Mouvements annuels, reproduction et compétition alimentaire chez un prédateur aviaire de la toundra, le labbe à longue queue

Thèse

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Résumé

La migration représente un déplacement saisonnier récurrent entre un site de reproduction et un site d'hivernage géographiquement distants. Les migrateurs profitent ainsi d'un environnement saisonnier où les conditions sont favorables à la reproduction avec des ressources abondantes et une réduction de la compétition et de la prédation. En contrepartie, migrer implique des contraintes phénologiques, en plus d'exposer les individus à une plus grande diversité d'environnements lors des déplacements. Il est toutefois difficile d'établir des liens entre les conditions rencontrées durant la période non-reproductrice et leurs répercussions sur la reproduction chez les migrateurs. L'objectif général de cette thèse est de mieux comprendre les principales étapes du cycle annuel et leurs interrelations chez le labbe à longue queue, un oiseau marin migrateur de longue distance exploitant la toundra arctique en été et les mers australes en hiver. Cette thèse se décompose en trois objectifs spécifiques : (1) examiner les mouvements annuels de cet abondant prédateur de la toundra arctique en décrivant sa migration transéquatoriale, sa phénologie et ses stratégies migratoires saisonnières; (2) évaluer les relations entre les périodes non-reproductrice et reproductrice via de possibles effets reportés réciproques, ainsi que les impacts directs de la disponibilité de sa principale source de nourriture estivale, les lemmings, sur sa reproduction; (3) étudier les mécanismes permettant la coexistence du labbe au sein d'une guilde de prédateurs aviaires partageant deux espèces de lemmings dont les populations fluctuent annuellement. De 2004 à 2019, la reproduction du labbe a été suivie sur l'Île Bylot (Nunavut) dans le Haut-Arctique canadien pour en estimer la phénologie et le succès. Parallèlement, les nids des principaux prédateurs aviaires présents dans la zone d'étude (harfang des neiges, goéland bourgmestre, buse pattue, labbe à longue queue) ont été géoréférencés et des pelotes de régurgitations récupérées afin d'identifier les proies consommées. De 2014 à 2019, 70 géolocalisateurs ont été déployés sur des labbes pour suivre leurs déplacements pendant une année entière. Les géolocalisateurs ont révélé que les labbes parcourent annuellement >32 000 km. Durant la période non-reproductrice, ils hivernent majoritairement dans la région d'*upwelling* du Benguela de l'Atlantique Sud et ils effectuent une halte migratoire printanière et automnale au large des Grands Bancs de Terre-Neuve, des régions océaniques hautement productives. Contrairement à la majorité des oiseaux, la migration d'automne est plus rapide que celle du printemps. Cette stratégie s'explique probablement par des contraintes écologiques au printemps ralentissant la progression vers l'Arctique, comme la présence de la banquise et la toundra enneigée, et des contraintes endogènes à l'automne incitant les individus à arriver rapidement au site d'hivernage pour amorcer la mue. Nous avons trouvé peu d'effets reportés de la période d'hivernage et de la migration printanière sur la reproduction. Toutefois, une réduction du temps en vol en hiver augmente la propension à nicher, alors qu’une arrivée trop hâtive au printemps la diminue. En revanche, une forte abondance de lemmings en été augmente la propension à nicher et le succès reproducteur, alors que pondre tardivement diminue celui-ci. Globalement, les conditions locales influencent fortement la reproduction, alors que les effets reportés ont un effet plutôt faible. Durant l’été, deux mécanismes permettent la coexistence de la guilde de prédateurs aviaires à laquelle le labbe appartient. D’abord, une ségrégation spatiale de l’habitat basée sur les préférences spécifiques réduit le chevauchement des territoires de nidification entre espèces. Ensuite, une ségrégation alimentaire dans les espèces et la taille des lemmings en fonction de la taille des prédateurs qui les consomment réduit le chevauchement des niches alimentaires. En l’absence du prédateur dominant, le harfang, un relâchement de la pression de compétition s’opère néanmoins sur le labbe, le plus petit prédateur, qui déplace sa niche alimentaire en consommant des proies plus grosses. Ces résultats suggèrent que les conditions variables et imprévisibles de l’Arctique comme les couvertures de neige et de glace, ainsi que l’abondance de lemmings influencent fortement le cycle annuel du labbe à longue queue et affectent davantage le succès reproducteur que la variabilité émanant de la période non-reproductrice. Cette thèse améliore notre compréhension des stratégies migratoires aviaires et du rôle de la compétition interspécifique dans un environnement caractérisé par une ressource pulsée, les lemmings.

Abstract

Migration represents a recurring seasonal movement between geographically distant breeding and wintering sites. Migrants thus benefit from a seasonal environment where conditions are favourable to reproduce with abundant resources, and low competition and predation. However, migrating involves phenological constraints, and exposes individuals to a greater diversity of environments. Nevertheless, it is difficult to establish links between conditions encountered during the non-breeding period and their impact on reproduction in migrants. The overall objective of this thesis is to better understand the main stages of the annual cycle and their interrelationships in the long-tailed jaeger, a long-distance migratory seabird exploiting the Arctic tundra in summer and the southern seas in winter. This thesis consists of three specific objectives: (1) examine the annual movements of this abundant Arctic tundra predator by describing its transequatorial migration, phenology and seasonal migratory strategies; (2) assess the relationships between non-breeding and breeding periods through potential reciprocal carry-over effects, as well as the direct impacts of the availability of its main food resource in summer, lemmings, on its reproduction; (3) investigate the mechanisms allowing coexistence of the jaeger within a guild of avian predators sharing two species of lemmings whose populations fluctuate annually. From 2004 to 2019, reproduction of jaegers was monitored on Bylot Island, Nunavut, in the Canadian High Arctic to estimate its phenology and success. Also, nests of the main avian predators present in the study area (snowy owl, glaucous gull, rough-legged hawk, long-tailed jaeger) were georeferenced and regurgitation pellets collected to identify the prey consumed. From 2014 to 2019, 70 geolocators were deployed on jaegers to track their movements throughout an entire year. Geolocators showed that jaegers travel >32 000 km annually. During the non-breeding period, they winter mostly in the Benguela upwelling region of the South Atlantic and they make a stopover off the Grand Banks of Newfoundland in spring and in fall, both highly productive oceanic regions. Unlike most birds, fall migration is faster than spring migration. This strategy is likely due to ecological constraints during the spring that slow progression towards the Arctic, such as the presence of sea-ice and the snow cover in the tundra, and endogenous constraints in the fall, prompting individuals to quickly arrive at the wintering site to start molting. We found few carry-over effects of the wintering period and spring migration on reproduction. However, reducing time spent flying during the winter increases breeding propensity, while arriving too early in spring has the opposite effect. Conversely, high lemming abundance during the summer increases breeding propensity and breeding success, while laying late decreases the latter. Overall, reproduction is strongly influenced by local conditions and weakly influenced by carry-over effects. During the summer, two mechanisms allow the coexistence of the guild of avian predators to which jaegers belongs. First, spatial segregation of habitat based on species-specific preferences reduces overlap of nesting territories between species. Second, food segregation based on lemming species and size according to the size of predators that consume them reduces the overlap of food niches. The absence of the dominant predator, the snowy owl, nonetheless triggers a competitive release on the smallest one, the jaeger, which shifts its food niche by consuming larger prey. These results suggest that variable and unpredictable conditions in the Arctic as snow and ice covers, and lemming abundance strongly influence the annual cycle of the long-tailed jaeger and influence reproductive performance more than the variability encountered during the non-breeding period. This thesis improves our understanding of bird migratory strategies and the role of interspecific competition in an environment characterized by a pulsed resource, lemmings.

Table des matières

Liste des tableaux

CHAPITRE 1

CHAPITRE 2

CHAPITRE 3

CHAPITRE 5

ANNEXES

Liste des figures

CHAPITRE 1

CHAPITRE 2

CHAPITRE 3

CHAPITRE 4

CHAPITRE 5

ANNEXES

Liste des annexes

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Avant-propos

Ma thèse se compose de sept sections incluant une introduction et une conclusion générale, rédigées en français, et cinq chapitres centraux présentés sous forme d'articles scientifiques révisés par les pairs, rédigés en anglais. L'introduction présente une revue de littérature sur l'état des connaissances actuelles des principales thématiques abordées dans cette thèse et présente les objectifs de recherche de chaque chapitre. Les chapitres 1, 2 et 5 sont publiés et la version présentée dans la thèse est identique à la version publiée. Trois annexes (S2.8 - S2.10) avec les données de migration individuelles ont toutefois été ajoutées au contenu publié pour le chapitre 2. Le chapitre 4 a été soumis à un journal scientifique avec comité de révision et le chapitre 3 est en préparation pour être soumis prochainement.

Le chapitre 1 intitulé « **Sexing a monomorphic plumage seabird using morphometrics and assortative mating** » a été publié en décembre 2019 dans la revue *Waterbirds* (https://doi.org/10.1675/063.042.0403). Gilles Gauthier est le principal coauteur de ce chapitre. Louis Bernatchez (Université Laval) et Jean-François Therrien (Hawk Mountain Sanctuary) ont contribué également à titre de coauteurs.

Le chapitre 2 intitulé « **Seasonal variations in migration strategy of a long-distance arctic-breeding seabird** » a été publié en octobre 2021 dans la revue *Marine Ecology Progress Series* (https://doi.org/10.3354/meps13905). L'article a été publié en tant que *Feature article* du volume 677 de la revue. Gilles Gauthier est le principal coauteur de ce chapitre, suivi de Joël Bêty (Université du Québec à Rimouski), Jean-François Therrien et Nicolas Lecomte (Université de Moncton) dont les contributions sont équivalentes.

Le chapitre 3 intitulé « **Weak carry-over effects and strong influence of local conditions on the reproduction of a long-distance migrant** » est présentement en cours de préparation en vue de la soumission. Gilles Gauthier est le principal coauteur de ce chapitre, suivi de Joël Bêty, Jean-François Therrien et Nicolas Lecomte dont les contributions sont équivalentes. Cet article sera soumis au journal *Ornithology* (*Auk*).

Le chapitre 4 intitulé « **High site fidelity and low mate change in an Arctic monogamous seabird** » a été soumis au journal *Ibis*. Gilles Gauthier est le principal coauteur de ce chapitre, suivi de Jean-François Therrien.

Le chapitre 5 intitulé « **Resource partitioning among avian predators of the Arctic tundra** » a été publié en décembre 2020 dans la revue *Journal of Animal Ecology* (https://doi.org/10.1111/1365-2656.13346). Gilles Gauthier est le principal coauteur, suivi d'une contribution équivalente de Dominique Fauteux (Musée Canadien de la Nature) et Jean-François Therrien.

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Schmidt, E., D. Fauteux, J.-F. Therrien, G. Gauthier, and Y. Seyer. 2020. Improving diet assessment of Arctic terrestrial predators with the size of rodent mandibles. Journal of Zoology 311:23–32. doi: https://doi.org/10.1111/jzo.12756.

Introduction

Contexte général

Les migrations animales fascinent les scientifiques depuis des siècles par leur diversité et leurs implications écologiques, physiologiques, comportementales et évolutives. Ce phénomène écologique est largement répandu à travers le règne animal, notamment chez les mammifères marins (Reeves et al. 2004, Stevick et al. 2011, Sterling et al. 2014) et terrestres (Thirgood et al. 2004, Côté et al. 2012), les insectes (Anderson 2009, Reppert et de Roode 2018), les poissons (Weng et al. 2007, Barthem et al. 2017) et les oiseaux (Garthe et al. 2016, Cooper et al. 2017, Robillard et al. 2018, Léandri-Breton et al. 2019). Néanmoins, les migrations aviaires suscitent un intérêt particulier par la capacité des oiseaux à franchir des distances phénoménales (e.g. la migration d'un pôle à l'autre de la sterne Arctique *Sterna paradisea*; Egevang et al. 2010) et d'importantes barrières écologiques (e.g. la traversée de l'Atlantique du pluvier grand-gravelot *Charadrius hiaticula*, un limicole de petite taille; Léandri-Breton et al. 2019).

Se déplacer dans le temps et l'espace permet aux oiseaux de réduire les variations extrêmes de leur environnement (Dingle 2014). Migrer les expose toutefois aux conséquences des changements climatiques planétaires majeurs qui affectent de manière différentielle la structure et le fonctionnement des écosystèmes (Pecl et al. 2017, Bonan et Doney 2018, IPCC 2019, Riddell et al. 2021, Kubelka et al. 2022). En effet, les migrateurs de longues distances sont particulièrement exposés aux conséquences de ces perturbations étant donné leur besoin de s'adapter à différents milieux durant leur cycle annuel (Crick 2004, Both et al. 2010, Marra et al. 2011). Ils doivent non seulement composer avec les modifications environnementales différentielles entre les aires de reproduction et d'hivernage, mais aussi avec les réponses de leurs proies (Both et Visser 2001, Crick 2004, Both et al. 2010, Doiron et al. 2015, Kubelka et al. 2022). La synchronie entre la reproduction et la disponibilité de nourriture chez ces migrateurs, un des principaux gages de succès (Perrins 1970), peut ainsi en être affectée (Stenseth et al. 2002, Crick 2004, Both et al. 2010, Doiron et al. 2015). Toutefois, alors que les changements climatiques affectent la disponibilité des ressources, la photopériode, un des plus importants stimuli environnementaux amorçant la migration (Berthold 1996, Gwinner 1996), n'est pas affectée (Both et Visser 2001). Ainsi, il importe de mieux connaître le cycle annuel des espèces migratrices pour bien comprendre comment elles réagiront ultimement à ces perturbations.

La migration aviaire

Au cours de leur cycle annuel, les oiseaux migrateurs ont trois activités importantes et exigeantes d'un point de vue énergétique pour lesquelles la synchronie temporelle avec les conditions environnementales est essentielle : la migration, la reproduction et la mue (Alerstam et al. 2003, Hedenström 2008, Newton 2011, Marmillot et al. 2016). La migration se définit alors comme un mouvement de masse directionnel et récurrent d'un nombre important d'individus impliquant un retour vers leur point de départ. Typiquement, il s'agit d'un déplacement saisonnier d'une population entre « deux mondes » (Greenberg et Marra 2005), soit deux sites séparés géographiquement, un site de reproduction et un site d'hivernage (Dingle et Drake 2007, Newton 2008, 2011, Rappole 2013, Dingle 2014). Ce déplacement permet aux animaux de profiter d'un environnement saisonnier et d'augmenter leur succès reproducteur avant de repartir lorsque les ressources diminuent en abondance et ne suffisent plus à assouvir leurs besoins (Fryxell et Sinclair 1988, Newton 2008, McKinnon et al. 2010, Dingle 2014).

Beaucoup d'oiseaux vivent dans des environnements saisonniers où les paramètres sont variables dans le temps et souvent prévisibles (Newton 2011). La migration est alors motivée par différents facteurs écologiques comme l'abondance des ressources, la qualité de l'habitat, le climat, la forte saisonnalité, la pression de prédation et la compétition intra ou interspécifique (Dingle et Drake 2007, Newton 2008, McKinnon et al. 2010). Les ressources abondantes, la longue photopériode, les milieux ouverts, la compétition limitée, la faible abondance de pathogènes et la faible pression de prédation font de l'Arctique un lieu de prédilection pour la nidification chez les oiseaux (Gilg et Yoccoz 2010, McKinnon et al. 2010). Les coûts de la migration sont alors compensés par les bénéfices encourus. Les oiseaux migrateurs peuvent ainsi parcourir de très longues distances à travers le globe et connecter des écosystèmes distants, mais en contrepartie s'exposer à une myriade de menaces en cours de route (Bairlein 2003, Newton 2008, Briedis et Bauer 2018).

La connectivité migratoire se définit par la force des liens entre différentes régions géographiques utilisées par des individus ou des populations migratrices à l'intérieur de l'aire de répartition annuelle de l'espèce (Webster et al. 2002, Marra et al. 2011). Elle représente la tendance qu'ont les individus provenant d'une aire de reproduction déterminée à se rejoindre sur une aire d'hivernage particulière ou sur les haltes migratoires, et inversement (Webster et al. 2002, Newton 2008). Autrement dit, il s'agit de la propension des populations à se mélanger ou à rester indépendantes tout au long de leur cycle annuel. La connectivité suit ainsi un gradient s'échelonnant de très forte, si tous les individus d'un site de reproduction se retrouvent sur le même site d'hivernage, à nulle, s'ils se répartissent à travers toute l'aire d'hivernage de l'espèce et que différentes populations s'y entremêlent (Webster et al. 2002, Webster et Marra 2005, Boulet et Norris 2006, Newton 2008).

Les couloirs et haltes migratoires utilisés, la vitesse de déplacement et les distances parcourues peuvent varier grandement entre les migrations pré-reproductrice (printemps) et post-reproductrice (automne; Kopp et al. 2011, Hedd et al. 2012, Dias et al. 2012, Adamík et al. 2016). Les oiseaux ont avantage à arriver tôt au printemps afin de débuter rapidement la reproduction et, dans certains cas, pour arriver avant leurs compétiteurs (Kokko 1999, Nilsson et al. 2013, Schmaljohann 2018). Un spectre de différentes stratégies permet d'atteindre ce but. À un extrême, les individus accumulent les ressources nécessaires à la reproduction sur les haltes migratoires avant d'atteindre l'aire de nidification hâtivement (*capital breeders*) et à l'autre, ils effectuent un sprint à la fin de la migration et profitent des ressources disponibles sur le site de reproduction (*income breeders*; Drent et Daan 1980, Alerstam 2006). Ces comportements favorisent généralement une stratégie de minimisation du temps durant la migration pré-reproductrice (Nilsson et al. 2013, Zhao et al. 2017) pour arriver à une date optimale au site de reproduction. À l'automne, plusieurs facteurs dont le succès reproducteur et la durée des soins parentaux peuvent influencer le départ ou la phénologie de la migration (Bogdanova et al. 2011, Newton 2011, Guilford et al. 2012, Catry et al. 2013). On note toutefois une grande variabilité dans les stratégies de migration entre les taxons (Schmaljohann 2018), mais également entre les saisons et les populations pour une même espèce (Klaassen et al. 2012, Dias et al. 2012, Bustnes et al. 2013).

Chez plusieurs espèces d'oiseaux, les patrons migratoires présentent de la variabilité en fonction du sexe ou du groupe d'âge des individus. Cette variabilité s'observe tant dans la phénologie que les aires d'hivernage exploitées ou les routes empruntées (Alerstam et al. 2003, Newton 2008, 2011, Balbontín et al. 2009, Paxton et Moore 2015, Thiebot et al. 2015). Ces différences sont habituellement attribuables au rôle différent des sexes dans la reproduction, ainsi qu'à la taille et la dominance (Newton 2008). Pour de nombreuses espèces, les mâles arrivent en premier au site de reproduction, souvent pour prendre possession des meilleurs territoires (Francis et Cooke 1986, Newton 2008, Paxton et Moore 2015). Ces derniers doivent toutefois balancer les risques plus élevés encourus par une arrivée trop hâtive (e.g. accès restreint à la nourriture en raison du couvert neigeux; Bêty et al. 2004) et les bénéfices ultimes de cette stratégie (e.g. meilleur succès reproducteur; Norris et al. 2004a). Par contre, chez d'autres espèces (e.g. mouette tridactyle *Rissa tridactyla;* Bogdanova et al. 2011), l'arrivée des deux sexes au site de reproduction est synchronisée, permettant la réunification des couples (Bried et Jouventin 2002, Gunnarsson et al. 2004).

En hiver, une ségrégation sexuelle des habitats se crée chez certaines espèces. Ainsi, les mâles s'approprient généralement les territoires de plus grande qualité offrant un meilleur accès aux ressources et/ou les territoires les plus proches du site de reproduction (Ornat et Greenberg 1990, Marra 2000, Newton 2008). La compétition pour les ressources près des aires de reproduction et les relations de dominance en fonction de la taille des individus influencent donc la distance de migration et le site d'hivernage utilisé (Alerstam et Hedenström 1998, Newton 2008). Les sites d'hivernage et de mue utilisés peuvent ensuite influencer la durée de la migration, le temps passé sur le site d'hivernage, de même que la phénologie de la migration (Saino et al. 2015, Paxton et Moore 2015).

L'étude de la migration

Depuis la fin du 19e siècle, la pose de bagues et de différents marqueurs sur les oiseaux permet le suivi temporel et spatial des migrations (Bairlein 2001, Newton 2008). L'augmentation du nombre d'oiseaux marqués récupérés et le développement de méthodes statistiques sophistiquées ont permis d'augmenter la résolution temporelle de l'étude des migrations par cette technique (Bairlein 2001). Au fil du temps, les observations visuelles d'individus marqués, le suivi des radars et surtout l'usage de la télémétrie se sont ajoutés et ont permis des études beaucoup plus détaillées des migrations (Bairlein 2003, Newton 2008, Fiedler 2009).

Les avancées technologiques des dernières décennies ont permis d'améliorer considérablement les suivis, notamment grâce aux émetteurs satellites et aux enregistreurs GPS qui permettent un suivi en temps réel des déplacements. Ces dispositifs ont permis l'acquisition d'informations très détaillées et précises sur la migration (e.g. routes, vitesse, phénologie), mais leur prix élevé restreint leur utilisation et la possibilité de déploiement à grande échelle, alors que leur taille importante limite leur usage sur les petites espèces (Bairlein 2003, Newton 2008, Fiedler 2009, Bridge et al. 2011). Des études ont d'ailleurs rapporté que l'usage de ces appareils affectait la reproduction (Ackerman et al. 2004, Whidden et al. 2007) et la survie (Hatch et al. 2000, Thaxter et al. 2016, Anderson et al. 2020) chez plusieurs espèces. Conséquemment, puisque l'usage de tels appareils peut conduire à une augmentation de la dépense énergétique, à l'altération de certains comportements individuels et à une diminution de la survie, de la probabilité de nicher et du succès reproducteur, il importe de faire preuve de vigilance dans leur utilisation et dans l'interprétation subséquente des résultats (Barron et al. 2010). L'utilisation de tels appareils peut d'ailleurs conduire à certains problèmes éthiques et à des enjeux de conservation plus importants dans le cas d'études d'espèces sensibles ou dont les populations sont menacées (Barron et al. 2010).

Avec la poursuite de la miniaturisation technologique et le développement des géolocalisateurs, il est aujourd'hui possible d'étudier les mouvements d'espèces de plus en plus petites (Fiedler 2009). Ces appareils de petite taille (i.e. aussi peu que 0.35 g) sont relativement peu coûteux et permettent des déploiements à large échelle (McKinnon et Love 2018). Les géolocalisateurs enregistrent l'intensité lumineuse, ce qui permet de calculer les variations quotidiennes et annuelles à partir desquelles il est possible d'établir la latitude en fonction de la durée du jour, et la longitude en fonction des heures de lever et coucher de soleil (Hill 1994, Lisovski et al. 2012). Par contre, des facteurs comme les conditions météorologiques, la topographie, la végétation et le comportement de l'animal peuvent ajouter du bruit aux données en ombrageant le capteur photosensible, induisant un biais dans l'estimation des positions (Lisovski et al. 2012). Bien que moins précis que les émetteurs satellites et GPS, ces appareils permettent tout de même d'établir à environ 140-186 km près la localisation des oiseaux (Welch et Eveson 1999, Phillips et al. 2004, Shaffer et al. 2005), une précision suffisante pour étudier les grands mouvements migratoires et les sites d'hivernage utilisés par des espèces parcourant annuellement plusieurs milliers de kilomètres. De plus, de récents développements méthodologiques permettent aujourd'hui d'améliorer le traitement des données, augmentant la précision des localisations estimées (Lisovski et al. 2019, Joo et al. 2020).

Des géolocalisateurs ont été déployés sur bon nombre d'espèces dans les dernières années (Weimerskirch et Wilson 2000, Stutchbury et al. 2009, Egevang et al. 2010, Garthe et al. 2016, Cooper et al. 2017, van Bemmelen et al. 2017, Léandri-Breton et al. 2019, Hromádková et al. 2020). Il a été démontré que leur impact était minimal sur la survie et le comportement malgré l'observation de légers effets au niveau endocrinien, et ce, même chez des espèces de petite taille (Carey 2011, Quillfeldt et al. 2012, Elliott et al. 2012, Kürten et al. 2019). Par contre, ces appareils n'étant que des enregistreurs de données, il faut recapturer les individus afin de récupérer les géolocalisateurs et leur contenu (Fiedler 2009, Bridge et al. 2013). Toutefois, pour des espèces longévives et fidèles au site de reproduction, ceci est peu contraignant avec des taux de retour atteignant parfois 100 % (Weimerskirch et Wilson 2000, Guilford et al. 2009, Bridge et al. 2013).

La reproduction chez les oiseaux

Le compromis entre le besoin pour les oiseaux d'acquérir les ressources nécessaires pour subvenir à leur propre survie et à celle de leur progéniture fait de la reproduction une activité coûteuse énergétiquement, tout comme la mue et la migration (Williams 1966, Martin 1987, Newton 2011). Ce coût se présente sous la forme d'une réduction dans l'efficacité d'autres fonctions essentielles chez un individu reproducteur et/ou dans la probabilité de survivre pour se reproduire à nouveau

(Williams 1966). C'est pourquoi, avant d'amorcer la reproduction et d'y investir son énergie, un oiseau est confronté à une importante décision qui peut entraîner des répercussions substantielles sur sa survie. En fait, se reproduire implique un compromis entre assurer la survie de sa progéniture actuelle sans compromettre ses chances de reproduction futures afin de maximiser son succès reproducteur à vie (*lifetime reproductive success*; Williams 1966, Calow 1979, Erikstad et al. 1998, Newton 2011).

La condition corporelle pré-reproductrice des adultes, la disponibilité de nourriture et la date d'arrivée au site de reproduction, dans le cas des migrateurs, peuvent affecter la décision individuelle de se reproduire, la date et la taille de ponte et, ultimement, le succès reproducteur (Erikstad et al. 1998, Bêty et al. 2003, Therrien et al. 2014a, Harms et al. 2015, Lamarre et al. 2017b). Si un adulte n'a pas acquis préalablement une condition corporelle suffisante, ou si les risques sont trop importants pour lui, il peut produire de plus petites couvées ou simplement éviter de se reproduire (Chastel et al. 1995a, 1995b, Bêty et al. 2003, Harms et al. 2015). D'ailleurs, chez des espèces longévives comme les oiseaux marins, lorsque les conditions ne sont pas favorables à la reproduction, il devient plus avantageux de ne pas se reproduire plutôt que de risquer sa propre survie pour élever des jeunes qui, à leur tour, ont peu de chance de survivre (Williams 1966, Calow 1979, Erikstad et al. 1998).

Pour maximiser leur succès reproducteur et leurs chances de survie, les oiseaux peuvent ajuster la taille et la phénologie de la ponte, un compromis prédit par la théorie (Rowe et al. 1994) et validé empiriquement sur des espèces se reproduisant sur capital (Bêty et al. 2003). La taille de ponte et le niveau de risques à prendre pour protéger la progéniture posent ainsi un dilemme au moment de la reproduction (Williams 1966). Une plus grande couvée à élever peut conduire à une augmentation de la mortalité des adultes ou à un plus faible nombre de jeunes à l'envol en raison du manque de ressources (Lack 1958, Charnov et Krebs 1974). Il est attendu, chez les espèces qui ont un taux de survie annuel élevé, que l'effort investi annuellement dans la reproduction soit moindre que chez celles où le taux de survie est plus faible (Williams 1966, Erikstad et al. 1998, Moreno 2003). C'est pourquoi la plupart des espèces longévives ont de petites couvées, parfois même un seul œuf dans le cas des espèces nidicoles (Gaston 2004).

La phénologie de la reproduction est un déterminant important de son succès, particulièrement dans les environnements saisonniers (Low et al. 2015, Doiron et al. 2015). Un défi chez les reproducteurs est donc de faire coïncider la période d'élevage des jeunes, généralement la période la plus exigeante, avec la période d'abondance et de disponibilité maximale de la nourriture (Perrins 1970, Martin 1987, Visser et al. 1998, Doiron et al. 2015). Trouver le moment idéal n'est pas simple puisque la disponibilité des ressources change durant la saison et les individus doivent anticiper plusieurs semaines à l'avance quand les conditions seront optimales pour élever un jeune (Perrins 1996). Ceci est particulièrement difficile dans le contexte actuel des changements climatiques puisque les oiseaux migrateurs, surtout les migrateurs de longue distance, doivent s'adapter aux modifications environnementales tout au long de leur trajet migratoire (Both et Visser 2001, Crick 2004, Both et al. 2010, Marra et al. 2011). De surcroît, ils doivent aussi s'adapter aux réponses variables dans la phénologie et l'abondance de leurs ressources alimentaires sur les sites de reproduction pour éviter une asynchronie (*mismatch*) entre leurs besoins et la disponibilité de ces ressources (Both et Visser 2001, Crick 2004, Both et al. 2010, Doiron et al. 2015, Grimm et al. 2015, Potvin et al. 2016).

Les pontes plus tardives sont souvent couronnées de moins de succès (Martin 1987, Lepage et al. 2000, Bêty et al. 2003, Harms et al. 2015). Ainsi, elles sont généralement plus petites, une stratégie qui permet de devancer la date d'éclosion et réduire le nombre de jeunes à nourrir, augmentant ainsi leurs chances de survivre (Rowe et al. 1994, Bêty et al. 2003, Descamps et al. 2011). Par ailleurs, une arrivée plus hâtive au site de reproduction engendre souvent une ponte plus hâtive, offrant un plus grand potentiel de succès que pour un nicheur tardif (Bêty et al. 2003, Harms et al. 2015). Cependant, nicher tôt peut avoir des effets délétères sur le succès reproducteur certaines années en raison de conditions météorologiques incertaines et pouvant devenir défavorables après l'initiation de la ponte (Perrins 1970, 1996, Bêty et al. 2004). Finalement, en cas d'échec de reproduction, un individu est confronté à un choix crucial, soit d'entreprendre ou non une deuxième nichée, une situation peu commune chez les espèces dont le cycle reproducteur est long (Martin 1987, Low et al. 2015).

Fidélité au partenaire

La fidélité des individus à leur territoire de reproduction et à leur partenaire peut affecter les composantes du *fitness* (i.e. succès reproducteur et survie; Jankowiak et al. 2018, Leach et al. 2020). En fait, chez les espèces monogames nicher avec un partenaire familier mène généralement à un meilleur succès reproducteur, contrairement à un individu qui niche avec un nouveau partenaire, particulièrement chez les espèces longévives (Black et Owen 1995, Ismar et al. 2010, Sommerfeld et al. 2015). Cette fidélité permet de réduire les coûts liés à la cour, la compétition pour le territoire, la perte d'opportunités de reproduction, ou encore au risque de trouver un partenaire de moins bonne qualité que le précédent (Choudhury 1995, Ismar et al. 2010, Jankowiak et al. 2018, Leach et al. 2020). De plus, il a été démontré chez certaines espèces que nicher avec un partenaire déjà connu et expérimenté permettait de devancer la date de ponte, laissant plus de temps pour élever les jeunes (González-Solís et al. 1999b, Sánchez-Macouzet et al. 2014, Lv et al. 2016).

Néanmoins, le divorce (i.e. prendre un nouveau partenaire pour se reproduire sans que l'autre ne soit mort) pourrait être parfois une stratégie pour maximiser le *fitness* si les bénéfices surpassent les coûts (Choudhury 1995, Naves et al. 2006). Un meilleur partenaire ou territoire, une augmentation de la performance reproductive, ou encore une augmentation de la viabilité de la progéniture représentent des bénéfices potentiels au divorce (Choudhury 1995). L'arrivée tardive d'un individu sur le site de reproduction, où la réunification des partenaires se fait souvent (Bried et Jouventin 2002, Gunnarsson et al. 2004), compte parmi les facteurs qui pourraient favoriser un changement de partenaire, particulièrement chez les espèces moins longévives (Choudhury 1995, Naves et al. 2006, Sánchez-Macouzet et al. 2014). Si le partenaire tarde à arriver, ou s'il est simplement mort pendant la période non-reproductrice, il devient plus avantageux de trouver assez rapidement un nouveau partenaire que d'attendre et risquer de perdre une opportunité de reproduction, ou de commencer à nicher plus tard, augmentant le risque d'échec.

Encore peu d'évidences suggèrent que le succès reproducteur de l'année antérieure peut affecter la probabilité de rétention d'un partenaire, mais Naves et al. (2006) ont démontré qu'un échec tôt en saison augmentait la probabilité de divorce la saison suivante. À l'inverse, plusieurs études ont rapporté l'absence de corrélation entre les deux facteurs, et ce, peu importe le moment de l'échec de reproduction (Choudhury 1995, Ismar et al. 2010, Sommerfeld et al. 2015). Ceci démontrerait que les coûts liés à la recherche d'un nouveau partenaire surpassent ceux liés au maintien du partenaire, même après un échec, dans beaucoup de cas (Sommerfeld et al. 2015). En revanche, une forte corrélation entre la fidélité au territoire de reproduction et au partenaire a été mise en évidence chez plusieurs espèces. Ainsi, dans la situation où le territoire de reproduction sert de point de réunification des couples, si un individu change de territoire, cela pourrait induire un divorce, faisant de ce dernier un effet secondaire de la fidélité au territoire de reproduction (Choudhury 1995, Bried et Jouventin 1999, 2002, Jankowiak et al. 2018).

Les effets reportés

Tout au long de leur cycle annuel, les oiseaux sont confrontés à des conditions environnementales, météorologiques, d'alimentation et de compétition variables et souvent défavorables. Or, les conditions rencontrées pendant une saison peuvent affecter la condition corporelle d'un individu immédiatement, mais peuvent aussi se prolonger au cours des saisons subséquentes, et ainsi affecter des processus comme la phénologie de la migration, la propension à se reproduire, la performance reproductive ou encore la survie (Marra et al. 1998, Bearhop et al. 2004, Harrison et al. 2011, Salton et al. 2015). De tels effets, appelés effets reportés, peuvent survenir à n'importe quelle saison, soit de l'hiver ou de la migration printanière vers la période de reproduction estivale ou encore de la reproduction estivale vers la migration automnale ou la période d'hivernage. Ces effets reportés se définissent donc comme l'ensemble des événements et des processus qui se produisent au cours d'une saison et qui affectent la performance individuelle au cours d'une saison subséquente (Norris 2005, Norris et Marra 2007, Harrison et al. 2011). Ils peuvent affecter les composantes du *fitness* (i.e. survie, reproduction) tant positivement que négativement (Marra et al. 1998, Norris 2005, Norris et Marra 2007, Harrison et al. 2011). Ainsi, les espèces migratrices peuvent subir les conséquences d'une exposition à certaines conditions plusieurs mois après y avoir été exposées ou même à des milliers de kilomètres de là (Gill et al. 2001, Saino et al. 2004), notamment avec des conséquences variables en fonction du sexe (Norris et al. 2004a, Salton et al. 2015, Saino et al. 2017).

Plusieurs exemples d'effets reportés chez les espèces migratrices vivant dans des environnements saisonniers ont été documentés. Par exemple, chez la paruline flamboyante (*Setophaga ruticilla*), les individus qui fournissent un important effort reproducteur ont tendance à décaler la mue pendant la migration, produisant des plumes de moindre qualité et retardant l'arrivée sur les aires d'hivernage. Ce faisant, ils sont contraints à des habitats de moindre qualité (Norris et al. 2004b). Parallèlement, un individu avec des plumes de moindre qualité en hiver aurait une capacité inférieure à s'alimenter ou à défendre un bon territoire (Gill et al. 2001, Harrison et al. 2011). En retour, l'utilisation de ces habitats de moindre qualité en hiver aurait un impact négatif sur le succès reproducteur subséquent, notamment parce que les individus qui hivernent dans les meilleurs habitats arriveraient plus tôt sur les aires de nidification et pourraient acquérir des territoires de meilleure qualité (Marra et al. 1998, Bearhop et al. 2004, Norris 2005, Paxton et Moore 2015). Chez l'hirondelle rustique (*Hirundo rustica*), une mue plus rapide sur l'aire d'hivernage résulte en une arrivée plus hâtive sur l'aire de nidification favorisant un meilleur succès reproducteur (Saino et al. 2004, 2015). Une reproduction plus tardive en raison de conditions défavorables pendant l'hiver ou la migration pourrait retarder l'envol des jeunes, affectant leur nourrissage en préparation à la migration (Norris et al. 2004a). Pour leur part, les oiseaux marins seraient particulièrement sensibles aux effets reportés lorsqu'ils quittent leur site de reproduction pour la haute mer où ils parcourent souvent de très longues distances (Shoji et al. 2015). Plusieurs cas d'effets reportés ont d'ailleurs été documentés au sein de ce groupe (Catry et al. 2013, Salton et al. 2015, Shoji et al. 2015, Crossin et al. 2016, Fayet et al. 2016, Desprez et al. 2018).

Ultimement, les effets reportés peuvent avoir des conséquences au niveau de la dynamique populationnelle (Norris 2005, Norris et Taylor 2006, Betini et al. 2013, Saino et al. 2017), notamment en fonction de la force de la connectivité migratoire (Norris et Marra 2007). En présence d'une forte connectivité, toute la population s'expose aux mêmes conditions locales et stress environnementaux, ce qui la rend plus vulnérable (Webster et al. 2002, Norris et Marra 2007, Briedis et Bauer 2018). Par exemple, dans le cas d'une forte connectivité, si un événement de mortalité de masse ou un stress quelconque se produit sur le site d'hivernage, l'ensemble de la population reproductrice diminuera. À l'inverse, une faible connectivité migratoire permet de tamponner l'effet grâce aux individus provenant d'autres sites d'hivernage qui eux ne sont pas affectés par cet événement.

La compétition interspécifique

La compétition interspécifique se définit comme étant la compétition entre des individus d'au moins deux espèces différentes pour une ressource commune limitée et se manifeste sous deux formes, soit par exploitation ou par interférence (Birch 1957, Krebs 2001, Gotelli 2008). D'abord, la compétition par exploitation survient lorsque des espèces interagissent indirectement (i.e. en utilisant la même ressource et en réduisant donc son abondance pour l'autre espèce), affectant tous les individus de manière plus ou moins égale (Schoener 1983, Krebs 2001). Puis, la compétition par interférence survient lorsque des espèces interagissent directement pour accéder à une ressource (e.g. par la défense d'un territoire de nidification). Dans ce contexte, une espèce va souvent dominer et monopoliser la ressource au détriment des autres (Schoener 1983, Krebs 2001).

La compétition, particulièrement par interférence, peut mener à une ségrégation temporelle ou spatiale dans l'exploitation d'une ressource (Carothers et Jaksić 1984). Pour réduire la superposition de niches et ainsi réduire la compétition interspécifique, une espèce peut alors déplacer sa niche et ajuster ses besoins, par exemple, en modifiant son utilisation de l'habitat ou encore ses techniques d'alimentation (MacArthur 1958, Ashmole 1968, Diamond 1970). Ceci est d'autant plus nécessaire pendant la période de reproduction alors que la compétition peut être très élevée en réponse à l'augmentation des besoins en ressources. Néanmoins, malgré la possibilité de ségréguer l'utilisation de certaines ressources, la présence d'une espèce peut avoir un fort impact négatif sur une autre, alors que cette dernière ne l'affecte que très peu, menant à de la compétition asymétrique (Minot 1981, Gotelli 2008).

Plusieurs études ont permis d'illustrer les mécanismes par lesquels des consommateurs partageant une ressource ou des aires d'alimentation communes arrivaient à coexister. L'exemple classique est celui des plaines de Serengeti où plusieurs prédateurs différencient leur régime alimentaire en sélectionnant une ou des proies en fonction de leur taille (Sinclair et al. 2003). Chez les oiseaux marins, il est fréquent que plusieurs espèces nichant au même site (e.g. une île) partagent les mêmes types de proies marines autour de ce site. Lorsque l'abondance d'une proie commune devient limitante, les espèces compétitionnent alors pour cette ressource. Ainsi, la diversité et la spécialisation des méthodes d'alimentation, le site précis d'alimentation utilisé et la période d'alimentation dans la journée permettent souvent à chaque espèce d'exploiter les mêmes proies de façon différente pour réduire la compétition (Ashmole 1968, Sealy 1973, Wilson 2010, Robertson et al. 2014). Chez les rapaces, une ségrégation des proies consommées, des territoires de nidification ou de la phénologie de la reproduction pour réduire le chevauchement entre la niche des espèces durant les périodes de grande demande énergétique tel l'élevage des jeunes a été observée (Poole et Bromley 1988, Restani 1991, Gerstell et Bednarz 1999).

Selon Lack (1946) et Wiens (1977), l'intensité de la compétition dans les écosystèmes est dynamique et varie temporellement. Ce faisant, l'augmentation de l'abondance d'une ressource contribue à réduire l'intensité de la compétition (Wiens 1977, Schoener 1983). Ainsi, dans un système où les ressources sont pulsées, les pics d'abondance conduisent souvent à une diminution de la compétition (Yang et al. 2008). Inversement, lorsque les ressources se raréfient, l'intensité de la compétition augmente (Wiens 1977, Schoener 1983). L'augmentation de la compétition mène alors à l'exploitation d'un plus grand spectre de ressources (Finke et Snyder 2008).

Le labbe à longue queue (*Stercorarius longicaudus*)

Écologie de la reproduction

Le labbe à longue queue, un oiseau marin longévif (survie annuelle de 91 %; Julien et al. 2013), est fortement pélagique, passant la quasi-totalité de sa vie en mer (Wiley et Lee 2020). Toutefois, en période de nidification, contrairement à la majorité des oiseaux marins, il change complètement son mode de vie pour devenir exclusivement terrestre environ deux semaines avant le début de la ponte (Maher 1970, Gilg et al. 2013, Ruffino et al. 2016, Wiley et Lee 2020). Durant cette période, il cesse complètement de s'alimenter en mer (voir la section *Migration et hivernage*) et s'alimente exclusivement de proies terrestres jusqu'à son retour en mer à la fin de la reproduction (Maher 1970, Andersson 1971, 1976a). Ainsi, les lemmings brun (*Lemmus trimucronatus*) et variable (*Dicrostonyx groenlandicus*) constituent les proies principales du labbe à longue queue sur la majorité des sites étudiés (Maher 1970, Andersson 1976a, Ruffino et al. 2016, Wiley et Lee 2020). Des proies alternatives sont néanmoins consommées, particulièrement lorsque les lemmings sont moins abondants. Parmi ces dernières se trouvent une part importante d'arthropodes, mais aussi des passereaux, des limicoles, et des baies dans certaines régions de l'Arctique (Maher 1970, Andersson 1971, 1976a, de Korte et Wattel 1988, Ruffino et al. 2016).

En général, la quête alimentaire du labbe à longue queue s'effectue à l'intérieur d'un territoire d'environ 1 km^2, soit dans un rayon de 600 à 700 m du nid (Maher 1970, Andersson 1971, 1976a). Pour nicher, les labbes s'installent préférentiellement en milieu mésique dans les premiers endroits découverts de neige au printemps, notamment sur de petits monticules de tourbe, un sol de gravier entouré de basse végétation, ou des flancs de collines à faible pente (Andersson 1971, de Korte 1985, Meltofte et Høye 2007). Cet environnement leur procure un point de vue sur l'entièreté du territoire facilitant sa défense (Andersson 1971). D'ailleurs, ces oiseaux étant territoriaux entre eux, ils repèrent tout intrus ou prédateur potentiel à grande distance et tentent de les repousser en les harcelant (de Korte 1986, Wiley et Lee 2020). Afin de garder le nid le plus cryptique possible et réduire le risque de prédation, les labbes ne construisent pas de structure, mais utilisent plutôt de légères dépressions dans le sol pour y pondre leurs œufs, le plus souvent deux mais jamais plus (Andersson 1971, 1976b).

Le labbe étant fidèle à son territoire de reproduction, il y revient année après année (Maher 1970, Andersson 1981, Meltofte et Høye 2007). Néanmoins, la densité de labbes sur les sites de reproduction est très variable annuellement, étant fortement influencée par l'abondance de proies. En effet, la densité peut atteindre environ 1 couple/km^2 lors des pics de lemmings, mais être très faible, voire nulle, en période de creux (Andersson 1976a, 1981, Gilg et al. 2006, Meltofte et Høye 2007, Therrien et al. 2014a, Julien et al. 2014). Le mâle et la femelle contribuent tous deux dans l'incubation et l'élevage des jeunes, mais avec une prépondérance pour la femelle, le mâle contribuant plus dans la défense du territoire et la chasse (Andersson 1971, de Korte 1985, Furness 1987). Un à deux jours après l'éclosion, les jeunes, nidifuges, quittent le nid pour s'alimenter et se camoufler, mais restent sur le territoire parental jusqu'à leur envol environ trois semaines plus tard (Maher 1970, Andersson 1971, 1976a). Lorsque l'élevage des jeunes est terminé, environ une dizaine de jours après le premier envol, les adultes entreprennent leur migration et abandonnent les jeunes à eux-mêmes (Wiley et Lee 2020).

Migration et hivernage

À ce jour, peu d'études se sont intéressées à la migration et la distribution hivernale du labbe à longue queue et les observations de l'espèce au large ou près des côtes sont peu nombreuses (Wiley et Lee 2020). Gilg et al. (2013) et van Bemmelen et al. (2017) ont toutefois suivi plusieurs individus à l'aide de géolocalisateurs et Sittler et al. (2011) à l'aide d'émetteurs satellites. Ils ont identifié les haltes migratoires et les sites d'hivernage utilisés par les populations européennes et de la côte est du Groenland. Après leur reproduction en région Arctique, les labbes de ces populations entreprennent une migration vers une halte migratoire au large des Grands Bancs de Terre-Neuve, suivi d'une migration de plusieurs milliers de kilomètres pour atteindre les sites d'hivernage le long de la côte ouest-africaine dans l'hémisphère austral. Ce faisant, les labbes figurent parmi les plus grands migrateurs transéquatoriaux.

Le régime alimentaire des labbes en mer, notamment sur les aires d'hivernage, est très peu connu (Furness 1987, Wiley et Lee 2020). Il a cependant été rapporté que les labbes se nourrissent de petits poissons et d'invertébrés capturés à la surface et qu'ils sont parfois attirés par les rejets des bateaux de pêche (Wiley et Lee 2020). Également, les Stercorariidae sont reconnus pour s'alimenter par kleptoparasitisme (Furness 1987). Or, le labbe à longue queue ne fait pas exception, mais ce comportement en mer serait moins présent que chez les autres espèces de cette famille, possiblement en raison de sa plus petite taille. Toutefois, il profiterait d'agrégations d'oiseaux de petite taille en mer pour s'alimenter. Par ailleurs, les sites d'hivernage utilisés par le labbe à longue queue coïncideraient avec des régions marines très productives, particulièrement l'*upwelling* du Benguela (Shannon et O'Toole 2003, Chavez et Messié 2009, Grecian et al. 2016). Cette zone d'hivernage, tout comme la halte migratoire en Atlantique Nord, constituent des sites utilisés par plusieurs espèces marines (Shannon et O'Toole 2003, Crawford 2007, Boertmann 2011, Scales et al. 2014, Davies et al. 2021).

À l'instar de la fidélité des labbes à leur site de reproduction (Maher 1970, Andersson 1981, Meltofte et Høye 2007), van Bemmelen et al. (2017) ont démontré une certaine fidélité dans les routes migratoires et les sites d'hivernage individuels. Malheureusement, il n'existe aucune information sur les trajets migratoires ou les sites d'hivernage des labbes à longue queue nichant en Arctique canadien.

Le réseau trophique de la toundra arctique

Le réseau trophique de la toundra arctique auquel le labbe à longue queue appartient en été est somme toute relativement simple étant composé d'un faible nombre d'espèces et présentant peu de structure d'habitat pour le supporter (Krebs et al. 2003, Gauthier et al. 2011, Legagneux et al. 2012b). Plusieurs espèces de prédateurs terrestres et aviaires y sont néanmoins présentes et dépendantes d'un faible nombre de proies potentielles pour y vivre (Krebs et al. 2003, Gilg et al. 2006, Gauthier et al. 2011, Legagneux et al. 2012b). Parmi les proies essentielles structurant l'écosystème de la toundra, on compte les lemmings brun et variable, deux espèces de taille similaire (Ims et Fuglei 2005, Schmidt et al. 2012, 2020). Il s'agit d'une ressource pulsée, car ces espèces présentent des fluctuations d'abondance pouvant aller jusqu'à 100 fois entre les années de pic et de creux (Gilg et al. 2006, Fauteux et al. 2015, Ehrich et al. 2020). Le lemming brun accomplit des cycles de grandes amplitudes tous les trois ou quatre ans, alors que le lemming variable subit des fluctuations de population de moindre amplitude (Gruyer et al. 2008, Fauteux et al. 2015). Ces fluctuations d'abondance peuvent avoir une grande influence sur la densité annuelle de prédateurs qui en dépendent pour leur reproduction et leur survie (Gilg et al. 2006, Therrien et al. 2014a).

La simplicité du réseau trophique de la toundra et l'absence de structure érigée peuvent mener à une forte compétition pour la ressource alimentaire entre les prédateurs aviaires. Parmi les principaux, on note le labbe à longue queue, le harfang des neiges (*Bubo scandiacus*), la buse pattue (*Buteo lagopus*) et le goéland bourgmestre (*Larus hyperboreus*). Le harfang des neiges, un spécialiste des lemmings, est une espèce irruptive et fortement nomade (Therrien et al. 2014a, 2014b, Holt et al. 2020). Sa présence sur un site de reproduction en Arctique dépend grandement de l'abondance de sa source de nourriture de prédilection, les lemmings (Gilg et al. 2006, Therrien et al. 2014a). Il s'agit en fait du plus gros prédateur aviaire de l'Arctique et son habitat de nidification, la toundra mésique, ressemble beaucoup à celui du labbe à longue queue. La buse pattue dépend aussi fortement des lemmings et son effort de reproduction est intimement lié à leur abondance (Therrien et al. 2014a, Terraube et al. 2015, Beardsell et al. 2016). Par contre, elle niche principalement en bordure des falaises, sur des affleurements rocheux et sur des versants escarpés, un habitat qui n'est pas utilisé par les labbes (Beardsell et al. 2016, Bechard et al. 2020). Le goéland bourgmestre, bien qu'il s'agisse d'une espèce marine, est un prédateur généraliste qui s'alimente surtout de ressources terrestres, notamment de lemmings, en été (Samelius et Alisauskas 1999, Gauthier et al. 2015). Il niche sur des îlots en bordure des lacs et des étangs, mais également en bordure de la mer et des deltas de rivière (Gauthier et al. 2015, Weiser et Gilchrist 2020), des sites peu fréquentés par les labbes. Néanmoins, cette espèce utilise un vaste territoire d'alimentation pendant la reproduction incluant l'habitat préféré par les labbes pour la reproduction. D'autres prédateurs aviaires sont aussi présents à faible densité et s'alimentent occasionnellement de lemmings (i.e. faucon pèlerin *Falco peregrinus*, faucon gerfaut *F. rusticolus*, labbe parasite *Stercorarius parasiticus*, grand corbeau *Corvus corax*; Gauthier et al. 2011). Finalement, deux prédateurs terrestres sont présents et s'alimentent aussi fortement de lemmings, soit le renard Arctique (*Vulpes lagopus*) et l'hermine (*Mustela erminea*; Gauthier et al. 2011). Qui plus est, la brièveté de l'été Arctique limite la fenêtre temporelle disponible pour la reproduction, restreignant la possibilité d'un décalage phénologique dans l'arrivée des migrateurs, la reproduction et l'exploitation des proies communes (Gauthier et al. 2011).

Objectifs de la thèse

Cette thèse s'insère parmi dans les études à long terme de l'écosystème arctique de l'Île Bylot, Nunavut (73°08 N, 80°00 O; Gauthier et al. 2011, 2013). Ce suivi écosystémique touche un grand nombre d'espèces aviaires et mammaliennes qui ont notamment été étudiées de manière approfondie pour mieux comprendre leur dynamique individuelle et les interactions trophiques (e.g. Legagneux et al. 2012b). Cependant, peu d'études à travers l'Arctique se sont attardées à l'écologie d'un des prédateurs aviaires les plus abondants de la toundra, le labbe à longue queue (Gilg et al. 2006, Meltofte et Høye 2007, Julien et al. 2013, 2014, Therrien et al. 2014a) et aucune en Arctique canadien ne s'est intéressée à sa migration (Sittler et al. 2011, Gilg et al. 2013, van Bemmelen et al. 2017). Parallèlement, encore peu d'études ont déterminé les effets à long terme des conditions hivernales chez les migrateurs de longue distance, car il est difficile d'établir un lien avec ce qui se passe entre les saisons chez les espèces exploitant différentes régions géographiques (Harrison et al. 2011, Salton et al. 2015, Clausen et al. 2015, Paxton et Moore 2015). Ceci est particulièrement le cas chez les oiseaux marins lorsqu'ils quittent l'aire de reproduction pour retourner en mer (Gjerdrum et al. 2008). Finalement, encore aucune étude ne s'est intéressée à la dynamique et aux mécanismes permettant la coexistence de plusieurs prédateurs aviaires qui s'alimentent de deux espèces de proies dont les populations fluctuent grandement entre les années, des conditions propices à une forte compétition interspécifique.

Dans un premier temps, cette thèse a pour objectif d'étudier la reproduction, la migration et l'hivernage du labbe à longue queue pour mieux comprendre comment ces phases de son cycle annuel s'influencent par le biais d'effets directs et reportés. Dans un second temps, elle vise à mieux comprendre les interactions entre le labbe à longue queue, sa principale source de nourriture estivale, les lemmings, et les autres prédateurs aviaires exploitant cette ressource en période de reproduction dans un milieu où toutes les conditions sont réunies pour favoriser une forte compétition interspécifique.

Organisation de la thèse

Le premier chapitre établit une relation entre les mesures morphométriques et le sexe des individus chez le labbe à longue queue. Étant donné l'absence de dimorphisme sexuel au niveau du plumage et le peu de distinction dans leurs comportements en période de reproduction, des analyses génétiques étaient nécessaires pour connaître le sexe. J'ai donc testé si une combinaison de mesures morphométriques pouvait représenter une méthode simple et fiable pour identifier avec exactitude le sexe des individus sur le terrain.

Le deuxième chapitre a d'abord comme objectif de documenter et décrire les routes migratoires et les aires d'hivernage exploitées par la population de labbes à longue queue nichant dans l'est de l'Arctique canadien à l'aide de géolocalisateurs. Ensuite, il vise à mieux comprendre les paramètres de ces trajets (i.e. vitesse, distance, durée…) pour dégager les patrons généraux en fonction du sexe des individus et au sein de la population en général. À la lumière de ces données, j'ai comparé les stratégies adoptées pendant les migrations d'automne et de printemps. L'objectif est de vérifier si le labbe utilise une stratégie de minimisation du temps en migration au printemps, comme observé chez beaucoup d'espèces d'oiseaux, particulièrement en Arctique où la saison de reproduction est courte et les contraintes temporelles très fortes.

Le troisième chapitre s'inscrit dans la suite du précédent et a pour objectif de tester la présence d'effets reportés réciproques entre la migration, la période d'hivernage et différents paramètres de la reproduction des labbes. De plus, il vise à vérifier l'influence des facteurs locaux (e.g. abondance de lemmings) sur les paramètres de la reproduction.

L‘objectif du quatrième chapitre est d'évaluer la fidélité interannuelle des labbes à leur partenaire et à leur site de reproduction en fonction du succès de la reproduction et, inversement, l'effet de cette fidélité sur la reproduction.

L'objectif du cinquième et dernier chapitre de ma thèse est de comprendre les mécanismes favorisant la coexistence de quatre prédateurs aviaires d'une même guilde se partageant une ressource commune, les lemmings. La simplicité du réseau trophique de l'Arctique du fait de la très faible diversité de proies et les irruptions périodiques d'abondance de ces proies représentent une situation où la compétition interspécifique devrait être intense. De plus, les variations dans la composition de la guilde de prédateurs entre les années de faible et de forte abondance de proies offrent une excellente opportunité pour examiner les conséquences d'un relâchement de la compétition sur les autres espèces de prédateurs et en particulier sur le labbe.

Chapitre 1 – Sexing a monomorphic plumage seabird using morphometrics and assortative mating

Labbe à longue queue

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1.1 Résumé

Identifier le sexe d'oiseaux présentant peu de dimorphisme sexuel sans recourir à des analyses génétiques est particulièrement complexe. L'objectif de cette étude était d'établir une méthode fiable basée sur des mesures morphométriques pour identifier le sexe du labbe à longue queue (*Stercorarius longicaudus*), une espèce présentant un faible dimorphisme de taille entre les sexes et aucun au niveau du plumage. L'étude a aussi vérifié la présence d'un appariement assorti basé sur la taille des individus pour déterminer si des différences intra-couple dans la taille pouvaient améliorer l'identification du sexe. Soixante-seize labbes, incluant 26 couples nicheurs, ont été mesurés et sexés génétiquement sur l'Île Bylot (Nunavut, Canada) durant les étés 2014 à 2018. Les oiseaux ont été pesés et mesurés (aile, tarse, tête, rectrices) et des plumes ont été prélevées à la poitrine pour identifier le sexe à l'aide d'analyses génétiques. Une première fonction discriminante basée sur la masse et la longueur d'aile a permis de sexer 83% des individus avec exactitude. Des évidences d'un appariement assorti positif basé sur la taille ont été notées, car la masse corporelle des individus à l'intérieur d'un couple était positivement reliée et 88% des femelles avaient une masse supérieure à celle de leur partenaire. Une seconde fonction considérant la masse, la longueur d'aile et des rectrices centrales et la masse du partenaire a permis d'augmenter le succès de classification à 92%. L'ajout d'informations sur le partenaire a réduit l'erreur de classification de moitié (17% vs 8%). Enfin, malgré le faible dimorphisme sexuel des labbes, l'utilisation d'une combinaison de mesures morphométriques a permis de sexer les individus avec confiance sans recourir à des analyses génétiques. De plus, considérer les mesures des deux partenaires d'un couple augmente considérablement l'exactitude du sexage grâce à la présence d'un appariement assorti.

Mots clés : Analyses discriminantes · Dimorphisme sexuel · Identification du sexe · Labbe à longue queue · Mesures morphométriques · Oiseaux marins · Sexage génétique · *Stercorarius longicaudus*

1.2 Abstract

This study aimed to establish a reliable method based on morphometrics to sex long-tailed jaeger (*Stercorarius longicaudus*), a species with slight differences in body size between sexes but no plumage differences. The presence of assortative mating based on size was also examined to determine if within-pair differences in size could improve sexing. Seventy-six long-tailed jaegers were measured, including 26 breeding pairs, on Bylot Island (Nunavut, Canada) during summers 2014-2018. Bird weight, wing chord, tarsus, head, and tail feathers were measured, and breast feathers were collected to determine sex with DNA extracts. A first discriminant function based on two variables (body mass and wing chord) accurately sexed 83% of birds. Some evidence for positive assortative mating based on size was found, as body mass of pair members was positively related, and 88% of females were heavier than their partner. A second discriminant function that included body mass, wing chord, length of the central tail feather, and partner's body mass accurately sexed 92% of birds. Adding a new morphometric and information from the partner allowed a reduction in sex misclassification by half (17% vs. 8%). In conclusion, external body measurements are useful to sex long-tailed jaegers, a slightly dimorphic species, and measurements of both members of a pair considerably improve the accuracy of sexing, likely due to the presence of assortative mating.

Key words: Discriminant analysis · Genetic sexing · Long-tailed jaeger · Morphometrics · Seabirds · Sex identification · Sexual dimorphism · *Stercorarius longicaudus*

1.3 Introduction

Being able to correctly identify the sex of animals in the wild is essential in many situations. Indeed, most life history traits and behavior of animals differ between sexes (Roff 1992, Dingle and Drake 2007, Dobson 2013). Many bird species present conspicuous sexual dimorphism in plumage or size, which easily allows sexing of individuals in hand or even at distance. However, sexing of individuals may be very challenging in species that exhibit little or no differences in plumage or size. This is the case in many seabirds, which are often monomorphic based on their external appearance and present small size differences between sexes (Fairbairn and Shine 1993).

The long-tailed jaeger (*Stercorarius longicaudus*) is a typical seabird species that does not exhibit conspicuous external sexual dimorphism. Although the species shows reverse size dimorphism (Wiley and Lee 1998), the size difference between male and female is subtle, and standard body measurements are unhelpful for sexing this species reliably according to Pyle (2008). Plumages are also virtually identical between the two sexes, even though Manning et al. (1956) reports that females are on average more extensively dusky on lower breast and belly than males within the same population. However, differences in coloration may be subjective and hard to observe, especially in the field. Behavioral observations can sometimes help sexing but are time-consuming and difficult to apply, especially in species where both sexes incubate, feed young, and defend the territory like jaegers (Furness 1987). Genetic analysis can reliably sex monomorphic species (Fridolfsson and Ellegren 1999). The Polymerase Chain Reaction (PCR) based method, commonly used in ecology, requires access to specialized laboratories and can be expensive. Even though recent *in situ* methods such as loop-mediated isothermal amplification (LAMP) are getting more popular, specialized equipment are still needed, and they may not be adapted to all field situations (Centeno-Cuadros et al. 2017, Koch et al. 2019).

As an alternative, attempts have been made to sex seabirds with a combination of morphometrics. Several statistical methods have been used to differentiate the sex of monomorphic birds, and Linear Discriminant Analysis (LDA) is most often used in the literature. Statistical models based on a combination of morphometrics were successfully developed to sex seabirds such as the Atlantic puffin (*Fratercula arctica*; Friars and Diamond 2011), Arctic tern (*Sterna paradisaea*; Devlin et al. 2004), black-legged kittiwake (*Rissa tridactyla*; Jodice et al. 2000), black-browed albatross (*Thalassarche melanophrys*; Ferrer et al. 2016), great skua (*Stercorarius skua*; Hamer and Furness 1991) and parasitic jaeger (*Stercorarius parasiticus*; Phillips and Furness 1997).

Some studies have shown that within-pair differences in external appearance can improve the accuracy of sexing (Ainley et al. 1985, Jodice et al. 2000, Fletcher and Hamer 2003). For example, in the short-tailed shearwater (*Puffinus tenuirostris*), within-pair comparison of morphometrics improved the accuracy of LDA models from 84% to 92% (Carey 2011). Within-pair differences are typically due to assortative mating, defined as a pattern of non-random mating between male and female, based on some phenotypic criteria (Jiang et al. 2013). It can be either positive, in which case individuals tend to mate with similar partners, or negative, in which case they avoid similar partners (Jiang et al. 2013). Even though assortative mating appears weaker in birds compared to other phyla, it was documented in several species including in the lesser snow goose (*Anser caerulescens*; Cooke et al. 1976), brant (*Branta bernicla*; Abraham et al. 1983), black grouse (*Lyrurus tetrix*; Rintamäki et al. 1998), brown noddy (*Anous stolidus*; Chardine and Morris 1989), parasitic jaeger (Furness 1987, Phillips and Furness 1997) and several falconids (Olsen et al. 1998). In all those situations, researchers were able to demonstrate that birds are not mating randomly with respect to their appearance. However, some studies did not find assortative mating based on morphometrics (black guillemot, *Cepphus grylle*; Berzins et al. 2009).

Our objective was to establish a reliable and simple method to sex long-tailed jaegers captured in the field with morphometrics. First, we examined if discriminant analysis based on a combination of body measurement could be used to sex long-tailed jaegers. Second, we determined if assortative mating based on size was present in this species, and if within-pair size differences could be used to improve the accuracy of sexing.

1.4 Methods

1.4.1 Study site and field methods

The fieldwork was conducted from 2007-2018 in the lowland tundra of Bylot Island (Nunavut) (73° 09′ 00.00″ N 79° 58′ 60.00″ W) in the Canadian High Arctic (Gauthier et al. 2013). A breeding population of long-tailed jaeger has been studied at this site since 2007. Nest searches were carried out annually in late June/early July and monitored until hatching. We captured males and females, marked them with metal and plastic bands, and took several body measurements. Birds were most often captured at the nest using a bownet trap, or in the nest vicinity using a bal-chatri trap with a live lemming inside, a noose carpet with quail or goose eggs, or a netgun when birds were not breeding.

All captured birds were weighed (± 0.5 g) with a Pesola spring scale, and we took six external body measurements. We checked the 0 on the spring scale daily, and adjusted it if needed. Culmen length (from the tip of the bill to the first feathers at the base of the maxillary), total head length (from the tip of the bill to the rear of the skull), and tarsus length (from inter-tarsal joint to the base of the toes) were measured with calipers (± 0.1 mm). We took two measurements of the rectrices with a ruler (± 0.5 mm): the longest central tail feather (R1) and the longest tail feather excluding R1. We measured wing chord from the carpal joint to the end of the longest primary feather using a stop-end ruler (± 0.5 mm). For birds that were measured more than once, we randomly selected one set of measurements for the analyses.

We estimated laying date of breeding pairs as follows. If the nest was found between laying of the first and second egg, laying date was considered to be the day before the visit. If only one egg was laid or if the nest was found after both eggs were laid, eggs were floated and the incubation stage was established based on Furness and Furness (1981) and Liebezeit et al. (2007). If the nest was visited at hatching, laying date was estimated by subtracting the mean incubation length (24 days; Maher 1970) to the hatching date.

1.4.2 Molecular sexing

We plucked three feathers on the breast of jaegers at the time of capture, or in a few cases, we took a blood sample (a few drops) from the brachial vein in order to sex birds using DNA analysis. Feathers were preserved in a paper envelope at ambient temperature and we extracted DNA from a small piece (3-5 mm) of pulp at the bottom of the calamus. Blood samples were preserved in Queen's lysis buffer (0.01 M Tris, 0.01 M NaCl, 0.01 M EDTA, and 1% n-lauroylsarcosine, pH 7.5) until analyses (Seutin et al. 1991). We used a salt extraction protocol modified from Aljanabi and Martinez (1997). The pulp sample was dropped in a solution of 440 µl of salt extraction buffer (0.4 M NaCl, 10 mM Tris–HCl and 2 mM EDTA), 44 µl of SDS 20% and 8 µl of proteinase K (20 mg/ml). The sample was incubated overnight at 50 to 57°C on a stirring plate, and 300 µl of 6 M NaCl solution was added to the sample. Sample was vortexed for 30 sec and then centrifuged at 10 300 rpm for 30 min. Six hundred microliters of supernatant was transferred into a new tube to which 600 µl of isopropanol (at -20°C) was added and mixed by gently inverting the tubes. The sample was incubated at -20°C for at least 1 hr and centrifuged at 13 000 rpm for 20 min. The supernatant was discarded and 200 µl of 70% ethanol (at -20°C) added to the tube. The sample was centrifuged at 13 000 rpm for 10 min and the supernatant discarded again. The pellet was washed a second time to remove all the remaining isopropanol. Samples were air-dried overnight at 37°C and resuspended in 50 µl of sterile water. Since the quantity of DNA was low in the samples, it was important to resuspend it in a small volume of water. The sample was refrigerated at 4°C overnight before DNA amplification.

DNA was amplified by a Polymerase Chain Reaction (PCR) based on Fridolfsson and Ellegren (1999) using a GeneAmp PCR System 9700 (Applied Biosystems). PCR reaction were done with a 10 µl volume composed of 5 µl of AccuStart II (Quantabio) PCR SuperMix, 0.25 µl of primers 2550F (5′-GTTACTGATTCGTCTACGAGA-3′) and 2718R (5′-ATTGAAATGATCCAGTGCTTG-3′), 2.5 µl of sterile water and 2 µl of DNA. The thermal profile was almost identical to the one described in Fridolfsson and Ellegren (1999) except the initial denaturing step lasted 4 min (instead of 2 min) and the extension in the 35 additional cycles lasted 45 sec (instead of 40 sec).

To determine the sex of the amplified DNA samples, a 3% agarose gel electrophoresis was conducted in TBE buffer with ethidium bromide staining. Eight microliters of each DNA sample was placed on the agarose gel under a current of 125 V for approximately 45 min. Sex was determined by the amplification of a part of the CHD1 gene. Under UV-light, males (homogametic ZZ) display a single band (CHD1W – 400 to 450 bp) while females (heterogametic ZW) display two bands (CHD1W – 400 to 450 bp, and CHD1Z – 600 to 650 bp).

1.4.3 Data analyses

Body mass can fluctuate over time and especially during the breeding season (Norberg 1981, Croll et al. 1991, Jones 1994), which could be a source of error when using this trait in the same analysis along with morphological measurements (van Franeker and ter Braak 1993, Lorentsen and Røv 1994). We verified if seasonal change in body mass could be a confounding factor by regressing this variable on breeding stage, estimated by number of days after laying as described above, using a linear mixed-effects model (one for each sex) with the capture year as random effect using the *nlme* package (Pinheiro et al. 2018). We used all breeding individuals captured from 2007-2018 for which the incubation date and the sex were known (n = 44 females and n = 40 males). We verified the amount of variation explained by the model using the marginal R^2_m for fixed effects (Nakagawa and Schielzeth 2013). Body mass was not significantly related to incubation stage in either females (slope = -0.83 g/day; 95% CI -1.89 to 0.22; $R^2_m = 0.07$) nor males (slope = -0.16 g/day; 95% CI -1.14 to 0.83; $R^2_m < 0.01$). Considering that most birds were measured between day 7 and 21 of the incubation period, this represents a potential mean mass loss of 11.7 g for females and 2.2 g for males over this 14 day period, or 3.7% and 0.8% of their body mass, respectively. We thus concluded that body mass could be used in our analyses without any correction.

To build equations to sex jaegers based on morphometrics, we used only birds captured from 2014-2018 because they were all measured by the same two experienced observers, which minimizes inter-individual variability. We did not attempt to do a correction for the observer and assumed that differences would be attributable to within-measurements error instead of between observers as in Devlin et al. (2004).

We used a Multivariate Analysis of Variance (MANOVA) with six morphometric characters to test for overall body size differences between sexes. We excluded culmen length because it was correlated with head length (Pearson $r = 0.52$; for all other measurements, $r \leq 0.35$). If the global MANOVA was significant, we further conducted univariate ANOVA on each measurement separately. MANOVA was done using a Pillai's Trace test because it is more robust to the deviation of the multivariate normality than the Wilk's Lambda (Quinn and Keough 2002).

We used Linear Discriminant Analysis (LDA) from the *caret* package (Kuhn 2018) with the leave-one-out cross-validation method to establish the best discriminant model. Data were scaled and centered by subtracting the mean and dividing by the standard deviation. Even if the dataset was unbalanced (see above), the prior probability was set to 0.5 for each sex since we had no reason to believe that the population was unbalanced. The model with the highest Youden's index (Youden 1950), Matthew's correlation coefficient (MCC) (Matthews 1975), and discriminant power (DP) (Blakeley et al. 1995) was considered as being the best-fitted model and selected to create the classification function. Homoscedasticity (homogeneity of the variance-covariance matrix) was tested using Box's M test ($\chi^2_{21} = 24.4$, $P = 0.27$) and univariate normality was verified with Shapiro-Wilk's test ($P > 0.05$ for all measurements except for tarsus [$W = 0.94$, $P = 0.002$] and tail excluding R1 [$W = 0.97$, $P = 0.03$]). Because the discriminant analysis is robust to the non-respect of the normality, data were not transformed (Tabachnick and Fidell 2007).

To evaluate the presence of assortative mating, we related morphometrics of pair members with a reduced major axis regression (*lmodel2* package; Legendre 2018). To evaluate within-pair differences, we performed a two-sided paired t-test for all morphometrics. We also simulated ($n = 200$ simulations) 26 random pairs (the same number as in our study) by randomly selecting with replacement females and males among the pool of individuals that we measured. For each simulation, we calculated the proportion of pairs where the female was heavier or had longer wing than their partner, and we related measurements of pair members together. Finally, we repeated the LDA by adding information from the partner to see if it could improve accuracy of our models. We added partners' variables that differed significantly within-pairs to those retained in models that presented an accuracy >80% in the previous LDA and reran all those models considering that the dataset was not exactly the same here (reduced sample size).

We evaluated the efficiency of the discriminant function equations developed in this study to sex long-tailed jaegers (see Results) by applying them to an independent dataset of birds measured on Bylot Island from 2007-2010 by another observer. All the analyses were done in R (R Core Team 2018).

1.5 Results

We used a sample of 76 individuals (43 females and 33 males) measured by the two experienced observers from 2014-2018 for the main analyses presented in this paper. Among those, we captured both members of 26 different breeding pairs, including three pairs that had the same male or female that mated with a different individual in a subsequent year. We used an additional sample of 26 individuals (10 females and 16 males) measured from 2007-2010, including four pairs, to test equations developed in the previous analyses. Most individuals used in the analyses were sexed using DNA, but in some cases (n = 7), only one member of a pair was sexed with molecular methods. As no same sex pairs of long-tailed jaeger were found based on DNA sexing of both partners (n = 29 pairs), the sex of those seven individuals was assigned based on their partner's sex.

The MANOVA showed a significant difference between males and females based on six morphometrics ($F_{1,69} = 11.1$, Pillai = 0.49, $P < 0.001$). However, univariate comparisons revealed significant differences only for wing chord and body mass (Table 1.1), with females being 10% heavier than males and their wing cord 2% longer than males on average. All measurements showed a high degree of overlap between the two sexes, even for wing chord and body mass (Figure 1.1).

Table 1.1 Morphometrics ($\bar{x}$ ± SD) of male and female long-tailed jaegers (*Stercorarius longicaudus*) and comparison between sexes based on a MANOVA (n = 76 individuals).

Variable	Female	Male	$F_{1,69}$	P
Head length (mm)	70.6 ± 1.8	71.0 ± 1.8	0.92	0.34
Tarsus length (mm)	43.5 ± 2.1	42.9 ± 1.5	1.89	0.17
Wing chord length (mm)	315.5 ± 5.6	308.5 ± 8.7	18.24	< 0.001
Tail length (R1) (mm)	298.5 ± 24.5	298.3 ± 21.1	< 0.01	0.97
Tail length (excluding R1) (mm)	128.9 ± 7.3	127.6 ± 7.7	0.62	0.43
Body mass (g)	317.8 ± 21.1	286.1 ± 18.5	46.74	< 0.001

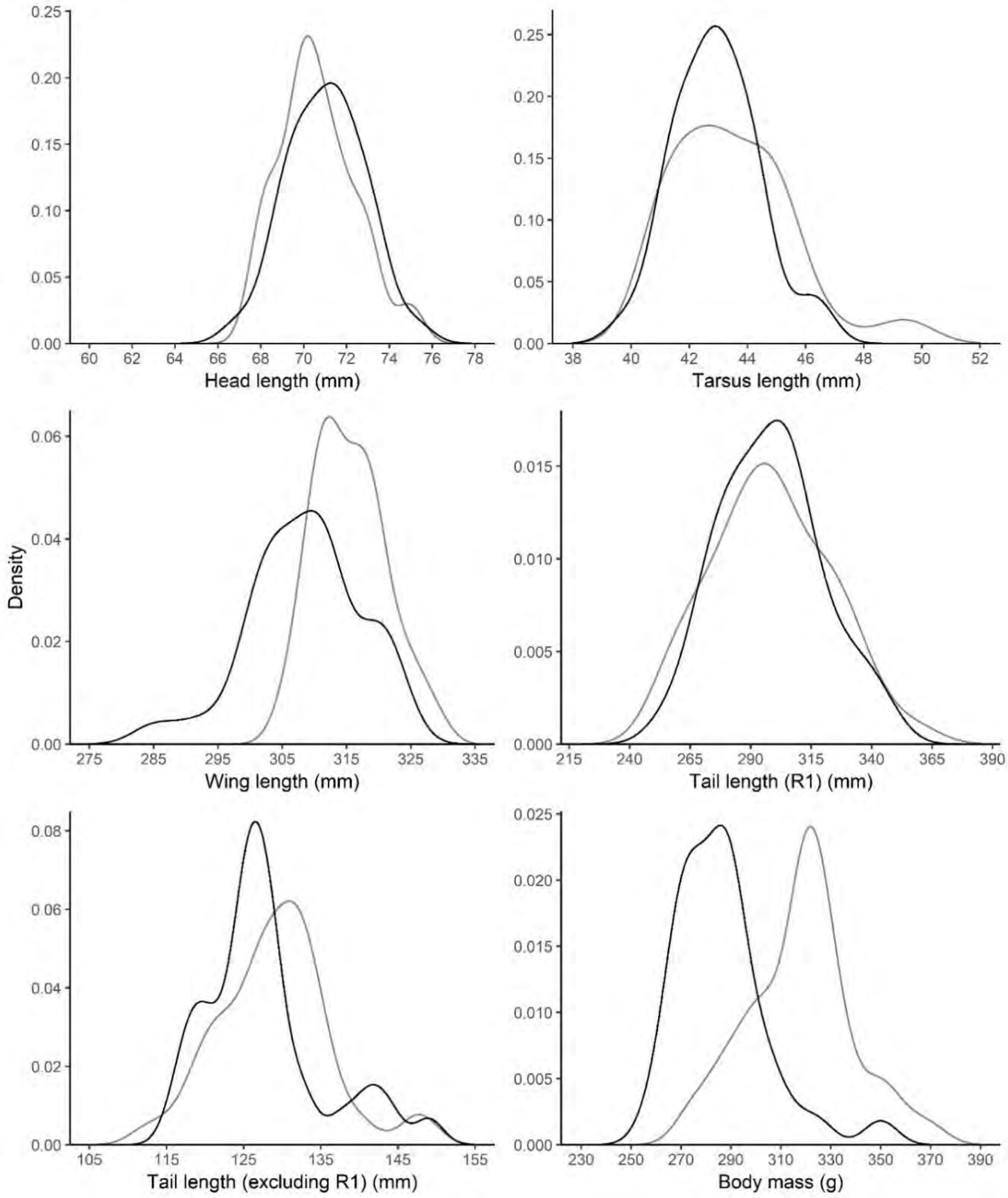

Figure 1.1 Density plot of six morphometrics of male (black curve) and female (grey curve) long-tailed jaegers (*Stercorarius longicaudus*) (n = 76).

Among the 25 LDA models tested, seven had an accuracy >80% to discriminate between males and females, and they included between one and three variables (Annexe S1.1, Table S1.1). The model that performed best had the two variables that differed significantly between sexes: body mass and wing chord. This model had the highest accuracy (82.9%), Youden's index (0.655), discriminant power (1.732) and MCC (0.653; Annexe S1.1, Table S1.1). According to this model, the classification function was:

Eq (1) $Score = 0.075 \cdot body\ mass + 0.119 \cdot wing\ chord - 59.915$

where a score higher than 0 classifies the individual as a female. The test correctly classified 83.7% of the females (sensitivity or true positives) and 81.8% of the males (specificity or true negatives; Altman and Bland 1994).

Body mass of individuals within pairs was positively related ($r^2 = 0.245$, $P = 0.01$) but not wing chord ($r^2 = 0.001$, $P = 0.86$). Within-pair comparisons showed significant sex differences again for only two variables: wing chord and body mass (Table 1.2). Within a pair, 85% of the females had a longer wing than males and 88% were heavier than males (Figure 1.2). For all other measurements, the difference between sexes within-pair was close to 0 (Figure 1.2). When individuals were paired randomly, body mass and wing chord of pair members were weakly related (average $r^2 = 0.042$ and 0.036, respectively) and rarely significant ($P < 0.05$ for 6.5% of simulations for body mass and 3.5% for wing chord). Moreover, on average 88% of the females were heavier than their mate (range: 69% to 100%) and 76% of the females had longer wings than their mate (range: 53 to 92%). We therefore examined if adding body mass or wing chord of partners could improve the accuracy of our LDA model to determine the sex of individuals.

Table 1.2 Results of the paired t-test for within-pair difference (female minus male) in six morphometrics (n = 26 pairs) of long-tailed jaeger (*Stercorarius longicaudus*).

Variable	Mean difference	t_{25}	P
Head length (mm)	-0.3	-0.81	0.42
Tarsus length (mm)	0.1	0.19	0.85
Wing chord length (mm)	6.1	3.79	< 0.001
Tail length (R1) (mm)	-6.8	1.30	0.20
Tail length (excluding R1) (mm)	1.4	0.84	0.41
Body mass (g)	29.8	6.81	< 0.001

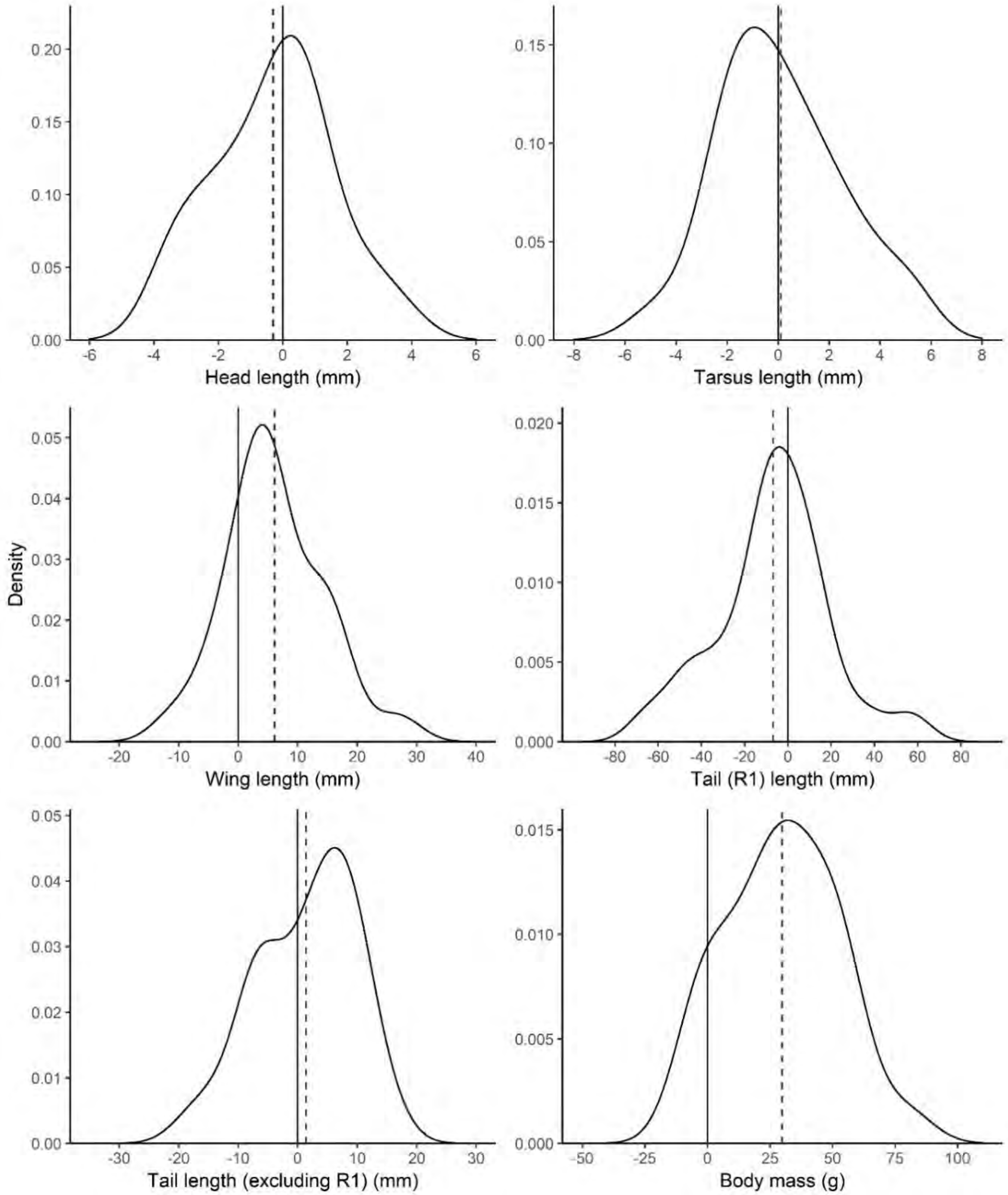

Figure 1.2 Density plot of the within-pair size difference for six morphometrics in long-tailed jaegers (*Stercorarius longicaudus*) (n = 26). The vertical solid line represents no difference (0) and a positive value means that females are bigger than males. The vertical dashed line represents the within-pair mean difference.

Adding partners' measurements to those of individuals improved their sex identification as several models using various combinations of variables had an accuracy >83% (Annexe S1.1,Table S1.2). The model that performed best included the body mass, wing chord and length of the central rectrice (R1) of the individual in combination with body mass of its partner. This model had an accuracy of classification of 92.3% (classification success equal in both sexes) and a discriminatory power of 2.740 (Annexe S1.1, Table S1.2). The classification function of this model was:

$$\text{Eq (2)}\quad \mathit{Score} = 0.113 \cdot \mathit{body\ mass} + 0.107 \cdot \mathit{wing\ chord} - 0.051 \cdot \mathit{tail\ length\ (R1)} - 0.129 \cdot \mathit{partner's\ body\ mass} - 13.525$$

where a score higher than 0 classifies the individual as a female.

When we tested Equation 1 on the dataset measured from 2007-2010, only 62% of the 26 individuals were correctly sexed. On the other hand, Equation 2 correctly sexed 100% of the eight individuals. Close examination of this dataset revealed that the mean body mass of females was 23.5 g lower than in the dataset we used to establish the function ($t_{51} = -3.17$, $P = 0.003$) though not for males (difference of 3.7 g, $t_{47} = -0.57$, $P = 0.57$).

1.6 Discussion

As previously reported (Wiley and Lee 1998), we found reversed size dimorphism in long-tailed jaegers. However, dimorphism was weak and only present for body mass and wing chord. Nonetheless, combining body mass and wing chord in a discriminant analysis allowed us to accurately sex 83% of the individuals. Interestingly, the model was simple as it required only two variables that are relatively easy to measure to predict the sex. Errors in taking those measurements are often quite small compared to other measurements such as tarsus, head length and culmen (Winker 1998).

The sex classification success that we obtained is comparable to other studies in seabirds which typically ranges from 72% to 93% based on individual measurements (Coulter 1986, Lorentsen and Røv 1994, Mallory and Forbes 2005, Mischler et al. 2015, Ferrer et al. 2016). A similar study in parasitic jaeger, a closely related species, produced a discriminant function to sex individuals with an accuracy of 91% using the same two variables as in our Equation 1 (Phillips and Furness 1997). The higher accuracy of their model compared to ours may be due to a higher dimorphism in that species, as females were 15% heavier than males on average.

Body mass must be used with caution when attempting to discriminate sexes because it varies over time, especially during the breeding season, and possibly differently between sexes (Norberg 1981, Croll et al. 1991, Jones 1994). However, we did not find any significant change in body mass according to the incubation stage in both sexes despite a trend for a decrease in females. Since most birds were measured over about half of the incubation period only (day 7 and 21), it is possible that this limited our ability to find a significant decrease in females. Thus, even though variation in body mass may be source of errors in some circumstances, our results suggest that it remains an important variable to discriminate the sex of long-tailed jaegers on the breeding ground.

We concluded that there is a positive assortative mating based on body mass, as heavy females tended to mate with heavy males and light females with light males on average, but not based on wing chord. Positive assortative mating, which occurs when individuals tend to mate to individuals similar to them, has been reported in a wide variety of species such as in brant (Abraham et al. 1983), feral pigeons (*Columba livia*; Johnston and Johnson 1989), parasitic jaegers (Phillips and Furness 1997) and in several falcon species (Olsen et al. 1998). Despite this positive assortative mating, it is interesting to see that within-pairs, 88% of females were still heavier and 85% had longer wings than their partner, which suggests that females also prefer to mate with males smaller than themselves. Female preference for a male smaller than them has been reported in many raptor and owls species that present reversed size dimorphism (Earhart and Johnson 1970, Andersson and Norberg 1981, Safina 1984). Nevertheless, we do not know exactly what is the mechanism leading to the mating pattern found in long-tailed jaeger, as we lack behavioral observations. For instance, we cannot totally exclude the possibility that the observed pattern of assortative mating could be a consequence of other confounding variables, such as selection for high-quality territories defended by heavy individuals.

A preference of females for males smaller than themselves can explain why including body mass of the partner in our discrimination analysis considerably improved the accuracy of our model to predict the sex. Indeed, the proportion of misclassified individuals decreased by half (17% vs. 8%) with the partner's measurement and the addition of the tail length to the model. Therefore, efforts should be made to capture and measure both members of a pair if sex identification is an important variable. Few studies attempted to improve the classification success using within-pair comparison and, to our knowledge, none did by developing new discriminant functions taking into consideration measurements from the other individual. Nevertheless, a simple within-pair comparison of the discriminant score reduced the proportion of misclassified individuals from 26-28% to 10-16% in two tern species (Fletcher and Hamer 2003, Devlin et al. 2004) and from 5-15% to 0-11% in cape petrel (*Daption capense*; Weidinger and van Franeker 1998).

When we tested Equation 1 with the set of measurements taken by another observer from 2007-2010, we were surprised of the poor success of the equation in assigning sex. The large difference in female body mass found between the two datasets may be responsible for this poor success. Several factors may explain this large difference, including annual effects, difference in the incubation stage at which individuals were measured or miscalibration of the spring scale. Among those, difference in incubation stage may be an important one, because birds were captured on average significantly later in the 2007-2010 dataset than in the 2014-2018 dataset used to establish the equations (23 days vs. 17 days of incubation, respectively; $t_{22} = 3.0$, $P = 0.006$). This further emphasizes the need to be cautious when using equations that include body mass, as mentioned above. However, it is reassuring to see that, when using Equation 2 with this same dataset, classification success was 100%. It thus appears that any factor that may have biased low female body mass in that other dataset was controlled by including body mass of the partner. This comparison therefore provides a strong argument to justify the measurement of both breeding partners and the use of our Equation 2. Furthermore, when measuring breeding individuals, we strongly suggest recording the reproductive phenology. Even though our data did not show any significant decrease in body mass of incubating females, more data covering the whole incubation period are needed to better document this. A decrease in female body mass throughout the incubation period would not be surprising, considering that females assume about two-third of the total incubation time in this species (Andersson 1971).

We were able to establish two simple equations to sex long-tailed jaegers based on morphological measurements. Depending on the objectives of the study, the sexing method we presented in this paper may be sufficient to avoid the need to do expensive and tedious DNA analyses to sex individuals. However, the timing of the measurements may affect the reliability of Equation 1 due to possible variations of female body mass during incubation. The equation should be most accurate when individuals are measured during mid-incubation, between 7 and 21 days. However, using measurements from the partner apparently overcomes this limitation and this is why, when working with breeding pairs, we recommend capturing both individuals. Also, geographical differences in size are possible between populations of the same species (Waugh et al. 1999, Angel et al. 2015) and differences in body mass between sites were previously reported for the long-tailed jaeger (Wiley and Lee 1998). Thus, care should be taken when applying these equations elsewhere in the Arctic.

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1.8 Supplementary material

Annexe S1.1 – Results of the linear discriminant analysis models

Chapitre 2 – Seasonal variations in migration strategy of a long-distance arctic-breeding seabird

Labbe à longue queue équipé d'un géolocalisateur à la patte

Référence de la publication :
Seyer, Y., G. Gauthier, J. Bêty, J.-F. Therrien, and N. Lecomte. 2021. Seasonal variations in migration strategy of a long-distance arctic-breeding seabird. Marine Ecology Progress Series 677:1–16.

2.1 Résumé

Plusieurs facteurs internes (reproduction, mue) et externes (saisonnalité, disponibilités des ressources) peuvent influencer les stratégies migratoires de longue-distance chez les oiseaux marins. Les stratégies minimisant la durée de migration au printemps sont les plus communes et permettent d'arriver au moment optimal pour débuter la reproduction. Notre objectif était de documenter les déplacements annuels (routes, sites d'hivernage) chez les deux sexes du labbe à longue queue (*Stercorarius longicaudus*), un migrateur de petite taille nichant en Arctique, pour ensuite comparer les stratégies employées au printemps et à l'automne (phénologie, halte, vitesse, distance). Nous voulions déterminer si les labbes utilisaient eux aussi une stratégie de minimisation du temps au printemps. Nous avons récupéré 43 trajets migratoires provenant de géolocalisateurs déployés sur les îles Bylot et Igloolik sur une période de 6 ans. À la fin de l'été, le départ en migration des labbes nichant dans l'Arctique canadien s'étalait sur une période d'environ 5 semaines et ils parcouraient en moyenne >32 000 km annuellement avant de revenir nicher, une des plus longues migrations documentées. Au printemps et à l'automne, la majorité des individus utilisaient une importante halte migratoire au large des Grands Bancs de Terre-Neuve et, en hiver, ils se répartissaient sur une vaste région de l'Atlantique Sud. Nos résultats ont démontré que la migration printanière était 40% plus longue et 32% plus lente qu'à l'automne, en plus de présenter une augmentation de 61% du temps passé sur l'eau (alimentation et/ou repos). Une stratégie de minimisation du temps à l'automne permettrait aux labbes d'atteindre rapidement les sites d'hivernage pour débuter leur mue. Au printemps, ils adopteraient plutôt une stratégie d'alimentation en continu en cours de migration (*fly-and-forage*) afin d'augmenter l'effort d'alimentation et d'accumuler des réserves énergétiques en prévision de conditions défavorables pouvant survenir à l'arrivée au site de reproduction.

Mots clés : Courant du Benguela · Déplacement hivernaux · Émetteurs satellites · Geolocalisateurs · Global Location Sensor · GLS · Labbe à longue queue · *Stercorarius longicaudus* · Suivis migratoires

2.2 Abstract

Long-distance migratory seabirds need to adjust their migration strategy according to internal (breeding, molting) and external factors (seasonality, resource availability). Time-minimizing strategies are common during spring migration to arrive at the optimal time to breed. We studied the annual movements and migration strategy of the long-tailed jaeger *Stercorarius longicaudus*, a small arctic-nesting seabird. First, we documented year-round movements (routes, wintering sites) of male and female jaegers breeding in the Canadian Arctic. We then compared their migration strategies between seasons (phenology, stopover use, travel distance, speed) to determine whether they adopt a time-minimizing strategy in spring. Over 6 yr, we collected 43 tracks from geolocators deployed on Bylot and Igloolik Islands. Jaegers departed the breeding site over a 5 wk period and traveled on average 32 375 km (round trip) before returning to breed, one of the longest documented migrations on Earth. Birds used a major stopover area east of the Grand Banks of Newfoundland in spring and fall, and wintered in high marine productivity areas of the South Atlantic. Unexpectedly, the spring migration was 40% longer and 32% slower than in fall, and birds increased their time spent on water (foraging and/or resting) by 61%. A time-minimizing strategy in fall may help to reach the wintering site rapidly and start molting early. In spring, a fly-and-forage strategy seems to be adopted to increase foraging effort, probably for the accumulation of body reserves before breeding and in anticipation of unfavorable conditions that may prevail at arrival on their arctic breeding site.

Key words: Benguela Current · Geolocators · Global Location Sensor · GLS · Long-tailed jaeger · Non-breeding movement · Satellite transmitters · *Stercorarius longicaudus* · Tracking

2.3 Introduction

Migratory seabirds can travel long distances across the planet, connecting distant ecosystems and exposing themselves to a diversity of environmental conditions and resources along the way. Migration path and phenology, and wintering area used, can have a strong impact on key demographic traits such as survival or reproduction if individuals are not at the right place at the right time (Norris et al. 2004a, Newton 2008, Klaassen et al. 2014, Senner et al. 2019). Because of seasonal and annual variations in resource availability, seabirds should adjust their migration strategy (e.g. timing of migration, travel speed, use of stopover and wintering areas) to maximize their fitness. In addition, intrinsic factors such as body condition and reproductive or molting state can also influence the migration strategy (Newton 2008, 2011, Alerstam 2011).

Migratory birds can face different environmental conditions and selection pressures during their pre-breeding (spring) and post-breeding (fall) migration (Newton 2008, Horton et al. 2016), which can lead to seasonal variation in optimal migration strategy (Nilsson et al. 2013, Zhao et al. 2017, Schmaljohann 2018). For instance, competition for breeding territories and high reproductive success in early breeders can favor birds arriving early and in good body condition on their breeding grounds (Kokko 1999, Waugh et al. 1999, Verhulst and Nilsson 2008). Under these conditions, individuals are expected to complete their spring migration as fast as possible, given constraints on flying speed and energy acquisition rate. Such a time-minimization strategy is commonly thought to play a major role during the pre-breeding migration (Hedenström and Alerstam 1997, Zhao et al. 2017) and may explain why spring migration is faster than fall migration in many long-distance migrants (Nilsson et al. 2013, Schmaljohann 2018). This may be especially important in species breeding at high latitudes where the summer is brief (Reséndiz-Infante and Gauthier 2020).

Seasonal variation in environmental conditions such as weather pattern or food availability on the wintering and stopover sites can also have a strong effect on migratory behavior, and the benefits of a fast spring migration can be counterbalanced by various costs (Schmaljohann 2018, Deng et al. 2019). For instance, unfavorable wind and limited resources at stopovers when individuals need to build up body reserves can reduce the pace of the spring migration (Petrie and Wilcox 2003, Kölzsch et al. 2016, Deng et al. 2019). Moreover, individuals nesting in highly seasonal environments, such as the Arctic, could suffer from unfavorable weather or food shortage if they arrive on their breeding grounds too early and in poor body condition (Bêty et al. 2004, Nuijten et al. 2014, Jean-Gagnon et al. 2018). In contrast, a high abundance of energy-rich food during late summer on the breeding grounds may allow prolonged non-stop flights in fall in some species, shortening the post-breeding migration (Bustnes et al. 2013, Alves et al. 2016, Kölzsch et al. 2016). The timing of the post-breeding molt is another factor that can influence the timing and speed of the fall migration (Jahn et al. 2013, Kulaszewicz and Jakubas 2015, Kiat and Izhaki 2016). Overall, the optimal migration strategies can vary between taxa (Schmaljohann 2018), and between populations of the same species (Klaassen et al. 2012, Bustnes et al. 2013) depending on environmental conditions and selection pressures faced by individuals during their entire annual cycle.

The long-tailed jaeger *Stercorarius longicaudus* (hereafter jaeger) represents a good study model to investigate seasonal variations in migratory behavior. It is a relatively small seabird that achieves one of the longest documented migrations on Earth, from its High Arctic breeding sites to its subtropical wintering areas in the southern hemisphere (Gilg et al. 2013, van Bemmelen et al. 2017). Jaegers are pelagic for most of the year, but they switch to the terrestrial environment to breed. Their breeding season is constrained by the short arctic summer and food abundance that often decreases as the summer progresses (Gauthier et al. 2011, Fauteux et al. 2015). They consume exclusively terrestrial prey during the summer, and they rely on lemming populations to breed successfully in most parts of their range (Maher 1970, Furness 1987, Therrien et al. 2014a). Once they acquire a territory, individuals can return and use the same site yearly (Maher 1970, Seyer et al. 2020). However, food accessibility can be highly unpredictable when approaching the arctic breeding ground and on arrival due to the timing of ice cover at sea and snowmelt on land, as well as cyclic population fluctuations in lemmings.

In this study, we document for the first time the year-round movements of long-tailed jaegers breeding in the Canadian Arctic by tracking more than 45 males and females. We first describe their fall and spring oceanic migratory routes and identify their main stopover and wintering sites. We then compare the marine productivity, a proxy of food availability, at the different wintering and stopover sites used by jaegers. We also analyze their migration strategy in fall and spring in terms of phenology, stopover location, travel distance, travel speed, and time spent in flight vs. on the water to determine if jaegers have a more rapid spring migration as found in many bird species. Due to the constraints imposed by the short arctic summer on their breeding grounds, we expected jaegers to adopt a time-minimizing migration strategy in spring.

2.4 Methods

2.4.1 Study site and field methods

The field work was conducted during the long-tailed jaeger breeding season (mid-June to early August) in 2008 and from 2014 to 2019 at Bylot Island (73°08’ N, 80°00’ W), and from 2016 to 2019 at Igloolik Island (69°39’ N, 81°54’ W). Both sites are located in Nunavut in the Canadian High Arctic. Nests of long-tailed jaegers are spaced out on the tundra, and systematic nest searches were carried out annually in late June and early July to find breeding pairs. Territorial pairs were identified by their alarm calls, and nests were found by spotting incubating birds returning to their nest. Some nests were also found opportunistically during other field activities on the outskirts of the main study area. All nests were georeferenced when found and monitored until hatching or failure. Because jaegers are faithful to their nesting site (Seyer et al. 2020), we also made systematic searches where marked jaegers previously nested.

We captured most jaegers at their nest using a bownet trap, but also sometimes in the nest vicinity using a noose carpet, a netgun, or a bal-chatri trap baited with a lemming. All captured birds were marked with metal and plastic numbered bands for individual identification and sexed by DNA analysis using feather pulp, except for a few birds in 2008 (see Seyer et al. 2019 for more details).

From 2014 to 2018, we equipped birds with a geolocator (light-level loggers; Intigeo-C65, Migrate Technology) attached to the plastic band with a cable tie through 2 small holes (Figure S2.1 in Annexe S2.1). Geolocators measured 14 × 8 × 6 mm and weighed 1 g, representing about 0.7% (geolocator with the band) of the body mass (female: 318 g, male: 286 g; Seyer et al. 2019). They were equipped with both light and wet-immersion sensors. We deployed 65 geolocators on Bylot Island (2014−2016: n = 20 yr^{-1}, 2018: n = 5) and 5 on Igloolik Island in 2016 between 20 June and 10 July (Table S2.1 in Annexe S2.2). We attempted to recover geolocators from 2015 to 2019 between 19 June and 10 July (i.e. during the incubation). Considerable effort was made to recapture breeding birds on their nest and non-breeding birds in their previous nesting territory using the capture methods previously described.

In 2008, we deployed 10 satellite transmitters (PTT-100, Microwave Telemetry) on adults (8 females, 2 unknown) from 1 to 12 July on Bylot Island (Table S2.1). The devices weighed 10 g, representing about 3% of the body mass following the recommendation of Phillips et al. (2003). Transmitters were attached with a backpack harness made of Teflon ribbons (Figure S2.2; Steenhof et al. 2006). All protocols were approved by the Animal Care Committee of Université Laval following the guidelines of the Canadian Council on Animal Care. All geolocator and satellite transmitter data are available in the Movebank Data Repository (Seyer et al. 2022a, 2022b).

2.4.2 Analyses of geolocator data

Geolocators sampled light intensity each minute and recorded its maximum value every 5 min. A wet-immersion sensor measured conductivity every 30 s and was programmed to record a wet count only for immersion in saltwater (value >63 on an arbitrary scale from 0–127; Fox 2013). Wet counts were summed, and the values were saved every 4 h.

Before deployment, we performed a calibration in an open field in southern Québec (46°44' N, 71°28' W; Annexe S2.8), and during the deployed period, we performed a Hill-Ekstrom calibration during the longest stable position (i.e. the wintering period; Lisovski et al. 2012). Twilight events were identified using the threshold method (Ekstrom 2004, Lisovski and Hahn 2012) with the *TwGeos* package (Lisovski et al. 2016) in R (other packages mentioned below are also in R). We set the threshold value to 1.15 lux to avoid noise in the night-time light levels. To determine the geographic locations, we analyzed light-level data using a Bayesian approach with the *SGAT* package (Wotherspoon et al. 2013). We simulated a total of 11 700 samples. We provided the model with (1) raw location estimates calculated with the threshold method, (2) a spatial mask where inland positions were less likely than at-sea positions, and (3) a movement model defining probable flight speed. We assumed a mean travel speed of 14 km·h^{-1} with a maximum at 61 km·h^{-1} (Spear and Ainley 1997, Sittler et al. 2011). More details about the geolocator data analysis are provided in Annexe S2.3.

Saltwater immersion data were used to estimate the maximum time spent in flight daily throughout the non-breeding period. Each wet count recorded was associated with a contact with saltwater. However, wet signals could not be assigned to a specific activity, as jaegers may be on the water to forage or to rest. In contrast, considering that jaegers are highly pelagic and seldom rest on land outside the breeding season (Wiley and Lee 2020), each dry period (no wet count) was associated with flight (Mejías et al. 2017, Schacter and Jones 2018, Studholme et al. 2019). Accordingly, a higher number of immersions was associated with less time spent in flight. At sea, some stercorariids use kleptoparasitism, with about 20% of the chases being successful (Furness 1987). The extent to which the small long-tailed jaeger relies on kleptoparasitism to feed is unclear, but it appears less important than in other members of the Stercorariidae (Furness 1987, Wiley and Lee 2020). Thus, we assumed that kleptoparasitism represented a negligible portion of the time spent flying.

Because jaegers become entirely terrestrial during breeding, we used a changepoint analysis (Killick and Eckley 2014) to identify the start and end of migration based on a sudden change in the daily number of immersions when the birds switch between marine and terrestrial lifestyles (Fauchald et al. 2019). To identify fall and spring migration stopovers, we looked at stationary periods estimated by the *ChangeLight* function in the *GeoLight* package (Lisovski and Hahn 2012) with a minimum duration of 3 d. Finally, to define the wintering period, we used a 3-step approach based on the 'Migratory Analytical Time Change Easy Detection' method (Chen et al. 2016, Doko et al. 2016). More details about the estimation of the start and end of these periods are provided in Annexe S2.3.

We calculated the total distance for each migration step by summing the distance between successive locations using the great-circle distance (*distVincentyEllipsoid* function in the *Geosphere* package; Hijmans 2019). Because geolocators are inaccurate in 24 h daylight regions, we estimated the distance traveled between the arctic breeding site and the first location estimated by the geolocator (or vice versa) based on the path recorded by satellite transmitters (see section *Migratory path and distance* in Results). To estimate the duration of migration, we calculated the difference between departure (or arrival) date from the breeding site and arrival (or departure) on the wintering site, excluding the stopover duration.

To estimate the duration of the stopover and the wintering periods, we calculated the difference between the arrival and departure dates at each site. Finally, to estimate the travel speed for each migration leg, we divided the distance traveled by its duration using only portions of the tracks recorded by the geolocators (i.e. excluding the segments in the Arctic where no positions were available).

We estimated the individual home range (75% utilization) and core area size (50% utilization) during the wintering and stopover periods using the kernel utilization distribution method with the *kernelUD* function of the package *adehabitatHR* (Calenge 2006). We used the bivariate normal kernel method and the least-square cross-validation algorithm to find the best smoothing parameter value (*h*, Table S2.2 in Annexe S2.3) controlling for the amount of variation in each component of the estimate (Worton 1989). We repeated the same methods for the home range and core area sizes at the population level or to compare males vs. females. To delimit the main wintering sites, we used the 50% minimum convex polygon for each site observed, considering separately all the locations recorded at each site.

2.4.3 *Analysis of satellite transmitter data*

Satellite transmitters were programmed to transmit a signal continuously during 6 h at 4 d intervals. We received the locations via the Argos system (Collecte Localisation Satellites 2016), and each location was assigned to a class (0, 1, 2, 3, A, B, Z) depending on its estimated precision. The estimated accuracy of the location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1500, <1500, <500, and <250 m, respectively, and classes A and B had no accuracy estimation. Locations of class Z failed and were excluded, and in the case of multiple records with the same time label, we retained the most accurate one. All remaining locations were filtered using a speed-distance-angle filter (*argosfilter* package; Freitas et al. 2008, Freitas 2012). We specified a speed threshold of 67 $km{\cdot}h^{-1}$, corresponding to the predicted mean + 1 SD ground flight speed of jaegers and skuas with tailwinds (Spear and Ainley 1997), a value slightly higher than the maximum flight speed recorded by Sittler et al. (2011). We used the default settings for distances and angles, removing locations requiring turning angles of 165° and 155° if the track leading to them was longer than 2.5 and 5.0 km, respectively (Freitas et al. 2008). Our 3-step filter retained 88 ± 3% (SD) of the original locations among individuals.

To avoid non-independence of spatial data because of the multiple recorded locations for each period of transmission, we averaged to a single mean daily location. We considered that a bird had started its migration when its movement at sea was directional without turning back for a 6 h recording period or when it reached a distance ≥150 km away from Bylot Island. Departure date was defined as the median between the previous recorded date and the first one recorded on migration. We applied the same method to estimate the arrival date on the fall stopover area off Newfoundland.

2.4.4 *Marine productivity*

We used marine productivity as a proxy of food availability at the main wintering and stopover sites used by jaegers. We used the MODIS-Aqua Level-3 chlorophyll *a* (chl *a*) data at 9 km resolution (NASA OB DAAC 2018), which is a good proxy of marine productivity (Ware and Thomson 2005). We calculated the mean annual concentration of chl *a* from 2002 to 2020 within each wintering site and the mean over 32 d in spring (23 April to 24 May) and in fall (29 August to 29 September) for stopover sites used by jaegers.

2.4.5 *Statistical analyses*

We assessed the influence of the period of the annual cycle on the total distance traveled with a linear mixed-effect model (LMM) based on a restricted maximum likelihood approach in the package *nlme*

(Pinheiro et al. 2018). We used bird IDs as a random factor for all LMMs because some individuals were monitored more than once. However, we applied linear models (LMs) when we had ≤ 2 individuals monitored twice to avoid overfitting and because the random effect explained a negligible portion of the variance. We used LMs to assess if sex affected the total distance traveled annually (from the breeding to the wintering site and back to the breeding site), and the size of the individual core wintering area. We also used LMs to compare the chl *a* concentration between the different wintering sites or between fall and spring stopovers.

We used LMMs to assess sex differences in departure date from the breeding site and to compare departure date from the breeding site and arrival date at the stopover between tracking devices (geolocators vs. satellite transmitters). We used LMMs or LMs to test the influence of sex or wintering site on the duration of stopover and wintering periods, arrival and departure dates from the wintering site, and arrival date at the breeding site. Finally, we used an LMM to test if the combined duration of migration and stopover changed between fall and spring migrations.

We assessed the influence of the period of the annual cycle on travel speed during migration and at stopovers and on the daily number of immersions (proxy of the time spent in flight vs. resting or foraging at sea) with LMMs. We tested the influence of sex, wintering site used, departure date from the breeding or wintering site, and type of tracking device on fall and spring migration travel speed with LMs or LMMs. Finally, we tested if the daily number of immersions varied according to travel speed and between fall and spring migrations using an LMM. For all LMMs, we calculated the marginal R^2 (for fixed effects) and the conditional R^2 (for fixed and random effects) based on Nakagawa and Schielzeth (2013). All analyses were done using the software R (R Core Team 2020) and we used a significance value (α) of 0.05. Means are presented ± SD throughout.

2.5 Results

We retrieved 42 geolocators (Bylot Island: n = 40; Igloolik Island: n = 2) 1−5 yr after deployment, giving an overall recovery rate of 60% (Table S2.1). We collected 43 tracks from 34 different individuals (19 females and 15 males), including 23 complete 2-way migrations (5 devices yielded no or little information; Annexe S2.9). We received positions of birds marked with satellite transmitters from 42−95 d after their deployment (Table S2.12; Annexe S2.10). None of the 10 individuals marked in 2008 with transmitters were ever seen again in the following breeding seasons up to 2019.

2.5.1 Migratory path and distance

Long-tailed jaegers departing the eastern Canadian Arctic traveled through Baffin Bay and Davis Strait to the North Atlantic and then crossed the ocean to the western African coast (Figure 2.1; Animation S1 in Annexe S2.11 at www.int-res.com/articles/suppl/m677p001_supp/). In the austral regions, most birds continued through the eastern part of the Atlantic Ocean. During both migrations, most individuals (fall: 88%, n = 43; spring: 83%, n = 23) had one major stopover located east of the Grand Banks of Newfoundland (Figure 2.2), while the others did not use any stopover. The fall stopover area of the population was more spatially restricted (60% smaller) than the spring one. Stopover sites were generally similar for males and females, although their core area overlapped more in fall (60–65% depending on sex) than in spring (33−39%; Figure S2.4 in Annexe S2.4).

The total distance traveled annually by jaegers estimated from geolocators averaged 61 344 ± 9 101 km (range = 43 227−76 021 km; n = 23). If we exclude the stopovers and the wintering period, they traveled on average 32 375 ± 6 546 km during migrations (range = 20 437−44 743 km; n = 23). The distance traveled during the spring migration, excluding the stopover, was significantly longer by about 20% compared to the fall (Table 2.1; Table S2.4 in Annexe S2.5) and the total distance traveled annually during migration did not differ between males (32 505 ± 6 482 km) and females (32 256 ± 6 890 km).

Table 2.1 Movement characteristics (mean ± SD) for different periods of the annual cycle of long-tailed jaegers breeding in the eastern Canadian Arctic and recorded with geolocators. Sample sizes (n) for the duration and the distance only include individuals tracked for the whole period, whereas those for travel speed and the number of daily immersions include incomplete tracks. Fall and spring migration periods exclude the stopover periods.

Period	n[a]	Distance (km)	Duration (d)	n[b]	Travel speed ($km \cdot d^{-1}$)	No of daily immersions
Fall migration	40	14 730 ± 3 053	42.7 ± 16.0	43	385 ± 90	1055 ± 269
Fall stopover	37[c]	3 682 ± 2 341	19.7 ± 12.8	37	190 ± 33	1112 ± 209
Wintering	26	20 487 ± 4 574	144.8 ± 34.4	40	149 ± 27	2005 ± 267
Spring migration	23	17 705 ± 4 610	63.6 ± 21.1	26	263 ± 60	1702 ± 303
Spring stopover	19[c]	5 597 ± 3 873	26.8 ± 16.0	19	199 ± 46	1872 ± 332

[a] Sample size for distance and duration

[b] Sample size for travel speed and daily number of immersions in saltwater

[c] Individuals with no fall or spring stopover were excluded

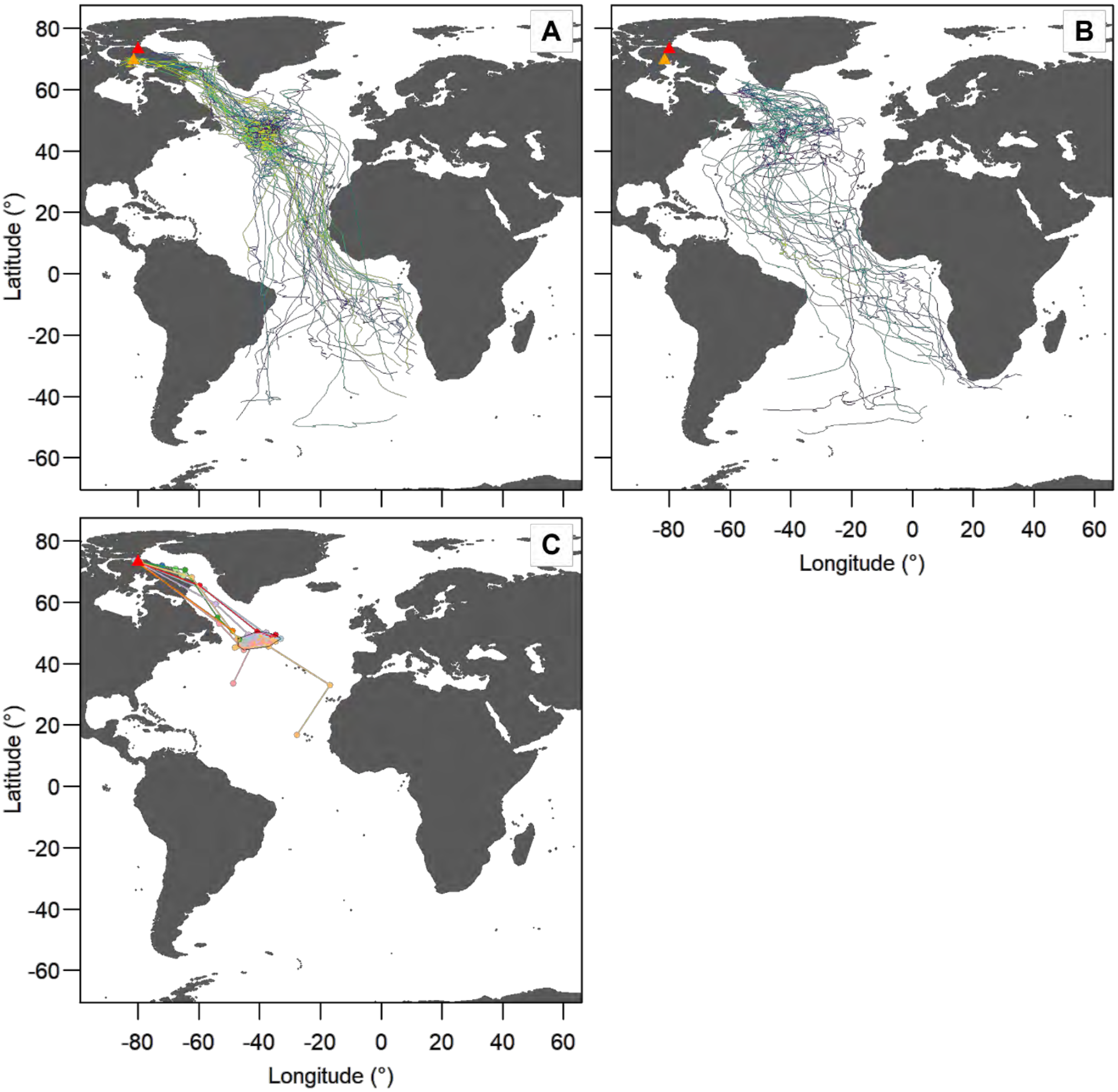

Figure 2.1 (A) Fall and (B) spring migratory paths of long-tailed jaegers breeding in the eastern Canadian Arctic on Bylot Island (red triangle) and Igloolik Island (orange triangle) and recorded with geolocators. (C) Fall migratory path of long-tailed jaegers recorded with satellite transmitters. Each point represents the mean daily location recorded every 4 d. The gray shaded area represents the 95% minimum convex polygon and delimits the fall stopover area. Each color represents a different individual.

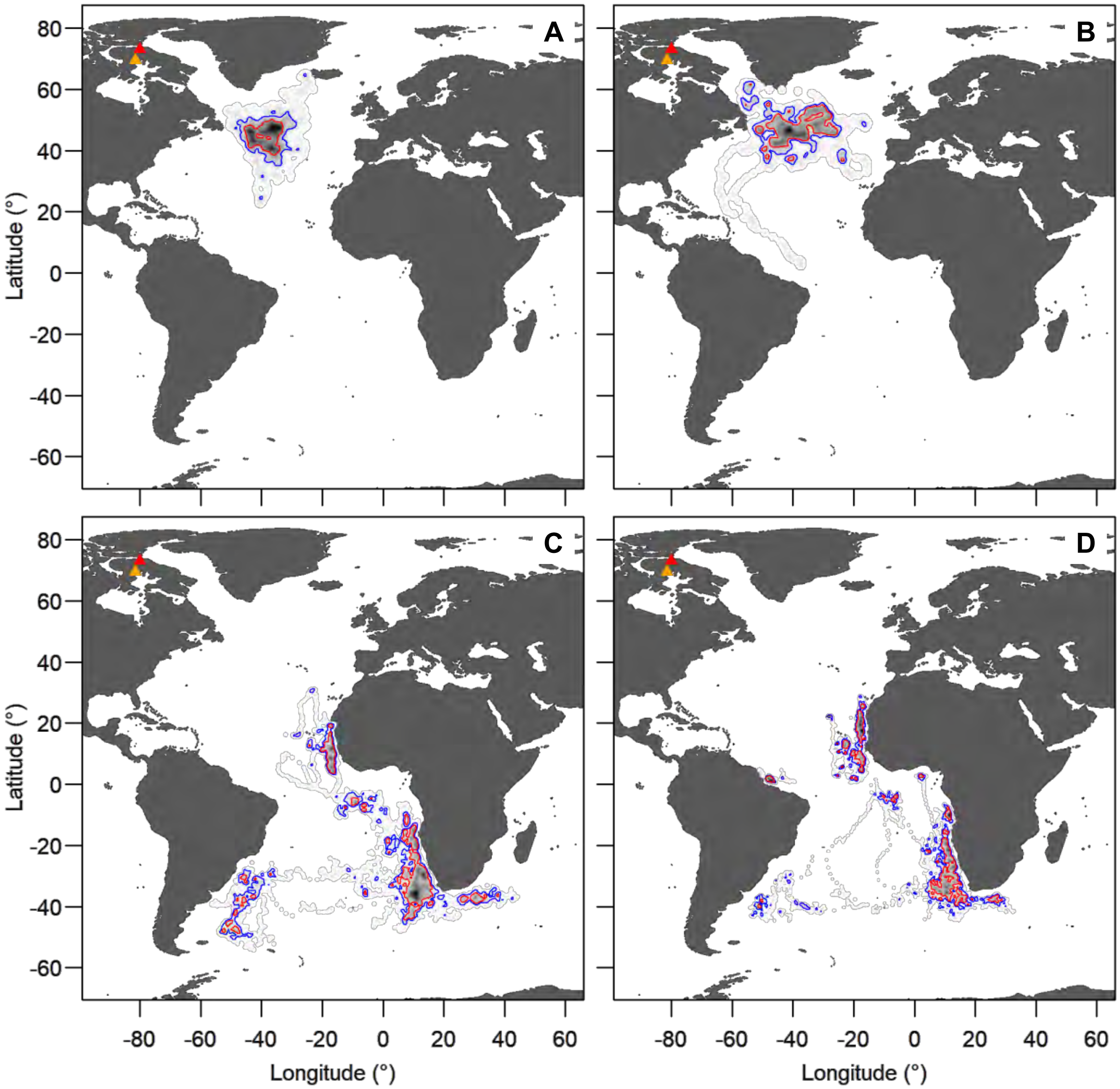

Figure 2.2 (A) Fall and (B) spring stopover sites, and winter distributions of (C) female and (D) male long-tailed jaegers breeding in the eastern Canadian Arctic on Bylot Island (red triangle) and Igloolik Island (orange triangle) and recorded with geolocators. Blue lines enclose the 75% area and red lines enclose the 50% core area used. Gray shading represents the intensity of the kernel utilization distribution based on all locations recorded during the period; darker colors represent a higher utilization.

2.5.2 Wintering period

Based on individual core area used, we were able to delimit 6 different wintering sites, all of which were associated with major oceanic currents, 4 in the eastern Atlantic (i.e. Canary, Guinea, Benguela, and Agulhas Currents) and 2 in the western Atlantic (i.e. North Equatorial and Brazil Currents; see

Figure 2.2 & Figure 2.3; Figure S2.5 in Annexe S2.4). The Benguela Current was the most heavily used site (68% of the individuals; n = 40), whereas other sites were used by about 3−15% of the individuals. Males and females used the same wintering sites (Figure 2.2). The mean size of individual core areas tended to be higher for females (290 414 ± 111 619 km^2; n = 14) than for males (223 285 ± 107 774 km^2; n = 12), but we found no significant difference (Table S2.4).

Among the individuals with a complete wintering period, 18 used only 1 site for the whole period: 10 in the Benguela Current, 4 in the Canary Current, 3 in the Brazil Current, and 1 in the Guinea Current. If we also consider incomplete wintering periods, individuals used on average 1.3 different sites during the winter (range: 1−2; n = 40). Individuals from the same pair did not systematically use the same wintering sites (Table S2.3 in Annexe S2.4).

2.5.3 Marine productivity

The second most heavily used wintering site (Canary Current) had the highest mean annual chl *a* concentration (1.14 ± 0.22 mg·m^{-3}; Figure 2.3; Figure S2.6 in Annexe S2.6) and was significantly higher than other wintering sites (Guinea: 0.19 ± 0.03, Benguela: 0.23 ± 0.02, Agulhas: 0.30 ± 0.03, North Equatorial: 0.31 ± 0.09, Brazil: 0.36 ± 0.04 mg·m^{-3}; Table S2.5 in Annexe S2.5). However, the Benguela and Agulhas Currents presented the lowest coefficients of variation through time, 8.6 and 9.8%, respectively, compared to 19.5% for the Canary Current (Figure S2.6). The mean 32 d chl *a* concentration was 3.8 times higher on the spring stopover than on the fall stopover (Figure S2.6, Table S2.5) but showed a similar coefficient of variation (18%).

2.5.4 Migration phenology

Jaegers marked with geolocators left Bylot Island over a 5 wk period (12 August ± 9 d, range: 23 July to 27 August; n = 41; Figure S2.7 in Annexe S2.7), and the 2 individuals from Igloolik Island left on 8 and 21 August. Departure dates did not differ between sexes (Table S2.6 in Annexe S2.5). Individuals marked with satellite transmitters had similar departure dates (17 August ± 4 d, range: 12 to 25 August; n = 9; Table S2.6). Jaegers arrived within 14 ± 5 d at the North Atlantic stopover site and at the same time for geolocators (26 August ± 10 d, range: 29 July to 8 September, n = 38) and satellite transmitters (24 August ± 4 d, range: 16 to 28 August, n = 7; Table S2.6). Jaegers stayed there about 20 ± 13 d (Table 2.1), but individuals wintering at the most distant sites (Benguela and Agulhas Currents) spent less time on the fall stopover than individuals wintering at the closest one (Canary Current; Table S2.6). Individuals arrived on their wintering site on 10 October ± 17 d (range: 1 September to 21 November; n = 40) and departed on 6 March ± 32 d (range: 14 January to 13 May;

n = 26). We found no difference in the arrival date to the different wintering sites, but the departure date from the northernmost wintering site (Canary) was 47 d later than for other sites and the duration of the wintering period was 32% longer (Table S2.6). We found no sex difference in the arrival and departure dates, nor in the duration of the wintering period (Table S2.6).

Jaegers arrived at the North Atlantic stopover site around 23 April ± 17 d (range: 20 March to 19 May; n = 19) and spent about 27 ± 16 d there (Table 2.1). Jaegers wintering at the southernmost site spent more time on the stopover than birds from the northernmost site. Females also spent more time than males (30 ± 18 vs. 15 ± 15 d) at the spring stopover, contrary to the fall period (12 ± 14 vs. 22 ± 12 d, respectively; Table S2.6). Arrival at the breeding site occurred over a 2.5 wk period (average: 3 June ± 4 d, range: 26 May to 13 June; n = 23), a shorter span than for the departure date. Arrival date did not differ between sexes or wintering sites (Table S2.6). Arrival date of individuals of the same pair was on average 5 ± 2.6 d apart (Table S2.3). The total time spent in migration and at the stopover was shorter in fall (60 ± 16 d) than in spring (86 ± 31 d; Table S2.6).

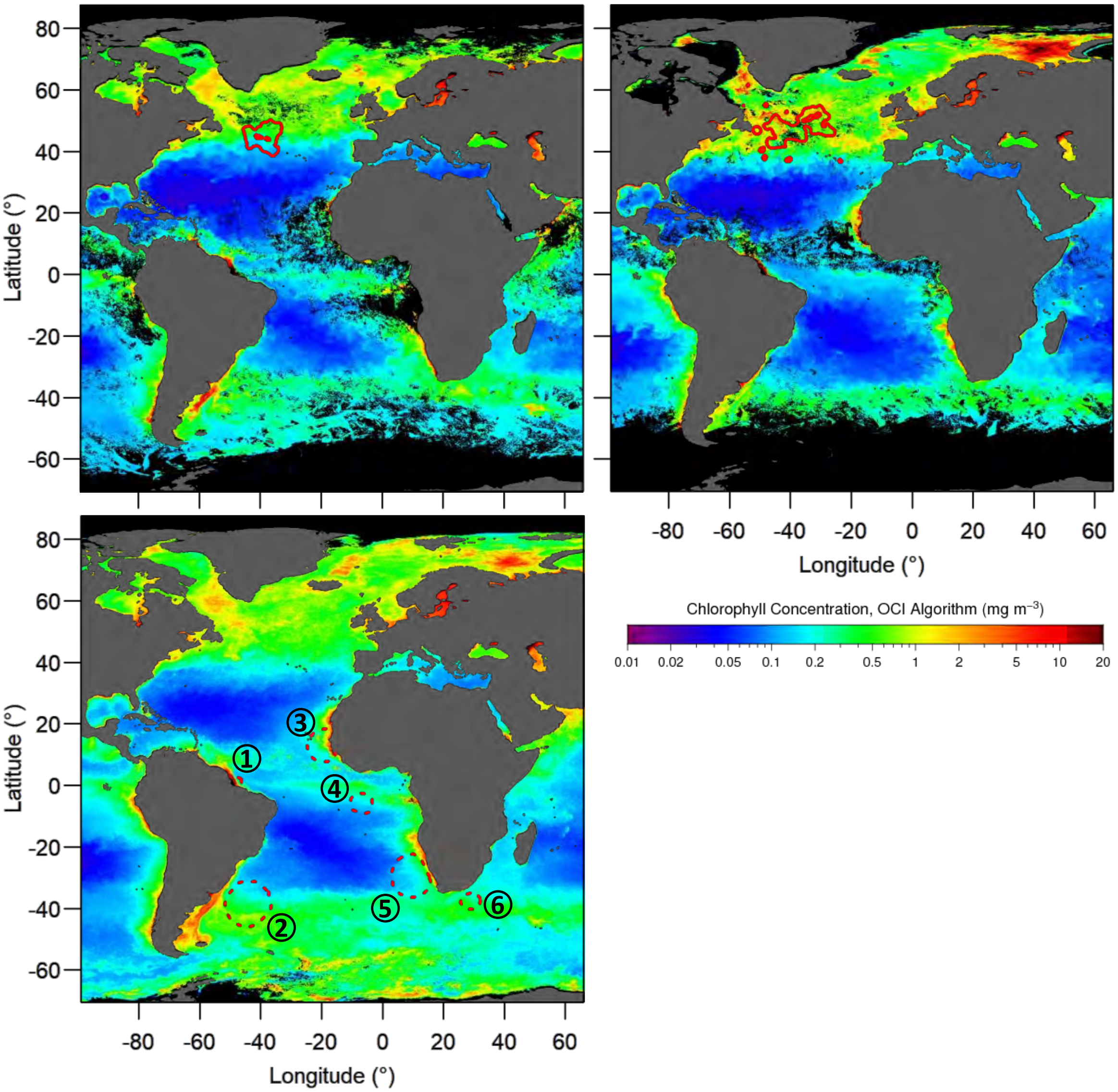

Figure 2.3 Oceanic chlorophyll *a* concentration estimated for various periods of the annual cycle of long-tailed jaegers in 2016. (A) Fall stopover (mean over 32 d); (B) spring stopover (mean over 32 d); (C) wintering period (annual mean). Red solid lines enclose the 50% core area used by jaegers during stopovers based on the kernel utilization distribution. Red dashed lines enclose the main wintering sites of jaegers based on the kernel utilization distribution. Currents are numbered: (1) North Equatorial, (2) Brazil, (3) Canary, (4) Guinea, (5) Benguela, and (6) Agulhas Current. Maps modified from NASA OB DAAC (2018).

2.5.5 Travel speed and immersions

The average daily travel speed differed between periods, ranging from 149 $\text{km}\cdot\text{d}^{-1}$ during the wintering period to 385 $\text{km}\cdot\text{d}^{-1}$ during the fall migration (Table 2.1; Table S2.4). Fall migration was on average 46% faster than spring migration (Table 2.1). When birds were using stopover areas, their daily travel speeds were similar in spring and fall but 27−33% higher than in winter (Table 2.1). Both sexes traveled at the same speed in fall and spring (Table S2.4). Average fall migration travel speed was similar for birds heading to different wintering sites, but birds wintering in the Guinea Current traveled at a slightly lower speed in spring compared to birds originating from other sites (Table S2.4). During spring, migration speed increased with the departure date from the wintering site, but not in fall (Figure 2.4; Table S2.4). Travel speed of birds tracked with satellite transmitters during the first part of the fall migration (428 ± 155 $\text{km}\cdot\text{d}^{-1}$; $n = 7$) was similar to birds tracked with geolocators (385 ± 90 $\text{km}\cdot\text{d}^{-1}$; $n = 43$; Table S2.4).

The average daily number of immersions in saltwater was 61% higher during the spring migration than during the fall migration (Table 2.1; Table S2.4). In spring, the daily number of immersions after the stopover was 12% higher than before the stopover (1857 ± 344 vs. 1658 ± 309 immersions per day) and equal to the stopover period (1872 ± 332; Table S2.4). The daily number of immersions also decreased as individual travel speed increased, and this relationship was steeper in spring than in fall (Figure 2.5; Table S2.4). The immersions were also 7–90% higher during the wintering period than in other periods (Table 2.1; Table S2.4).

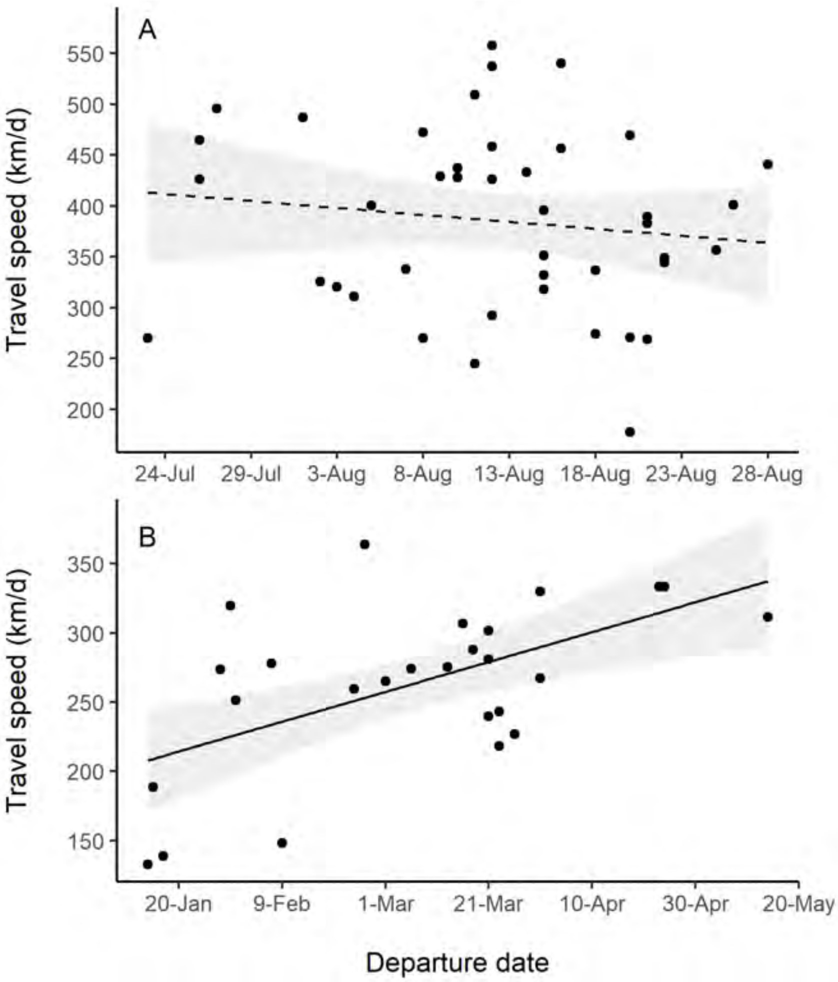

Figure 2.4 Relationship between travel speed during migration and departure date (A) from the breeding site and (B) from the wintering site in long-tailed jaegers. Each point represents the mean travel speed during fall or spring migration for 1 individual. Solid line represents a significant relationship and dashed line a non-significant one (gray shading is the 95% confidence interval).

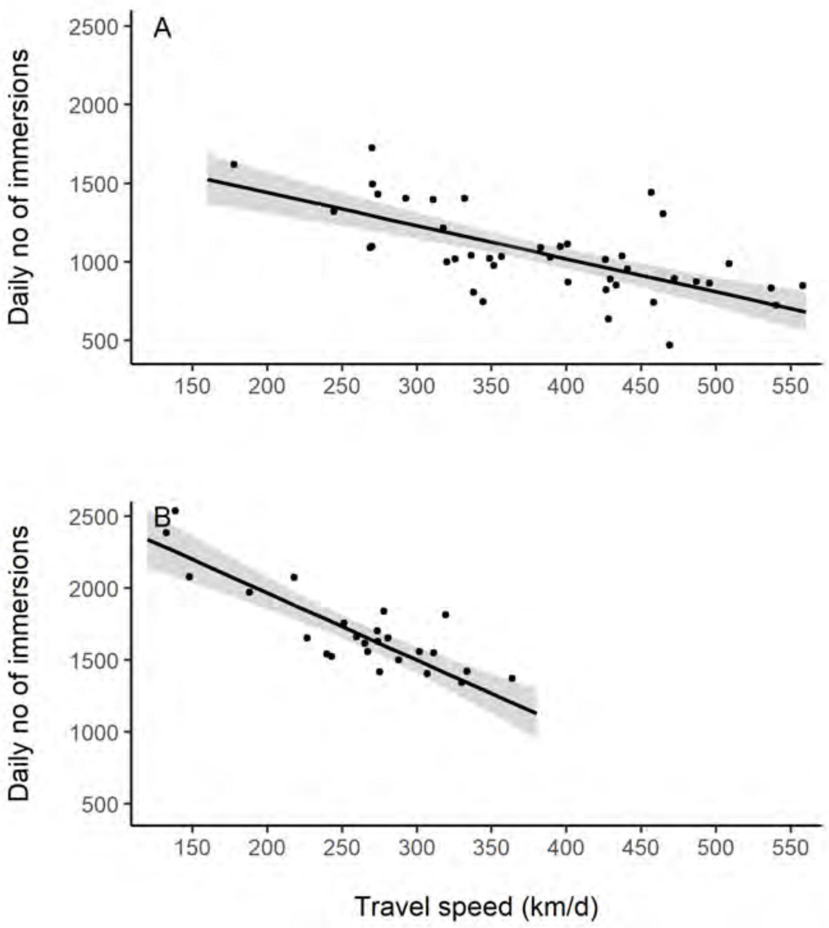

Figure 2.5 Relationship between the daily number of immersions in saltwater and travel speed during (A) fall and (B) spring migrations of long-tailed jaegers. Each point represents the mean number of immersions during fall or spring migration for one individual. Solid line represents a significant relationship (gray shading is the 95% confidence interval).

2.6 Discussion

We documented for the first time the annual movements and migration phenology of the Canadian population of long-tailed jaegers, long-distance migrants breeding in the Arctic. We confirmed the presence of a major stopover in the North Atlantic and found that their main wintering sites are located in the austral region of the Atlantic Ocean, predominantly off the African coast. Contrary to most migratory bird species, and especially species breeding in the Arctic where the reproductive season is very short, jaegers traveled faster during the fall migration than during the spring migration and did not adopt a time-minimizing strategy during the spring migration.

2.6.1 Migratory path

The migration of long-tailed jaegers roughly followed a figure-eight pattern, turning clockwise in the North Atlantic and somewhat counter-clockwise in the South Atlantic. This pattern is displayed by several other trans-equatorial migrating seabirds (González-Solís et al. 2007, Egevang et al. 2010, Hedd et al. 2012). Jaegers breeding in the Eurasian Arctic displayed a similar migratory route across the Atlantic Ocean to those breeding in the Canadian Arctic and also showed a similar wider migratory path in spring compared to the fall (Gilg et al. 2013, van Bemmelen et al. 2017). These paths do not follow the shortest distance between the breeding and wintering sites but they follow the dominant winds in the Atlantic (González-Solís et al. 2007, Felicísimo et al. 2008, Egevang et al. 2010). Therefore, these paths probably represent an energy-optimization strategy to benefit from tailwinds (Alerstam 2011).

Long-tailed jaegers breeding in the eastern Canadian Arctic used the same stopover area in the North Atlantic during both spring and fall migrations. Located east of the Grand Banks of Newfoundland, this area was used for 3 to 4 wk by most individuals. It is associated with the subpolar front between the Grand Banks and the Charlie-Gibbs fracture zone. It is recognized as a hotspot for seabirds because of its important productivity and predictability, especially in spring as also shown by our results (Boertmann 2011, Scales et al. 2014, Davies et al. 2021). Many seabirds use this area either as a stopover (e.g. Cory's shearwater *Calonectris borealis*, Arctic tern *Sterna paradisaea*, European and Greenlandic long-tailed jaegers) or as a wintering site (e.g. great skua *Stercorarius skua*, sooty shearwater *Ardenna grisea*, Cory's shearwater; Egevang et al. 2010, Dias et al. 2011, Magnúsdóttir et al. 2012, Hedd et al. 2012, Gilg et al. 2013, van Bemmelen et al. 2017, Davies et al. 2021). This area should therefore be considered as a major refueling stop for the migrating long-tailed jaegers and reinforces the need to protect it to ensure the sustainability of many seabird populations (Davies et al. 2021).

2.6.2 Wintering period

We identified 6 main wintering sites used by long-tailed jaegers breeding in eastern Canada. These sites were predominantly located in the south Atlantic Ocean and most jaegers wintered, at least partly, in the Benguela Current. European and eastern Greenlandic populations are also concentrated along the west African coast in winter, from the Guinea to the Benguela Current, with the latter site being the most heavily used site (Gilg et al. 2013, van Bemmelen et al. 2017). Overall, these results indicate a weak migratory connectivity in long-tailed jaegers, as individuals originating from the same breeding site can spread over several distant wintering sites and are mixed with birds originating from different breeding populations. Weak migratory connectivity makes it more difficult to target particular areas to protect specific populations that could be in trouble (Webster et al. 2002).

Jaegers wintered in areas of high marine productivity; thus, presumably in predictable and food-rich areas. All of their wintering sites, especially the 2 most heavily used, the Benguela and Canary Currents, are influenced by strong upwellings leading to high productivity. The Benguela Current is one of the most important and stable upwelling regions in the world, providing high productivity year-round (Chavez and Messié 2009). It is a known wintering area for many seabird species (e.g. Cory's shearwaters, Sabine's gull *Xema sabini*; Dias et al. 2011, Stenhouse et al. 2012, Davis et al. 2016), and is also an important migratory passage (e.g. Arctic tern; Egevang et al. 2010) and breeding (e.g. cape gannet *Morus capensis*; Crawford 2007) area for other species. Its consistent productivity between years probably makes this area more attractive for jaegers than other sites. Despite a high marine productivity, the Canary Current is influenced by strong seasonality (Chavez and Messié 2009) and displays important inter-annual variability.

Gilg et al. (2013) suggested that by concentrating their activity at sites heavily used by other seabirds, jaegers may incur additional benefits due to their occasional kleptoparasitic habit, but this hypothesis remains to be validated. Moreover, it is possible that long-tailed jaegers benefit from fishing vessels, which also concentrate in upwelling and high productivity areas, by feeding on fishing discards from ships (Wiley and Lee 2020). However, this may pose a risk for their survival due to bird bycatch associated with fisheries (Dias et al. 2019).

2.6.3 Travel speed and phenology

Migratory birds often travel faster in spring than in fall, which allows them to arrive early on the breeding site before competitors and at the optimal time for breeding (Kokko 1999, Alerstam 2011, Nilsson et al. 2013, Schmaljohann 2018). However, our results showed the opposite in long-tailed jaegers, with the fall migration being the faster one, as previously found by Gilg et al. (2013). Jaegers may use this strategy to arrive rapidly at their wintering site and start molting their flight feathers as soon as possible. Although information on molting pattern is limited in this species (Wiley and Lee 2020), van Bemmelen et al. (2018) showed that molt only starts after completion of the fall migration, once birds have reached their wintering site. This pattern is common in long-distance migrants (Alerstam 1990, Kjellén 1994, Newton 2011), including seabirds (Voelker 1997, Lee et al. 2020). As molting can reduce flight efficiency, birds rarely molt flight feathers during long-distance migrations and especially in fall when feathers are old and worn (Newton 2011).

Jaegers traveled a greater distance and spent much more time traveling and on stopovers in spring than in fall. This pattern differs from other seabirds that follow similar migratory paths. For instance, Arctic terns migrate 1.5 times faster in spring than in fall while covering similar distances (Egevang et al. 2010, Hromádková et al. 2020). The slower travel speed in spring and the higher number of daily immersions (more time in contact with saltwater) compared to fall provide evidence that jaegers adopt some sort of fly-and-forage migration strategy in spring (Strandberg and Alerstam 2007). This is especially true after the spring stopover when jaegers increased their number of immersions compared to before the stopover, suggesting a reduction of time spent in flight and an increase in foraging and/or resting on the water. It is unlikely that the fly-and-forage strategy is due to a lower food availability considering the higher marine productivity found at the stopover site in spring compared to fall (Figure S2.6; NASA OB DAAC 2018). Jaegers may use a fly-and-forage strategy to increase their feeding effort during the spring migration and the stopover in anticipation of unfavorable conditions that may prevail upon arrival at the breeding site. Extensive sea-ice cover restricts access to open water in spring in the Arctic. Thus, feeding opportunities are likely limited to a few polynyas or the mouth of thawing rivers in the Baffin Bay and Foxe Basin regions in spring (Hunt 1991, Barber and Massom 2007). On land, lemming density varies considerably between years (Fauteux et al. 2015), and the presence of snow cover in spring greatly reduces their accessibility to avian predators (Therrien et al. 2015). Therefore, the high unpredictability of arctic marine and terrestrial food resources in spring may favor increased feeding at sea during the stopover and the last portion of their migration. This would allow birds to arrive in good body condition and invest in reproduction shortly after arrival while minimizing the risk of starvation (de Korte 1985, Lamarre et al. 2017b, Jean-Gagnon et al. 2018). Our results thus support the idea that migratory seabirds that depend on terrestrial prey on their arctic breeding grounds may reduce travel speed in spring to prevent adverse effects on their fitness (Bêty et al. 2004, Nuijten et al. 2014, Deng et al. 2019).

In spring, the spread of arrival dates at the breeding site was almost halved compared to the spread of departure dates in late summer (2.5 vs. 5 wk), a pattern typical of what we would expect for most species. In spring, the timing of arrival can be critical because laying date is an important determinant of breeding success, especially in the Arctic due to the shortness of the breeding season (Bêty et al. 2004, Reséndiz-Infante and Gauthier 2020). A concentrated arrival period may appear contradictory with their slow travel speed during spring migration. However, jaegers may adjust their arrival date by changing their travel speed near the end of the migration in response to local environmental conditions. Unfortunately, we could not verify this hypothesis due to the lack of positions at high latitudes in spring with the 24 h daylight. In the fall, departure dates may be less critical and depend on weather conditions or food availability on the breeding grounds (Newton 2008).

2.6.4 Sex variability

Our results suggest no or few sex differences in the phenology, migratory movements, and wintering site. Parental roles in avian reproduction often contribute to sex differences in the migration phenology, with males typically arriving earlier in spring to defend a good territory (Alerstam 2011, Newton 2011, De Felipe et al. 2019). Size dimorphism could also explain differences in the migratory distance (Müller et al. 2015). The absence of sex-specific differences in jaegers is thus not surprising, as males and females have rather similar roles and investment in reproduction (Furness 1987), and size dimorphism is small (Seyer et al. 2019). The few pairs that we tracked did not migrate together and used different wintering sites most of the time. Thus, pair reunification could also be an additional factor behind the smaller variance in arrival dates during spring compared to the departure dates in late summer. A synchronous arrival should facilitate pair reunification on the breeding territory. Indeed, a long interval between the arrival of pair members may increase the chances that the first arriving bird decides to form a new pair bond to avoid losing a breeding opportunity (Choudhury 1995, González-Solís et al. 1999b).

2.6.5 Negative impact of satellite transmitters

The signal of all individuals marked with satellite transmitters was lost within a few weeks after the start of the fall migration, as also reported by Sittler et al. (2011) on the same species. Despite important field efforts to monitor jaegers for >10 yr at the breeding site, none of the 10 marked individuals was ever resighted, unlike individuals marked with geolocators (minimum return rate of 74%, n = 70). This strongly suggests that satellite transmitters installed as backpack harnesses had a negative impact on the survival of long-tailed jaegers, as reported in other seabirds (great skuas, Thaxter et al. 2016; herring gulls *Larus argentatus*, Anderson et al. 2020). Thaxter et al. (2016) suggested that a reduction in flight agility and foraging efficiency could have affected the kleptoparisitic behavior of skuas. It is also possible that the device and/or the harness affected flight performance during their long migration, created friction on the skin, or compromised insulation due to feather wear, thus increasing mortality due to exhaustion (Thaxter et al. 2016). If plumage gets damp, pelagic seabirds do not have the possibility to rest on land to dry, which may rapidly lead to death due to chilling. Even though satellite transmitters respected the 3% of body mass rule (Phillips et al. 2003), this additional weight may also have affected survival through an increase in energy expenditure during their long migration. However, transmitters apparently had a minimal effect on travel speed and migration phenology since these parameters were similar to those of individuals tracked with geolocators during early migration. Nonetheless, for future research on long-tailed jaegers, we strongly recommend the use of small and light devices such as geolocators to avoid the problems reported here and by Sittler et al. (2011).

2.7 Conclusions

We reported for the first time migratory movements of long-tailed jaegers breeding in the Canadian Arctic. Only a few arctic seabirds are long-distance trans-equatorial migrants like long-tailed jaegers (Egevang et al. 2010, Stenhouse et al. 2012, Davis et al. 2016, Hromádková et al. 2020). Although several of these species share similar migratory paths and stop over areas (Davies et al. 2021), the optimal migration strategies appear species specific. Contrary to most other species, the fall migration of arctic-nesting jaegers was 46% faster and more direct than the spring migration. A time-minimizing strategy in fall may be partly favored by the need to molt as soon as possible after the completion of the migration. In spring, a fly-and-forage strategy could be the best strategy, as higher foraging effort during migration may allow birds to arrive in the Arctic in good body condition, hence in a better position to face unpredictable and adverse environmental conditions.

Documenting travel paths of long-distance migrating seabirds allows the identification of key areas for the conservation of these species, such as the eastern end of the Grand Banks of Newfoundland or the Benguela Current in the case of long-tailed jaegers. This provides baseline information to evaluate how threats such as climate warming or increased fishing activity may potentially affect these distant areas and ultimately the seabirds using them. Furthermore, integrating events and constraints faced during the entire annual cycle can increase our ability to explain variations in migration strategies used by seabirds or demographic trends observed at their breeding site due to carry-over effects. Ultimately, this will improve our ability to take proper conservation actions when needed.

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2.9 Supplementary material

Annexe S2.1 – Attachment of tracking devices

Annexe S2.2 – Deployment information of tracking devices

Annexe S2.3 – Details on the geolocator analysis method

Annexe S2.4 – Wintering and stopover areas

Annexe S2.5 – Output of linear models

Annexe S2.6 – Chlorophyll concentration

Annexe S2.7 – Phenology of the annual cycle

Annexe S2.8 – Détails supplémentaires sur la calibration des géolocalisateurs récupérés

Annexe S2.9 – Données individuelles des labbes à longue queue suivis à l'aide d'un géolocalisateur

Annexe S2.10 – Données individuelles des labbes à longue queue suivis à l'aide d'un émetteur satellite

Annexe S2.11 – Animated migratory tracks of long-tailed jaegers. Available at www.int-res.com/articles/suppl/m677p001_supp/

Chapitre 3 – Weak carry-over effects and strong influence of local conditions on the reproduction of a long-distance migrant

Labbe à longue queue en incubation sur son nid

En préparation :
Seyer, Y., G. Gauthier, J. Bêty, J.-F. Therrien, and N. Lecomte. Weak carry-over effects and strong influence of local conditions on the reproduction of a long-distance migrant.

3.1 Résumé

Les animaux qui migrent peuvent relier des écosystèmes éloignés et les conditions rencontrées à chaque site peuvent ensuite les affecter via des effets reportés. Cela est particulièrement vrai chez certains oiseaux marins comme le labbe à longue queue (*Stercorarius longicaudus*), un migrateur de longue distance devenant exclusivement terrestre en période de reproduction. L'objectif de cette étude était de tester les effets reportés réciproques entre les périodes de reproduction, de migration et d'hivernage chez cette espèce en évaluant les effets reportés potentiels (1) des paramètres du mouvement et de la phénologie pendant la période non-reproductrice (hivernage et migration printanière) sur les paramètres de la reproduction et (2) du succès reproducteur sur la phénologie de la migration automnale. Nous avons également examiné si les conditions locales, notamment l'abondance de lemmings au site de reproduction, influençaient les paramètres de la reproduction et pouvaient moduler les effets reportés. Pendant 15 ans, nous avons suivi la reproduction des labbes et la densité de lemmings sur l'Île Bylot dans l'Arctique canadien, et nous avons étudié leurs déplacements pendant la période non-reproductrice à l'aide de géolocalisateurs. Nous avons trouvé peu d'effets reportés de la période non-reproductrice et de sa phénologie sur la date d'arrivée en Arctique ou sur les paramètres de la reproduction. Toutefois, augmenter le temps passé en vol en hiver et arriver hâtivement au site de reproduction diminuaient la propension à nicher. En revanche, la propension à nicher et le succès reproducteur étaient fortement liés à l'abondance locale de lemmings et le succès reproducteur des nicheurs hâtifs était plus élevé que celui des nicheurs tardifs. La phénologie de la migration automnale était devancée pour les individus échouant la reproduction sans toutefois en changer la durée. La reproduction du labbe était ainsi faiblement affectée par les effets reportés mais fortement influencée par les conditions locales. La forte saisonnalité et l'imprévisibilité de la toundra arctique (ressources pulsées, moment de la fonte de la neige au printemps) en comparaison aux environnements océaniques exploités durant la période non-reproductrice pourraient expliquer ces résultats.

Mots clés : Géolocalisateurs · Hivernage · Labbe à longue queue · Lemming · Migration · Oiseaux marins · Propension à nicher · *Stercorarius longicaudus* · Succès reproducteur · Toundra

3.2 Abstract

Migratory animals often connect distant ecosystems during their annual cycle and conditions encountered at any of these sites can impact them later on through carry-over effects (COEs). This is especially true in some seabird species like the long-tailed jaeger (*Stercorarius longicaudus*), a long-distance migrant that completely switch from a marine to a terrestrial lifestyle to breed. The aim of this study was to test for reciprocal COEs between reproduction, migration, and wintering periods in this species by assessing potential COEs of (1) movement parameters and phenology during the non-breeding season (winter and spring periods) on reproductive parameters (breeding propensity, laying date, and breeding success), and of (2) breeding success on phenology of fall migration. We also examined whether local food resources at the breeding site (lemming abundance) influenced reproductive parameters and could modulate COEs. Over 15 years, we monitored jaeger reproduction and lemming densities on Bylot Island in the Canadian Arctic, and we used geolocators to study their movements during the non-breeding season. We found few COEs of the movement parameters and phenology during the non-breeding season on arrival date in the Arctic or on reproductive parameters, although increased time spent flying during the winter and early arrival at the breeding site decreased breeding propensity. In contrast, local conditions affected several reproductive parameters as breeding propensity and breeding success were both strongly related to lemming abundance, and breeding success of early breeders was higher than that of late breeders. The phenology of fall migration was advanced for failed breeders but duration stayed constant. Reproduction of long-tailed jaegers was therefore weakly influenced by COEs but strongly by local conditions. The high seasonality and unpredictability of the Arctic tundra (e.g. pulsed resources, timing of spring snowmelt) in comparison to the oceanic environment used during the non-breeding season could explain these results.

Key words: Breeding propensity · Breeding success · Geolocators · Lemming · Long-tailed jaeger · Migration · *Stercorarius longicaudus* · Seabirds · Tundra-nesting · Wintering

3.3 Introduction

Migratory animals often use resources from several distant and very different ecosystems, such as the terrestrial and marine ones. These links across ecosystems can affect the population dynamics of many species (Webster et al. 2002, Bauer et al. 2016) and even the structure of food webs through nutrient exchange (Gauthier et al. 2011, Zwolicki et al. 2013, Robillard et al. 2021). During their annual cycle, long-distance migrants must pass through different types of environments that change seasonally. They need to use sites when enough resources are available and which are predictable over time (Newton 2008, Gilg and Yoccoz 2010). Environmental changes occurring along the migratory route pose additional challenges for animals as they may need to adjust their migration strategy (e.g. route, phenology) to minimize negative impacts while taking advantage of new opportunities (Parmesan and Yohe 2003, Trautmann 2018, Kharouba et al. 2018, Reséndiz-Infante et al. 2020). Moreover, they need to arrive at the breeding site at the right time to avoid a mismatch between reproduction and the phenology and abundance of their prey (Both and Visser 2001, Crick 2004, Both et al. 2010, Doiron et al. 2015, Potvin et al. 2016).

Many studies have shown that conditions encountered during migration and the winter period (e.g. weather condition, food abundance, competition, disturbance) can subsequently affect the reproductive performance (Marra et al. 1998, Morrissette et al. 2010, Legagneux et al. 2012a, Salton et al. 2015). These are called carry-over effects (COEs), i.e. events and processes occurring in one season that result in individuals making the transition between seasons in different levels of condition, affecting individual performance during a subsequent period (Norris 2005, Norris and Marra 2007, Harrison et al. 2011). Although COEs from the winter or spring migration on the subsequent reproduction are most often documented, events occurring during the breeding season can also affect processes occurring at later stages such as molting and fall migration (Norris et al. 2004b, Catry et al. 2013, Low et al. 2015, Shoji et al. 2015, Fayet et al. 2016).

COEs do not act alone but usually in combination with conditions prevailing during the current season. Indeed, reproductive decision such as whether to initiate breeding or not, and when and how much to invest in reproduction will likely be influenced both by COEs and conditions on the breeding ground (Morrissette et al. 2010, Legagneux et al. 2012a). For instance, timing of breeding is an important determinant of reproductive success in seasonal environments (Low et al. 2015), as early breeders usually have a higher reproductive success than late breeders (Perrins 1970, Lepage et al. 2000, Harms et al. 2015). Timing of breeding or clutch size can be strongly affected by local conditions like food availability, weather or presence of competitors (Rowe et al. 1994, Erikstad et al. 1998, Therrien et al. 2014a). However, arrival date at the breeding site and body condition, which will often depend on events occurring during the migration or the preceding winter period, can also impact these breeding decisions (Rowe et al. 1994, Bêty et al. 2003, Descamps et al. 2011, Harms et al. 2015).

The long-tailed jaeger (*Stercorarius longicaudus*), a small-size seabird, performs one of the longest migration on Earth from its breeding site in the High Arctic to wintering sites scattered throughout the southern oceans (van Bemmelen et al. 2017, Seyer et al. 2021). Moreover, they switch from a marine lifestyle for most of the year to an entirely terrestrial one during the summer when they are highly reliant on lemmings to breed (Therrien et al. 2014a, Seyer et al. 2020), a pulsed resource displaying large interannual fluctuations in abundance (Fauteux et al. 2015). Their very long migration and ecosystem switch expose jaegers to diverse environments throughout their annual cycle. Thus, these conditions have a strong potential to lead to COEs effects across seasons and, in combination to local conditions, affect their reproduction (Webster et al. 2002, Norris and Marra 2007, Briedis and Bauer 2018).

The aim of this study was to test for reciprocal COEs between reproduction, migration, and the wintering period in the long-tailed jaeger. We first evaluated potential COEs of events occurring during the non-breeding season (i.e. movement parameters and phenology, wintering site used) on subsequent reproductive parameters (i.e. breeding propensity, laying date and breeding success) of individuals. We expected an earlier laying and an improved breeding success for individuals arriving earlier in spring. We then examined whether reproductive parameters were also influenced by environmental conditions encountered on the breeding ground (local lemming abundance). Finally, we evaluated whether reproductive success affected the fall migration phenology. We expected failed breeders to leave the terrestrial environment and begin and complete their migration earlier than successful breeders.

3.4 Methods

3.4.1 Study area and study species

The field work was conducted during the jaeger breeding seasons (mid-June to early August) on Bylot Island (Nunavut; 73°08’ N 80°00’ W) in the Canadian High Arctic. The area is composed of rolling hills with gentle slopes, low-elevation plateaus, and lowlands. Mesic tundra dominates the landscape, but wetlands associated with ponds and polygons are common in lowlands (Gauthier et al. 2011). The mesic tundra is dominated by prostrate shrubs and a sparse cover of forbs and graminoids. The main study site (35 km^2) was the Qarlikturvik Valley, a large glacial valley, and a secondary site (25 km^2), situated 30 km to the south, was located at the center of a large snow goose (*Chen caerulescens*) nesting colony. Two rodent species are present at the study site, the brown lemming (*Lemmus trimucronatus*), which displays large-amplitude fluctuations of abundance every 3-4 years, and the collared lemming (*Dicrostonyx groenlandicus*), which shows weak amplitude fluctuations (Gruyer et al. 2008, Gauthier et al. 2013).

Long-tailed jaegers nest on the tundra in open areas, mostly moist and mesic meadows on flat terrain, and to a lesser extent in mesic tundra on gentle slopes (Seyer et al. 2020, Wiley and Lee 2020). During the breeding period, jaegers feed primarily on lemmings (Seyer et al. 2020) but also on young passerines and shorebirds, arthropods and berries (Maher 1970, Andersson 1971, 1976a). Their main nest predators are the Arctic fox (*Vulpes lagopus*) and the glaucous gull (*Larus hyperboreus*; Wiley and Lee 2020).

3.4.2 Field methods

3.4.2.1 Nest monitoring

We carried out systematic nest searches along parallel transects spaced out by 400 m in late June and early July to find breeding pairs at the main study site from 2004 to 2019. Breeding jaegers are easy to detect due to their alarm call when intruders are up to 200 m from their nest (Andersson 1971, Wiley and Lee 2020). At the secondary study site, nests were found opportunistically since 2015. All nests were georeferenced when found (data availability: Gauthier et al. 2020).

Active nests were visited every 1-2 weeks until hatching to check their content. The laying date was defined as the date the first egg was laid, and it was estimated from one of the three following techniques. When a nest was found between laying of the first and second egg, we considered the laying date was the day before the visit. If a nest was found with 2 eggs (maximum clutch size, Andersson 1976b) or if only one egg was laid, eggs were floated and we estimated the incubation stage based on Furness and Furness (1981) and Liebezeit et al. (2007). If a nest was visited at hatching, we estimated the laying date by subtracting the mean incubation length (24 d; Maher 1970) to hatching date of the first egg. Because jaeger chicks leave the nest within two days after hatching and are hard to find on the tundra, we defined breeding success as the probability that at least one young successfully left the nest. Success was confirmed by the presence of chicks or aggressive adults in the nest vicinity after hatch or by the presence of small shell fragments in nests visited after hatch. Success could be confirmed only for nest located at the main study site (Qarlikturvik Valley).

3.4.2.2 Bird capture

We captured breeding jaegers at their nest from 2007 to 2019 using a bownet trap, or in the nest vicinity using a noose carpet, a netgun, or a bal-chatri trap with a live lemming inside. All captured birds were marked with metal and coded plastic bands that could be read at a distance. Several individuals were also equipped with a geolocator (light-level loggers; Intigeo-C65, Migrate Technology, Cambridge, United Kingdom) attached to the plastic band (see Seyer et al. 2021 for more details; data availability: Seyer et al. 2022a).

3.4.2.3 Lemming monitoring

We live-trapped lemmings annually from 2004 to 2019 in two permanent 11-ha grids in the center of the main study site, one in wet tundra habitat and one in mesic habitat (see Fauteux et al. 2015 for methodological details). Three-day trapping sessions were conducted twice (mid-June and mid-July), and all captured lemmings were identified to species, marked, and released. Lemming densities were estimated with spatially explicit capture-recapture models for each trapping period and grid (see details in Fauteux et al. 2015). We averaged June and July lemming densities to avoid an underestimation of the early summer lemming density (hereafter lemming density) in late snowmelt years. Finally, we averaged densities between both grids, and we summed densities of each species.

3.4.3 Movement analysis

We deployed 65 geolocators from 2014 to 2018 and we recovered 40 of them from 2015 to 2019, which yielded 41 tracks from 32 different individuals (some individuals received >1 geolocator). Among these, we had 23 complete migrations including the returning date to the breeding ground after a full year. Geolocators sampled light intensity each minute and recorded its maximum value every 5 min, and a wet-immersion sensor recorded when in contact with saltwater (value >63 on an arbitrary scale from 0 to 127; Fox 2013). We estimated the locations of individuals with light intensity data twice daily throughout the annual cycle with the threshold method (Ekstrom 2004, Lisovski and Hahn 2012) using a Bayesian approach implemented in the *SGAT* package (Wotherspoon et al. 2013) in R (other packages mentioned below are also in R).

We used a changepoint analysis with the *cpt.meanvar* function from the package *changepoint* (Killick and Eckley 2014) to identify a sudden change in the daily number of immersions when jaegers finished breeding and switched to a marine lifestyle to migrate, and conversely, when they arrived to breed in the subsequent year. We summed the daily number of immersions and calculated a 3-d running mean. A visual inspection of changepoint plots allowed us to select the transitions corresponding to the beginning of the fall and the end of the spring migration.

To define the wintering period, we used a three-step approach based on the “Migratory Analytical Time Change Easy Detection” method (Chen et al. 2016, Doko et al. 2016). First, we performed a changepoint analysis to identify sudden changes in an ordered sequence of data for three parameters: latitude, longitude, and net-squared displacement (NSD), which corresponds to the straight-line distance between the starting location (i.e. the breeding site), and any other subsequent location. During the wintering period, we expected the three parameters to present flat and stable lines as birds should be staying in the same region. Second, a visual inspection of these parameters (latitude, longitude, NSD) plotted together with the migratory path helped to identify the beginning and the end of the wintering period. Finally, we validated the dates with those estimated from the stationary periods revealed by the *ChangeLight* function from the package *GeoLight* (Lisovski and Hahn 2012) for the same time period (i.e. winter; see Seyer et al. 2021 for more details).

Analyses of geolocator data yielded several variables: departure and arrival date at the breeding and wintering sites, duration of spring and fall migrations, time spent at the wintering site, distance travelled, travel speed, and daily number of immersions during both migrations and at the wintering site, and main wintering site used (see Seyer et al. 2021 for details). Several of these variables were correlated (Annexe S3.1). For subsequent analyses, we selected parameters that were the most biologically meaningful and with low correlation between them. We selected daily number of immersions at the wintering site (a proxy of the time spent in flight vs. foraging or resting at sea; Seyer et al. 2021), distance travelled at the wintering site, duration of spring migration, spring migration travel speed, and arrival date at breeding site to test the influence of the non-breeding period on reproductive parameters. To test the influence of reproductive success on fall migration, we selected departure date from the breeding site, duration of fall migration, and arrival date at wintering sites.

3.4.4 Statistical analyses

We used generalized linear models (GLMs) to assess the influence of daily number of immersions and distance travelled at the wintering site, and spring migration duration and travel speed on arrival date at the breeding site of jaegers marked with geolocators. We used GLMs to assess the influence of daily number of immersions and distance travelled at the wintering site, spring migration travel speed, and arrival date at the breeding site on breeding propensity (binomial distribution in this case) and laying date.

Because jaegers are faithful to their wintering site (Y. Seyer, unpubl. data, van Bemmelen et al. 2017), we considered that individuals equipped at least once with a geolocator always wintered at the same site, even if their wintering site was determined in a single year. Thus, we included all breeding attempts of these individuals either in a generalized linear mixed model (GLMM; *lme4* package; Bates et al. 2015) to assess the influence of the wintering site used on laying date or in a GLM to assess the influence of the wintering site used on breeding success. Bird ID was set as random factor and we calculated marginal R^2_m (for fixed effects) and conditional R^2_c (for fixed and random effects) based on Nakagawa and Schielzeth (2013). We also examined the influence of wintering site used on breeding propensity with a GLMM, but we restricted the dataset to the period when jaegers equipped with geolocators were searched actively at the study site annually (individuals that were never resighted at the breeding site were excluded). This method allowed us to increase the sample size for these analyses.

We used a GLMM with binomial distribution to assess the influence of lemming density on breeding propensity and used bird IDs as random factor. We only used jaegers equipped with a geolocator to estimate breeding propensity as intensive nest searches were conducted to locate them. We used GLMs to assess the influence of lemming density on laying date and clutch size (with a binomial distribution in the latter case) using all nests monitored during the study period. We considered clutch size as a dichotomic variable because jaegers lay one or two eggs. We used GLMs to examine if the phenology of fall migration (i.e. departure date from the breeding site, arrival date at the wintering site, duration of the fall migration) differed between successful and failed breeders. Two models were tested with either lemming density or laying date as covariate and breeding success as response variable. We repeated the same analysis by expressing laying date as deviation of the annual mean to control for annual variation in nesting phenology.

Breeding success was analyzed as a daily survival rate (DSR) of nests using a binary response variable (success or failed hatched) modeled with the logistic-exposure method (Shaffer 2004). Breeding success was estimated as $(DSR)^{24}$, where 24 is the duration of the incubation period from the laying of the first egg to hatching. All tested models were kept as simple as possible because of the small sample size available for some variables and the sparsity of the data. Analyses were done using the software R version 4.1.0 (R Core Team 2021). Means are presented with standard errors throughout the results and slopes (β) with their 95% confidence intervals.

3.5 Results

3.5.1 *Influence of the non-breeding season on reproductive success*

Arrival on Bylot Island of jaegers marked with geolocators (June 3 ± 0.9 d, n = 23) was not influenced by the spring migration as arrival date was not related to either the duration or the travel speed of the spring migration (Table 3.1). However, an increase in the daily number of immersions and a decrease in the distance travelled at the wintering site tended to delay arrival date in spring (Table 3.1; Figure 3.1).

The breeding propensity of jaegers was positively related to the daily number of immersions at wintering site as well as arrival date at breeding site (Table 3.2; Figure 3.2). On average, each day of delay after May 26 increased the breeding propensity by 4%. However, breeding propensity was not affected by the wintering site used, the distance travelled at the wintering site, or the spring migration travel speed. Similarly, laying date was not affected by the wintering site used, daily number of immersions and the distance travelled at the wintering site, spring migration travel speed, or arrival date at breeding site (Table 3.2; Figure 3.2). Breeding success did not vary according to the wintering site used (Table 3.2).

Table 3.1 Slope parameters (β) and their 95% confidence intervals (CI) of models examining the links between parameters of the wintering and spring migration periods and arrival date of long-tailed jaegers equipped with geolocators at their breeding site, Bylot Island, Nunavut, Canada, 2014-2019. n: Sample size. *K*: Number of parameters. Dates were expressed as day of the year for statistical analyses.

Response variable	Explanatory variable	*K*	β	CI	R^2	n
Arrival date at breeding site	Daily number of immersions at the wintering site	3	0.012	[-0.003; 0.028]	0.11	22
Arrival date at breeding site	Distance travelled at the wintering site	3	-0.0003	[-0.0007; 0.0001]	0.11	23
Arrival date at breeding site	Duration of spring migration	3	0.00	[-0.06; 0.06]	0.00	23
Arrival date at breeding site	Spring migration travel speed	3	-0.018	[-0.060; 0.024]	0.03	23

3.5.2 Local determinant of reproductive success

We monitored a total of 406 nests of long-tailed jaegers and we could determine the outcome of 279 nests. The breeding propensity of jaegers increased with lemming density (β = 2.61 [1.39, 5.73], $R^2_m = 0.67$, $R^2_c = 0.72$, n = 94; Figure 3.3; analysis restricted to marked individuals); an increase from 1 to 2.5 lemmings per ha increased the breeding propensity from 0.04 to 0.66. The mean laying date of jaegers was June 18 ± 0.3 d (Figure 3.4) and was not affected by lemming density (β = -0.21 [- 0.54, 0.13], n = 218). The annual proportion of 2-egg clutches was high in most years (mean: 0.88 ± 0.03; n = 11 yrs; Figure 3.4) although the probability of laying two eggs instead of one tended to increase with lemming density (β = 0.14 [-0.04, 0.34], n = 361). The mean annual breeding success of initiated nests was 0.44 ± 0.10 and highly variable between years (range: 0−0.95; n = 13 yr; Figure 3.4). The breeding success increased with lemming density (β = 0.43 [0.31, 0.56], n = 279); an increase of 1 lemming per ha increased the probability of successful breeding by 11% on average. In contrast, the probability of successful breeding decreased by 3.9% on average with each day of delay in laying (β = -0.15 [-0.21, -0.09], n = 169; Figure 3.5; results did not change when laying date was expressed as deviations of annual mean).

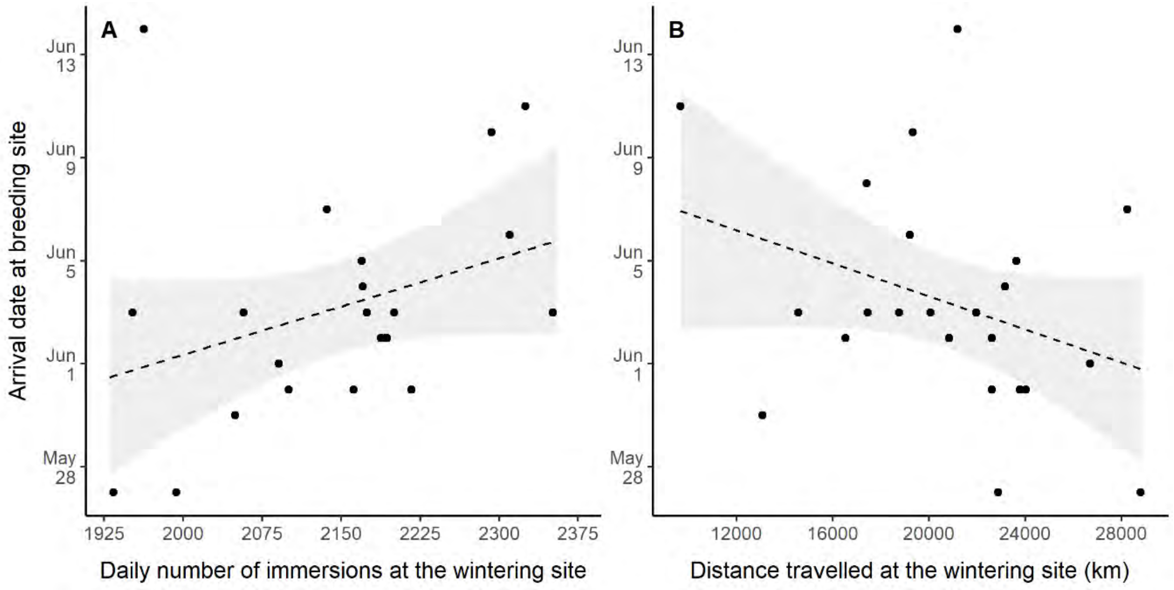

Figure 3.1 Arrival date at breeding site of long-tailed jaegers in relation to A) the daily number of immersions at the wintering site or B) distance travelled at the wintering site (n = 22 and 23, respectively) on Bylot Island, Nunavut, Canada, 2014-2019. Dashed lines represent non-significant relationships. The gray shaded area represents the 95% confidence intervals.

Table 3.2 Slope parameters (β) and their 95% confidence intervals (CI) of models examining the links between parameters of the wintering and spring migration periods and the subsequent breeding parameters of long-tailed jaegers equipped with geolocators at their breeding site, Bylot Island, Nunavut, Canada, 2014-2019. R^2_m: Marginal R-squared for fixed effects (linear mixed-effect models) or R-squared (generalized linear models). R^2_c: Conditional R-squared for fixed and random effects. n: Sample size. *K*: Number of parameters. Reference levels were set as *not nesting* for breeding propensity, *failed breeding* for breeding success, and *Benguela current* for the wintering site. Dates were expressed as day of the year for statistical analyses.

Response variable	Explanatory variable	*K*	β	CI	R^2_m	R^2_c	n
Breeding propensity[*]	Wintering site: Agulhas c.	6	1.27	[-0.18; 2.92]	0.04	0.04	87
	Wintering site: Brazil c.		0.58	[-1.20; 2.35]			
	Wintering site: Canary c.		0.35	[-0.76; 1.45]			
	Wintering site: Guinea c.		0.58	[-1.61; 2.76]			
Breeding propensity	Daily number of immersions at wintering site	2	0.005	[0.002; 0.010]	0.22	-	37
Breeding propensity	Distance travelled at the wintering site	2	0.0000	[-0.0002; 0.0002]	0.00	-	23
Breeding propensity	Spring migration travel speed	2	0.011	[-0.009; 0.035]	0.05	-	23
Breeding propensity	Arrival date at breeding site	2	0.23	[0.00; 0.56]	0.14	-	23
Laying date[†]	Wintering site: Agulhas c.	6	0.30	[-2.72; 3.31]	0.02	0.10	48
	Wintering site: Brazil c.		-0.82	[-4.27; 2.62]			
	Wintering site: Canary c.		1.07	[-1.53; 3.71]			
Laying date	Daily number of immersions at wintering site	3	-0.002	[-0.010; 0.006]	0.02	-	15
Laying date	Distance travelled at the wintering site	3	0.0000	[-0.0002; 0.0003]	0.02	-	10
Laying date	Spring migration travel speed	3	-0.017	[-0.047; 0.013]	0.11	-	12
Laying date	Arrival date at breeding site	3	-0.09	[-0.43; 0.25]	0.03	-	10
Breeding success[†]	Wintering site: Agulhas c.	5	-0.13	[-1.38; 1.13]	-	-	61
	Wintering site: Brazil c.		0.18	[-1.07; 1.43]			
	Wintering site: Canary c.		-0.59	[-1.73; 0.55]			

[*] Data set includes information for jaegers monitored at least once with a geolocator for all the years they nested between 2015-2019. Bird ID was set as random factor.

[†] Data set includes information for jaegers monitored at least once with a geolocator for all the years they nested between 2008-2019. Bird ID was set as random factor.

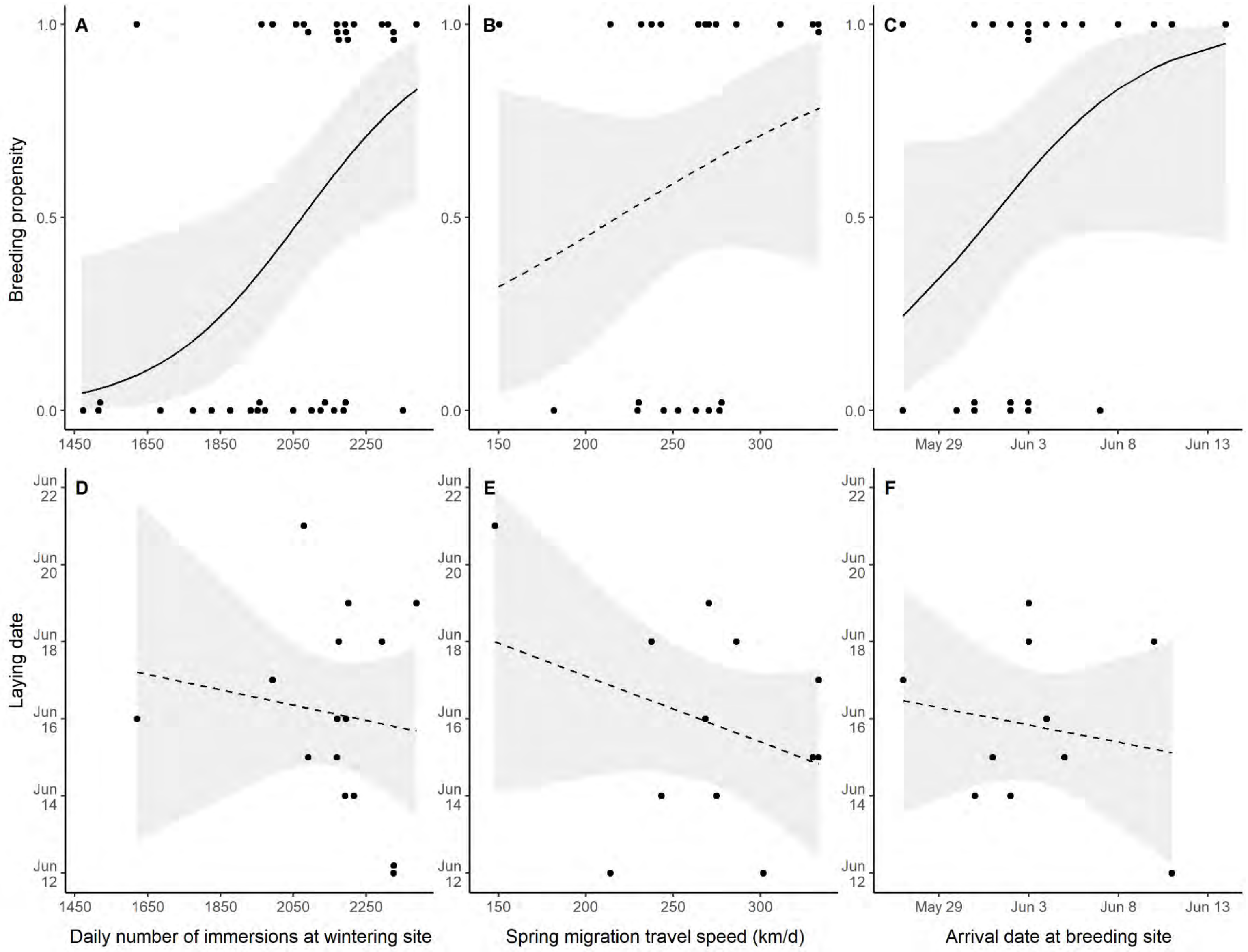
A
B
C
D
E
F
Breeding propensity
1.0
0.5
0.0
Laying date
Jun 22
Jun 20
Jun 18
Jun 16
Jun 14
Jun 12
1450
1650
1850
2050
2250
150
200
250
300
May 29
Jun 3
Jun 8
Jun 13
Daily number of immersions at wintering site
Spring migration travel speed (km/d)
Arrival date at breeding site

Figure 3.2 Breeding propensity or laying date of long-tailed jaegers in relation to daily number of immersions at the wintering site (A, n = 37; D, n = 15), spring migration travel speed (B, n = 23; E, n = 12), and arrival date at their breeding site (C, n = 23; F, n = 10) on Bylot Island, Nunavut, Canada, 2014-2019. Solid lines represent significant relationships and dashed lines non-significant ones. The gray shaded area represents the 95% confidence intervals.

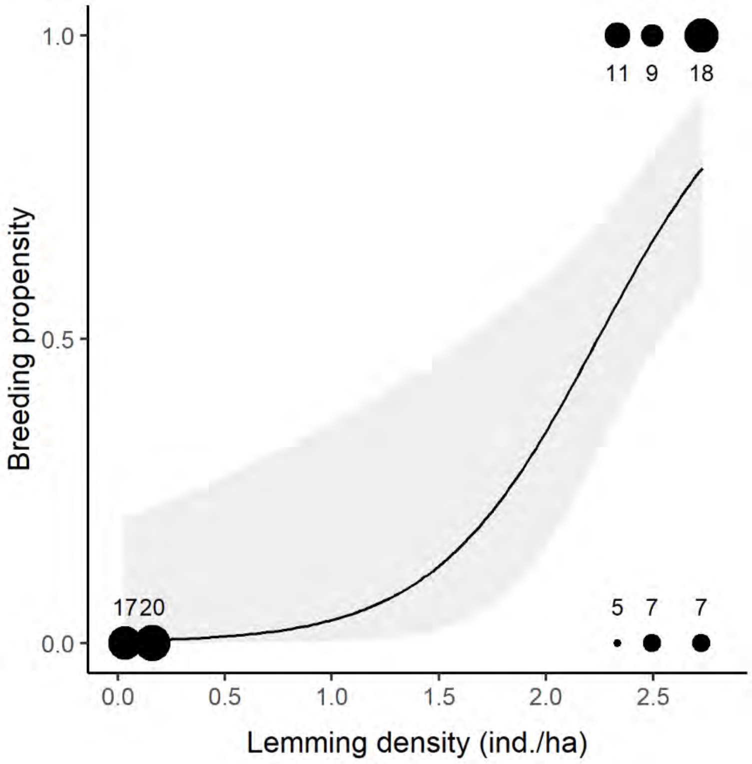

Figure 3.3 Breeding propensity of long-tailed jaegers (n = 94) in relation to lemming density on Bylot Island, Nunavut, Canada, 2015-2019. Numbers above or below each data points represent the annual sample size and the size of the dots is proportional it. Solid line represents significant relationships. The gray shaded area represents the 95% confidence intervals.

3.5.3 Influence of reproductive success on fall migration

Compared to failed breeders, jaegers that bred successfully departed about 10 d later from the breeding site (successful breeders: August 17 ± 1.2 d, n = 15 vs. failed: August 7 ± 2.8 d, n = 12; $\beta = 9.53$ [3.95, 15.12] , $R^2 = 0.31$) and arrived about 2 weeks later at the wintering site (October 17 ± 5.2 d, n = 14 vs. October 3 ± 3.3 d, n = 10; $\beta = 13.34$ [-0.01, 26.69], $R^2 = 0.15$). Nevertheless, the duration of the fall migration did not differ between successful and failed breeders (61.7 ± 4.6 d, n = 14 vs. 58.4 ± 3.3 d, n = 10; $\beta = 3.27$ [-8.68, 15.23]).

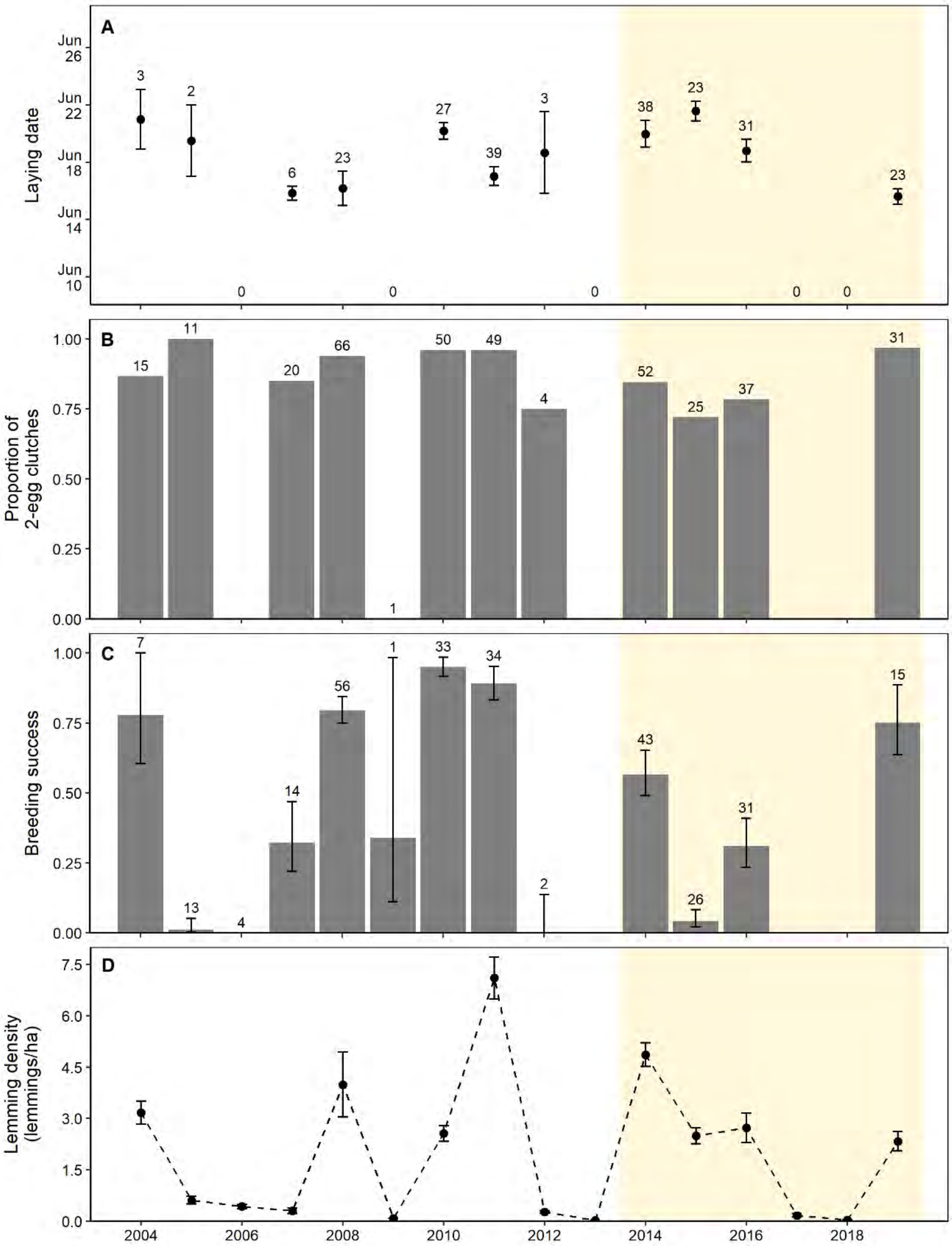

Figure 3.4 A) Laying date (mean ± SE), B) proportion of 2-egg clutches and C) estimated breeding success (mean ± SE) of long-tailed jaegers, and D) lemming density (mean ± SE) on Bylot Island, Nunavut, Canada, 2004-2019. Numbers above each column or data points represent the annual sample size. Yellow shaded area represents years when geolocator data were collected.

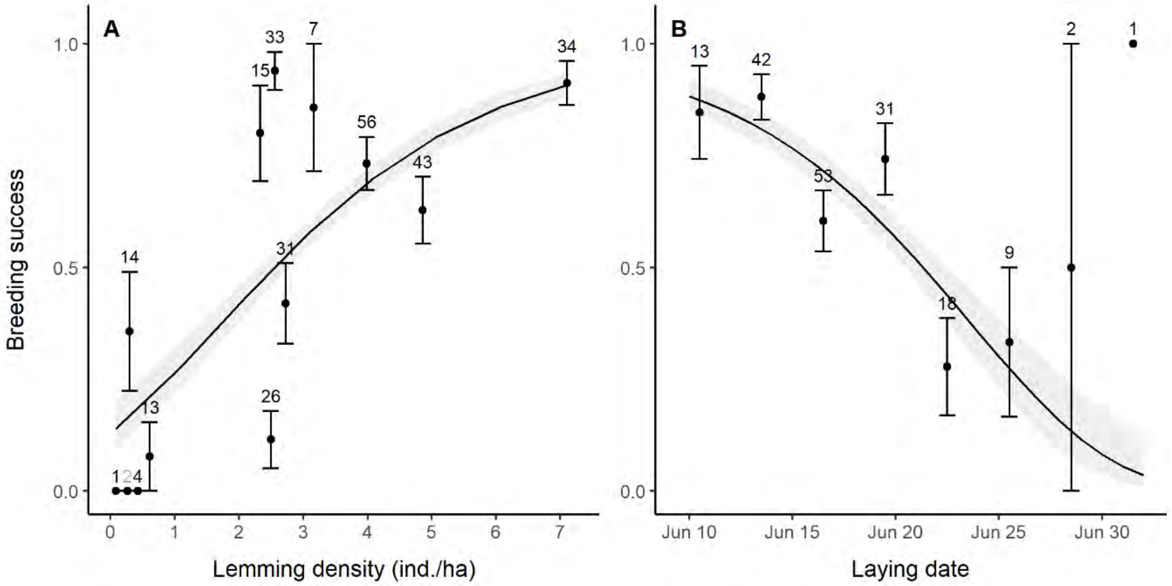

Figure 3.5 Breeding success of long-tailed jaegers in relation to A) lemming density or B) laying date (n = 279 and 169, respectively) on Bylot Island, Nunavut, Canada, 2004-2019. Even though analyses were performed on individual data points, for sake of clarity, we presented the mean breeding success by year (A) or by 3 d bin (B) classes and added standard errors. Numbers above each data points represent the sample size of each class. Solid lines represent significant relationships. The gray shaded area represents the 95% confidence intervals.

3.6 Discussion

We showed that the reproduction of a long-distance arctic migrant is heavily driven by food availability at the breeding site but appears to be weakly affected by events occurring during the non-breeding season through COEs. The unpredictability of the highly seasonal arctic environment (e.g. pulsed resources, variable spring snowmelt) creates variable breeding conditions (Therrien et al. 2014a, Beardsell et al. 2016) and may have overridden potential COEs driven by the conditions encountered during migration and the wintering period. Nonetheless, spending a high proportion of time in flight during the winter decreased the probability of breeding. Moreover, this is one of the few studies showing that early arrival at the breeding site may have deleterious effects on the probability of nesting.

3.6.1 Effects of winter and spring migration on reproductive success

Arrival date at the breeding site was not influenced by the duration of the spring migration, although individuals wintering closer to the breeding site left more than 45 d later, spent less time in migration and travelled faster than those spending the winter 7500 km further away (Seyer et al. 2021). Leaving earlier for the northbound migration at the most distant sites may be a strategy to compensate the additional cost of a longer migration without delaying arrival date at the breeding site (Oppel and Powell 2009). Although individuals wintering closer to the breeding site may sometimes arrive earlier to breed (Hötker 2003, Bregnballe et al. 2006), the costs of wintering further can be offset by the quality of the wintering and stopover sites used (Alves et al. 2012). The absence of effects of travel speed during migration on arrival date to the breeding site suggests that individuals are able to compensate the higher cost of migrating faster or for longer distance by using highly productive sites during wintering and stopover periods (Seyer et al. 2021). It is possible that adjustment of the arrival date occurs during the last steps of the migration, as the birds reach arctic waters. For instance, the annual extent of sea ice may constrain jaegers in their migration, forcing them to slow down and contributing to synchronize their arrival over a short time frame (Nuijten et al. 2014, Seyer et al. 2021).

The shortness of the arctic summer probably also favors an arrival at the breeding site over a short period. From laying to fledging, reproduction lasts about 50 d, forcing jaegers to start breeding within a few days after territories are free of snow (Andersson 1976a, Wiley and Lee 2020). Although early breeders usually have a high reproductive success (Perrins 1970, Lepage et al. 2000), arriving too early may also entail some costs as suggested by the reduced breeding propensity of jaegers arriving earliest. Only a few studies previously demonstrated this effect in other species, especially in the Arctic (Bêty et al. 2004, Legagneux et al. 2016, Jean-Gagnon et al. 2018). This may not be surprising as conditions in early summer can be highly unpredictable at those latitudes: access to lemmings on land may be limited by the snow cover (Therrien et al. 2015), access to the marine environment may be limited by the ice cover (Hunt 1991), and extreme weather conditions like late snow storm may occur (Moore et al. 2005). Thus, birds arriving too early may deplete their body reserves due to lack of feeding opportunities, which may force them to forego breeding.

A high proportion of time spent in flight during the winter, as revealed by the immersion counts, may indicate that these individuals were spending less time foraging or resting at sea and traveling longer distances in search of good foraging areas. This could explain why these birds had a reduced breeding propensity. It was previously shown that seabirds displaying a high level of activity during the winter (i.e. more time spent flying, higher foraging effort, less resting) occasionally skip a reproduction to improve their reproductive performance in the following year (Kazama et al. 2013, Shoji et al. 2015). This strategy can compensate for poor body condition, sometimes carried over from the previous breeding season, or poor foraging conditions at the wintering site. Nonetheless, other breeding parameters (laying date, breeding success) were not influenced by movement parameters of the wintering or spring migration periods. Despite some differences in primary productivity among wintering sites used by jaegers (Seyer et al. 2021), we found no effect of the site used over a range of 8500 km on reproductive parameters, which further suggests that the higher energetic costs to reach a distant wintering site may be compensated by benefits such as the richness and predictability of resources. It is also possible that the energetic cost of migration may not be so high in a species that uses gliding as a primary flight mode (Pennycuick 2008).

The highly variable and unpredictable conditions at the breeding site may have overridden potential COEs, especially when breeding conditions were very poor or very good (Legagneux et al. 2012a). Alternatively, a low variability in conditions encountered, either due to the relative stability of the oceanic environment or the use of areas with a high and fairly constant productivity by the majority of the population (Seyer et al. 2021), may have limited the potential to detect COEs (Oppel and Powell 2009). However, the small sample available may have also hampered our ability to detect potential COEs from the non-breeding period on reproduction.

3.6.2 Local determinant of reproductive success

Previous studies documented a close relationship between lemming density, the main food of many avian predators in the Arctic, and breeding effort of those predators at the population level as indexed by local nest density (Gilg et al. 2006, Therrien et al. 2014a, Seyer et al. 2020). They pointed out that a minimal lemming density is required to breed, including for long-tailed jaegers. While body condition could be sufficient to lay eggs, a low lemming abundance during the crash phase may not provide enough resources to raise chicks. Our analysis at the individual level confirmed that most jaegers take the decision of not breeding under these conditions (i.e. breeding probability reaches 50% only when lemming density exceeds ~2 lemmings per ha), which is expected in a long-lived species with potentially many other breeding opportunities (Drent and Daan 1980, Erikstad et al. 1998, Weimerskirch 2002, Descamps et al. 2011). Once lemming density is sufficient to allow jaegers to breed, food resource apparently has little influence on timing of breeding or clutch size. Clutch size is relatively fixed in this species (>85% of individuals lay 2 eggs in most years) and could be partly determined by body condition of birds. As long-tailed jaegers are using oceanic environments, which are relatively stable temporally (Seyer et al. 2021), body condition of birds at arrival may not vary so much between years. Unlike other species nesting in seasonal environments (Bêty et al. 2003, Moore et al. 2005, Descamps et al. 2011, Harms et al. 2015), laying date was not determined by arrival date at the breeding site in jaegers although sample size for this analysis was quite small.

Although lemming abundance had little influence on the reproductive investment once individuals had decided to breed, it did have a strong positive effect on breeding success. This is probably due to an increased predation rate on eggs by foxes and gulls in years of low lemming abundance (Bêty et al. 2002, Gauthier et al. 2015, Lamarre et al. 2017a, Duchesne et al. 2021, Beardsell et al. in press). However, although abandoned nests are rarely found, it is also possible that reduced nest attentiveness by jaegers in years of low food abundance increases the vulnerability of eggs to predation as foxes increase their daily activity time and travel longer distance in those years (Beardsell et al. in press). We also observed a strong seasonal decline in breeding success over the span of laying dates. The shortness of the breeding season, a temporal decrease in resource availability, and a temporal increase in predation pressure and resource competition are all factors that could contribute to the reduced success of late breeders (Gauthier et al. 2011, Fauteux et al. 2015, Seyer et al. 2020).

3.6.3 Effects of reproductive success on fall migration

Post-breeding departure from the breeding site occurred over a long time span (5 weeks) and this was partly due to the early departure of failed breeders, as commonly observed in seabirds (Bogdanova et al. 2011, Guilford et al. 2012, Catry et al. 2013). In late summer, feeding conditions may be better at sea than on land as lemming density often decreases during the season (Fauteux et al. 2015), and competition for resources with other lemming predators increases (Seyer et al. 2020). This probably motivates failed breeders to depart for migration as soon as reproduction is over and return to the marine environment, the primary habitat of jaegers. Thus, birds can rapidly change from a breeding to a migrating state when the former one is over. Because jaegers start molting their flight feathers only when they reach their wintering area (van Bemmelen et al. 2018), they probably are in a hurry to complete their fall migration (Seyer et al. 2021), and the similar length of fall migration between failed and successful breeders strongly reinforces this idea.

3.7 Conclusions

The presence of weak COEs of movement parameters and phenology during the non-breeding season on reproduction suggests that conditions encountered at the breeding site override those encountered during the period spent at sea in a small, long-distance migrant. The high variability and the low predictability of the arctic environment at the time of breeding due to a pulsed resource could explain this phenomenon. As long-tailed jaegers apparently favor their own survival over reproduction when local resources are scarce, arriving in good condition is likely not sufficient to have a large effect on reproduction. Moreover, jaegers have the ability to quickly move over long distances at sea, which may help them to find food-rich areas during the non-breeding period and buffer environmental effects. Nonetheless, considering that the few COEs detected were at the individual level and not related to the wintering site used, it may be more a matter of individual ability to exploit a specific wintering site than a matter of how good the conditions encountered are at this wintering site. It is thus possible that factors that we could not test such as age, sex or individual quality may have mask other potential COEs (Marra et al. 1998, Balbontín et al. 2009, Harrison et al. 2011, Bogdanova et al. 2011). Further studies are needed to better understand potential reciprocal effects between the wintering, migratory and reproductive periods of long-distance migrants at the individual level and their consequences on life-history traits.

3.8 Acknowledgments

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3.9 Supplementary material

Annexe S3.1 – Spearman correlation coefficients of migratory variables

Chapitre 4 – High site fidelity and low mate change in an Arctic monogamous seabird

Couple de labbes à longue queue

Soumis :
Seyer, Y., G. Gauthier, and J.-F. Therrien. High site fidelity and low mate change in an Arctic monogamous seabird.

4.1 Résumé

La monogamie est répandue chez les oiseaux marins et la fidélité au partenaire ainsi qu'au site de reproduction est commune chez ces espèces marines longévives. Toutefois, l'asynchronie dans la date d'arrivée au site de reproduction, où a généralement lieu la réunification des couples, peut mener au divorce et engendrer des coûts comme un retard de la ponte et une réduction du succès reproducteur. En revanche, la familiarité à un site de reproduction augmente habituellement le succès reproducteur. Nos objectifs étaient d'abord de déterminer le niveau de fidélité du labbe à longue queue (*Stercorarius longicaudus*) à son partenaire et à son territoire de reproduction, et ensuite d'évaluer l'influence du succès reproducteur sur sa fidélité au site et au partenaire, et vice-versa. Les labbes sont uniques parmi les oiseaux marins car ils deviennent exclusivement terrestres durant la période de reproduction. Nous avons suivi la reproduction et l'appariement d'un total de 65 labbes (69 couples au total) sur l'Île Bylot dans l'Arctique canadien sur une période de 13 ans. Les labbes déplaçaient relativement peu la position de leur nid entre deux événements de reproduction dans des années différentes (304 m en moyenne) et ils avaient un taux de rétention minimal du partenaire de 79% chez les mâles et 85% chez les femelles. Suivant un succès de reproduction, la fidélité au site était plus élevée pour les individus fidèles à leur partenaire que ceux avec un nouveau partenaire, et inversement en cas d'échec. Nous n'avons noté aucun effet du succès reproducteur sur la probabilité de conserver un partenaire l'année suivante et aucun effet d'un changement de partenaire sur la date d'initiation de la ponte et le succès reproducteur. La courte durée de l'été arctique et la grande imprévisibilité des ressources dans la toundra favorisent sans doute une grande fidélité des labbes à leur site et à leur partenaire, en plus de réduire les bénéfices potentiels d'un changement de partenaire suivant un échec de reproduction.

Mots clés : Fidélité · Labbe à longue queue · Monogamie · Nidification · Reproduction · *Stercorarius longicaudus* · Toundra

4.2 Abstract

Social monogamy is widespread in seabirds and mate and nest site fidelity are common in those long-lived species. However, asynchronous arrival at the breeding site, where pair reunification usually occurs, may lead to divorce and entail some costs such as delayed laying or reduced reproductive success. Site familiarity often increases the breeding success. Our aim was to determine the level of fidelity to mate and site of long-tailed jaegers (*Stercorarius longicaudus*), and to assess the influence of breeding success on site and mate fidelity, and conversely. Jaegers are unique among seabirds as they become exclusively terrestrial during the breeding period. We monitored reproduction and pairing of 65 jaegers (69 pairs) on Bylot Island in the Canadian Arctic over 13 years. Jaegers moved a relatively short distance between breeding attempts in different years (304 m on average) and minimum mate retention was 79% for males and 85% for females. Site fidelity was higher for successful breeders that were faithful to their mate compared to those that had a new mate, and conversely for failed breeders. There was no effect of breeding success on the probability to retain a mate the subsequent year, and no effect of remating on laying date and breeding success. The shortness of the arctic summer and the high unpredictability of resources on the tundra likely favor a high site and mate fidelity in jaegers and reduce potential benefits of remating following a breeding failure.

Key words: Breeding · Long-tailed jaeger · Mate faithfulness · Monogamy · Reproduction · *Stercorarius longicaudus* · Tundra-nesting

4.3 Introduction

Social monogamy is ubiquitous in birds and is the mating system of more than 90% of the species, many of which are also faithful to their mate between years (Lack 1968). This strategy is particularly beneficial in long-lived species as site and mate fidelity are important factors that can affect reproductive success. Familiarity with a partner and a site can reduce the risks and costs incurred by reproduction (Dow and Fredga 1983, Choudhury 1995, Bried and Jouventin 2002, Sánchez-Macouzet et al. 2014). Breeding with a familiar mate usually increases breeding success as it can reduce the cost related to courtship or territory acquisition (Choudhury 1995, Catry et al. 1997, Ismar et al. 2010, Jankowiak et al. 2018, Leach et al. 2020). It can also enhance coordination between partners for incubation shifts, chick feeding and the timing of foraging trips, thus improving reproductive performance (Bried and Jouventin 2002).

Seabird pairs usually reunite at the breeding site after spending the nonbreeding period separated at sea. Therefore, synchrony in arrival time at the breeding site may play a role in mate fidelity (Bried and Jouventin 2002). Asynchrony could cause divorce since waiting for the arrival of a partner will delay laying and lead to reduced reproductive success (Choudhury 1995, Naves et al. 2006, Sánchez-Macouzet et al. 2014). This is especially true in highly seasonal environments where breeding early is generally advantageous (Perrins 1970, Bêty et al. 2003, Low et al. 2015). Under these circumstances, pairing with a new partner may be beneficial. To varying degrees, previous breeding failures were found to trigger divorce (Choudhury 1995, Naves et al. 2006, Ismar et al. 2010, Culina et al. 2015, Sommerfeld et al. 2015). However, the strong association between site and mate fidelity, especially in seabirds, may act as a confounding factor, making reunification with the same individual a side-effect of site-faithfulness (Choudhury 1995, Bried and Jouventin 1999, 2002, Jankowiak et al. 2018).

The long-tailed jaeger (*Stercorarius longicaudus*), a small, long-lived seabird (Julien et al. 2013), breeds all over the Arctic tundra and performs one of the longest trans-equatorial migration annually (van Bemmelen et al. 2017, Seyer et al. 2021). During the breeding season, jaegers completely switch from a marine to a terrestrial lifestyle. They rely on a small inland territory to forage throughout the reproductive period and become highly dependent on lemming abundance to breed, a pulsed resource with cyclic fluctuations (Andersson 1981, Therrien et al. 2014a). Even though these socially monogamous birds were previously assumed to be faithful to their mate and nesting territory, the rate of mate change of long-tailed jaegers has not been quantified using individual based ringing data (Maher 1970, Andersson 1981, Seyer et al. 2020).

Our aim was to determine the level of fidelity of long-tailed jaegers to their mate and nesting territory based on marked individuals. We assessed the influence of previous breeding success on site and mate fidelity, and conversely, the consequences of remating on breeding success. Because of the high temporal variability in resources abundance (i.e. lemming), we were expecting the influence of breeding success on mate fidelity to be limited, but that success should be reduced after remating.

4.4 Methods

4.4.1 Study area and study species

The field work was conducted during the jaeger breeding season (mid-June to early August) on Bylot Island, Nunavut (73°08' N 80°00' W) in the Canadian High Arctic. The main study site (35 km^2) was the Qarlikturvik Valley, a large glacial valley, and the secondary site (25 km^2), situated 30 km to the south, was located at the center of a large snow goose (*Chen caerulescens*) nesting colony (see Seyer et al. 2020 for additional details on the study area).

4.4.2 Field methods

We carried out systematic nest searches along parallel transects spaced out by 400 m in late June and early July to find breeding pairs throughout the main study site from 2007 to 2019. Breeding jaegers are easy to detect due to their alarm call when intruders are up to 200 m from their nest (Andersson 1971, Wiley and Lee 2020). At the secondary study site, nests were found opportunistically since 2015. All nests were georeferenced when found. We captured breeding jaegers at their nest using a bownet trap, or in the nest vicinity using a noose carpet, a netgun, or a bal-chatri trap baited with a live lemming inside during the incubation period. All captured birds were marked with metal and a coded plastic band that could be read at a distance (~50 m). A few body feathers were plucked to sex the birds by DNA analysis (see Seyer et al. 2019 for details). Jaegers encountered during nest searches or nest visits were checked for the presence of plastic bands and the codes were read at a distance whenever possible, either with binoculars or on high resolution photos of individuals.

Active nests were visited every 1-2 weeks until hatching to check their content. The laying date was defined as the date the first egg was laid. If the nest was found between laying of the two eggs (maximum clutch size, Maher 1970), we considered the laying date was the day before the visit. If the nest was found after the end of laying, they were floated to estimate the incubation stage (Furness and Furness 1981, Liebezeit et al. 2007). If a nest was found at hatching, we estimated the laying date by subtracting the mean incubation length (24 d; Maher 1970) to the hatching date. Since jaeger chicks leave the nest soon after hatching and are hard to find on the tundra, we defined breeding success as the probability that at least one young successfully left the nest. Success was confirmed by the presence of chicks or aggressive adults in the nest vicinity or by the presence of small shell fragments in nests visited after hatch. We considered individuals to be divorced when both members of a pair were confirmed to be still alive and at least one was observed breeding with another partner (Choudhury 1995). Nesting data are available online (Gauthier et al. 2020).

4.4.3 Statistical analyses

We used generalized linear models (GLMs) to explore the influence of breeding success in the previous year, mate fidelity (same partner as the previous year) and their interaction on the interannual nest displacement distance, and the influence of mate fidelity on the laying date. We scaled laying date to the annual mean (i.e. individual date minus annual mean) to correct for interannual environmental variability. We used GLMs with a binomial distribution to assess the impact of mate or site fidelity on the breeding success and the influence of breeding success on mate fidelity the following year. All analyses were done using the software R (R Core Team 2021). Means are presented with standard errors throughout the results and slopes (β) with their 95% confidence intervals.

4.5 Results

From 2007 to 2019, we observed 69 breeding pairs during 8 years of reproduction (jaegers skip breeding when lemmings are too scarce). These pairs were composed of 65 different individuals (30 females, 29 males, 6 unknown) marked with coded bands and were sighted on average 1.8 times between years (range: 1 to 5).

On average, jaeger nests where at least one pair member returned were separated by 304 ± 30 m (range: 4 to 769 m) in different years. We found that an interaction between previous breeding success and mate fidelity influenced nest site fidelity ($\beta = 374.1$ [46.5, 701.6], $R^2 = 0.14$, $n = 36$; Figure 4.1). Following a successful breeding, jaegers that retained their mate nested at a smaller distance the subsequent year than those that did not retain their mate. Conversely, failed breeders that retained their mate moved further on the subsequent breeding season than those that changed mate. We found no relationship between breeding success and nest displacement distance from the previous year breeding ($\beta = -0.001$ [-0.004, 0.002], $n = 41$).

Overall, 72% of the males ($n = 32$) retained their mate whereas 28% were seen nesting in a subsequent year with a new mate. Among these, if we exclude females presumed to be dead (due to satellite transmitters; Seyer et al. 2021), then minimum mate retention was 79% ($n = 29$). For females, 85%

retained their mate (n = 27) and 15% had a new one. Among all individuals that changed mate, we were able to confirm in only one case that the mate had survived and renested elsewhere with a new partner. We found no evidence that breeding success affected the probability to retain the mate in subsequent breeding events (β = -0.08 [-1.62, 1.52], n = 31). Breeding with a new partner had no influence on the laying date (β = 1.04 [-0.38, 2.45], n = 32) nor on the breeding success (β = 1.10 [- 0.36, 2.78], n = 36).

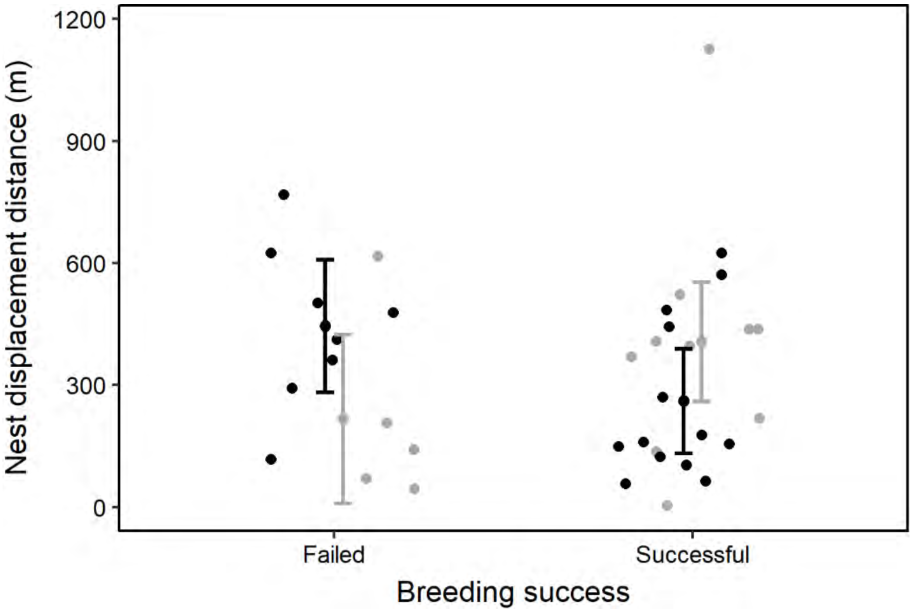

Figure 4.1 Nest displacement distance (m) of long-tailed jaegers breeding at Bylot Island (n = 35) depending on breeding success and mate fidelity (black: mate retained; gray: mate not retained). Error bars represent the 95% confidence intervals.

4.6 Discussion

Our results provide the first evidence of relatively high nest site and mate fidelity in long-tailed jaegers based on individually marked birds, thus providing support to underlying hypotheses of previous demographic models (Barraquand et al. 2014). Site fidelity was affected by both previous breeding success and mate retention. The longer distance moved by failed breeders compared to successful ones is a pattern commonly observed in birds (Dow and Fredga 1983, Switzer 1993, Hakkarainen et al. 2001, Sommerfeld et al. 2015). Breeding failure may serve as an index of site quality, and this may encourage individuals to look for a higher quality site in their territory or to move to another territory to nest. Curiously, the pattern was reversed in birds that changed mate. Perhaps this is because the challenge of finding a new mate overrules potential effects of previous breeding success. Moreover, when mating with a new partner, site selection may be affected by the previous success of both pair members, one of which is unknown in this case. Thus, our results confirm the strong association between nest and mate fidelity as previously showed for other species (Choudhury 1995, Bried and Jouventin 1999, 2002, Jankowiak et al. 2018).

Based on our raw estimates of mate retention rate and assuming an annual survival rate of 91% in long-tailed jaegers (Julien et al. 2013), we could estimate that only 12% of the males and 6% of the females divorced annually. A low divorce rate in pairs where both members survive is further confirmed by a single observation of a divorced pair where both pair members mated with a different individual in subsequent years. Even though we lack precision in our estimated divorce rates because of the small sample size, our results showed that it stands below the median rate of 14% for seabirds (see review in Mercier et al. 2021) and is similar to the great skua (*Catharacta skua*; Catry et al. 1997). Laying date was not influenced by mate fidelity contrary to what was previously demonstrated for other species (González-Solís et al. 1999a, Sánchez-Macouzet et al. 2014, Lv et al. 2016) including for great skua (Catry et al. 1997). This suggests that when the previous partner is not returning to the breeding site, individuals may start searching for a new mate shortly after arrival to avoid missing or delaying a breeding attempt. Indeed, as breeding late in the season often reduces success (Perrins 1970, Bêty et al. 2003), a pattern also found in jaegers (Seyer et al. in prep), the benefits of remating may exceed the costs in those situations (Sánchez-Macouzet et al. 2014).

Previous studies on this population showed an average delay of 14 d between the mean arrival and laying dates of jaegers and a synchronous arrival of previous pair members (5 d apart on average; Seyer et al. 2021, in prep). Though courtship behavior of jaegers remains unknown (Wiley and Lee 2020), Furness (1987) reported that even faithful pairs take a few days before remating after they reencounter on the nesting territory. Considering that seabirds generally do not remain together during the nonbreeding period (Bried and Jouventin 2002, Seyer et al. 2021) and the short pre-laying period upon arrival, there is a strong pressure for synchronous arrival at the breeding site. Accordingly, the initial formation of a new pair is believed to be based on temporal assortative mating, allowing synchronicity in arrival in subsequent years (Furness 1987). Otherwise, asynchronous arrival may quickly lead to a divorce due to time constraints (Naves et al. 2006). This strategy probably serves to reduce the costs associated with the loss of a mate and could explain why laying date was not affected by mate retention.

As found in many seabird populations (González-Solís et al. 1999a, Ismar et al. 2010, Sommerfeld et al. 2015, but see Bried and Jouventin 1999, Culina et al. 2015, Mercier et al. 2021), we found no effect of past breeding success on mate retention. Similarly, we found no effect of mate retention on the breeding success as reported by Ismar et al. (2010) and Jeschke et al. (2007) but see Sommerfeld et al. (2015). Finding a new mate and territory may involve temporal and energetic costs associated with prospection and fighting, which brings a risk of missing a breeding attempt (Choudhury 1995, Jankowiak et al. 2018). This risk is especially severe for species breeding in an environment where the reproductive season is very short as in the Arctic (Mercier et al. 2021). Current reproductive success may be a poor predictor of reproductive success the following year due to the high interannual variability of resources on the tundra (i.e. lemming abundance). This may favor mate retention, perhaps an adaptation to buffer temporal variability as supported by Botero and Rubenstein (2012). Thus, the benefits of retaining a mate probably exceed the costs of remating following a breeding failure in long-tailed jaegers. The similarities in the roles and investment in reproduction between partners (Furness 1987, Wiley and Lee 2020) and the fact that food acquisition largely occurs in a small inland territory (Andersson 1971) may also be contributing factors. This may help to reduce the inefficiency associated to breeding with a new mate (Choudhury 1995, van Rooij and Griffith 2013), which is often encountered in seabirds that need to synchronize their feeding trips at sea during breeding.

4.7 Acknowledgments

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Chapitre 5 – Resource partitioning among avian predators of the Arctic tundra

Couple de labbes à longue queue partageant un lemming brun

Référence de la publication :
Seyer, Y., G. Gauthier, D. Fauteux, and J.-F. Therrien. 2020. Resource partitioning among avian predators of the Arctic tundra. Journal of Animal Ecology 89:2934–2945.

5.1 Résumé

La compétition interspécifique joue un rôle clé dans la structure des communautés écologiques. La toundra arctique, un écosystème à faible productivité, supporte un réseau trophique simple où plusieurs espèces de prédateurs s'alimentent d'une même ressource connue pour ses larges fluctuations d'abondance, les lemmings. Nous avons étudié les mécanismes pouvant réduire la compétition intraguilde et permettant la coexistence de quatre prédateurs aviaires (harfang des neiges, goéland bourgmestre, buse pattue et labbe à longue queue) se nourrissant de cette ressource pulsée que sont les lemmings. Nous avons déterminé si une ségrégation alimentaire basée sur la taille et l'espèce des proies consommées ainsi qu'une ségrégation spatiale des territoires de nidification pouvaient permettre cette coexistence. Finalement, nous avons vérifié si l'absence d'harfangs, un prédateur irruptif dominant, entrainait un relâchement de la compétition sur le plus petit prédateur, le labbe, en lien avec les proies consommées et les territoires de nidification. Pendant 14 ans, nous avons suivi l'abondance des populations de lemmings, ainsi que la reproduction des prédateurs aviaires sur l'Île Bylot. Nous avons géoréférencé les sites de nidification de ces prédateurs et récolté des pelotes de régurgitation pour y récupérer les mandibules de lemmings afin d'inférer l'espèce et la taille des proies. Les résultats ont démontré la présence d'une ségrégation alimentaire en fonction de la taille des prédateurs, les plus gros consommant les plus gros lemmings et inversement. Tous les prédateurs consommaient plus de lemmings variables que de lemmings bruns par rapport à leur disponibilité. Toutefois, la buse et le goéland consommaient surtout des lemmings variables, alors que les bruns dominaient le régime alimentaire du harfang et du labbe. En l'absence d'harfangs, les labbes consommaient des proies de plus grande taille, suggérant un relâchement à court terme de la compétition. Parallèlement, nous avons trouvé un chevauchement faible à modéré dans les territoires de nidification des différentes espèces et aucune évidence de changement dans celui des labbes en l'absence d'harfangs. La distribution spatiale des espèces semblait donc être le reflet de leurs préférences d'habitat spécifiques. Ainsi, une ségrégation spatiale agirait comme principal mécanisme de partage des ressources entre ces prédateurs aviaires et, secondairement, une ségrégation par la taille et les espèces de proies consommées. Néanmoins, la compétition pour les ressources serait toujours présente et mènerait à un déplacement de la niche écologique du plus petit prédateur de la guilde. La compétition interspécifique pourrait donc jouer un rôle prépondérant dans la structure d'écosystèmes simples, peu productifs et caractérisés par une ressource pulsée.

Mots clés: Régime alimentaire · Compétition interspécifique · Labbe · Lemming · Territoire de nidification · Harfang · Taille de proies · Rapaces

5.2 Abstract

Interspecific competition can play a key role in structuring ecological communities. The Arctic tundra is a low productivity ecosystem supporting simple food webs, but several predators often feed on the same prey species, lemmings, known for their large-amplitude population fluctuations. We examined mechanisms involved in reducing intra-guild competition and allowing coexistence of four avian predators (snowy owls, glaucous gulls, rough-legged hawks and long-tailed jaegers) feeding on a pulsed resource (brown and collared lemmings). We compared the size and species of prey consumed by predators to see if resource partitioning occurred. We also verified if spatial segregation in nesting areas could be another mechanism allowing coexistence. Finally, we tested if the absence of the snowy owl, a dominant and irruptive species, triggered a competitive release on the smallest predator, the jaeger, with respect to prey size and nesting area used. We monitored the breeding of predators and lemming abundance over a 14-year period on Bylot Island, Canada. We mapped their nesting sites and collected regurgitation pellets to recover lemming mandibles, which were used to infer prey species and size. The size of lemmings consumed varied among species with the largest predators consuming the largest lemmings and the smallest predators consuming the smallest lemmings. All predators consumed more collared than brown lemmings compared to their availability although owls and jaegers consumed relatively more brown lemmings compared to gulls and hawks. Jaegers consumed larger lemmings in the absence of owls than in their presence, suggestive of a short-term competitive release. We found moderate to low overlap in nesting areas among predators and no evidence of their expansion in the absence of owls, suggesting that spatial distribution is caused by species-specific habitat preferences. The main mechanism to partition food resources among these avian predators is spatial segregation, and secondarily prey size and species. However, we found evidence that food competition is still present and leads to a niche shift in the smallest predator of the guild. Interspecific competition may thus be a pervasive force in simple, low productivity food webs characterized by pulsed resources.

Key words: Diet · Interspecific competition · Jaeger · Lemming · Nesting territory · Owl · Prey size · Raptors

5.3 Introduction

The importance of interspecific competition in ecological communities is a long-standing debate in ecology (Dhondt 2012). Some argue that interspecific competition is a key factor structuring ecological communities when resources are limited and shared among several consumers (Hutchinson 1959, Hardin 1960, MacArthur and Levins 1967, Schoener 1983). In contrast, others argue that the role of competition in communities is limited, especially when resources are varying temporally (Wiens 1977, Connell 1983). Several studies have examined how temporal fluctuations in resources affect the strength of competition but with contrasting results as some found that resource pulses promote species coexistence while others found that they increase competition (Chesson and Warner 1981, Ostfeld and Keesing 2000, Yang et al. 2008). Experiments have shown that species sharing the same resource in the same environment need to differentiate their niche to coexist or they will go extinct (Gause 1934, MacArthur and Levins 1967). Therefore, considerable efforts have been devoted to determine the mechanisms used by species to reduce competition and allow coexistence.

Species can coexist by changing their foraging technique, foraging sites, habitat or reproductive phenology (MacArthur 1958, Ashmole 1968). Various studies have unravelled the mechanisms through which multiple consumers sharing prey can minimize interspecific competition, for instance by partitioning resources or foraging areas. A classic example is the Serengeti ecosystem where many predators differentiate their diet by selecting one or a few prey species based on size (Sinclair et al. 2003). Another case is the resource partitioning by desert seed-eating ants and rodents based on seed size (Davidson 1977, Brown and Davidson 1977). Specialization on various prey types to avoid competition among coexisting raptors has also been documented (Poole and Bromley 1988, Restani 1991, Gerstell and Bednarz 1999). However, very few studies have examined how multiple predators sharing only one or two main prey species could coexist in an ecosystem characterized by a low productivity and large resource pulses, a situation where strong interspecific competition could be expected.

The Arctic tundra is a low productivity ecosystem with minimal habitat structuring that supports relatively simple food webs (Krebs et al. 2003, Legagneux et al. 2014). In the High Arctic, several species of mammalian (foxes, mustelids) and avian (raptors, seabirds) predators often feed primarily on only one or two species of lemmings (Gilg et al. 2006, Legagneux et al. 2012b). The most common avian predators of lemmings in the Canadian Arctic include two specialist species, the snowy owl *Bubo scandiacus* and the rough-legged hawk *Buteo lagopus*, a semi-specialist species, the long-tailed jaeger *Stercorarius longicaudus*, and a generalist species, the glaucous gull *Larus hyperboreus*.

Lemmings are well known for their large amplitude, multi-annual population fluctuations where abundance can vary 100-fold or more between peaks and lows, which can be considered a resource pulse (Krebs 2011, Ehrich et al. 2020). A diverse array of top predator species feeding on one or two highly fluctuating prey species are conditions that should lead to intense interspecific competition. Examining how these species can coexist together in the simple tundra ecosystem is of special interest considering that predator–prey interactions appear to be a driver of lemming fluctuations in many parts of the Arctic (Gilg et al. 2003, Therrien et al. 2014a, Fauteux et al. 2016).

We examined mechanisms involved in reducing intra-guild competition for limited resources among four common avian predators of the Arctic tundra. The main prey of these predators in the Canadian Arctic are two rodent species, the brown *Lemmus trimucronatus* and the collared lemming *Dicrostonyx groenlandicus*. We first hypothesized that these predators partition the resource by specializing on prey of different size and different species. Accordingly, we predicted that the body mass of lemmings consumed would be proportional to the predator body size, with larger species consuming larger lemmings and vice versa. We also examined if spatial segregation due to species-specific preference in nesting habitat could be another mechanism allowing coexistence. In this system, the jaeger and the owl are the two species that overlap the most in their habitat use but the owl is only present at the study site in years of peak lemming abundance (Therrien et al. 2014a, 2014b). We therefore hypothesized that the absence of the largest predator, the snowy owl, would trigger a short-term competitive release on the smallest predator, the long-tailed jaeger. We predicted that in years when snowy owls are absent, (a) the size of lemmings consumed by the long-tailed jaeger would increase, but not the size of prey consumed by the rough-legged hawk and the glaucous gull, and (b) the spatial distribution of jaeger territories would expand into areas normally occupied by owls, but it will stay constant for gulls and hawks.

5.4 Methods

5.4.1 Study site and field methods

Fieldwork was conducted during the breeding season (May–August) in the Qarlikturvik Valley of Bylot Island (Nunavut; 73°08′N 80°00′W) in the Canadian High Arctic over a 58 km^2 area (Figure 5.1; Gauthier et al. 2011). The study area is composed of a large glacial valley with a mixture of wet meadows and mesic tundra in lowlands. The valley is surrounded by rolling hills and low-elevation plateaus near the sea and more mountainous areas upstream. Streams and rivers running through surrounding hills and plateaus have created gullies, narrow valleys and ravine with frequent outcrops and small cliffs. The mesic tundra is dominated by prostrate shrubs and a sparse cover of forbs and graminoids, whereas wet tundra is mainly composed of graminoids growing through a thick moss layer in fens.

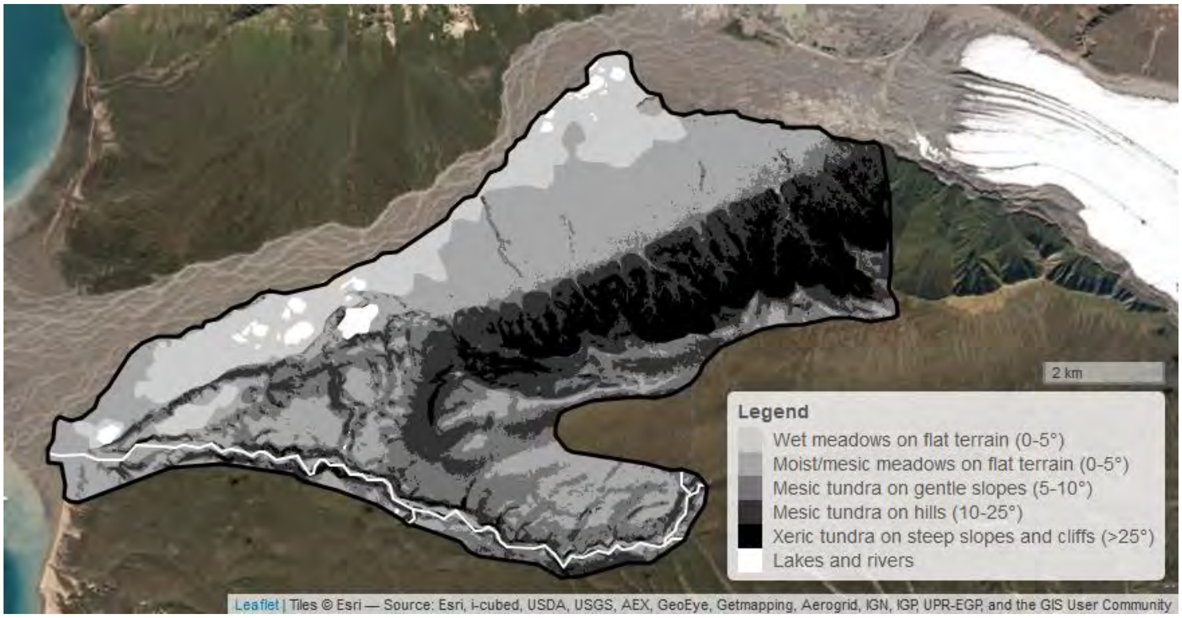

Figure 5.1 Main habitat types found in the 58 km^2 study area (Qarlikturvik Valley, Bylot Island, Nunavut; delimited by the thick black line) according to the wetness of the terrain and steepness of slopes. Digital elevation model (DEM) used to create the map is from Porter et al. (2018) and basemap from ESRI (2020).

Snowy owls are an irruptive and highly nomadic species and their summer diet is almost exclusively composed of lemmings (Therrien et al. 2014a, 2014b). Mean body mass is 1 700 g for males and 2 150 g for females (Richards and Gaston 2018; J.-F. Therrien, unpubl. data). Rough-legged hawks also feed predominantly on lemmings and their breeding effort is related to annual abundance of small mammals (Beardsell et al. 2016). Their mean body mass is 950 g for males to 1 200 g for females (Richards and Gaston 2018; J.-F. Therrien, unpubl. data). Long-tailed jaegers are seabirds breeding on the tundra in summer where they rely heavily on lemmings but also on some other prey (small birds, arthropods; Maher 1970). Their mean body mass is 290 g for males and 320 g for females (Seyer et al. 2019) and their breeding effort is also related to lemming abundance (Maher 1970). Glaucous gulls have a more diversified diet than the other species and includes lemmings, bird eggs and young, fish and invertebrates (Gauthier et al. 2015). The mean body mass is 1 700 g for males and 1 350 g for females (G. Gauthier, unpubl. data; Richards and Gaston 2018). Other avian predators present at the study area are the peregrine falcon *Falco peregrinus*, the gyrfalcon *Falco rusticolus* and the parasitic jaeger *Stercorarius parasiticus* but they occur at low density and feed only occasionally on lemmings (Fauteux et al. 2016). Two mammalian predators are also present, the Arctic fox *Vulpes lagopus* and the ermine *Mustela erminea*, and both feed heavily on lemmings (Gauthier et al. 2011).

Only two rodent species are present at the study site, the brown lemming and the collared lemming and they are similar in size [adult brown lemmings, 51 ± 14 g (mean ± SD), n = 1 450; adult collared lemmings 57 ± 12 g, n = 155; Gauthier 2020]. The brown lemming is the most abundant species and shows large-amplitude fluctuations of abundance every 3–4 years, whereas collared lemmings show weak amplitude population fluctuations (Gruyer et al. 2008, Fauteux et al. 2015). Brown lemmings typically prefer moist grass and sedge habitats in wet and mesic tundra, whereas collared lemmings tend to prefer drier habitats, mostly mesic and xeric habitat, but can also be found in wet habitat (Morris et al. 2000, Naughton 2012).

5.4.2 Nest monitoring and pellet analysis

The breeding activity of avian predators was studied from 2004 to 2017. Nest searches were carried annually to find all breeding pairs in the study area. Linear transects spaced out by 400 m were surveyed in lowlands and gentle slope areas to locate jaeger and gull nests, and survey routes along ridges in hilly terrain were systematically walked for owls and hawks in their potential breeding habitat. Because gulls and hawks are often faithful to their old nesting structures, previously used nest sites were revisited.

Active nests were georeferenced and visited every 1–2 weeks until hatching. Fresh regurgitation pellets were collected at a subsample of nests or nearby perching sites in the breeding territory. At the first visit, old pellets and prey remains were removed from the nest and discarded to collect only fresh pellets during the following visits. Pellets were placed in paper bags and air-dried for 2 weeks or dried in an oven for 48 hr before dissection. Overall, we collected and analysed 176 pellets of snowy owls, 327 pellets of glaucous gulls, 239 pellets of rough-legged hawks and 402 pellets of long-tailed jaegers. Pellets were not collected for all four species every year, except in 2008, because nests of some species were scarce or failed early in some years or because of reduced field effort.

Pellets were dissected to extract intact lemming mandibles and we identified them to species based on Naughton (2012). We measured the ramus–molar toothrow (RMT) as described in Schmidt et al. (2020) of either the left or right mandibles of each lemming found depending on which side was the most numerous in each pellet. The body mass of lemmings consumed was estimated from their RMT measurement based on the equations provided by Schmidt et al. (2020) for Nunavut. Because those equations overestimated the body mass of lemmings with very large mandibles, we truncated estimates to a maximum value of 105 g for brown lemmings (n = 2) and 118 g for collared lemmings (n = 4).

5.4.3 Lemming monitoring

We live-trapped lemmings annually in two permanent 11-ha grids located in the centre of the study area, one in wet tundra habitat and one in mesic habitat (Fauteux et al. 2015). Each grid had 144 trapping stations (100 from 2004 to 2006) separated by 30 m according to a Cartesian plane, and one Longworth trap was set at each station. Each trap was visited every 12 hr for 3–4 consecutive days during three trapping sessions in June, July and August (see Fauteux et al. 2015, for details). We identified all captured lemming to species, weighed them, and individually tagged them.

Lemming densities were estimated with spatially explicit capture–recapture analyses with the *secr* package (Efford 2020; see details in Fauteux et al. 2015) for each trapping period and grid. We assumed that trapped lemmings were representative of the population of prey available for predators in years when pellets were collected. However, we recognize that density estimates were based on only two trapping grids and may not capture all spatial variability especially with respect to the relative abundance of each species. To avoid pseudo-replication, we only considered the body mass of an individual the first time it was trapped.

5.4.4 Spatial analysis

We mapped habitat types in the study area based on Duclos et al. (2006) and Porter et al. (2018). Habitat types were wet meadows and moist/mesic tundra, both on flat terrain (0–5° slopes), mesic tundra on gentle slopes (5–10°), mesic tundra on hills (10–25°) and xeric tundra on the steepest slopes (>25°; Figure 5.1).

We estimated the area used by each predator species within the study area based on the location of nests found. We estimated the nesting area of each species using the adaptive local convex hull polygon (*a*-LoCoH) method (Getz et al. 2007). The *a*-LoCoH is based on the minimum convex polygon method in combination with a nonparametric kernel method (see Annexe S4.1 for more details on the method). We used the 90% isopleth to delimit the core area used for nesting by each species across years, hereafter called the nesting area. We delimitated the area used by each species of predators by combining the nests found in the years of presence of owls (2004, 2008, 2010, 2014) and the years of absence of owls (2005–2007, 2009, 2011–2013, 2015–2017). We estimated the overlap in the area used for nesting by each pair of species in years with and without owls. We also calculated the annual density of nests for each species over the entire study area and within the nesting area of each species as defined above.

To estimate if the presence of an owl nest influenced territory settlement by jaegers, we used two approaches. First, we created buffer zones of 500 and 1000 m around each owl nest and counted the number of jaegers nesting in these zones when owls were nesting. We selected the previous or following year, when owls were absent, and counted the number of nests in the same buffer zones. For this analysis, we did not consider years when no jaeger nest was found to avoid a false exclusion effect. We then estimated the proportion of all jaeger nests found annually in the study area that were located within these buffer zones. Second, we measured the annual displacement of jaeger nests between years with and without owls. To do so, we measured the distance between each owl nest and all jaeger nests within a 1000-m radius of owl nests that year. We measured again the distance from the position of these owl nests and all jaeger nests found within the same radius in the previous or the following year when owls were absent.

We also determined the influence of owl nests on the annual displacement of individual jaeger nests using a sample of marked birds (see Seyer et al. 2019, for details). We only used the nests of individuals for which we knew their location in more than 1 year, excluding cases with a gap of >2 years between nest locations. We first used jaeger nests located <1000 m from an owl nest to measure the distance between their nest in the year of owl presence and in the previous or following year. Second, we used the same method to calculate the displacement of jaeger nests located >1000 m from an owl nest.

5.4.5 Statistical analyses

To determine if there were differences in body mass of lemmings consumed among the predators and with available lemmings (i.e. trapped), we used linear mixed-effect models (LMMs) based on a restricted maximum likelihood approach (REML) from the package *nlme* (Pinheiro et al. 2018). For all models, we used the nest ID as random factor because more than one pellet was collected at each nest. For the lemmings available, we used trapping grid and year as a single random effect (i.e. each combination of grid and year was assigned a different ID). We tested for differences in body mass of lemmings consumed and available (both species combined) in the presence of owls (M1, Table S4.2 in Annexe S4.2) and in their absence (M2). A limitation of our analysis is that pellets of each species were not collected in all years (see Table S4.3). To examine if pooling years could be a source of bias, we repeated the previous analysis for the single year (2008) that we collected pellets from all four species (model M1a). We also tested for a difference in body mass of lemmings consumed in the presence and absence of owls for each of the other avian predators (M3, M4, M5, Table S4.2). Finally, we compared the body mass of available lemmings for years with and without owls (M6, Table S4.2). We repeated the previous analysis only for the years when pellets were collected for each predator separately. We calculated the marginal R^2_m (for fixed effects) and the R^2_c (for fixed and random effects) based on Nakagawa and Schielzeth (2013). We evaluated normality for fixed and random effects and homoscedasticity visually with Q–Q plot and residuals in relation to fitted values plot respectively. For all models, we ln-transformed lemming body mass to obtain a normal distribution.

We used a stepwise model selection procedure to select the best fitted log-linear model to compare the proportion of brown versus collared lemmings in the prey consumed by the different avian predators in years with and without owls. We started from the saturated model including the three main effects (lemming species, predator species and owl presence) and we did a backward selection based on AIC (Burnham and Anderson 2002). We performed separate analyses to compare the proportion of brown lemmings consumed by the predators versus those available: one in the years of owl presence and the other in the years of owl absence.

We compared nest density for the entire study area and within the estimated nesting area of each species between predator species and years with and without owls using a linear model. We used a two-sided t-test to compare the number of jaeger nests found within a 500-m or a 1000-m radius around an owl nest or the proportion of these nests among all nests found to the number or proportion in the year before or after owl presence. To compare jaeger nest displacement in the presence versus absence of owls, we used a LMM based on a REML approach. Since some jaeger nests were within a 1000-m radius of more than one owl nest, we used the nest ID as a random factor. To compare the inter-annual nest displacement of marked jaegers, we used a LMM with the band number (individual ID) as a random effect. We did all the analyses using the software R (R Core Team 2019).

5.5 Results

5.5.1 Resources partitioning

We measured a total of 534 mandibles, 283 in years with snowy owls and 251 in years without (Table S4.4). Over a 14-year period, lemming abundance was high during 7 years and low during the other 7 years, with annual densities varying from 2.5 to 6.5 lemmings/ha and from 0 to 0.5 lemmings/ha respectively. Owls were found nesting in the study area during 4 years (2004, 2008, 2010 and 2014) but were absent in 3 other years (2011, 2015 and 2016) when lemming densities were high.

Table 5.1 Slope parameters (β) and their 95% confidence intervals (CI) for models M1 to M6. Response variables (body mass of lemmings consumed or available) are detailed in Table S4.2. Nest ID was used as random factor for all the models. R^2_m: Marginal R-squared for fixed effects. R^2_c: Conditional R-squared for fixed and random effects. σ^2_i: Variance of the random effect intercept. σ^2_r: Variance of the random effect residuals.

Model no*	Explanatory variable	β	Low CI	High CI	R^2_m	R^2_c	σ^2_i	σ^2_r
M1	Owl Gull Hawk Jaeger	0.433 0.638 0.335 -0.227	0.235 0.412 0.090 -0.430	0.632 0.864 0.580 -0.025	0.143	0.305	0.043	0.184
M2	Gull Hawk Jaeger	0.351 0.503 0.171	0.153 0.315 0.031	0.549 0.691 0.311	0.134	0.208	0.015	0.160
M3	Owl presence	-0.264	-0.490	-0.037	0.059	0.441	0.100	0.146
M4	Owl presence	-0.113	-0.452	0.226	0.014	0.348	0.069	0.135
M5	Owl presence	0.348	0.134	0.562	0.134	0.161	0.006	0.192
M6	Owl presence	0.057	-0.091	0.205	0.004	0.077	0.014	0.181

* Reference group were as follow: M1 and M2: Lemming available; M3, M4, M5 and M6: Owl absent

In the presence of owls, the mean mass of lemmings consumed by the three largest predators (owls, gulls and hawks) was similar, although it tended to be higher in gulls, and was heavier than those available (i.e. live-trapped; Table 5.1, model M1; Figure 5.2A). In contrast, jaegers consumed lemmings lighter than those available and those eaten by all other predators. In the absence of owls, the mass of lemmings consumed differed again between jaegers and hawks but not between jaegers and gulls, and all predators consumed lemmings heavier than those available (Table 5.1, model M2; Figure 5.2B). When restricting the analysis to 2008, the pattern was similar though fewer significant differences were found, potentially due to smaller sample size (Table S4.5; Figure S4.1).

When comparing species individually, the body mass of lemmings consumed by jaegers was higher in absence than in the presence of owls [43.7 g (35.8, 49.2) vs. 33.5 g (27.5, 37.8), M (95% CI) respectively; Table 5.1, model M3] and the trend was similar for hawks but not statistically significant [63.9 g (46.4, 77.9) vs. 56.6 g (43.1, 66.9); Table 5.1, model M4]. Lemmings consumed by gulls were lighter in the absence than in the presence of owls [52.1 g (42.7, 58.8) vs. 73.5 g (61.6, 81.9); Table

5.1, model M5]. Finally, the body mass of lemmings available did not differ much between years without and with owls [37.2 g (32.4, 40.5) vs. 39.2 g (34.8, 42.3) respectively; Table 5.1, model M6]. We found the same results when we restricted the previous analysis only to years when pellets were collected for each species (Table S4.6).

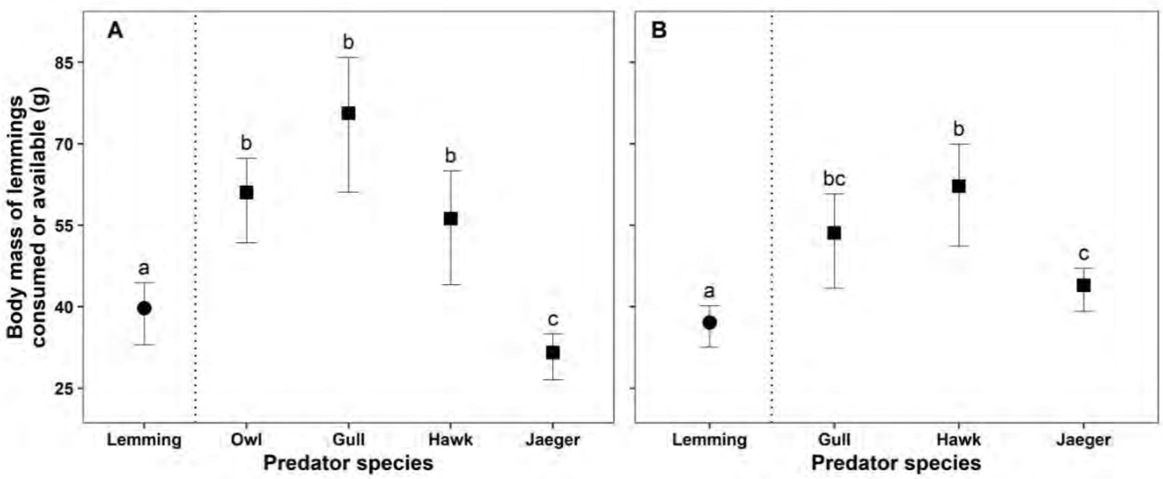

Figure 5.2 Body mass (g) of lemmings consumed by different predator species (square) or available (live-trapped lemmings; circle) A) in presence of owls (model M1) and B) in absence of owls (model M2; Table 5.1). Estimated means and 95% CI calculated from LMMs were back-transformed to match the scale of the original data. Means with the same letters do not differ significantly.

All predators consumed both lemming species (Figure 5.3). The preferred model examining the effect of predator species and owl presence on the proportion of lemming consumed retained all two-way interactions between lemming species, predator species and owl presence (Table S4.7). Jaegers, hawks and gulls consumed slightly more brown than collared lemmings in years when owls were present (interaction lemming × owl presence; Table 5.2; Figure 5.3). The proportion of brown lemmings consumed by jaegers was higher than that by hawks or gulls, and higher in hawks than in gulls (interactions lemming × predator species, Table 5.2). When owls were present, the proportion of brown lemmings they consumed was similar to jaegers and hawks but higher than gulls (Table S4.8). Regardless of the presence or absence of owls, all predators consumed brown lemmings in lower proportion than their availability, and conversely for collared lemmings (interactions lemming × predator species; Table S4.8).

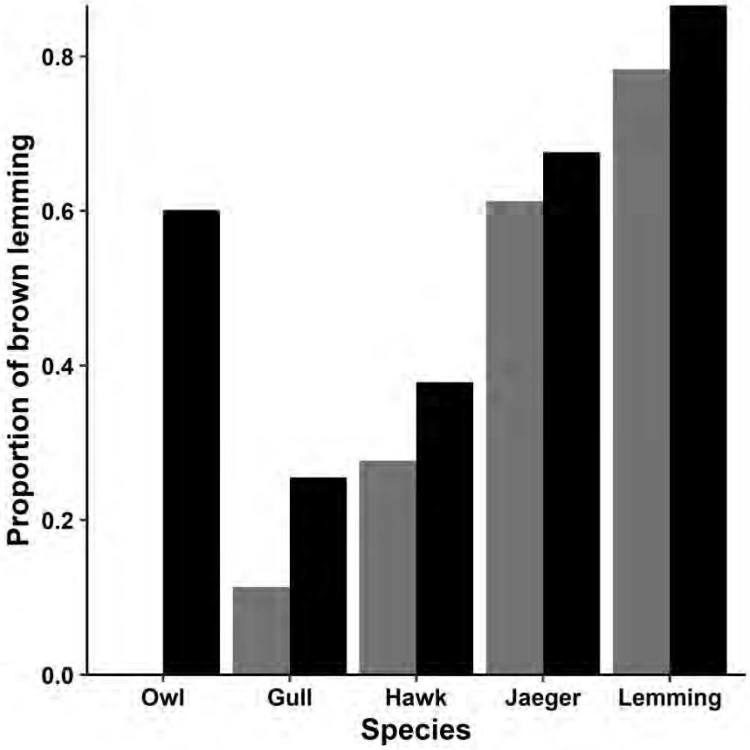

Figure 5.3 Proportion of brown vs. collared lemmings in the diet of different predator species and in the lemmings available (live-trapped lemmings) in presence of owls (black) or in absence (gray).

Table 5.2 Slope parameters (β) and their 95% confidence intervals (CI) from the log-linear analysis comparing the proportion of brown vs. collared lemmings in the prey consumed by three avian predators in presence or absence of owls. Reference levels are collared lemming, hawks and owl absent.

Explanatory variable	β	CI
Brown lemming	-0.953	[-1.424, -0.507]
Gull	-0.229	[-0.642, 0.177]
Jaeger	0.191	[-0.167, 0.553]
Owl presence	-0.709	[-1.152, -0.283]
Brown lemming × Gull	-0.764	[-1.462, -0.094]
Brown lemming × Jaeger	1.359	[0.860, 1.876]
Brown lemming × Owl presence	0.447	[-0.001, 0.903]
Gull × Owl presence	0.693	[0.113, 1.282]
Jaeger × Owl presence	-0.275	[-0.794, 0.246]

5.5.2 Spatial partitioning

We found 216 nests in years of owl presence (jaeger: 122, hawk: 16, gull: 42, owl: 36), and 211 nests in their absence (jaeger: 91, hawk: 15, gull: 105). Nest density over the whole study area varied according to the predator species and owl presence (interaction species × owl presence: $F_{2,29} = 8.19$, $P = 0.002$; Table 5.3). Nest density of jaegers and hawks was much higher in the presence of owls but not for gulls. When restricting the analysis to the nesting area used by each species, nest density did not differ between the years of owl presence or absence for all species ($F_{1,29} = 0.12$, $P = 0.72$; interaction: $F_{2,29} = 5.62$, $P = 0.58$; Table 5.3). However, the gull nest density within their nesting range was about 10 times higher than the other species ($F_{3,29} = 79.0$, $P < 0.001$).

In years with owls, the nesting area covered 17.2 km^2 for jaegers, 4.0 km^2 for hawks, 0.5 km^2 for gulls and 10.6 km^2 for owls (Figure 5.4). The habitat and topography of these nesting areas differed among species (Table S4.9). Gulls used predominantly wet meadows associated with lakes on flat terrain; hawks mainly used xeric tundra on steep slopes, cliffs and to a lesser extent mesic tundra on hills; jaegers used mostly moist/mesic meadows on flat terrain; and owls used almost equally moist/mesic meadows on flat terrain and mesic tundra on gentle slopes and hills. Almost 30% of the nesting area of owls overlapped with that of jaegers and 9% with the hawks while 17% of the nesting area of jaegers and 24% of hawks overlapped with that of owls (Table 5.4). In the absence of owls, the extent of the nesting areas was reduced for jaegers (12.9 km^2) and hawks (1.6 km^2) but not for gulls (0.9 km^2; Figure 5.4). The nesting habitat of each species remained similar in those years (Table S4.9) and the nesting area of jaegers did not substantially overlap with other species (Table 5.4).

Table 5.3 Nest density (mean ± SE) of predators within the whole study area and only within the nesting area (nest/km^2) in years of presence (n = 3 years) and absence (n = 8) of owls (NA: not applicable).

	Study area		Nesting area	
	Owl present	Owl absent	Owl present	Owl absent
Snowy owl	0.17 ± 0.05	NA	0.88 ± 0.23	NA
Glaucous gull	0.21 ± 0.03	0.20 ± 0.02	11.05 ± 1.92	12.37 ± 1.16
Rough-legged hawk	0.09 ± 0.03	0.03 ± 0.01	1.00 ± 0.3	1.16 ± 0.43
Long-tailed jaeger	0.62 ± 0.13	0.18 ± 0.07	1.37 ± 0.23	0.70 ± 0.27

Table 5.4 Overlap between the nesting areas of each species in presence / absence of owls. Table should be read as the % of the nesting area of the species in row overlapped by the nesting area of the species in column (NA: not applicable).

	Long-tailed jaeger	Rough-legged hawk	Glaucous gull	Snowy owl
Long-tailed jaeger	-	0.2 / < 0.1	0.9 / 1.3	17.1 / NA
Rough-legged hawk	0.8 / 0.2	-	0 / 0	24.4 / NA
Glaucous gull	31.7 / 17.9	0 / 0	-	0 / NA
Snowy owl	27.9 / NA	9.2 / NA	0/NA	-

We found no difference between years with and without owls in the number or proportion of jaeger nests located within a 500-m radius around owl nest locations (Table 5.5). With a 1000-m radius, the number of jaeger nests was lower in the absence than in the presence of owls, but the proportion of nests remained the same (Table 5.5). We found no difference in the distance between owl and jaeger nests within the 1000-m radius around owl nests when comparing years with and without owls ($F_{1,49} = 0.26$, $P = 0.61$). Finally, the mean distance between nest locations of the same individual jaegers in different years was 325 m (n = 36, SE = 49) for those located >1000 m away from an owl nest and 483 m (n = 10, SE = 143) for those nesting <1000 m, a non-significant difference ($F_{1,13} = 1.05$, $P = 0.32$).

Table 5.5 Comparison of the abundance of long-tailed jaeger nests around snowy owl nests between years of owl presence and absence. Radius: radius of the buffer zone around owl nests. Number of nest is the absolute count of nest. Proportion of all the nests found annually located within the buffer zone.

Radius (m)	Method	Owl present		Owl absent		t-test	
		Mean	SE	Mean	SE	t_6	P
500	n of nest	1.5	0.9	1.0	0.4	0.52	0.62
	Proportion of nests	0.07	0.04	0.07	0.03	-0.05	0.96
1000	n of nest	9.0	1.1	3.8	1.3	3.18	0.02
	Proportion of nests	0.37	0.10	0.25	0.07	0.98	0.37

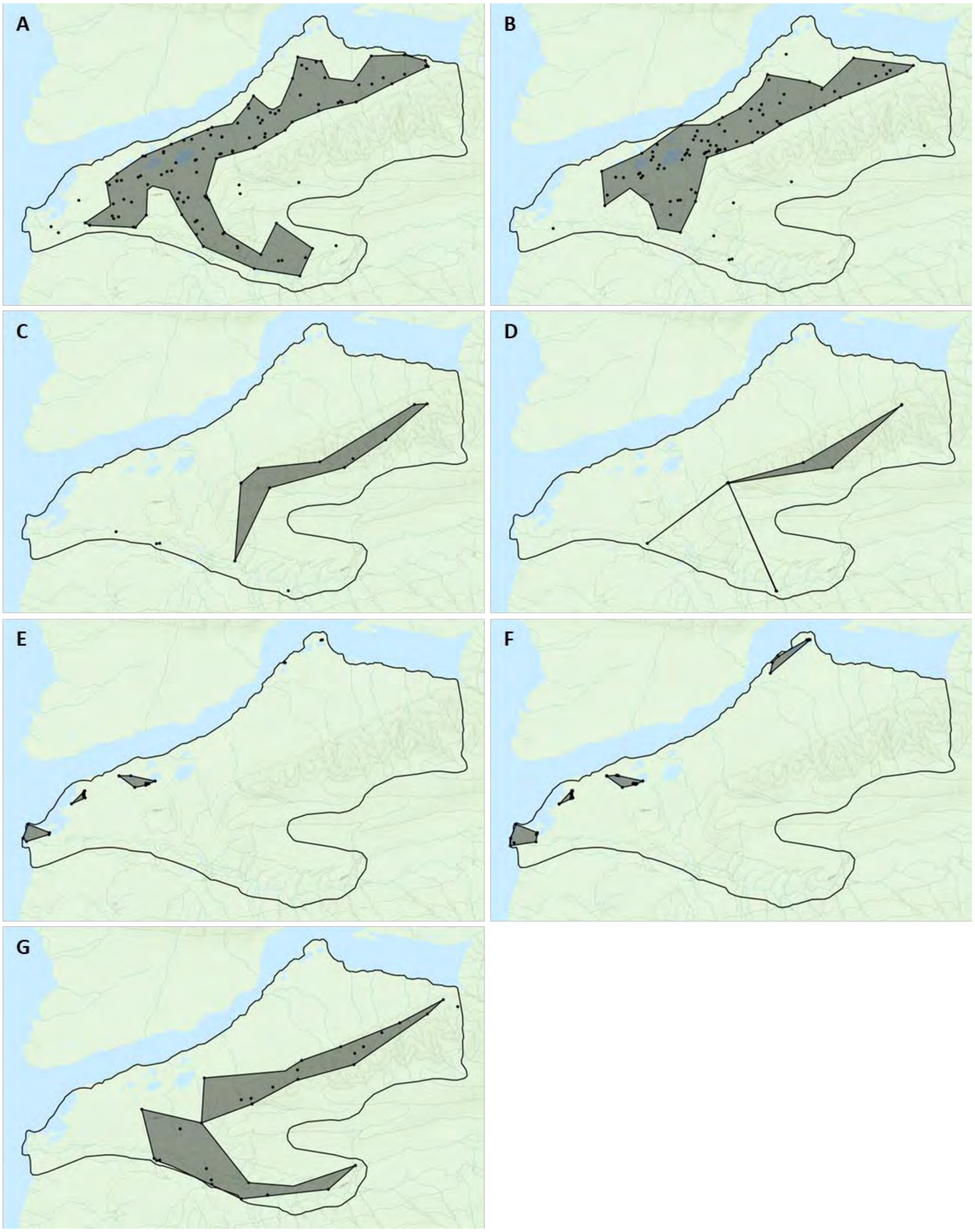

Figure 5.4 Local Convex Hull (LoCoH) polygons of the area covered by 90% of the nests (defined as the nesting area; gray shading) of long-tailed jaeger (A-B), rough-legged hawk (C-D), glaucous gull (E-F), and snowy owl (G) in years of presence (left panel) and absence (right panel) of owls. The black dots represent the position of each nest (some nest may overlap between years). The outer black line polygon represents the borders of the study area.

5.6 Discussion

Our 14-year study allowed us to gain a better understanding of the intensity of interspecific competition and of mechanisms promoting coexistence among a guild of avian predators exploiting temporally fluctuating resources in a low productivity environment. The irruptive behaviour of one predator, the snowy owl, in response to resource pulses created the conditions for a short-term natural competitive release experiment. We showed that resource partitioning according to prey body size and, to a lesser extent, prey species was a mechanism that reduced competition but it was modulated by the presence or absence of the dominant predator, the snowy owl. We also found that spatial segregation according to habitat was an important mechanism to minimize competition but that segregation changed little in the presence or absence of the largest competitor. Finally, the smallest predator of the guild was apparently affected the most by competition.

5.6.1 Resource partitioning based on prey size and species

Even though the four avian predators in our system all feed on lemmings, each of them specialized on prey of different size and used the two lemming species differently. As we hypothesized, larger predators generally consumed larger lemmings and this effect was most pronounced in the smallest predator, the long-tailed jaeger. Owls and jaegers overlapped in their habitat use and both fed mostly on brown lemmings contrary to hawks and gulls, which consumed mostly collared lemmings. It is therefore not surprising to observe a short-term competitive release on jaegers when owls, the largest and most dominant predator, are absent. Indeed, jaegers consumed lemmings that were on average smaller than those available in the presence of owls but heavier than those available when owls were absent. This clearly suggests a strong competition between these two species and a negative effect of the presence of owls on resources use by jaegers.

We observed weak resource partitioning based on prey size among the three largest predators but we found differences in lemming species consumed. Although all predators consumed collared lemmings in greater proportion than their relative availability, as also noted by Therrien et al. (2014a), this proportion was highest in gulls, intermediate in hawks and lowest in owls. The high consumption of collared lemmings by hawks can be explained by their preference to nest in more xeric habitat, where collared lemmings should be more prevalent than brown lemmings (Morris et al. 2000, Naughton 2012). However, the proportion of collared lemming consumed by gulls is surprisingly high considering that they breed mainly in wet meadows, the preferred habitat of brown lemmings. Glaucous gulls are generalist predators that feed on a wide range of prey and habitats (Samelius and Alisauskas 1999, Gauthier et al. 2015) and our results suggest that they may often hunt away from their nest, in mesic habitat. The fact that all predators consumed more collared than brown lemmings compared to their availability is consistent with the idea of a greater vulnerability of the former to predation (Reid et al. 1995, Therrien et al. 2014a), which is possibly due to behavioural differences (Morris et al. 2019) since both species are of similar size.

Temporal segregation in resource use is another mechanism that can reduce interspecific competition. In the guild of avian predators studied by Poole and Bromley (1988) in the Canadian Arctic, interspecific variation in the timing of breeding, especially between common ravens *Corvus corax* and gyrfalcons, reduced temporal overlap of the chick-rearing periods and thus attenuated competition when resource demand is highest. In our system, timing of breeding is similar for all species except for owls that breed earlier. However, because of their lengthy breeding season, their brood-rearing period largely overlaps with the three other species. Therefore, temporal segregation in resource use is weak as the period of highest food requirement is largely synchronous among species. Moreover, except for gulls that partially switch from lemmings to geese after chick hatching (Gauthier et al. 2015), the diet composition for the three other predators is dominated by lemmings throughout the summer (Maher 1970, Hakala et al. 2006, Therrien et al. 2014a).

5.6.2 Spatial resource partitioning

The four avian predators generally used different habitats for nesting and the overlap in nesting area was moderate to small. All these species are territorial during the breeding season and their foraging activity predominantly occurs in their breeding territory (Maher 1970, Holt et al. 2020, Pokrovsky et al. 2020) except perhaps gulls, which range over a larger area during breeding (Gauthier et al. 2015). The use of different nesting habitats may thus be a primary mechanism allowing these species to feed on the same prey and reduce competition in an environment where vertical habitat structuring is absent. In avian predators, species that overlap the most in their nesting habitat should overlap the least in their diet (Restani 1991, Pokrovsky et al. 2020). In agreement with this, the largest overlap in nesting area used among the four predators was between jaegers and gulls, the two species that differed the most in the lemming species used.

Jaegers and hawks showed some overlap in nesting area with owls. Wiklund et al. (1998) suggested that interference competition between snowy owls and rough-legged hawks could explain their mutual avoidance observed across a range of study sites in Siberia. We found no evidence for this as both species bred in good numbers in high lemming years. The diversity of landscape present in our study area and the tendency for each species to use different nesting habitats may have facilitated this coexistence. Moreover, rough-legged hawks in North America tend to be site faithful and reuse the same territory (Bechard and Swem 2002, Beardsell et al. 2016) whereas in Siberia they tend to be more nomadic (Pokrovsky et al. 2020).

Contrary to our initial prediction, we found no evidence that owls excluded jaegers from potential breeding habitat even though both predators feed mostly on brown lemming. The settlement pattern of jaegers was similar and they used approximately the same area regardless of the presence or absence of owls. Because jaegers do not reuse old nests, the position of the nesting site is a new decision every year. Nonetheless, the presence of a large and close competitor did not affect the distribution of nesting jaegers contrary to what was observed in a guild of forest owls (Kajtoch et al. 2015, 2016). The current distribution pattern of jaegers appears to be governed primarily by habitat preference rather than interference competition although spatial segregation with owls may have evolved in response to past competition. Although spatial partitioning may be an important mechanism to reduce food competition among these avian predators, the reduction in prey size consumed by jaegers when owls are present indicate that competition is still present between these two species, possibly due to their partial overlap in habitat use. This also suggests that competition may be mostly by exploitation with owls preying on large lemmings, which in turn force jaegers to rely on smaller prey.

Overlap in nesting areas among gulls, jaegers and hawks tended to decrease in the absence of owls, which was largely a consequence of jaegers and hawks having reduced nesting areas in those years. This is likely because lemming abundance was lower in the years of owl absence than presence, and thus the breeding effort of these two species was reduced. Nonetheless, the reduction of overlap in nesting areas of these species in years of low lemming abundance could be an additional mechanism reducing food competition when the resource is most limiting.

5.6.3 Competition in fluctuating environments

Numerous studies have reported intense interspecific competition, either by interference or exploitation, in various raptor guilds (Restani 1991, Wiklund et al. 1998, Gerstell and Bednarz 1999, Hakkarainen et al. 2004). The Arctic tundra is rather unique in having several sympatric avian predators feeding mostly on the same prey, lemmings, a pulsed resource with large inter-annual fluctuations in abundance. In accordance with Wiens (1977), and Lack (1946) in the case of raptors, we found that intensity of competition is dynamic and varied as resources fluctuated temporally. However, contrary to the conventional wisdom, we found that competition was more intense when the resource was abundant rather than scarce (Wiens 1977, Schoener 1983). This occurs because snowy owls, the largest and most dominant predator, are present in the system only when lemmings are abundant and other species (jaegers, hawks) increase their breeding effort in those years. Therefore, resource pulses increase interspecific competition by attracting more species and higher densities due to the high mobility of avian predators (Therrien et al. 2014a). Interestingly, under these conditions, predators consumed a larger spectrum of lemming size than when they are scarce even if the size of available lemmings remains the same. Thus, as competition increases, resource partitioning leads to a greater breadth of resource exploitation, as reported by Finke and Snyder (2008) in an insect consumer community.

Spatial segregation in nesting areas through species-specific habitat preferences appears to be the primary mechanism allowing the coexistence of predators in our system, and secondarily a differential use of resources according to species and size. Due to its importance in promoting coexistence in this low productivity ecosystem, it is possible that species-specific habitat preference may be a ghost of competition between these predators in the distant past (Rosenzweig 1981, Dhondt 2012). Despite spatial and resources partitioning, the smallest species of the guild appears to suffer from asymmetric exploitative competition and is forced to shift its feeding niche by relying on smaller prey size than what they would consume in the absence of its strongest competitor. However, we do not have data to evaluate the consequences of this shift in resource use on the reproductive success of jaegers. Nonetheless, our study shows that interspecific competition could be a pervasive force in a relatively simple and low productivity arctic food web where avian predators play a prominent role (Therrien et al. 2014a) and result in a niche shift for some species.

5.7 Acknowledgments

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collected the data in the field and conducted the laboratory analyses; Y.S. conducted the statistical analyses and wrote the manuscript with the assistance of G.G., D.F. and J.-F.T. All contributed to the revision of the manuscript and gave the final approval for publication

5.8 Supplementary material

Annexe S4.1 – Details of the *a*-LoCoH method

Annexe S4.2 – Supplementary tables and figure

Conclusion

Ma thèse ajoute certaines des pièces manquantes à la compréhension globale du fonctionnement des écosystèmes arctiques et, plus particulièrement, aux études à long terme du système modèle de l'Île Bylot (Gauthier et al. 2011, 2013). Elle approfondit les connaissances fondamentales sur un des principaux prédateurs aviaires de la toundra arctique, le labbe à longue queue, et ses interactions interspécifiques. Les connaissances apportées par cette thèse améliorent la compréhension de la phénologie de la migration et de la reproduction, de même que les liens entre elles et l'hivernage chez cet oiseau marin migrateur transéquatorial (Chapitre 2 et Chapitre 3), ce que peu d'études ont réalisé à ce jour. Près de 15 ans de suivi du régime alimentaire et de la reproduction d'une guilde de prédateurs aviaires à la distribution circumpolaire ont mis en lumière les mécanismes favorisant leur coexistence malgré un amalgame de conditions favorisant une forte compétition alimentaire (Chapitre 5). J'ai démontré l'omniprésence de la compétition interspécifique dans un réseau trophique relativement simple et à faible productivité, réfutant au passage l'idée que l'augmentation de la disponibilité des ressources réduit la compétition interspécifique. Également, mes travaux accroissent nos connaissances sur la fidélité au site et au partenaire de reproduction chez une espèce longévive exploitant un environnement saisonnier et imprévisible (Chapitre 4). Finalement, ma thèse a permis de décrire l'appariement entre les individus et de proposer une méthode d'identification du sexe chez le labbe à longue queue, une espèce présentant un très faible dimorphisme sexuel (Chapitre 1).

Dimorphisme sexuel et appariement des individus

Connaître le sexe des individus revêt une importance particulière en écologie, car il peut grandement affecter le comportement et les traits d'histoires de vie. Ma thèse a permis de développer une équation simple à partir de la longueur d'aile et de la masse corporelle d'un individu pour identifier son sexe. Par une approche novatrice, j'ai également mis au point une équation pour sexer avec une plus grande exactitude les individus nicheurs en ajoutant à ces paramètres la masse du partenaire. Ainsi, simplement à l'aide de données faciles à récolter sur le terrain il est possible d'identifier le sexe d'un individu et de son partenaire sans utiliser de méthodes génétiques coûteuses et laborieuses. Ayant dorénavant la capacité d'identifier le sexe des individus avec une assez grande précision, j'ai pu déceler la présence d'un appariement assorti positif chez les labbes; les grosses femelles s'apparient avec de gros mâles, mais presque toujours plus petits qu'elles ce qui démontre que l'appariement ne se fait pas aléatoirement (Chapitre 1).

L'appariement non aléatoire des labbes pourrait contribuer à l'arrivée synchrone des mâles et des femelles sur un court intervalle de temps, et par le fait même, au fort taux de fidélité des labbes à leur partenaire (79 – 85 %) et à l'emplacement de leur nid (Chapitre 4). En fait, la préférence des labbes pour un partenaire similaire réduit le bassin d'individus disponibles, diminuant la probabilité de trouver un nouvel individu en cas de divorce, et ainsi augmentant la probabilité de manquer une opportunité de reproduction. La durée de la reproduction et la brièveté de l'été arctique pourraient aussi contribuer à ces fortes fidélités. Cependant, les mécanismes menant à l'appariement des individus chez le labbe à longue queue sont encore nébuleux. Néanmoins, si on suppose que la réunification des couples a bel et bien lieu sur terre, mes résultats appuient l'idée qu'elle se produit durant un court intervalle juste après leur arrivée.

Migrer de l'Arctique jusqu'aux mers australes

Le cœur de ma thèse repose sur le suivi de 43 migrations annuelles complètes ou partielles de labbes à longue queue nichant dans l'est de l'Arctique canadien à l'aide de géolocalisateurs. Il s'agit de la première étude portant sur cette population, mais surtout de la plus grande étude phénologique sur l'espèce et la seule s'étant attardée à la variabilité sexuelle des paramètres de la migration (Chapitre 2). Les analyses suggèrent l'existence d'une faible connectivité migratoire chez cette espèce en démontrant que les labbes de l'Arctique canadien utilisent les mêmes aires d'hivernage que les populations européennes et groenlandaises (Gilg et al. 2013, van Bemmelen et al. 2017). L'échantillon considérable d'individus suivis a aussi permis de quantifier l'importance relative de différents sites d'hivernage et de démontrer l'utilisation par près de 70 % des individus de la région d'*upwelling* du Benguela au large de l'Afrique du Sud, une zone de grande importance pour beaucoup d'espèces marines (Crawford 2007, Egevang et al. 2010, Dias et al. 2011, Stenhouse et al. 2012, Davis et al. 2016). J'ai aussi noté une absence de variation entre les sexes dans les paramètres et la phénologie de la migration, ce qui est en accord avec le très faible dimorphisme sexuel des labbes (Chapitre 1) et la contribution similaire du mâle et de la femelle dans la reproduction, l'élevage des jeunes et la défense du territoire (Furness 1987, Wiley et Lee 2020).

L'étude approfondie de la migration du labbe à longue queue a permis de documenter leur stratégie migratoire contre-intuitive. La stratégie la plus communément observée chez les oiseaux implique une migration rapide au printemps pour arriver hâtivement sur les sites de reproduction, particulièrement lorsque la compétition pour les ressources et les territoires est forte et où la saison de reproduction est courte. À l'automne, la migration est généralement plus lente alors que la nécessité d'arriver rapidement au site d'hivernage est faible (Nilsson et al. 2013, Schmaljohann 2018). Or, bien que le labbe à longue queue niche en Arctique où toutes ces contraintes sont réunies (Gauthier et al. 2011, Therrien et al. 2014a), incluant une forte compétition pour les ressources et le territoire (Chapitre 5), les analyses ont démontré l'adoption d'une stratégie migratoire opposée (Chapitre 2). La présence de contraintes climatiques à l'arrivée des labbes en Arctique, comme la présence de banquise et de territoire enneigé, réduit la disponibilité de la nourriture et les avantages d'une arrivée hâtive. De plus, le fort taux de fidélité des couples (Chapitre 4), l'importance de l'appariement assorti (Chapitre 1), la quasi-absence de dimorphisme sexuel (Chapitre 1), le besoin de constituer des réserves d'énergie avant l'arrivée au site de reproduction (de Korte 1985) et la diminution de la propension à nicher liée à une arrivée trop hâtive (Chapitre 3) appuient l'idée du besoin d'une arrivée relativement synchrone des labbes en Arctique à une date optimale.

Effets reportés réciproques entre la migration, l'hivernage et la reproduction

Il a préalablement été démontré que les labbes font preuve de flexibilité dans leur migration en adaptant les routes empruntées pour s'ajuster aux conditions environnementales rencontrées (van Bemmelen et al. 2017). Or, mes analyses ont démontré qu'ils étaient également capables de flexibilité dans la phénologie de leur migration automnale (Chapitre 3). L'absence de ségrégation temporelle dans la reproduction des prédateurs pour réduire la compétition interspécifique (Chapitre 5), l'augmentation de la demande énergétique au moment de nourrir les jeunes et la diminution de la disponibilité des lemmings avec l'avancement de la saison de reproduction (Fauteux et al. 2015) sont toutes des contraintes liées à l'environnement arctique. Ainsi, la déplétion des ressources en Arctique avec l'avancement de la saison serait une des principales raisons qui motive les labbes à entamer hâtivement la migration automnale suivant un insuccès de reproduction pour ainsi retrouver des conditions plus favorables en mer. Cette capacité à amorcer la migration hâtivement quand la reproduction échoue permet d'arriver tôt sur les sites d'hivernage pour entreprendre la mue et ainsi éviter le chevauchement de cette activité énergétiquement coûteuse avec la migration (van Bemmelen et al. 2018).

Le labbe à longue queue étant fidèle à son site d'hivernage (van Bemmelen et al. 2017), il est possible de croire que l'issue de la reproduction n'affecte pas la sélection du site d'hivernage contrairement à ce qui a été observé par Catry et al. (2013) chez un autre oiseau marin migrateur de longue distance. Ce faisant, la sélection des sites d'hivernage pourrait être faite lors de la première migration automnale, menant ensuite à la fidélité à ce site, bien que chez certaines espèces des changements dans les sites utilisés puissent survenir avec l'âge (Alerstam et Hedenström 1998, Newton 2011). De plus, puisque ma thèse n'a décelé à peu près aucun effet reporté de la période non-reproductrice sur la reproduction, il est possible d'avancer que la richesse et la stabilité des sites utilisés en hiver et en migration tamponnent les effets de la reproduction précédente. Les patrons observés durant les dernières étapes de la migration printanière, notamment l’usage d’une halte migratoire commune à la quasi-totalité de la population et l’ajustement de la stratégie migratoire après cette dernière (i.e. diminution du temps passé en vol; Chapitre 2), favorisent vraisemblablement l’accumulation de réserves d’énergie et l’ajustement de l’arrivée en Arctique pour éviter de subir les contrecoups des aléas environnementaux dus à la banquise et l’enneigement. Ainsi, cette étape ultime de la migration pourrait à son tour atténuer la variabilité rencontrée pendant la période non-reproductrice. Finalement, en Arctique, la variabilité interannuelle, l’imprévisibilité des conditions et la disponibilité des ressources alimentaires permettraient de tamponner tout effet reporté potentiel émanant de la période non-reproductrice. Ce faisant, la décision de nicher et l’issue de la reproduction dans un environnement hautement variable annuellement seraient majoritairement influencés par les conditions locales plutôt que par des effets reportés des saisons précédentes.

Compétition et ségrégation dans une guilde de prédateurs

Le rôle capital des lemmings dans le régime alimentaire des prédateurs de l’Arctique et son influence sur leur reproduction ont déjà été démontrés (Gilg et al. 2006, Therrien et al. 2014a). Toutefois, ma thèse a permis de mieux définir la manière dont les populations de lemmings bruns et variables influençaient le partage des ressources entre les principaux prédateurs aviaires (Chapitre 5). En effet, mes résultats ont mis en lumière deux mécanismes modulant la compétition interspécifique et permettant la coexistence des prédateurs. Le premier implique une ségrégation des proies basée sur leur taille et, dans une plus faible mesure, l’espèce. Le second implique pour sa part une ségrégation de l’habitat réduisant la compétition pour les proies.

Quatorze ans de suivi de nidification et d’étude du régime alimentaire en Arctique ont démontré le dynamisme de la compétition interspécifique, mais aussi l’effet contre-intuitif provoqué par une ressource pulsée sur l’intensité de la compétition. Habituellement, l’intensité de la compétition diminue avec l’augmentation de la disponibilité des ressources, et inversement (Wiens 1977, Schoener 1983). Or, ma thèse a mis en évidence l’augmentation de l’intensité de cette compétition lorsque la disponibilité des ressources augmente. Lorsque les ressources sont abondantes, la guilde de prédateurs se diversifie en accueillant un prédateur aviaire nomade, le harfang des neiges (Therrien et al. 2014b). À l’inverse, lorsque l’abondance de proies diminue, les autres prédateurs diminuent leur effort reproducteur (Andersson 1981, Therrien et al. 2014a, Beardsell et al. 2016), relâchant l’intensité de la compétition. Cette variabilité de l’intensité de la compétition est surtout ressentie chez le labbe à longue queue, le plus petit prédateur de la guilde, qui ajuste sa niche alimentaire en fonction de la présence ou l'absence du harfang. Ceci démontre la plasticité du régime alimentaire chez cette espèce marine qui devient exclusivement terrestre pour la reproduction.

Limites de l'étude

Bien que tous les efforts possibles aient été faits pour s'assurer de la robustesse des interprétations et des conclusions de cette thèse, quelques bémols seraient toutefois à apporter à certains résultats. L'âge est un paramètre important pouvant affecter les comportements individuels, notamment pendant la migration et la reproduction (Hunt 1980, Choudhury 1995, Alerstam et Hedenström 1998, Newton 2011). Malheureusement, je n'ai pu le considérer dans cette thèse, car les individus étudiés ont tous été marqués adultes, d'autant plus qu'après plus de 10 ans de marquage sur l'Île Bylot, aucun individu marqué jeune n'a encore été réobservé. L'impossibilité de considérer l'âge pourrait avoir induit un biais dans certaines analyses, notamment celles sur les effets reportés, la fidélité des labbes à leur partenaire et leur territoire de nidification et la phénologie de la migration. En effet, le niveau de fidélité au partenaire tout comme l'effort de reproduction peuvent être plus faibles chez de jeunes individus (Weimerskirch 1992, Choudhury 1995, Ens et al. 1996, Newton 2011).

L'utilisation de géolocalisateurs présente aussi certaines limites dans la précision des localisations estimées. La précision d'environ 150-200 km dans l'estimation des localisations limite l'interprétation à fine échelle spatiale des déplacements durant les périodes de migration et de séjour (Phillips et al. 2004, Lisovski et al. 2019). De plus, l'imprécision dans l'estimation de la latitude augmente durant les périodes d'équinoxes puisque la durée du jour est similaire partout sur le globe et près de l'équateur où elle varie très peu (Hill 1994, Ekstrom 2004, Lisovski et al. 2019). Dans les régions polaires, où l'ensoleillement est de 24 h, l'estimation de la longitude devient à son tour impossible en raison de l'absence de lever et de coucher de soleil (Lisovski 2018).

Malgré un effort de terrain substantiel cumulant six campagnes pour déployer 70 géolocalisateurs et en récupérer 42 (60 %), certaines données ont été corrompues. Un problème technique avec une série de géolocalisateurs a causé un arrêt prématuré de l'enregistrement des données de 14 appareils, laissant des trous béants dans les suivis migratoires. Malheureusement, cela a restreint la quantité d'information récoltée au printemps par rapport à l'automne. Ainsi, l'échantillon utilisé pour tester la présence d'effets reportés des périodes d'hivernage et de la migration printanière sur la reproduction demeure limité. Au Chapitre 3, j'explique la faible occurrence d'effets reportés par la variabilité et l'imprévisibilité des conditions en Arctique et la capacité d'ajustement des labbes lors des dernières étapes de leur migration. Toutefois, un échantillonnage plus complet aurait incontestablement permis d'éliminer certains doutes qui persistent sur la présence possible de certains effets reportés.

Finalement, en raison d'un effort de terrain variable entre les années dû à la disponibilité du personnel, aux conditions météorologiques et à l'abondance de lemmings, l'étude du régime alimentaire présente un échantillon débalancé entre les années et les espèces. Puisque Gauthier et al. (2015) ont démontré une variation intra-annuelle du régime alimentaire d'un prédateur aviaire de la toundra arctique en période de reproduction, il aurait été pertinent d'explorer si une telle variabilité existe chez les autres prédateurs. Or, malgré le grand nombre de pelotes de régurgitation récupérées et disséquées (Chapitre 5), il a été impossible de tester la présence de variation intra-annuelle dans l'utilisation des proies de cette guilde de prédateurs. Outre le goéland bourgmestre, un prédateur généraliste (Gauthier et al. 2015), il est assumé que les autres prédateurs spécialistes (i.e. harfang des neiges, buse pattue) et semi-spécialistes (i.e. labbe à longue queue) maintiennent le même régime alimentaire pendant toute la saison. Bien que le plan d'échantillonnage ait limité cette possibilité, il aurait été souhaitable de tester pour la présence d'une éventuelle variation intra-annuelle du régime alimentaire pour infirmer la possibilité qu'un certain degré de ségrégation temporelle (e.g. Poole et Bromley 1988) agisse en tant qu'autre mécanisme permettant la coexistence de ces prédateurs aviaires.

Perspectives de recherche

Bien que les cinq chapitres de ma thèse constituent un apport significatif à notre compréhension de la dynamique des écosystèmes arctiques et aux connaissances fondamentales d'un prédateur majeur de l'Arctique canadien jusqu'alors peu connu, plusieurs questions restent en suspens. En effet, mon étude a aidé à mieux comprendre les mécanismes impliqués dans la ségrégation des ressources alimentaires et spatiales sur les aires de reproduction entre les espèces. Elle a apporté de nouvelles évidences quant au dynamisme et à l'intensité de la compétition interspécifique en fonction des fluctuations temporelles des ressources. Toutefois, cette étude ne s'est concentrée qu'aux relations interspécifiques. Sachant que les labbes restent sur terre en été et qu'ils repoussent leurs congénères de leur territoire (Furness 1987, Wiley et Lee 2020), il serait intéressant d'approfondir l'étude au niveau des interactions intraspécifiques et à une échelle spatiale plus fine pendant la reproduction. L'utilisation d'appareils avec une grande précision spatiale (e.g. GPS; Bridge et al. 2011) permettrait de caractériser l'utilisation individuelle du territoire, l'implication de chaque parent dans la reproduction et l'élevage des jeunes, ainsi que le comportement d'alimentation des labbes. Une approche à l'aide de tels moyens technologiques mettrait à jour de vieilles études qui ont caractérisé pour la toute première fois les comportements du labbe à longue queue (e.g. Maher 1970, Andersson 1971, 1981) et permettrait de quantifier précisément ces comportements. Une analyse à fine échelle spatiale de l'utilisation du territoire de nidification chez un prédateur comme le labbe améliorerait ainsi notre compréhension de son dynamisme et sa plasticité entre les années de faible et de forte abondance de proies. La densité de couples nicheurs diminue avec la diminution des proies (cette thèse; Gilg et al. 2006, Therrien et al. 2014a), mais il n'a jamais été démontré explicitement que ce phénomène entrainait l'utilisation d'un plus vaste territoire, ce qui pourrait entrainer une compétition intraspécifique accrue. Une telle étude en utilisant le labbe à longue queue comme modèle contribuerait ainsi à mieux comprendre la variabilité dans l'utilisation de l'espace à fine échelle chez des espèces qui dépendent de ressources pulsées, mais qui ne sont pas nomades comme c'est le cas du harfang des neiges.

Dans un autre ordre d'idée, selon la liste rouge des espèces menacées de l'Union Internationale pour la Conservation de la Nature (UICN), le labbe à longue queue représente une préoccupation mineure, notamment en raison de sa forte population, sa distribution holarctique et sa stabilité temporelle (BirdLife International 2018). Cependant, l'Arctique et les milieux marins subissent des pressions croissantes en raison des changements climatiques et de l'augmentation des activités anthropiques (Moritz et al. 2002, IPCC 2019, Dias et al. 2019). Or, comme mentionné précédemment, ma thèse présente pour la toute première fois des données sur la migration et la distribution hivernale de la population canadienne de labbes à longue queue. Ces informations aideront à mieux anticiper les risques auxquels l'espèce pourrait être exposée étant donné la tendance climatique actuelle. La contribution de ma thèse à l'augmentation des connaissances sur la distribution hivernale de l'espèce pourrait mener à l'identification et à la délimitation de zones marines d'intérêt en migration et sur les aires d'hivernage pour l'espèce ainsi que pour d'autres espèces d'oiseaux marins, à l'image des travaux de Davies et al. (2021).

À la suite des échecs rencontrés avec le déploiement d'émetteurs satellites attachés à l'aide de harnais sur le dos de labbes à longue queue (Sittler et al. 2011, Chapitre 2), Harrison et al. (2022) ont déployé de plus petits émetteurs sur deux individus en utilisant une méthode d'attachement différente. Cette étude a démontré que cette méthode ouvre la possibilité de suivre les déplacements de labbes à longue queue sans affecter leur survie. Ainsi, avec la miniaturisation continuelle des enregistreurs de données, il serait envisageable, connaissant les grandes étapes de la migration du labbe et sa phénologie, d'utiliser dans le futur des appareils plus précis que les géolocalisateurs comme des émetteurs satellites, des GPS ou des accéléromètres (Bridge et al. 2011, Brown et al. 2013) et de cibler des périodes spécifiques du cycle vital pour maximiser l'acquisition des données. Ce faisant, il serait possible d'acquérir une image plus précise de la distribution hivernale de l'espèce et des haltes migratoires pour raffiner les informations encore déficientes sur leur mode de vie hivernal, notamment sur leur alimentation, le kleptoparasitisme, la compétition interspécifique ou les interactions avec les pêcheries. En effet, les géolocalisateurs nous ont renseignés sur le temps passé en vol ou en contact avec l'eau en mer. Or, nous ignorons la répartition du temps passé au repos vs en alimentation lors d'un contact avec l'eau, une information pourtant cruciale, ou encore le temps passé à kleptoparasiter lorsque l'oiseau est en vol. L'utilisation d'un accéléromètre couplée au capteur d'immersions des géolocalisateurs contribuerait à élucider la question et ainsi mieux comprendre la stratégie migratoire des labbes, surtout au printemps.

Bien que ma thèse ait levé le voile sur les stratégies migratoires d'un migrateur de longue distance, plusieurs zones grises persistent. Des études récentes ont démontré des différences dans les stratégies migratoires en termes de vitesse de déplacement, de phénologie, de durée de séjours ou de tactique d'acquisition des ressources en fonction d'un gradient latitudinal des sites de reproduction utilisés (Briedis et al. 2016, Loon et al. 2017, Lamarre et al. 2021). L'augmentation de la distance à parcourir entre les sites de reproduction et d'hivernage, ainsi que les contraintes environnementales en migration pourraient expliquer ces stratégies variables qui minimisent les risques et optimisent les bénéfices pour la reproduction et la survie. Mes analyses suggèrent que la stratégie migratoire des labbes est davantage dictée par des contraintes environnementales au printemps, comme la glace de mer, l'enneigement au site de reproduction et ultimement l'accès à la nourriture, et endogènes à l'automne, comme la mue. Il est toutefois pertinent de se demander si cette stratégie diffèrerait pour les individus nichant ailleurs en Arctique.

En Amérique du Nord, les labbes nichent de la Baie d'Hudson (61° N) à l'Île d'Ellesmere (82° N), en passant par l'Île Bylot (73° N; Wiley et Lee 2020). La durée de la saison estivale et la fenêtre disponible à la nidification rétrécissent à mesure que l'on monte en latitude. Étudier les effets des contraintes temporelles et environnementales sur le comportement des dernières étapes de la migration (temps en vol vs sur l'eau, vitesse de déplacement), la date d'arrivée au site de reproduction, l'intervalle d'arrivée des labbes sur le site, la propension à nicher et ultimement la fidélité des labbes à leur partenaire dévoilerait peut-être une plasticité géographique dans les stratégies de l'espèce. De plus, étant donnée l'importance de la synchronie dans le retour au site de reproduction pour favoriser la réunification des couples, l'augmentation des contraintes temporelles liées aux latitudes les plus élevées pourrait augmenter les coûts liés à la fidélité des couples comme la hausse des opportunités de reproduction manquées en cas d'asynchronie dans la phénologie d'arrivée des partenaires, augmentant ainsi le taux de divorce. L'application d'un protocole standardisé sur un gradient nord-sud de l'aire de reproduction de la population canadienne de labbes à longue queue permettrait d'étudier l'ajustement de la stratégie migratoire aux conditions locales.

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Annexes

Annexe S1 – Documentation supplémentaire pour le Chapitre 1

Annexe S1.1 – Results of the linear discriminant analysis models

Table S1.1 Results of the 25 linear discriminant analysis models tested to predict the sex of individual long-tailed jaegers (*Stercorarius longicaudus*) using various combinations of their morphometrics. Models are sorted from the highest to the lowest accuracy.

#	Model	Accuracy	95% CI	MCC	Youden	DP
11	Body mass + Wing	0.829	0.725 – 0.906	0.653	0.655	1.732
9	Body mass + Head + Tail	0.816	0.710 – 0.895	0.634	0.639	1.683
10	Body mass + Head	0.816	0.710 – 0.895	0.634	0.639	1.683
4	Body mass + Wing + Tail (R1)	0.816	0.710 – 0.895	0.629	0.632	1.643
7	Body mass + Wing + Tail	0.816	0.710 – 0.895	0.629	0.632	1.643
12	Body mass	0.803	0.695 – 0.885	0.611	0.616	1.608
8	Body mass + Head + Wing	0.803	0.695 – 0.885	0.604	0.609	1.562
6	Body mass + Head + Wing + Tail	0.789	0.681 – 0.875	0.581	0.586	1.487
2	Body mass + Head + Tarsus + Wing + Tail (R1)	0.776	0.666 – 0.864	0.557	0.562	1.418
3	Body mass + Head + Wing + Tail (R1)	0.776	0.666 – 0.864	0.557	0.562	1.418
5	Body mass + Head + Tarsus + Wing + Tail	0.776	0.666 – 0.864	0.557	0.562	1.418
1	Body mass + Head + Tarsus + Wing + Tail (R1) + Tail	0.763	0.652 – 0.853	0.535	0.539	1.352
18	Head + Wing + Tail	0.737	0.623 – 0.831	0.464	0.464	1.117
19	Head + Wing	0.737	0.623 – 0.831	0.464	0.464	1.117
15	Head + Wing + Tail (R1)	0.711	0.595 – 0.809	0.416	0.418	0.982
21	Wing + Tail (R1)	0.697	0.581 – 0.798	0.392	0.395	0.920
17	Head + Tarsus + Wing + Tail	0.697	0.581 – 0.798	0.382	0.381	0.897
13	Head + Tarsus + Wing + Tail (R1) + Tail	0.684	0.567 – 0.786	0.357	0.357	0.832
14	Head + Tarsus + Wing + Tail (R1)	0.684	0.567 – 0.786	0.357	0.357	0.832
22	Wing	0.632	0.513 – 0.739	0.256	0.257	0.582
23	Tail	0.579	0.460 – 0.691	0.178	0.178	0.408
20	Head + Tail	0.566	0.447 – 0.679	0.140	0.141	0.315
16	Head	0.566	0.447 – 0.679	0.126	0.127	0.282
25	Tarsus	0.539	0.421 – 0.655	0.102	0.101	0.231
24	Tail (R1)	0.105	0.047 – 0.197	-0.793	-0.800	-2.514

Table S1.2 Results of the 28 linear discriminant analysis models tested to predict the sex of individual long-tailed jaegers (*Stercorarius longicaudus*) using various combinations of their morphometrics, and body mass and wing chord of their partner. Models are sorted from the highest to the lowest accuracy.

#	Model	Accuracy	95% CI	MCC	Youden	DP
30	Body mass + Wing + Tail (R1) + Partner's Body mass	0.923	0.815 – 0.979	0.846	0.846	2.740
44	Body mass + Wing + Tail (R1) + Partner's Body mass + Partner's Wing	0.904	0.790 – 0.968	0.808	0.808	2.493
27	Body mass + Wing + Partner's Body mass	0.885	0.766 – 0.956	0.772	0.769	2.310
46	Body mass + Partner's Body mass + Partner's Wing	0.885	0.766 – 0.956	0.772	0.769	2.310
41	Body mass + Wing + Partner's Body mass + Partner's Wing	0.885	0.766 – 0.956	0.769	0.769	2.246
45	Body mass + Wing + Tail + Partner's Body mass + Partner's Wing	0.885	0.766 – 0.956	0.769	0.769	2.246
33	Body mass + Head + Wing + Partner's Body mass	0.865	0.742 – 0.944	0.736	0.731	2.161
47	Body mass + Head + Wing + Partner's Body mass + Partner's Wing	0.865	0.742 – 0.944	0.736	0.731	2.161
29	Body mass + Head + Partner's Body mass	0.865	0.742 – 0.944	0.731	0.731	2.063
31	Body mass + Wing + Tail + Partner's Body mass	0.865	0.742 – 0.944	0.731	0.731	2.063
42	Body mass + Head + Tail + Partner's Body mass + Partner's Wing	0.865	0.742 – 0.944	0.731	0.731	2.063
43	Body mass + Head + Partner's Body mass + Partner's Wing	0.865	0.742 – 0.944	0.731	0.731	2.063
28	Body mass + Head + Tail + Partner's Body mass	0.846	0.719 – 0.931	0.692	0.692	1.880
32	Body mass + Partner's Body mass	0.846	0.719 – 0.931	0.692	0.692	1.880
34	Body mass + Wing + Partner's Wing	0.846	0.719 – 0.931	0.692	0.692	1.880
40	Body mass + Head + Wing + Partner's Wing	0.846	0.719 – 0.931	0.692	0.692	1.880
37	Body mass + Wing + Tail (R1) + Partner's Wing	0.827	0.697 – 0.918	0.654	0.654	1.731
38	Body mass + Wing + Tail + Partner's Wing	0.827	0.697 – 0.918	0.654	0.654	1.731
7	Body mass + Wing + Tail	0.808	0.675 – 0.904	0.623	0.615	1.674
11	Body mass + Wing	0.808	0.675 – 0.904	0.617	0.615	1.604
4	Body mass + Wing + Tail (R1)	0.808	0.675 – 0.904	0.617	0.615	1.604
12	Body mass	0.788	0.653 – 0.889	0.581	0.577	1.490
9	Body mass + Head + Tail	0.769	0.632 – 0.875	0.545	0.538	1.387
8	Body mass + Head + Wing	0.769	0.632 – 0.875	0.538	0.538	1.328
39	Body mass + Partner's Wing	0.769	0.632 – 0.875	0.538	0.538	1.328
36	Body mass + Head + Partner's Wing	0.750	0.611 – 0.860	0.510	0.500	1.291
10	Body mass + Head	0.750	0.611 – 0.860	0.503	0.500	1.238
35	Body mass + Head + Tail + Partner's Wing	0.731	0.590 – 0.844	0.467	0.462	1.142

Annexe S2 – Documentation supplémentaire pour le Chapitre 2

Annexe S2.1 – Attachment of tracking devices

Figure S2.1 Attachment of a geolocator (Intigeo-C65, Migrate Technology) on a plastic band on a long-tailed jaeger. © Yannick Seyer

Figure S2.2 Attachment of a satellite transmitter (PTT-100, Microwave Telemetry) on the back of a long-tailed jaeger. © Denis Sarrazin

Annexe S2.2 – Deployment information of tracking devices

Table S2.1 Summary of the deployment period of all geolocators (geo) recovered and satellite transmitters (sat) deployed on Bylot Island (n_{geo} = 40; n_{sat} = 10) and on Igloolik Island (n_{geo} = 2). Last date of recording: date the device stopped working if it was not working at recovery.

Sex	Device type	Device ID[a]	Site deployed	Date deployed	Date recovered	Last day of recording	No days of recording
U[b]	sat	84009	Bylot	Jul. 9, 2008	-	Aug. 27, 2008	49
U	sat	84014	Bylot	Jul. 9, 2008	-	Oct. 12, 2008	95
F	sat	84007	Bylot	Jul. 1, 2008	-	*NA*[c]	0
F	sat	84008	Bylot	Jul. 12, 2008	-	Sep. 4, 2008	54
F	sat	84010	Bylot	Jul. 11, 2008	-	Aug. 22, 2008	42
F	sat	84011	Bylot	Jul. 2, 2008	-	Aug. 29, 2008	59
F	sat	84012	Bylot	Jul. 5, 2008	-	Sep. 27, 2008	85
F	sat	84013	Bylot	Jul. 1, 2008	-	Sep. 9, 2008	70
F	sat	84015	Bylot	Jul. 2, 2008	-	Aug. 16, 2008	46
F	sat	84016	Bylot	Jul. 10, 2008	-	Sep. 21, 2008	74
F	geo	F634	Bylot	Jul. 6, 2014	Jun. 25, 2016	Dec. 7, 2015	519
F	geo	F637	Bylot	Jul. 7, 2014	Jun. 26, 2015	Jun. 12, 2015	340
F	geo	F638	Bylot	Jul. 7, 2014	Jun. 23, 2015	Mar. 13, 2015	341
F	geo	F641	Bylot	Jul. 8, 2014	Jun. 27, 2016	Mar. 25, 2015	260
F	geo	F915	Bylot	Jul. 5, 2014	Jun. 26, 2015	-	356
F	geo	R833	Bylot	Jun. 23, 2015	Jun. 25, 2016	-	368
F	geo	R834	Bylot	Jun. 25, 2015	Jun. 27, 2016	-	368
F	geo	R838	Bylot	Jul. 4, 2015	Jun. 27, 2016	Apr. 25, 2016	296
F	geo	R840	Bylot	Jul. 5, 2015	Jun. 22, 2019	-	0
F	geo	R842	Bylot	Jul. 7, 2015	Jul. 6, 2016	-	365
F	geo	R846	Bylot	Jul. 8, 2015	Jun. 27, 2016	-	355
F	geo	R847	Bylot	Jul. 8, 2015	Jul.5, 2016	-	363
F	geo	R849	Bylot	Jul. 8, 2015	Jul. 5, 2016	-	363
F	geo	R850	Bylot	Jul. 9, 2015	Jul. 9, 2016	-	366
F	geo	X568	Bylot	Jun. 23, 2016	Jun. 24, 2017	Mar. 5, 2017	255
F	geo	X569	Bylot	Jun. 24, 2016	Jun. 22, 2019	Aug. 19, 2016	56
F	geo	X571	Bylot	Jun. 30, 2016	Jun. 21, 2017	Dec. 18, 2016	171
F	geo	X576	Bylot	Jul. 5, 2016	Jun. 25, 2018	Dec. 23, 2016	171
F	geo	X584	Bylot	Jul. 10, 2016	Jun. 25, 2019	Mar. 5, 2017	238
F	geo	X595	Igloolik	Jul. 8, 2016	Jul. 7, 2017	Dec. 11, 2016	156
F	geo	BK188	Bylot	Jun. 25, 2018	Jun. 23, 2019	-	363
M	geo	F636	Bylot	Jul. 6, 2014	Jun. 24, 2016	Aug. 7, 2014	32
M	geo	F639	Bylot	Jul. 7, 2014	Jun. 23, 2016	Jan. 21, 2016	563
M	geo	F643	Bylot	Jul. 9, 2014	Jun. 28, 2019	Nov. 24, 2015	503
M	geo	F908	Bylot	Jun. 30, 2014	Jun. 25, 2015	-	360
M	geo	F909	Bylot	Jun. 30, 2014	Jun. 23, 2016	Jul. 26, 2015	391
M	geo	F913	Bylot	Jul. 5, 2014	Jul. 3, 2015	-	363
M	geo	R837	Bylot	Jul. 4, 2015	Jun. 21, 2019	Dec. 18, 2016	533
M	geo	R839	Bylot	Jul. 4, 2015	Jun. 27, 2016	-	359
M	geo	R843	Bylot	Jul. 7, 2015	Jun. 27, 2018	Dec. 14, 2016	526
M	geo	R845	Bylot	Jul. 8, 2015	Jun. 27, 2016	-	355
M	geo	R848	Bylot	Jul. 8, 2015	Jul. 5, 2016	-	363
M	geo	X567	Bylot	Jun. 20, 2016	Jun. 19, 2017	Oct. 9, 2016	110
M	geo	X570	Bylot	Jun. 30, 2016	Jun. 21, 2017	Mar. 22, 2017	264
M	geo	X575	Bylot	Jul. 5, 2016	Jun. 26, 2019	-	0

Sex	Device type	Device ID[a]	Site deployed	Date deployed	Date recovered	Last day of recording	No days of recording
M	geo	X578	Bylot	Jul. 6, 2016	Jun. 28, 2017	Dec. 16, 2016	163
M	geo	X582	Bylot	Jul. 8, 2016	Jul. 5, 2019	Jan. 14, 2017	189
M	geo	X583	Bylot	Jul. 10, 2016	Jul. 5, 2019	Aug. 30, 2016	52
M	geo	X585	Bylot	Jul. 10, 2016	Jul. 5, 2017	Nov. 7, 2016	119
M	geo	X596	Igloolik	Jul. 8, 2016	Jul. 10, 2017	Jan. 5, 2017	180
M	geo	BK187	Bylot	Jun. 25, 2018	Jun. 26, 2019	-	366
M	geo	BK191	Bylot	Jun. 27, 2018	Jun. 23, 2019	-	360

[a] Four birds were equipped with different geolocators on different years (F913 & R837, R850 & X584, X578 & BK191, X585 & BK187).

[b] Sex unknown

[c] The bird never left Bylot Island

Annexe S2.3 – Details on the geolocator analysis method

Analysis of geolocator data

We estimated sunset and sunrise using the threshold method (Ekstrom 2004, Lisovski and Hahn 2012) with the *TwGeos* package (Lisovski et al. 2016) in *R*. We set the threshold value to 1.15 lux, the lowest value we could use to avoid noise with the night-time light levels. Because on-site calibration of geolocators is impossible due to 24-h daylight during summer in the Arctic, we performed a 7 to 16 d calibration in an open field in southern Quebec (46°44'N, 71°28'W) in May and/or June to determine a zenith angle. As we were expecting the birds to be in different habitats (land vs. sea) and at very different latitudes during summer and winter, we calculated a different zenith angle on the wintering site, a stationary period during which average shading intensity should be constant (Lisovski et al. 2012). For 19 migratory tracks, we used the open-field calibration zenith angle during the breeding period, the Hill-Ekstrom calibration zenith angle (Lisovski et al. 2012) during the wintering period, and the mean of these zenith angles during migratory periods. For 24 migratory tracks, we obtained very unlikely locations with this approach, thus we only used the open-field calibration zenith angle. Estimated zenith angles ranged from 93.0° to 99.3°.

To determine the geographic locations, we analyzed light-level data using a Bayesian approach with the *SGAT* package (Wotherspoon et al. 2013), which uses the Metropolis algorithm to create its Markov Chain Monte Carlo simulations (Sumner et al. 2009). We used three independent chains with 1000 samples for the burn-in distribution, 900 samples for the tuning distribution, and 2000 samples to define the posterior distribution. Each sample represents one set of estimated geographic locations. We provided the model with 1) raw location estimates calculated with the threshold method, 2) a spatial mask where the likeliness of the position decreased gradually inland, up to 5 times less likely >100 km inland than over the sea, but not impossible, and 3) a movement model defining probable flight speed following a gamma distribution (mean = 1.4, SD = 0.08). We assumed a mean travel speed of 14 $km \cdot h^{-1}$ with a maximum at 61 $km \cdot h^{-1}$ (Spear and Ainley 1997, Sittler et al. 2011). To avoid too long and unrealistic paths, we limited the time available to travel between consecutive twilights between 7 to 12 h. This was necessary for 19 tracks, especially around equinoxes when twilight estimation is less accurate because of equal day length (Lisovski and Hahn 2012), or when convergence of the model was impossible. While this approach discarded unrealistic latitudinal estimation, some uncertainty persisted around the equinoxes.

Migration phenology and characterization

Since long-tailed jaegers become entirely terrestrial during the breeding period, we expected a sudden change in the number of immersion events when they switched from the marine to the terrestrial environment, and vice versa. To estimate the departure and arrival dates on the breeding site, we used the immersion data as suggested by Fauchald et al. (2019). Because these data are recorded at relatively short intervals, we smoothed them before further analysis. We summed the wet events daily and calculated a 3-d running mean (*caTools* package; Tuszynski 2020). We used the *cpt.meanvar* function from the package *changepoint* (Killick and Eckley 2014, Killick et al. 2016) with a binary segmentation algorithm (Scott and Knott 1974). A visual inspection of changepoint plots allowed us to select the transitions corresponding to the beginning of the fall migration and the end of the spring migration. We validated these dates with the first location estimated after the departure from the breeding site, and the last one recorded at the end of the migration respectively. Usually, these locations were south of Baffin Island because of the 24-h daylight in summer. When the first location recorded out of the breeding site was prior to the departure date estimated by the changepoint method ($n = 3$; mean difference of 1.7 d), we chose the one estimated from the location.

To define fall and spring stopovers, we looked at the stationary periods estimated by the *ChangeLight* function (*GeoLight* package; Lisovski and Hahn 2012). We used a minimum stationary period of 3 consecutive days and a probability threshold for site change (quantile) of 0.85. We used the *mergeSites* function to join stationary periods separated by single outliers and a maximum distance threshold of 200 km.

To define wintering period, we used a three-step approach based on the MATCHED (Migratory Analytical Time Change Easy Detection) method (Chen et al. 2016, Doko et al. 2016). First, we performed a changepoint analysis to identify sudden changes in an ordered sequence of data for three parameters: latitude, longitude, and net-squared displacement (NSD), which corresponds to the straight-line distance between the starting location (i.e. the breeding site), and any other subsequent location. The changepoint analysis with a binary segmentation algorithm marked the changes in mean and variance (*cpt.meanvar*) for these three parameters (Figure S2.3). During the wintering period, we expected the three parameters to present flat and stable lines as birds should be staying in the same region. Since jaegers are coming back to the same breeding site, we were expecting a double sigmoid function between these parameters and time over a full-year period (Bunnefeld et al. 2011). Second, a visual inspection of these parameters (latitude, longitude, NSD) plotted with the migratory path helped to identify the beginning and the end of the wintering period. Finally, we validated the dates with those estimated from the stationary periods revealed by the *ChangeLight* function for the same time period (i.e. winter).

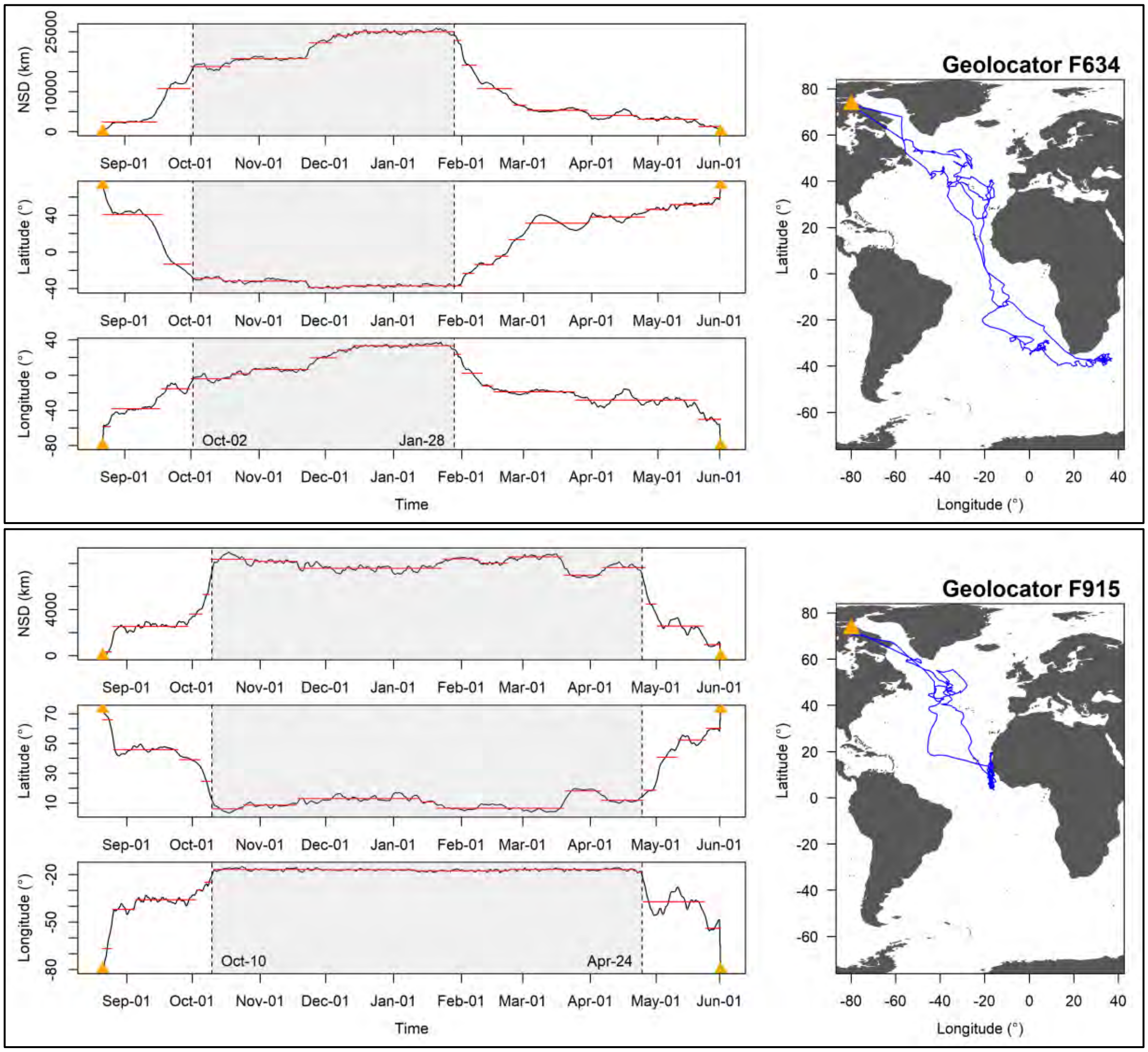

Figure S2.3 Annual pattern of three movement parameters, net-squared displacement (NSD), latitude and longitude, for two individuals marked with geolocators on Bylot Island. The red lines display the segments identified by the binary segmentation changepoint analysis, which are separated by sudden changes in parameter values. The gray shaded area represents the wintering period defined by the visual inspection of the changepoints for NSD, latitude and longitude together, and validated by the migratory path (blue line). The orange triangle represents the breeding site, and the period individuals are at the site.

Table S2.2 Optimal value of smoothing parameter (*h*) estimated by the bivariate normal kernel method and the least-square cross-validation algorithm for the individual and population kernel distribution estimations in long-tailed jaegers during the fall and spring stopover and wintering periods.

Parameter		Individual	Population
Fall		0.39 – 1.88	0.68
Winter		0.17 – 0.90	0.35
Spring		0.46 – 1.08	0.73
Male	Fall	-	0.67
	Winter	-	0.30
	Spring	-	0.80
Female	Fall	-	0.75
	Winter	-	0.42
	Spring	-	0.71

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Annexe S2.4 – Wintering and stopover areas

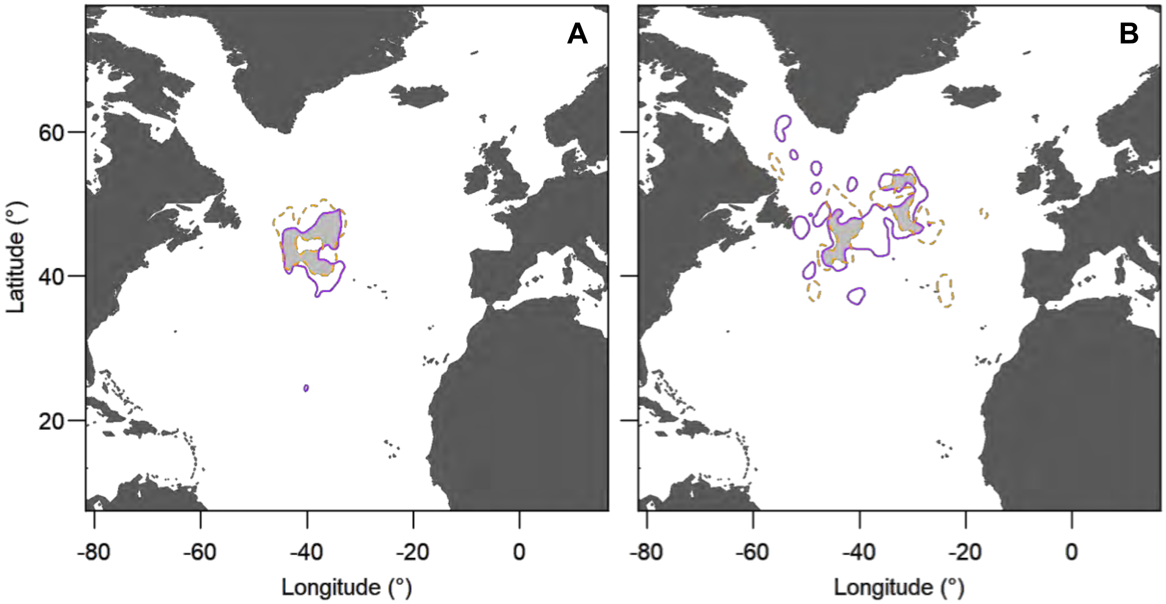


Figure S2.4 (A) Fall and (B) spring stopover core areas of female (purple solid line) and male (orange dashed line) long-tailed jaegers recorded with geolocators. The gray shading represents the overlap between sexes. The fall stopover core area of females overlapped at 65% with the one of males and at 60% for males. During spring stopovers, these overlaps dropped respectively to 33% and 39%.

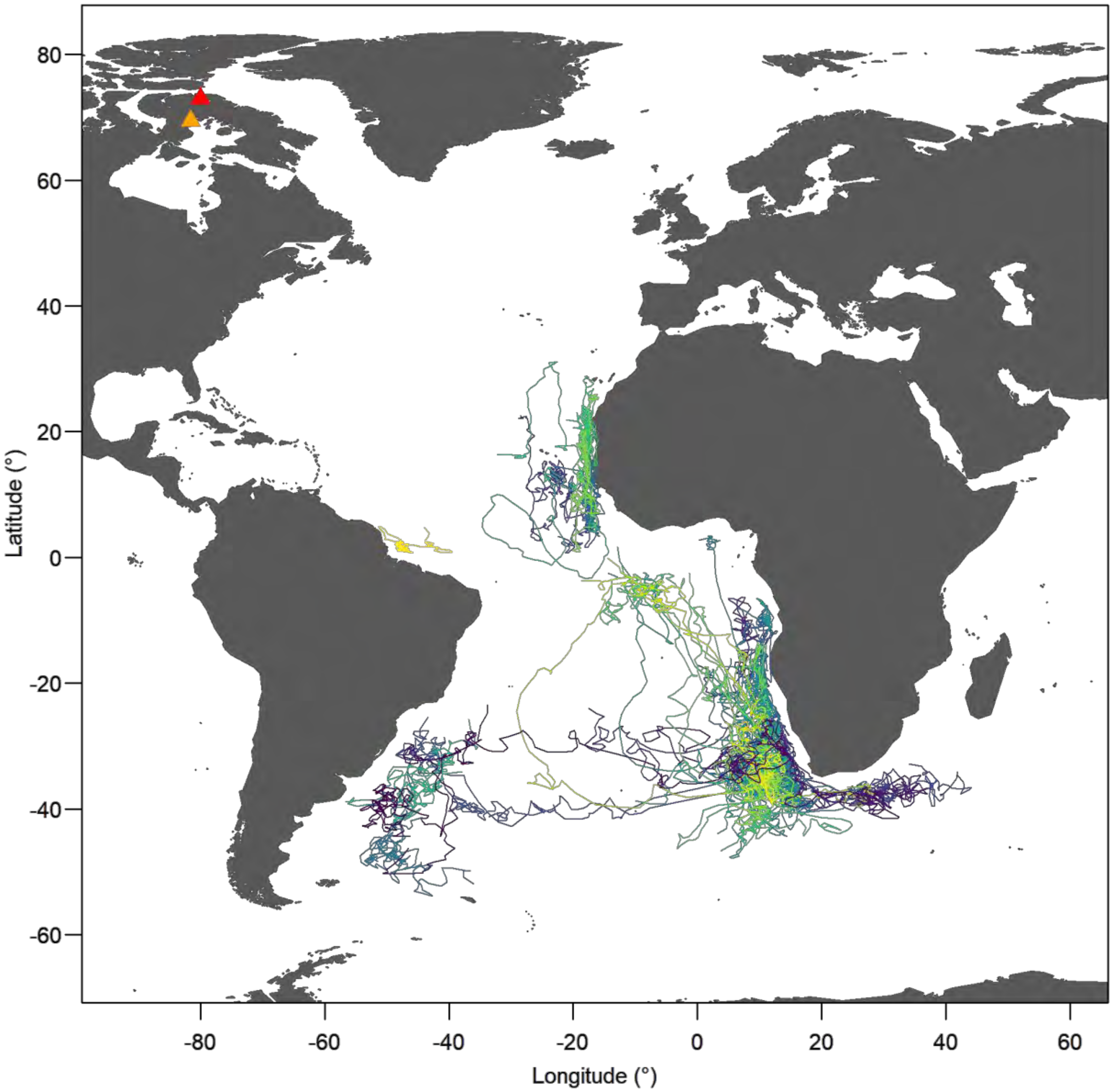


Figure S2.5 Movement during the wintering period of long-tailed jaegers breeding in the eastern Canadian Arctic on Bylot Island (red triangle) and Igloolik Island (orange triangle) and recorded with geolocators. Each color represents a different individual.

Table S2.3 Within-pair comparison of the migration phenology and wintering sites used by long-tailed jaegers breeding in the eastern Canadian Arctic and recorded with geolocators. Pairs were nesting together at deployment and at recovery (pair 1-4) or sighted together if they were not nesting (pair 5-6). Wintering sites: main site comes first. *NA*: Information not available due to device failure.

Pair	ID	Sex	Departure from breeding site	Wintering sites	Arrival at breeding site
1	F915 F913	F M	Aug 20 Aug 21	Canary C. Benguela C.	Jun. 5 Jun. 1
2	R838 R839	F M	Aug 20 Aug 20	Benguela C. Benguela C.	*NA* Jun. 10
3	R846 R845	F M	Aug 8 Aug 16	Brazil C. Benguela C.	May 30 Jun. 1
4	R847 R848	F M	Aug 10 Aug 14	Canary C. Canary C.	Jun. 13 Jun. 5
5	X571 X570	F M	Aug 2 Aug 6	Benguela C. Canary C.	*NA* *NA*
6	BK188 BK187	F M	Jul 27 Aug 10	Benguela C./Brazil C. Brazil C.	May 27 Jun. 2

Annexe S2.5 – Output of linear models

Table S2.4 Slope parameters (β) and their 95% confidence intervals (CI) of models examining the links between different movement parameters and sex, stage of the annual cycle or wintering sites of long-tailed jaegers or tracking device. R^2_m: Marginal R-squared for fixed effects (linear mixed-effect models) or adjusted R-squared (linear models). R^2_c: Conditional R-squared for fixed and random effects. n: Sample size.

Response variable	Explanatory variables[a]	β	Low CI	High CI	R^2_m	R^2_c	n
Total distance traveled[b]	Spring migration	2 935	1 346	4 523	0.14	0.47	63
Total distance traveled[c]	Male	-248.4	-6 063.6	5 566.9	0.05	-	23
Size of the wintering core area[c]	Male	-67 128	-15 6338	22 082	0.05	-	26
Travel speed[d]	Fall migration	236.3	212.2	260.4	0.72	0.74	164
	Fall stopover	40.9	15.9	65.8			
	Spring migration	115.0	87.4	142.6			
	Spring stopover	50.8	20.1	81.4			
Fall migration travel speed[c]	Male	-36.9	-92.7	18.9	0.04	0.04	42
Spring migration travel speed[c]	Male	22.8	-26.2	71.7	0.00	-	26
Fall migration travel speed[e]	Agulhas C.	16.7	-144.5	177.9	0.02	0.02	39
	Benguela C.	-13.5	-136.8	109.8			
	Brazil C.	20.1	-151.8	192.0			
	Guinea C.	-16.0	-176.2	144.1			
	North Equatorial C.	-46.4	-258.3	165.4			
Spring migration travel speed[e]	Agulhas C.	-55.8	-130.8	19.3	0.39	-	26
	Benguela C.	-9.5	-65.2	46.2			
	Brazil C.	14.9	-60.1	89.9			
	Guinea C.	-149.0	-234.1	-64.0			
Fall migration travel speed	Departure date from breeding site	-1.37	-5.18	2.43	0.02	0.02	42
Spring migration travel speed	Departure date from winter site	1.08	0.43	1.73	0.30	-	26
Fall migration travel speed[f]	Satellite transmitters	42.9	-40.0	125.8	0.02	0.02	49
Daily immersions[d]	Fall migration	-950.2	-1062.9	-837.5	0.70	0.72	164
	Fall stopover	-893.7	-1 010.9	-776.4			
	Spring migration	-315.1	-446.5	-183.8			
	Spring stopover	-146.7	-290.8	-2.6			

Response variable	Explanatory variables[a]	β	Low CI	High CI	R^2_m	R^2_c	n
Daily immersions in spring[g]	Stopover	214.1	47.1	381.1	0.08	0.45	66
	Migration after stopover	199.6	32.6	366.6			
Daily immersions[b]	Travel speed	-2.11	-2.77	-1.45	0.79	0.85	67
	Spring migration	1 034.0	602.4	1 465.6			
	Travel speed x Spring migration	-2.55	-4.02	-1.08			

[a] Dates were expressed as day of the year for statistical analyses.

Reference levels: [b] Fall migration; [c] Female; [d] Wintering period; [e] Canary C.; [f] Geolocators; [g] Migration before stopover

Table S2.5 Slope parameters (β) and their 95% confidence intervals (CI) of models examining the links between chlorophyll *a* concentration and wintering or stopover sites of long-tailed jaegers. R^2: adjusted R-squared. n: Sample size.

Response variable	Explanatory variables	β	Low CI	High CI	R^2	n
Chlorophyll *a* concentration[a]	Agulhas C.	-0.57	-0.62	-0.52	0.92	114
	Benguela C.	-0.68	-0.73	-0.64		
	Brazil C.	-0.50	-0.54	-0.45		
	Guinea C.	-0.77	-0.82	-0.72		
	North Equatorial C.	-0.58	-0.63	-0.53		
Chlorophyll *a* concentration[b]	Spring stopover	0.58	0.53	0.64	0.93	37

Reference levels were as follow: [a] Canary C.; [b] Fall stopover

Table S2.6 Slope parameters (β) and their 95% confidence intervals (CI) of models examining the links between migration phenology and sex or wintering site of long-tailed jaegers or tracking device. Wintering site refers to the furthest site reached during the winter. R^2_m: Marginal R-squared for fixed effects (linear mixed-effect models) or adjusted R-squared (linear models). R^2_c: Conditional R-squared for fixed and random effects. n: Sample size.

Response variable[a]	Explanatory variables	β	Low CI	High CI	R^2_m	R^2_c	n
Departure from breeding site[b]	Male	4.19	-1.18	9.55	0.06	0.06	43
Departure from breeding site[c]	Satellite transmitters	6.28	0.13	12.43	0.08	0.08	50
Arrival to fall stopover[c]	Satellite transmitters	-1.02	-8.84	6.80	0.00	0.14	44
Duration of the fall stopover[d]	Male	7.41	0.54	14.28	0.52	0.52	40
	Agulhas C.	-21.78	-37.63	-5.92			
	Benguela C.	-18.97	-30.99	-6.96			
	Brazil C.	4.13	-12.65	20.91			
	Guinea C.	-17.11	-34.58	0.36			
	North Equatorial C.	-10.33	-32.75	12.08			
Arrival to wintering site[d]	Male	9.93	-3.07	22.92	0.11	0.54	40
	Agulhas C.	-8.10	-37.36	21.17			
	Benguela C.	-1.81	-24.16	20.54			
	Brazil C.	6.12	-23.54	35.79			
	Guinea C.	-1.55	-37.51	34.41			
	North Equatorial C.	-4.97	-44.83	34.88			
Departure from wintering site[d]	Male	16.86	-3.15	36.88	0.48	-	26
	Agulhas C.	-60.27	-97.12	-23.43			
	Benguela C.	-39.96	-67.23	-12.68			
	Brazil C.	-42.27	-79.12	-5.43			
	Guinea C.	-81.82	-124.61	-39.03			
Duration of the wintering period[d]	Male	7.8	-18.8	34.4	0.21	-	26
	Agulhas C.	-52.0	-100.9	-3.1			
	Benguela C.	-37.2	-73.4	-1.0			
	Brazil C.	-49.0	-98.0	-0.1			
	Guinea C.	-76.5	-133.3	-19.7			
Duration of the spring stopover[d]	Male	-14.94	-28.70	-1.18	0.30	-	23
	Agulhas C.	37.06	9.78	64.35			
	Benguela C.	10.01	-8.07	28.10			
	Brazil C.	10.07	-14.10	34.25			
	Guinea C.	13.82	-22.07	49.71			

Response variable[a]	Explanatory variables	β	Low CI	High CI	R^2_m	R^2_c	n
Arrival to breeding site[d]	Male	-0.57	-4.62	3.48	0.02	-	23
	Agulhas C.	-5.00	-13.03	3.03			
	Benguela C.	-4.93	-10.26	0.39			
	Brazil C.	-3.10	-10.21	4.02			
	Guinea C.	0.71	-9.85	11.28			
Duration of migration and stopover combined[e]	Spring migration	21.5	9.7	33.2	0.16	0.21	69

[a] Dates were expressed as day of the year for statistical analyses

Reference levels were as follow: [b] Female; [c] Geolocators, [d] Female and Canary C.; [e] Fall migration

Annexe S2.6 – Chlorophyll concentration

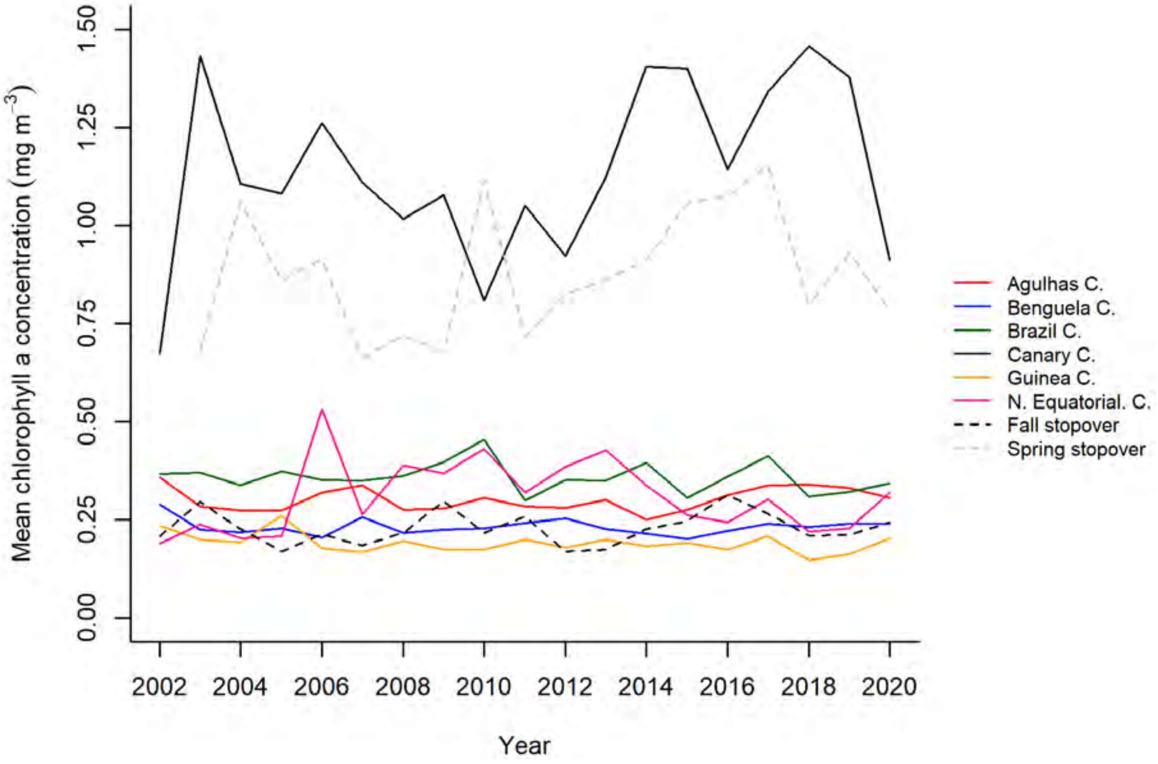


Figure S2.6 Mean annual chlorophyll *a* concentration estimated for the wintering sites (solid line) used by long-tailed jaegers breeding on Bylot Island and Igloolik Island and mean chlorophyll *a* concentration estimated over 32 d for the North Atlantic stopover sites (dashed line) during fall and spring stopover periods. Chlorophyll *a* data were estimated from NASA OB DAAC (2018).

Literature cited

NASA OB DAAC. 2018. NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Chlorophyll Data; 2018 Reprocessing. URL: https://oceancolor.gsfc.nasa.gov/l3/ (accessed 29 March 2021). Greenbelt, MD, USA.

Annexe S2.7 – Phenology of the annual cycle

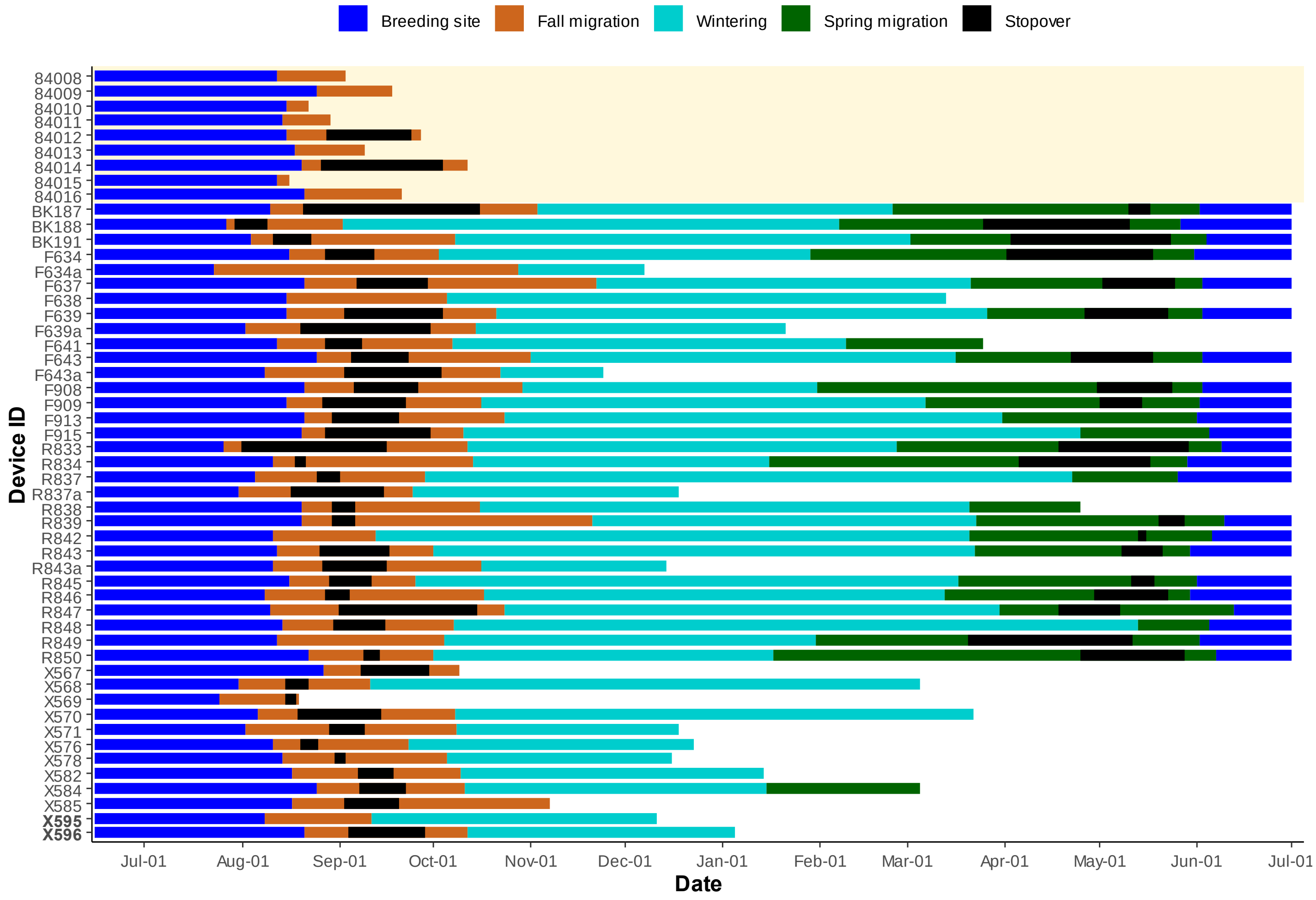


Figure S2.7 Phenology of the annual cycle of long-tailed jaegers recorded with satellite transmitters (yellow shaded area) or geolocators breeding on Bylot Island or Igloolik Island (device IDs X595 and X596 at bottom, in bold).

Annexe S2.8 – Détails supplémentaires sur la calibration des géolocalisateurs récupérés

Table S2.7 Période de calibration des géolocalisateurs récupérés sur l'Île Bylot (n = 40) et l'Île Igloolik (n = 2). Site de calibration : 46°44' N 71°28' O.

Géolocalisateur	Période de calibration
F634, F637, F638, F639, F641, F643, F908, F909, F913, F915	13 juin – 20 juin 2013
R833, R834, R837, R838, R839, R842, R843, R845, R846, R847, R848, R849, R850	9 mai – 25 mai 2015
X567, X568, X569, X570, X571, X576, X578, X582, X584, X585, X595, X596	14 mai – 28 mai 2016
BK187, BK188, BK 191	21 mai – 3 juin 2018

Figure S2.8 Installation des géolocalisateurs (Intigeo-C65, Migrate Technology) au site de calibration dans un milieu ouvert à Québec (QC, Canada; 46°44’N, 71°28’O). © Yannick Seyer

Annexe S2.9 – Données individuelles des labbes à longue queue suivis à l'aide d'un géolocalisateur

Table S2.8 Description des variables présentées sur les fiches individuelles des labbes à longue queue équipés d'un géolocalisateur entre 2014 et 2019.

Géolocalisateur : Numéro d'identification de l'appareil. La lettre « A » est ajoutée pour la seconde année de migration enregistrée par un même appareil

Bague de métal : Numéro d'identification de la bague métallique du USGS

Marqueur auxiliaire : Numéro d'identification et couleurs du marqueur auxiliaire auquel est attaché le géolocalisateur

Site : Site de déploiement et de récupération de l'appareil (Île Bylot : 73°08' N, 80°00' O; Île Igloolik : 69°39' N, 81°54' O)

Sexe : Sexe de l'individu déterminé par analyse génétique

Déploiement : Date de déploiement de l'appareil

Récupération : Date de récupération de l'appareil

Dernier enregistrement : Date où l'appareil a cessé de fonctionner s'il ne fonctionnait plus à la récupération

Nombre de localisations : Nombre total de localisations estimées entre le déploiement et la récupération de l'appareil (chaque point sur la carte correspond à une localisation, généralement une à midi et une à minuit)

Migration automnale / Halte automnale / Aire d'hivernage / Migration printanière / Halte printanière : Étapes de la période non-reproductrice. L'automne fait référence au déplacement vers le site d'hivernage et le printemps au retour vers le site de reproduction. L'information sur les migrations exclue la période de halte migratoire.

Début : Date de commencement de l'étape de la période non-reproductrice

Fin : Date de fin de l'étape de la période non-reproductrice

Durée : Durée de l'étape de la période non-reproductrice en jours

Distance : Distance parcourue pendant l'étape de la période non-reproductrice en km

Vitesse : Vitesse de déplacement pendant l'étape de la période non-reproductrice en km/jour

Immersions : Nombre d'immersions en eau salée pendant l'étape de la période non-reproductrice

Site d'hivernage : Site(s) d'hivernage utilisé(s) par l'individu en ordre d'importance

Année 1 : Année (saison de reproduction) du déploiement de l’appareil (ou saison de reproduction précédent la deuxième année de migration pour les appareils ayant enregistré plus d’une migration)

Année 2 : Année (saison de reproduction) suivant le déploiement de l’appareil ou suivant la deuxième année de migration pour les appareils ayant enregistré plus d’une migration)

Nicheur : Individu nicheur (oui) ou non-nicheur (non)

Initiation : Date de ponte estimée du premier œuf

Éclosion : Date d’éclosion estimée du premier œuf

Succès : Succès ou échec de la reproduction déterminée en fonction du succès à l’éclosion des œufs. (*Probable* : présence d’évidence d’éclosion, mais non confirmé par la présence de jeunes)

Taille de ponte : Nombre d’œufs pondus par le couple

Partenaire : Numéro d’identification de la bague du partenaire identifié au même nid pour un individu reproducteur

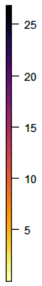
n.d. : Donnée non-disponible

- : non-applicable

Détails supplémentaires sur les cartes :

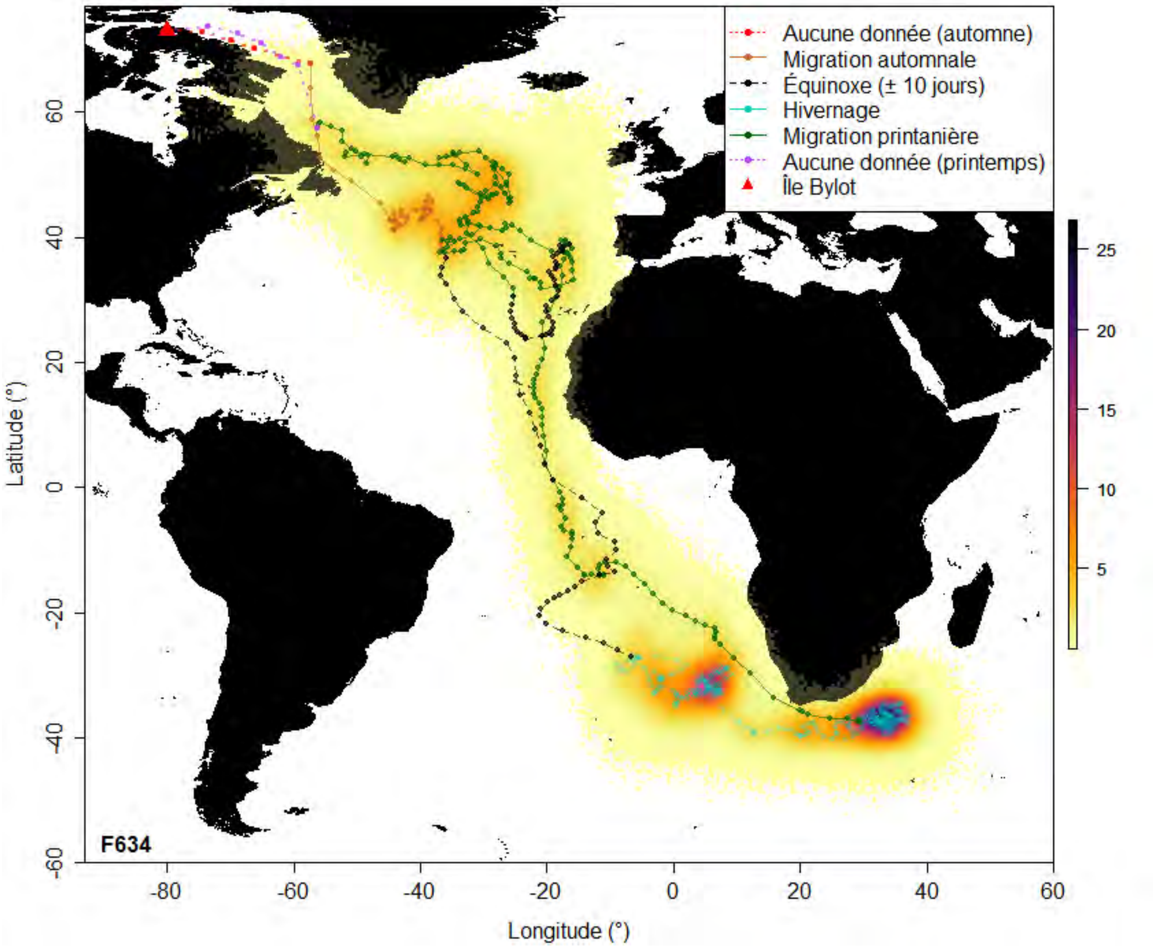
- La première section du trajet migratoire à l’automne (┈●┈) et la dernière section au printemps (┈●┈) couvrent une zone où l’estimation des localisations par les données de lumière est hautement imprécise en raison de l’été Arctique (24 h d’ensoleillement). Ces sections du trajet ont été inférées pour les individus nichant à l’Île Bylot à partir du trajet le plus probable déterminé par les émetteurs satellites déployés en 2008 de manière à relier le site de reproduction de l’individu à la première localisation enregistrée en mer à l’automne, et inversement, de la dernière localisation estimée en mer au printemps au site de reproduction. Les données d’immersions ont confirmé la présence des individus en mer plutôt que sur terre pendant cette section du trajet migratoire.

- L’échelle de couleur illustrée sur chacune des cartes (voir image ci-contre) représente la densité des localisations probables estimées par les 11 700 simulations réalisées par la méthode de Monte-Carlo par chaînes de Markov (MCMC). Chaque simulation représente un trajet probable. L’échelle est ajustée selon la taille d’échantillon de chaque individu et la densité maximale de points observés. La couleur jaune représente une faible densité de localisations et les couleurs plus foncées une plus forte densité. La densité de points n’a pas été représentée à ± 10 jours des équinoxes d’automne et de printemps.



Géolocalisateur	F634	**Sexe**	Femelle
Bague de métal	0944-02563	**Site**	Bylot
Marqueur auxiliaire	15 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
6 juillet 2014	25 juin 2016	7 décembre 2015	560



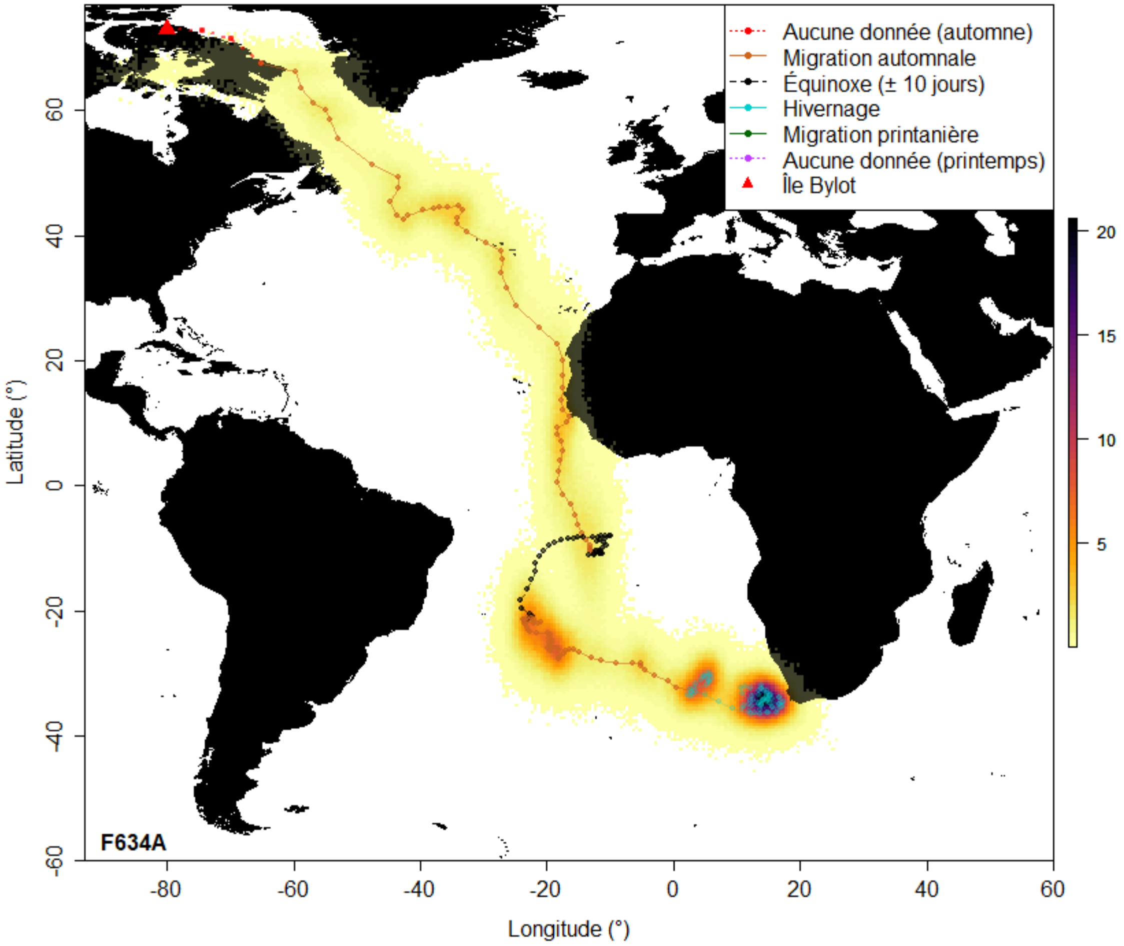
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	16 août	2 oct.	26	15 212	540	124
Halte automnale	27 août	12 sept.	15	2 926	190	167
Hivernage	2 oct.	28 jan.	118	22 621	191	360
Migration printanière	28 jan.	31 mai	76	23 114	274	284
Halte printanière	1 avril	18 mai	47	12 148	262	282

Site d'hivernage	Aiguilles, Benguela

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	17 juin	-	non	2	0944-02818
Année 2	non	-	-	-	-	-

Géolocalisateur	F634A	**Sexe**	Femelle
Bague de métal	0944-02563	**Site**	Bylot
Marqueur auxiliaire	15 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
6 juillet 2014	25 juin 2016	7 décembre 2015	227

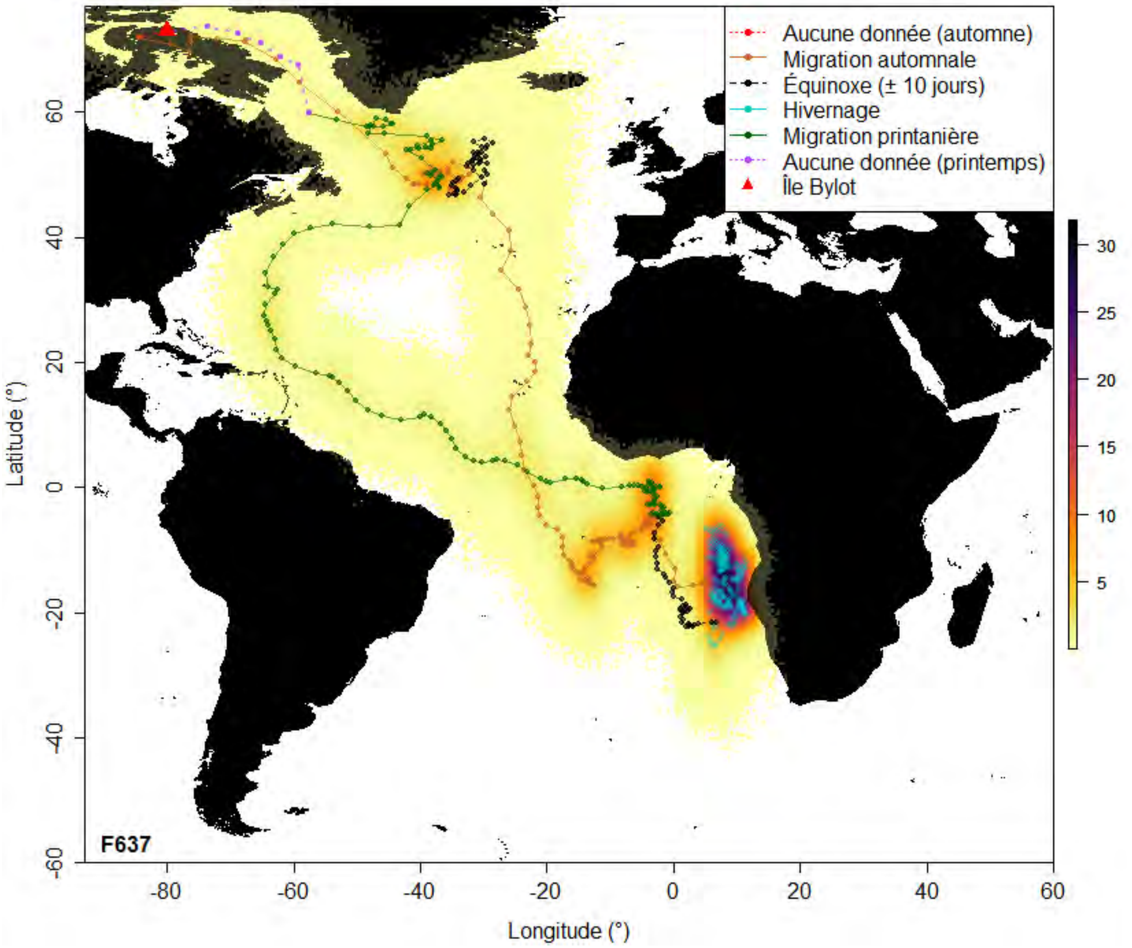


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	23 juil.	27 oct.	73	20 572	270	286
Halte automnale	-	-	0	-	-	-
Hivernage	27 oct.	n.d.	≥ 40	≥ 7 834	194	396
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	non	-	-	-	-	-
Année 2	oui	18 juin	-	non	1	0944-02570

Géolocalisateur	F637	**Sexe**	Femelle
Bague de métal	0944-02819	**Site**	Bylot
Marqueur auxiliaire	19 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
7 juillet 2014	26 juin 2015	12 juin 2015	563

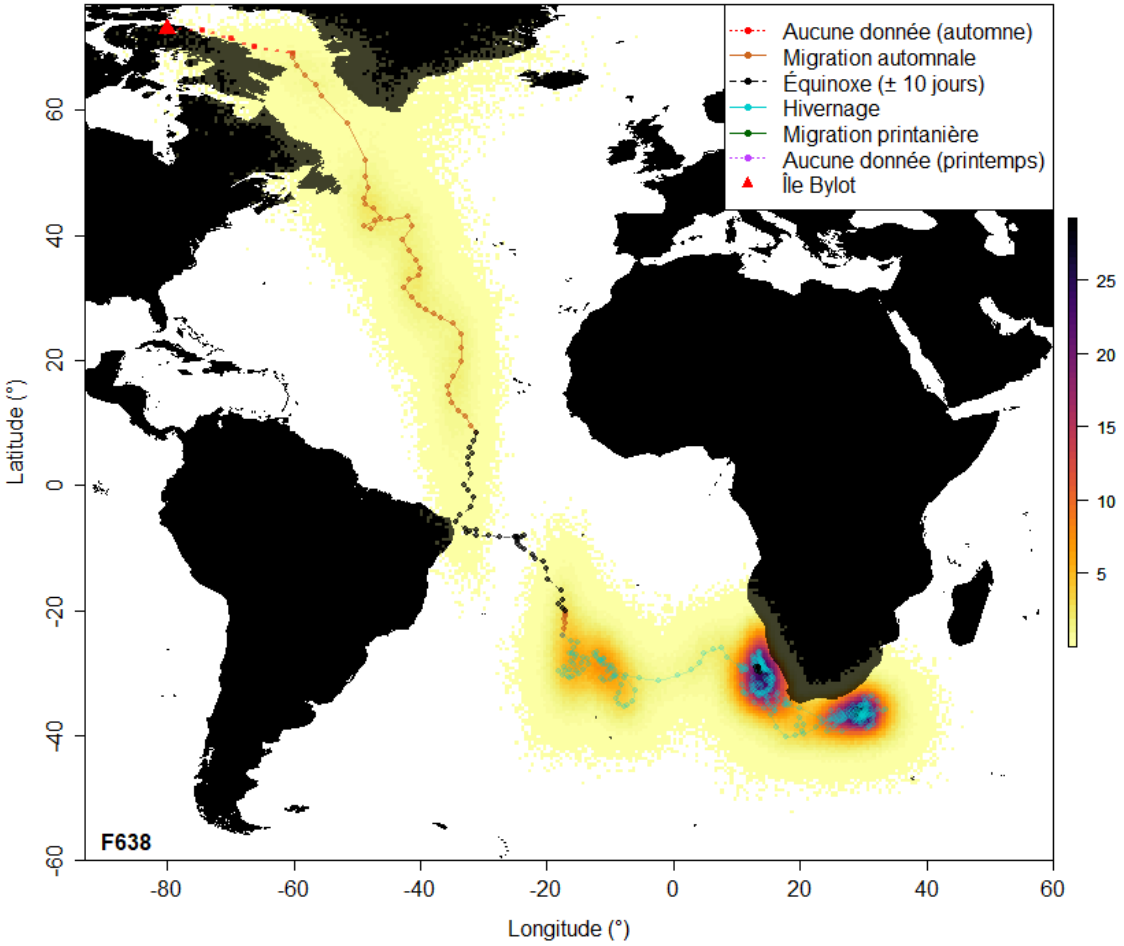


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	21 août	21 nov.	68	18 389	269	181
Halte automnale	6 sept.	29 sept.	22	4 523	202	188
Hivernage	21 nov.	21 mars	120	20 069	167	365
Migration printanière	31 mars	3 juin	51	14 492	240	260
Halte printanière	2 mai	25 mai	23	7 607	333	275
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	19 juin	13 juil.	oui	2	0944-02542
Année 2	oui	19 juin	-	non	2	0944-02542

Géolocalisateur	F638	**Sexe**	Femelle
Bague de métal	0944-02820	**Site**	Bylot
Marqueur auxiliaire	20 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
7 juillet 2014	23 juin 2015	13 mars 2015	407



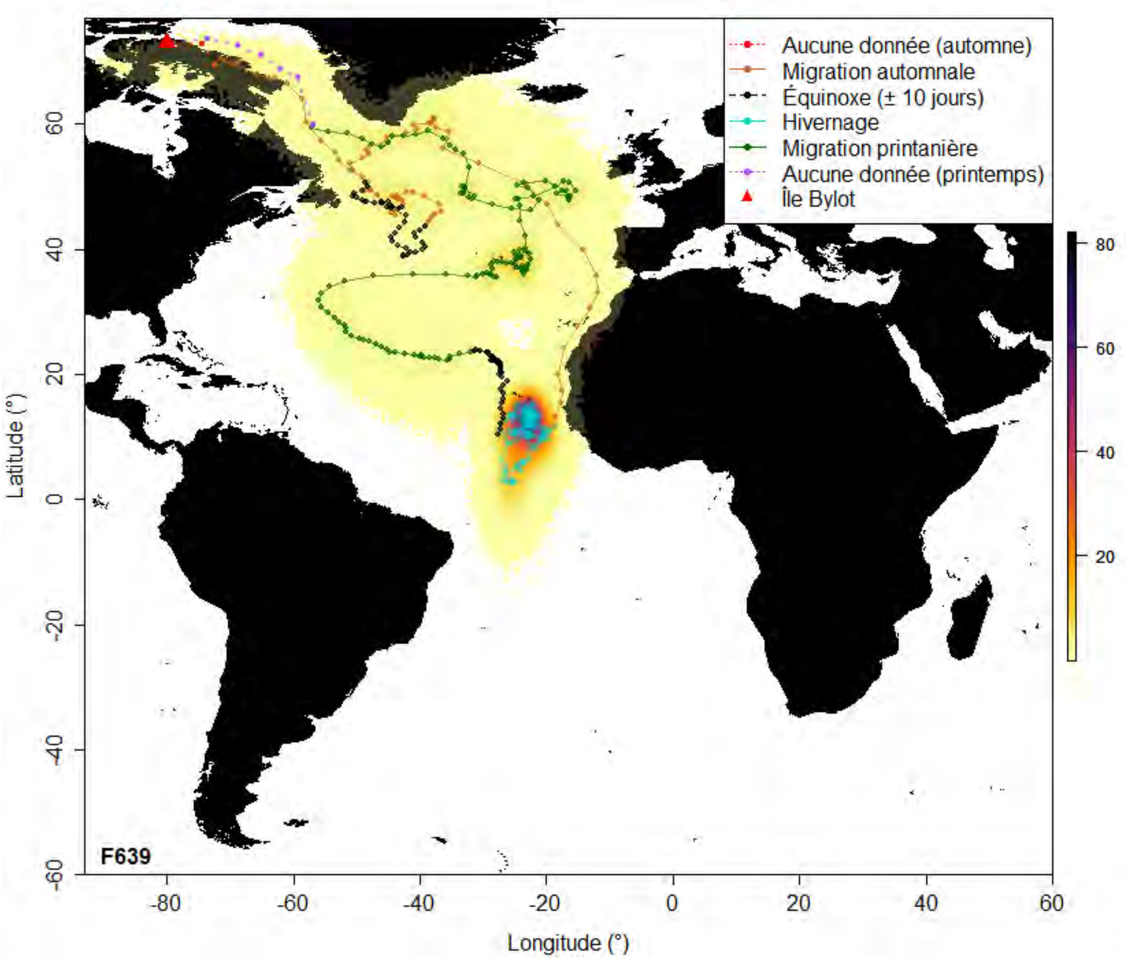
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	15 août	5 oct.	46	15 364	318	198
Halte automnale	-	-	0	-	-	-
Hivernage	5 oct.	n.d.	≥ 159	≥ 27 810	175	365
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage Aiguilles, Benguela

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	16 juin	-	non	1	0944-02821
Année 2	oui	16 juin	-	non	2	0944-02821

Géolocalisateur	F639	**Sexe**	Mâle
Bague de métal	0944-02822	**Site**	Bylot
Marqueur auxiliaire	21 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
7 juillet 2014	23 juin 2016	21 janvier 2016	566

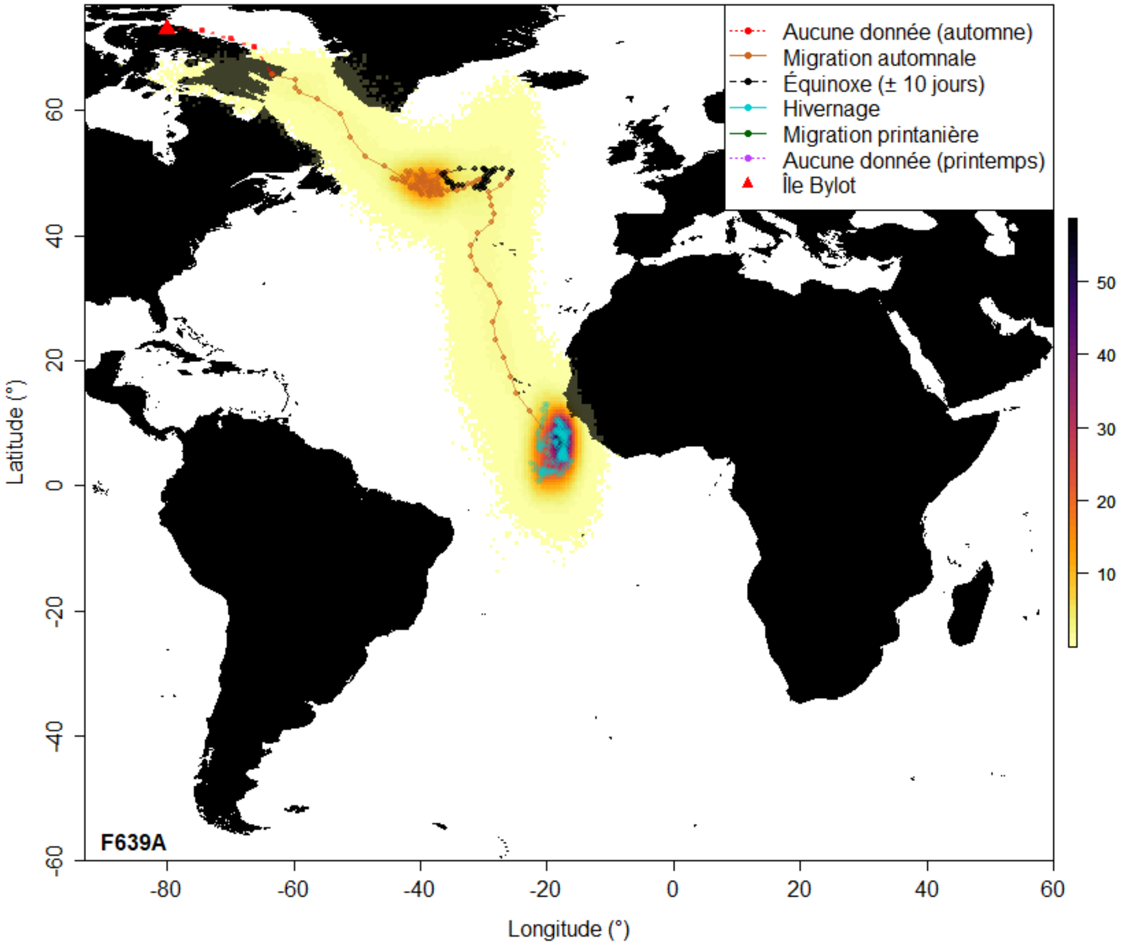


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	15 août	20 oct.	32	11 746	352	160
Halte automnale	2 sept.	4 oct.	31	5 622	179	184
Hivernage	20 oct.	26 mars	157	17 436	111	325
Migration printanière	26 mars	3 juin	42	11 548	227	276
Halte printanière	26 avril	23 mai	27	6 195	230	267
Site d'hivernage	Canaries					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	19 juin	n.d.	probable	2	n.d.
Année 2	non	-	-	-	-	-

Géolocalisateur	F639A	**Sexe**	Mâle
Bague de métal	0944-02822	**Site**	Bylot
Marqueur auxiliaire	21 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
7 juillet 2014	23 juin 2016	21 janvier 2016	341

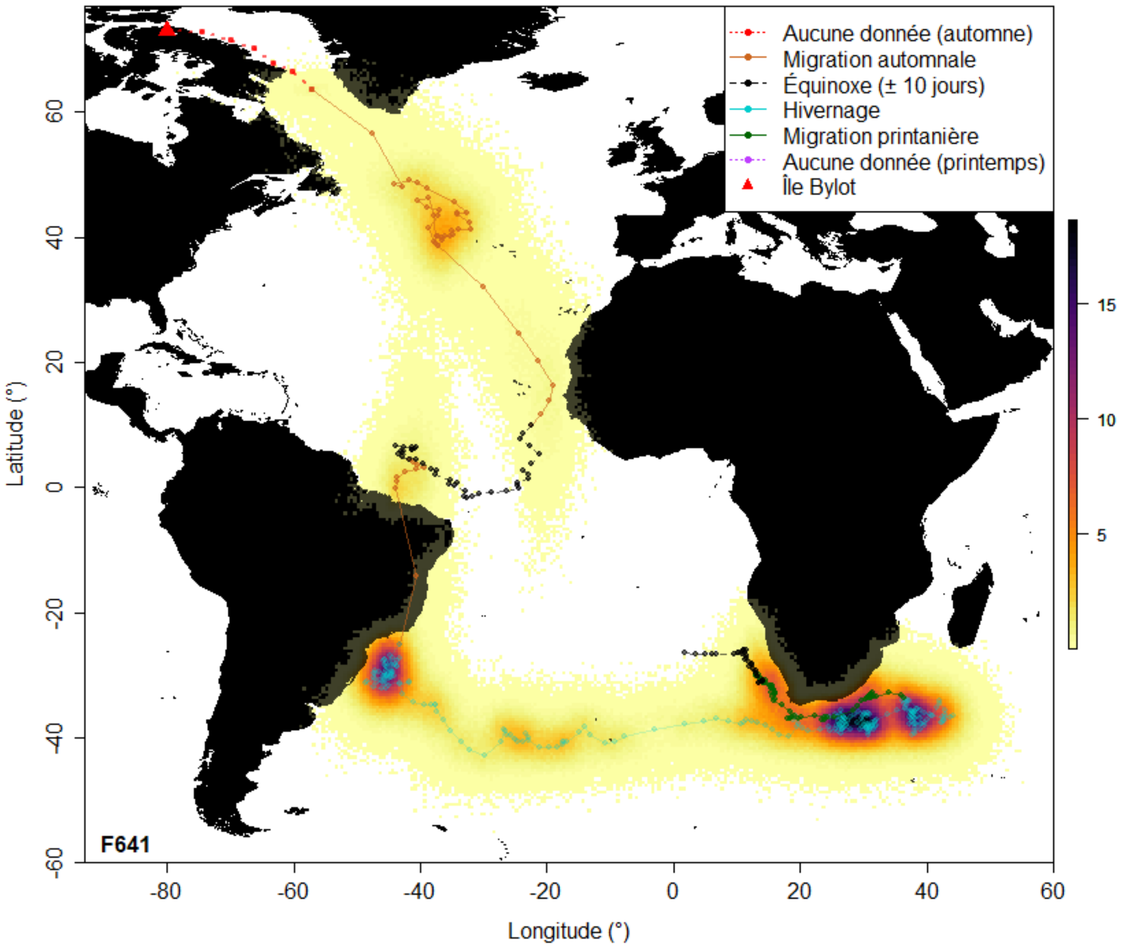


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	2 août	14 oct.	31	11 297	326	164
Halte automnale	19 août	30 sept.	41	5 628	136	195
Hivernage	14 oct.	n.d.	≥ 99	≥ 13 229	134	270
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Canaries					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	non	-	-	-	-	-
Année 2	oui	15 juin	-	non	2	0944-02857

Géolocalisateur	F641	**Sexe**	Femelle
Bague de métal	0944-02825	**Site**	Bylot
Marqueur auxiliaire	24 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
8 juillet 2014	27 juin 2016	25 mars 2015	427



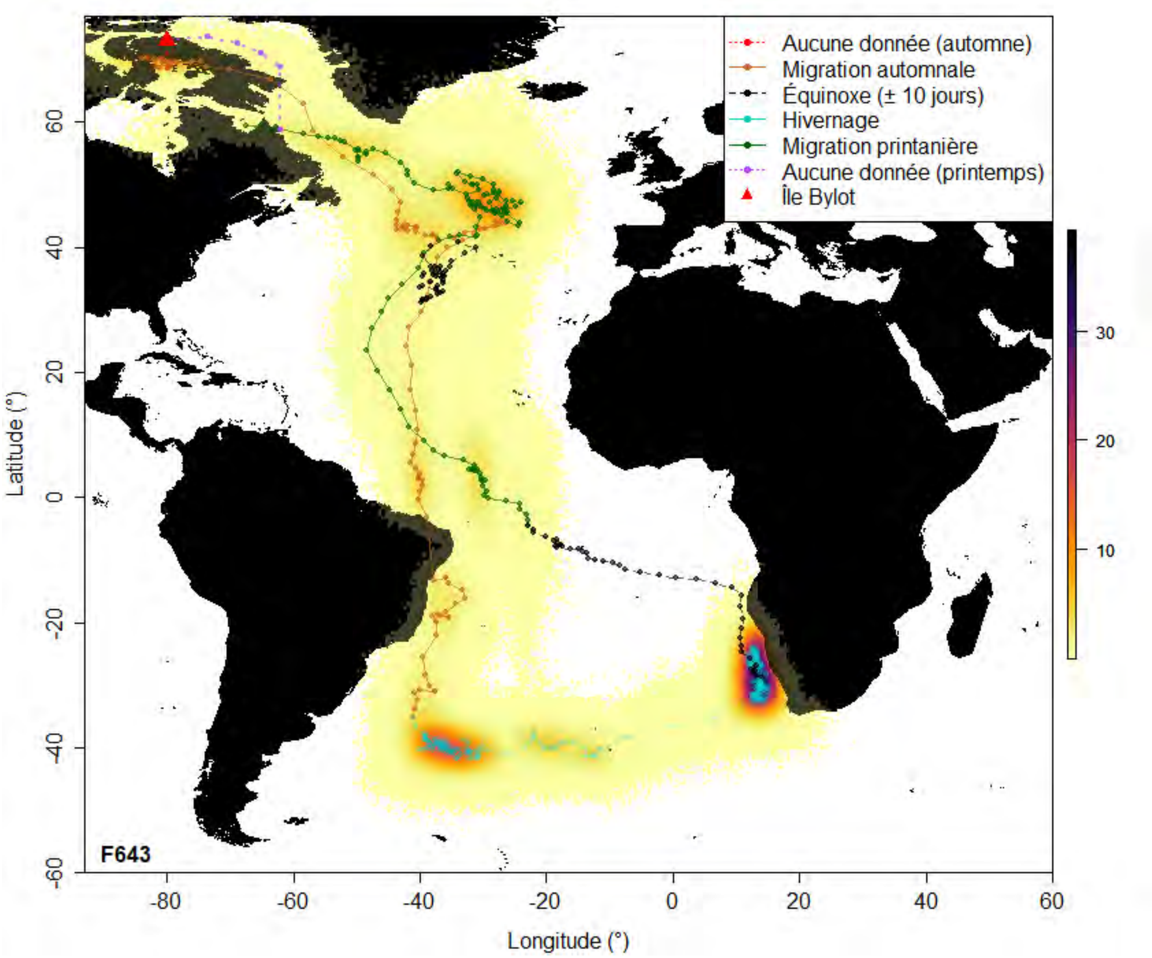
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	12 août	6 oct.	33	19 437	537	139
Halte automnale	27 août	8 sept.	11	2 383	209	209
Hivernage	6 oct.	9 fév.	126	23 643	188	345
Migration printanière	9 fév.	n.d.	≥ 44	≥ 6 532	148	340
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage Aiguilles, Brésil

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	17 juin	n.d.	probable	2	0944-02826
Année 2	oui	21 juin	-	non	2	n.d.

Géolocalisateur	F643	**Sexe**	Mâle
Bague de métal	0944-02827	**Site**	Bylot
Marqueur auxiliaire	26 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
9 juillet 2014	28 juin 2019	24 novembre 2015	572

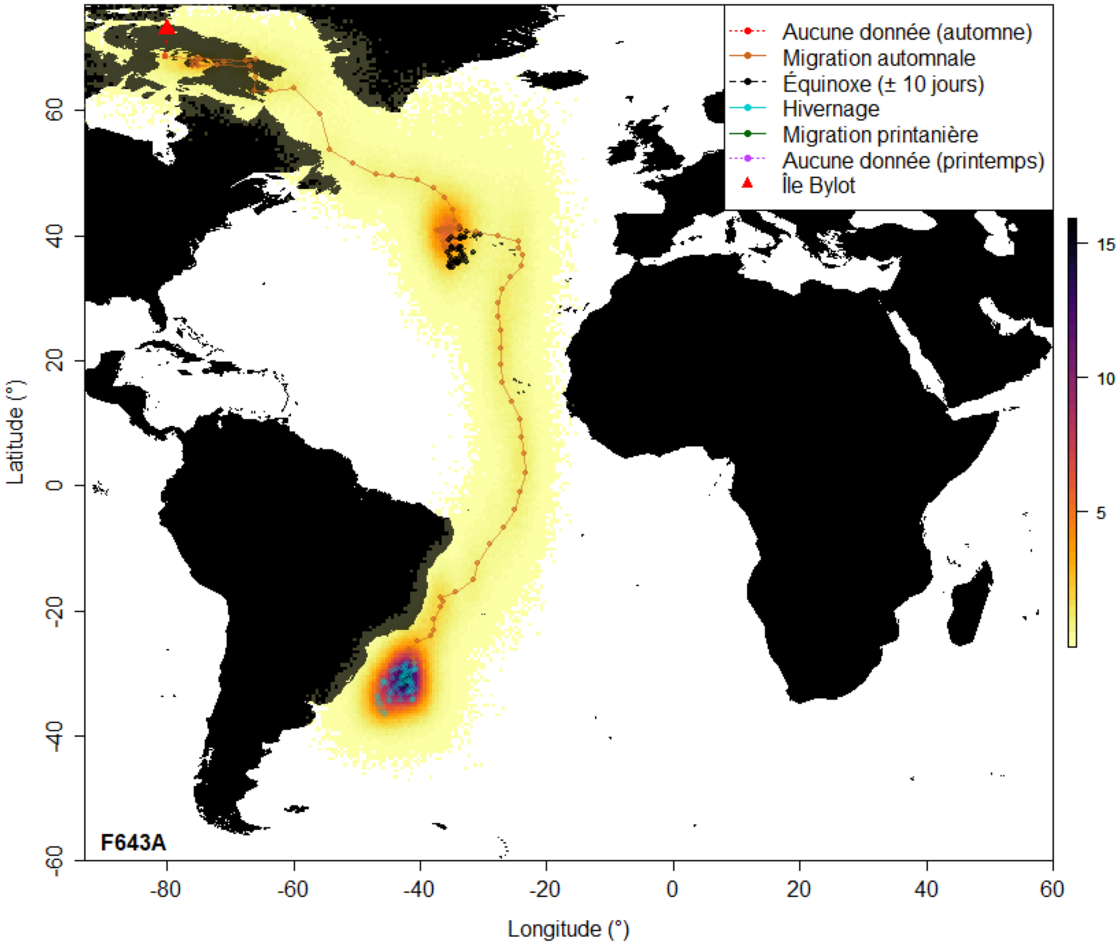


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	25 août	31 oct.	50	19 088	357	167
Halte automnale	4 sept.	23 sept.	18	4 017	218	183
Hivernage	31 oct.	16 mars	136	21 962	162	391
Migration printanière	16 mars	3 juin	53	18 468	307	237
Halte printanière	22 avril	18 mai	26	5 492	211	322
Site d'hivernage	Benguela, Brésil					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	18 juin	12 juil.	oui	2	0944-02828
Année 2	non	-	-	-	-	-

Géolocalisateur	F643A	**Sexe**	Mâle
Bague de métal	0944-02827	**Site**	Bylot
Marqueur auxiliaire	26 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
9 juillet 2014	28 juin 2019	24 novembre 2015	190

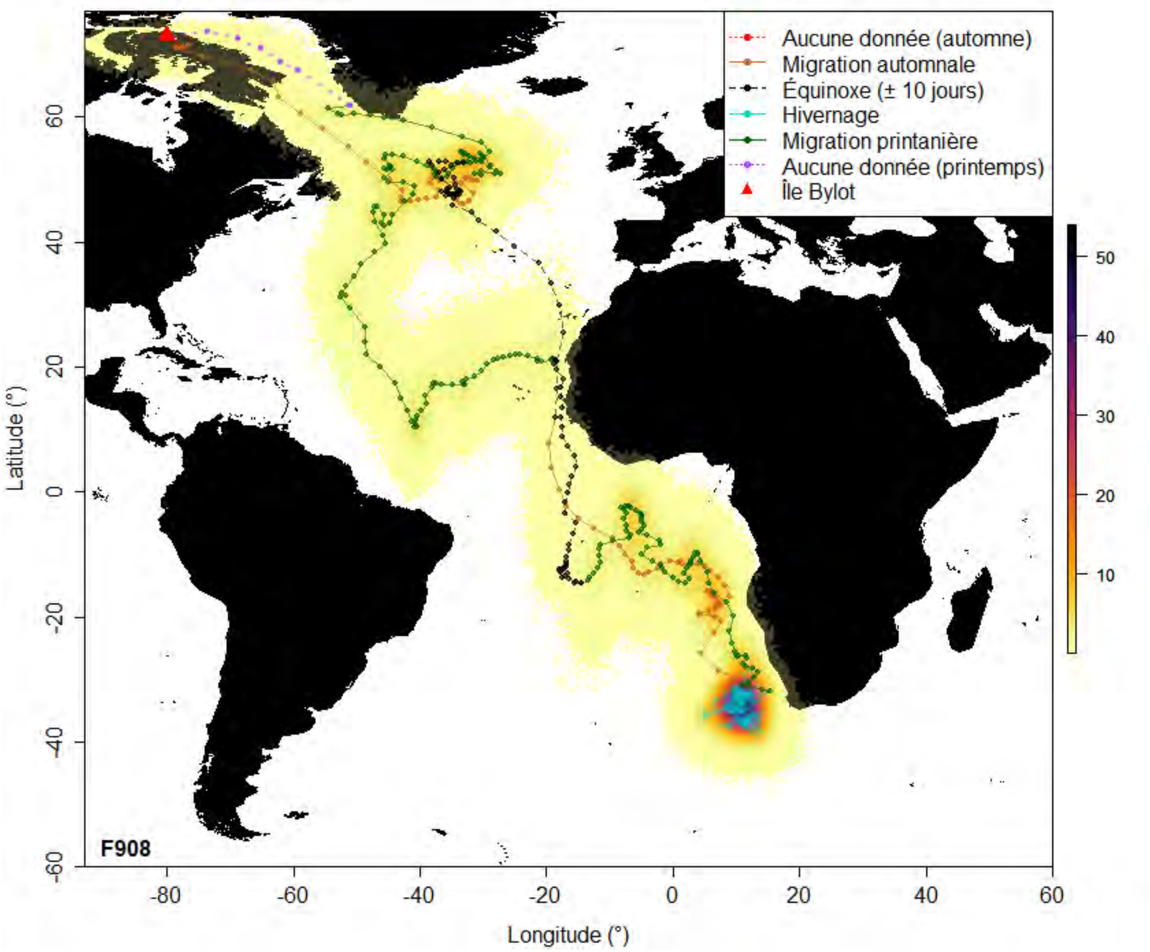


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	8 août	22 oct.	32	15 502	472	147
Halte automnale	2 sept.	3 oct.	31	5 434	176	229
Hivernage	22 oct.	n.d.	≥ 33	≥ 6 252	190	257
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Brésil					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	non	-	-	-	-	-
Année 2	non	-	-	-	-	-

Géolocalisateur	F908	**Sexe**	Mâle
Bague de métal	0944-02556	**Site**	Bylot
Marqueur auxiliaire	03 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
30 juin 2014	25 juin 2015	-	561

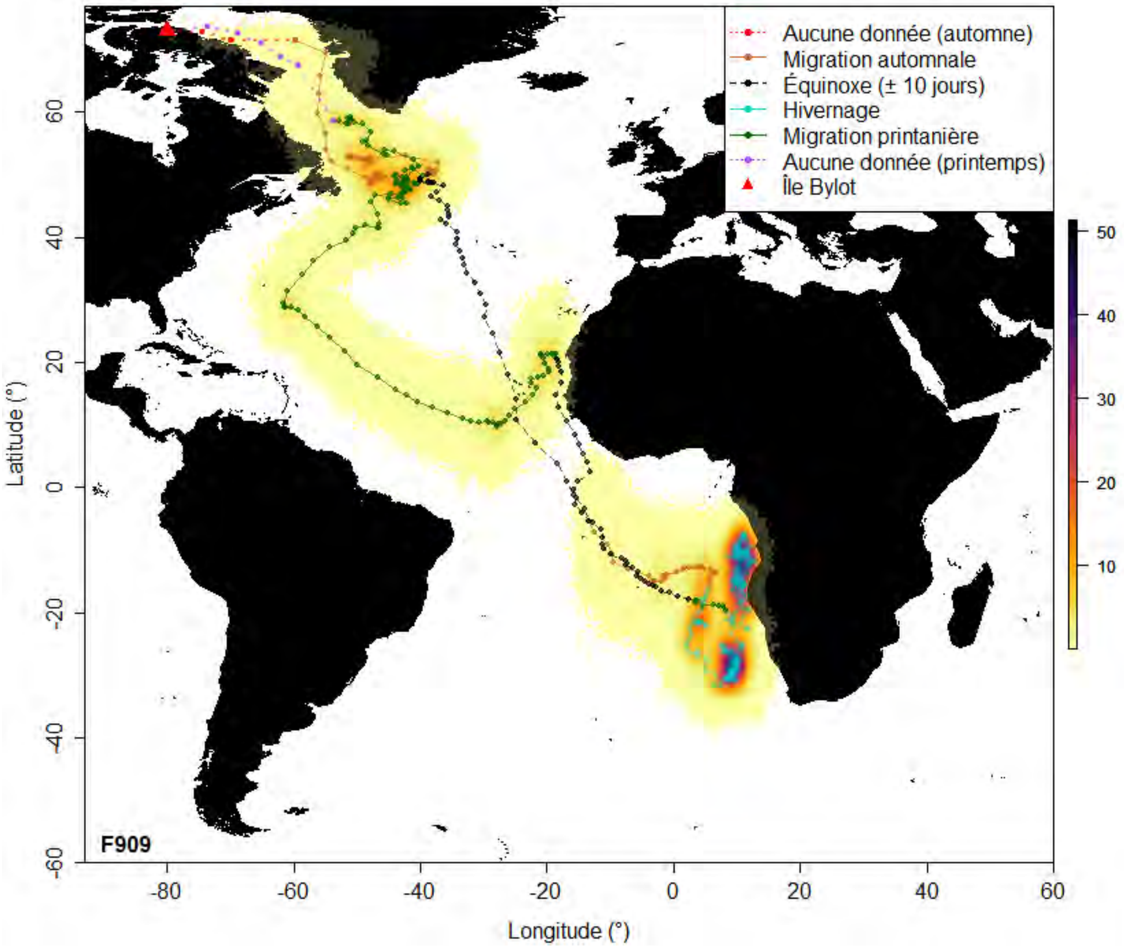


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	21 août	29 oct.	47	18 452	383	178
Halte automnale	5 sept.	26 sept.	20	4 091	200	145
Hivernage	29 oct.	31 jan.	95	14 560	154	362
Migration printanière	31 jan.	3 juin	97	26 290	251	294
Halte printanière	30 avril	24 mai	24	4 244	177	310
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	14 juin	8 juil.	oui	2	0944-02524
Année 2	oui	18 juin	-	non	2	0944-02524

Géolocalisateur	F909	**Sexe**	Mâle
Bague de métal	0944-02814	**Site**	Bylot
Marqueur auxiliaire	04 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
30 juin 2014	23 juin 2016	26 juillet 2015	554

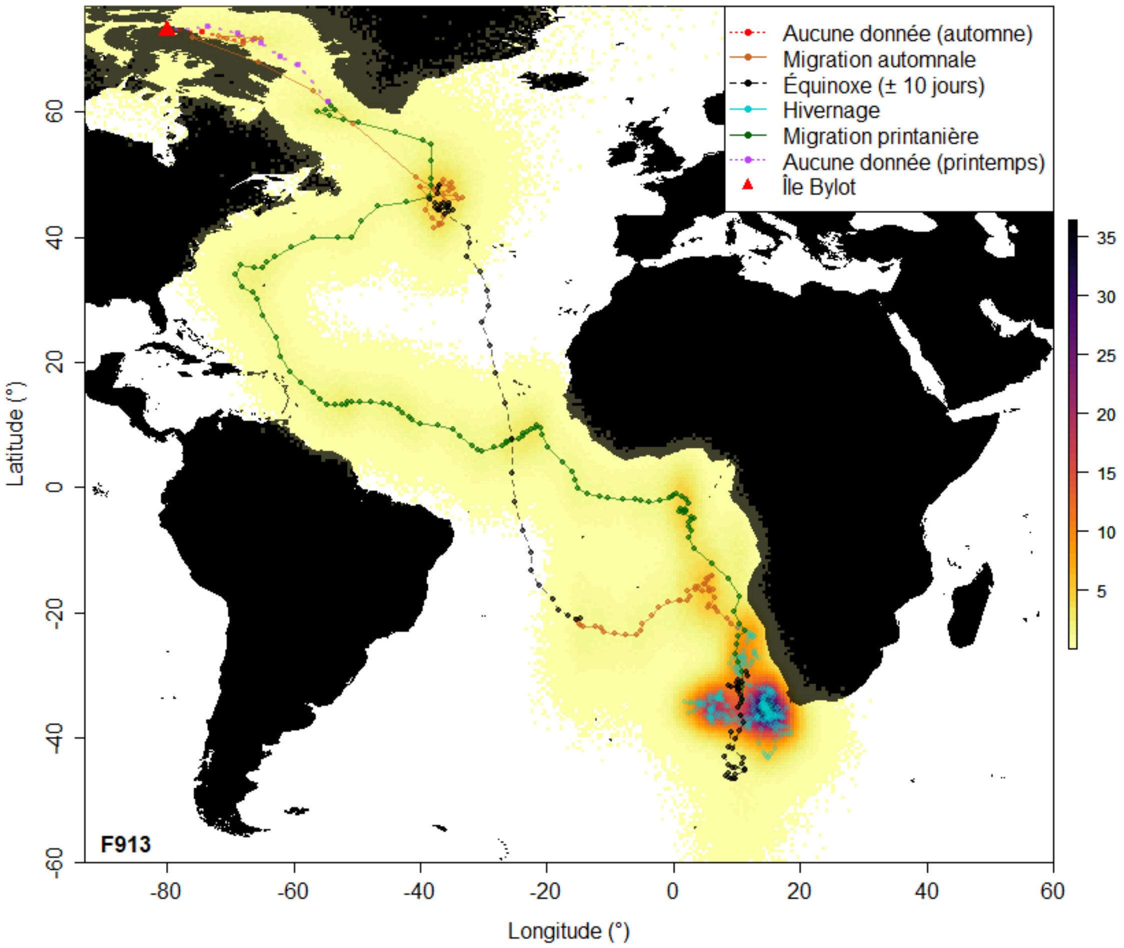


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	15 août	16 oct.	29	12 424	396	179
Halte automnale	26 août	22 sept.	26	5 015	190	186
Hivernage	16 oct.	6 mars	142	20 828	147	364
Migration printanière	6 mars	2 juin	67	20 437	274	272
Halte printanière	1 mai	14 mai	14	2 768	203	248
Site d’hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	14 juin	-	non	2	0944-02590
Année 2	non	-	-	-	-	-

Géolocalisateur	F913	**Sexe**	Mâle
Bague de métal	0944-02521	**Site**	Bylot
Marqueur auxiliaire	10 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
5 juillet 2014	3 juillet 2015	-	559



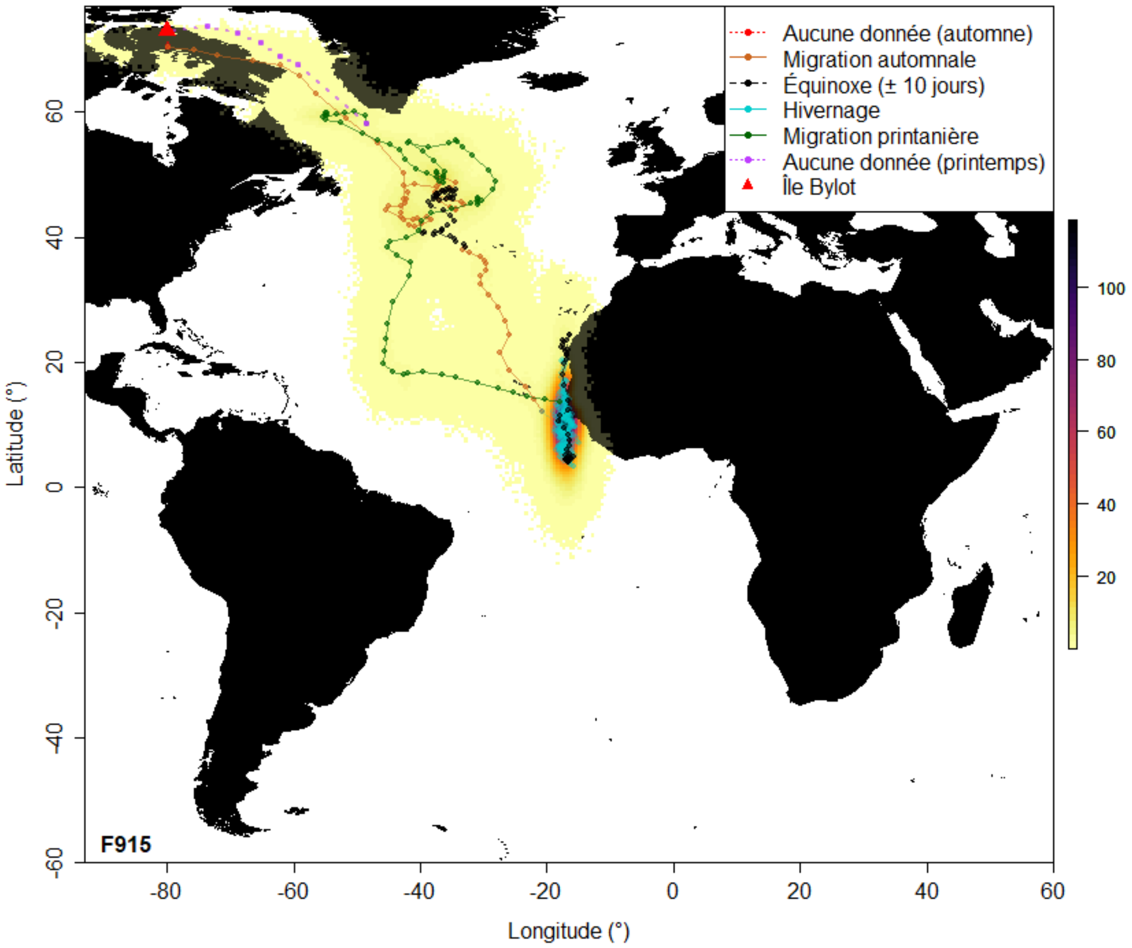
	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	21 août	23 oct.	43	17 305	389	167
Halte automnale	29 août	20 sept.	21	4 309	205	155
Hivernage	23 oct.	31 mars	159	26 703	168	348
Migration printanière	31 mars	1 juin	61	21 805	330	224
Halte printanière	-	-	0	-	-	-

Site d'hivernage	Benguela

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	17 juin	11 juil.	oui	2	0944-02816
Année 2	oui	15 juin	-	non	2	0944-02816

Géolocalisateur	F915	**Sexe**	Femelle
Bague de métal	0944-02816	**Site**	Bylot
Marqueur auxiliaire	12 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
5 juillet 2014	26 juin 2015	-	564

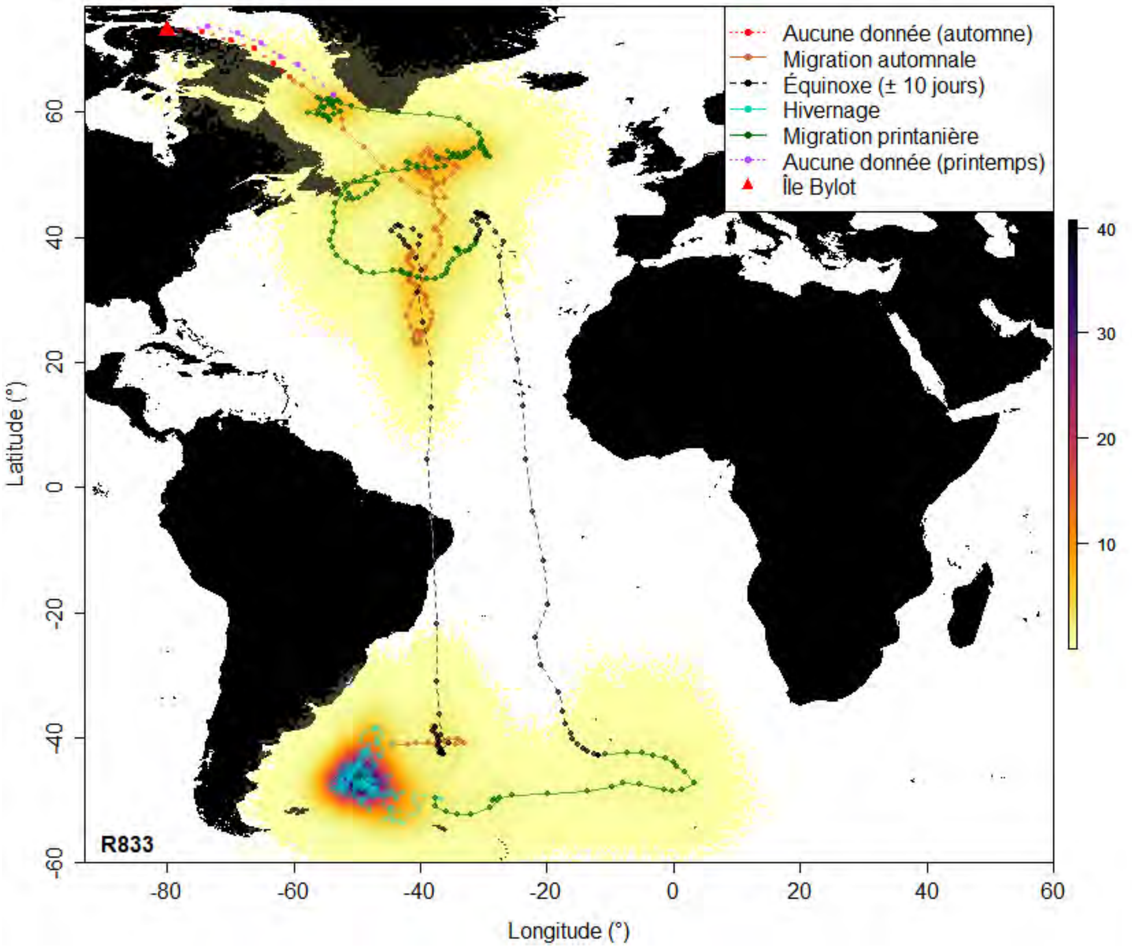


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	20 août	10 oct.	16	7 956	469	74
Halte automnale	27 août	30 sept.	33	6 491	194	146
Hivernage	10 oct.	24 avril	197	23 631	120	361
Migration printanière	24 avril	5 juin	36	14 302	333	425
Halte printanière	-	-	0	-	-	-
Site d'hivernage	Canaries					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	17 juin	11 juil.	oui	2	0944-02521
Année 2	oui	15 juin	-	non	2	0944-02521

Géolocalisateur	R833	**Sexe**	Femelle
Bague de métal	0944-02524	**Site**	Bylot
Marqueur auxiliaire	02 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
23 juin 2015	25 juin 2016	-	617

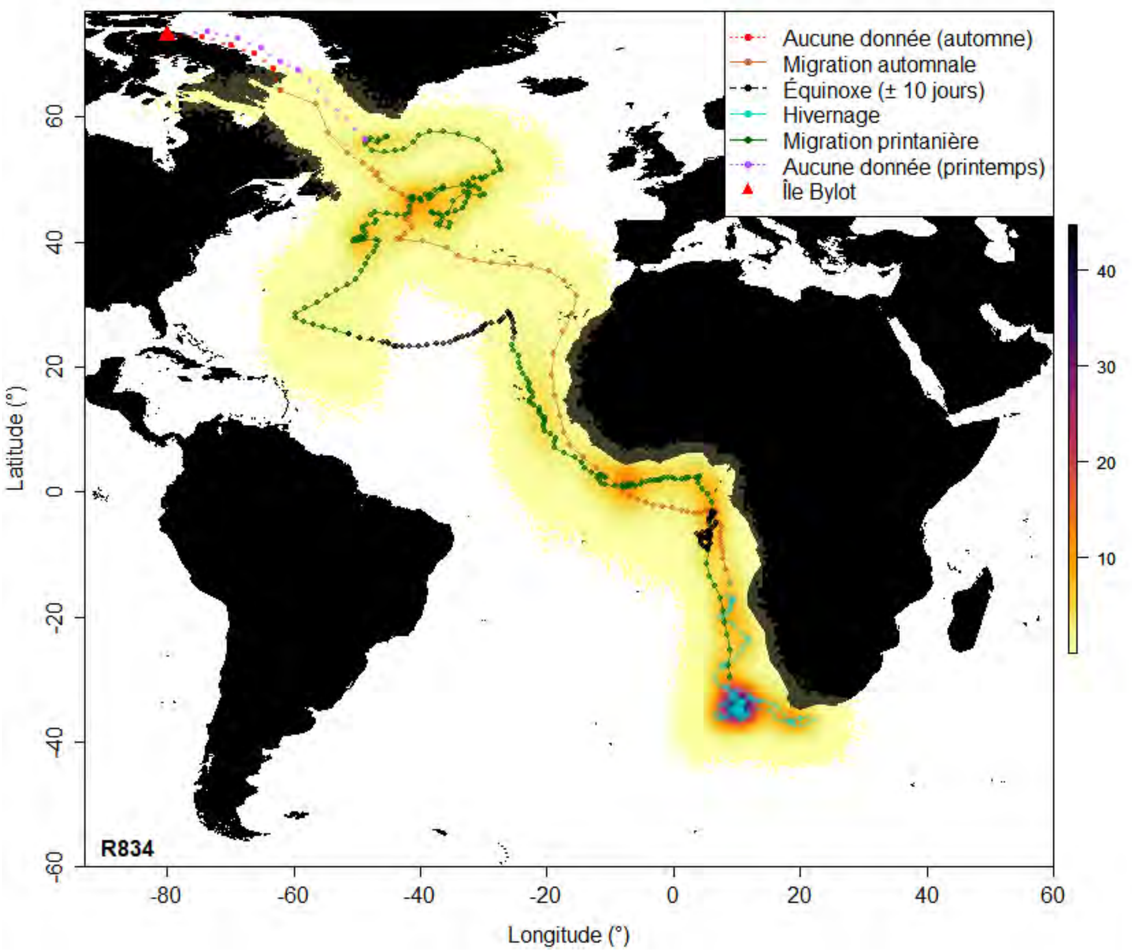


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	26 juil.	11 oct.	31	15 511	465	208
Halte automnale	31 juil.	16 sept.	46	8 615	186	193
Hivernage	11 oct.	25 fév.	137	19 334	141	382
Migration printanière	25 fév.	9 juin	54	21 379	364	226
Halte printanière	18 avril	29 mai	42	7 649	183	306
Site d'hivernage	Brésil					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	18 juin	-	non	2	0944-02556
Année 2	oui	17 juin	11 juil.	oui	2	0944-02556

Géolocalisateur	R834	**Sexe**	Femelle
Bague de métal	0944-02841	**Site**	Bylot
Marqueur auxiliaire	31 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
25 juin 2015	27 juin 2016	-	583

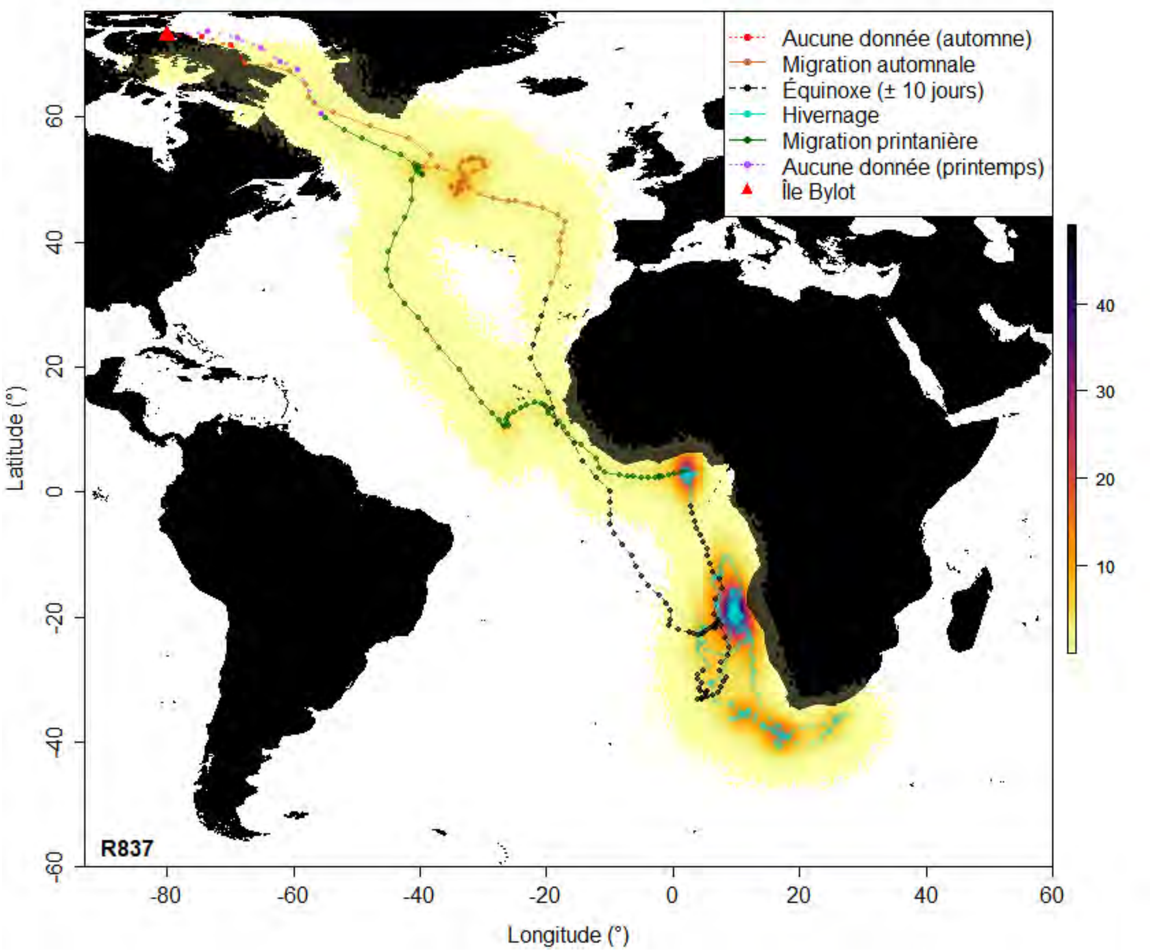


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	11 août	13 oct.	61	16 200	245	215
Halte automnale	17 août	21 août	3	554	163	211
Hivernage	13 oct.	15 jan.	94	13 075	138	341
Migration printanière	15 jan.	29 mai	92	19 895	188	328
Halte printanière	5 avril	17 mai	42	6 947	166	312
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	23 juin	-	non	1	n.d.
Année 2	non	-	-	-	-	-

Géolocalisateur	R837	**Sexe**	Mâle
Bague de métal	0944-02521	**Site**	Bylot
Marqueur auxiliaire	10 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
4 juillet 2015	21 juin 2019	18 décembre 2016	564

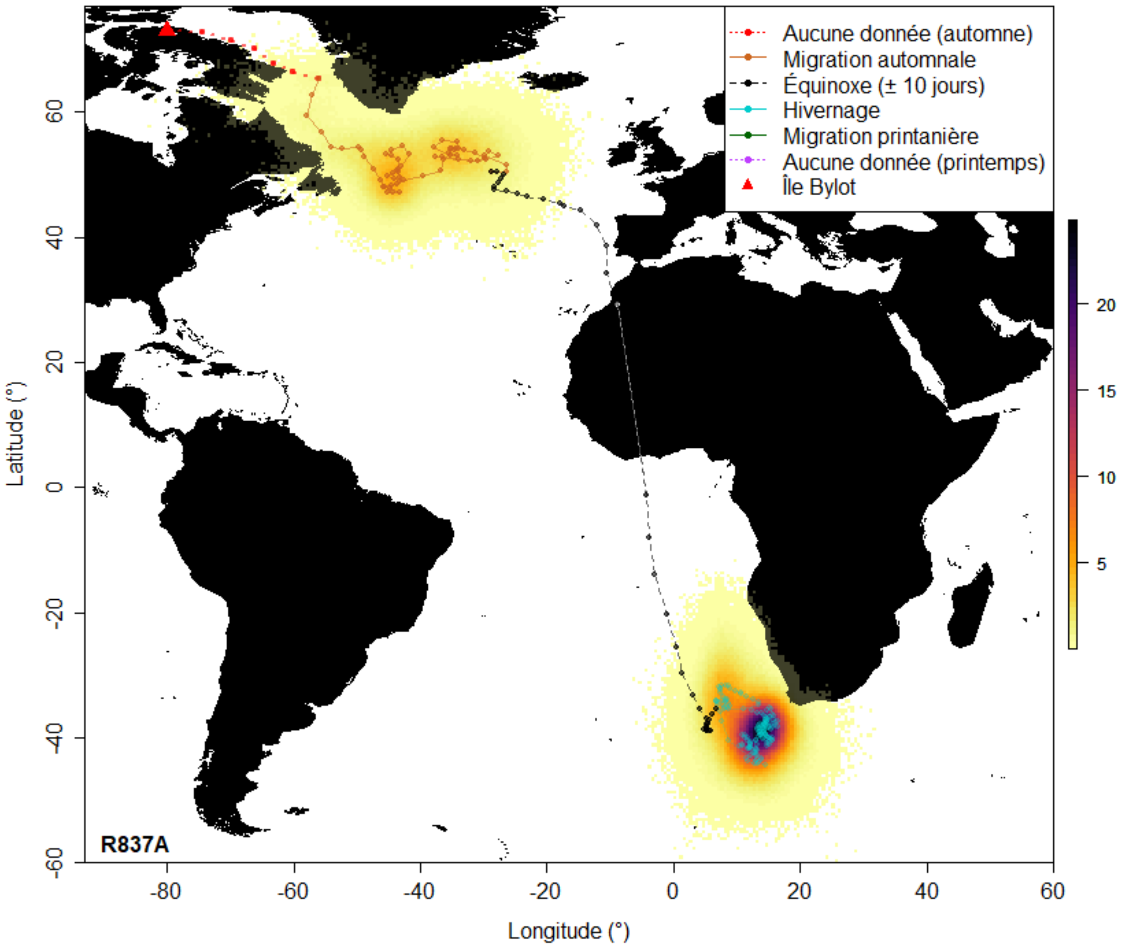


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	5 août	28 sept.	35	14 907	401	181
Halte automnale	24 août	1 sept.	7	952	129	164
Hivernage	28 sept.	22 avril	208	28 814	139	331
Migration printanière	22 avril	26 mai	33	12 774	333	239
Halte printanière	-	-	0	-	-	-
Site d’hivernage	Benguela, Guinée					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	15 juin	-	non	2	0944-02816
Année 2	oui	16 juin	-	non	2	0944-02816

Géolocalisateur	R837A	**Sexe**	Mâle
Bague de métal	0944-02521	**Site**	Bylot
Marqueur auxiliaire	10 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
4 juillet 2015	21 juin 2019	18 décembre 2016	257

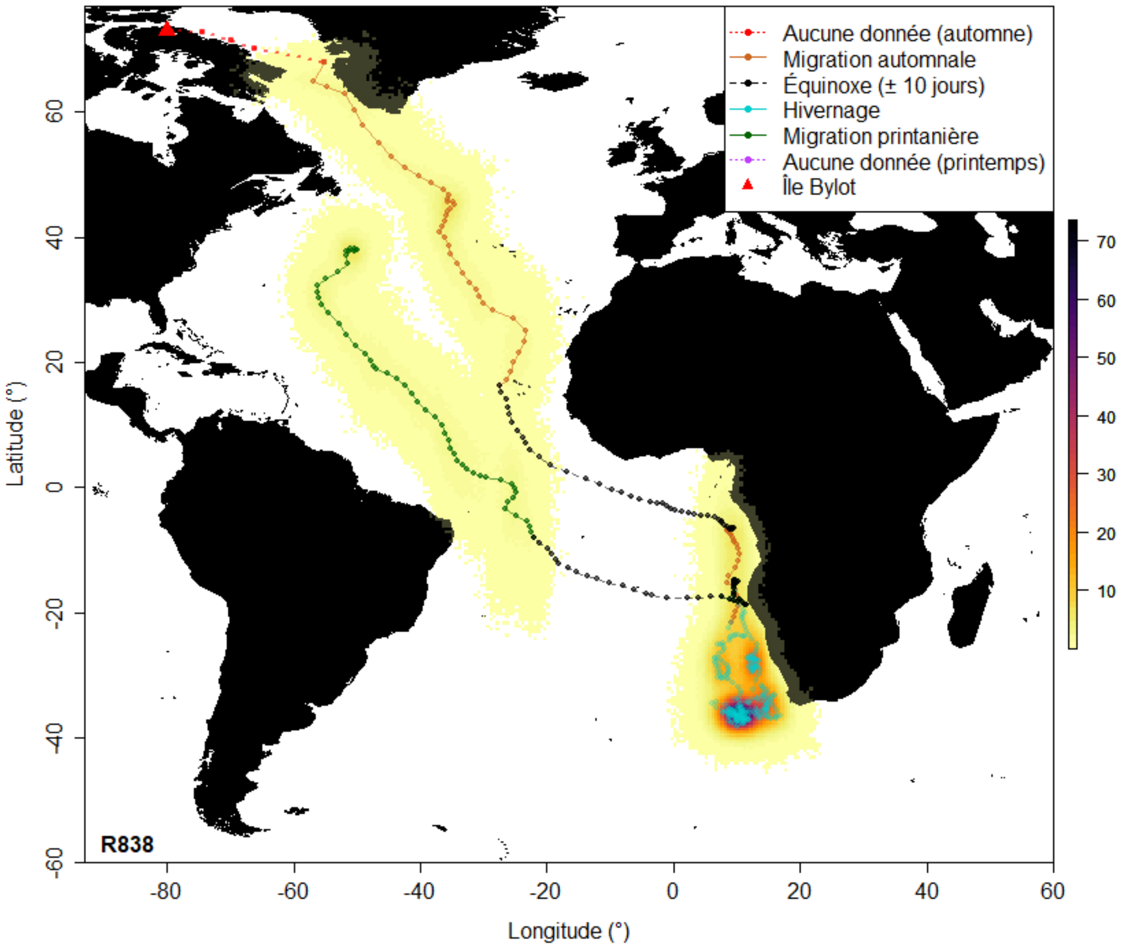


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	31 juil.	24 sept.	14	13 489	847	199
Halte automnale	16 août	15 septé	29	6 976	238	188
Hivernage	24 sept.	n.d.	≥ 85	≥ 12 602	148	281
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	16 juin	-	non	2	0944-02816
Année 2	non	-	-	-	-	-

Géolocalisateur	R838	**Sexe**	Femelle
Bague de métal	0944-02564	**Site**	Bylot
Marqueur auxiliaire	33 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
4 juillet 2015	27 juin 2016	25 avril 2016	490

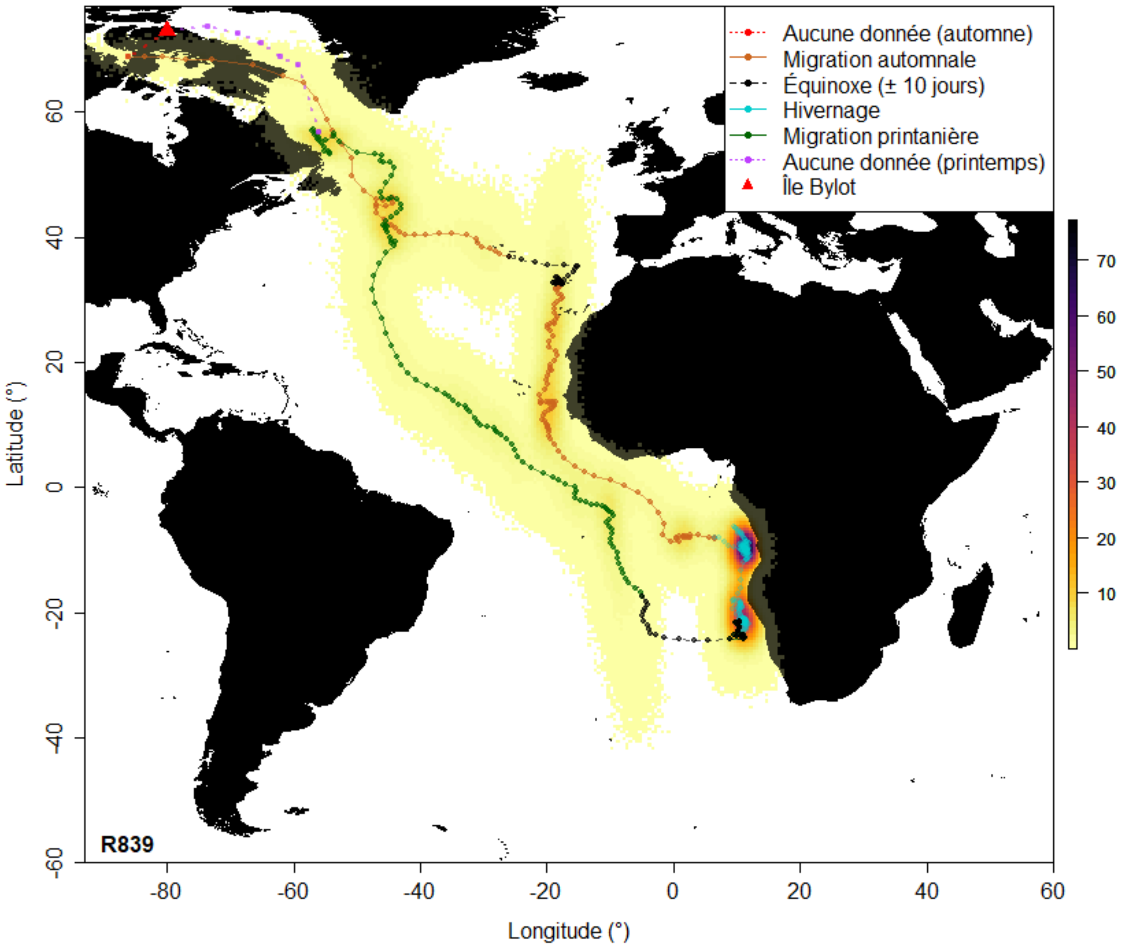


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	20 août	15 oct.	47	13 905	271	244
Halte automnale	29 août	6 sept.	7	1 289	174	290
Hivernage	15 oct.	20 mars	157	17 518	111	387
Migration printanière	20 mars	n.d.	36	≥10 733	302	260
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	19 juin	13 juil.	probable	2	0944-02565
Année 2	oui	11 juin	-	non	2	0944-02565

Géolocalisateur	R839	**Sexe**	Mâle
Bague de métal	0944-02565	**Site**	Bylot
Marqueur auxiliaire	34 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
4 juillet 2015	27 juin 2016	-	561

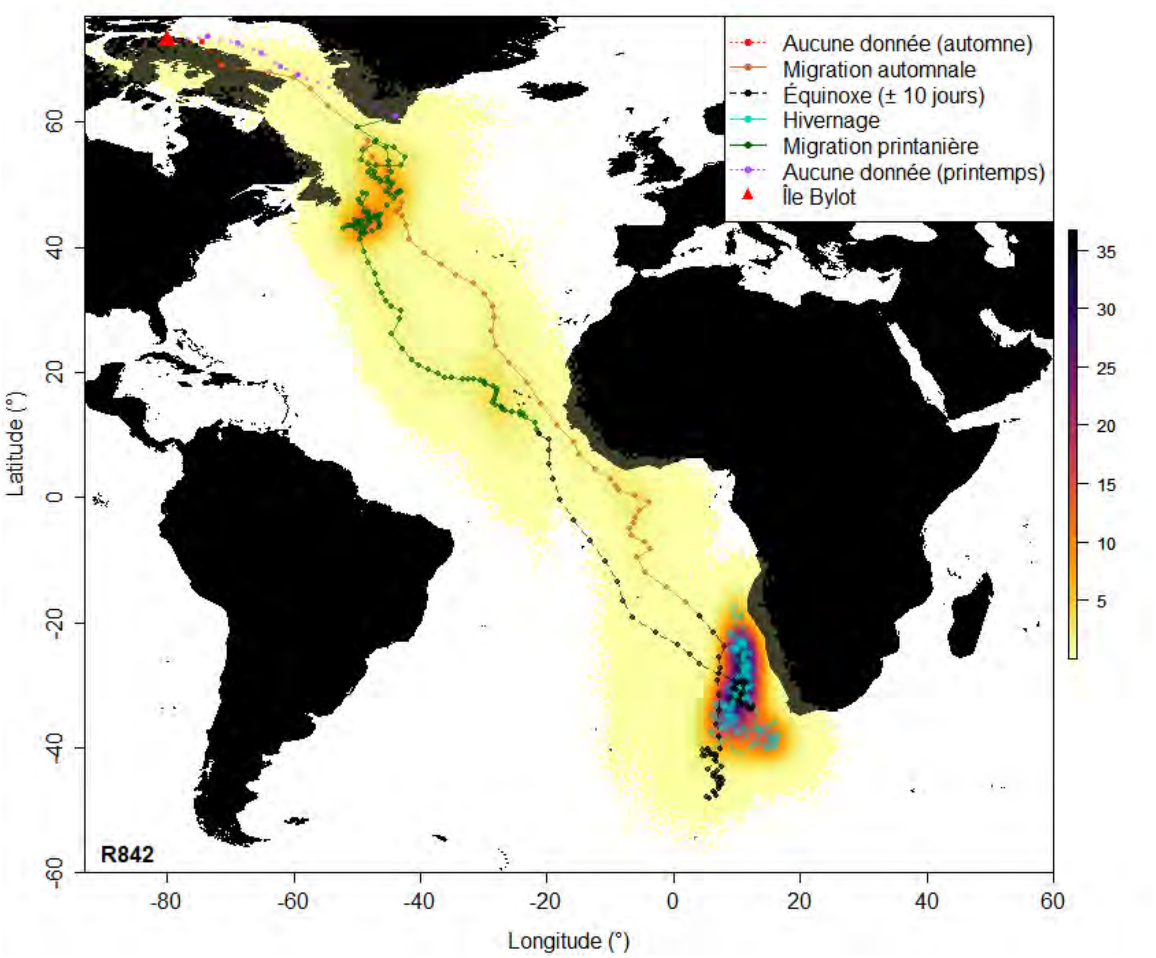


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	20 août	20 nov.	84	15 455	178	267
Halte automnale	29 août	6 sept.	7	1 489	202	169
Hivernage	20 nov.	22 mars	123	9 666	78	387
Migration printanière	22 mars	10 juin	59	15 277	218	346
Halte printanière	19 mai	28 mai	8	1 341	163	477
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	19 juin	13 juil.	probable	2	0944-02564
Année 2	oui	11 juin	-	non	2	0944-02564

Géolocalisateur	R842	**Sexe**	Femelle
Bague de métal	0944-02844	**Site**	Bylot
Marqueur auxiliaire	37 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
7 juillet 2015	6 juillet 2016	-	573

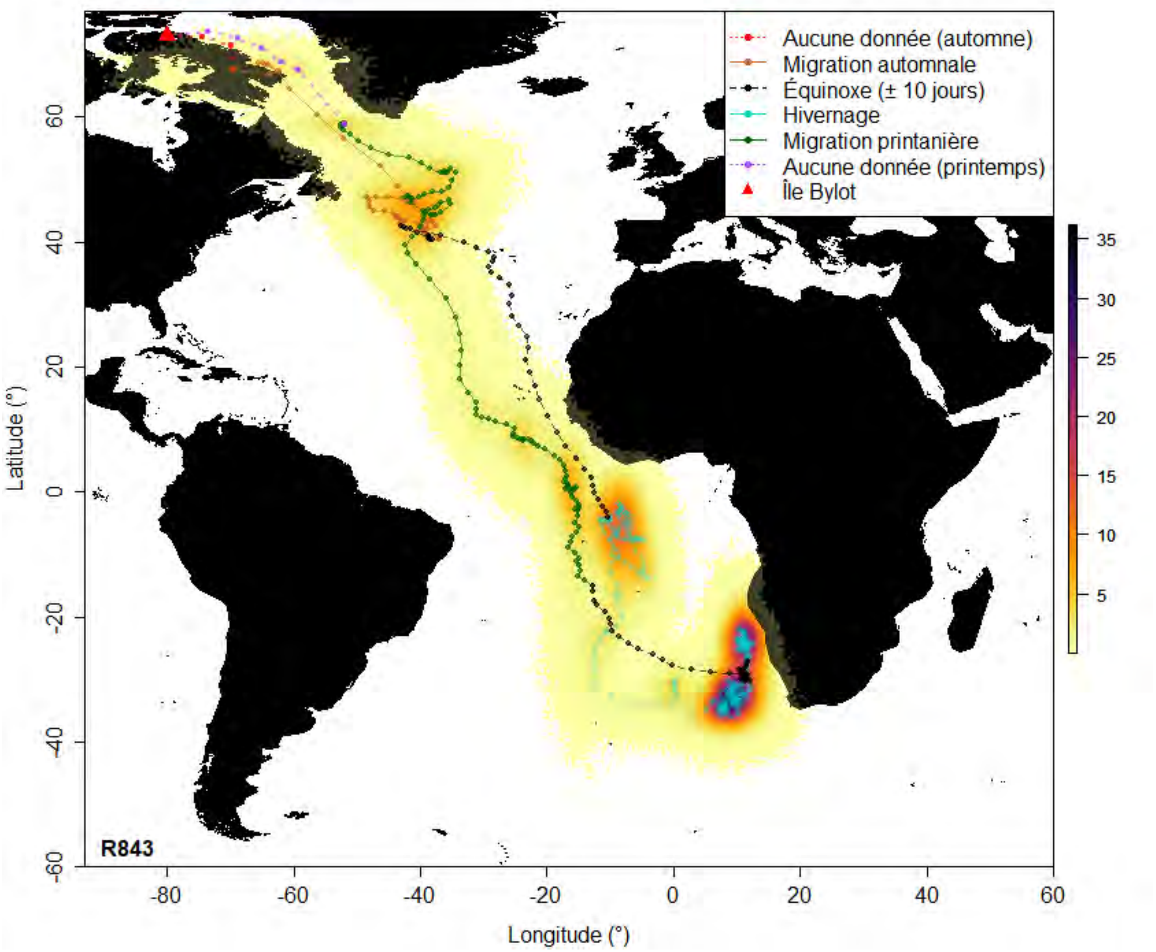


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	11 août	12 sept.	25	13 351	509	158
Halte automnale	-	-	0	-	-	-
Hivernage	12 sept.	20 mars	190	28 261	148	356
Migration printanière	20 mars	6 juin	68	21 330	281	275
Halte printanière	13 mai	16 mai	3	510	172	275
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	20 juin	14 juil.	oui	2	0944-02843
Année 2	non	-	-	-	-	-

Géolocalisateur	R843	**Sexe**	Mâle
Bague de métal	0944-02845	**Site**	Bylot
Marqueur auxiliaire	38 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
7 juillet 2015	27 juin 2018	14 décembre 2016	567

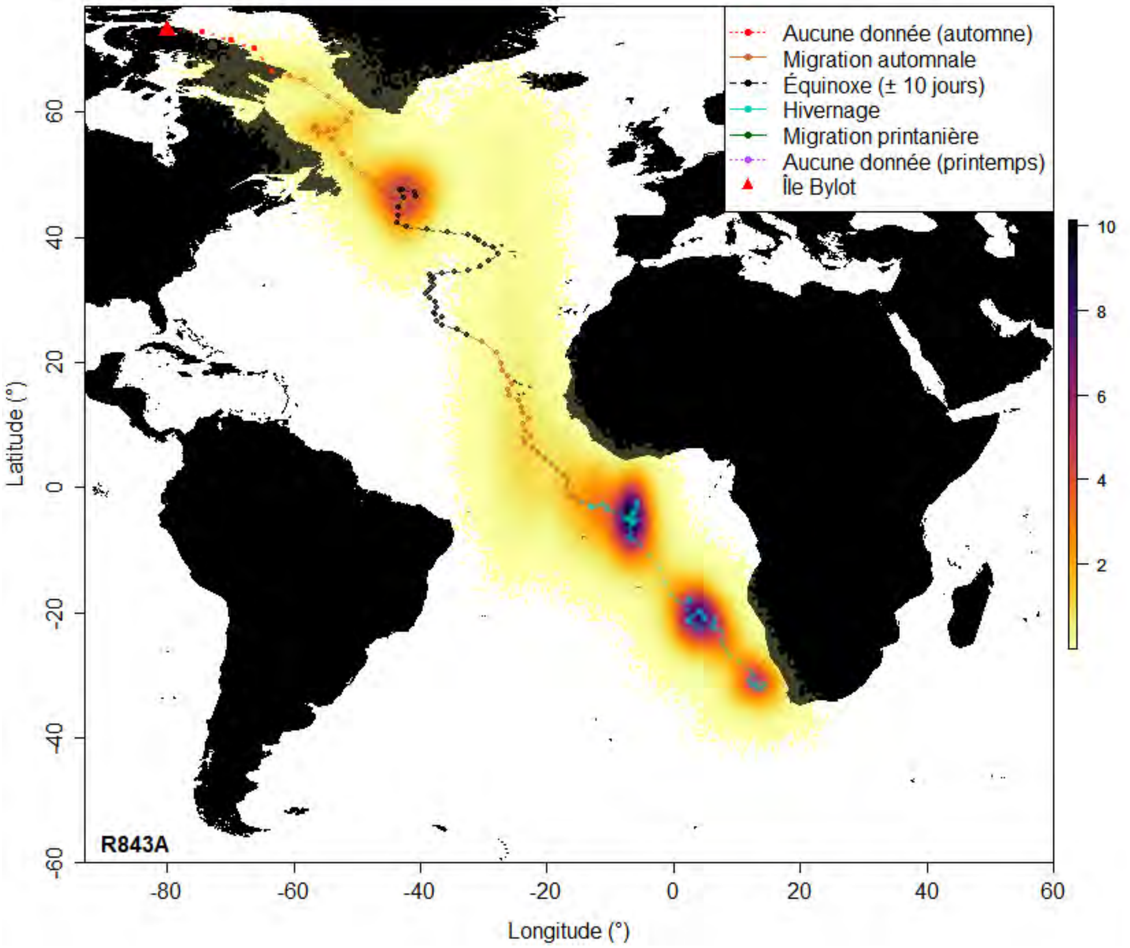


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	12 août	30 sept.	20	9 917	458	119
Halte automnale	25 août	17 sept.	22	3 732	167	186
Hivernage	30 sept.	22 mars	174	24 022	138	349
Migration printanière	22 mars	30 mai	55	15 418	243	251
Halte printanière	8 mai	21 mai	13	2 241	173	275
Site d'hivernage	Benguela, Guinée					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	22 juin	16 juil.	probable	2	0944-02846
Année 2	non	-	-	-	-	-

Géolocalisateur	R843A	**Sexe**	Mâle
Bague de métal	0944-02845	**Site**	Bylot
Marqueur auxiliaire	38 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
7 juillet 2015	27 juin 2018	14 décembre 2016	233

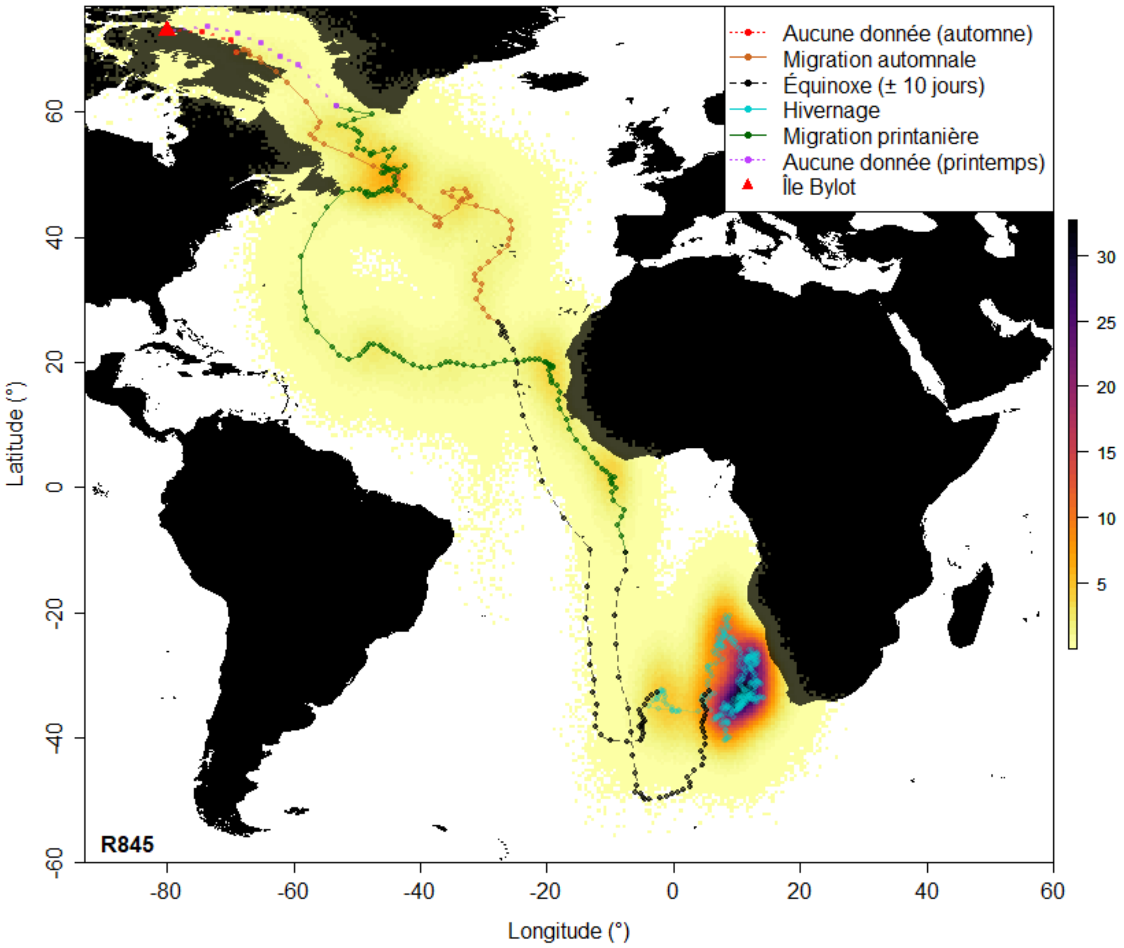


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	11 août	16 oct.	37	12 076	292	231
Halte automnale	26 août	16 sept.	20	4 498	221	204
Hivernage	16 oct.	n.d.	≥ 59	≥ 8 704	148	300
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela, Guinée					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	non	-	-	-	-	-
Année 2	non	-	-	-	-	-

Géolocalisateur	R845	**Sexe**	Mâle
Bague de métal	0944-02847	**Site**	Bylot
Marqueur auxiliaire	40 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
8 juillet 2015	27 juin 2016	-	575

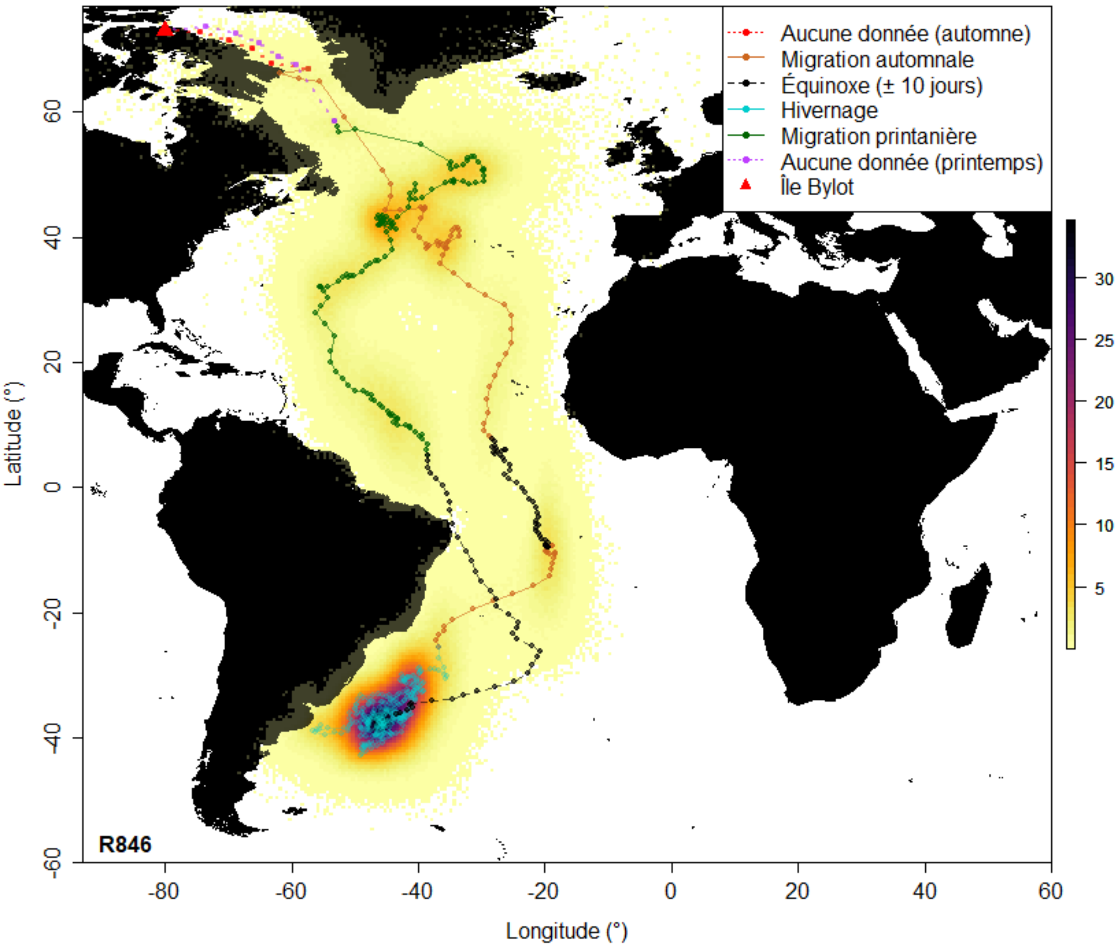


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	16 août	25 sept.	27	13 165	457	227
Halte automnale	28 août	11 sept.	13	3 546	264	163
Hivernage	25 sept.	17 mars	175	22 620	130	364
Migration printanière	17 mars	1 juin	65	20 600	288	254
Halte printanière	11 mai	18 mai	8	1 220	159	305
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	21 juin	15 juil.	oui	2	0944-02848
Année 2	oui	13 juin	-	non	3	0944-02848

Géolocalisateur	R846	**Sexe**	Femelle
Bague de métal	0944-02848	**Site**	Bylot
Marqueur auxiliaire	41 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
8 juillet 2015	27 juin 2016	-	568



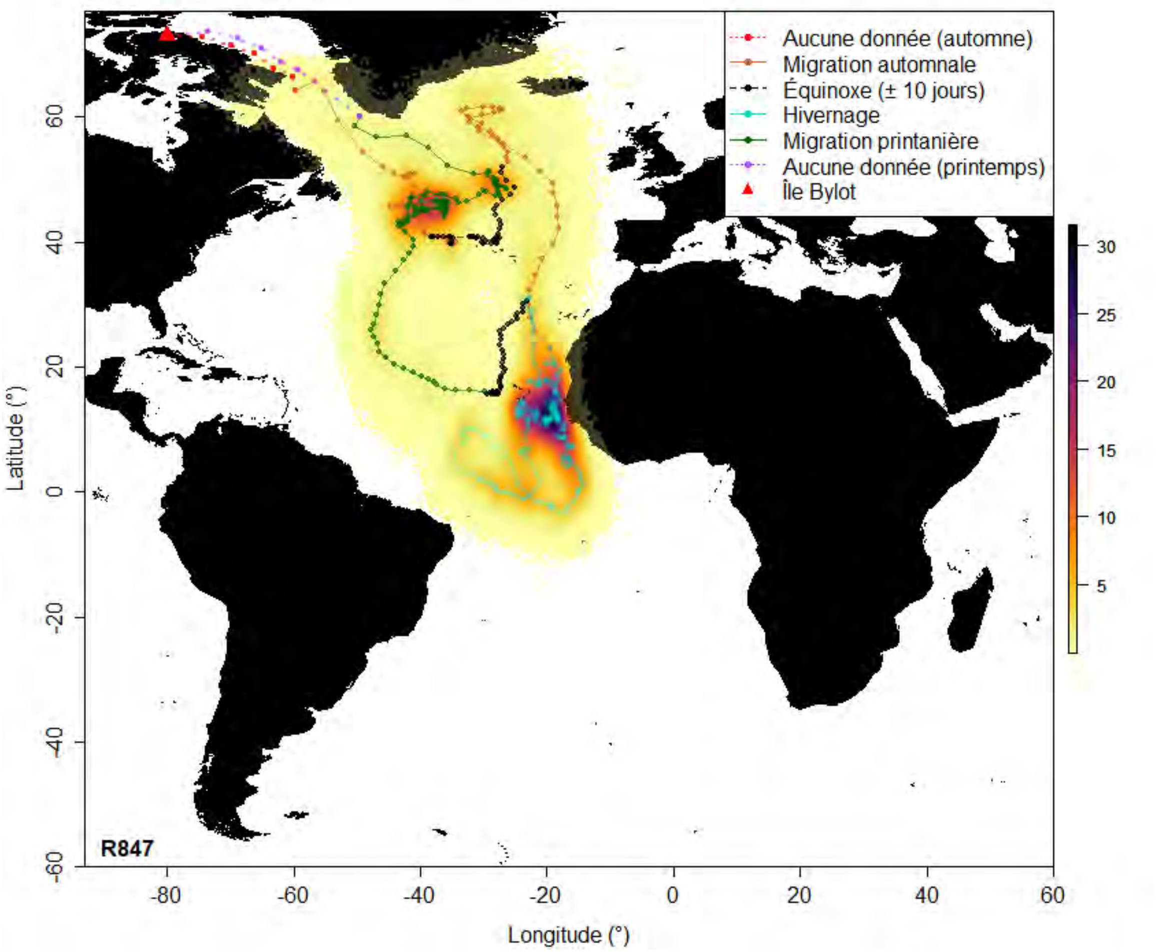
	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	8 août	16 oct.	55	16 076	270	182
Halte automnale	27 août	4 sept.	7	1 127	152	206
Hivernage	16 oct.	12 mars	148	23 781	160	370
Migration printanière	12 mars	30 mai	53	16 793	275	238
Halte printanière	29 avril	23 mai	24	4 039	169	325

Site d'hivernage Brésil

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	21 juin	15 juil.	oui	2	0944-02847
Année 2	oui	13 juin	-	non	3	0944-02847

Géolocalisateur	R847	**Sexe**	Femelle
Bague de métal	0944-02849	**Site**	Bylot
Marqueur auxiliaire	42 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
8 juillet 2015	5 juillet 2016	-	548

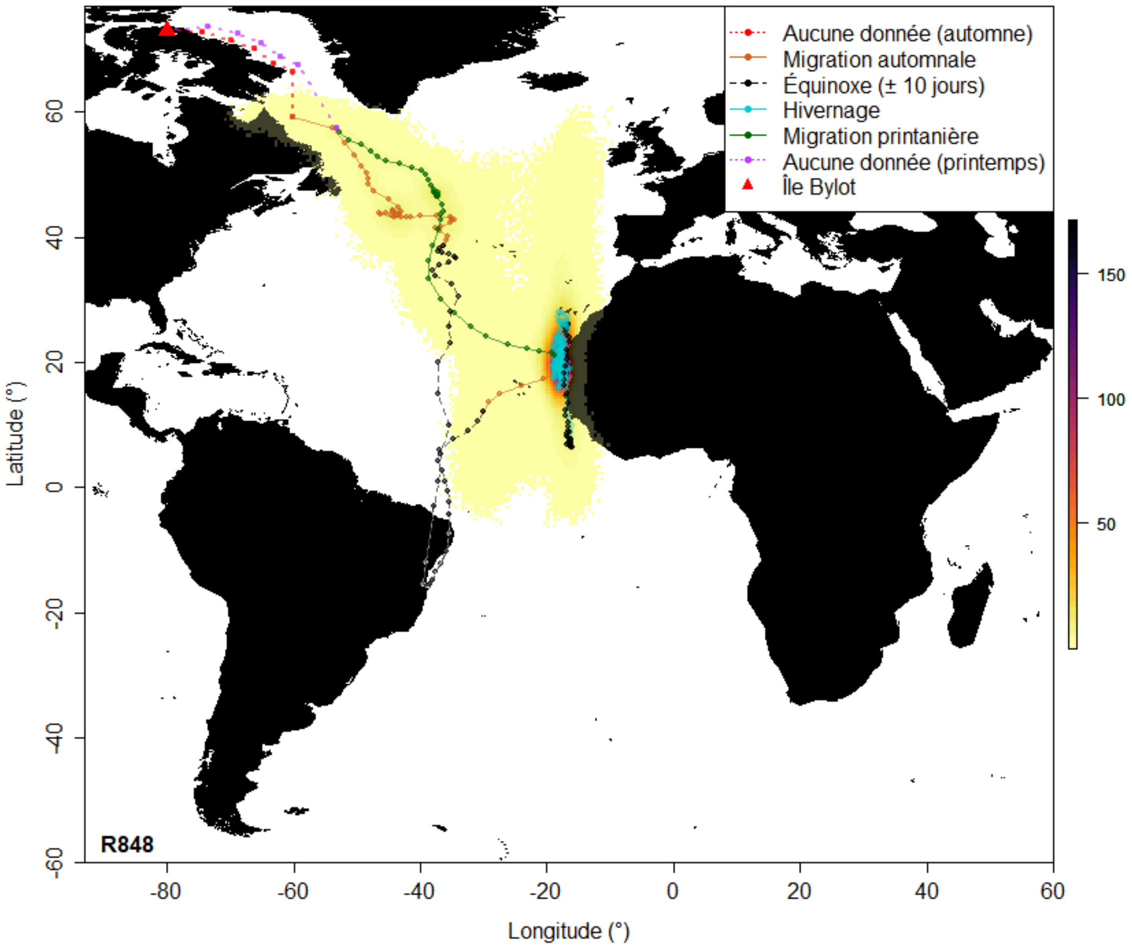


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	10 août	23 oct.	17	8 684	428	106
Halte automnale	31 août	15 oct.	44	7 671	173	173
Hivernage	23 oct.	30 mars	159	21 177	133	326
Migration printanière	30 mars	13 juin	36	11 754	267	256
Halte printanière	18 mars	7 mai	20	3 165	161	303
Site d'hivernage	Canaries					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	24 juin	n.d.	n.d.	2	0944-02850
Année 2	oui	26 juin	n.d.	n.d.	2	0944-02850

Géolocalisateur	R848	**Sexe**	Mâle
Bague de métal	0944-02850	**Site**	Bylot
Marqueur auxiliaire	43 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
8 juillet 2015	5 juillet 2016	-	565

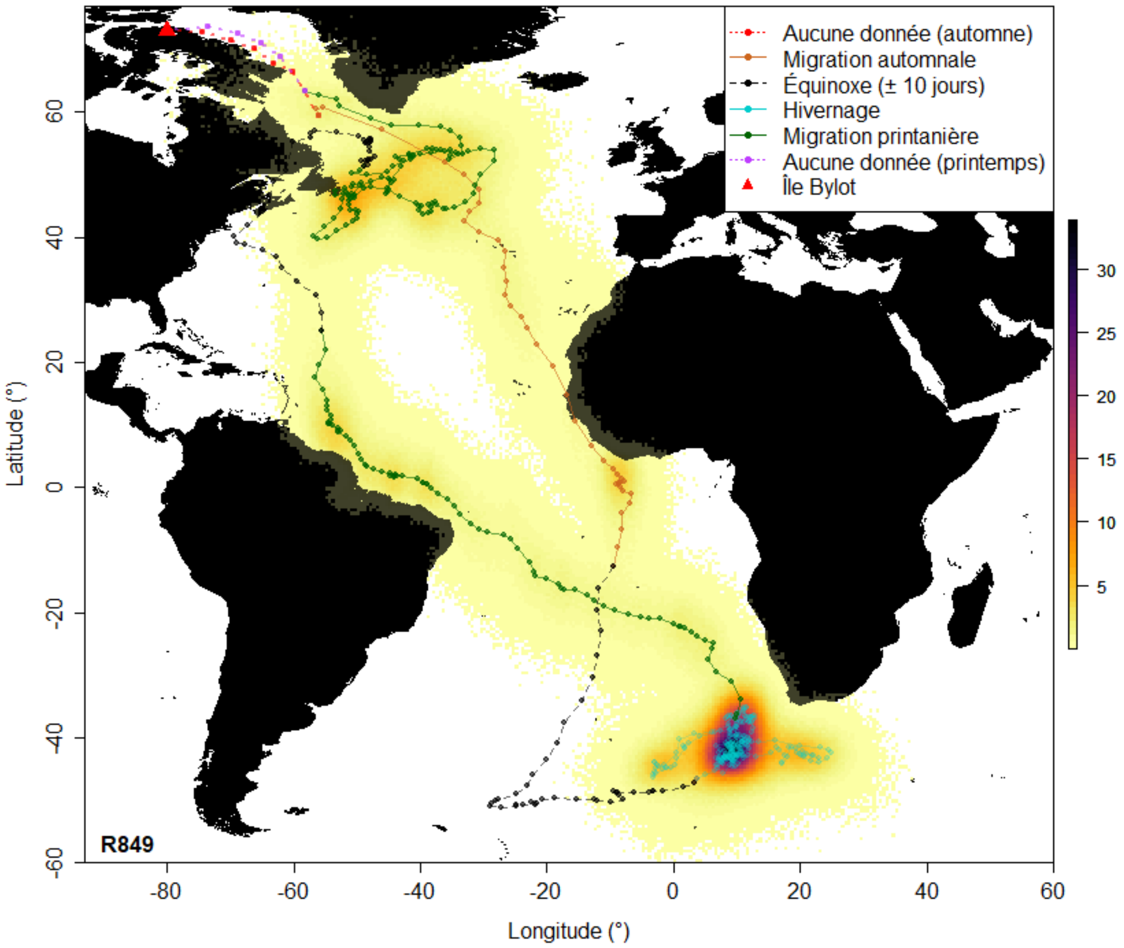


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	14 août	7 oct.	28	14 208	433	136
Halte automnale	30 août	15 sept.	17	2 427	147	185
Hivernage	7 oct.	13 mai	220	19 196	87	384
Migration printanière	13 mai	5 juin	19	8 049	311	251
Halte printanière	-	-	0	-	-	-
Site d'hivernage	Canaries					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	24 juin	n.d.	n.d.	2	0944-02849
Année 2	oui	26 juin	n.d.	n.d.	2	0944-02849

Géolocalisateur	R849	**Sexe**	Femelle
Bague de métal	0944-02851	**Site**	Bylot
Marqueur auxiliaire	44 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
8 juillet 2015	5 juillet 2016	-	547

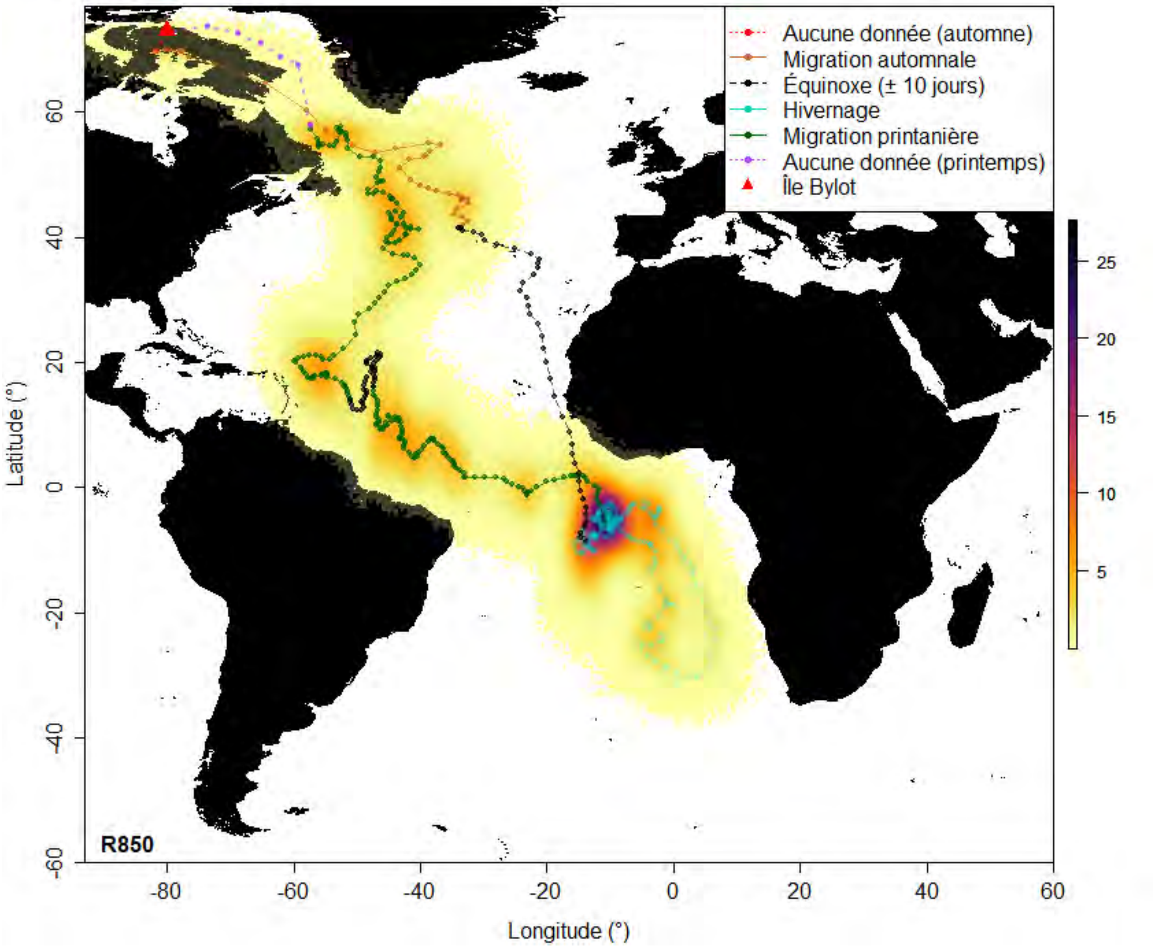


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	12 août	4 oct.	42	19 681	426	166
Halte automnale	-	-	0	-	-	-
Hivernage	4 oct.	30 jan.	119	18 746	158	343
Migration printanière	30 jan.	2 juin	62	21 209	319	301
Halte printanière	20 mars	11 mai	53	10 482	199	292
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	24 juin	n.d.	n.d.	2	0944-02852
Année 2	oui	n.d.	-	non	2	n.d.

Géolocalisateur	R850	**Sexe**	Femelle
Bague de métal	0944-02853	**Site**	Bylot
Marqueur auxiliaire	30 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
9 juillet 2015	9 juillet 2016	-	560

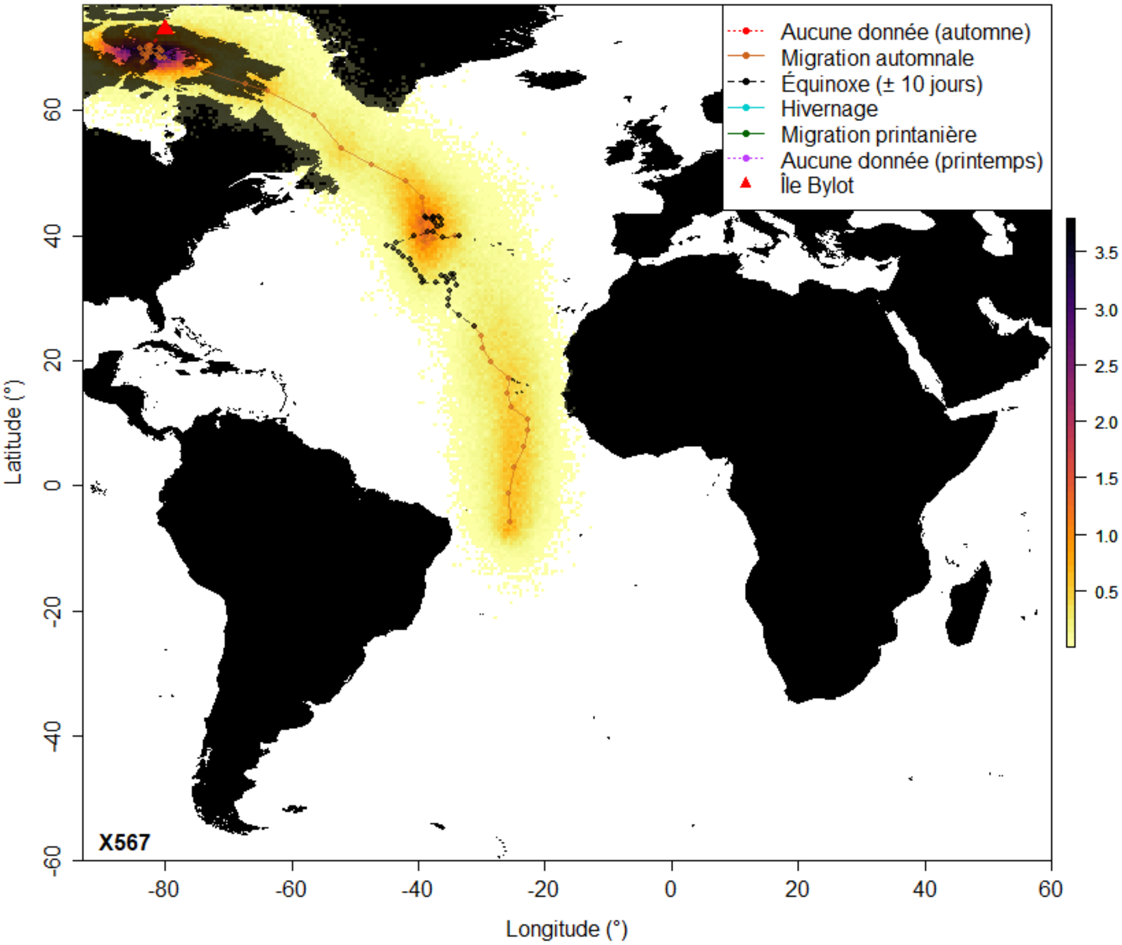


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	22 août	30 sept.	32	11 404	349	169
Halte automnale	8 sept.	14 sept.	5	863	159	153
Hivernage	30 sept.	17 jan.	109	17 403	160	255
Migration printanière	17 jan.	7 juin	102	16 219	139	421
Halte printanière	25 avril	28 mai	33	6 161	187	431
Site d'hivernage	Guinée					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	24 juin	n.d.	n.d.	2	n.d.
Année 2	oui	1 juil.	n.d.	n.d.	2	0944-02871

Géolocalisateur	X567	**Sexe**	Mâle
Bague de métal	0944-02570	**Site**	Bylot
Marqueur auxiliaire	47 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
20 juin 2016	19 juin 2017	9 octobre 2016	83



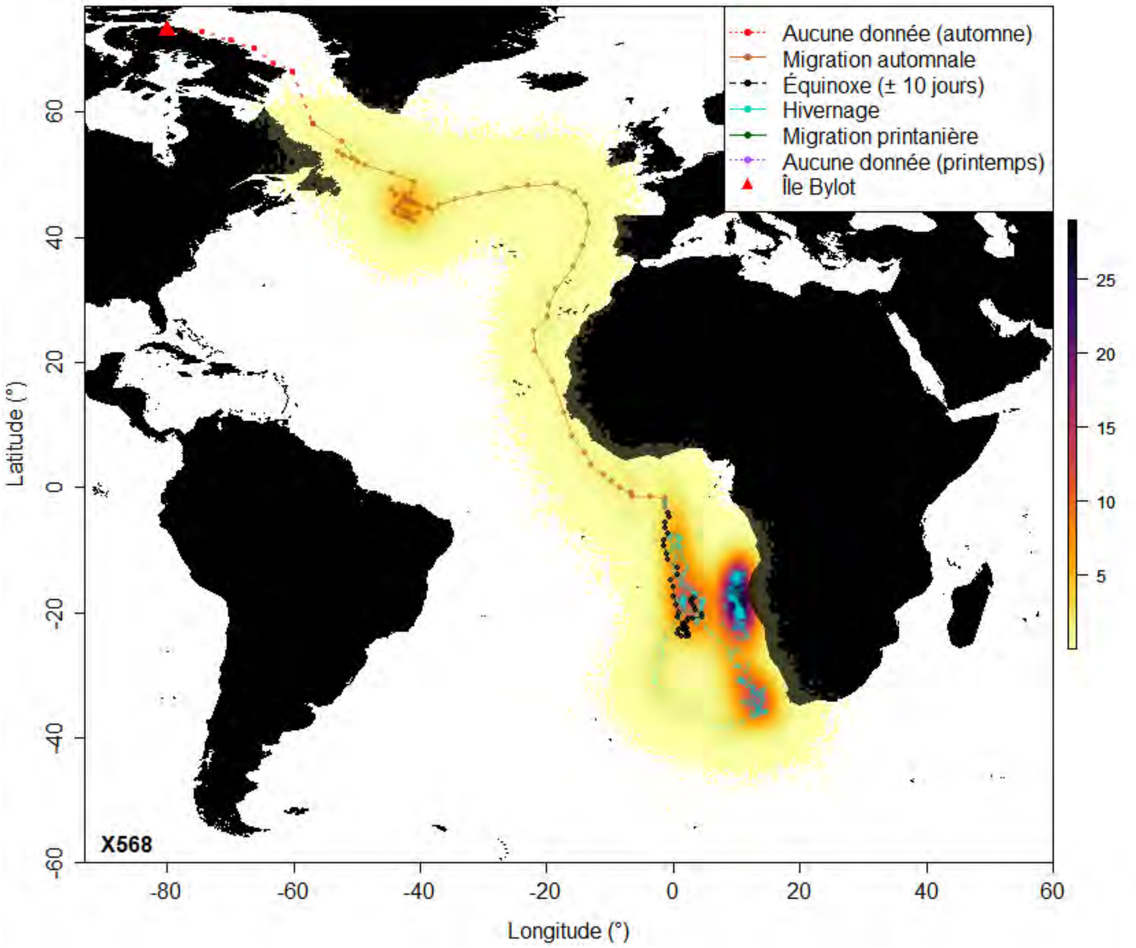
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	27 août	n.d.	20	9 362	441	149
Halte automnale	7 sept.	29 sept.	≥ 22	≥ 5 302	242	180
Hivernage	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage n.d.

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	18 juin	-	non	1	0944-02563
Année 2	non	-	-	-	-	-

Géolocalisateur	X568	**Sexe**	Femelle
Bague de métal	0944-02585	**Site**	Bylot
Marqueur auxiliaire	48 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
23 juin 2016	24 juin 2017	5 mars 2017	389

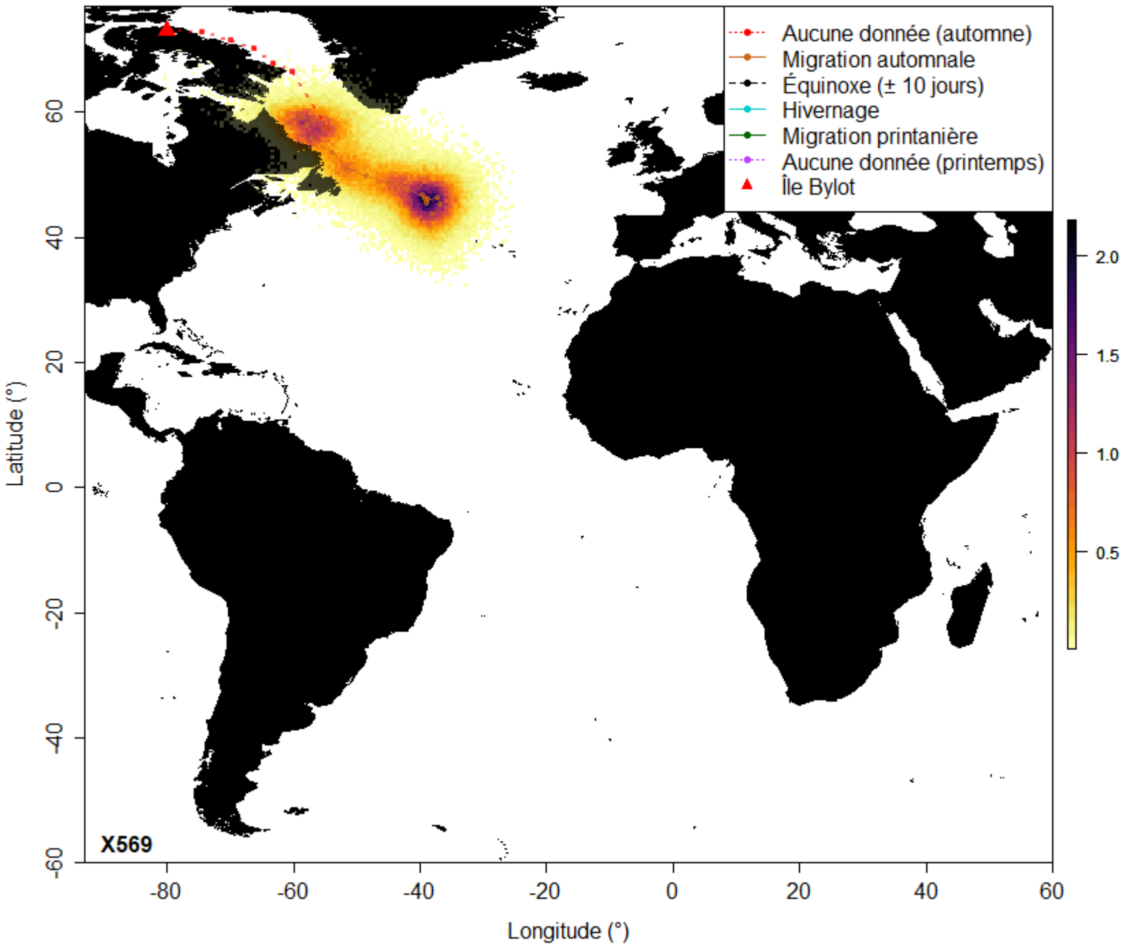


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	31 juil.	10 sept.	25	14 372	487	146
Halte automnale	14 août	22 août	7	1 406	191	140
Hivernage	10 sept.	n.d.	≥ 162	≥ 26 940	166	327
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d’hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	16 juin	-	non	2	0944-02559
Année 2	non	-	-	-	-	-

Géolocalisateur	X569	**Sexe**	Femelle
Bague de métal	0944-02857	**Site**	Bylot
Marqueur auxiliaire	49 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
24 juin 2016	22 juin 2019	19 août 2016	17

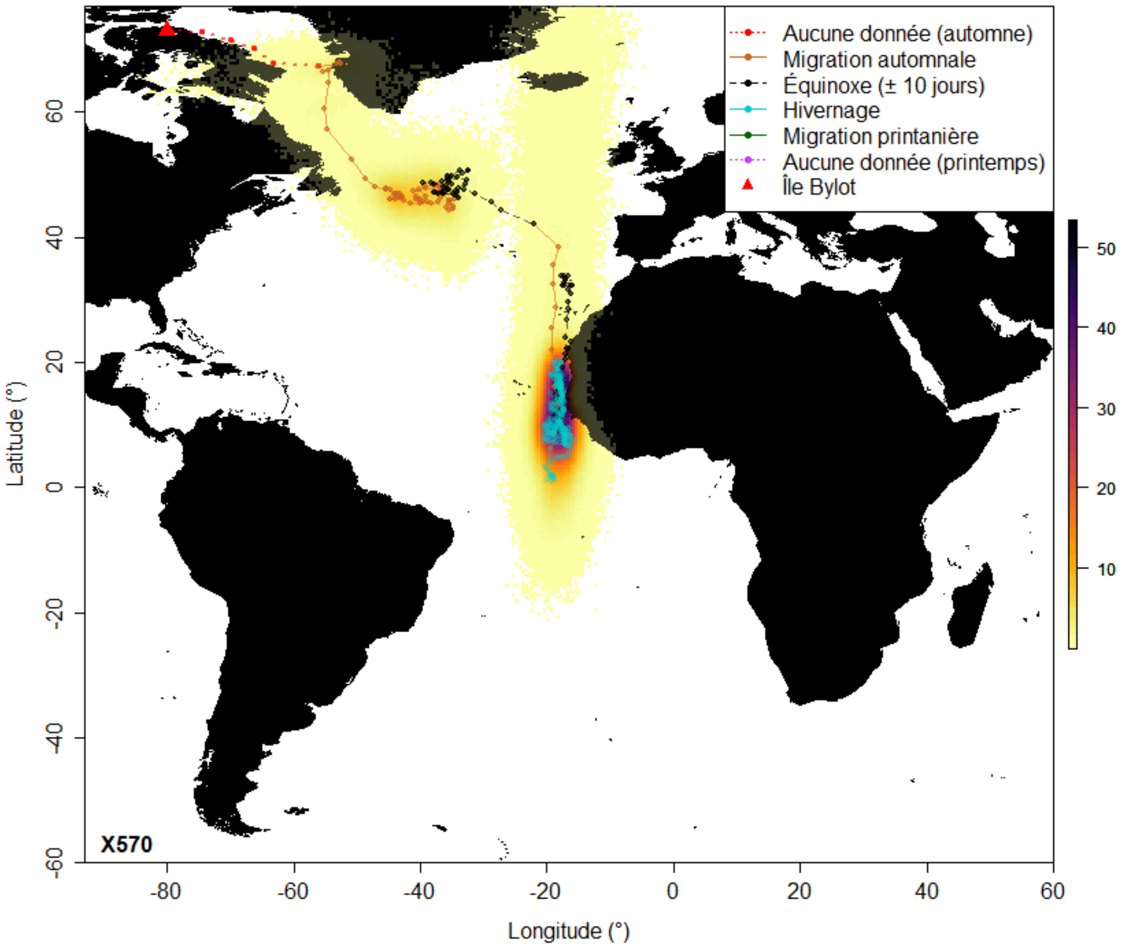


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	25 juil.	n.d.	≥ 5	≥ 4 384	426	134
Halte automnale	14 août	18 août	≥ 3	≥ 760	229	128
Hivernage	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	n.d.					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	15 juin	-	non	2	0944-02822
Année 2	non	-	-	-	-	-

Géolocalisateur	X570	**Sexe**	Mâle
Bague de métal	0944-02859	**Site**	Bylot
Marqueur auxiliaire	50 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
30 juin 2016	21 juin 2017	22 mars 2017	443



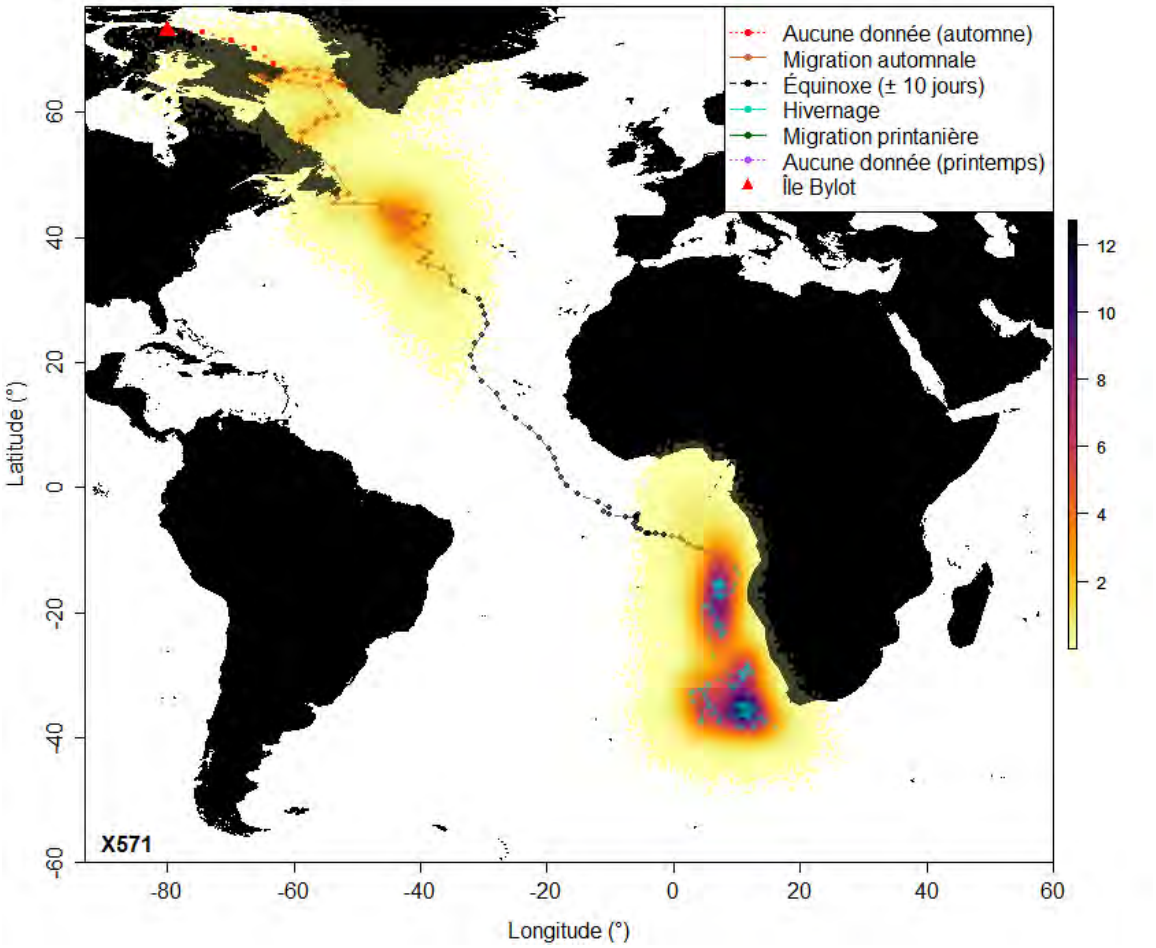
	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	6 août	7 oct.	32	12 024	338	131
Halte automnale	18 août	14 sept.	26	4 495	170	165
Hivernage	7 oct.	n.d.	≥ 164	≥ 21 721	132	354
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage Canaries

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	17 juin	-	non	2	0944-02860
Année 2	non	-	-	-	-	-

Géolocalisateur	X571	**Sexe**	Femelle
Bague de métal	0944-02860	**Site**	Bylot
Marqueur auxiliaire	51 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
30 juin 2016	21 juin 2017	18 décembre 2016	248

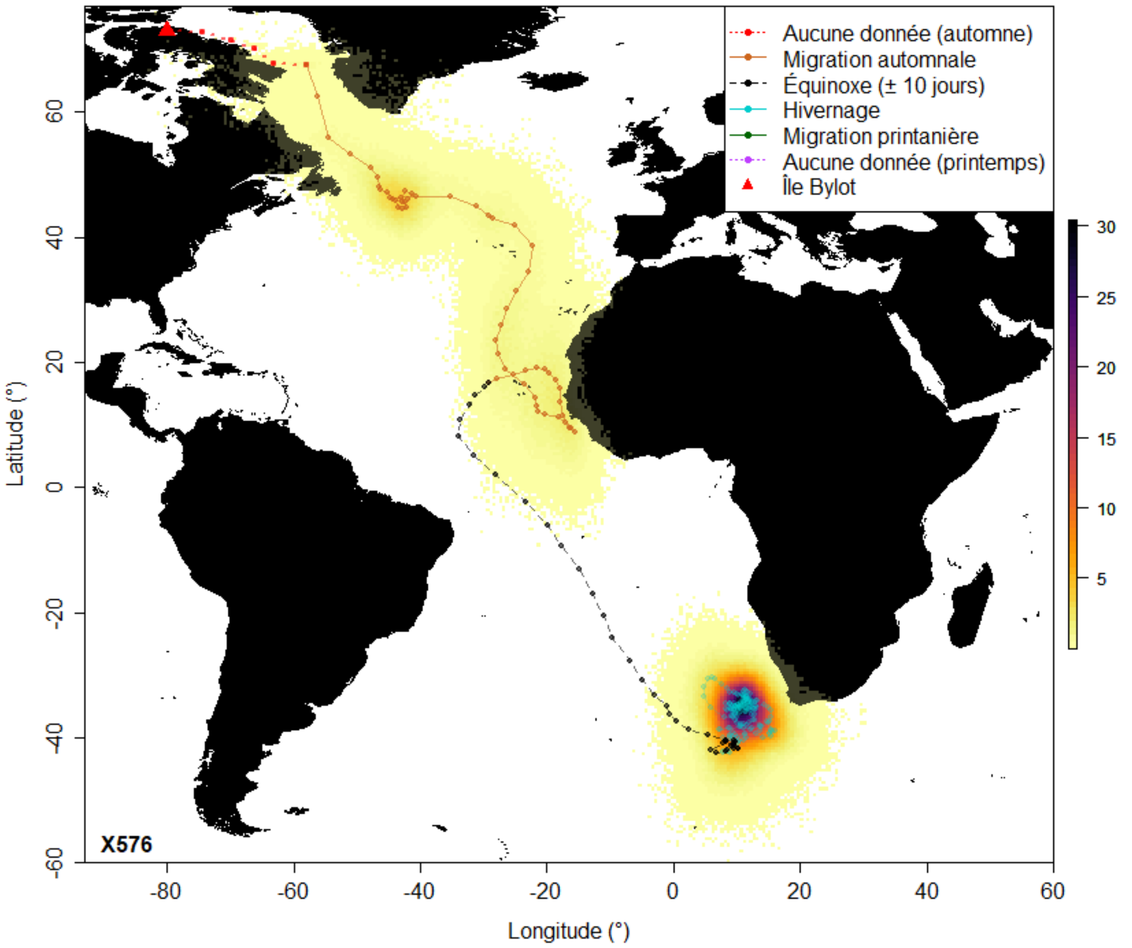


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	2 août	8 oct.	42	15 159	320	164
Halte automnale	28 août	9 sept.	11	2 669	235	186
Hivernage	8 oct.	n.d.	≥ 71	≥ 14 053	198	296
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	17 juin	-	non	2	0944-02859
Année 2	non	-	-	-	-	-

Géolocalisateur	X576	**Sexe**	Femelle
Bague de métal	0944-02864	**Site**	Bylot
Marqueur auxiliaire	57 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
5 juillet 2016	25 juin 2018	23 décembre 2016	259

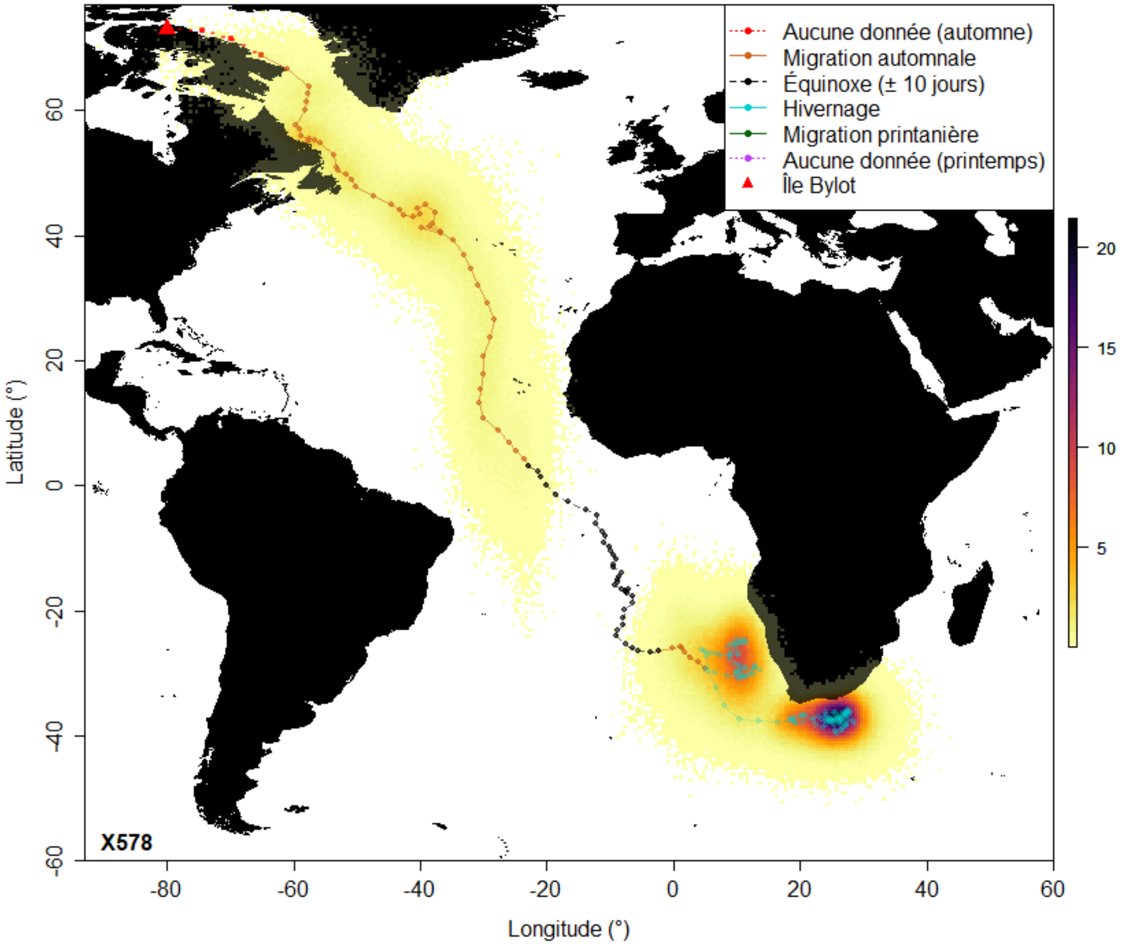


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	11 août	23 sept.	33	19 793	558	137
Halte automnale	19 août	25 août	5	1 014	189	209
Hivernage	23 sept.	n.d.	≥ 91	≥ 13 921	153	328
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	20 juin	n.d.	n.d.	2	0944-02863
Année 2	non	-	-	-	-	-

Géolocalisateur	X578	**Sexe**	Mâle
Bague de métal	0944-02866	**Site**	Bylot
Marqueur auxiliaire	59 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
6 juillet 2016	28 juin 2017	16 décembre 2016	239

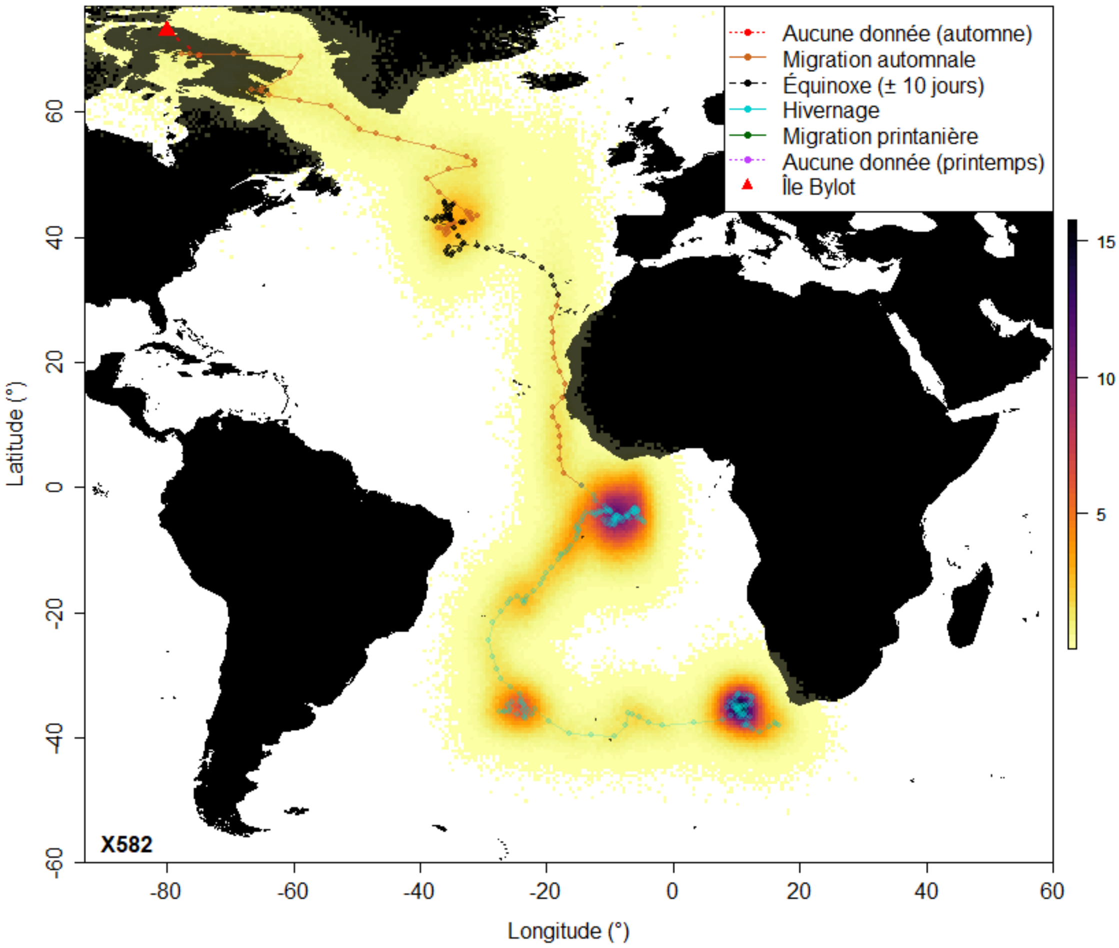


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	14 août	5 oct.	44	15 681	332	230
Halte automnale	30 août	3 sept.	3	817	240	209
Hivernage	5 oct.	n.d.	≥ 72	≥ 11 693	163	312
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Aiguilles, Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	21 juin	n.d.	n.d.	2	0944-02865
Année 2	non	-	-	-	-	-

Géolocalisateur	X582	**Sexe**	Mâle
Bague de métal	0944-02870	**Site**	Bylot
Marqueur auxiliaire	64 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
8 juillet 2016	5 juillet 2019	14 janvier 2017	290



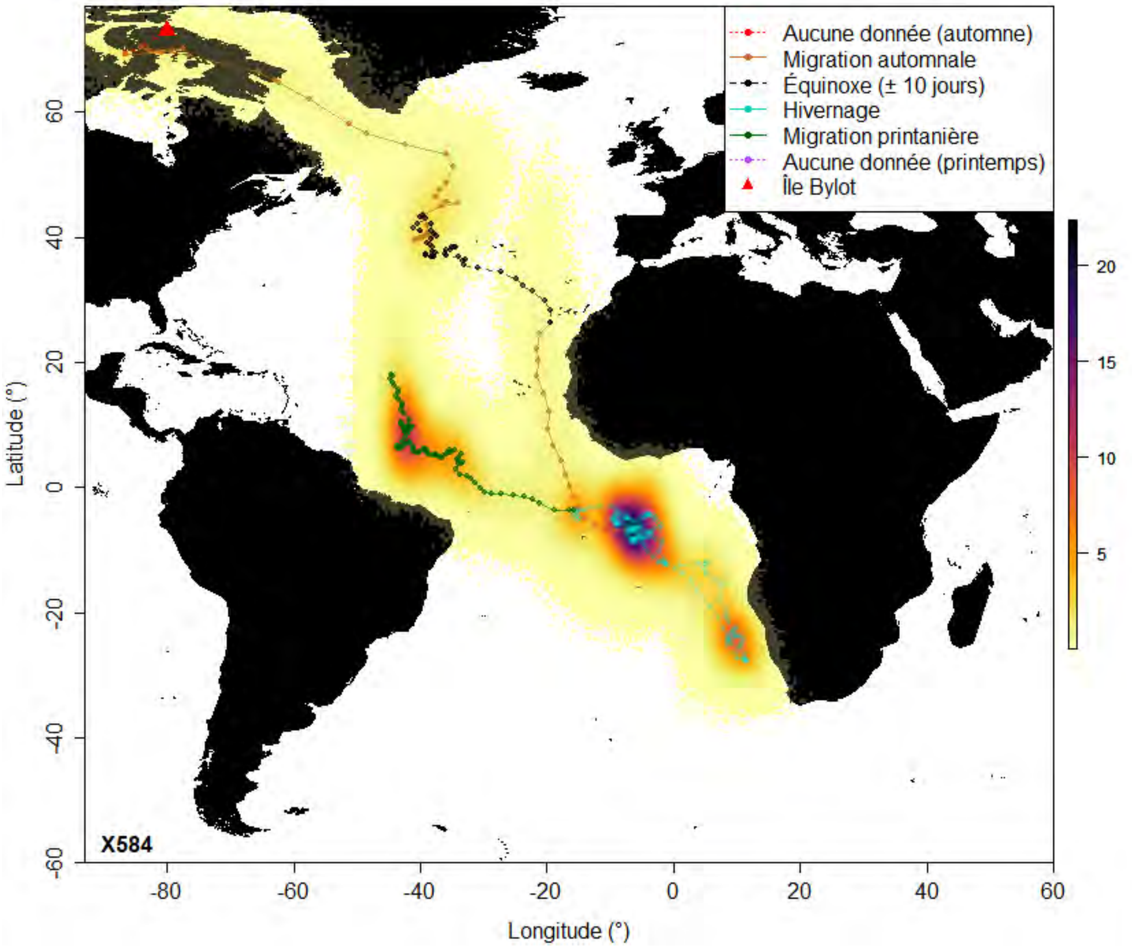
	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	17 août	9 oct.	40	14 077	337	170
Halte automnale	7 sept.	18 sept.	11	1 522	138	166
Hivernage	9 oct.	n.d.	≥ 96	≥ 17 985	187	255
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage Benguela, Guinée

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	18 juin	14 juil.	probable	1	0944-02869
Année 2	non	-	-	-	-	-

Géolocalisateur	X584	**Sexe**	Femelle
Bague de métal	0944-02853	**Site**	Bylot
Marqueur auxiliaire	30 (jaune-noir)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
10 juillet 2016	25 juin 2019	5 mars 2017	382

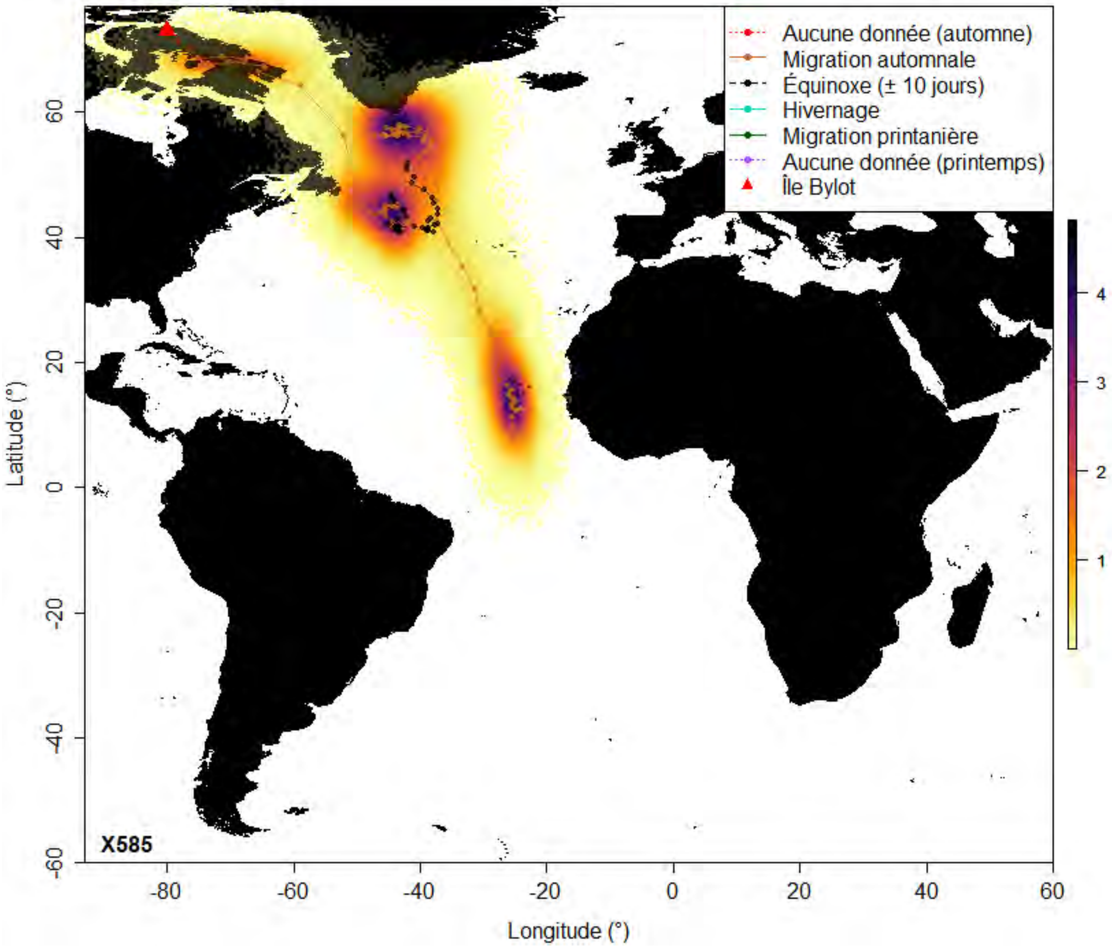


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	25 août	10 oct.	32	13 369	401	141
Halte automnale	7 sept.	22 sept.	15	2 296	153	154
Hivernage	10 oct.	14 jan.	96	15 000	155	246
Migration printanière	14 jan.	n.d.	≥ 50	≥ 6 571	133	397
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela, Guinée					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	1 juil.	n.d.	n.d.	2	0944-02871
Année 2	non	-	-	-	-	-

Géolocalisateur	X585	**Sexe**	Mâle
Bague de métal	0944-02856	**Site**	Bylot
Marqueur auxiliaire	67 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
10 juillet 2016	5 juillet 2017	7 novembre 2016	149



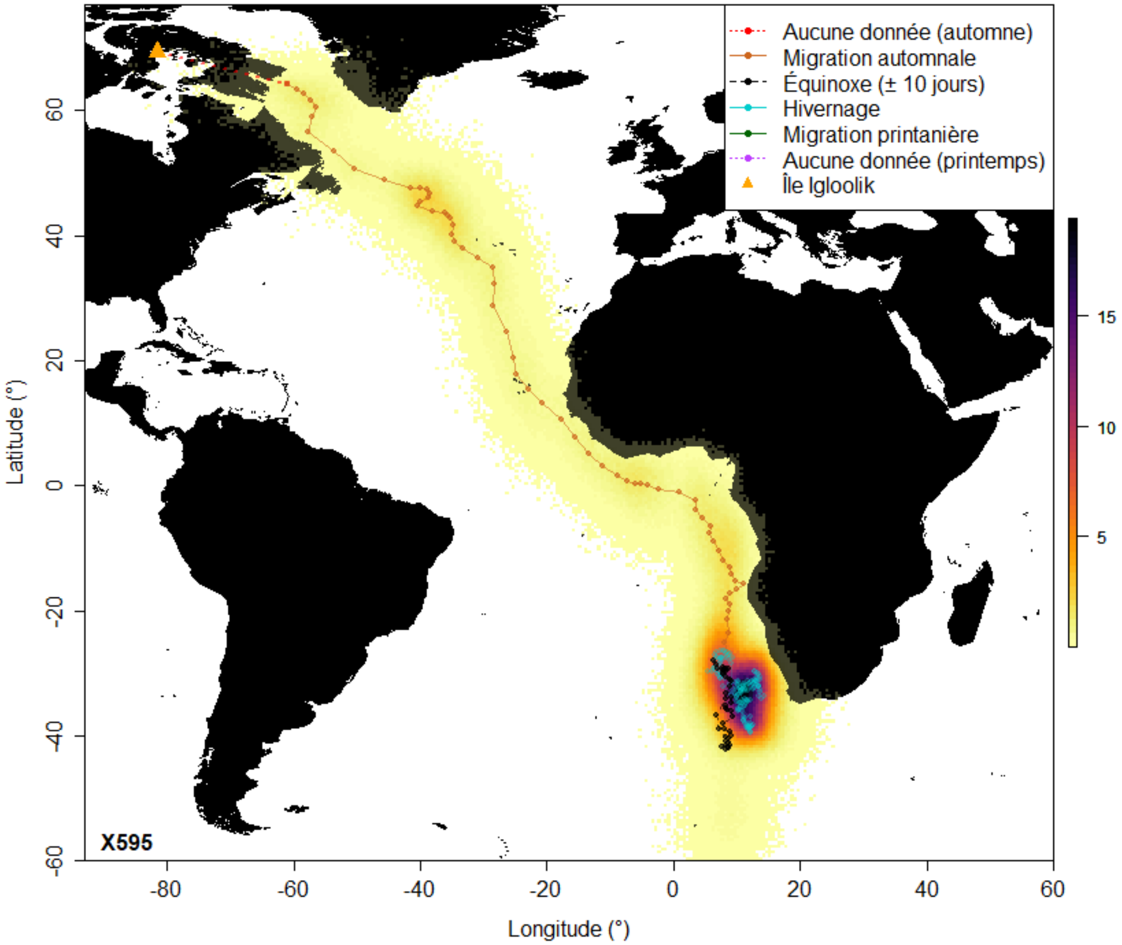
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	17 août	n.d.	≥ 58	≥ 16 362	274	235
Halte automnale	2 sept.	20 sept.	≥17	≥ 2 879	165	205
Hivernage	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage	n.d.

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	15 juin	9 juil.	oui	2	0944-02872
Année 2	non	-	-	-	-	-

Géolocalisateur	X595	**Sexe**	Femelle
Bague de métal	1034-06899	**Site**	Igloolik
Marqueur auxiliaire	12 (vert-blanc)		

Déploiement	**Récupération**	**Dernier enregistrement**	**Nombre de localisations**
8 juillet 2016	7 juillet 2017	11 décembre 2016	247

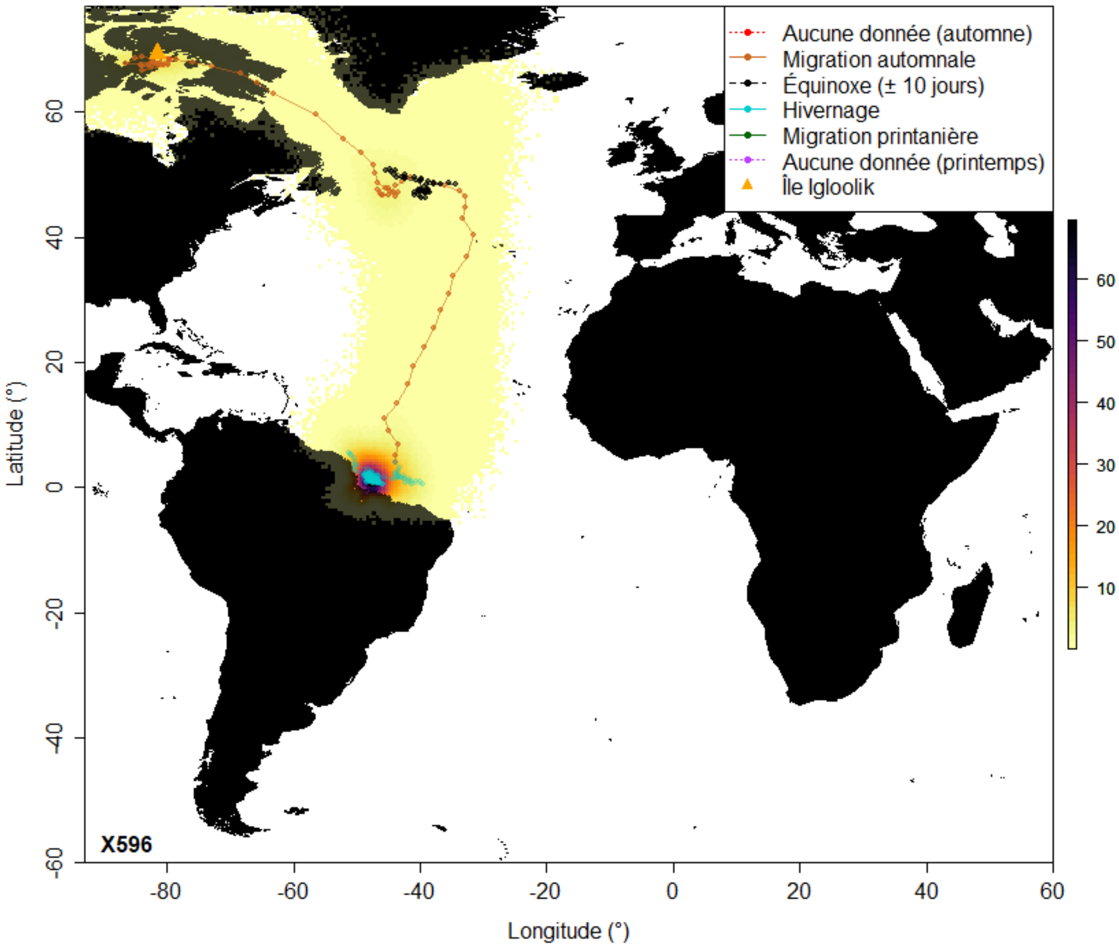


	Début	**Fin**	**Durée**	**Distance**	**Vitesse**	**Immersions**
Migration automnale	8 août	11 sept.	33	15 072	429	143
Halte automnale	-	-	0	-	-	-
Hivernage	11 sept.	n.d.	≥ 91	≥ 12 013	132	267
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Site d'hivernage	Benguela					

	Nicheur	**Initiation**	**Éclosion**	**Succès**	**Taille de ponte**	**Partenaire**
Année 1	oui	21 juin	15 juil.	probable	n.d.	n.d.
Année 2	oui	n.d.	n.d.	probable	2	1034-06802

Géolocalisateur	X596	**Sexe**	Mâle
Bague de métal	1034-06802	**Site**	Igloolik
Marqueur auxiliaire	13 (vert-blanc)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
8 juillet 2016	10 juillet 2017	5 janvier 2017	274



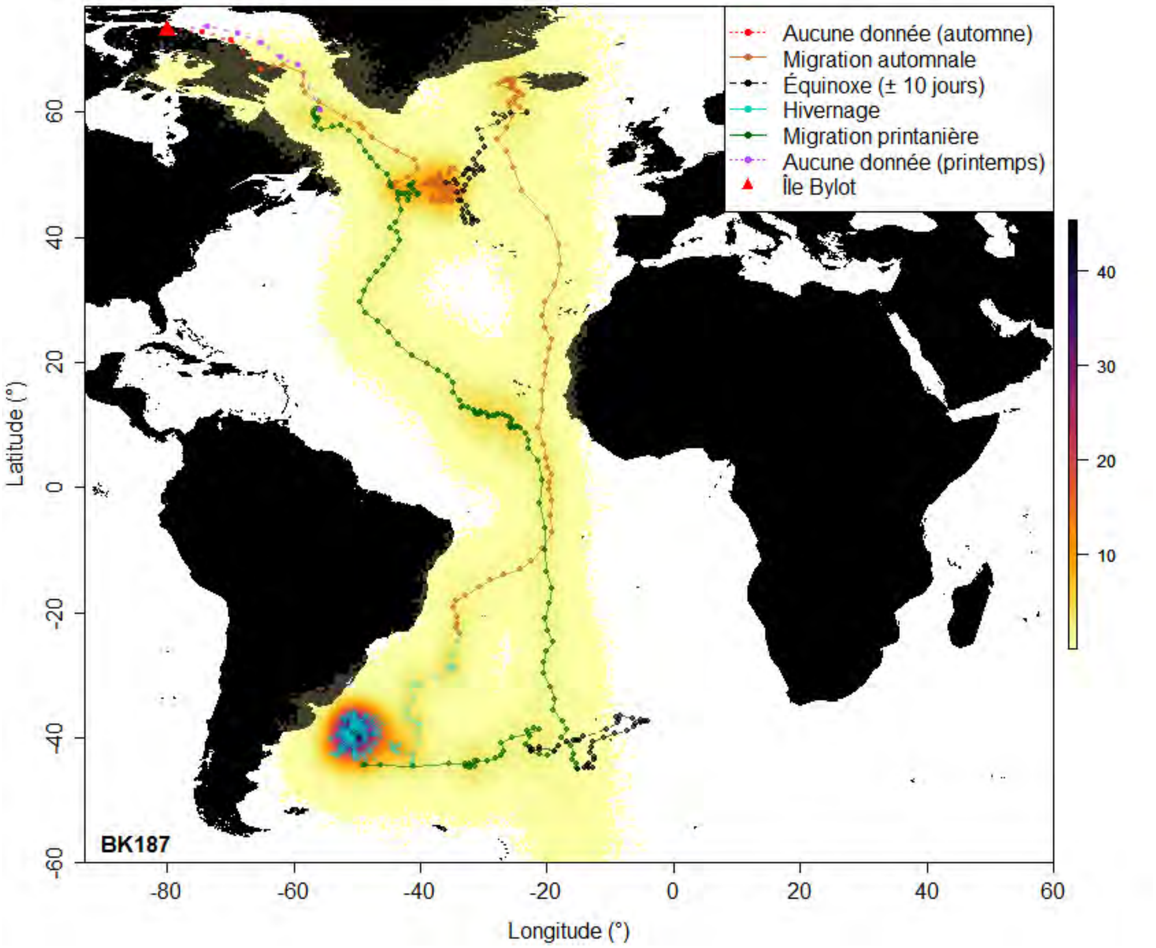
	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	21 août	11 oct.	28	10 602	344	125
Halte automnale	3 sept.	28 sept.	24	4 174	171	150
Hivernage	11 oct.	n.d.	≥ 82	≥ 9 415	115	256
Migration printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Halte printanière	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Site d'hivernage Nord équatorial

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	oui	27 juin	21 juil.	oui	2	1034-06803
Année 2	oui	n.d.	n.d.	probable	2	1034-06899

Géolocalisateur	BK187	**Sexe**	Mâle
Bague de métal	0944-02856	**Site**	Bylot
Marqueur auxiliaire	67 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
25 juin 2018	26 juin 2019	-	579

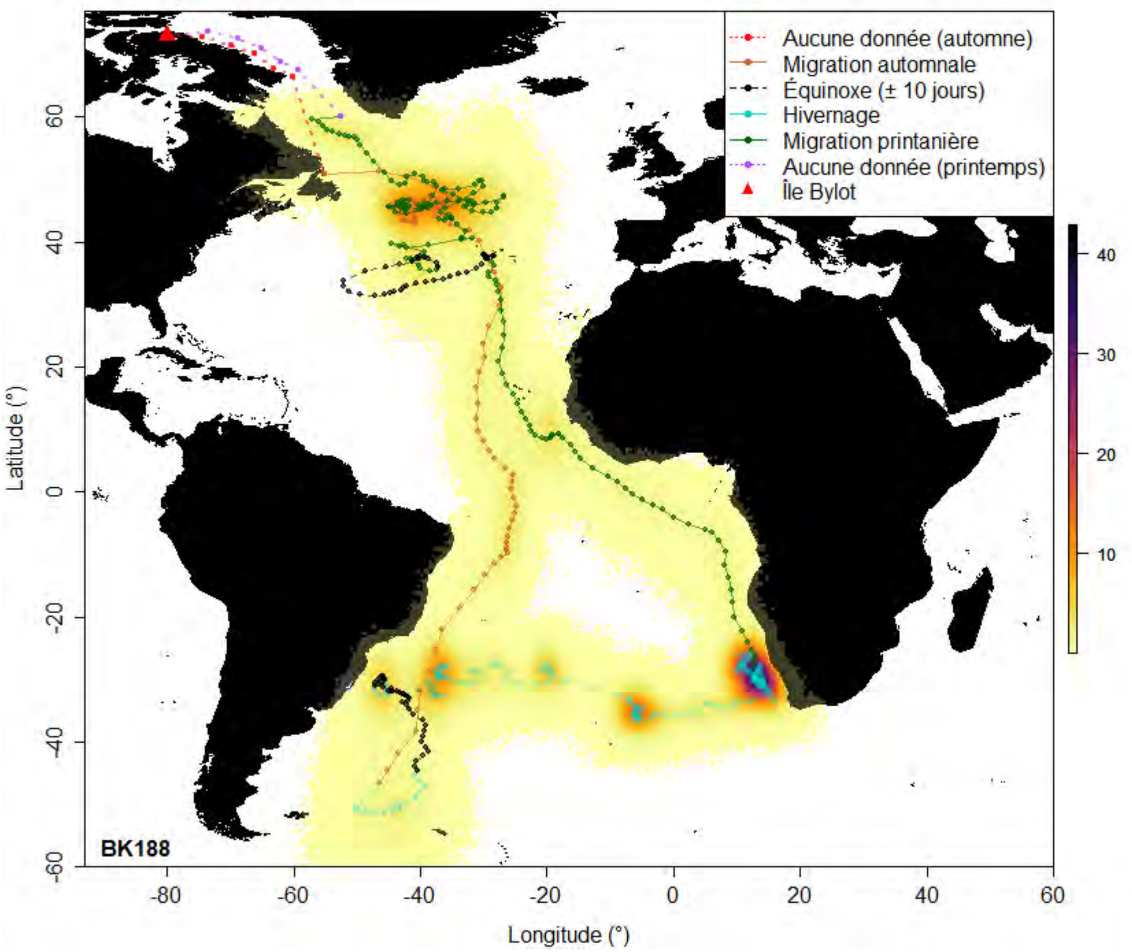


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	10 août	3 nov.	30	14 273	437	173
Halte automnale	20 août	15 oct.	56	10 246	183	195
Hivernage	3 nov.	23 fév.	113	16 536	146	364
Migration printanière	23 fév.	2 juin	85	24 022	260	274
Halte printanière	10 mai	17 mai	7	1 106	158	294
Site d'hivernage	Brésil					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	non	-	-	-	-	-
Année 2	non	-	-	-	-	-

Géolocalisateur	BK188	**Sexe**	Femelle
Bague de métal	0944-02872	**Site**	Bylot
Marqueur auxiliaire	70 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
25 juin 2018	23 juin 2019	-	603

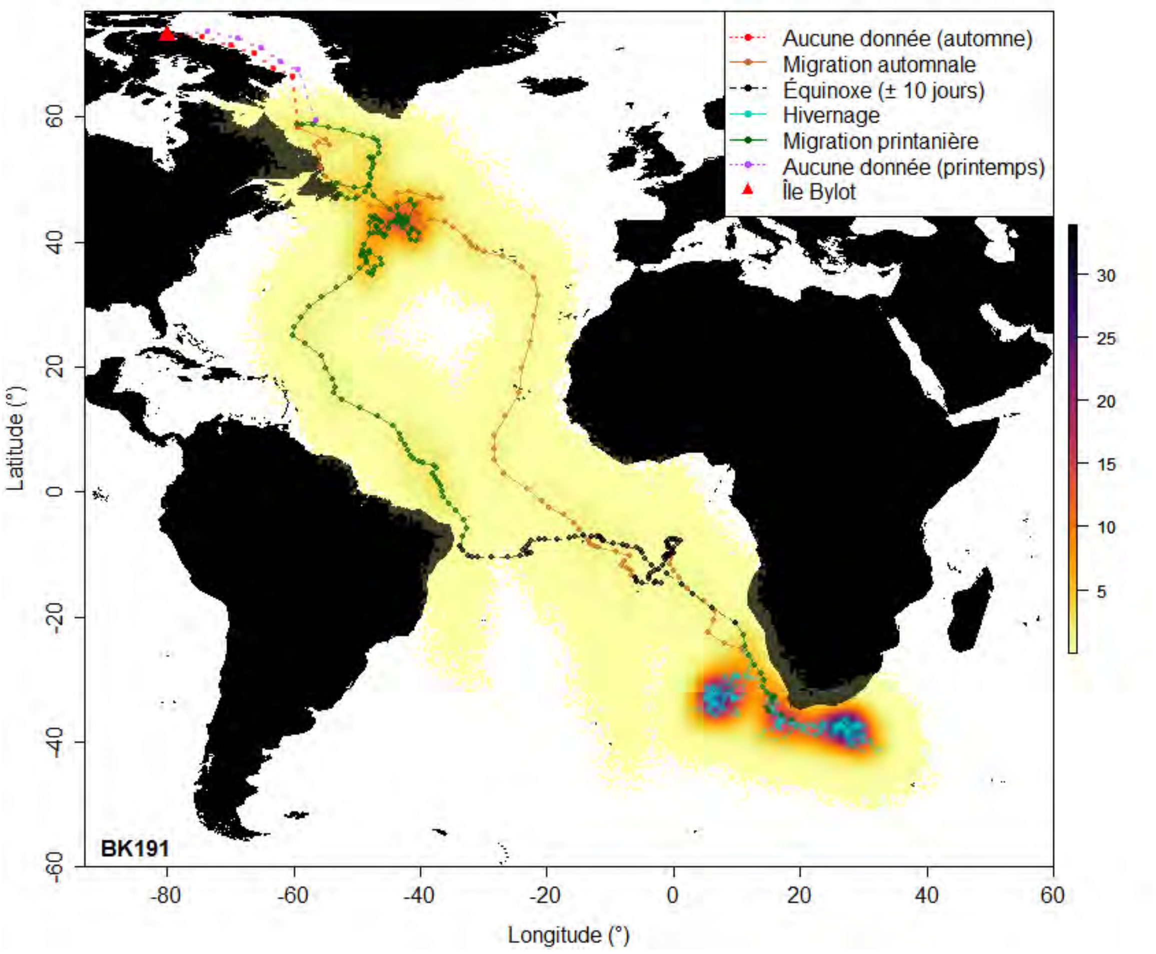


	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	27 juil.	1 sept.	26	15 837	495	141
Halte automnale	29 juil.	9 août	10	2 346	227	211
Hivernage	1 sept.	7 fév.	159	22 885	144	322
Migration printanière	7 fév.	27 mai	60	18 766	278	309
Halte printanière	25 mars	10 mai	47	9 316	200	305
Site d'hivernage	Benguela, Brésil					

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	non	-	-	-	-	-
Année 2	non	-	-	-	-	-

Géolocalisateur	BK191	**Sexe**	Mâle
Bague de métal	0944-02866	**Site**	Bylot
Marqueur auxiliaire	59 (jaune-noir)		

Déploiement	Récupération	Dernier enregistrement	Nombre de localisations
27 juin 2018	23 juin 2019	-	605



	Début	Fin	Durée	Distance	Vitesse	Immersions
Migration automnale	4 août	7 oct.	52	18 181	311	231
Halte automnale	10 août	23 août	12	2 870	232	241
Hivernage	7 oct.	1 mars	145	23 167	159	361
Migration printanière	1 mars	4 juin	42	13 267	265	275
Halte printanière	2 avril	23 mai	51	13 716	268	297

Site d'hivernage Aiguilles, Benguela

	Nicheur	Initiation	Éclosion	Succès	Taille de ponte	Partenaire
Année 1	non	-	-	-	-	-
Année 2	oui	16 juin	-	non	2	0944-02885

Table S2.9 Synthèse des informations sur la phénologie de la migration annuelle des labbes à longue queue nichant dans l'est de l'Arctique canadien et suivis par des géolocalisateurs (ID). La durée de chacune des périodes est exprimée en jour. n.d. : Donnée non-disponible. - : non-applicable.

ID	Migration automnale			Halte migratoire			Période d'hivernage			Migration printanière			Halte migratoire		
	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée
F634	16 août	2 oct.	26	27 août	12 sept.	15	2 oct.	28 jan.	118	28 jan.	31 mai	76	1 avril	18 mai	47
F634A	23 juil.	27 oct.	73	-	-	0	27 oct.	n.d.	≥ 40	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
F637	21 août	21 nov.	68	6 sept.	29 sept.	22	21 nov.	21 mars	120	31 mars	3 juin	51	2 mai	25 mai	23
F638	15 août	5 oct.	46	-	-	0	5 oct.	n.d.	≥ 159	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
F639	15 août	20 oct.	32	2 sept.	4 oct.	31	20 oct.	26 mars	157	26 mars	3 juin	42	26 avril	23 mai	27
F639A	2 août	14 oct.	31	19 août	30 sept.	41	14 oct.	n.d.	≥ 99	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
F641	12 août	6 oct.	33	27 août	8 sept.	11	6 oct.	9 fév.	126	9 fév.	n.d.	≥ 44	n.d.	n.d.	n.d.
F643	25 août	31 oct.	50	4 sept.	23 sept.	18	31 oct.	16 mars	136	16 mars	3 juin	53	22 avril	18 mai	26
F643A	8 août	22 oct.	32	2 sept.	3 oct.	31	22 oct.	n.d.	≥ 33	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
F908	21 août	29 oct.	47	5 sept.	26 sept.	20	29 oct.	31 jan.	95	31 jan.	3 juin	97	30 avril	24 mai	24
F909	15 août	16 oct.	29	26 août	22 sept.	26	16 oct.	6 mars	142	6 mars	2 juin	67	1 mai	14 mai	14
F913	21 août	23 oct.	43	29 août	20 sept.	21	23 oct.	31 mars	159	31 mars	1 juin	61	-	-	0
F915	20 août	10 oct.	16	27 août	30 sept.	33	10 oct.	24 avril	197	24 avril	5 juin	36	-	-	0
R833	26 juil.	11 oct.	31	31 juil.	16 sept.	46	11 oct.	25 fév.	137	25 fév.	9 juin	54	18 avril	29 mai	42
R834	11 août	13 oct.	61	17 août	21 août	3	13 oct.	15 jan.	94	15 jan.	29 mai	92	5 avril	17 mai	42
R837	5 août	28 sept.	35	24 août	1 sept.	7	28 sept.	22 avril	208	22 avril	26 mai	33	-	-	0
R837A	31 juil.	24 sept.	14	16 août	15 sept.	29	24 sept.	n.d.	≥ 85	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
R838	20 août	15 oct.	47	29 août	6 sept.	7	15 oct.	20 mars	157	20 mars	n.d.	36	n.d.	n.d.	n.d.
R839	20 août	20 nov.	84	29 août	6 sept.	7	20 nov.	22 mars	123	22 mars	10 juin	59	19 mai	28 mai	8
R842	11 août	12 sept.	25	-	-	0	12 sept.	20 mars	190	20 mars	6 juin	68	13 mai	16 mai	3
R843	12 août	30 sept.	20	25 août	17 sept.	22	30 sept.	22 mars	174	22 mars	30 mai	55	8 mai	21 mai	13
R843A	11 août	16 oct.	37	26 août	16 sept.	20	16 oct.	n.d.	≥ 59	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
R845	16 août	25 sept.	27	28 août	11 sept.	13	25 sept.	17 mars	175	17 mars	1 juin	65	11 mai	18 mai	8
R846	8 août	16 oct.	55	27 août	4 sept.	7	16 oct.	12 mars	148	12 mars	30 mai	53	29 avril	23 mai	24
R847	10 août	23 oct.	17	31 août	15 oct.	44	23 oct.	30 mars	159	30 mars	13 juin	36	18 mars	7 mai	20
R848	14 août	7 oct.	28	30 août	15 sept.	17	7 oct.	13 mai	220	13 mai	5 juin	19	-	-	0
R849	12 août	4 oct.	42	-	-	0	4 oct.	30 jan.	119	30 jan.	2 juin	62	20 mars	11 mai	53
R850	22 août	30 sept.	32	8 sept.	14 sept.	5	30 sept.	17 jan.	109	17 jan.	7 juin	102	25 avril	28 mai	33
X567	27 août	n.d.	20	7 sept.	29 sept.	≥ 22	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X568	31 juil.	10 sept.	25	14 août	22 août	7	10 sept.	n.d.	≥ 162	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X569	25 juil.	n.d.	5	14 août	18 août	≥ 3	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X570	6 août	7 oct.	32	18 août	14 sept.	26	7 oct.	n.d.	≥ 164	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X571	2 août	8 oct.	42	28 août	9 sept.	11	8 oct.	n.d.	≥ 71	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X576	11 août	23 sept.	33	19 août	25 août	5	23 sept.	n.d.	≥ 91	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

ID	Migration automnale			Halte migratoire			Période d’hivernage			Migration printanière			Halte migratoire		
	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée	Début	Fin	Durée
X578	14 août	5 oct.	44	30 août	3 sept.	3	5 oct.	n.d.	≥ 72	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X582	17 août	9 oct.	40	7 sept.	18 sept.	11	9 oct.	n.d.	≥ 96	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X584	25 août	10 oct.	32	7 sept.	22 sept.	15	10 oct.	14 jan.	96	14 jan.	n.d.	≥ 50	n.d.	n.d.	n.d.
X585	17 août	n.d.	58	2 sept.	20 sept.	≥17	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X595	8 août	11 sept.	33	-	-	0	11 sept.	n.d.	≥ 91	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
X596	21 août	11 oct.	28	3 sept.	28 sept.	24	11 oct.	n.d.	≥ 82	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
BK187	10 août	3 nov.	30	20 août	15 oct.	56	3 nov.	23 fév.	113	23 fév.	2 juin	85	10 mai	17 mai	7
BK188	27 juil.	1 sept.	26	29 juil.	9 août	10	1 sept.	7 fév.	159	7 fév.	27 mai	60	25 mars	10 mai	47
BK191	4 août	7 oct.	52	10 août	23 août	12	7 oct.	1 mars	145	1 mars	4 juin	42	2 avril	23 mai	51

Table S2.10 Synthèse des informations sur la distance parcourue (km) et la vitesse de déplacement (km/jour) de la migration annuelle des labbes à longue queue nichant dans l'est de l'Arctique canadien et suivis par des géolocalisateurs (ID). n.d. : Donnée non-disponible. - : non-applicable.

ID	Distance parcourue					Vitesse de déplacement				
	Migration automnale	Halte migratoire automnale	Période d'hivernage	Migration printanière	Halte migratoire printanière	Migration automnale	Halte migratoire automnale	Période d'hivernage	Migration printanière	Halte migratoire printanière
F634	15 212	2 926	22 621	23 114	12 148	540	190	191	274	262
F634A	20 572	-	≥ 7 834	n.d.	n.d.	270	-	194	n.d.	n.d.
F637	18 389	4 523	20 069	14 492	7 607	269	202	167	240	333
F638	15 364	-	≥ 27 810	n.d.	n.d.	318	-	175	n.d.	n.d.
F639	11 746	5 622	17 436	11 548	6 195	352	179	111	227	230
F639A	11 297	5 628	≥ 13 229	n.d.	n.d.	326	136	134	n.d.	n.d.
F641	19 437	2 383	23 643	≥ 6 532	n.d.	537	209	188	148	n.d.
F643	19 088	4 017	21 962	18 468	5 492	357	218	162	307	211
F643A	15 502	5 434	≥ 6 252	n.d.	n.d.	472	176	190	n.d.	n.d.
F908	18 452	4 091	14 560	26 290	4 244	383	200	154	251	177
F909	12 424	5 015	20 828	20 437	2 768	396	190	147	274	203
F913	17 305	4 309	26 703	21 805	-	389	205	168	330	-
F915	7 956	6 491	23 631	14 302	-	469	194	120	333	-
R833	15 511	8 615	19 334	21 379	7 649	465	186	141	364	183
R834	16 200	554	13 075	19 895	6 947	245	163	138	188	166
R837	14 907	952	28 814	12 774	-	401	129	139	333	-
R837A	13 489	6 976	≥ 12 602	n.d.	n.d.	847	238	148	n.d.	n.d.
R838	13 905	1 289	17 518	≥ 10 733	n.d.	271	174	111	302	n.d.
R839	15 455	1 489	9 666	15 277	1 341	178	202	78	218	163
R842	13 351	-	28 261	21 330	0 510	509	-	148	281	172
R843	9 917	3 732	24 022	15 418	2 241	458	167	138	243	173
R843A	12 076	4 498	≥ 8 704	n.d.	n.d.	292	221	148	n.d.	n.d.
R845	13 165	3 546	22 620	20 600	1 220	457	264	130	288	159
R846	16 076	1 127	23 781	16 793	4 039	270	152	160	275	169
R847	8 684	7 671	21 177	11 754	3 165	428	173	133	267	161
R848	14 208	2 427	19 196	8 049	-	433	147	87	311	-

ID	Distance parcourue					Vitesse de déplacement				
	Migration automnale	Halte migratoire automnale	Période d’hivernage	Migration printanière	Halte migratoire printanière	Migration automnale	Halte migratoire automnale	Période d’hivernage	Migration printanière	Halte migratoire printanière
R849	19 681	-	18 746	21 209	10 482	426	190	158	319	199
R850	11 404	863	17 403	16 219	6 161	349	159	160	139	187
X567	9 362	≥ 5 302	n.d.	n.d.	n.d.	441	242	n.d.	n.d.	n.d.
X568	14 372	1 406	≥ 26 940	n.d.	n.d.	487	191	166	n.d.	n.d.
X569	≥ 4 384	≥ 760	n.d.	n.d.	n.d.	426	229	n.d.	n.d.	n.d.
X570	12 024	4 495	≥ 21 721	n.d.	n.d.	338	170	132	n.d.	n.d.
X571	15 159	2 669	≥ 14 053	n.d.	n.d.	320	235	198	n.d.	n.d.
X576	19 793	1 014	≥ 13 921	n.d.	n.d.	558	189	153	n.d.	n.d.
X578	15 681	817	≥ 11 693	n.d.	n.d.	332	240	163	n.d.	n.d.
X582	14 077	1 522	≥ 17 985	n.d.	n.d.	337	138	187	n.d.	n.d.
X584	13 369	2 296	15 000	≥ 6 571	n.d.	401	153	155	133	n.d.
X585	≥ 16 362	≥ 2 879	n.d.	n.d.	n.d.	274	165	n.d.	n.d.	n.d.
X595	15 072	-	≥ 12 013	n.d.	n.d.	429		132	n.d.	n.d.
X596	10 602	4 174	≥ 9 415	n.d.	n.d.	344	171	115	n.d.	n.d.
BK187	14 273	10 246	16 536	24 022	1 106	437	183	146	260	158
BK188	15 837	2 346	22 885	18 766	9 316	495	227	144	278	200
BK191	18 181	2 870	23 167	13 267	13 716	311	232	159	265	268

Table S2.11 Superficie de l’aire d’hivernage (en km^2) des labbes à longue queue nichant dans l’est de l’Arctique canadien déterminée par une méthode d’estimation par noyau (*Kernel density estimation*) pour une utilisation à 95 %, 75 % et 50 %. ID représente le numéro du géolocalisateur. n.d. : Donnée non-disponible.

ID	Utilisation à 95 %	Utilisation à 75 %	Utilisation à 50 %
F634	2 201 659	1 034 514	448 206
F634A	689 149	355 235	180 914
F637	1 221 724	644 696	296 797
F638	1 857 072	843 774	344 687
F639	695 448	325 359	140 393
F639A	627 671	295 946	132 873
F641	2 560 769	1 095 835	454 096
F643	1 112 851	436 029	190 154
F643A	668 118	371 370	192 377
F908	678 836	316 818	154 379
F909	1 110 946	533 892	240 018
F913	1 357 673	724 889	349 598
F915	431 471	230 973	116 006
R833	983 670	459 263	214 416
R834	1 046 813	490 577	202 669
R837	2 023 071	940 370	398 152
R837A	783 837	378 368	175 898
R838	941 749	435 960	174 455
R839	249 350	104 797	42 048
R842	1 630 779	794 426	357 638
R843	1 337 527	583 152	242 838
R843A	861 742	418 487	195 218
R845	1 356 965	675 774	308 436
R846	1 158 386	628 757	325 598
R847	2 203 257	1 050 209	461 107
R848	380 916	183 547	84 451
R849	1 045 390	461 158	205 344
R850	1 838 515	799 170	334 013
X567	n.d.	n.d.	n.d.
X568	1 841 007	883 034	382 843
X569	746 692	391 455	198 363
X570	1 527 698	778 353	363 156
X571	822 365	402 626	176 874
X576	849 552	405 306	181 039
X578	1 845 513	812 478	339 743
X582	974 164	446 471	197 036
X584	734 214	418 213	218 182
X595	160 572	53 702	23 696
X596	982 712	453 813	214 041
BK187	1 612 960	715 294	278 409
BK188	1 323 053	656 595	314 915
BK191	2 201 659	1 034 514	448 206

Annexe S2.10 – Données individuelles des labbes à longue queue suivis à l’aide d’un émetteur satellite

Table S2.12 Synthèse des paramètres de la migration automnale individuelle des labbes à longue queue suivis par des émetteurs satellites déployés sur l’Île Bylot en 2008 (n = 9). La vitesse de déplacement réfère à celle entre l’Île Bylot et la halte migratoire. ID : Numéro d’identification de l’émetteur satellite. n.d. : Donnée non-disponible.

ID	Date de départ	Distance Île Bylot – Halte migratoire (km)	Date d’arrivée à la halte migratoire	Durée de la halte migratoire (jour)	Vitesse de déplacement (km/jour)
84008	12 août	3 370	21 août	≥ 13.5	354
84009	25 août	n.d.	n.d.	n.d.	n.d.
84010	15 août	n.d.	n.d.	n.d.	n.d.
84011	14 août	3 239	27 août	≥ 2.2	242
84012	15 août	3 638	28 août	27.5	263
84013	18 août	3 137	25 août	≥ 15.2	490
84014	20 août	3 215	26 août	39.8	490
84015	12 août	2 909	16 août	≥ 0.2	689
84016	21 août	3 166	28 août	≥ 24.7	470

Annexe S3 – Documentation supplémentaire pour le Chapitre 3

Annexe S3.1 – Spearman correlation coefficients of migratory variables

Table S3.1 Spearman correlation coefficients (above black diagonal) and their significance levels (below black diagonal) of the main variables estimated from geolocator data. Light gray cells represent the variables selected to analyze the influence of the non-breeding season on reproductive success and dark gray ones the influence of the reproductive success on fall migration. Values in bold highlight the coefficients and p-values of selected variables. Sample size varies from 23 to 41 depending on the variable.

	Departure from breeding site	Duration – Fall migration	Immersions – Fall migration	Speed – Fall migration	Distance – Fall migration	Arrival at wintering site	Duration – Wintering period	Immersions – Winter period	Distance – Wintering period	Departure from wintering site	Arrival at breeding site	Duration – Spring migration	Immersions – Spring migration	Speed – Spring migration	Distance – Spring migration
Departure from breeding site		**-0.17**	0.03	-0.17	-0.02	**0.28**	-0.31	0.13	0.02	-0.03	0.19	-0.05	0.23	-0.25	-0.07
Duration – Fall migration	**0.32**		0.35	-0.50	0.23	**0.86**	-0.27	0.32	-0.41	0.18	0.27	-0.05	-0.32	-0.08	0.04
Immersions – Fall migration	0.85	0.03		-0.64	0.37	0.28	-0.24	0.32	-0.33	-0.13	-0.03	0.29	-0.19	0.00	0.16
Speed – Fall migration	0.29	<0.01	<0.01		-0.18	-0.55	0.32	-0.22	0.29	-0.01	-0.07	-0.11	0.04	0.30	0.17
Distance – Fall migration	0.89	0.16	0.02	0.27		0.13	-0.44	0.31	-0.07	-0.37	-0.21	0.37	-0.09	0.04	0.23
Arrival at wintering site	**0.09**	**<0.01**	0.09	<0.01	0.44		-0.38	0.33	-0.39	0.14	0.25	-0.05	-0.15	-0.20	0.03
Duration – Wintering period	0.13	0.18	0.24	0.11	0.03	0.06		0.10	0.67	0.82	0.01	-0.83	-0.45	0.60	-0.29
Immersions – Winter period	0.43	0.05	0.05	0.18	0.06	0.05	0.64		**0.26**	0.29	**0.24**	**-0.15**	-0.44	**0.34**	0.15
Distance – Wintering period	0.91	0.01	0.04	0.08	0.66	0.02	<0.01	**0.12**		0.40	**-0.33**	**-0.51**	-0.41	**0.46**	-0.02
Departure from wintering site	0.87	0.37	0.51	0.94	0.07	0.49	<0.01	0.15	0.04		0.21	-0.96	-0.46	0.45	-0.34
Arrival at breeding site	0.40	0.21	0.88	0.74	0.34	0.25	0.97	**0.27**	**0.12**	0.33		**-0.03**	0.15	**-0.05**	-0.24
Duration – Spring migration	0.81	0.81	0.19	0.61	0.08	0.83	<0.01	**0.51**	**0.01**	<0.01	**0.91**		0.48	**-0.36**	0.57
Immersions – Spring migration	0.25	0.11	0.36	0.85	0.66	0.45	0.02	0.03	0.04	0.02	0.50	0.02		-0.57	-0.15
Speed – Spring migration	0.21	0.70	0.99	0.14	0.84	0.33	<0.01	**0.09**	**0.02**	0.02	**0.81**	**0.09**	<0.01		0.24
Distance – Spring migration	0.74	0.84	0.44	0.40	0.26	0.88	0.15	0.45	0.93	0.09	0.27	<0.01	0.47	0.23	

Annexe S4 – Documentation supplémentaire pour le Chapitre 5

Annexe S4.1 – Details of the *a*-LoCoH method

The local convex hull polygon (LoCoH) method is based on the minimum convex polygon method combined with a non-parametric kernel method (Getz et al., 2007). Basically, the method works by creating convex hulls for every point in the dataset and then iteratively joining them from the smallest to the largest, dividing them into a set of nonparametric kernels based on the isopleths. The use of LoCoH method instead of parametric kernels method is better to delimit geographical features (lakes, rivers, boundaries). The adaptive LoCoH (*a*-LoCoH) method is a modification of the fixed *k*-LoCoH method (*k*-nearest neighbor convex hulls method – *k*-NNCH or *k*-LoCoH) (Getz et al., 2007).

For every point in the dataset, a hull that includes the maximum number of points for which the sum of the distances between these points and a root point is less or equal to a threshold value *a* is built. Contrary to the *k*-LoCoH method, the number of points included in the construction of the LoCoH kernels is changing depending on their distance from the root point. Thus, the radius of the circle that circumscribes each local convex hull is affected by the distance between each point. Smaller convex hulls are found in high use areas, giving clearly defined isopleths in areas with high concentration of data (Getz et al., 2007).

We selected the optimal threshold value following a two steps process, as described by Getz et al. (2007) and Stark et al. (2017). First, we defined heuristic parameter values noted *a* as the maximum distance between any two nests in the data set (Table S4.1). We defined these raw values for each species in presence and absence of owls. These values served as starting points from which we refined the estimation to determine the optimal values noted *a** (Table S4.1). To do so, we rounded each *a* value to the nearest multiple of 50 m and visually assessed the maps to select the most accurate one, i.e. the one that best matches the data. Knowing the topography and the vegetation through the study area as well as the nest distribution of each predator species over a 14 years period, we used the minimum spurious hole covering (MSHC) rule to select the appropriate *a** by ensuring areas that were never used (no nest throughout the years) were excluded from the polygons. The MSHC rule is a technique used to select the smallest value of a (the *a**-value) that produces a covering that matches the topology of the area and the distribution of the dataset (Getz and Wilmers, 2004). Even if this rule is somehow subjective, Getz et al. (2007) demonstrated that *a*-LoCoH method is quite robust to changes in the value of *a*.

We used the 90% isopleth provided by the *a*-LoCoH analysis to delimit the core area used for nesting by each species across all years. The number of nests included in this isopleth usually exceeded this threshold (jaeger: 94% and 91%; gull: 90% and 99%; hawk: 94% and 100%; owl: 97%, for years with and without snowy owls, respectively).

Table S4.1 Heuristic parameter value (*a*) (maximum distance between any two nest in m) and optimal estimated value (*a**) to delimit the area used by each species of avian predators in presence or absence of snowy owls.

	Owl present		Owl absent	
	a	*a**	*a*	*a**
Snowy owl	10 725	7 150	-	-
Glaucous gull	11 340	2 200	11 481	4 300
Rough-legged hawk	10 636	5 250	9 156	7 500
Long-tailed jaeger	12 947	5 500	12 501	9 450

Literature cited

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Stark, D. J., I. P. Vaughan, D. A. Ramirez Saldivar, S. K. S. S. Nathan, and B. Goossens. 2017. Evaluating methods for estimating home ranges using GPS collars: A comparison using proboscis monkeys (*Nasalis larvatus*). PLoS ONE 12:e0174891.

Annexe S4.2 – Supplementary tables and figure

Table S4.2 Candidate models used to compare the body mass of lemmings consumed among the four avian predator species and with the lemmings available from live trapping (variable species; M1, M2), and the impact of the presence or absence of snowy owls (variable owl presence) on the size of the prey consumed by the other predators (M3, M4, M5). Nest IDs were used as the random factor for all models and body mass were ln-transformed. Number of parameters (*K*) and observations (n) are also reported.

Model No	Response variable	*K*	n	Explanatory variable
M1	Body mass of lemmings consumed and available in presence of snowy owls	7	1201*	Species
M2	Body mass of lemmings consumed and available in absence of snowy owls	6	676	Species
M3	Body mass of lemmings consumed by long-tailed jaegers	4	213	Owl presence
M4	Body mass of lemming consumed by rough-legged hawks	4	102	Owl presence
M5	Body mass of lemmings consumed by glaucous gulls	4	91	Owl presence
M6	Body mass of lemmings available from live trapping	4	1343	Owl presence

* n = 303 when model M1 was applied to year 2008 only (model M1a).

Table S4.3 Sample size of intact mandibles measured annually for each predator species. Each mandible represents a different individual.

Year	2004	2007	2008	2010	2014	2015	2016	2017
Snowy owl	47	-	47	34	-	-	-	-
Glaucous gull	-	44	47	-	-	-	-	-
Rough-legged hawk	-	-	8	6	23	2	52	11
Long-tailed jaeger	-	-	56	9	6	72	70	-

Table S4.4 Sample size of lemming mandibles measured in pellets of each predator species in presence or absence of owls. Numbers in parenthesis represent the total number of nest sampled.

Owl status	Species	Snowy owl	Glaucous gull	Rough-legged hawk	Long-tailed jaeger	Total
Owl present	Brown lemming	77	12	14	48	151
	Collared lemming	51	35	23	23	132
	Total	128 (16)	47 (18)	37 (11)	71 (31)	283 (76)
Owl absent	Brown lemming	0	5	18	87	110
	Collared lemming	0	39	47	55	141
	Total	0 (0)	44 (9)	65 (7)	142 (22)	251 (38)
	Total	128	91	102	213	534

Table S4.5 Slope parameters (β) and their 95% confidence intervals (CI) for model M1a. Nest IDs were used as random factor and body mass were ln-transformed. R^2_m: Marginal R-squared for fixed effects. R^2_c: Conditional R-squared for fixed and random effects. σ^2_i: Variance of the random effect intercept. σ^2_r: Variance of the random effect residuals.

Model no*	Explanatory variable	β	Low CI	High CI	R^2_m	R^2_c	σ^2_i	σ^2_r
M1a	Owl	0.429	-0.002	0.859	0.274	0.429	0.055	0.201
	Gull	0.726	0.334	1.117				
	Hawk	0.437	-0.177	1.050				
	Jaeger	-0.229	-0.618	0.161				

* Reference group is Lemming available

Table S4.6 Slope parameters (β) and their 95% confidence intervals (CI) of the LMMs comparing the mean body mass of the lemmings available in presence and in absence of snowy owls for each predator species while considering only years when pellets were collected (Table S4.3). R^2_m: Marginal R-squared for fixed effects. R^2_c: Conditional R-squared for fixed and random effects. *K*: Number of parameters. n: Sample size.

Species of predator*	Explanatory variable	β	Low CI	High CI	R^2_m	R^2_c	*K*	n
Gull	Owl presence	-0.045	-0.464	0.373	0.001	0.007	4	200
Hawk	Owl presence	0.116	-0.027	0.258	0.016	0.061	4	1148
Jaeger	Owl presence	0.084	-0.056	0.225	0.008	0.045	4	1134

* Reference group for all the models is owl absent

Table S4.7 Stepwise selection of the best log-linear model comparing the proportion of brown vs. collared lemmings consumed by three different avian predators in presence or absence of owls. Backward model selection from the saturated model was based on AIC. The saturated model included the three main effects (Lemming, Predator, Owl), the three two-way interactions and the three-way interaction. Lemming: lemming species (brown or collared); Predator: avian predator species (gull, hawk, jaeger); Owl: presence or absence of snowy owls. *K*: Number of parameters.

Removed effect	Deviance	*K*	AIC
Step 1: Test of three-way interaction			
Saturated model	0.000	12	85.47
Three-way interaction removed	1.199	10	82.67
Step 2: Test of two-way interactions			
Model without three-way interaction	1.199	10	82.67
Lemming × Owl interaction removed	5.028	9	84.49
Predator × Owl interaction removed	13.529	9	91.00
Lemming × Species interaction removed	69.325	9	146.79

Table S4.8 Slope parameters (β) and their 95% confidence intervals (CI) from the log-linear analysis comparing the proportion of brown vs. collared lemmings in the prey consumed by four different avian predators and in the lemming available (live-trapped lemmings) in (A) presence of owls and (B) absence of owls. Reference levels are collared lemming, and lemmings from live trapping.

	Explanatory variable	β	CI
A)	Brown lemming	1.864	[1.678, 2.060]
	Owl	-0.872	[-1.207, 0.552]
	Gull	-1.249	[-1.639, -0.885]
	Hawk	-1.669	[-2.139, -1.244]
	Jaeger	-1.669	[-2.139, -1.244]
	Brown lemming × Owl	-1.452	[-1.853, -1.047]
	Brown lemming × Gull	-2.935	[-3.656, -2.279]
	Brown lemming × Hawk	-2.361	[-3.075, -1.681]
	Brown lemming × Jaeger	-1.129	[-1.651, -0.582]
B)	Brown lemming	1.286	[1.060, 1.523]
	Gull	-0.858	[-1.243, -0.492]
	Hawk	-0.672	[-1.031, -0.326]
	Jaeger	-0.515	[-0.854, -0.184]
	Brown lemming × Gull	-3.341	[-4.427, -2.469]
	Brown lemming × Hawk	-2.246	[-2.859, -1.672]
	Brown lemming × Jaeger	-0.828	[-1.236, -0.417]

Table S4.9 Percentage of various habitat types present in the nesting area of each predator in years of presence (n = 3 years) and absence (n = 8) of snowy owls (see Figure 5.1; for definition of habitat type).

Habitat type	Long-tailed jaeger		Rough-legged hawk		Glaucous gull		Snowy owl
	Presence	Absence	Presence	Absence	Presence	Absence	
Wet meadows on flat terrain	12.1	13.4	0.0	0.0	68.9	64.3	0.0
Moist/mesic meadows on flat terrain	59.2	67.1	7.3	1.1	30.4	34.9	24.3
Mesic tundra on gentle slope	18.0	15.0	11.6	2.3	0.7	0.8	28.3
Mesic tundra on hills	10.2	4.5	36.2	39.6	0.0	0.0	33.3
Xeric tundra on steep slopes and cliffs	0.5	0.0	44.9	57.0	0.0	0.0	14.1

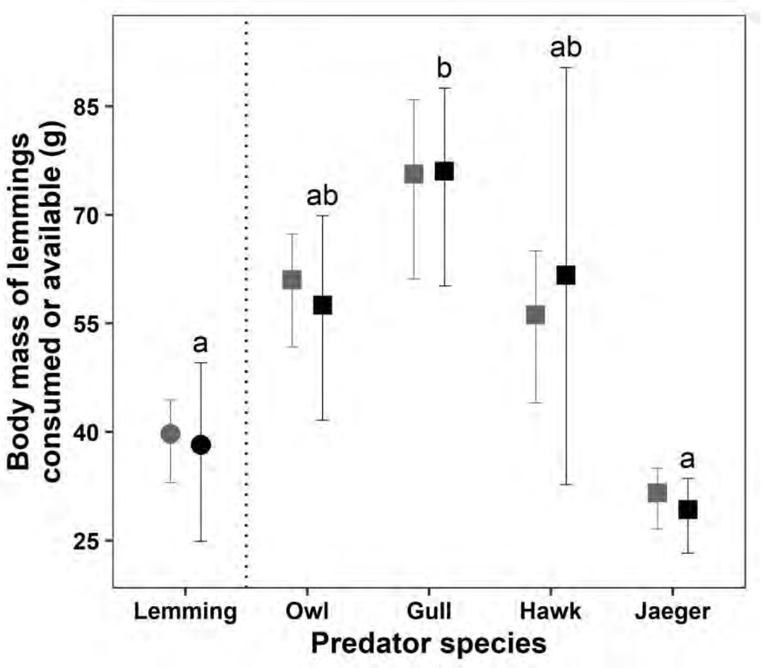

Figure S4.1 Mean body mass (g) of lemmings consumed by different predator species (square) or available (live-trapped lemmings; circle) in 2008 (black) and in all years of owl presence pooled (gray; from Figure 5.2A). Estimated means and 95% CI calculate from LMMs were back-transformed to match the scale of the original data. Mean with the same letters do not differ significantly in 2008.