) and are most often restricted to reed habitats. Consequently, we expect some degree of synchrony in the variation of their departure probabilities during the study period. However, the Sedge warbler (SW) and the Reed warbler (RW) are trans-saharan migrants (Bibby & Green 1981b) while the Bluethroat (BT) includes both trans-saharan and non-trans-saharan migrants (Ellegren 1990, 1991). Our hypothesis is that variation of departure probability should show a higher degree of synchrony between SW and RW than between either species and BT.

In the capture-mark-recapture framework (hereafter CR), how to estimate synchrony of bird departure from stopover sites has not received as much attention as demographic parameters such as survival or breeding probability (Grosbois *et al.* 2009, Lahoz-Monfort *et al.* 2011, 2013). Comparisons of departure probability from a stopover site among species have already been conducted in the CR framework (Schaub *et al.* 2008, Moore *et al.* 2017). However, these comparisons are based on models that estimate departure probability separately for each species, which are then compared. Models integrating several species have never been developed and the synchrony in the variation of departure probability has never been quantified. Thanks to the recent development of multi-species capture recapture models (Grosbois *et al.* 2009, Lahoz-Monfort *et al.* 2011), it is now possible to measure synchrony using random effects.

The advantage of this approach lies in the fact that it is possible to quantify the variation of departure probability directly within the model and thus create synchrony indices. Here, we used a multi-species CR model to study synchrony in the variation of departure probability from stopover sites between the above-mentioned species (SW, RW and BT). The stopover behaviour of these species has already been studied separately (Arizaga, Barba, Alonso, & Vilches, 2010; Arizaga, Mendiburu, *et al.*, 2011; Roques *et al.*, 2020; Schaub *et al.*, 2008; Schaub, Pradel, Jenni, & Lebreton, 2001), but to date no attempt has been made address synchrony in departure probability, nor to identify synchronizing agents.

Methods

Data sampling

Data collection was conducted at three ringing sites in France (Donges, France: 47.308591, -2.029212; Île du Massereau: 47.259583, -1.891654; Saint-Vigor-d'Ymonville: 49.455245, 0.361095).

The first two stations are located in the Loire Estuary and the third in the Seine Estuary (Fig.1), and provide suitable reed habitats for stopovering songbirds. Data from marked individuals have been collected using a standardized mist-netting protocol (including tape-luring; B. Bargain, C. Vansteenwegen, & J. Henry, 2002). Each captured bird was identified and ringed. The three most abundant reed-songbirds were the Sedge Warbler (*Acrocephalus scirpaceus*), the Reed Warbler (*Acrocephalus schoenobaenus*) and the Bluethroat (*Luscinia svecica*). These species stopover at this place on the way to wintering areas located in sub-Saharan Africa or Spain (for the two species of warblers), and to North Africa reed areas for the Bluethroat (Arizaga et al., 2016; Shirihai & Svensson, 2018). The SW and the RW weigh around 12g, and the BT is heavier with a mean mass around 16g. These species mostly depend on reedbeds to feed during stopovers. In spite of different feeding specialisations, (Bibby & Green 1981, Bibby & Thomas 1985, Fontanilles *et al.* 2019) reedbeds are places where food is abundant and diverse, and the three species stopover at the same place to refuel.

Among all migrant songbirds that stop at a site, only a small fraction stays several days to rest and refuel (i.e. actual stopover; Warnock, 2010). The majority either continues migration by the following night, or moves to another nearby stopover place (i.e., transients; Bächler & Schaub, 2007; Schaub et al., 2008). As we aim to study the departure probability of birds that stayed over at the site, we selected capture-recapture data from birds that were caught at least twice, in two different days. This restriction excludes most transients (Mills *et al.* 2011, Taylor *et al.* 2011, Sjöberg *et al.* 2015). Hence, the stopover duration estimated here applies only to the part of the population passing by the site and that stays for at least 2 days. At Donges, the final sample included data from 1349 They had Sedge warblers, 277 Reed warblers and 230 Bluethroats from 2009 to 2014 (very few recaptures happened between years). The latest recapture at the site occurred on average 3.75 ± 3.48 (SD), 7 ± 5.62 (SD) and 6.46 ± 5.29 (SD) days after the first capture for SW, RW, and BT, respectively. Concerning Ile du Massereau, 580 Sedge warblers, 188 Reed warblers and 87 Bluethroats were captured from 2014 to 2016, and the latest recapture occurred on average 4.48 ± 3.84 (SD), 5.52 ± 4.91 (SD) and 7.06 ± 5.19 (SD) days after the first capture. Last, at Saint-Vigor-D'Ymonville 317 Sedge warblers, 163 Reed warblers and 73 Bluethroats were captured from 2007 to 2009, with the latest recapture occurring on average 3.91 ± 3.02 (SD), 6.08 ± 4.91 (SD) and 7.08 ± 5.01 (SD) days after the first capture.

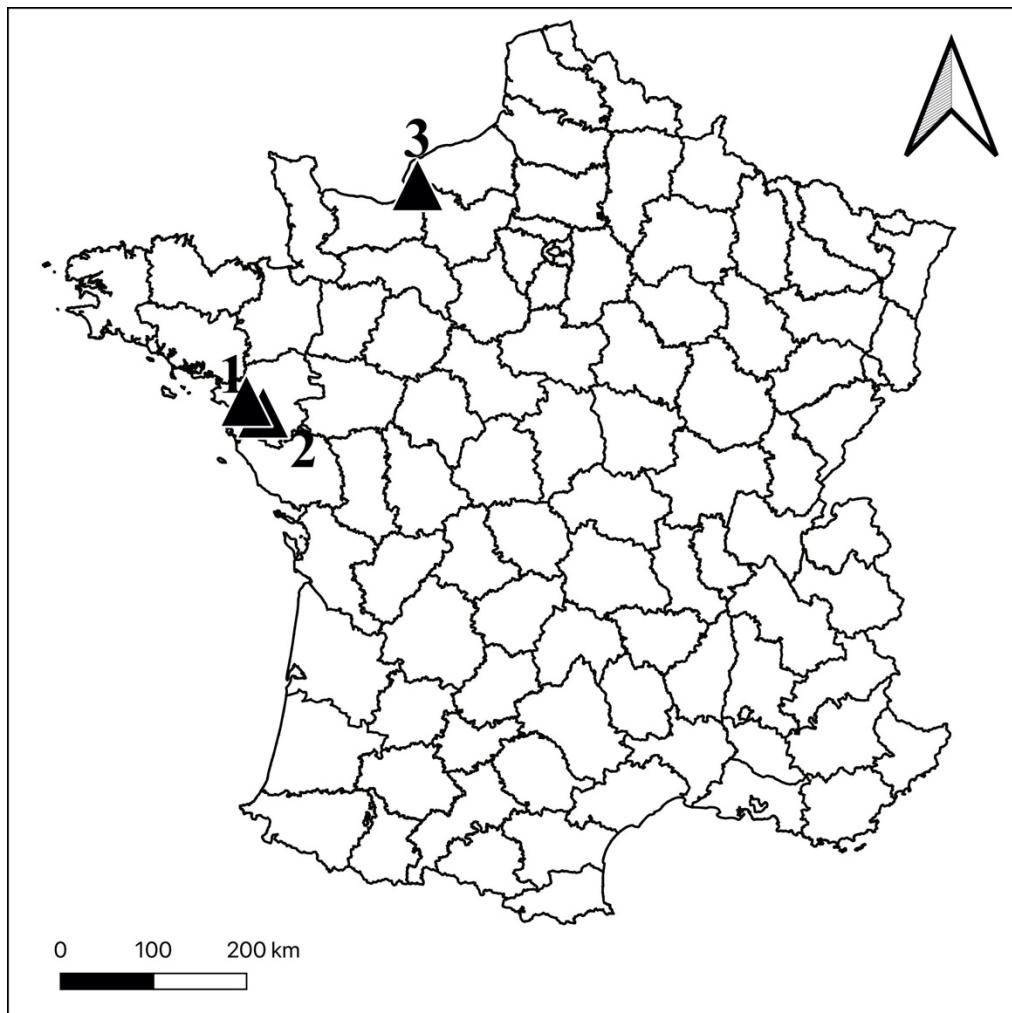


Figure 1: Locations of the three ringing stations in France. 1: Donges, 2: Île du Massereau, 3: Saint-Vigor-D'Ymonville.

Weather Variables

In order to test the hypothesis that weather conditions generate synchrony in departure probability, we used daily records of wind speed (in $m.s^{-1}$), wind direction (in $^{\circ}$), atmospheric pressure (in Hpa) and relative humidity (in %). Data come from local meteorological stations close to ringing sites. Depending on its direction, wind can either facilitate flight (tailwind) or increase the cost of flight (headwind). To integrate both wind effects, the wind covariate was computed as (Arizaga, Belda, et al., 2011):

$$\text{wind} = V \cos[\alpha_T - (180^{\circ} + \alpha_W)],$$

where V is wind speed (in $m.s^{-1}$), α_T the assumed departure direction (180° for Donges and Île du Massereau; 210° for Saint-Vigor-d'Ymonville according to recovery data and south migration direction, Dehorter and CRBPO 2015), and α_W the direction the wind (Åkesson *et al.* 2002).

To avoid the statistical problem inherent to collinearity between weather variables, we ran a Principal Component Analysis (PCA) at each site (See Supporting Information) with the following weather variables: Relative humidity (in %), atmospheric pressure (in Hpa) and wind (Eq. 1). As Axis 1 accounts for more than 50% of the variation in weather conditions at each site, we used first axis from the PCA conducted at each site as the weather covariate to integrate in the CR model.

Statistical Analysis

We used a Bayesian, state-space formulation of an open population capture-recapture model that incorporates entry probabilities to a sampling area (Pledger *et al.* 2008, Lyons *et al.* 2016, Roques *et al.* 2020). This formulation allows modelling both birds' arrival at and departure from the stopover site. The parameters of the model are:

$\phi_{y,t,s}$ Probability of staying in the sampling area between sampling occasions (days) t and $t+1$, in year y , for species s

$\eta_{y,t,s}$ Probability of arriving at the stopover area at sampling occasion t , in year y , for species s given that the individual was not there before

$p_{y,t,s}$ Probability of capture at the sampling occasion t in year y for species s given that the individual has arrived but not yet departed

Our model contains one submodel for the state process (states are “not yet arrived”, “present in the study area”, “departed”), and another submodel for the observations encoded in the individual capture histories. The observation process is conditional on the true state. For each individual capture history h_i , there is a true state history accounted for by the vector z_i . This vector of binary state variables describes if an individual i is present, $z_{i,t} = 1$, or not, $z_{i,t} = 0$, in the stopover area on day t .

The state process is defined as:

$$z_{i,t}|z_{i,t-1} \sim Bernoulli\left(\phi_{t-1}z_{i,t-1} + \eta_t \prod_{j=1}^{t-1}(1 - z_{i,j})\right)$$

The term $\prod_{j=1}^{t-1}(1 - z_{i,j})$ is here to model the availability of the individual to enter in the stopover area and is equal to 1 when the individual has not yet entered the stopover area, and 0 when it has already entered.

As the binary observations are conditionally independent Bernoulli random variables, the link between the state and observation processes is given by the following equation:

$$h_{i,t}|z_{i,t} \sim Bernoulli(z_{i,t}, p_t)$$

This means that if an individual i has not yet entered the stopover area or has left it ($z_{i,t} = 0$), then $h_{i,t} = 0$ with probability equal to 1. If $z_{i,t} = 1$, then the capture history $h_{i,t}$ is a Bernoulli trial with probability p_t , which is the probability of capture at time t . This formulation allows us to estimate the time since arrival (TSA) for each individual. This TSA covariate is a non-observable variable that can be computed with the sum of the true states $z_{i,t}$, which represents the presence of the individual i at time t at the stopover area:

$$TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s}$$

Use modified the formulation of Lahoz-Monfort et al., (2011) and Grosbois et al., (2009) who studied synchrony in survival between species, and used random effects in the model for departure probability. We treated year-specific day effect (t) as a random effect that is common to all the species: $\delta_t \sim N(0, \sigma^2_\delta)$. The second random effect, depends on year (y), day (λ), and species (s), and accounts for the species-specific part in variation in departure probability: $\varepsilon_{t,s} \sim N(0, \sigma^2_{\varepsilon_s})$. We ran three models, one without covariate (A) and two with covariates (B,C):

$$\text{logit}(\phi_{y,t,s}) = \alpha_s + \delta_t + \varepsilon_{t,s} \quad (A)$$

$$\text{logit}(\phi_{y,t,s}) = \alpha_s + \delta_{y,t} + \varepsilon_{y,t,s} + \beta_s * TSA_{i,t} \quad (B)$$

$$\text{logit}(\phi_{y,t,s}) = \alpha_s + \delta_{y,t} + \varepsilon_{y,t,s} + \beta_1 * PCA1_t \quad (C)$$

$\alpha_{y,s}$ is the intercept for species s in year y , β_s is the species-specific slope for TSA, and β_1 is the slope for weather conditions. As we are using multiple independent years within the same analysis, this formulation allows integrating data from multiple years (which can be seen as replicas) to estimate the variances of the common (σ^2_δ) and species-specific random terms ($\sigma^2_{\varepsilon_s}$). The advantage of this approach is to estimate variances with a larger amount of data. However, this formulation ignores the possible variation of synchrony between years.

Consequently, we used the site with the largest sample size (Donges) to extend this formulation and allow the variances to vary among years, and obtain year-specific estimates of synchrony. Here the random effects are $\delta_{y,t} \sim N(0, \sigma^2_{\delta_y})$ for the common day and year effect, and $\varepsilon_{y,t,s} \sim N(0, \sigma^2_{\varepsilon_{y,s}})$, for the species-specific term. Then, we ran the above-mentioned three versions of the model (A, B, C).

Using the estimated parameters, a species-specific intra-class correlation coefficient (ICC_s) can be calculated to quantify synchrony:

$$ICC_s = \frac{\sigma^2_\delta}{\sigma^2_\delta + \sigma^2_{\varepsilon_s}}$$

ICC_s quantifies the synchrony in variation of departure probability of species s with the other species, or to say it differently, the quantity of between-day variance that is accounted by the common random term δ_t . When σ^2_δ is large compared with $\sigma^2_{\varepsilon_s}$, then ICC_s is large and the between-day variation for that species is mostly synchronous with the other species. This formulation of ICC_s can be extended to calculate a year- and species-specific intra-class correlation coefficient:

$$ICC_{y,s} = \frac{\sigma^2_{\delta_y}}{\sigma^2_{\delta_y} + \sigma^2_{\varepsilon_{y,s}}}$$

To quantify the effect of environmental covariates to the synchrony between species-specific departure probability, we can compare models used the method in Grosbois et al. (2009) and Lahoz-Monfort et al. (2011). All models (A, B and C) include random effects, but model A does

not include covariates and contains only a species-specific intercept by year (α_s). For model A the residual variance is $\hat{\sigma}_\delta^2$ is denoted by $\hat{\sigma}_\delta^2(res)$, and the total variance for model B and C is denoted $\hat{\sigma}_\delta^2(tot)$. From these estimated variances, we can compute a coefficient C_δ which quantifies to the contribution of the focal covariate to the interspecific synchrony in departure probability:

$$C_\delta = 1 - \frac{\hat{\sigma}_\delta^2(res)}{\hat{\sigma}_\delta^2(tot)}$$

As previously, this coefficient can be extended to a year-specific contribution of covariates to synchrony. Here the residual variance $\hat{\sigma}_{\delta_y}^2$ from model A is denoted by $\hat{\sigma}_{\delta_y}^2(res)$, and the total variance for model B and C is noted $\hat{\sigma}_{\delta_y}^2(tot)$. the new coefficient is denoted C_{δ_y} and quantifies the contribution of the focal covariate to the interspecific synchrony in departure probability in year y:

$$C_{\delta_y} = 1 - \frac{\hat{\sigma}_{\delta_y}^2(res)}{\hat{\sigma}_{\delta_y}^2(tot)}$$

We used Nimble on R 3.6.1 with RStudio Version 1.2.5001 to run models ,with package nimble (de Valpine *et al.* 2017). We used 300 000 iterations with a burnin of 200 000. Chain mixing and convergence of the parameters were checked (Kéry & Schaub 2011). The nimble code is available in the Supporting Information.

Results

Multisites

Interspecific synchrony (ICC_s) and the fraction of variation accounted for by the covariates (C_δ) were calculated from estimates of model A (without covariates). For SW, ICCs values range between 0.6 and 0.8 at the three sites, ICCs values are higher (around 0.9) in RW and BT (Table 1). Results are consistent among sites, and the credible intervals are narrow enough to be confident about the mean values (Table 1). This provides evidence of a high degree of synchrony in the variation of daily departure probability between the three species at the three sites. The variation explained by TSA (C_δ TSA) is high at the three sites, with a mean equal to 0.921 at Donges, 0.901 at St Vigor d'Ymonville and 0.77 at l'île du Massereau (Table 1). Conversely, the fraction of variation explained by the environmental covariates is generally low, with a mean value of 0.012 at

Donges, 0.137 at St Vigor d'Ymonville and 0.001 at l'Île du Massereau. Overall, the number of individuals captured does not seem to affect the estimation of ICC_s because the credible intervals for RW and BT are generally narrower than for SW, which is the most abundant species.

Table 1. Estimates of species-specific intra-class correlation coefficients (ICC_s), and covariates contributions (C_δ) from the estimated residual and total variance of the common (δ_t) and species-specific ($\varepsilon_{t,s}$) random effect terms (standard deviations of the ICC_s are shown in parentheses).

	DONGES	ST VYGOR	ILE DU
	D'YMONVILLE	MASSEREAU	
SEDGE WARBLER	0.61 (± 0.13)	0.78 (± 0.11)	0.85 (± 0.13)
	<i>n=1349</i>	<i>n=317</i>	<i>n=580</i>
REED WARBLER	0.93 (± 0.10)	0.96 (± 0.07)	0.97 (± 0.08)
	<i>n=277</i>	<i>n=163</i>	<i>n=188</i>
BLUETHROAT	0.95 (± 0.07)	0.94 (± 0.08)	0.81 (± 0.12)
	<i>n=240</i>	<i>n=73</i>	<i>n=87</i>
$C_\delta \text{ TSA}$	0.921	0.901	0.770
$C_\delta \text{ Environment}$	0.012	0.137	0.001

Multiple years at the Donges station

The species-specific ICC_s varies among years, but except in year 2010 and 2013, the values are similar to what we found in the previous section: ICC for SW lied between 0.5 and 0.7 but was higher in RW and BT (Table 2). However, the standard deviations of these estimated $\text{ICC}_{y,s}$ are three to four times larger than what we found previously when we estimated a unique ICC_s per species on all the years (Table 2). The estimation of synchrony is thus more precise when integrated all years to estimate a single ICC per species. Contrary to what we found in the previous section, the number of individuals seems to affect the precision of the estimation; the smallest standard

deviation corresponds to SW in year 2011, and to the largest number of individuals (Table 2). The fraction of the variation accounted for by the covariates is consistent with the results in the previous section: TSA captures most of the variation of the year-specific common random term (δ_y). However, weather conditions seem to account for 50% of the variation in year 2009, 17% in year 2011, 3% in year 2014 and 0% in the other years (Table 2). Contrary to the contribution of TSA to synchrony, the contribution of the weather conditions varies among years.

Fig.2 shows the variation of the daily departure probability of the three species in August. There are peaks of departure probability mostly during the third decade of August (estimated departure probabilities for the other years are available in the Supplementary Material). SW showed an earlier peak than the two others species, which could be responsible for the lower ICCs in all sites and years in this species (Fig.2 and Table 1 & 2). In addition, even if they do not have the same intensity, the increases in departure probability are synchronized between species, which is consistent with the estimated values of the ICCs.

Table 2. Estimates of species and year-specific intra-class correlation coefficients (ICC_s) and year-specific covariates contributions ($C_{\delta,y}$) from the estimated residual and total variance of the common ($\delta_{y,t}$) and species-specific ($\varepsilon_{y,t,s}$) random effect terms for the Donges station (standard deviations of the ICC_s are shown in parentheses).

	2009	2010	2011	2012	2013	2014
SEDGE WARBLER	0.59 (± 0.31)	0.45 (± 0.32)	0.74 (± 0.21)	0.46 (± 0.31)	0.26 (± 0.24)	0.69 (± 0.24)
	<i>n=54</i>	<i>n=29</i>	<i>n=777</i>	<i>n=376</i>	<i>n=45</i>	<i>n=68</i>
REED WARBLER	0.65 (± 0.30)	0.37 (± 0.34)	0.83 (± 0.22)	0.78 (± 0.28)	0.45 (± 0.35)	0.78 (± 0.28)
	<i>n=79</i>	<i>n=29</i>	<i>n=27</i>	<i>n=36</i>	<i>n=31</i>	<i>n=75</i>

BLUETHROAT	0.53 (± 0.27)	0.30 (± 0.33)	0.82 (± 0.25)	0.73 (± 0.28)	0.62 (± 0.34)	0.80 (± 0.21)
	<i>n</i> =81	<i>n</i> =45	<i>n</i> =18	<i>n</i> =21	<i>n</i> =10	<i>n</i> =55
<hr/>						
C_δ TSA	0.97	0.69	0.89	0.91	0.79	0.91
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C_δ Environment	0.52	0	0.17	0	0	0.3
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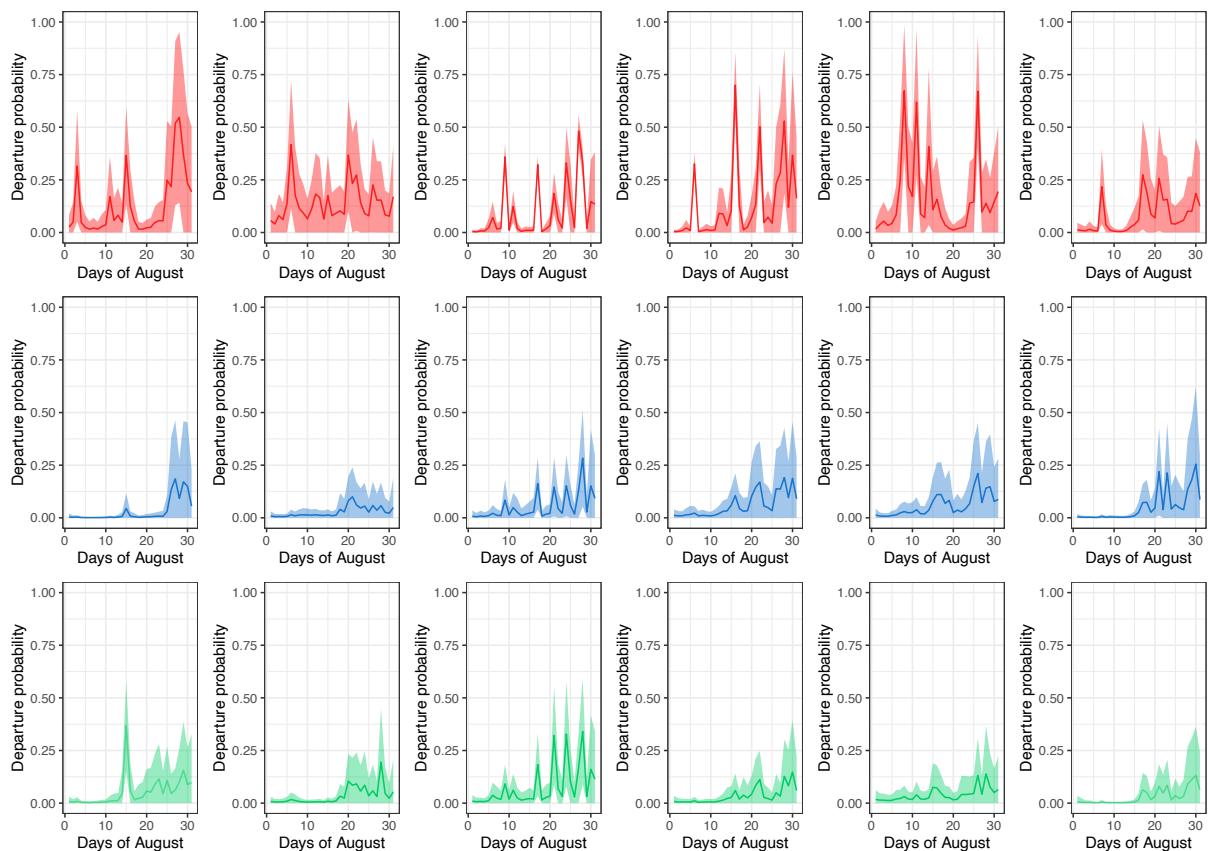


Figure 2: Daily departure probability of the three species in August, from 2009 to 2014, with standard deviations. Red: Sedge warbler, Blue: Reed Warbler, Green: Bluethroat. Solid lines represent the mean and the shaded areas around the mean are the standard deviations around the mean.

Discussion

Synchrony in departure probability

The high synchrony in the variation of departure probability suggests that birds leave the stopover area in “waves” (Figure 2). Even if nocturnal long distant songbird species are not supposed to constitute flocks during night migration (Gauthreaux Jr. 1972, Balcomb 1977), their departures from stopover sites seem to coincide in departure waves. These peaks of departures result in high nocturnal migration intensity; this phenomenon has first been detected by ornithologists during moon-watching sessions (Nisbet & Drury, 1969, Gauthreaux Jr. 1972, Liechti *et al.* 1995, Zehtindjiev & Liechti 2003) and then by radar studies (Richardson 1979, Lupi *et al.* 2016, Weissnau *et al.* 2016). These methods do not allow identifying species, but sometimes orders like *passeriformes*, *charadriiformes* (Schmaljohann *et al.* 2008, Zaugg *et al.* 2008, Nilsson *et al.* 2018, Schmid *et al.* 2019). This study is the first to explicitly measure synchrony in departure probability from a stopover site and we detected these peaks of departures with a capture-recapture dataset.

One may think that weather conditions drives these behaviours. However, even if weather conditions play a role in the decision to depart from stopover sites (Erni *et al.* 2002, Schaub *et al.* 2004, Ma *et al.* 2011, Grönroos *et al.* 2012, Sjöberg *et al.* 2015, Dossman *et al.* 2016), they do not are not the main driver of this decision here. Weather conditions seem to only strongly affect departure decisions when they are harsh (heavy rain, heavy headwind; Schmaljohann, Lisovski, & Bairlein, 2017; Wikelski *et al.*, 2003). Our results provide evidence that TSA is the most important synchronizing agent of departures. As captures took place during fall migration in our dataset, we expected that the individuals follow more the energy-minimization strategy rather than the time-minimization one (Hedenstrom & Alerstam 1997). TSA can be viewed as an integrative metric which reflects changes in the bird internal state (Roques *et al.* 2020); in this view our results are consistent with some recent studies suggesting that the internal state of the bird (fuel stores, body condition, restness) is the most important factor in the decision to depart from a stopover site (Eikenaar & Schlafke 2013, Cohen *et al.* 2014, Moore *et al.* 2017, Schmaljohann & Eikenaar 2017, Anderson *et al.* 2019, Roques *et al.* 2020).

However, Anderson et al., (2019) recently showed that migration distance can influence the strategy employed by individuals: depending on their destination, birds may use time-minimization or energy-minimization strategy. Unfortunately, our study design does not allow us to know where

the birds come from and where they go. SW and RW are strictly trans-saharans migratory birds and are widely spread in Europe during breeding seasons (Shirihai & Svensson 2018). Contrary to SW and RW, some populations of BT overwinter in Portugal or Northern Africa while some go to Senegal (Arizaga *et al.* 2015, 2016). These different overwintering sites seem to correspond to different subspecies of BT and different geographical origins (Arizaga & Tamayo, 2013; Arizaga *et al.*, 2015, 2016). However, as our study took place during fall migration in August, most of our birds are first-year individuals and thus harder to separate into subspecies. Moreover, knowledge concerning morphometric criteria specific to subspecies was sufficient at the time our data were collected. If subspecies could be identified during ringing session at stopover sites, this information could be used in our model to test the hypothesis that subspecies use different departure strategies at the same stopover site (Arizaga, Mendiburu, *et al.*, 2011).

Also, to extend our knowledge about the synchrony in departure probability of songbirds, it would be interesting to use our model on partially migratory birds (Lundberg 1988). As these birds may not (or less) be under time or energy pressure, the drivers of synchrony (or asynchrony) should be more related to local weather conditions. Trans-saharans *and* partially migratory birds could exhibit asynchrony in departure probability from stopover sites.

Modelling and possible developments

We modified capture-recapture models already developed to study synchrony in survival (Grosbois *et al.* 2009, Lahoz-Monfort *et al.* 2011), and used them to study the synchrony in departure probability from stopover sites. This model allows distinguishing the underlying processes generating synchrony in departure probability. We also extended these models to integrate multiple replicates (here ringing seasons) to obtain more precise estimates of synchrony indices. Complementary studies at the individual levels with recent GPS or telemetry tools (Anderson *et al.* 2019) would provide additional information. Also, it would be interesting to extend this model to integrate data from multiple sources, such as telemetry and radar data (Anderson *et al.* 2019, Liechti *et al.* 2019). Combining different data sources in the same model would help estimate departure probability and its daily variations with more accuracy.

Apart from detecting synchrony in departure probability, this model is flexible both in terms of possible extensions. For example, this model could be transformed to study synchrony in departure probability at the spatial level by adding a site dependent random effect ($\gamma_{t,l}$) as follow:

$$\text{logit}(\phi_{t,l}) = \alpha_s + \delta_t + \gamma_{t,l}$$

Where $\gamma_{t,l} \sim N(0, \sigma^2_{\gamma_l})$ is the value of the site-specific random effect at time t and at location l .

The synchrony index between sites can be computed as follows:

$$ICC_l = \frac{\sigma^2_{\delta}}{\sigma^2_{\delta} + \sigma^2_{\gamma_l}}$$

ICC_l would then represent the synchrony in variation of departure probability between sites for the studied species. However, this excludes the possibility to integrate several species in the model and hence to look at how the variations of departure probabilities of a specific species s at a site l are synchronized with the variations of departure probability of the same species s at the other sites. In order to do this, we would need to add a new random effect. This random effect $\lambda_{t,s,l}$ would be species- (s) and site-specific (l) and denoted by $\lambda_{t,s,l} \sim N(0, \sigma^2_{\lambda_{s,l}})$. The new model also including the species-specific random effect $\varepsilon_{t,s}$ and the site and species-specific intercept $\alpha_{s,l}$ would then be:

$$\text{logit}(\phi_{t,s,l}) = \alpha_{s,l} + \varepsilon_{t,s} + \lambda_{t,s,l}$$

This model would allow evaluating how species s at site l behaves compared to the same species at the other locations.

$$ICC_{s,l} = \frac{\sigma^2_{\varepsilon_s}}{\sigma^2_{\varepsilon_s} + \sigma^2_{\lambda_{s,l}}}$$

This extension would allow including all the species and all the locations in the same model, and also computing many different synchrony indexes within the same framework by changing the random effects included in the model. The estimation and the convergence of random effects often take a long time and convergence can be hard to reach.

Last, as competition between species is thought to influence behaviour at stopover sites, especially if food resources are not sufficient (Jenni & Schaub 2003), the model can also be extended test hypotheses concerning relationship between the presence (or abundance) of one species and the decisions of others by adding a term in the departure probability equation its effect on synchrony.

Conclusion

Comparing departure decisions from stopover sites in several species using tools designed to quantify the degree of synchrony in departure decisions is of great interest for management of stopover areas but also to raise and test new hypotheses about bird migration. The processes underlying individual decisions (and thus synchrony) are complex and we need more data about local movement (Mills *et al.* 2011, Taylor *et al.* 2011), body condition (Anderson *et al.* 2019, Klinner *et al.* 2020), and migration distance (Anderson *et al.* 2019). The class of models we developed here is flexible, such models can be used with capture-recapture data to test hypotheses at different spatial and temporal scales, using data from different taxonomic groups or groups characterized by different migration strategies (eg partial *vs* obligatory migrants) and open new perspectives to study bird migration.

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5 Article 4: Utilité de la métrique “durée de halte estimée” dans la gestion et la conservation des zones de halte migratoire

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5.1 Estimated Stopover duration as a tool for conservation and management of stopover areas

Estimated Stopover duration as a tool for conservation and management of stopover areas

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Abstract

Migratory birds are highly dependent on the quality of stopover habitats throughout their migratory journey. These habitats are currently under an increasing number of threats: climate change, pollution, habitat loss. However, the effects of habitat loss or habitat quality deterioration, unless they are specifically monitored, are often detected only when they are severe, or indirectly, when a bird population is declining. Yet, anthropogenic effects can slowly impact the behaviour of stopovering migratory birds before being detected. Stopover duration is usually monitored through bird ringing, by computing the minimum stopover duration (MSD), i.e. the time elapsed between the first and the last day of capture. We used simulations to evaluate the ability of MSD to detect a decrease in stopover duration over time. In parallel, we estimated stopover duration (ESD) through recent capture-recapture modelling. Unlike MSD that underestimates stopover duration, ESD estimates it correctly and, more importantly, detects declining trends that are not detected by MSD. Hence, ESD is a more robust tool for management and conservation of stopover habitats and migratory birds.

Introduction

Migratory birds represent almost 20% of the bird species of the world (Birdlife International 2008, Kirby *et al.* 2008). On the journeys between breeding and wintering areas they need to stop at places to replenish their reserves (Alerstam 1990). These “stopover areas” are critical for success of the journey (Kirby *et al.* 2008). Migratory birds thus depend not only on the quality of breeding or wintering habitat, but also on that of the many areas where they stop throughout migration (Mehlman *et al.* 2005, Moore 2018, Cohen *et al.* 2019). Consequently, the conservation of migratory birds must be considered at the level of the whole flyway (Kirby *et al.* 2008).

The importance of stopover areas for migratory birds lies in the relationship between migrants and habitat during the stopover. Stopovering implies arriving to the stopover site, resting to recover from extreme physical exercise, and looking for suitable habitat to replenish reserves (Alerstam & Lindström 1990, Cohen *et al.* 2014b). To select a suitable stopover site, nocturnal migrating birds

can use cues such as songs and calls of conspecifics (Herremans 1990, Mukhin *et al.* 2008). Habitat selection is an important step in the stopover process because body condition, migration timing, survival and fitness depend on the quality of the stopover habitat (Ktitorov *et al.* 2010, Sheehy *et al.* 2011, Cohen *et al.* 2012, Klinner *et al.* 2020). However birds cannot allocate a large amount of time to prospect for best habitats because of time and energy constraints (Hedenstrom & Alerstam 1997, Cohen *et al.* 2014b).

The stopover areas concentrating a large amount of birds are usually areas providing a substantial amount of food resources. However, a large part of these habitats are currently under different anthropogenic threats (Kirby *et al.* 2008, Gardner & Davidson 2011, Mitsch & Hernandez 2013, Zöckler 2014). Habitat loss, climate change, habitat pollution or even pollution of surrounding areas drastically impact the quality of these habitats and food abundance (Kirby *et al.* 2008, Sheehy *et al.* 2011, Shobrak 2011, Murray & Fuller 2015). This is especially true for wet areas where billions of birds stopover each year to rest and refuel (Kirby *et al.* 2008, Gardner & Davidson 2011). If habitat loss or substantial pollution can easily be detected, discrete but important changes can occur and affect habitat quality. Detecting these changes require constant monitoring of many physical and biophysical features of the habitat (Adamus 1992). The effort needed to monitor all the main stopover areas (or surrounding areas) is prohibitively large.

Substantial stopover habitat changes and discrete ones can negatively affect the ability of individuals to find resources and affect their behaviour at stopover sites (Gillespie & Fontaine 2017). If food resources are scarce, individuals replenish their reserves at a slower pace or try to locate a more productive area (Ktitorov *et al.* 2010, Cohen *et al.* 2014b, Schmaljohann & Eikenaar 2017). This can result in changes in stopover duration (Jenni & Schaub 2003, Schmaljohann & Eikenaar 2017, Schmaljohann 2018). Hence, stopover duration can be a tool to detect changes in habitat quality. Nevertheless, true stopover duration is not directly observable because the detection of stopovering birds is imperfect (Schaub *et al.* 2001). This is especially true for songbirds that spend most of the time feeding into reeds or bushes (Schaub *et al.* 2001, Schmaljohann & Eikenaar 2017). Mist-netting, ringing and capture-recapture are appropriate methods to monitor bird behaviour (Davidson *et al.* 1999, Bairlein 2003, Baillie & Schaub 2009). Minimum stopover duration (hereafter MSD, the number of days between the first and last capture of marked individuals) can be directly measured at stopover sites. Bird ringing is already widely used by managers and scientists across the world to monitor the state of migrating populations (Baillie &

Schaub 2009) and alert to changes in bird numbers at stopover areas (Jiguet *et al.* 2011). Our idea is not to evaluate the health of populations but to detect possible changes in stopover habitat quality through changes in estimated stopover duration. MSD is known to strongly underestimate true stopover duration (Schaub *et al.* 2001, Schmaljohann & Eikenaar 2017, Roques *et al.* 2020). Thanks to the development of capture-recapture (CR) models (Schaub & Jenni 2000, Péron *et al.* 2007, Lyons *et al.* 2016, Roques *et al.* 2020), it is now possible to estimate true stopover duration while accounting for imperfect detection at stopover sites. Our hypothesis is that the performance of MSD as a tool to detect variation in stopover duration over years is outperformed by that of estimates of stopover duration that account for imperfect detection of free ranging bird species. Our goal is to use simulations to compare the ability of MSD and ESD to detect decreasing trends of stopover duration over time, and evaluate the relevance of these indicators as tools for management of stopover areas. Also, we discussed how different trends of ESD can be interpreted concerning birds decisions and habitat quality at the studied stopover place or along the flyway.

Methods

Modelling

We used a recent state-space formulation of an open CR model (Pledger *et al.* 2008, Lyons *et al.* 2016, Roques *et al.* 2020) to analyse simulated datasets where stopover duration decreases over 5 years. The CR model is parameterized with entry probability in the sampling area (Crosbie & Manly 1985, Schwarz & Arnason 1996). The parameters of the model are:

ϕ_t Probability of staying in the sampling area between days t and $t+1$,

η_t Probability of arriving at the stopover area on day t given that the individual was not present before,

p_t Probability of capture (encounter) in day t given the individual has arrived but not yet departed.

This model explicitly separates the state process (the true, partially observable state of the bird) from the observation process (what investigators see in the field). The true state of an individual is either “present in the stopover” or “not present in the stopover area”. If the true state “not present” occurs before the first capture and or after the last capture, the bird is not yet arrived or already departed, respectively. The observations are simply “seen” or “not seen” or more specifically

captured or not captured with mist-netting. The true state is accounted for by vector \mathbf{z}_i , and the observations (the observed capture history) by vector \mathbf{h}_i . The true state of the individual i at time t is represented by $z_{i,t}$ and the observation by $h_{i,t}$. The dynamics of state \mathbf{z} from occasion t to the following $t+1$ is modelled using Bernoulli variable as follows:

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli} \left(\phi_{t-1} z_{i,t-1} + \eta_t \prod_{j=1}^{t-1} (1 - z_{i,j}) \right)$$

The term $\prod_{j=1}^{t-1} (1 - z_{i,j})$ is used to model the availability of the individual for entering the stopover area and is equal to 1 when the individual has not yet entered the stopover area, and 0 afterwards.

The observation process (dependent on the state process) is also modelled using a Bernoulli variable as follows:

$$h_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t}, p_t)$$

This means that if an individual i has not yet entered the stopover area or has left it ($z_{i,t} = 0$), then $h_{i,t} = 0$ with probability equal to 1. If $z_{i,t} = 1$, then the capture history $h_{i,t}$ is a Bernoulli variable with probability p_t , the probability of capture at time t .

This state-space formulation allows computing multiple derived parameters from the state-process vector \mathbf{z}_i (Pledger *et al.* 2008, Lok *et al.* 2019, Roques *et al.* 2020). Here we will focus on the ESD formulation described in Lyons et al. (2016), which is given by the following equation:

$$\text{ESD} = \frac{\sum_i \sum_t z_{i,t}}{n}$$

where n is the number of individuals and z the true state variable (which defines if an individual was present or not at the stopover site at day t).

Simulations

We ran different simulations with a decreasing staying probability resulting in a decreasing stopover duration over the years. Arrival probability was set constant to 0.3. The only non-fixed parameter was detection probability p . We simulated datasets under four mean detection probabilities: 0.8,

0.5, 0.3 and 0.15. The latter value is the closest to detection probabilities common in field studies (Schaub *et al.* 2001, Roques *et al.* 2020). We simulated all the datasets with a decreasing value of the probability of staying in the sampling area (ϕ) equal to 0.9, 0.8, 0.7, 0.6 and 0.5, from year 1 to 5, respectively. The number of capture occasions (days) was fixed to 15 days and the number of individuals was 1000. Individuals that are never seen when simulating the capture histories (histories containing only zeros) are removed. Hence all our datasets represent a ringing season where birds are captured during 15 days each year. We replicated our simulations 10 times per ringing season with the same parameter values. Hence, we analysed 10 datasets*4 different capture probabilities*5 ringing seasons = 200 datasets. We estimated ESD for each dataset and compared it to MSD.

We used Markov chain Monte Carlo algorithms (MCMC) to approximate the Bayesian posterior distributions of model parameters. We used MCMC chains of 30,000 iterations with a burn-in period of 15,000 and performed analyses using JAGS (Hornik *et al.* 2003) and program R version 3.6.1 (R Development Core Team 3.0.1. 2013). R codes used to perform these models are available in the Supplementary Material. In order to test the ability of ESD and MSD to detect a decreasing trend of stopover duration, we performed Generalized Least Squares (GLS) models (Guéry *et al.* 2019) for each scenario with the R package “nlme” (Pinheiro *et al.* 2020). To compute a variance for each year of each scenario, we randomly selected 1000 values from the Bayesian posterior distributions of mean stopover durations for each sample, which resulted in a variance for each year computed from randomly selected 10 000 values. Using GLS to quantify the significance of a trend allows us to take the distribution of the parameter into account instead of simply use the mean of the parameter, which can lead to biased conclusions about the significance of a trend or a parameter (Guéry *et al.* 2019).

Results

Our model correctly estimated stopover duration in the three different scenarios where capture probability was ≥ 0.3 but slightly underestimated stopover duration when $p=0.15$ and $\phi \leq 0.8$ (Figure 1). The values are pretty constant regardless of the scenario. As expected, MSD always underestimated true stopover duration, with an increasing bias as capture probability decreases. Our model also correctly detected the decreasing trend in stopover duration in the four capture probability scenarios (Figure 1, left column and Table 1). In contrast, MSD detected this decreasing

trend in only three capture probability scenarios ($p=0.8$, $p=0.5$ and $p=0.3$; Figure 1, right column and Table 1). With $p=0.15$ (Figure 1, bottom right corner), this trend could not be detected with MSD detecting (non-significant p-value, Table 1) and the true stopover duration was strongly underestimated (Figure 1).

Table 1: Slope coefficients and p-values from the Generalized Least Squares analyses (GLS) for the four different capture probability scenarios. ESD: Estimated Stopover Duration, MSD: and Minimum Stopover Duration. Values in bold stand for the non-significant trend in stopover duration over years.

	ESD		MSD	
<i>Capture probability</i>	<i>slope</i>	<i>p-value</i>	<i>slope</i>	<i>p-value</i>
p=0.8	-0.21	<0.001	-0.20	<0.001
p=0.5	-0.23	0.002	-0.20	<0.001
p=0.3	-0.27	0.006	-0.19	<0.001
p=0.15	-0.30	0.01	-0.04	0.104

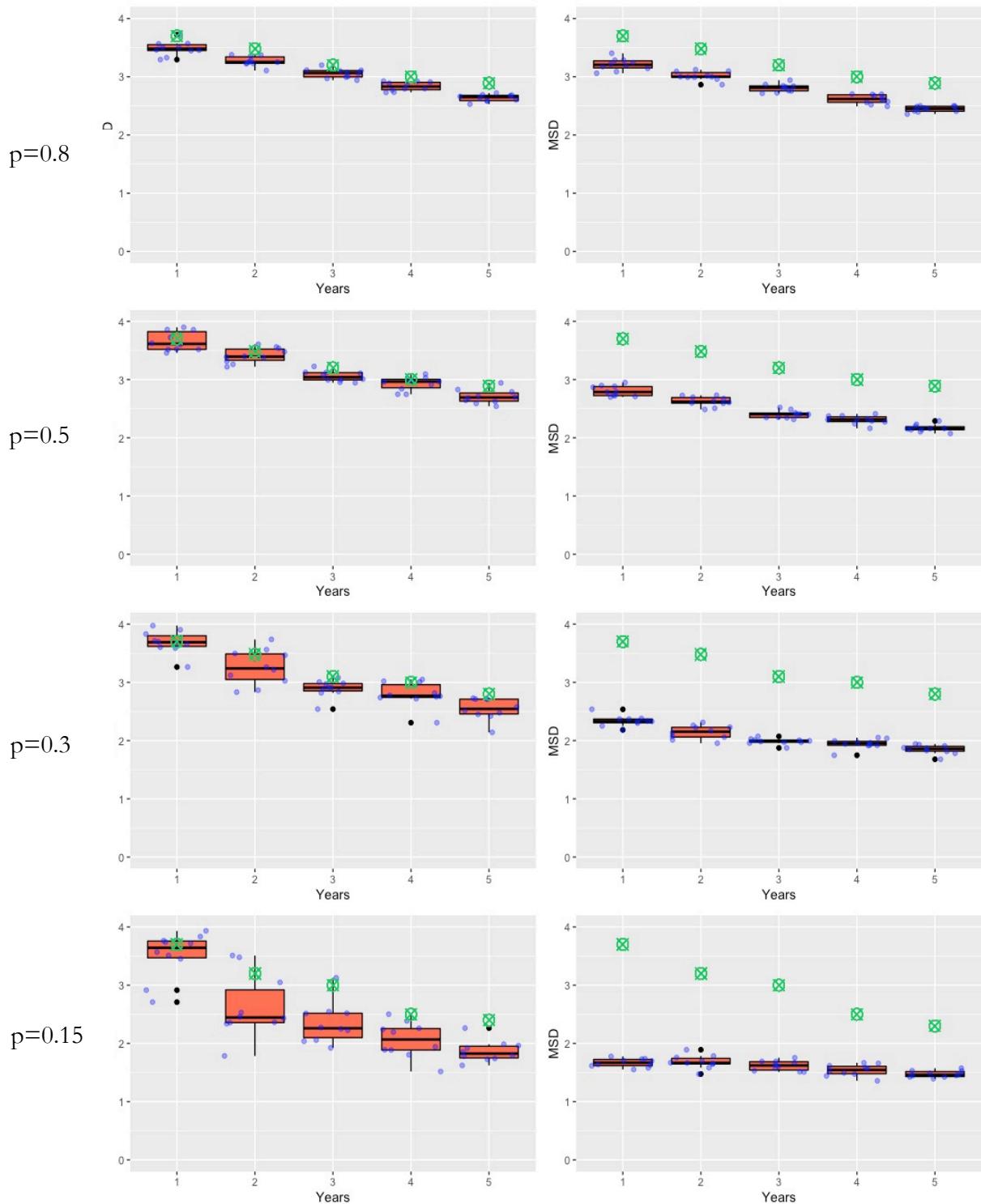


Figure 1: Mean estimated stopover duration (ESD) and minimum stopover duration (MSD) for four different capture probabilities 0.8, 0.5, 0.3, 0.15. The blue dots stand for the values of each of the 10 mean yearly ESD and MSD. The green barred circles stand for the mean true stopover duration in the 10 simulated datasets for each year.

Discussion

Our results show that MSD is unable to detect a decreasing trend in true stopover duration when detectability is under 0.3. We used a large range of values of detection probability, when the usual values of daily detection probability in stopovering birds is around 0.15 (Schaub *et al.* 2001, 2004, Salewski *et al.* 2007, Schmaljohann & Eikenaar 2017, Roques *et al.* 2020). This means that the most realistic scenario is the one where $\phi=0.15$: our results show that MSD is not a robust metric to study the changes in the behaviour of stopovering birds. Apart from underestimating stopover duration when detectability is low, MSD fails to detect the variation in stopover duration over years or seasons, and thus prevents investigators from detecting any trend in true stopover duration. ESD performs better to detect temporal variations in stopover duration than MSD. But, ESD slightly underestimated the true stopover duration when $\phi\leq0.8$. As our goal is to detect a trend, this is not of great importance in our case. Also, cases when ϕ is constant during a ringing season is not really realistic because staying probabilities can widely vary between days (days with perfect or adverse weather conditions, days at the end of the period). This underestimation may disappear when ϕ is time dependent. Further simulations will address this aspect.

Warning to changes in habitat quality or population health state

The usefulness of ESD lies in the stopover behaviour of birds. Birds use stopover areas to rest and refuel, all of these activities contribute to the total stopover duration (Alerstam & Lindström 1990, Schmaljohann & Eikenaar 2017, Schmaljohann 2018). Changes in stopover duration can reflect different processes.

First, if food resources become locally scarcer, competition increases and birds relocate to more suitable habitat more rapidly than if resources were abundant (Ktitorov *et al.* 2010, Cohen *et al.* 2014b). This situation caused by habitat changes will shorten stopover duration locally. But, shorter durations can also reflect a degradation of habitat quality at a stopover site upstream: if birds do not relocate in a more suitable habitat, they will increase their stopover duration (compared to previous years) to refuel at the needed level of energy reserves. Hence, if they are under time pressure (Cohen *et al.* 2014a), they will shorten the stopover duration at the next stopover site (Ktitorov *et al.* 2010; which may be our monitored site). Indeed, the overall migration travel of migratory birds is optimized in terms of energy or time: individuals stop at selected places (to whom

they show fidelity; Yohannes *et al.* 2007) where food is sufficient to optimize the journey (Hedenström & Alerstam 1997, Alerstam 2011). Hence, a decreasing trend in stopover duration should alert to potential changes at the studied stopover area or upstream. These changes may be caused by decreased in food abundance, or increased pollution, competition, or predation (Kirby *et al.* 2008, Brown *et al.* 2017, Moore 2018). Once again, this highlights the importance of addressing the conservation of migratory birds at the level of the entire flyway (Kirby *et al.* 2008).

Second, an increasing trend in stopover duration can also be due to a decrease in local food abundance. If food is less abundant at the studied stopover area, birds will refuel at a slower pace (Ktitorov *et al.* 2010). Hence, acquiring a sufficient amount of fuel stores will take longer than usual. As above, this can also be due to changes in food availability at a stopover area up the flyway where habitat quality is poorer. In this case birds arrive at the studied stopover area with lower fuel stores and will need more time to replenish their reserves.

It is important to keep in mind that a trend in stopover duration may not be induced by habitat changes at the studied stopover area or along the flyway. Such trends can also be explained by habitat changes at breeding or wintering areas. For example, climate change can modify the phenology of food at breeding areas and make birds breed earlier than usual (Both & te Marvelde 2007, Moller *et al.* 2008, Chmura *et al.* 2020, Hällfors *et al.* 2020). Birds will then depart earlier than usual from breeding sites, but as climate change effects are not linear along a flyway, stopover areas may not be affected and birds may arrive earlier than usual and thus be constrained to wait for the peak in food abundance.

ESD can be a very useful tool to warn about changes at the population level, the flyway level, or the stopover habitat one. Counts of migratory soaring birds at bottlenecks are already used in this way; they can warn of substantial changes of population health state (Vansteelant *et al.* 2020). ESD should be part of the toolbox routinely used at stopover areas to assess habitat quality or population state.

Benefits of using estimated stopover duration as a tool for conservation and management

Using ESD as a tool for management and conservation has several advantages. Long-term tinging data is already available at many stopover areas around the world (Davidson *et al.* 1999, Kirby *et al.* 2008, Baillie & Schaub 2009). These data can be directly used to assess the variation of ESD over

time and do not require additional funds to implement new monitoring protocols. Funding bird migration monitoring is getting more and more difficult and these monitoring programmes require a substantial time investment by field ornithologists. Explicitly stating the potential of this type of data, including the new potential inherent to the development of new analytical tools would help managers raise funding to continue these programmes. In our view ESD is a useful tool at several levels: to detect changes occurring in the habitat and the population, to help managers make decisions, and to justify the continuation and the funding of bird ringing monitoring projects.

Nevertheless, practitioners should be aware of the fact that estimating ESD *via* CR models requires data large enough sample to precisely estimate stopover duration. Hence, this method cannot be used in situations where only a few birds are daily trapped in mist-nets. One interesting extension of these statistical models is to also use the counts of birds at the stopover area to estimate the population size which can be monitored over the years (McGowan *et al.* 2015, Lyons *et al.* 2016, Lok *et al.* 2019).

Future developments

Capture-recapture models designed to estimate stopover duration are not currently available in widely used CR programs such as MARK (White & Burnham 1999) for example. Consequently, these models are not yet easily usable by managers and field ornithologists who are not used to programming with R and the BUGS language (Hornik *et al.* 2003, R Development Core Team 3.0.1. 2013, de Valpine *et al.* 2017). It would be very useful to develop this type of model as an application directly usable by managers and field ornithologists. SHINY applications currently provide this opportunity and make R analyses more user friendly through a dedicated interface directly accessible on a dedicated server (Chang *et al.* 2020). This development would promote the existence of a network of ringing stations where stopover duration is monitored each year, and may help discover large scale patterns of stopover duration variation, habitat quality variation or population changes.

Conclusion

We demonstrated the usefulness of estimating stopover duration rather than using observed minimum duration for conservation and management purposes of species or habitat. Stopover habitats as well as bird populations are increasingly under threats from different sources, and changes in either of them are sometimes hard to detect. ESD is more efficient at detecting such

changes than MSD. We strongly recommend the use of estimated stopover duration with recent capture-recapture models in order to address changes in stopover duration. Transferring this tool to managers of stopover areas will improve our approach to the conservation of habitats and bird populations.

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6 Conclusion et perspectives

6.1 Remarques générales

L'objectif principal de mon travail de thèse pourrait être résumé par deux questions principales : « Quels sont les déterminants du départ d'un site de halte migratoire et comment étudier ces derniers à travers des jeux de données de baguage déjà existants ? ». Ces questions sont très vastes et pourraient constituer un travail de recherche de toute une vie ; c'est d'ailleurs déjà le cas pour certains scientifiques qui travaillent activement sur la migration des oiseaux depuis des décennies. Malgré tout, les résultats obtenus durant ces trois années de thèse ont permis de caractériser ces décisions avec des outils d'analyse de données évitant des biais connus mais non-encore pris en compte dans l'immense majorité des études, et de révéler des déterminants de ces décisions qui seraient restés indétectés ou auraient été sous-estimés sans l'utilisation de ces outils. Cette thèse a aussi permis de valoriser des jeux de données parfois récoltés sur plusieurs dizaines d'années. Dans cette générale, j'aborderai les apports biologiques et écologiques de chacun des articles présentés dans les chapitres ci-dessus et discuterai d'une métrique particulière utilisée dans cette thèse : le temps depuis l'arrivée ou Time Since Arrival (TSA). Les résultats obtenus ici ne peuvent en effet être compris sans connaître la nature de cette métrique, ses limites, mais aussi ce qu'elle a de différent et novateur par rapport aux métriques utilisées dans la littérature. Ensuite j'aborderai les futurs développements méthodologiques des modèles de Capture-Marquage-Recapture (CMR) susceptibles de nous permettre une compréhension encore plus fine des facteurs impliqués dans la décision de départ d'un site de halte migratoire. Enfin, je finirai par les implications potentielles que le type de résultats et d'analyses présentés dans ce document peuvent avoir en termes de gestion (ceci est en partie déjà développé dans l'article 4).

Il est important de souligner que la migration des oiseaux réserve encore d'innombrables inconnues quant aux comportements précis des individus pendant leurs vols, leurs décisions sur site de halte, leur orientation, la mise en place de nouvelles voies de migration et bien d'autres aspects. Cette thèse n'avait pas vocation à tout explorer mais se focalisait sur la modélisation de la décision de départ à partir de données de CMR. Des travaux complémentaires permettront à l'avenir de découvrir ou de préciser de nombreux aspects encore inconnus de la migration des oiseaux.

6.2 Écologie de la halte migratoire

Parmi les 4 articles de cette thèse, 3 s'intéressent aux comportements des oiseaux migrants lors de leurs haltes migratoires. Ces 3 parties apportent donc des connaissances sur la biologie et l'écologie de la halte migratoire.

Article 1. Le premier article avait comme objectif de mesurer la part relative des facteurs internes et externes dans la décision de départ d'un site de halte ; il a révélé que l'état interne de l'oiseau (approché grâce à un proxy qu'est le temps depuis l'arrivée) est prédominant par rapport aux conditions météorologiques au temps t dans la décision de départ. Cependant les conditions météorologiques ont pu au préalable indirectement influencer l'état interne de l'oiseau en complexifiant l'accès à la ressource (Jenni & Schaub 2003, Schmaljohann & Eikenaar 2017, Schmaljohann *et al.* 2017). Mais il en est de même si l'on mesure directement la condition corporelle de l'oiseau et son taux d'engrassement. Les mesures de condition corporelle précises s'avèrent compliquées sur les oiseaux de petite taille. En effet, le poids n'apparaît par exemple pas comme un bon proxy de la condition corporelle car il explique au plus 50 à 60% de la variation de la condition corporelle (Schwilch & Jenni 2001, Schmaljohann & Eikenaar 2017). La condition corporelle peut cependant être approchée grâce à un indice : the scaled mass index (SCI; Peig & Green 2009). Ce rapport permet de d'identifier la variation du poids entre individus qui n'est pas due à la différence de taille des oiseaux et pourrait être utilisé comme un indice de condition corporelle. Mais utiliser cette métrique pose deux problèmes.

Le premier problème est que les oiseaux ne sont pas nécessairement pesés à chaque recapture dans les jeux de données de baguage, ce qui impliquerait, pour utiliser la condition corporelle mesurée dans des analyses, de supprimer tous les individus à qui il manque au moins une pesée dans l'histoire de capture. Ceci réduirait fortement la taille des jeux de données, qui tendraient en outre à inclure plutôt les oiseaux capturés peu de fois au détriment de ceux capturés un plus grand nombre de fois mais pour lesquels la pesée n'a pas été systématiquement réalisée (Mills *et al.* 2011, Taylor *et al.* 2011). Le second problème est d'ordre méthodologique: utiliser une covariable individuelle continue comme le SCI dans le cadre d'une étude utilisant le protocole de récolte de données et les modèles de CMR implique de tenter de prédire la valeur de SCI pour chaque individu n'étant pas capturé à une occasion de capture (King *et al.* 2008, Schofield & Barker 2011). Cela peut être fait

en intégrant dans le modèle de CMR un modèle théorique de variation temporelle de cette covariable durant le séjour de l'individu dans un site de halte. Cependant nous n'avons à l'heure actuelle pas d'idée précise de ce modèle de variation de SCI, ni de la manière dont les conditions environnementales impactent cette variation. Même les études expérimentales manipulant des oiseaux ne fournissent pas de tel modèle (qu'il faut définir de manière formelle afin de l'intégrer dans un modèle statistique).

Ce dernier point pourrait par ailleurs nous amener au questionnement suivant : sachant que les individus capturés sont manipulés et que cette manipulation peut induire une perte de masse (Schwilch & Jenni 2001), les variations de la condition corporelle des individus capturés sont-elles représentatives de l'ensemble de la population faisant halte ? Répondre à cette question nécessiterait d'approfondir notre connaissance des impacts de la capture sur la condition corporelle de l'oiseau pendant sa halte migratoire. C'est pour cela que l'une des idées principales de cet article est d'utiliser le temps depuis l'arrivée comme un proxy de l'état interne de l'oiseau, voire de sa condition corporelle, dans le but d'évaluer le rôle que joue cette composante dans la décision de départ du site, et de le comparer à celui des conditions environnementales. Ceci nous a permis de progresser dans l'évaluation de l'importance relative des facteurs internes *versus* facteurs externes dans la décision de départ d'un site de halte migratoire.

Le temps depuis l'arrivée intègre certainement de multiples aspects, pas seulement l'état de forme ou la condition corporelle de l'oiseau, et résulte de plusieurs processus. Il est donc possible qu'il dépende de l'accès à la ressource, qu'il reflète aussi le temps de repos et le taux d'engraissement, eux-mêmes influencés par les conditions météorologiques sur les sites où les fenêtres météorologiques favorables à la migration sont rares. En conséquence, il n'est pas surprenant qu'il soit le facteur numéro 1 influençant la probabilité de départ dans nos analyses. La nature intégratrice du TSA fait que cette métrique englobe beaucoup des déterminants du départ d'un site de halte. Ce peut être jugé comme une qualité tout comme un défaut : cette métrique permet d'étudier le départ des sites de haltes migratoires sans ignorer l'effet de l'état interne individuel même si les données disponibles ne donnent pas accès à une mesure directe de cet état. Elle permet donc l'utilisation de très nombreux jeux de données historiques et de longues séries temporelles dont la récolte a commencé avant que des méthodes alternatives de suivi du comportement individuel pendant la halte migratoire ne soient disponibles, ou dont la taille d'échantillon très conséquente reste incompatible avec l'équipement des individus par des dispositifs électroniques

encore coûteux. Le fait de ne pas avoir à manipuler les individus à chaque capture permet également de limiter le dérangement et le stress. Cependant, cette métrique ne permet pas d'étudier les détails des interactions entre état individuel interne et facteurs externes, ni l'effet de ces interactions sur la décision de départ. Le fait de détecter une influence des facteurs environnementaux en plus du TSA sur cette décision peut montrer que les conditions environnementales immédiates contribuent à déterminer le départ, alors que le TSA intègre également l'interaction entre ces conditions depuis l'arrivée sur le site de halte, le comportement de recherche de nourriture, et les processus physiologiques de repos et d'engraissement. Enfin, l'intégration de TSA comme covariable dans les modèles de capture-recapture ralentit considérablement la vitesse de calcul et limite les possibilités d'optimisation du temps de calcul (voir plus bas, section Futures analyses et développements des modèles de CMR).

Article 2. Le deuxième article s'attachait, lui, à évaluer si les déterminants du départ des sites de halte variaient en fonction du site. Les sites étaient caractérisés par des conditions environnementales différentes, et correspondaient à des routes migratoires contrastées. Nous avions, d'une part un site peu humide avec globalement peu de vent, positionné sur une voie de migration terrestre, et d'autre part, un site littoral humide et venté, où les oiseaux se préparaient à un vol au-dessus de l'océan durant lequel ils n'avaient pas la possibilité de se poser. Les analyses ont dévoilé que les oiseaux restaient plus longtemps que ce qui était théoriquement nécessaire pour refaire leurs réserves et qu'ils avaient tendance à choisir des conditions de vent avantageuses au moment du départ. Ceci est cohérent avec l'hypothèse que les individus adoptaient une stratégie de minimisation de l'énergie dépensée. Les oiseaux se préparant à un vol au-dessus de l'océan ont aussi un temps de halte moyen plus long, ce qui peut être expliqué par un besoin énergétique plus important. La météo était aussi *a priori* plus importante dans la décision de départ pour les oiseaux se préparant à un vol au-dessus de l'océan. Cette étude réutilisant des jeux de données déjà analysés par le passé, mais ici avec des méthodes d'analyses récentes, a permis d'identifier des déterminants du départ et de tester une hypothèse émise dans le cadre de la théorie de la migration optimale (minimisation du temps versus minimisation de l'énergie consacrée au trajet migratoire; Alerstam & Lindström 1990, Schmaljohann 2018, Anderson *et al.* 2019) et de préciser les comportements des oiseaux migrants utilisant différentes routes migratoires et faisant face à différentes barrières physiques. Ces résultats sont en accord avec une étude récente sur les limicoles migrants nord-américains (Anderson *et al.* 2019) concluant que les espèces ayant une distance de migration inférieure à 7500km utilisent une stratégie de minimisation de l'énergie dépensée durant la

migration postnuptiale, quand ceux ayant une distance de migration supérieure à 9000km ont tendance à utiliser une stratégie de minimisation du temps en migration. L'espèce étudiée ici correspond au premier cas de figure (Gratto-Trevor *et al.* 2012, Brown *et al.* 2017).

Article 3. Enfin le troisième article visait à quantifier la synchronie des probabilités de départ quotidiennes de plusieurs espèces de passereaux paludicoles. Cet article a révélé que ces probabilités étaient fortement synchronisées et que le temps depuis l'arrivée était la variable qui générait en grande partie cette synchronie. Cette étude est l'une des premières à quantifier la synchronie dans le départ d'un site de halte et met en évidence des phénomènes bien connus que sont les vagues de départ de sites de migration. Plus globalement, cela montre que les individus appartenant à un même cortège d'espèces (passereaux paludicoles) semblent se comporter de la même manière vis-à-vis des décisions de départ d'un site de halte. Ceci renforce la généralité des conclusions quant aux comportements des passereaux migrants transsahariens lors de leurs haltes.

Pour aller plus loin sur la question de la synchronie, il serait intéressant de l'étudier dans le contexte des arrivées sur un site de halte migratoire. Si l'arrivée sur le site suivant est conditionnée par le départ du précédent, les observations de terrains tendent à suggérer que les conditions météorologiques ont plus d'influence sur les arrivées que sur les départs (Deppe *et al.* 2015, Bradarić *et al.* 2020). Si l'on étudiait les arrivées sur un site, l'hypothèse serait que les variations de probabilités d'arrivée quotidiennes tendent à être synchrones entre les espèces, et que les processus générant cette synchronie sont plutôt d'ordre météorologique. Les conditions météorologiques (notamment les régimes de vents) pourraient influencer le choix du site de halte et non directement le fait d'arriver (Vansteelant *et al.* 2017, Bradarić *et al.* 2020).

6.3 Après le départ, l'arrivée ?

Il y a malheureusement un important manque de connaissances sur les arrivées des oiseaux sur les sites de halte migratoire, et la plupart des études se focalisent plutôt sur les départs. Les outils de géolocalisation récents pourraient permettre de remédier à cela sur certaines espèces mais les petits passereaux ne peuvent à l'heure actuelle pas être équipés de balise GPS, les dispositifs n'étant pas assez miniaturisés (McKinnon & Love 2018). Ceci peut cependant être étudié en équipant les oiseaux de radio émetteurs et en plaçant sur le terrain des réseaux d'antennes capables de détecter le passage d'oiseaux déjà équipés (Fiedler 2009). Ceci a déjà été en partie réalisé pour la traversée des passereaux dans le golfe du Mexique (Deppe *et al.* 2015) mais le nombre d'individus équipés

reste faible et l'étude se plaçait dans un contexte de franchissement d'une barrière géographique importante qu'est le golfe du Mexique. Dans le contexte européen, un réseau d'antennes capables de détecter le passage d'oiseaux équipés d'un radio émetteur a été développé sur les côtes de la mer du Nord (plus particulièrement sur l'île d'Helgoland en Allemagne, Schmaljohann & Klinner 2020) et a déjà permis de documenter la stratégie étonnante d'un rougegorge familier (*Erythacus rubecula*) équipé d'un radio transmetteur très léger : parti d'Allemagne, il a été détecté sur les côtes Néerlandaises avant de traverser la mer du Nord pour rejoindre les côtes Britanniques pour y passer l'hiver. Ces technologies permettent de suivre les départs tout comme les arrivées, et ouvrent d'innombrables possibilités d'études sur le sujet. Le facteur limitant sera la plupart du temps le nombre d'oiseaux équipés passant par ces réseaux d'antennes pour pouvoir dégager des patrons généraux.

Pour tenter de dégager des patrons plus globaux, les modèles utilisés durant cette thèse intègrent des probabilités quotidiennes d'arrivées (relatives à l'ensemble des jours de suivi : les individus du jeu de données doivent tous arriver) sur le site de halte migratoire (Lyons *et al.* 2016, Lok *et al.* 2019). Il serait ainsi possible d'utiliser des covariables pour expliquer les variations de la probabilité d'arrivée sur site. On pourrait alors penser à utiliser des données météorologiques à $j-1$ ou $j-2$ dans des contrées en amont du site de halte ou alors directement utiliser les conditions locales au temps t . Le moment précis de la saison (par exemple le nombre de jours écoulés depuis le début du mois d'août) est aussi central dans l'arrivées des oiseaux sur un site de halte migratoire (Arizaga *et al.* 2011, Stanley *et al.* 2012, Deppe *et al.* 2015) et ce pour être coordonnés avec les pics de nourriture. Il est possible que les probabilités d'arrivées journalières des individus sur le site de halte résultent d'une interaction entre la météorologie locale ou en amont et le moment précis de la saison de migration. Une autre piste pour étudier les arrivées serait d'inverser les histoires de captures individuelles (Pradel 1996) et considérer le départ comme l'arrivée. Comme précédemment, s'en suivrait l'ajout de covariables pour mieux comprendre les déterminants de l'arrivée sur un site de halte. Les jeux de données utilisés dans cette thèse pourraient permettre d'étudier la halte migratoire dans son ensemble, de l'arrivée jusqu'au départ.

6.4 Futures analyses et développements des modèles CMR

Dans la perspective d'approfondir la connaissance des décisions de départ des oiseaux migrateurs et de l'influence de l'état interne de l'individu et sa condition corporelle sur cette décision, de nombreux développements et adaptations des modèles de CMR sont possibles.

Mieux comprendre la relation entre le temps depuis l'arrivée et la condition corporelle fait partie des verrous importants pour l'étude de la migration. Ouvrir ce verrou nécessite des développements méthodologiques. Il est en effet nécessaire de connaître la durée de halte dans son ensemble et de ne pas considérer le premier jour de capture comme le jour d'arrivée sur le site de halte. Il est possible et même fortement probable que l'individu soit arrivé quelques jours avant la première capture, et qu'il ait pu dans un premier temps se reposer. L'individu peut perdre du poids durant les premiers jours de sa halte à cause de la transformation/dégradation de son hypertrophie musculaire engendrée par un vol sur une longue distance (Gaunt *et al.* 1990, Rayner 1990). Il en est de même lors du dernier jour de capture, qui est souvent considéré comme le jour de départ. Dans le cas où l'on prend uniquement la période entre première et dernière capture pour étudier la relation entre la condition interne de l'individu et ses décisions, la relation étudiée entre temps depuis l'arrivée et état interne ne repose que sur un temps de séjour partiel et il est donc impossible de l'intégrer dans un modèle théorique de variation temporelle de la condition pendant la halte au sein d'un modèle de CMR. Les nouvelles technologies de radio-tracking miniaturisées pourraient cependant nous aider à définir et calibrer ce genre de modèle de CMR, qui pourrait ensuite être utilisé sur des milliers d'individus (ce que ne permet pas le radio-tracking pour des raisons de coût, Bairlein 2003, Bairlein & Schaub 2009, Robinson *et al.* 2010). En effet, il serait possible de détecter l'arrivée sur site d'un individu déjà équipé et de tenter de le capturer plusieurs fois au cours de sa halte pour évaluer la progression de sa prise de masse et de son engrangement. En répétant cela sur plusieurs individus, des patrons de variation de l'état interne pourraient être décrits et par la suite intégrés dans des modèles de CMR prenant en compte la condition corporelle comme un prédicteur de la décision de départ. Cela permettrait de clarifier la relation entre temps depuis l'arrivée et état interne de l'individu.

Un autre aspect important de l'étude des haltes migratoires concerne les transients. Les transients sont des individus qui n'utilisent pas réellement le site comme site de halte mais qui peuvent être capturés dans les filets pendant un déplacement entre deux zones situées à proximité du site étudié. Ce peut également être des individus qui arrivent sur ce site après un important vol de migration

et se relocalisent très rapidement sur un site aux alentours (Bächler & Schaub 2007, Salewski *et al.* 2007, Mills *et al.* 2011, Taylor *et al.* 2011). Le problème que pose ce type de comportement est que ces individus ne sont pas disponibles pour la capture durant les occasions de capture suivantes (les jours suivants leur arrivée par exemple); ils sont assimilés à des individus qui sont partis. Ce comportement tend à biaiser la probabilité de départ avec les modèles tels qu'ils existent si la question principale porte sur les individus utilisant bel et bien le site pour faire leurs réserves en vue d'un prochain vol. Si les transients sont très nombreux dans le jeu de données, ce qui peut être le cas avec les passereaux en halte migratoire (Mills *et al.* 2011, Taylor *et al.* 2011, Cohen *et al.* 2014, Schmaljohann & Klinner 2020), au-delà du fait de biaiser les estimations de la probabilité de départ, ce sous-échantillon peut poser des problèmes de convergence des modèles d'estimation de paramètres tels que la probabilité de départ. Durant la thèse, j'ai tenté d'utiliser une probabilité d'assignation au statut « résident » ou « transient » à l'intérieur des modèles de CMR. Cependant les modèles ne convergeaient pas. Nous ne sommes donc pas allés plus loin concernant ce point et avons préféré, comme c'est le cas dans la plupart des études, ne considérer que les individus capturés au moins deux fois. Cependant, la probabilité de détection étant généralement faible (inférieure à 0.15, Schaub & Jenni 1999, Schaub *et al.* 2001, Moore *et al.* 2017, Schmaljohann & Eikenaar 2017), des individus capturés une seule fois peuvent très bien être des individus faisant réellement halte sur le site. Pour améliorer les techniques analytiques des décisions en prenant en compte le maximum d'individus, la gestion des transients dans les modèles de CMR étudiant la halte migratoire fait partie des développements nécessaires pour de futures études.

Étant donné qu'il existe des centaines voire des milliers de jeux de données de baguage déjà récoltés à travers le monde, parallèlement au développement des nouvelles technologies pour le suivi de la migration, il est primordial de continuer à adapter au mieux les outils de modélisation pour pouvoir tirer des informations de ces jeux de données parfois récoltés depuis plus de 40 ans. Au-delà de l'avancée des connaissances sur l'écologie de la halte migratoire, cela permettrait aussi d'approfondir les réactions des oiseaux migrants face à l'évolution du climat (Both & te Marvelde 2007, Kirby *et al.* 2008, Chmura *et al.* 2020) et la pression anthropique sur les habitats de halte qui devient de plus en plus importante dans certains secteurs (Mehlman *et al.* 2005, Kirby *et al.* 2008, Moore 2018).

Au-delà du développement des modèles à proprement parler, les analyses de CMR réalisées dans cette thèse requièrent des temps de calculs non négligeables allant de 3 jours à presque un mois.

Même si une partie de la thèse a consisté à optimiser ces modèles, notamment à l'aide de Nimble (de Valpine *et al.* 2017), la dimension « nombre de jours » reste trop importante dans la perspective de développement d'un outil destiné à l'usage de gestionnaires. Il serait donc intéressant d'étudier différentes pistes, notamment si l'on vise l'estimation du temps de halte sans s'intéresser aux covariables qui l'influencent. Différents outils pourraient alors être utilisés pour augmenter significativement la vitesse de calcul. Il y a notamment Template Model Builder (TMB, Kristensen *et al.* 2016a, b) qui pourrait permettre d'optimiser la vitesse de calcul de manière substantielle. TMB est une librairie R où l'on écrit directement le modèle en langage C++, ce qui demande un temps d'apprentissage non négligeable pour qui n'est pas habitué à ce langage. Cet outil a déjà démontré une diminution de la vitesse de calcul très importante notamment pour les modèles de capture-recapture (jusqu'à 6000 fois plus rapide que Jags, un autre programme également accessible par R ; Hornik *et al.* 2003). Cependant il semblerait que, dans la perspective où l'on continuerait d'utiliser le temps depuis l'arrivée comme covariable individuelle, ces outils ne sont pas mobilisables car ils ne formalisent pas explicitement le processus latent non observable qui nous permet de calculer, à chaque occasion, un temps depuis l'arrivée. En résumé, dans une perspective de mise à disposition de ces modèles pour les gestionnaires, TMB apparaît comme une alternative prometteuse. *A contrario*, dans la perspective d'étudier plus finement les déterminants du départ d'un site de halte migratoire, les approches Bayésiennes avec l'utilisation de Nimble restent *a priori* le meilleur compromis entre puissance et flexibilité (de Valpine *et al.* 2017).

6.5 Apports quant à la gestion des sites de halte

Les différents chapitres de cette thèse ont mis en évidence l'aspect prépondérant du temps de halte dans la décision de départ d'un site, et également que ce dernier s'avère généralement plutôt long (environ 10 jours) durant la migration postnuptiale pour les passereaux transsahariens. Ceci indique que les événements météorologiques sont secondaires dans la décision de départ de ces individus. Du point de vue de la gestion d'un site accueillant plusieurs espèces de passereaux migrants, il est donc primordial que le milieu soit assez riche pour accueillir des centaines d'individus sur une période minimum de 10 jours avant la première capture de l'espèce et 10 jours après la dernière capture. La qualité, de même que la quiétude d'un site doivent être considérés sur une période plus large que la simple différence entre première et dernière capture. De plus, les outils statistiques permettant de mesurer la part relative de l'état de l'oiseau *versus* les conditions météorologiques dans la décision de départ d'un site de halte permettraient de classer les sites de halte en

différenciant (i) ceux où les oiseaux font une halte longue et où le temps depuis l'arrivée est déterminant dans la décision de départ *versus* (ii) les sites de halte où le temps de halte est plutôt court et où les conditions météorologiques sont plus déterminantes. Il serait possible de prioriser des efforts de protection sur les sites utilisés par les oiseaux pour refaire leurs réserves.

Partant du point de vue développé dans l'article 4 sur l'utilité du temps de halte estimé comme outil pour la gestion et la conservation, il serait très utile qu'une application de type SHINY (Beeley 2013, Chang *et al.* 2020) soit développée en partenariat avec des gestionnaires et bagueurs pour leur permettre de suivre l'évolution des zones de halte à travers le baguage. Les gestionnaires pourront alors détecter directement des changements sur les zones de halte dont ils s'occupent et avertir sur le fait qu'il faudrait se pencher sur l'état de la population de l'espèce en question. Il faudrait une application informatique qui permettrait à l'utilisateur de charger son jeu de données, qui serait ensuite transformé en histoires de captures, et qui permettrait de choisir entre une analyse « temps minimum de halte » et « temps de halte estimé ». C'est dans ce but que j'ai commencé à développer un squelette d'application (voir Figure 1).

Bien entendu ce début de développement ne constitue qu'une esquisse de ce à quoi pourrait ressembler ce type d'application. Cependant, grâce à cet exemple on peut voir la facilité d'utilisation et le potentiel d'analyses à grande échelle que ce genre d'outil peut apporter. Cela est d'autant plus vrai que ces applications peuvent être directement disponibles sur une page internet dédiée ne demandant pas d'installation spécifique de logiciel. Toutefois, avant d'aller plus loin dans le développement d'applications directement utilisables par les gestionnaires, un temps d'optimisation du modèle sera nécessaire (voir discussion précédente sur l'optimisation du temps de calcul) pour que le temps d'analyse d'un jeu de données contenant entre 100 et 1000 individus sur un minimum de 15 jours puisse prendre moins d'une heure de calcul. Si une telle application était disponible pour que les gestionnaires et bagueurs puissent analyser directement leurs jeux de données de baguage, il faudrait aussi l'étendre pour calculer certaines métriques synthétiques liées à la migration, telles que les dates des pics de captures au cours du temps, ou encore de la date moyenne où 50% des captures saisonnières ont été réalisées. L'application pourrait donc ne pas se limiter à l'estimation du temps de halte et permettrait plus globalement de réaliser des analyses sur les jeux de données issues des protocoles liés à l'étude de la halte migratoire ou plus largement à la phénologie de la migration. Pour que ce genre d'outil soit à la fois utile aux gestionnaires et aux scientifiques, il conviendrait de réaliser des enquêtes sur les besoins spécifiques de chacun. Ce type

d'outil pouvant facilement permettre des analyses à large échelle, il constitue probablement l'avenir de l'étude de la migration à travers les données de baguage, parallèlement à l'avènement des technologies de tracking individuel qui permettront, elles, de mieux connaître les mouvements des oiseaux sur un site de halte et de prendre en compte l'ensemble du territoire utilisé par un oiseau en halte (Buler *et al.* 2007, Mills *et al.* 2011, Taylor *et al.* 2011, Cohen *et al.* 2014, Bayly *et al.* 2019).

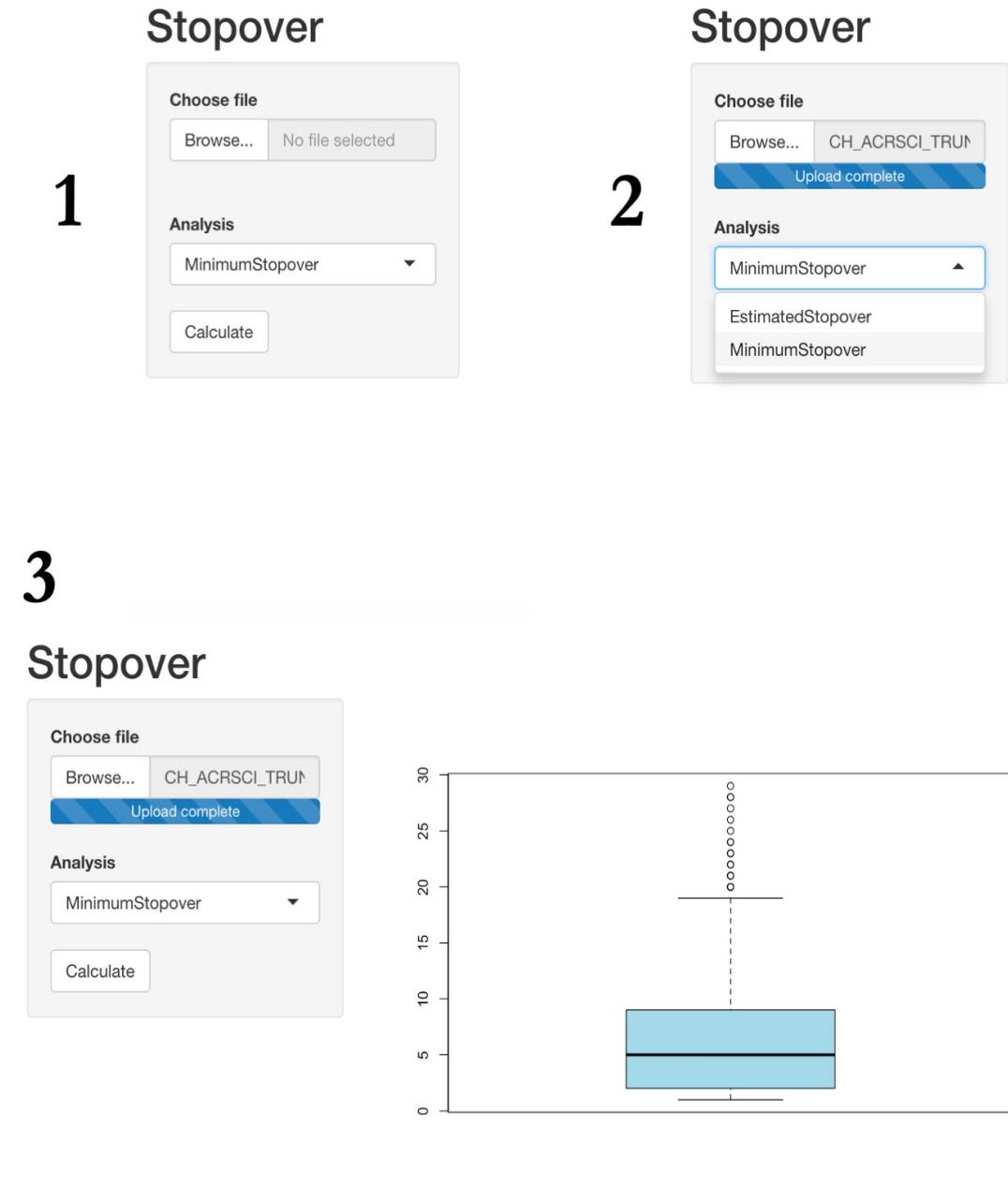


Figure 13 : Exemple d'un squelette d'application SHINY pour estimer le temps de halte à partir de jeux de données de baguage d'oiseaux.

6.6 Possible futur de l'étude de la halte migratoire ?

Cette thèse aura permis d'étudier certains aspects de l'écologie de la halte migratoire en utilisant des techniques analytiques conçues pour tenir compte du fait qu'un individu n'est pas nécessairement contacté sur un site alors qu'il y est présent, et de montrer que la valorisation des jeux de données de baguage déjà existants peut encore apporter des connaissances établies en utilisant de grands échantillons, chose que l'engouement actuel pour les technologies de tracking individuel ne peut encore faire. Elle aura aussi permis de profiler les applications possibles de techniques analytiques récentes en termes de gestion et de suivi à long terme.

On pourrait envisager deux grandes tendances pour les années à venir dans les études sur la halte migratoire. D'un côté la miniaturisation des outils de tracking individuel vont permettre de préciser les décisions de départ et l'utilisation spatiale d'un site de halte au niveau individuel. De l'autre, la continuité des suivis par baguage va permettre de constituer des jeux de données permettant de documenter de manière plus fiable les changements de comportements lors de la halte migratoire à des échelles de temps plus larges, un enjeu important face aux changements globaux. Ceci permettra de suivre les variations de comportement des oiseaux lors d'une halte migratoire et plus largement de suivre l'état des populations d'oiseaux migrants à long terme. Les outils de modélisation permettront aussi de faire des prédictions concernant les réactions de ces oiseaux face aux différentes changements et pressions, et ainsi de réaliser des préconisations de gestion de sites ou de populations dans le but de prévenir d'éventuelles chutes des effectifs. Ceci nécessite le développement d'outils accessibles à la fois aux gestionnaires, aux bagueurs et aux scientifiques.

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7 Annexes

7.1 Annexes de l'Article 1

Supplementary Material

When to depart from a stopover site? Time-since-arrival matters more than weather conditions

7.1.1 CORRELATION BETWEEN WEATHER COVARIATES

Table 1 : Pearson correlation coefficient between weather covariates (the * indicates the level of significance respectively <0.05, <0.01, <0.001)

	Wind	Temperature	Humidity	Cloudcover	Δ Pressure
Wind		-0.245***	0.239***	0.138**	0.41***
Temperature			-0.122*	0	-0.07
Humidity				0.390***	0.06
Cloudcover					-0.08
Δ Pressure					

7.1.2 SUMMARY OF WEATHER COVARIATES

Table 2 : Summary of the weather covariates during the study period

	Mean	Standard deviation
Wind Speed	5.4 m.s ⁻¹	2.6
Temperature	17.7°C	1.65

Humidity	84.2%	7.16
Cloudcover	3.98	2.75
Pressure	1015.06 Hpa	5.52

7.1.3 JAGS CODE

Computation time on our dataset with 5610 individuals (683 adults and 4927 juveniles) and 30 capture occasions: 23 days with 60 000 iterations and 2 chains

```

model {

# Priors and constraints

a~dnorm(0,0.01) #intercept

b~dnorm(0,0.01) #TSA

c~dnorm(0,0.01) #wind

e~dnorm(0,0.01) #cloudcover

f~dnorm(0,0.01) #humidity

j~dnorm(0,0.01) #Deltapressure1

celsius~dnorm(0,0.01) #Temperature

#prior on age effect

for (age in 1:2){

age_effect[age]~dnorm(0,tau_age)

}

tau_age<- 1 / (sd_age*sd_age)
}
```

```

sd_age~dunif(0, 2)

#prior year effect

for (a in 1:20){

year_effectdep[a]~dnorm(0,tau_dep)

}#a

tau_dep<- 1 / (sd_dep*sd_dep) #Hyperparameter

sd_dep~dunif(0, 2)

# prior recapture probability, 1.5 relies to a mean value of recapture probability for this #dataset
#(previous analyses)

logit_pm~dnorm(-1.5,0.01)

tau_p<- 1 / (sd_p*sd_p)

sd_p~dunif(0, 2)

for ( a in 1:20){

for (t in 1:n.occasions) {

logit(p[a,t])<- l_p[a,t]

l_p[a,t]~dnorm(logit_pm, tau_p)

}#t

}#a

```

```
# prior for entry probs 20=number of years
```

```
for( a in 1:20){
```

```
  for (t in 1:(n.occasions)) {
```

```
    eta[a,t]~dunif(0,1)
```

```
  }#t
```

```
}#a
```

```
# Likelihood
```

```
for (i in 1:M) {
```

```
# First occasion
```

```
z[i,1] ~ dbern(eta[group[i],1])
```

```
zstop[i,1]<- z[i,1]
```

```
prod1mz[i,1]<- 1
```

```
# Observation process
```

```
mup[i,1] <- z[i,1] * p[group[i],1] * visit[group[i],1]
```

```
y[i,1] ~ dbern(mup[i,1])
```

```
# Subsequent occasions
```

```
for (t in 2:n.occasions) {
```

```
# State process
```

```

zstop[i,t]<-zstop[i,t-1]+z[i,t] #update TSA

prod1mz[i,t]<-prod1mz[i,t-1]*(1-z[i,t-1])

logit(phi[i,t-1])<-a+b*zstop[i,t-1]+c*wind[group[i],t-1]+e*cloudcover[group[i],t-
1]+f*humidity[group[i],t-1]+j*delta1[group[i],t-1]+celsius*temp[group[i],t-
1]+age_effect[ages[i]]+year_effectdep[group[i]]

```

```

mu[i,t] <- phi[i,t-1] * z[i,t-1] + eta[group[i],t] * prod1mz[i,t]

z[i,t] ~ dbern(mu[i,t])

```

Observation process

```

mup[i,t] <- z[i,t] * p[group[i],t] * visit[group[i],t]

y[i,t] ~ dbern(mup[i,t])

```

} # t

} # i

stopover duration

```

for (i in 1:M) {

  stop[i] <- sum(z[i,1:n.occasions])}

  zes <- mean(stop[])
}

}

```


7.2 Annexes de l'Article 2

More Than Just Refuelling: Lengthy Stopover and Selection of Departure Weather by Sandpipers Prior to Transoceanic and Transcontinental Flights

Supporting information

7.2.1 Appendix S1. Details about environmental covariates and Principal Component Analysis

Table S1: Mean and standard deviation of the weather variables at both sites.

Wind = 24 hour change in the surface tailwind vector, see methods.

	KENT ISLAND	SIBLEY LAKE
CLOUDCOVER	4.4 ± 3.3	6.0 ± 3.1
WIND	0.54 ± 7.1	0.3 ± 6.4
HUMIDITY	47.8 ± 14.9	73.9 ± 17.2
TEMPERATURE	22.7 ± 5.6	17.2 ± 3.8
PC1	-0.8 ± 1.3	0.8 ± 1.1
PC2	-0.16 ± 1.2	0.2 ± 0.9
NDAYS	74	75

Table S2: Pearson correlation coefficients of weather variables at Kent Island (Upper part of the table) and Sibley Lake (lower part of the table). The *** indicate the level of significance, respectively <0.05, <0.01, <0.001.

	CLOUDCOVER	WIND	HUMIDITY	TEMPERATURE
CLOUDCOVER		-0.19	0.54***	-0 .30**
WIND	-0.43**		0.02	-0.27*
HUMIDITY	0.36***	0.26*		-0 .64***
TEMPERATURE	-0 .47***	0.04	-0 .39***	

Table S3: Correlations between weather covariates and Principle Components. Eigenvalues and % of variance of PC axes are also displayed.

	PC 1	PC 2	PC 3	PC 4
CLOUDCOVER	0.77	-0.32	0.54	0.05
WIND	-0.20	0 .92	0.27	0.14
HUMIDITY	0.87	0.12	-0.31	0.34
TEMPERATURE	-0.82	-0.40	0.10	0.38
EIGENVALUE	2.08	1.14	0.49	0.29
% OF VARIANCE	51.99	28.61	12.19	7.21

CUMULATIVE % OF VARIANCE	51.99	80.60	92.79	100.00
---	-------	-------	-------	--------

7.2.2 Appendix S2. JAGS code of the statistical model used in our study

```

model {
  # Priors and constraints
  a~dnorm(0,0.1)
  b[1]~dnorm(-1,0.1)T(0) #adult
  b[2]~dnorm(-1,0.1)T(0) #juv
  beta1~dnorm(0,0.1)
  beta2~dnorm(0,0.1)

  # prior capture probability
  logit_pm~dnorm(-1.2,0.1) # env p 0.3
  tau_p<- 1 / (sd_p*sd_p) #Hyperparameter 2
  sd_p~dunif(0, 2)

  for (t in 1:n.occasions) {
    logit(p[t])<- l_p[t]
    l_p[t]~dnorm(logit_pm, tau_p)
  }

  # prior visual recapture psight
  logit_psight~dnorm(-1.2,0.1) # env p 0.3
  tau_psight<- 1 / (sd_psight*sd_psight) #Hyperparameter 2
  sd_psight~dunif(0, 2)

  for (t in 1:n.occasions) {
    logit(psight[t])<- l_psight[t]
    l_psight[t]~dnorm(logit_psight, tau_psight)
  }

  # prior for entry probs

  for (t in 1:(n.occasions)) {
    for (a in 1:2){
      eta[t,a]~dunif(0,1)
      } #a age
    } # t
  }
}

```

```

# Likelihood
for (i in 1:M) {

  # First occasion
  z[i,1] ~ dbern(eta[1], age[i])
  zstop[i,1]<- z[i,1]
  prod1mz[i,1]<- 1

  # Observation process
  theta[i,1,2] <- z[i,1] * p[1]
  theta[i,1,1]<-1-theta[i,1,2]
  theta[i,1,3]<-0
  theta[i,1,4]<-0

  y[i,1] ~ dcat(theta[i,1,])

  # Subsequent occasions
  for (t in 2:n.occasions) {
    # State process

    zstop[i,t]<-zstop[i,t-1]+z[i,t]
    prod1mz[i,t]<-prod1mz[i,t-1]*(1-z[i,t-1])

    logit(phi[i,t-1])<-a+b[age[i]]*zstop[i,t-1]+beta1*PCA1[t-1,1]+beta2*PCA2[t-1,1]

    mu[i,t] <- phi[i,t-1] * z[i,t-1] + eta[t, age[i]] * prod1mz[i,t]
    z[i,t] ~ dbern(mu[i,t])

    # Observation process
    theta[i,t,1]<-1-theta[i,t,2]-theta[i,t,3]+theta[i,t,4]
    theta[i,t,2]<-p[t]*(1-psight[t]*tagged[i,t])*z[i,t]
    theta[i,t,3]<-psight[t]*tagged[i,t]*(1-p[t])*z[i,t]
    theta[i,t,4]<-p[t]*psight[t]*tagged[i,t]*z[i,t]

    y[i,t] ~ dcat(theta[i,t,])
    #y[i,t]<-Y[i,t]-1
  } # t
} # i

# stopover duration
for (i in 1:M) {
  stop[i] <- sum(z[i,1:n.occasions])
}

```

7.3 Annexes de l'article 3

Supporting Information

7.3.1 Principal component analyses of the weather variables

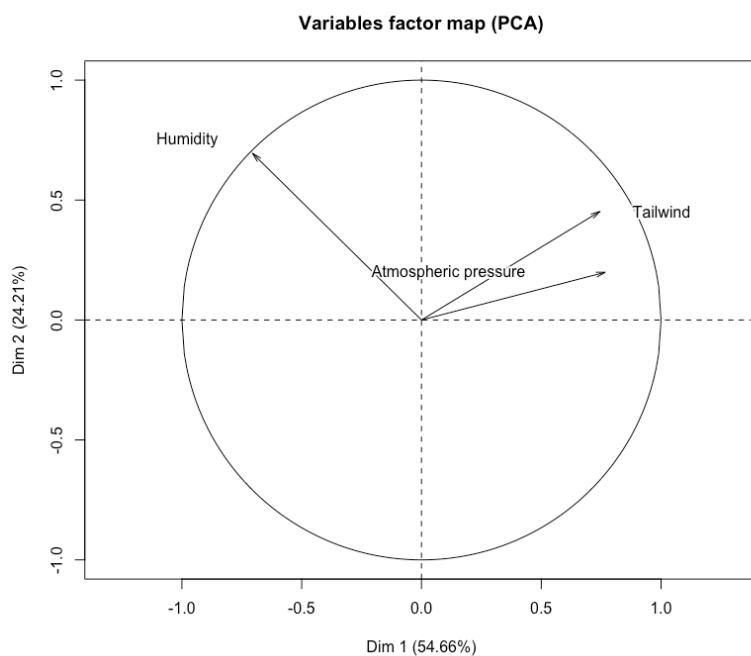


Figure 1 : Principal component analysis of the weather variables at the Donges ringing station

Table 1 : Percentage of Contribution of each weather covariate to each axe.

	DIMENSION 1	DIMENSION 2
HUMIDITY	30.3	66.4
PRESSURE	35.9	5.44
TAILWIND	33.8	28.17

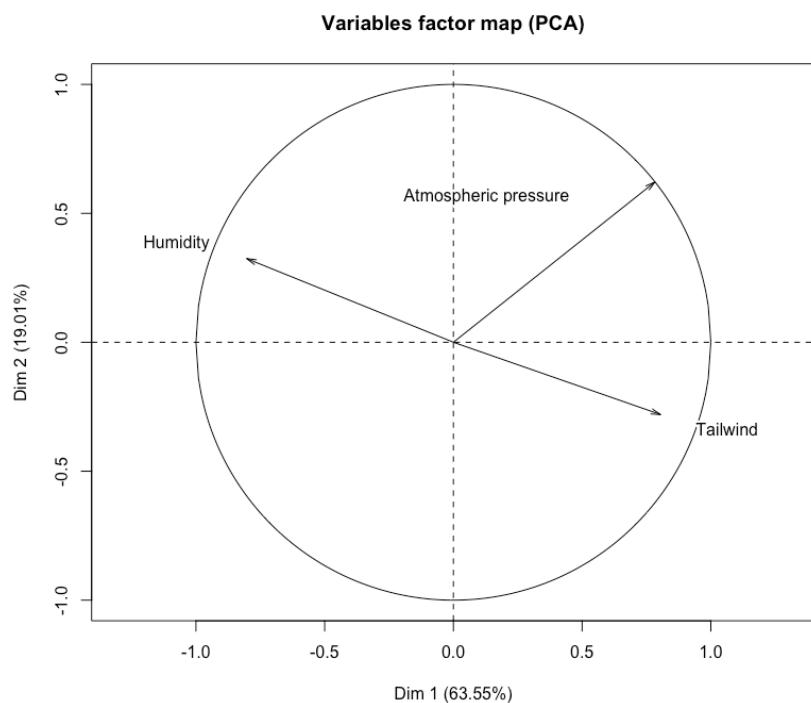


Figure 2 : Principal component analysis of the weather variables at the île du Massereau ringing station

Table 2 : Percentage of Contribution of each weather covariate to each axe.

	DIMENSION 1	DIMENSION 2
HUMIDITY	33.8	18.5
PRESSURE	32.2	67.7
TAILWIND	34.0	13.8

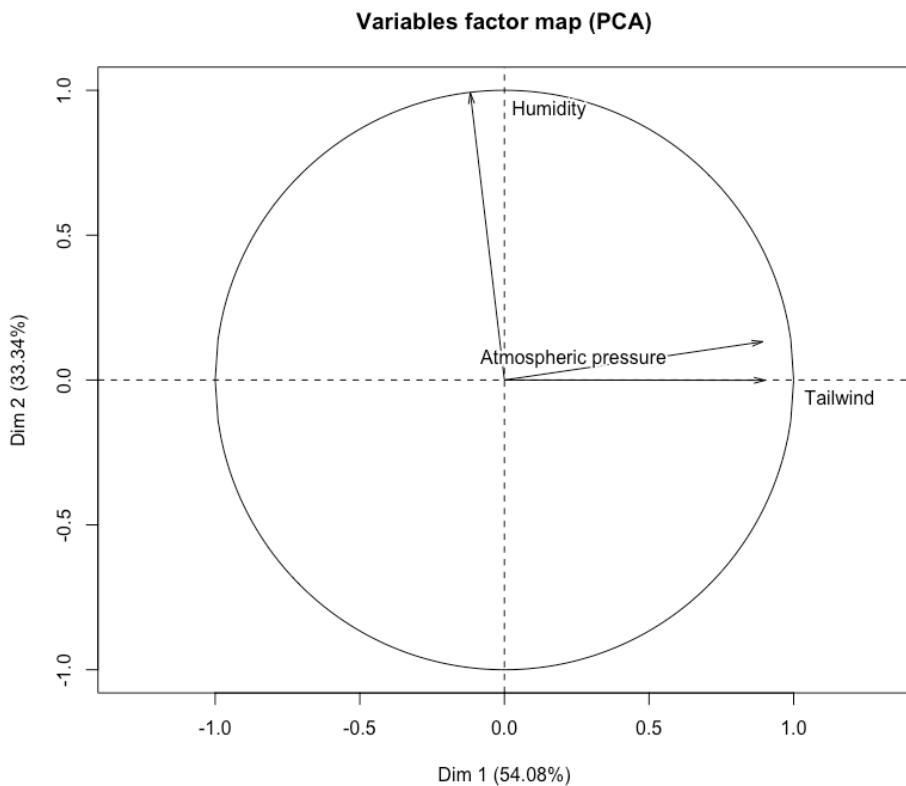
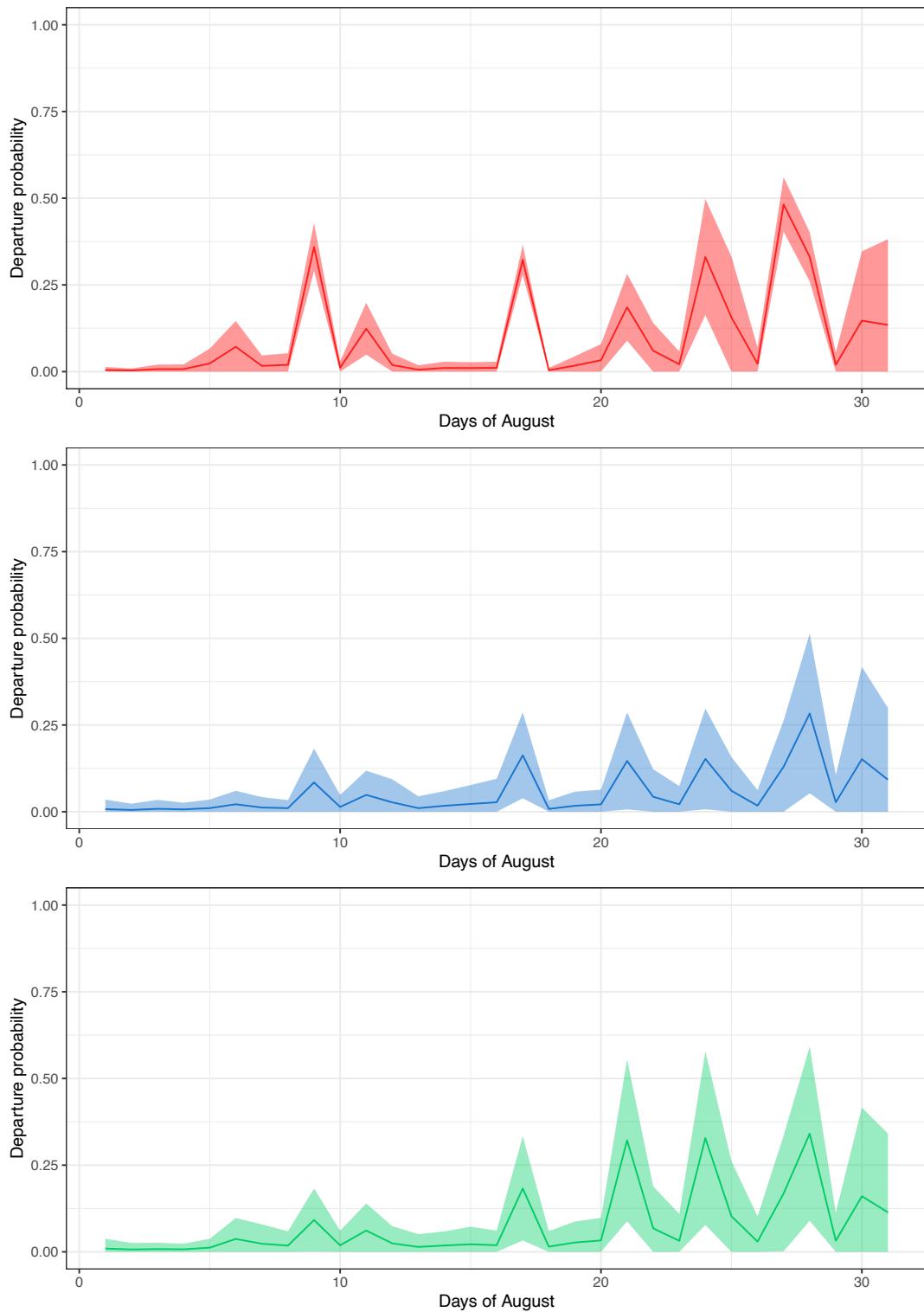


Figure 3: Principal component analysis of the weather variables at the Saint-Vigor-d'Ymonville ringing station

Table 3: Contribution of each weather covariate to each axe (%).

	DIMENSION 1	DIMENSION 2
HUMIDITY	0.9	98.2
PRESSURE	48.1	1.7
TAILWIND	50.0	0.1

7.3.2 Example of synchronized Departure probabilities at the Donges ringing station in 2011



7.3.3 Nimble and R code to run the model

Nimble code for multi-species capture-recapture model incorporating a synchrony index in departure probability

```
library(nimble)

## Load capture histories

load('CH_ACRSCH_DONGES9_14')
load('CH_ACRSCI_DONGES9_14')
load('CH_LUSSVE_DONGES9_14')

# Load year vectors

load('year_ACRSCH_DONGES9_14')
load('year_ACRSCI_DONGES9_14')
load('year_LUSSVE_DONGES9_14')

## Nimble code

code <- nimbleCode({
```

Priors for sd and sd2

```
sd.d ~ dunif(0, 10)
```

```

sigma2.d <- sd.d^2

for (esp in 1:3){

  sd.eSp[esp] ~ dunif(0, 10)

  sigma2.eSp[esp] <- sd.eSp[esp]^2

}

## intercept and TSA slope per species

for(esp in 1:3) {

  b[esp]~ dnorm(0, 0.1)

  for (yrs in 1:6){

    a[yrs,esp] ~ dnorm(0, 0.1)

  }

}

## Priors for phi.est, eta , time and species specific random terms

for (yrs in 1:(nbyears)) {

  for(t in 1:(n.occasions)) {

    delta[yrs,t] ~ dnorm(0, sd = sd.d)

    ## Species-specific random effect terms

    for(esp in 1:3) {

      p[yrs,t,esp] ~ dunif(0, 1)

      eta[yrs,t,esp] ~ dunif(0, 1)

      epsilon[yrs,t,esp] ~ dnorm(0, sd = sd.eSp[esp])

    }

  }

}

```

```

for (i in 1:M) {

  for (t in 1:n.occasions){

    logit(phi.est[i,t]) <- a[year[i],sp[i]] + b[sp[i]]*TSA[i,t]+ delta[
year[i],t] + epsilon[year[i],t,sp[i]]

  }

}

## Likelihood

for(i in 1:M) {

  ## First occasion

  z[i,1] ~ dbern(eta[year[i],1,sp[i]])

  prod1mz[i,1] <- 1

  TSA[i,1] <- z[i,1]

  ## Observation process

  mup[i,1] <- z[i,1] * p[year[i],1,sp[i]]

  y[i,1] ~ dbern(mup[i,1])

  ## Subsequent occasions

  for (t in 2:n.occasions) {

    ## State process

    prod1mz[i,t] <- prod1mz[i,t-1] * (1 - z[i,t-1])

    TSA[i,t] <- TSA[i,t-1]+z[i,t]

    mu[i,t] <- phi.est[i,t-1] * z[i,t-1] + eta[year[i],t,sp[i]] * prod1m

    z[i,t]

    z[i,t] ~ dbern(mu[i,t])

    ## Observation process
}

```

```

mup[i,t] <- z[i,t] * p[year[i],t,sp[i]]

y[i,t] ~ dbern(mup[i,t])

}

}

## stopover duration

for (i in 1:M) {

stp[i] <- sum(z[i,1:n.occasions])

}

zes <- mean(stp[1:M])

})


```

```

known_state_ch <- function(ch) {

state <- ch

for (i in 1:dim(ch)[1]){

if(sum(ch[i,])!=0){

n1 <- min(which(ch[i,]==1))

n2 <- max(which(ch[i,]==1))

state[i,n1:n2] <- 1

}

}

state[state==0] <- 0

return(state)

```

```

}

# bind capture histories and year vectors

lCH <- rbind(CH_ACRSCH_DONGES9_14, CH_ACRSCI_DONGES9_14, CH_LUSSVE_DONGES9_14)

lyear<-c(year_ACRSCH_DONGES9_14,year_ACRSCI_DONGES9_14,year_LUSSVE_DONGES9_14 )

sp <- c(rep(1, dim(CH_ACRSCH_DONGES9_14)[1]),
       rep(2, dim(CH_ACRSCI_DONGES9_14)[1]),
       rep(3, dim(CH_LUSSVE_DONGES9_14)[1]))

M <- dim(lCH)[1]
n.occasions <- dim(lCH)[2]
z.init <- known_state_ch(lCH)

constants <- list(M = M, n.occasions = n.occasions, sp = sp, year=lyear, nbyears=length(unique(lyear)))

data <- list(y = lCH)

inits <- list(sd.d = 1,
               a = matrix(1,6,3),
               b = rep(1,3),

```

```

sd.eSp = rep(1,3),
delta = matrix(0,length(unique(lyear)),n.occasions),
p = array(0.5, c(length(unique(lyear)),n.occasions,3)),
eta = array(0.5, c(length(unique(lyear)),n.occasions,3)),
epsilon = array(0, c(length(unique(lyear)),n.occasions,3)),
z = z.init)

Rmodel <- nimbleModel(code, constants, data, inits)
Rmodel$calculate()

params <- c('sd.d', 'a','b', 'sd.eSp', 'zes')

conf <- configureMCMC(Rmodel, monitors = params)

Rmcmc <- buildMCMC(conf)

Cmodel <- compileNimble(Rmodel)
Cmcmc <- compileNimble(Rmcmc, project = Rmodel)

if(FALSE) {
  compiledList <- compileNimble(list(model=Rmodel, mcmc=Rmcmc))

  Cmodel <- compiledList$model; Cmcmc <- compiledList$mcmc
}

```

```
ni <- 300000  
nt <- 1  
nb <- 200000  
nc <- 1  
  
set.seed(0)  
  
system.time(samples <- runMCMC(Cmcmc, niter = ni, thin = nt, nburnin = nb,  
nchains = nc))
```


7.4 Annexes Article 4

R and JAGS code to run a model estimating stopover duration (ESD)

First, we will load the packages (R2jags), set the working directory and load the capture histories (CH)

```
library('R2jags')
setwd("~/Documents/Thèse/Gestion/")
load("CH")
```

Now, let's write the model into a text file to provide it to JAGS for the analysis. The txt file of the model will be saved in the previously set working directory.

```
sink("model_stopover.txt")
cat("model {
## Priors

#prior for recapture probability and remaining probability

for (i in 1:nind){

for (t in 1:n.occasions){

logit(phi[i,t])<-mean.phi
p[i,t]<-mean.p

}#t

}#i


mean.p~dunif(0,1) #mean recapture probability
mean.phi~dnorm(0,0.01) #mean remaining probabiliy


# prior for entry probabilities

for (t in 1:n.occasions){
```

```

eta[t]~dunif(0,1)

}

## Likelihood

for (i in 1:nind) {

# First occasion

z[i,1] ~ dbern(eta[1])

prod1mz[i,1]<- 1

# Observation process

mu1[i,1] <- z[i,1] * p[i,1]

y[i,1] ~ dbern(mu1[i,1])


# Subsequent occasions

for (t in 2:n.occasions) {

# State process

prod1mz[i,t]<-prod1mz[i,t-1]*(1-z[i,t-1])

mu2[i,t] <- phi[i,t-1] * z[i,t-1] + eta[t] * prod1mz[i,t]

z[i,t] ~ dbern(mu2[i,t])


# Observation process

mu1[i,t] <- z[i,t] * p[i,t-1]

y[i,t] ~ dbern(mu1[i,t])
}

```

```

} # t

} # i

##Derived parameters

# stopover duration computed from the sum of the true states z

for (i in 1:nind) {

stop[i] <- sum(z[i,1:n.occasions])

}

zes <- mean(stop[])

}

", fill=TRUE)

sink()

```

The model is thus written. Now we need to set the data and the initial values to provide to JAGS. To help the model to converge we can give it the true states of the individual that we can deduce from the capture history (fill z with 1 between first and last capture) using the known.state.ch function (Kery & Schaub 2011)

```

known.state.ch <- function(ch){

state <- ch

for (i in 1:dim(ch)[1]){

if(sum(ch[i,])!=0){

n1 <- min(which(ch[i,]==1))

n2 <- max(which(ch[i,]==1))

state[i,n1:n2] <- 1

}

```

```

    }

state[state==0] <- NA

return(state)

}

```

Now we create the data file

```
jags.data <- list(y = CH, nind= dim(CH)[1], n.occasions = dim(CH)[2], z=k
nown.state.ch(CH))
```

Now we will give initial values to z for the model using the function ch.init.z. (Kery & Schaub 2011)

```
ch.init.z <- function(ch){

  for (i in 1:dim(ch)[1]){

    if(sum(ch[i,]!=0)){

      n1 <- min(which(ch[i,]==1))

      n2 <- max(which(ch[i,]==1))

      ch[i,n1:n2] <- NA

    } #else {ch[i,dim(CH)[2]]=1}

  }

  return(ch)
}

inits <- function(){list(z=ch.init.z(CH)) }
```

Now we set that we want to monitor the stopover duration called zes in our model. Also we set the number of iterations, number of chains and the burn-in.

```
parameters <- c("zes")
```

```
# MCMC settings
```

```
ni <- 15000
```

```
nt <- 3
```

```
nb <- 7500
```

```
nc <- 2
```

Now let's run the model previously created with the associated data files.

```
stopover <- jags(jags.data, inits, parameters, "model_stopover.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb)

## module glm loaded

## Compiling model graph

## Resolving undeclared variables

## Allocating nodes

## Graph information:

## Observed stochastic nodes: 9365

## Unobserved stochastic nodes: 6672

## Total graph size: 58455

##

## Initializing model
```

In Bayesian analyses it is important to check the chain mixing the Rhat value to be sure of the good convergence of the model parameters (Rhat need to be less than 1.2).

This first command will show a summary of the estimated parameters with the mean value, the standard deviation, credible intervals and Rhat.

```
stopover
```

```

## Inference for Bugs model at "model_stopover.jags", fit using jags,
## 2 chains, each with 15000 iterations (first 7500 discarded), n.thin =
3

## n.sims = 5000 iterations saved

##          mu.vect sd.vect    2.5%    25%    50%    75%   97.5%
## zes        3.971  0.127  3.740  3.882  3.966  4.054  4.240
## deviance 4115.982 49.143 4020.814 4082.206 4115.694 4148.119 4210.413

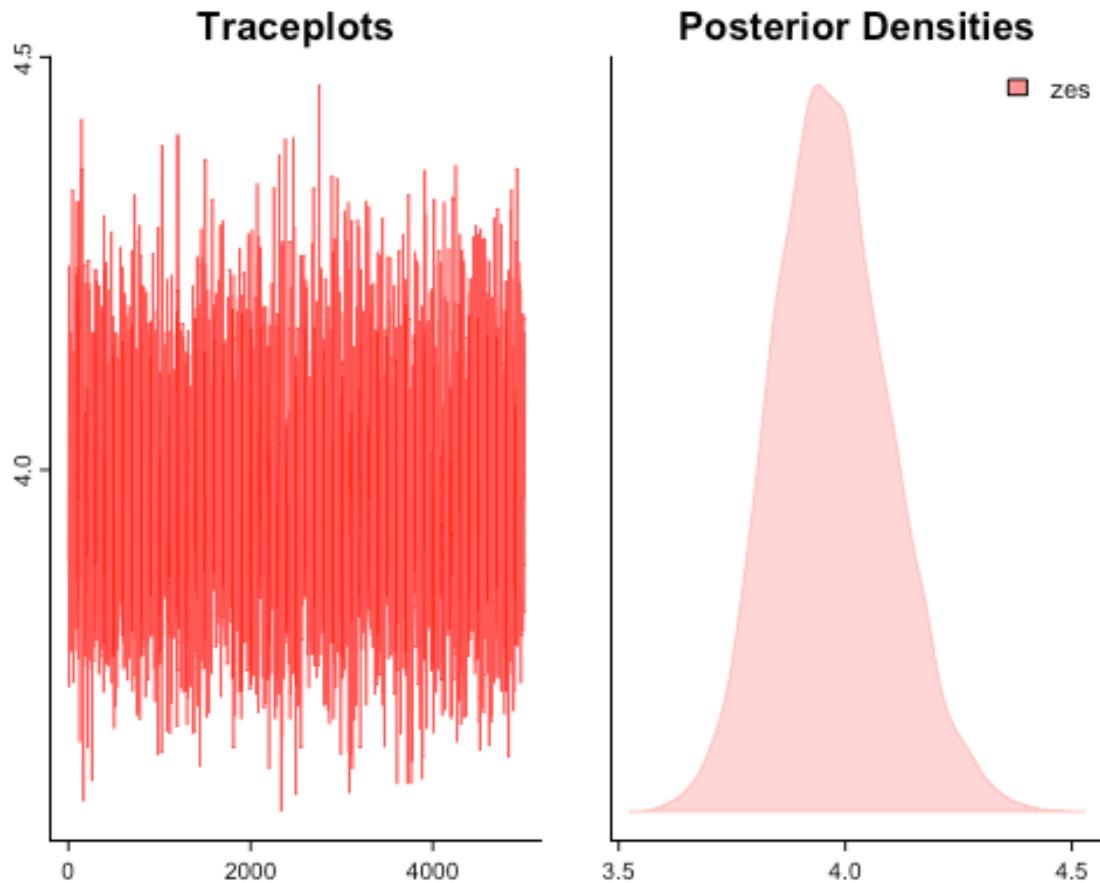
##          Rhat n.eff
## zes        1.007   310
## deviance 1.003   840

##
## For each parameter, n.eff is a crude measure of effective sample size,
## and Rhat is the potential scale reduction factor (at convergence, Rhat=
1).

##
## DIC info (using the rule, pD = var(deviance)/2)
## pD = 1206.3 and DIC = 5322.3
## DIC is an estimate of expected predictive error (lower deviance is bett
er).

```

Then let's plot chain mixing and posterior distributions.



The chain mixing is good and fast (see Kery and Schaub 2011 for more information). The estimation of stopover duration is around 3.9 days. Let's compare this value to the minimum stopover duration (MSD) computable from the capture histories.

```
min_stopover=NULL

for (i in 1:dim(CH)[1]){
  first=min(which(CH[i,]==1))
  last=max(which(CH[i,]==1))
  min_stopover[i]=(last+1)-first
}
mean(min_stopover)

## [1] 2.537453
```

The estimated stopover duration is here more than 1 day longer than the minimum stopover duration.

References

- Kéry, M., & Schaub, M. (2011).** Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.
- Lyons, J. E., Kendall, W. L., Royle, J. A., Converse, S. J., Andres, B. A., & Buchanan, J. B. (2016).** Population size and stopover duration estimation using mark–resight data and Bayesian analysis of a superpopulation model. *Biometrics*, 72(1), 262-271.

7.5 Chapitre 12 du livre: Demographic Methods Across the Tree of Life

Chapter 12 Survival Analyses

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Abstract

Survival analyses are a key tool for demographers, ecologists and evolutionary biologists. In this chapter, we present the most common methods for conducting survival analyses and illustrate their use for species across the tree of life. We discuss the challenges associated with various types of survival data, and methods to model species with complex life cycle and include the impact of environmental factors and individual heterogeneity. We cover the analysis of ‘known-fate’ data collected in lab conditions, using the Kaplan-Meier estimator and Cox’s proportional hazard regression analysis. Alternatively, survival data collected on free-ranging populations usually involve individuals missing at certain monitoring occasions, and unknown time at death. We provide an overview of capture-mark-recapture (CMR) models, from single-state to multi-state and multi-event models, and of their use in animal and plant demography to estimate demographic parameters (including survival, access to reproduction, dispersal) while correcting for imperfect detection of individuals. We discuss various inference frameworks available to implement CMR models using a frequentist or Bayesian approach. Only humans are an exception among free-ranging populations, with the existence of several consequent databases with perfect knowledge of age and cause of death for all individuals. We present a brief overview of the most common models used to describe mortality patterns over age and time on human mortality data. Throughout the chapter, the focus is placed on seven case studies, which involve lab organisms, free-ranging birds, reptiles and plant populations, and human populations. Each example includes data and codes, together with step-by-step guidance to run the survival analysis.

Keywords (5-10):

tardigrade, sex uncertainty, tag loss, stopover decision, *Cypripedium parviflorum*, mortality models, Bayesian Survival Trajectory Analysis, JAGS, e-surge, marked.

Introduction

Fitness differences among individuals are the bedrock of ecological and evolutionary dynamics (Stearns 1992). Survival is without doubt one major component of fitness, which makes of survival analyses a key tool for demographers, ecologists and evolutionary biologists (Metcalf and Pavard 2007).

Assessing survival is not always an easy task. This is because individuals die only once in a lifetime, therefore precluding repeated measurements on the same individual, and death is rarely directly observed. However, a diversity of monitoring techniques exists to gather survival data for species across the tree of life, from short-living lab organisms, plants exhibiting dormancy, to long-living and elusive wild vertebrates (see chapter 4 and chapter 5). Each monitoring technique leading to a peculiar type of survival data, a plethora of methods exist to estimate survival, from simple non-parametric estimators, to more or less complex semi-parametric and fully parametric models fitted in a continuous or in a discrete manner (reviewed in e.g. Wienke 2010, Miller 2011, Klein et al. 2016, Canudas-Romo et al. 2018, Cox 2018). The choice of method is guided by the type of survival data (e.g. collecting age at death or monitoring live individuals with perfect or imperfect detection), the species life-history (e.g. single or numerous stages or ages) and the environment it experiences (e.g. controlled conditions versus variable environments).

The aim of this chapter is not to provide another extensive review of the existing techniques for survival analyses, but rather to illustrate and contrast the most commonly used methods to estimate survival across the tree of life. The focus is placed on eight case studies of survival analyses in lab organisms, free-ranging animal and plant populations and in human populations. While it is relatively straightforward to gather survival data and assess survival using simple models under controlled lab conditions (Klein 2016; see section 2), monitoring survival in free-ranging populations often require more sophisticated capture-mark-recapture (CMR) techniques to deal with imperfect detection of individuals (Williams et al. 2002, see section 3). Indeed, survival data are often ‘incomplete’ in free-ranging populations, timing and cause of death can be hard to assess,

and multiple environmental factors are at play in influencing survival (see section 3, see also chapters 4, 5 and 6). Humans are an exception, with the existence of several consequent databases with perfect knowledge of age and cause of death for several human populations, such as the Human Mortality Database (2019). A great diversity of mortality models has been developed specifically to analyse age at death data in human demography (e.g. Canudas-Romo et al. 2018, see section 4).

1. What is survival analysis and why do we need it?

1.1. Time matters

Survival analysis is used to analyze the time up to a specific event is going to occur. The event is generally death, but can be of another kind (e.g. reproduction, migration, or exposure to a pathogen). Survival data usually involve following a set of individuals over a specific period of time and recording the time of occurrence of the event of interest.

1.2. Censoring and missing data

By nature, survival data have some particularities: survival cannot take a negative value, survival data are often censored, and missing data are frequent. Right censoring occurs when an individual remains alive after the end of the study or drops out of the study, e.g. due to permanent emigration (Klein et al. 2006). Left-censoring occurs when we cannot observe the time when the event occurred, e.g. an individual was already exposed to a pathogen before the study started (Klein et al. 2006). Other types of missing data are common, because individuals cannot always be observed at all occasions (see chapter 3 and section 3). We need survival analyses to avoid introducing bias, because ordinary linear regression cannot effectively handle the censoring of observations and missing data (but see section 3).

1.3. Known fate data versus imperfect detection

In presence of data referred to as ‘know-fate’ data, survival can be modelled in a continuous manner using continuous distributions (e.g. Gompertz, Weibull, Makeham, Siler). The survival function

$S(t)$ is the probability that an individual survives up to a certain time t . The hazard function $h(t)$ represents the instantaneous event rate for an individual who has already survived to time t . Both functions are related, the hazard relates to the death rate, while survival reflects its cumulative non-occurrence. One might choose to model survival when the data involve counts of individuals alive at different points in time while mortality models can be preferred to model age at death data.

Alternatively, CMR models are used to estimate survival when the data involve individuals missing at certain monitoring occasions, and unknown time at death (Lebreton et al. 1992, see chapter 5). CMR models involve estimating survival probability in between consecutive occasions as a function of a set of covariates, while accounting for the imperfect detection of individuals at each occasion (e.g. a marked individual might be present in the study area at a given occasion, but missed). Fully parametric or semi-parametric approaches are available to model survival, transition, or detection in CMR models (examples in section 3).

In both cases, survival or mortality can be modelled using a non-parametric (see example in section 2), semi-parametric (see example in section 4) or fully parametric model (see examples in section 3 and 4).

2. Survival analyses in the lab: when it's (almost) all under control

2.1. Monitoring survival in the lab

In the lab, gathering survival data usually involve counting the number of individuals alive at different times or simply collecting the exact time at death. Collecting survival data is generally easier than in the wild because individuals are available for monitoring at all times during the study, and the influence of external variables is limited and often controlled. A common objective is to analyse differences in survival functions between groups of individuals that present different characteristics, e.g. various genotypes; groups of individuals exposed to various treatments; age, sex, and life history differences

2.2. Kaplan-Meier estimator and log-rank tests

Laboratory experiments generate data sometimes referred to as ‘known fate’ data, in which the probability of detection is 1 and thus does not need to be accounted for when estimating survival. The survival function $S(t)$, is usually estimated using the non-parametric Kaplan-Meier (KM) estimator (Kaplan and Meier 1958). For each time interval, it is calculated as the number of individuals surviving divided by the number of individuals at risk. Censored individuals who have dropped out of the study are not counted in the denominator. The cumulative survival probability is calculated by multiplying probabilities of surviving from one interval to the next. A plot of the KM survival probability against time provides a useful summary that can be used to estimate parameters such as median survival time. The smaller the time intervals, the smoother the survival curve.

Graphically, a vertical gap between the survival curves of different groups means that at a specific time point, one group has a greater fraction of individuals surviving while a horizontal gap means that it took longer for one group to experience a certain fraction of deaths. The log-rank test (Peto et al, 1977) is often used to compare the survival distributions of two or more groups. It is a non-parametric test based on a chi-square statistic, which makes no assumptions about the survival distributions. It assumes that the groups have the same survival as the null hypothesis. When the log-rank statistic is large, it is evidence for a significant difference in the survival times between the groups.

KM curves and log-rank tests are very useful in assessing whether a categorial covariate (e.g. treatment A vs. treatment B; males vs. females) affects survival. However, it does not allow investigating the effects of multiple or continuous covariates (e.g. weight, age) and to know how much more at risk one group is than another.

2.3. Cox’s proportional hazards to adjust for covariates

An alternative method is the Cox's proportional hazards regression analysis (Cox, 1972). It is a semi-parametric method, which can be used to assess simultaneously the effect of several risk factors (both categorial and continuous covariates) on survival time. It is analogous to a multiple regression in which the response variable is the hazard measuring the instantaneous rate of the event. It assumes a constant proportional hazard across groups over time, i.e. the ratio of the risk of dying at a particular point in time in one group over another group is constant over time. Proportionality tests are used to evaluate this assumption (e.g. Miller 2011, see Supplementary Information S1 for an example). Models allowing for different assumptions, such as accelerated failure time (AFT) models, are discussed for example in Kirkwood and Sterne (2003) and Klein et al. (2016).

2.4. Example of a stress assay in an unconventional resistant organism: the tardigrade

Tardigrades hold their own phylum that stands in between the phylum Arthropoda and Nematoda (Image 1). They are renowned organisms for their ability to cope with the harshest environments, such as exposure to organic solvents, extreme temperatures (from -272 to 151°C) or high radiation doses, at any stage of their life (e.g. Jönsson et al, 2005). Most notably, some tardigrades have survived a ten days flight in the vacuum of space, and at a depth of 180 km below the surface of the earth (Ono et al. 2016). However, it seems that the genetic “toolbox” that ensures the uncommon resistance of these organisms to extreme stress is not shared by all tardigrade species. The resistance of tardigrade species can be assessed and compared under controlled conditions in the lab.

[Image 1 about here]

In this example, we illustrate the use of KM survival curve and log-rank test to evaluate the effect of the chemical stressor on tardigrades survival time. We use a Cox Proportional Hazard model to assess the effect of the chemical stressor while taking into account tardigrades age. Full procedure including data and R script to run the analysis using the R package *survival*, are provided in Supplementary Information S1.

3. Survival analyses in the wild: dealing with uncertainty and variable environments

In free-ranging animal and plant populations, CMR field methods are generally used to gather survival data (procedure described in chapter 5). A plethora of CMR models exist to estimate demographic parameters (including survival, access to reproduction, dispersal) while accounting for imperfect detection of individuals (e.g. Lebreton et al. 1992, Williams et al. 2002, Schaub et al. 2004, Pradel et al. 2005).

Hereafter, we introduce principle of CMR analysis and the main types of CMR models. We then provide an overview of their use in animal and plant demography with step-by-step study cases.

3.1. Overview of CMR models

3.1.1. Principle

Within a typical CMR protocol designed to estimate survival probabilities, individuals are sampled on discrete occasions (often ≥ 3 occasions), at which they may be detected or not. Data collected in the field is then encoded into encounter histories organized by individual or cohort (see details in White and Burnham 1999). The simplest way to codify the encounter histories is by using binary codes “1” and “0” specifying if the individual has been detected or not. However, when additional information reflecting the state of the individual (e.g. breeder vs. non-breeder, different resighting sites, epidemiological states) is collected, encounter histories may include additional codes (see multi-state and multi-event capture-recapture frameworks below). Moreover, individual covariates can also be recorded and included at the end of the individual encounter histories either in order to categorize individuals (e.g. males and females, age class, different populations) or by indicating a particular quantitative individual trait (e.g. size) (White and Burnham 1999).

Models for the analysis of capture-mark-recapture data are classically based on multinomial distributions that describe on one hand the biological processes and on the other hand the observational processes, conditional to the biological ones. In the simplest case, the probabilities involved are, ϕ_i , probability of surviving the time interval $i, i+1$ and p_i the probability to detect a

live individual at occasion i . More complex models (see section 3.4.2 and 3.4.3 below) actuate multinomial rather than binomial biological processes and observational processes but the basic structure remains the same.

3.1.2. Single-state models

The Cormack-Jolly-Seber (CJS) model was the first CMR model (with an earlier formulation: the Jolly-Seber (JS) model; Jolly 1965, Seber 1965) to allow the estimation of demographic parameters under the assumption of an open population (i.e. open to birth, immigration, death, and emigration, a.k.a. B.I.D.E. models). Under the CJS approach, apparent survival (ϕ_i) is the probability that an individual alive at time i will be alive at time $i+1$, while resighting (p_i) is the probability that an individual alive and present just before time i is seen (and marked) on that occasion (Lebreton *et al.* 1992). Apparent survival is generally not referred to simply as ‘survival’ because it may be confounded by permanent emigration of marked individuals out of the study site, and by long-term vegetative dormancy in plants. Further, apparent survival is the probability to survive during the interval between two monitoring occasions and thus not at a specific monitoring occasion. In contrast, resighting is an estimator of detection of previously seen individuals during the monitoring occasion.

CMR models rely on several assumptions, the most important of which are that marked individuals are independent, tags are not lost, and the past history does not influence the fate of the individual (i.e. no trap response or negative effect of capture on survival). Pollock *et al.* (1990) developed a series of goodness-of-fit tests based on contingency tables for the CJS model to assess the validity of the assumptions. Later, directional tests for the detection of specific effects were derived (trap-dependence, Pradel 1993; transients, Pradel *et al.* 1997). The availability of informative goodness-of-fit tests makes the CJS model a common ‘umbrella’ model in model selection procedure (Lebreton *et al.* 1992). The CJS model can be easily expanded to age-dependent

parameters when new animals are released at different ages or in multiple cohorts, or reduced assuming parameters are constant over time (examples in Lebreton et al. 1992).

The CJS model, and its extensions, have been, and still are, extensively used in the ecological literature as they provide a suitable analytical framework to address multiple questions that tackle variability in survival over time (Lebreton et al. 1992), with external covariates (e.g. Grobois et al. 2008), changes in recruitment probabilities (e.g. Pradel and Lebreton 1999), recapture processes (e.g. Sanz-Aguilar et al. 2010) or evolutionary trade-offs (Tavecchia et al. 2001). However, the CJS model is based on capture-recapture data obtained from a single population and cannot explicitly frame observations of animals moving across multiple sites or between relevant biological states.

3.1.3. Multi-state models

Multi-state models extend the CJS model by making the parameters state-specific (Arnason 1973; Schwartz 1993). Thus, apparent survival (ϕ^{jk}) is now the probability that an individual alive in state j on monitoring occasion i survives to occasion $i+1$ and, during the latter occasion, transits to state k . This parameter may be decomposed into two parameters unseen in the CJS model: state-specific survival (S_i^j) and state-transition (Ψ_i^{jk}). Here, state-specific survival (S_i^j) is the probability that an individual alive in state j at monitoring occasion i survives to monitoring occasion $i+1$, irrespective of the state of the individual at the latter occasion. State-transition (Ψ_i^{jk}) is the probability, conditional on survival, of changing or moving from state j at time i to state k at time $i+1$ assuming that the individual survived the interval between the two occasions. Additionally, multi-state models estimate resighting (p_i^j), defined as the probability that an individual alive and in state j at monitoring occasion i is also observed in that occasion.

This multisite-multi-state formulation allows to address questions on survival and movement probabilities in metapopulation systems (e.g. Balkiz et al. 2010), but it also provides a suitable

framework for the study of between-state transitions to study evolutionary trade-offs (Nichols and Kendall 1995), recruitment probability (e.g., Jenouvrier et al. 2008) or to mix information of different types, i.e. recoveries and recaptures (e.g. Lebreton et al. 1999). The multisite – multi-state and robust design models have also been successfully applied to model dispersal to unobservable sites or transition to unobservable states, i.e. places or states through which animals can move but in which they cannot be seen, or unobservable dormancy states in plants (Kendall and Nichols 2002). In the unobservable site/state probability of detection is fixed to zero and for this reason they are often referred to as ‘ghost’ sites/states (Jenouvrier et al. 2008, Balkiz et al. 2010). Grosbois and Tavecchia (2003) applied this idea to unobservable transitions. They considered the probability of dispersal as a two-step process, one accounting for the probability of leaving a given site and a second, conditional to this, incorporating the probability of settling into a new site. A similar approach was used by Schaub and Pradel (2004) to estimate the relative importance of different causes of death. However, multisite-multi-state models have an important limitation: they assume that the state or the site in which an individual is observed is always certain.

3.1.4. Multi-event models

State uncertainty is a general problem in CMR models, but it might be particularly relevant in some studies. For example, the study of the evolutionary trade-off between survival and reproduction relies on the fact that the breeding state of the individuals observed is always determined correctly. This can be true in most cases, but sometimes it can be difficult to determine with certainty whether an animal or plant is: breeding or not, is healthy or affected by a particular disease, or even if it is a male or a female. Pradel (2005) solved this problem by generalizing the multisite-multi-state model into a multi-event framework. In this new framework, individuals are still assumed to move across different states through survival and transition processes but a new parameter, the initial state probability, appears. Usually, field observations are not fully informative of biological processes. By formally separating the ‘real’ state process from the observational process-events, Pradel

included a parameter to account for state uncertainty, i.e. the probability to not assign or erroneously assign a given state to an individual. Multi-event models provide a solution to estimate sex and/or age dependent survival in species with cryptic or little age and/or sexual dimorphism (see section 3.4.1). Transients can be considered as a particular initial state, and modelled directly using multi-event models (Genovart et al. 2012, Santidrian et al. 2017). More than uncertainty about the state of an individual, multi-event models allow to explicitly model unobserved heterogeneity among individuals. Indeed, latent state mixture models can be easily implemented within the multi-event framework, a model particularly suitable to frame individual heterogeneity or frailty (Gimenez, Cam and Gaillard 2018). Other approaches, e.g. using individual random effects can also be used to implement frailty (e.g. Cam et al. 2016, Hamel et al. 2018 , see also section 3.2).

Multi-event and multi-state models can be used to address many other ecological and evolutionary questions. If individual states can change over time, multi-event also allows modeling the transition dynamics between e.g. breeding states (Desprez et al. 2013) or epidemiological status (Benhaiem et al. 2018). Lagrange et al. (2014) developed multi-event models able to study dispersal among numerous sites for birds and amphibians. Tavecchia et al. (2012), modelled mortality due to different causes of mortality of radiotagged individuals, while accounting for the loss of the radio signal (see section 3.4.2). Multi-event models have also been used to model survival when marks identifying individuals are lost (even totally, see Badia-Boher et al. 2019). The multi-event approach can be also used to exploit supplementary information and estimate survival, dispersal and/or recruitment in partially monitored populations (Tavecchia et al. 2016; Sanz-Aguilar et al. 2016). Finally, trap-responses and memory effects can be modeled into the multi-event approach (Rouan et al. 2009; Pradel and Sanz-Aguilar 2012).

3.2. Environmental variability and individual heterogeneity in CMR models

Within a CMR model, survival, transition and/or detection parameters can be assumed to be a function of external covariates (Lebreton et al. 1992). This formulation allows the inclusion of

environmental effects in a regression-like framework, by including e.g. climatic variables, or individual time-invariant characters such as genotype. Multifactorial effects of environmental covariates can also be modeled using hierarchical models (King et al. 2009), e.g. to study evolutionary processes in the wild (Cubaynes et al. 2012). However, time-varying individual covariates, such as body weight, are tricky because when an individual is not detected, the value of the covariate is unknown. Inference can be based on a conditional likelihood approach using only the observed covariate values (trinomial approach; Catchpole et al. 2008) or missing values of can be imputed from an underlying distribution (e.g. multiple imputation; Worthington et al. 2015). However, methods of imputation are sensitive to the underlying model and the number of missing values (Langrock and King 2013). One possibility is to discretize the covariate and use a multi-state model (Fernández-Chacón et al. 2015, Gimenez, Cam and Gaillard 2018).

Unfortunately, we often do not measure all covariates influencing demographic parameters. Individuals may also react in different ways to environmental variation depending on unobservable individual states. This leads to unobserved (latent) individual heterogeneity (see chapter 9). Ignoring latent individual heterogeneity may lead to flawed inference about the ecological or evolutionary processes at hand (Cam et al. 2016, Hamel et al. 2018), such as senescence patterns (Cam and Monnat 2000, Service 2000, Peron et al. 2010). Latent individual heterogeneity can be framed using finite mixtures or as individual random effects (see Gimenez, Cam and Gaillard 2018 for a review about how to implement individual heterogeneity in CMR models).

3.3. Inference framework

Implementation of CMR models can be carried out either using a frequentist or Bayesian approach. A different philosophy stands behind each approach, and there is a long-standing debate about whether ecologists should use one or the other (e.g. Lele and Dennis 2009). While the frequentist approach may be faster, the Bayesian approach allows a great flexibility in the model writing which can be useful to tackle analytical complexity, such as choosing underlying distributions for model parameters, or fitting temporal random effects (e.g. Kery and Schaub 2011). Another appeal of

the Bayesian approach is the possibility to include prior knowledge on biological parameters to facilitate the estimation, e.g. information on body weight or survival of a closely-related species (MacCarthy et al. 2005). The Bayesian approach of CMR models uses the state-space formulation (SSM) that clearly distinguishes the observation process (detection) from the underlying demographic process of interest (transition between states; e.g. Gimenez et al. 2007, Royle 2008, Kery and Schaub 2011). The observation process being conditional to the state process. The SSM formulation therefore allows to easily implement complex multifactorial observation processes and combine multiple sources of information (e.g. Buoro et al. 2012, see Supplementary Information S5 for a SSM formulation of the Jolly-Seber model).

Prior to model fitting, goodness-of-fit tests are generally performed to check the validity of the assumptions behind a CMR model, e.g. using the R2ucare package (Gimenez et al. 2018). In the frequentist approach, model implementation can be carried out using program MARK and the widely used RMark package (White and Burnham 1999, Laake 2013), marked (Laake 2013) or E-SURGE (Choquet et al. 2009). Common tools for model comparisons include the Akaike Information Criterion and its variants (AICc, QAIC, wAIC; Burnham and Anderson 2002), which serves to rank the models, calculate weights of evidence for each of them or for a particular effect (Burnham and Anderson 2002). The Analysis of Deviance (Anodev) is also used to calculate the proportion of variance explained by a specific covariate (Grosbois et al. 2008). In the Bayesian approach, models can be implemented using program Jags (Plummer 2003), R packages such as rjags (Plummer et al. 2018) or BaSTA (Colchero et al. 2012). Posterior predictive checks can be used for performing model assessment (Chambert et al. 2014) and information criterion such as DIC or wAIC are often used for model comparison (Hooten and Hobbs 2015). Further details about implementation both in a frequentist and Bayesian framework can be found in McCrea and Morgan (2014).

Hereafter, we develop study cases in animal and plant demography showing how to implement CMR models in a frequentist framework using program E-SURGE and R package marked (Laake et al. 2013), and in a Bayesian framework using package BaSTA and rjags.

3.4. Study cases in animal demography

3.4.1. Estimating sex-dependent survival when sex assignment is uncertain: a multi-event model of the Balearic Wall Lizard (*Podarcis lilfordi*)

In this example, we consider the possibility of erroneous assignment of sex to a newly captured individuals, a situation common to the monitoring of species, for example, with little sexual dimorphisms. In CMR analyses, erroneously assigning sex at the beginning of the capture history leads to bias in the estimated survival difference between the sexes. Here, our aim is to estimate sex-specific survival rates in the Balearic wall lizards, a small species endemic of the Balearic archipelago, Spain. Immature males are sometimes difficult to be sexed in the field and can be confounded with mature females. Sex-specific survival rates can be estimated by accounting for the uncertainty on sex assignment using a multi-event CMR model to separate the ‘real’ sex of the individuals (state) from the ‘apparent’ (observed) sex (event). In this model, we considered four events (type of observations) which code three states (“real” state of the individual). Data, together with step-by-step instructions to implement the models in E-SURGE and interpret the results, are provided in Supplementary Information S2.

3.4.2. Survival and the issue of tag-loss: study case of the Red Kite (*Milvus milvus*)

Tag-loss is a common issue in wildlife monitoring of marked individuals and can lead to underestimated survival (Arnason and Mills, 1981). To cope with this issue, ecologists have developed advanced methodological tools: from multiple-marking to advanced statistical methods

to integrate tag-loss in the individual state (Cowen and Schwarz 2006, Tavecchia et al. 2012). Here is one case study to integrate the loss of a remote tracking device in the multi-event modeling framework.

The use of remote tracking devices (radio-satellite and GSM/GPS transmitters) to collect detailed individual history data is increasingly common in the ecological literature (see Chapter 3 and chapter 5). A problem in estimating survival from tracking data is that the lifespan of the remote signal is commonly shorter than the lifespan of the individual that carries the device. In this case the survival probability refers to the lifespan of the radio signal and not to the one of the animal. When animals are marked with tags or rings in addition to the radio device, their encounter history can follow the loss of the radio signal. In this example, we illustrate how multi-event models can accommodate the loss of the signal and provide unbiased estimate of survival in the presence of radio-loss or radio-failure using a real dataset on Red Kite in the island of Mallorca. Data, together with step-by-step instructions to implement the models in E-SURGE, and interpret the results, are provided in Supplementary Information S3.

3.4.3. Bayesian implementation using the R package BaSTA

The R package Bayesian Survival Trajectory Analysis (BaSTA; Colchero et al. 2012) provides a set of tools that complement other CMR methods when users want to estimate age-specific mortality from CMR datasets where times of birth are known only for few individuals (or none). Several parametric mortality models are available in BaSTA, including the exponential, Gompertz, Weibull, logistic, Makeham and Gompert-Makeham models. In order to include all records in the analysis, BaSTA estimates the missing ages at birth and at death, which reduces the bias in the estimation of the mortality and cumulative survival functions. An example of implementation is provided in Supplementary information S4.

3.4.4. Bayesian state-space formulation of the JS model to study stopover decisions of migratory birds using JAGS

Migratory birds cannot realize their journey between breeding and wintering areas in a single flight of thousands kilometres and usually stop-over at places where they can replenish their energy reserves. At these stopover places individuals are not easy to detect. Studying the stopover decisions of migratory birds is a typical case where the detectability need to be taken into account to be able to make strong ecological inference. In this example the survival between two capture occasions (ϕ) is considered as the remaining probability at the stopover place and thus $1-\phi$ is the departure probability between two occasions. As individuals may arrived in the stopover area before first capture, the model needs to not be conditional on the first capture (as in the CJS model). Thus, we can use the JS model parametrized with entry probabilities noted as η_i for the probability to entry in the stopover area between time i and $i+1$ if not previously entered (Schwarz and Arnason 1996). This SSM formulation of the JS model allows an easy implementation in the Bayesian framework and a straightforward computation of the stopover duration (Lyons et al. 2016). We can also easily incorporate the effect of a weather covariate on the departure probability. The implementation of this example with R and JAGS is provided in Supplementary S5.

3.5. Study cases in plant demography

Plants do not move, but certain aspects of their ecologies, such as vegetative dormancy, variable sprouting times, and complex growth patterns, can make them just as challenging to work with as animals.

3.5.1. Linear modeling of plant survival

The most common method to analyze survival using plant resighting datasets is using linear analysis under a logistic, generalized linear model (GLM), or generalized linear mixed model (GLMM) framework, with survival modeled assuming a binomial distribution (e.g. Salguero-

Gómez et al. 2012). This method assumes that at the very least, the resighting of previously observed individuals is nearly perfect, because any phenomenon decreasing re-detection would be observed as mortality and yield biased survival estimates. In cases where re-detection is not perfect, some have argued that this approach is still useful provided that monitoring datasets are particularly long and large, and that re-detection is still above 90% (Shefferson et al. 2018). However, in studies of vegetative dormancy-prone perennials, dormancy will increasingly be confused with mortality as study length decreases. In the final year of a study, there will be no ability to differentiate the dead from the dormant. This suggests that the final one to three years of data in a study should be used simply to assign dormancy within the remaining data, and that survival should not be estimated for those years. This loss of estimable years adds value to long datasets, particularly those over 10 years long.

We illustrate the use of linear modeling for survival analysis in plants using a case study on *Cypripedium parviflorum*, the North American small yellow lady's slipper, using data collected from 1994 to 2003 within a larger population from Illinois state in the United States. These data were previously used in e.g. Shefferson et al. (2018). Using the R packages lme4 for model fitting and MuMin for model comparison, we show that non-flowering plants have decreasing survival with increasing size, while flowering plants have increasing survival with increasing size. Full procedure including data and R script to run the analysis, are provided in Supplementary Information S6.

3.5.2. CMR survival analysis for plants

Plant population ecologists have long used field methods that may be considered in the same vein as mark-recapture methods in wildlife ecology. However, the application CMR methods to plant population ecology is very recent. In one of the first studies to use mark-recapture analyses in plants, Alexander et al. (1997) faced all of these problems in a population of the Mead's milkweed, *Asclepias meadii*. This population consists of plants that grow in high densities and do not always produce aboveground tissue in a growing season. Closed population mark-recapture analysis allowed them to produce estimates of population size unbiased by these challenges. Expanding on

this work, Shefferson et al. (2001) proposed the use of open population mark-recapture models to estimate annual survivorship in populations in which living individuals do not always sprout in a growing season. Since then, CMR studies have blossomed in plant population ecology, with extensions into the estimation of transition rates among life-history stages (e.g. Shefferson et al. 2003), estimation of the demographic impacts of herbivory (e.g. Kéry and Gregg 2004), investigations into relationships among life-history traits (e.g. Shefferson et al. 2003), tests of correlation with climatic factors (e.g. Shefferson and Tali 2007), the estimation of minimal recruitment levels necessary to sustain populations (Slade *et al.* 2003), and theoretical papers inspired by the problem of unobserved life stages (Kendall and Nichols 2002).

In this example, we also use the *Cypripedium parviflorum* dataset, in combination with the R package *marked* (Laake et al. 2013), to investigate costs of reproduction using CMR models. Full procedure including data and R script to run the analysis, are provided in Supplementary Information S7.

4. Mortality analysis in human populations

Modelling mortality in human populations is relatively easier than in non-human ones. For a given group of individuals, we often know their age-at-death, calendar year of the event and their sex. Thanks to these reliable data sources, methodological advances have been produced since De Moivre (1725) and Gompertz (1825). These long-standing demographic and statistical developments have been often drawn by political, military and economic reasons. Below, we present a brief overview of the most common models used to describe mortality patterns over age and/or time on human mortality data.

4.1. Human data and assumptions

For a given sex, we usually have deaths and exposures to the risk of death arranged in two matrices, whose rows and columns are classified by age at death, and year of death. The stochastic

assumption behind mortality has a central role in modeling it. The most suitable distribution when we observe mortality data is the Poisson distribution. The aim of any mortality model is to seek for a parsimonious, yet satisfactory description of the so-called force of mortality $\mu_{i,j}$, given observed deaths $d_{i,j}$, and exposures $e_{i,j}$. One could estimate force of mortality in a fully non-parametric framework computing the death rates $\mu_{i,j} \approx \frac{d_{i,j}}{e_{i,j}}$. Simple plots of rates over age and/or time are good tools for a first presentation of mortality development. Commonly, rates are plotted on a logarithmic scale to better acknowledge differences. A relatively strong assumption behind is that within the Poisson distribution mean and variance are equal. When the observed variance is larger than the theoretical one, we often attribute this feature either to overdispersion, or to some hidden patterns in the data. Specific methods for coping with this issue have been proposed in the literature for all models below, though they will not be presented in this chapter. For a comprehensive overview of them see, e.g. Cameron and Trivedi (2013). Furthermore, binomial distribution could be used when we deal with probability of dying (deaths divided by persons-at-risk) and the multinomial distribution has been suggested for modeling mortality from a cohort perspective (Canudas Romo et al., 2018).

4.2. Parametric models over age

Parametric models for a suitable representation of the variation of mortality over age have been proposed since Gompertz (1825). He observed that after a certain age, a “law of geometric progression pervades, in an approximate degree, large portions of different tables of mortality” (Gompertz, 1825, p. 514). He thus suggested representing force of mortality as:

$$\mu_i = ae^{bi}. \quad (1)$$

where a represents the mortality at time zero (usually age 30/40) and b is the rate of increase of mortality and is frequently used as a measure of the rate of aging.

Makeham (1860) extended Gompertz' equation by adding a constant, an age-independent term, $c > 0$, to account for risks of death that do not depend on age:

$$\mu_i = c + ae^{bi}. \quad (2)$$

Human mortality often shows a levelling-off above certain ages (often 80) (Vaupel, 1997). Logistic models have been proposed to portray this feature. Perks (1932) was the first to proposed a logistic modification of the Gompertz-Makeham models. A logistic function to model the late-life mortality deceleration can be given by

$$\mu_i = c + \frac{ae^{bi}}{1+ae^{bi}}. \quad (3)$$

where α capture the mortality deceleration at oldest ages. This law of mortality can be derived when heterogeneity is assumed in a proportional hazard setting. Commonly called the Gamma-Gompertz model, (3) is the hazard at a population level when standard mortality is described as a Gompertz and frailty values are assumed to be Gamma distributed (Wienke, 2010).

A simplified version of the previous logistic law has been proposed by Kannisto (1992):

$$\mu_i = c + \frac{ae^{bi}}{1+ae^{bi}}. \quad (4)$$

Heligman and Pollard (1980) derived a descriptive model, covering the whole age range. Here we propose a version for death rates:

$$\mu_i = A^{(i+B)^C} + De^{-E(lni - lnF)^2} + \frac{GH^i}{1+GH^i}. \quad (5)$$

where A, B . . . , H are the eight parameters in the model. Each component aims to describe mortality at childhood, during young-adult ages and at older ages. It is easy to see that such

parameterization can cause difficulties in the estimation procedure. Moreover, it would be hard to disentangle the physical meaning of each parameter (Booth and Tickle, 2008).

Another three-component, competing-risk mortality model has been proposed by Siler (1983). Initially developed for animal survival data, this model has been recently used in human demography, especially for simulating possible scenarios in mortality developments (Canudas-Romo, 2018). This model aims at portraying the whole of the age range with five parameters:

$$\mu_i = a_1 e^{-b_1 i} + a_2 + a_3 e^{b_3 i} \quad (6)$$

4.3. Over parametrized models: the example of the Lee-Carter

Moving to a two-dimensional perspective and given the wealth of data, traditional demographic methods for analyzing mortality surfaces, i.e. data on deaths and exposures cross-classified by age and year of occurrence, tend to apply a high number of parameters leading to all but parsimonious models. A typical example of this kind is the widely used model introduced by Lee and Carter (1992). In its original formulation, this approach reduces the complexity of the whole surface by introducing the following bi-linear model for the log-death-rates:

$$\ln(m_{ij}) = \alpha_i + \beta_i \kappa_j + \varepsilon_{ij}, \quad i = l, \dots, m \quad (7)$$

$$j = l, \dots, n$$

where α_i , β_i and κ_j are vectors of parameters to be estimated, and ε_{ij} represents the error term. Interpretation of the parameters are straightforward: α_i and β_i describe the general shape of mortality and the fixed rate of mortality improvement at age i respectively, and κ_j is a time-varying index which captures the general level of mortality. The variance ε_{ij} in Lee and Carter (1992) is assumed to be constant for all i and j . As presented, the Lee-Carter model (LC) is under-determined

and requires additional constraints on the parameters to be successfully estimated. Usually, the model is centered by $\sum \beta_i = 1$, $\sum \kappa_j = 0$.

As pointed out in Section 4.1, a Poisson assumption is more suitable for estimating mortality models and a further development of the Lee-Carter model was devoted to this issue (Brouhns et al., 2002). In Supplementary Information S7 we will provide computational details for estimating the LC model within a Poisson framework.

In the last decades, further variants of this model have been proposed for enhancing several features of the model (e.g. Booth et al. 2002).

4.4. Semi-parametric models: the example of P-splines

A compromise between simple parametric and over-parametrized models could be found in the area of semi-parametric statistics. Without the aim of producing estimated parameters with physical meanings and searching for a good fit to the data, smoothing approaches have been lately developed in the study of nonlinear phenomena. Among numerous options, we will mention here (and illustrate with more details in Supplementary Information S7) a methodology which is particularly suitable for the analysis of mortality developments: B-splines with penalties, known as P-splines. In a unidimensional setting, applications to mortality have been proposed by Currie et al. (2004) and Camarda (2008). Estimation of a model for the complete mortality surface will be achieved by a specific R package: MortalitySmooth (Camarda, 2012). It is noteworthy that, being an extremely flexible tool, this methodology can be easily implemented for the analysis of demographic phenomena other than mortality. The main idea of the P-splines is to construct an intentionally over-parametrized model and simultaneously to restrict, via a penalty, all redundant features for achieving a wisely parsimonious description of the data. Instead of smoothing a given structure, this approach used local supports such as equally-spaced B-splines over ages and/or years, and penalty term(s) on the associated coefficients.

4.5. Implementation example

We use data from the Human Mortality Database (2019) on Japanese females from year 1960 to 2016 and from age 0 to 100 to fit the models described above. Guidance with R script are provided in Supplementary Information S8.

Concluding remarks

This chapter has illustrated how the choice of a specific method for survival analysis is driven by the research question (e.g. comparing survival across groups vs assessing the effects of environmental predictors), the species life history (more or less easy to monitor) and its living environment (controlled vs. stochastic environments) which determines the type of survival data (e.g. proportion of individuals alive, CMR data, or age at death).

With the rising of new monitoring techniques allowing to gather more and more detailed data at the individual level (see chapter 5) has come the developments of advanced statistical tools for survival analyses, including multi-event models and hierarchical models. More than simply assessing survival to feed population projection models (see chapters 9, 10, 11 and 14), modern survival analyses have addressed questions about evolutionary trade-offs (e.g. Nichols and Kendall 1995), static versus dynamic heterogeneity in demographic parameters (e.g. Cam et al. 2016; Gimenez et al. 2018), assessing senescence (e.g. Peron et al. 2010), or quantifying heritability of demographic parameters in the wild (e.g. Papaïx et al. 2010). Addressing more and more complex questions has brought new challenges into the field of survival analyses. Among others, current methodological developments deal with methods to implement models with numerous states, predict age at death, or consider dependence among individuals when estimating survival.

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Résumé

Chaque année des dizaines de millions d'oiseaux migrateurs voyagent entre leurs aires de reproduction et leurs aires d'hivernage. Ce voyage de plusieurs milliers de kilomètres implique des contraintes météorologiques et énergétiques qui conduisent les oiseaux à effectuer des haltes migratoires. Les contraintes énergétiques forcent ainsi les oiseaux à refaire leurs réserves d'énergie durant ces haltes pour pouvoir effectuer de nouveau un vol de plusieurs centaines de kilomètres. En conséquence de cela, plus de 80% du temps total de migration est passé sur les sites de halte. Mieux comprendre les déterminants du départ d'un site de halte migratoire est ainsi crucial pour mieux appréhender le phénomène de la migration dans sa globalité ainsi que les variations de fitness d'une espèce. C'est pourquoi cette thèse, à l'interface entre modélisation et écologie de la migration, vise à obtenir une meilleure compréhension des décisions d'oiseaux migrateurs lors de leurs haltes à partir de données de capture-marquage-recapture récoltées parfois depuis des décennies. En plus de cela, les potentielles implications en termes de gestion d'un site de halte seront abordées. La thèse s'articule ainsi sous la forme de 4 parties principales présentant différents cas d'études relatifs à l'analyse de données de capture-marquage-recapture d'oiseaux sur des sites de halte migratoire.

Abstract

Every year tens of millions of migratory birds travel between their breeding and wintering grounds. This journey of several thousand kilometres involves meteorological and energy constraints that lead the birds to make migratory stops. The energy constraints force the birds to replenish their energy reserves during these stopovers in order to be able to make another flight of several hundred kilometres. As a result, more than 80% of the total migration time is spent at stopover sites. A better understanding of the determinants of the departure from a migratory stopover site is therefore crucial to better apprehend the migration phenomenon as a whole as well as the variations in fitness of a species. This is why this thesis, at the interface between modelling and migration ecology, aims to obtain a better understanding of the decisions made by migratory birds during their stopovers based on capture-marking-recapture data collected sometimes for decades. In addition to this, the potential implications in terms of the management of a stopover site will be addressed. The thesis is divided into 4 main parts presenting different case studies on the analysis of capture-tagging-recapture data of birds on migratory stopover sites.