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Yohan Sassi

To cite this version:

Yohan Sassi. De l'individu au groupe : étude du comportement de vol des vautours fauves. Ecologie, Environnement. Université de Montpellier, 2023. Français. NNT : 2023UMONG121 . tel-05262046

HAL Id: tel-05262046

https://theses.hal.science/tel-05262046v1

Submitted on 15 Sep 2025

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Écologie et biodiversité

École doctorale GAIA

Unité de recherche CEFE – UMR 5175

De l'individu au groupe : étude du comportement de vol des vautours fauves

Présentée par Yohan SASSI
Le 04 décembre 2023

Sous la direction de Olivier Duriez et Yann Tremblay

Devant le jury composé de

Claire Doutrelant, Directrice de recherche, Centre d'Écologie Fonctionnelle et Évolutive	Présidente du jury
Judy Shamoun-Baranes, Professeure, Université d'Amsterdam	Rapportrice
François Sarrazin, Professeur, Muséum National d'Histoire Naturelle	Rapporteur
Alexandre Millon, Maître de conférence, Université d'Aix-Marseille	Examinateur
Olivier Duriez, Maître de conférence, Centre d'Écologie Fonctionnelle et Évolutive	Directeur de thèse
Yann Tremblay, Chargé de recherche, Institut de Recherche pour le Développement	Co-directeur de thèse

UNIVERSITÉ DE MONTPELLIER

À mes parents,

© Olivier Duriez

Remerciements

Ce travail n'est pas l'œuvre d'un individu solitaire, mais bien le fruit de nombreuses collaborations et rencontres dont chacune a été riche d'apprentissage. À toutes et tous, impliqués de près ou de loin dans cette aventure, je tiens à vous faire part de ma gratitude et de ma reconnaissance pour l'aide apportée durant ces trois années. Je ferai de mon mieux, je vous l'assure, pour n'oublier personne dans mes remerciements, en revanche si votre nom n'apparait pas, ne doutez pas, je vous remercie grandement.

Mes premiers remerciements s'adressent naturellement à mes directeurs de thèse, **Olivier Duriez** et **Yann Tremblay** sans qui cette aventure n'aurait pas été possible. Je vous remercie de m'avoir donné la chance de candidater à l'école doctorale sur ce sujet de thèse, nous voilà 3 ans plus tard, après une belle aventure et un sacré bout de chemin parcouru. Merci de m'avoir fait confiance et de m'avoir soutenu tout au long de ce parcours. J'ai beaucoup appris à vos côtés, et je vous en suis reconnaissant.

Olivier, merci pour ta profonde gentillesse et ta remarquable générosité. Merci pour les aventures de terrain, que ce soit pour les captures vautours, le STOC ou encore le cluedo vautour ! Les captures de vautours ont toujours eu un goût particulier en ta présence. Si il y a bien une de tes phrases que je retiendrai c'est : « les vautours ne vivent pas dans le même espace-temps que nous… ». Bien que n'ayant pas compris de suite, j'ai rapidement réalisé à quel point ça pouvait être long d'attendre que les vautours viennent manger dans la cage… Mais on a réussi ! Je te remercie d'ailleurs d'avoir pris le temps de me former au baguage et à la pose de balise GPS. Merci pour l'opportunité de faire le STOC à Teyran avec toi, je n'oublierai jamais ton sourire lorsque je t'ai amené ton premier loriot pour le baguage. Merci pour l'initiation au cluedo vautour, Millau qui fait des allers-retours cette année… plutôt TMB ou les Cuns ? Une enquête bien rigolote à mener. Merci pour l'opportunité de travailler avec le Rocher des Aigles, et merci pour la découverte du club de plongée Objectif Bleu.

Yann, merci pour la découverte de la théorie sur la sélection naturelle de la blague. Il faut en faire beaucoup, c'est aux autres de trier ! Merci pour les parties de cochons sur Matlab. Merci pour l'accueil au Sénégal, les expériences sur place resteront gravées dans ma mémoire : la plage des mamelles, la plongée à Ngor, l'île de Kousmar, la manip croix au Hakuna, le New Africa… mais aussi les discussions sur les grands sujets de la vie le soir. Merci pour l'accueil à Sète, les discussions au bas de la Stèle Georges Brassens, toujours très intéressantes.

Je veux aussi remercier les membres de mon jury de thèse d'avoir accepté d'évaluer mon travail. Merci aux rapporteurs : **Judy Shamoun-Baranes** et **François Sarrazin**, merci aussi aux examinateurs : **Claire Doutrelant** et **Alexandre Millon.** Merci à **Elise Huchard**, **Francesco Bonadonna** et **Damien Farine**, pour vos conseils et vos retours sur mes idées lors des comités de suivi de thèse.

Mes remerciements vont maintenant à toutes les personnes avec qui j'ai fait des captures vautours. À l'équipe de la LPO Aude, la grande aventure des captures a commencé avec vous, le début a été laborieux mais la persévérance a porté ses fruits. Un immense merci à **Lise Dauverne**, **Yves Roullaud**, **Mathieu Vaslin** et **Anna Terras** pour l'accueil à Quillan et les moments passés sur le terrain ensemble. Je remercie aussi la LPO Grands Causses, et particulièrement **Thierry David** ainsi que **Robert Straughan** pour les curées auxquelles j'ai pu assister sur le charnier historique de Cassagne, un spectacle toujours aussi fascinant. Au Pays-basque, l'aventure de la capture n'a pas été des plus simple non plus, je remercie SAIAK et particulièrement **Isabelle Rebours** et **Michel Clouet** pour leur motivation sans faille et leur persévérance. Après s'être occupé des poussins, une première française, nous aurons fini par réussir à capturer « les vautours » adultes aussi. À ces occasions j'ai aussi pu faire la rencontre de deux personnages : **Didier Peyrusqué** et **Germain Besson**. Merci de m'avoir fait descendre avec vous dans les nids de vautour, en toute sécurité, et d'avoir partagé cette expérience extraordinaire. Merci aussi pour votre bonne humeur communicative, vos blagues et vos histoires toutes aussi intéressantes (et drôles) les unes que les autres. À tous lecteurs de cette section, si vous rencontrez ces personnages, demandez à connaître l'histoire des cou courts et des cou longs… À l'équipe de **Vautour en Baronnie** et à celle du **Vercors**, merci pour la capture effectuée ensemble dans ce si bel endroit. Mes remerciements pour les aventures de terrain ne pourraient pas être complets sans un immense merci au plus grand trappeur dont j'ai eu la chance de croiser la route : **Samuel Perret**. On aura fait de la route ensemble, on aura (beaucoup) attendu ensemble, et au final capturer quelques oiseaux ensemble. Merci pour ta bienveillance, et tous les bons moments que l'on a partagés lors des missions ! Je n'oublierai pas notre course de vélos pour enfants aux 28ème Rencontres Vautours. Encore merci !

Merci à la direction du Rocher des Aigles à Rocamadour, **Raphael Arnaud** et **Dominique Maylin**. Je vous suis extrêmement reconnaissant de m'avoir laissé mener mes expériences de thèse sur vos petits protégés, de m'avoir toujours très bien accueilli sur place et pour votre bienveillance. Merci aussi à tous les soigneurs avec qui j'ai pu travailler, aussi bien l'hiver que lors des expériences de vol l'été. Merci à **Oriane Trizinsky**, **Justine Pumo**, **Fanny Baldissier**, **Sylvain Bardet, Jean Michel Soulhié**, **Frédérique Aimé** et **Basile Nouzières**. Un remerciement particulier à toi Basile, toujours volontaire pour les expériences, même quand tu avais mille autres choses à faire. Merci pour les virées plus ou moins tardives à la recherche des oiseaux qui avaient décidé de dormir dehors. Je resterai impressionné par ton affection profonde pour chacun des oiseaux dont tu t'occupes, pour ton efficacité dans le travail que tu leur fais faire et pour ta maîtrise de la VHF. Merci pour l'ambiance au Rocher, toujours un plaisir de passer du temps avec vous sur l'esplanade, à voir évoluer ces oiseaux dans le canyon de l'Alzou.

Je souhaite aussi remercier l'ensemble des gens avec qui j'ai noué des amitiés durant ces années à Montpellier. **Jeanne** et **Fanny**, à nos premières soirées ensemble, la tête dans le caisson, sur le guidon d'un vélo avec une boite de chaussure à la main et une partie de tennis à 2h du matin. Oui c'est possible, oui c'est mémorable même. Pour l'ensemble des nombreux autres moments que nous avons partagés, un grand merci. Merci à toi **Val**, pour les soirées à

la Roqueturière, aux tap-tap-cans et aux beer-pongs, et pour m'avoir accueilli quand je n'avais plus de maison. Merci **Gus**, pour les chansons endiablées de Louise Attaque, les parties d'escalade nocturne des arbres du bois de Montmaure, et le soutien lors de l'écriture de cette thèse. Je remercie aussi tous les autres qui ont fait de la vie à Montpellier un sacré bon moment : **Jan**, **Sofia**, **Lilian**, **Nico**, **Martin**, **Constance**, **Nick**, **Vaish**, **Kat**, **Paul**, **Maurine**, **Mike**, **Nathan**, **Pierre**, **Lucie**, **Begum**, **Robin**, **Arthur**, **Alex**, **Sofie**, **Adrien** … et à l'ensemble des gens croisé au bois de Montmaure où les apéros du CEFE font rage.

Merci à l'ensemble des amis de longue date : **Romain**, **Ianis**, **Titi**, **Charlou**, **Alex**, **Mallau**, **Mathieu**, **Marina**, **Aymeline**, **Aymeric**, **Gaby**, **Mathilde** et tous ceux qui me connaissent depuis assez longtemps pour savoir que c'est pas ce que l'on aurait imaginé.

Merci aux membres permanents et précaires de mon équipe : Mouvement - Abondance - Distribution (MAD) du CEFE. D'abord merci à mes co-bureau, **Noa** et **Romain** depuis un petit bout de temps. Avec l'arrivée plus récemment de **Jérémy** et **Sarah**. Merci aux docs, post-doc et ingé de l'équipe. Merci **Ana**, **Marion** et **Louise** pour votre extrême bienveillance. À toi, la **DeLonghi Magnifica S**, merci, tu as été d'une aide capitale pour finir ce travail, le seul défaut que je te trouve, c'est que tu n'ai pas l'option perfusion. Pour finir avec l'équipe je remercie les stagiaires écureuils, particulièrement la team **Jeanne** & **Léa** pour votre bonne humeur !

Les tables de la rotonde au 3ème étage, merci d'avoir accueilli nombre de parties de coinche. Merci à l'ensemble des personnes qui ont participé, de manière plus ou moins assidue, à ce moment qui est devenu au fil du temps presque une tradition de la pause midi. Merci aussi aux transfuges de l'équipe NCS, particulièrement à **Ninon** et **Thibaut**.

Un petit mot pour toi **Ben**, toi qui connais les coulisses de cette thèse. Je suis reconnaissant de toute l'aide que tu m'as apporté, tes conseils, tes idées, ton efficacité et ton soutien. J'ai beaucoup appris avec toi, et je t'en remercie.

Samson, merci. C'est par opposition à la longueur de mon propos que je souhaite t'exprimer l'ampleur de mes remerciements. Merci pour tout, vraiment.

Marie, merci de ton soutien durant les épreuves de la vie, de la thèse et surtout sur la fin qui n'a pas été de tout repos. Merci d'être la personne que tu es, et merci pour tous les moments que nous avons partagés et pour ceux qui arrivent. Merci pour les grandes sorties : l'Afrique du Sud, l'Islande, mais aussi pour les plus modestes : sorties oiseaux où nous partons à 18h sous la pluie (en espérant qu'elle s'arrête avant d'arriver au spot) dans l'espoir de trouver 2 chouettes. Merci pour tout !

Et pour finir, j'adresse mes plus chaleureux remerciements à vous ma famille sans qui je ne serais pas arrivé jusqu'ici. Merci à mes parents, **Chrystelle** et **Stéphane**, pour votre soutien, votre compréhension et votre amour durant toutes ces années. J'espère que vous serez fiers de moi. Je remercie les beau-parents : **Thierry** et **Delphine**, qui eux, bien que

contraints à me supporter, ont aussi joué un rôle important dans ma construction. **Mélodie**, **Matys**, merci d'être vous, ma sœur, mon frère, vous avez des rôles clés dans ma vie. Les mots sont faibles pour exprimer toute ma gratitude, mais le cœur y est. Aux membres élargis de ma famille, merci de m'avoir encouragé et fait vivre tant de moments de joie.

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I. Introduction

I.1. Se déplacer, une question de survie nécessitant de multiples décisions

I.1.1. Patrons de déplacement : résultats observables d'une suite de décisions

Le déplacement est une caractéristique fondamentale du règne animal. Défini comme le changement d'emplacement d'un organisme dans le temps, le déplacement représente une condition *sine qua non* à la survie d'un organisme. Ainsi, au moins une fois dans leur vie les animaux se déplacent, même ceux considérés comme sessiles tel que les bivalves (Haris, 1990). A l'état larvaire, les bivalves forment le zooplancton et peuvent entreprendre des migrations verticales dans la colonne d'eau (Bandara et al., 2021). Même après s'être installées sur des rochers, les moules (*Dreissena polymorpha*) adultes peuvent encore ajuster leur position (Toomey et al., 2002). Bien qu'omniprésents dans le règne animal, les patrons de déplacements prennent des formes très variées (Teitelbaum & Mueller, 2019). Par exemple, certains animaux sont fidèles à un lieu particulier (*e.g.* colonie/nid) et y retournent fréquemment (Harel et al., 2016; Rosenberg & McKelvey, 1999), alors que d'autres alternent entre deux lieux, potentiellement très éloignés l'un de l'autre, au rythme des saisons (*i.e.*

espèces migratrices, Alerstam et al., 2003). Certains vont restreindre leurs déplacements dans une zone particulière formant leur domaine vital (Burt, 1943) alors que d'autres au contraire explorent de nouveaux endroits pour tout ou partie de leur vie, ces derniers étant considérés comme nomades (Wheat et al., 2017). La diversité de ces patrons de déplacement est le résultat observable des décisions prises par les animaux avant et pendant le déplacement, à la lumière de leur état interne, de leurs capacités de locomotion, de navigation et en réponse aux facteurs environnementaux (Nathan et al., 2008). Ces trois composantes inhérentes à l'animal ainsi que les facteurs environnementaux sont combinés par Nathan *et al.* (2008) dans le cadre du paradigme de l'écologie du déplacement (Figure I.1) afin d'appréhender les patrons de déplacement observés de manière holistique.

Pourquoi se déplacer ? Surveiller son territoire (*e.g.* comportement de patrouille, Watts & Mitani, 2001), éviter les prédateurs (*e.g.* Laundré et al., 2001; Laundre et al., 2010; Lima & Dill, 1990), se reproduire (*e.g.* dispersion à la maturité sexuelle, Bowler & Benton, 2005) ou rechercher de la nourriture (Pinaud & Weimerskirch, 2007) sont autant de motivations internes qui peuvent pousser un individu à se déplacer. En effet, les proies, par exemple, ont tendance à éviter les zones dans lesquelles le risque de prédation est élevé, impactant leur domaine vital mais aussi leurs stratégies de recherche alimentaire (Creel et al., 2005; Hernández & Laundré, 2005; Tolon et al., 2009). Le statut de reproduction et les traits d'histoire de vie d'un individu peuvent aussi largement influencer ses patrons de déplacement. À l'inverse des organismes ayant des traits d'histoire de vie de type r (*i.e.* durée de vie réduite et forte fécondité, Stearns, 1992), ceux de type K (longévif et fécondité faible, Stearns, 1992), qui souvent possèdent un investissement parental important, doivent ajuster leur aire de prospection en période d'élevage de façon à maximiser le gain énergétique par unité de temps, pour optimiser la survie de leur progéniture (Drent & Daan, 1980). L'état interne de l'individu définit donc sa motivation à entreprendre un déplacement et représente la première brique du paradigme de l'écologie du déplacement.

Où aller ? Décider où se déplacer implique que l'animal ait une idée de ce qu'il peut trouver, où et quand il peut le trouver. Pour cela, les animaux sont capables de collecter un certain nombre d'informations sur leur environnement au travers de leurs sens (Dall et al., 2005). De manière très directe, écouter les signaux d'écholocation des autres chauves-souris à la recherche de proies (Dechmann et al., 2009), ou observer des oiseaux marins plonger à la recherche de poissons (Thiebault et al., 2014) permet respectivement aux petits noctilions (*Noctilio albiventris*) et aux fous du Cap (*Morus capensis*) en quête de nourriture d'obtenir des informations cruciales quant à la disponibilité de nourriture. Décider où aller peut aussi s'appuyer sur une connaissance à long terme de certains patrons spatio-temporels de disponibilité d'une ressource, créés par l'intermédiaire de processus cognitifs tels que l'apprentissage et la mémoire. À force d'expérience et d'interaction avec l'environnement, ces processus permettent aux animaux d'interpréter les informations collectées, de les conserver et d'élaborer une représentation mentale de leur environnement (Fagan et al., 2013; Gallistel, 1993; Shettleworth, 2001). Par exemple, certaines espèces telles que le guillemot de Troïl

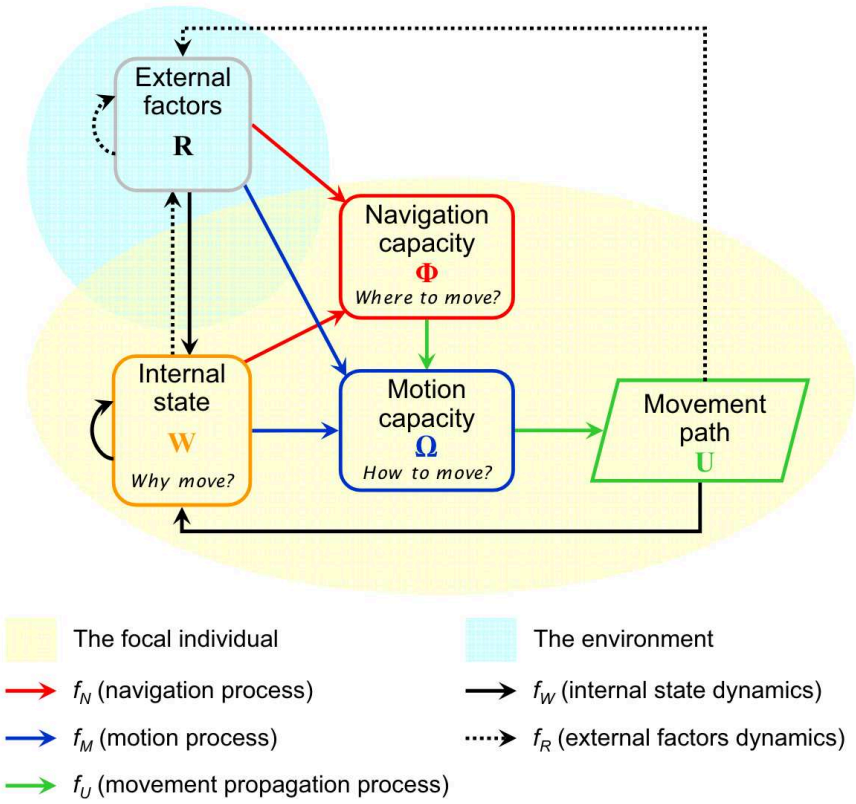


Figure I.1 : Paradigme de l'écologie du déplacement. La fond jaune regroupe les composantes liées à l'individu : son état interne (orange), ses capacités de locomotions (bleu) et de navigation (rouge). La quatrième composante, en gris sur le fond bleu, représente l'ensemble des facteurs externes susceptibles d'influencer le déplacement de l'individu. Les flèches indiquent les relations d'influence entre les différentes composantes. Adapté et traduit depuis Nathan et al. (2008).

(*Uria aalge*, Montevecchi et al., 2003) ou le fou de Bassan (*Morus bassanus*, Davoren et al., 2010) semblent mobiliser leur mémoire pour prendre la direction des régions où la densité de proie est élevée. En route vers une zone mémorisée, l'animal continue potentiellement à traiter des signaux sensoriels afin de maintenir le bon cap ou de naviguer au mieux dans l'environnement. Lors de leur voyage vers leurs zones d'hivernage ou de reproduction, de nombreuses espèces d'oiseaux migrateurs comme le bruant à couronne blanche (*Zonotrichia leucophrys gambelii*), mais aussi les tortues vertes (*Chelonia mydas*), utilisent des repères magnétiques comme boussoles naturelles pour ajuster leurs trajectoires (Åkesson et al., 2005; Åkesson & Hedenström, 2007; Benhamou et al., 2011; Luschi et al., 2007). Par conséquent, les capacités de navigation et les capacités cognitives des organismes jouent un rôle déterminant dans les prises de décisions et les patrons de déplacements qui en résultent.

Comment s'y rendre ? Les capacités de locomotion, qui correspondent à la capacité d'un individu à se mouvoir, limitent les alternatives lorsqu'il s'agit de savoir comment se rendre dans un endroit visé. Le mode de locomotion d'un individu est le résultat de l'interaction entre ses propriétés biomécaniques (systèmes musculaire, squelettique, nerveux, respiratoire et circulatoire) et son environnement (Dickinson et al., 2000). En réponse à ces

contraintes et pour y faire face, plusieurs modes de déplacements ont été sélectionnés, comme la marche, la course ou le saut en milieu terrestre, la nage en milieu aquatique ainsi que le vol en milieu aérien. Chez les oiseaux, des caractéristiques comme la taille des individus et leur charge alaire (*i.e.* le rapport entre sa masse et la surface portante de ses ailes) contraignent fortement la technique de vol. Certaines espèces se sont spécialisées dans le vol battu (*e.g.* passereaux, canards), alors que d'autres, les plus lourds, comme les albatros ou les rapaces n'utilisent quasiment que le vol plané. Ce type de vol est nettement plus économique en termes de dépenses énergétiques (Duriez et al., 2014; Shepard, 2022).

Au-delà des trois composantes précédentes inhérentes à l'animal, des facteurs externes peuvent aussi jouer un rôle clé dans les patrons de déplacement observés chez les animaux. Les conditions météorologiques et la configuration du paysage ont le potentiel d'influencer les déplacements aériens. Comme l'eau, l'air est un fluide dynamique dans lequel la force des courants, les turbulences ou même les courants ascendants peuvent réduire ou augmenter les coûts de déplacement des animaux en fonction des conditions locales (Alma et al., 2016; Chapman et al., 2011; Shepard et al., 2013), ce qui a un impact sur les niveaux d'activité des individus (*e.g.* chez les insectes : Mason, (2017), les chauves-souris : Safi et al., (2013), les oiseaux : Kogure et al., (2016)). La présence de congénères au travers de décisions à la majorité lors des déplacements (Strandburg-Peshkin et al., 2015), de compétiteur autour des ressources (Papageorgiou & Farine, 2020) ou même de potentiels prédateurs par le risque qu'ils imposent (Lima & Dill, 1990) façonnent eux aussi les patrons de déplacements dans le paysage. Enfin, de nombreuses études montrent que les niveaux d'hétérogénéité et l'imprévisibilité des sources de nourriture peuvent avoir un fort impact sur les déplacements des organismes et cela à plusieurs échelles, depuis le choix des sites de haltes migratoires (Gillespie & Fontaine, 2017), jusqu'aux stratégies de recherche alimentaire. Selon le gradient de prévisibilité de la ressource, les stratégies de recherche peuvent aller d'un déplacement aléatoire jusqu'à un trajet stéréotypé et répété (Riotte-Lambert et al., 2017; Riotte-Lambert & Matthiopoulos, 2020; Tello-Ramos et al., 2015).

I.1.2. La recherche de nourriture : une activité cruciale dans la vie des animaux

Parmi les multiples activités qui occupent la vie quotidienne des animaux, se nourrir pour acquérir l'énergie nécessaire à leurs fonctions vitales, à leur croissance, à leur survie et à leur reproduction est crucial (Roff, 1993). L'approvisionnement (« foraging » en anglais) regroupe plusieurs phases, la recherche, la manipulation et la consommation d'une source de nourriture. L'optimisation des stratégies d'approvisionnement, par l'action concomitante des mutations et de la sélection naturelle, générations après générations, agit sur ces phases, favorisant les individus qui maximisent les bénéfices et/ou minimisent les coûts associés à la recherche, la manipulation et à la consommation de la ressource. Cette optimisation du gain énergétique net à long terme, supposé être une composante majeure du succès reproducteur des individus (« fitness », Cezilly & Benhamou, 1996), est un point central dans la théorie de l'approvisionnement optimal (Pyke, 1984; Stephens, 2008; Stephens & Krebs, 1986;

Weimerskirch, 2018). Le compromis entre l'énergie acquise et l'énergie ou le temps consacré à son acquisition est fortement influencé par la source de nourriture elle-même, par sa prévisibilité dans l'espace et dans le temps et par sa qualité nutritionnelle, mais aussi par les stratégies que les animaux emploient pour choisir, rechercher, manipuler et consommer leur nourriture. Dans cette thèse, je me concentrerai sur la première phase, chercher et trouver une source de nourriture dans l'environnement. Pour ce faire, les animaux doivent prendre une multitude de décisions afin de maximiser leur taux de rencontre avec la source de nourriture et, en fin de compte, élaborer des stratégies de recherche spécifiques (Bell, 2012). Par exemple, les hérons alternent entre des déplacements et des phases d'embuscade précédant les captures, tandis que les abeilles mellifères se déplacent dans l'environnement à la recherche de fleurs porteuse de nectar. Ces stratégies, respectivement d'embuscade et de maraude, nécessitent de décider quand se déplacer, à quelle vitesse, dans quelles directions, etc. Ces décisions influencent largement les chances de trouver des ressources (Alpern et al., 2011; Bartumeus et al., 2016; Pyke, 1984).

Dans l'environnement, les ressources sont souvent distribuées de manière hétérogène dans l'espace (Charnov, 1976; MacArthur & Pianka, 1966) : abondantes et regroupées dans des parcelles, rares voir complètement absentes entre celles-ci. Le concept est facilement visualisable au travers d'exemples tels que les bancs de poissons dans l'océan recherchés par des dauphins, ou encore un massif de fleurs au sein d'un jardin dans lequel peuvent butiner des abeilles. La disponibilité des ressources alimentaires est aussi plus ou moins prévisible dans le temps et dans l'espace (Riotte-Lambert & Matthiopoulos, 2020). Les fleurs, agrégées dans le massif et se remplissant de nectar à un rythme spécifique représentent une source de nourriture particulièrement prévisible pour les bourdons ou les colibris (Temeles et al., 2006; Thomson, 1996). A l'inverse, prédire où et quand un banc de poisson sera disponible dans l'immensité de l'océan semble bien plus complexe. Optimiser la recherche de nourriture revient donc à savoir où aller afin de cibler le bon endroit au bon moment et ainsi réduire au maximum la probabilité de ne pas trouver de nourriture. Pour cela, il est nécessaire que les individus acquièrent et utilisent les informations disponibles dans l'environnement afin de prendre des décisions adaptées en réponse à cet environnement changeant (Dall et al., 2005).

L'optimisation du gain énergétique net à long terme peut aussi passer par l'optimisation du déplacement en lui-même lors de la recherche de nourriture. Les animaux se déplacent dans des milieux hétérogènes, dont les caractéristiques physiques dictent la dépense d'énergie nécessaire au déplacement et façonnent un « paysage énergétique » (Shepard et al., 2013). L'énergie physique disponible dans ce paysage énergétique influence grandement les stratégies de déplacement des animaux : exploitation des vents favorable par les espèces aériennes (Weimerskirch et al., 2000) ou des courants par les espèces aquatiques (Johansen et al., 2020; Mansfield et al., 2017) ; a contrario l'évitement des pentes abruptes, de la végétation dense et des couvertures neigeuses pour les espèces terrestres (Carnahan et al., 2021; Halsey & White, 2017; Lempidakis et al., 2018; Strandburg-Peshkin et al., 2017). Spécifiquement, le milieu aérien est hétérogène, dynamique et difficile à prévoir. Il offre des conditions de vol qui peuvent très rapidement changer et donc drastiquement impacter le coût énergétique du vol. Le vol étant le mode de déplacement le plus coûteux en énergie chez les

vertébrés (Norberg, 1996), pour les oiseaux a la recherche d'une source de nourriture imprévisible, la collecte d'informations devient cruciale non seulement pour qu'ils puissent prendre des décisions leur permettant de maximiser leur probabilité de trouver de la nourriture, mais aussi afin de réduire au maximum leurs coûts de déplacement (Dall et al., 2005; Williams & Safi, 2021).

I.2. Utilisation de l'information: pour le prochain « pas » et jusqu'à la stratégie de recherche alimentaire

I.2.1. Nature des informations disponibles

Selon Danchin et al., (2004) deux catégories principales d'informations sont accessibles ou générées par les individus : les informations personnelles et les informations sociales. Les informations personnelles sont acquises par le biais d'une perception directe par l'individu de l'environnement auquel il est exposé (*i.e.* par l'intermédiaire de ses sens). Ces informations peuvent être mémorisées et remobilisées lors de décisions futures. Les informations sociales, quant à elles, sont obtenues indirectement par l'observation des interactions entre d'autres individus et l'environnement. Parmi les informations sociales, on distingue les signaux volontaires (*e.g.* les vocalisations pour signaler la présence d'un prédateur, Gill & Bierema, 2013) des signaux involontaires (*e.g.* les déplacements comme marqueur de la possibilité de se mouvoir dans ces conditions environnementales, Okasaki et al., 2020; Williams et al., 2018). Ces derniers ne pouvant pas être cachés sont donc qualifiés d'informations publiques (Valone, 1989, 2007). L'acquisition d'information sociale est coûteuse en énergie car elle nécessite de maintenir une attention aux diverses sources d'information et d'être capable de les interpréter (Dunlap & Stephens, 2016; Jaumann et al., 2013; Kotrschal et al., 2013). En revanche, dès lors que l'information personnelle est plus coûteuse à acquérir, ou ne réduit pas suffisamment l'incertitude face à une situation, alors ces informations sociales procurent des bénéfices. En utilisant ces différentes sources d'informations pour anticiper ou réagir à l'environnement auquel ils sont ou seront confrontés, les animaux peuvent ainsi produire une réponse plus efficace (Thiebault et al., 2014).

I.2.2. Influence de la prévisibilité de la ressource sur l'utilisation de l'information dans les stratégies de recherche

Lors de la recherche d'une ressource prévisible dans le temps et/ou l'espace, l'utilisation d'information personnelle basée sur la mémoire d'expériences passées peut être avantageuse. Par exemple, après avoir détecté et mémorisé le rythme de production de nectar des fleurs, certains animaux développent un comportement de prospection routinière des inflorescences. Ils peuvent ainsi visiter les inflorescences dans un ordre précis et répétitif, avec un intervalle de temps entre les visites calé sur le rythme de remplissage des fleurs, afin d'arriver successivement sur les sites où la probabilité de trouver la ressource est la plus

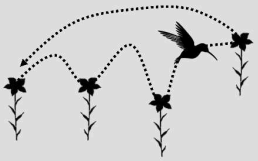
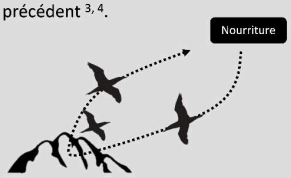
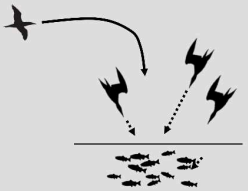
Ressource alimentaire	Prévisible (spatialement ou temporellement)	Imprévisible (disponibilité > 1 aller/retour)	Imprévisible (disponibilité < 1 aller/retour)
Stratégie de prospection	**Prospection routinière (« traplining »)** : l'individu visite de façon répétée, suivant une séquence ordonnée, certains sites [1], ou le fait de manière périodique, à intervalles de temps réguliers [2]. 	**Centre d'information** : partage passif d'information par un individu de retour d'un site d'alimentation, à la colonie. Il peut être suivi lorsqu'il repart, car il est probable qu'il repart sur le site précédent [3, 4]. 	**Recrutement local**: Regroupement d'individus autour d'une source de nourriture à la suite d'une détection opportuniste du comportement alimentaire d'autres individus [5].  **Réseau**: Organisation spatiale synchronisée permettant aux individus d'optimiser la prospection en gardant un contact visuel avec les congénères [6]. 
Utilisation d'information sociale	- (pas nécessaire)	+ (obligatoire)	+ (obligatoire)

Figure I.2 : Illustration des relations entre prévisibilité de la ressource, stratégie de prospection alimentaire et informations utilisées. 1 : Tello-Ramos et al. 2015 ; 2 : Berger-Tal & Bar-David, 2015 ; 3 : Tremblay et al. 2014 ; 4 : Harel et al. 2017 ; 5 : Thiebault et al. 2014 ; 6 : Assali et al. 2017.

grande. Ce comportement routinier (souvent appelé « traplining », par analogie au trappeur réalisant régulièrement le même circuit pour relever ses pièges, Figure I.2) a été décrit chez différentes espèces de mammifères (Garber, 1988; Lemke, 1984), oiseaux (Tello-Ramos et al., 2015) et insectes (Janzen, 1971; Lihoreau et al., 2013). Cette stratégie permet de minimiser la distance parcourue et le temps investi dans la recherche de la ressource tout en maximisant le gain énergétique puisque la probabilité de trouver des ressources régulièrement renouvelées est élevée. Ainsi, du point de vue de la théorie de l'approvisionnement optimal, le traplining est une stratégie optimisant l'équilibre coût/bénéfice face à une ressource alimentaire prévisible dans le temps et l'espace.

Pour les ressources réparties de manière hétérogène dans l'environnement, éphémères et imprévisibles, l'utilisation exclusive d'informations personnelles pour les décisions de déplacement peut être sujette à des erreurs (Fawcett et al., 2014). L'acquisition d'informations actualisées permet de réduire l'incertitude quant à la disponibilité d'une ressource, ce qui conduit à un déplacement plus efficace (où les gains sont supérieurs aux coûts, par unité de temps). Prenons pour exemple le cas des grands oiseaux planeurs comme le condor des Andes (*Vultur gryphus,* Shepard et al., 2011) ou encore les cigognes blanches (*Ciconia ciconia,* Nagy et al., 2018), qui prennent de la hauteur en s'élevant dans les courants d'air ascendants, et convertissent la hauteur acquise en distance en planant à travers le paysage, jusqu'au courant ascendant suivant. Une fois que la décision de quitter un courant ascendant est prise, ils doivent s'assurer que le vol plané les mènera au courant ascendant suivant avant

d'atteindre le sol. Bien que les caractéristiques du paysage et les conditions météorologiques puissent être utilisées par l'oiseau pour se rendre dans des zones favorables à la présence de courants ascendants, ces ressources éphémères peuvent ne pas être disponibles lorsque l'oiseau en aura besoin (Williams et al., 2020). La présence d'un individu prenant de la hauteur indique la présence d'un courant ascendant et transmet involontairement cette information aux autres oiseaux partageant le même espace aérien. L'utilisation de cette information sociale pourrait réduire drastiquement l'incertitude d'un individu autour de la découverte de son prochain courant ascendant. Ceci éviterait à l'individu de subir les coûts énergétiques associés au vol battu et/ou à un nouveau décollage dans le cas où aucun courant ascendant n'a été trouvé (Duriez et al., 2014). Cette utilisation d'information sociale devrait faciliter la prise de décision individuelle dans tout système où des individus cherchant la même ressource partagent un espace (*e.g.* chez les babouins olive, *Papio anubis*, Strandburg-Peshkin et al., 2017). Ce devrait aussi être le cas lorsque des preuves de leurs déplacements persistent dans le paysage sous la forme d'indices qui se dégradent progressivement. Pour les espèces terrestres par exemple, les empreintes et les pistes laissées aux abords des rives d'un cours d'eau indiquent probablement un chemin approprié pour le traverser. Ainsi, les individus en déplacement fournissent involontairement des informations cruciales concernant le paysage énergétique, qui pourraient être collectées et utilisées par d'autres afin d'effectuer un déplacement optimal (Shepard et al., 2013; Williams & Safi, 2021).

Alors que l'utilisation combinée de ces deux sources d'information pour réduire l'incertitude sur la disponibilité de la ressource physique nécessaire au déplacement est peu documentée, leur utilisation dans la recherche de nourriture est bien connue. Chez les oiseaux marins par exemple, se fier uniquement à la détection visuelle directe des bancs de poissons, dans un environnement aussi vaste et dynamique que l'océan, représenterait un effort considérable. Par conséquent, ils ne se concentrent pas seulement sur la recherche de nourriture, mais aussi sur la collecte d'indices de présence des proies par l'intermédiaire d'autres individus, potentiellement d'espèces différentes (Tremblay et al., 2014). Inféodés au milieu terrestre de par leur mode de reproduction, ces oiseaux effectuent des va-et-vient entre l'océan pour trouver de la nourriture et la colonie pour nourrir leurs poussins, un comportement qualifié d'approvisionnement à partir d'un lieu central (« central-place forager » en anglais). La colonie et les radeaux (groupe d'oiseaux posés à la surface de l'eau aux abords de la colonie) jouent le rôle de « centre d'information » (Figure I.2) où les individus ne s'étant pas nourri peuvent récupérer des informations sur la localisation d'une ressource. En suivant des oiseaux s'étant manifestement déjà nourris lorsque ces derniers repartent du nid, ou en partant dans la direction opposée à ceux qui rentrent d'une zone de nourrissage, ils débutent ainsi leur trajet vers une source potentielle de nourriture (Burger, 1997; Thiebault et al., 2014; Ward & Zahavi, 1973; Weimerskirch et al., 2010). Une fois en mer, les oiseaux sont attirés par la présence, le comportement de chasse et de nourrissage de prédateurs de sub-surface (poissons et mammifères marins) et d'autres oiseaux (conspécifiques ou hétérospécifiques) qui renseignent de la présence de nourriture (*e.g.* chez les fous du Cap, Thiebault et al., 2014). Ce processus de recrutement local (« local-enhancement » en anglais,

Figure I.2, Pöysä, 1992; Thorpe, 1956) donne lieu à des concentrations d'oiseaux en groupes mono-spécifiques ou pluri-spécifiques autour de bancs de proies.

À plus grande échelle, les individus conservant des individus éloignés dans leur champ de perception, pourraient également détecter des changements dans le comportement de ces individus, et ainsi de groupes éloignés, indiquant la découverte de nourriture. Dès lors, ils obtiendraient cette information et convergeraient vers le point d'intérêt. L'information se propagerait ainsi de groupes en groupes, et atteindrait des individus qui n'y auraient pas eu accès par détection directe. En considérant les groupes d'oiseaux marins comme des nœuds et le transfert d'informations comme des liens, une stratégie de recherche en réseau (« foraging network » en anglais, Figure I.2) pourrait émerger de cette distribution d'oiseaux marins. Les individus formant ce réseau bénéficieraient d'un effort de recherche multiplié par le nombre de participants, diminuant par conséquent le temps de recherche de nourriture. Ce processus a récemment été observé en milieu marin (Assali et al., 2017), et suggéré depuis longtemps chez des espèces terrestres comme les vautours à la recherche de carcasses (Houston, 1974; Jackson et al., 2008). Ainsi, à partir des décisions individuelles basées sur l'utilisation combinée d'informations personnelles et sociales, une stratégie de recherche collective à plus grande échelle peut émerger.

I.2.3. Coûts potentiels de l'utilisation de l'information sociale

Ces stratégies de recherche collective, reposant sur le partage d'information, entraînent l'agrégation rapide d'un grand nombre d'individus sur la même zone et impliquent un partage de la ressource. Si l'information est diffusée involontairement, le premier individu à exploiter la ressource, qui a investi du temps et de l'énergie pour la découvrir, peut pâtir de la venue d'autres individus. Dans le cas d'une ressource épuisable et/ou monopolisable, la compétition entre individus pour la ressource peut devenir importante, impactant plus souvent les individus en bas de la hiérarchie de dominance (Goss-custard et al., 1998; Stillman et al., 2000). Cette influence de la hiérarchie sur les stratégies de recherche de nourriture, où les individus de rang inférieur explorent et trouvent de la nourriture alors que les dominants en profitent, a été observée chez certaines espèces d'oiseaux sociaux comme la grue cendrée (*Grus grus*), l'huîtrier-pie (*Haematopus ostralegus*), le moineau domestique (*Passer domesticus*) ou encore la bernache nonnette (*Branta leucopsis*) (Alonso et al., 1997; Liker & Barta, 2002; Stahl et al., 2001; Stillman et al., 2000).

Un système où le découvreur, qui devient l'informateur, est désavantagé par rapport aux individus naïfs, qui deviennent informés de la présence de ressource sans effort de recherche, a été décrit comme celui d'un jeu entre producteurs (d'information) et chapardeurs (système « producers-scroungers », Barnard & Sibly, 1981). Bien que le modèle original considère les individus comme spécialisés dans l'une ou l'autre des deux stratégies, les modèles décrivant les stratégies d'utilisation de l'information au sein d'un groupe lors de la recherche de nourriture prédisent que les individus alternativement produisent ou profitent de l'information (Clark & Mangel, 1984; Giraldeau & Dubois, 2008; Mesoudi et al., 2016). En effet, pour que le partage d'information au sein des stratégies de recherche alimentaire soit

maintenu au cours de l'évolution, il est nécessaire que le coût individuel du partage de la ressource soit inférieur aux bénéfices apportés par l'échange de cette information. Par exemple, l'échange d'information sur la localisation des proies peut bénéficier aux prédateurs en augmentant leur taux de rencontre avec des proies (Boyd et al., 2016; Thiebault et al., 2014) et/ou en augmentant leur taux de capture de proies (Thiebault et al., 2016).

Par conséquent, chez les espèces sociales, les individus doivent relever le défi de trouver un compromis entre ces bénéfices associés à l'utilisation d'information sociale et les coûts dûs notamment à la compétition pour la ressource. Ce compromis détermine en fin de compte l'équilibre entre l'utilisation des informations personnelles et sociales dans la recherche d'une ressource imprévisible.

I.3. Les grands planeurs comme sujet d'étude, cas des vautours (fauves)

I.3.1. Une double contrainte: se déplacer avec les ascendances, se nourrir sur des carcasses

Les vautours sont des oiseaux charognards, regroupés au sein de deux familles géographiquement et taxonomiquement distinctes (Jarvis et al., 2014) : les Accipitridae d'une part, 15 espèces réparties dans les régions dites de l'Ancien Monde (Afrique, Asie et Europe), et les Cathartidae d'autre part, sept espèces distribuées sur l'ensemble du continent Américain, dans les régions dites du Nouveau Monde. Leurs ressemblances morphologiques et comportementales résultent d'un processus de convergence évolutive (Hertel, 1994) vers une niche écologique commune : les vautours sont les seuls vertébrés terrestres nécrophages obligatoires (Campbell, 2015; Ruxton & Houston, 2004).

Les nécrophages obligatoires sont dépendants de la disponibilité en cadavres d'animaux, aussi bien sauvages que domestiques (Campbell, 2015), pour leur survie et leur reproduction. En réponse à ce régime alimentaire très spécifique, les vautours ont dû s'adapter pour chercher, trouver et consommer une source de nourriture dont la disponibilité est éphémère et imprévisible aussi bien dans le temps que dans l'espace (Cortés-Avizanda et al., 2014; Yang et al., 2008). N'ayant pas les adaptations morphologiques pour tuer (*i.e.* des serres sans forces de préhension avec de courtes griffes émoussées) et comme il est difficile de prédire où et quand un animal va mourir de manière naturelle, les vautours sont contraints de se déplacer sur de grandes distances tous les jours pour espérer trouver un animal mort, et ainsi compenser l'imprévisibilité spatiale et temporelle de leurs ressources alimentaires. Malgré leur très bonne acuité visuelle (Mitkus et al., 2018) et pour certains vautours du Nouveau Monde un très bon odorat (Potier et al., 2019) leur permettant de localiser les carcasses de loin, il n'est pas rare qu'ils ne trouvent pas de quoi se nourrir pendant plusieurs jours. En conséquence, il est crucial pour ces oiseaux d'économiser au maximum l'énergie acquise par l'alimentation dans tous leurs comportements.

Les vautours possèdent un métabolisme de base relativement bas (Prinzinger et al., 2002) et sont également capables de stocker de grandes réserves énergétiques leur permettant

de jeûner plusieurs jours, et jusqu'à trois semaines (Bahat, 1995; Bahat et al., 1998; Spiegel et al., 2013). Mais comment concilier le besoin de parcourir plusieurs dizaines, voire centaines, de kilomètres par jour tout en économisant l'énergie, alors que le vol est le mode de déplacement le plus coûteux en énergie chez les vertébrés (Norberg, 1996) ? Les vautours ont donc dû adopter un type de vol peu coûteux en énergie : le vol à voile. Le vol à voile consiste essentiellement à planer, en utilisant les différents courants d'air ascendants disponibles dans l'environnement pour reprendre de la hauteur, le tout en évitant au maximum de battre des ailes (Pennycuick, 1972; Shepard, 2022; Shepard et al., 2011). Par exemple, le plus grand rapace terrestre volant du monde, le condor des Andes, utilise cette technique pour voler des heures durant en ne battant des ailes qu'un pourcent du temps (Williams et al., 2020). Ces rares battements sont associés quasi-exclusivement au décollage et à l'atterrissage. En vol, la dépense énergétique des vautours est extrêmement basse, équivalente à celle lorsqu'ils sont posés, au repos (Duriez et al., 2014).

Afin de se déplacer tout au long de la journée sans battre des ailes, ces grands planeurs utilisent deux types de courants d'air ascendants : les ascendances thermiques et les ascendances orographiques (Figure I.3). Ces dernières sont produites à l'issue de la rencontre du vent avec un relief qui dévie la masse d'air vers le haut de la pente. En volant parallèlement au relief (Duerr et al., 2015), les vautours stabilisent leur hauteur de vol, voire même gagnent de la hauteur, tout en poursuivant leur trajet. Les ascendances thermiques, quant à elles, se matérialisent sous la forme de bulles d'air chaud émanant des surfaces exposées au soleil. Ces bulles d'air s'élèvent alors dans le ciel. À la manière d'un ascenseur, les vautours entrent dans ces bulles, décrivent des cercles pour s'y maintenir et gagnent de la hauteur sans effort (la vitesse de chute de l'oiseau (généralement inférieure à 1 m/s) étant surpassée par sa vitesse d'ascension dans la bulle d'air chaud (entre 1 et 5 m/s, Williams et al., 2018). La bulle d'air se dilate en montant, ce qui permet aux oiseaux de décrire des cercles de plus en plus grands au fur et à mesure de leur ascension (diamètre variant entre 40 et 120 m, Williams et al., 2018). Avec l'augmentation du diamètre des cercles ils peuvent réduire leur angle d'inclinaison, ils deviennent ainsi plus efficaces et accélèrent leur vitesse ascensionnelle.

Alors que les ascendances orographiques sont relativement prévisibles, puisqu'il suffit qu'il y ait du vent et de détecter sa direction pour prédire au-dessus de quelles pentes il faut se placer pour bénéficier de l'ascendance, les ascendances thermiques sont beaucoup plus éphémères et imprévisibles. En effet, bien qu'il y ait des zones propices à la formation de thermiques, ou qu'elles soient rendues visibles par la formation de cumulus lorsqu'elles touchent la couche limite et condensent, elles ne produisent pas de flux continus d'air ascendant. L'air s'élève plutôt en séquences de bulles ou d'anneaux plus ou moins rapprochés dans le temps (Bradbury, 1989; Shepard, 2022). Il peut arriver que des thermiques soient alignés et successivement disponibles, formant des « routes de thermique » (« thermal streets ») dans lesquels les vautours peuvent maintenir leur altitude de vol, voir en gagner, tout en maintenant un déplacement rectiligne (« linear soaring », Pennycuick, 1998). Après être sortis d'un thermique, lors de la phase de plané, si les vautours ne parviennent pas à détecter un nouveau courant ascendant, ils peuvent être contraints de passer au vol battu, ou pire,

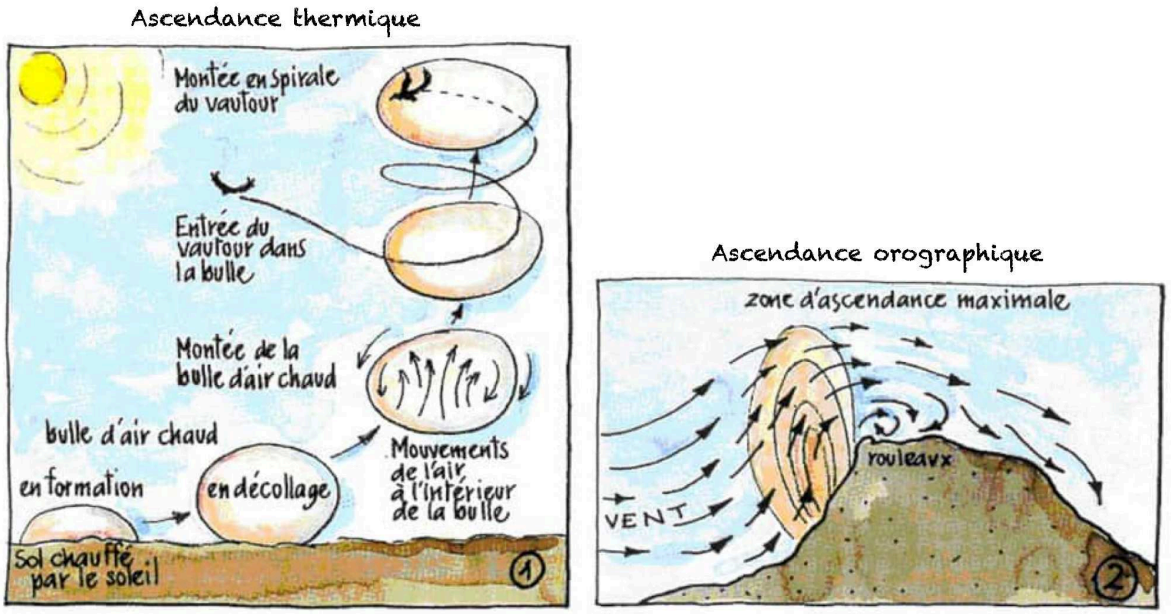


Figure I.3 : Différents types de courants ascendants utilisés par les oiseaux planeurs. (1) Représente le processus de formation d'une ascendance thermique. Le soleil chauffe le sol, lui-même par son rayonnement chauffe l'air à proximité, qui s'élève sous forme de bulles. (2) Il y a création d'une ascendance orographique dès lors que le vent heurte un relief et s'élève le long de la pente. © *Mouze 1998.*

d'atterrir et de décoller à nouveau, ce qui augmente considérablement leur dépense énergétique (Duriez et al., 2014; Horvitz et al., 2014). Ainsi, les vautours, qui ont tendance à principalement utiliser des ascendances thermiques (Scacco et al., 2023), sont doublement contraints. Premièrement, ils sont contraints par la nécessité de trouver des ascendances thermiques afin d'explorer le paysage. Ceci est d'autant plus vrai pour le vautour fauve (*Gyps fulvus*) qui, possedant une envergure variant entre 2,4 et 2,8 m et une surface alaire de 1 m² pour un poids de 8 à 11 kg, a la charge alaire la plus importante des grands vautours, avec 8 kg/m^2 contre 6.3 et 5.6 kg/m^2 pour le vautour moine (*Aegypius monachus*) et le gypaète barbu (*Gypaetus barbatus*) respectivement (Campbell, 2015; Duriez données non publiées). Pour prendre de la hauteur il a donc besoin de courants ascendants plus puissants que ce qui est nécessaire pour les autres espèces de grands vautours européens. Et deuxièmement, ils sont aussi contraints par la nécessité de trouver des carcasses pour survivre et se reproduire.

I.3.2. Bénéfices et coûts de la recherche en groupe

Les vautours peuvent compter sur leurs congénères pour les aider à trouver ces ressources dans leur environnement. En effet, le vautour fauve, la plus sociale des quatre espèces européennes, niche en colonies, sur des falaises, avec des nids espacés de seulement quelques mètres parfois. Lors des déplacements de prospection alimentaire, les vautours semblent former plusieurs petits groupes. Après la découverte d'une carcasse, plusieurs

dizaines, voire centaines de vautours s'agrègent autour et consomment rapidement la viande disponible (Bosè et al., 2012; Moreno-Opo et al., 2015; Mundy et al., 1992). Cette vie permanente en groupe offre une multitude d'opportunités de collecter de l'information sociale pour affiner les décisions individuelles.

À l'instar des oiseaux marins en période de reproduction, les vautours fauves présentent aussi un comportement de « central-place forager » (Harel et al., 2017). Lors du départ en prospection depuis la colonie, le premier défis que ces grands planeurs doivent relever est de trouver des courants ascendants pour prendre de la hauteur. L'utilisation de leur mémoire et de leurs capacités sensorielles peuvent facilement les mener vers des zones favorables à la création d'ascendances, puis en observant les autres oiseaux avec qui ils partagent l'espace aérien, ils peuvent collecter de l'information en temps réel, sur la disponibilité d'une ascendance. Ils l'utilisent ensuite pour adapter leur comportement de vol et leurs trajectoires afin de rejoindre leurs congénères et ainsi profiter de l'ascendance à leur tour (Figure I.4, H. J. Williams, King, et al., 2018). Par conséquent, les individus utilisent un mélange d'informations personnelles et sociales pour savoir où trouver et quand passer au thermique suivant afin de continuer à gagner de la hauteur sans effort.

Une fois en vol, la recherche de nourriture débute. Le défi est à nouveau relativement complexe, trouver via la vue une source de nourriture imprévisible : des carcasses d'animaux, distribuées dans un environnement ouvert, vaste et hétérogène (Campbell, 2015; Ruxton & Houston, 2004). Malgré cette imprévisibilité, ces charognards sont réputés pour leur efficacité à détecter les carcasses dans l'environnement. En effet, quelques minutes seulement après qu'un vautour ait détecté une carcasse, de nombreux congénères venant de toutes les directions tombent du ciel pour se poser autour de la carcasse (Figure I.5A). Ceci est le résultat d'un comportement d'attraction par recrutement local (« local enhancement », décrit de longue date chez les vautours, Buckley, 1996; Houston, 1974) suite à l'interprétation du comportement de l'individu découvreur, qui observe la carcasse en décrivant des cercles en vol descendant, comme signal de la présence d'une carcasse. Les individus les plus proches rejoignent le découvreur au-dessus de la carcasse et adoptent le même comportement, attirant des vautours venant de plus en plus loin, comme une réaction en chaîne (Figure I.4). Pour que l'information de la découverte puisse percoler aussi rapidement, Tristram (1867), cité par Houston (1974) fait l'hypothèse que les vautours se répartissent dans l'espace afin de former un réseau (« foraging network ») dans lequel la distance interindividuelle leur permet de continuellement garder un œil sur leurs congénères en vol, et de rapidement s'agréger dès que l'un d'eux trouve une carcasse (Cortés-Avizanda et al., 2014; Houston, 1974; Jackson et al., 2008). Cette stratégie de réseau, testée par modélisation informatique, serait beaucoup plus efficace que les stratégies basées sur l'utilisation d'information personnelles uniquement (*i.e.* la recherche aléatoire ou le « traplining », démontrée comme marginale, Fluhr et al., 2017; Monsarrat et al., 2013) lorsque les ressources alimentaires sont peu prévisibles et diluées dans le paysage (comme le sont les carcasses, Cortés-Avizanda et al., 2014; Deygout et al., 2010). Bien que cette hypothèse ait été formulée il y a un siècle et demi, testée et prouvée efficace par modélisation informatique, elle n'a jamais été démontrée empiriquement en raison de la difficulté technique d'enregistrer simultanément les positions de plusieurs dizaines de

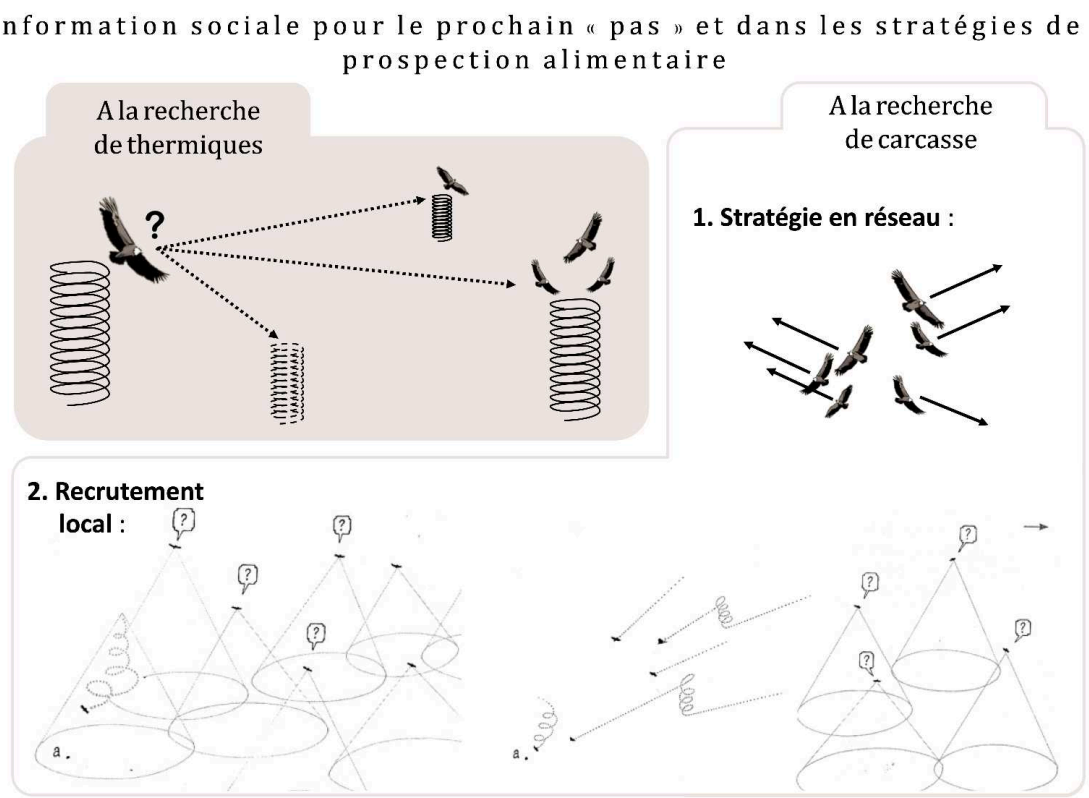


Figure I.4. Utilisation de l'information sociale par les vautours. Les spirales représentent des ascendances thermiques. Par leur vol circulaire et le gain de hauteur, les congénères donnent involontairement une information sur la disponibilité d'un thermique. Lors de la recherche de carcasse, l'hypothèse d'une stratégie en réseau suggère la dispersion de groupes d'individus qui scannent le sol afin d'optimiser la recherche alimentaire tout en gardant leurs congénères en vue. Il peuvent rapidement s'agréger autour de la carcasse (a) par le phénomène de recrutement local. Interprétant le vol circulaire descendant comme un signal de découverte d'une carcasse. © *Adapté de Deygout et al. 2010, pour la stratégie en réseau. Déom, 2008, Volume n°91 de La Hulotte : « Tonton Griffon », pour le recrutement local. Éric Corbeyran et Chico Pacheco, pour les silhouettes de vautours fauves.*

vautours volant à haute altitude, ainsi le doute subsiste quant à l'utilisation de cette stratégie par les vautours.

Une fois rassemblés autour de la carcasse, c'est le moment de la curée, le repas des vautours. Les vautours fauves sont les premiers à intervenir sur une carcasse, ils assurent la majeure partie du travail d'équarrissage et d'élimination des germes pathogènes dans l'écosystème en consommant rapidement les tissus mous comme les viscères et les muscles (Campbell, 2015). Le cadavre est entamé par les orifices naturels et les endroits où la peau est la plus fine. Rapidement plusieurs becs pointus et coupants se mettent à tirer le cuir des animaux dans toutes les directions, accélérant l'accès à la chair. S'ensuit une mêlée dans

Figure I.5 : Le repas des vautours : « La curée ». (A) L'arrivée massive de vautours lorsque le premier individu s'est posé à proximité de la carcasse. (B) La carcasse est entamée, chaque vautours essaie de récupérer sa part, en entrant par les côtés et en ressortant par le dessus. (C) La mêlée vue de l'intérieur, une amat de bec et de plumes à la recherche de leurs mets favoris : viscères, muscles, organes. (D) Au fur et à mesure que la curée avance, la viande sur la carcasse s'amenuise, il faut avoir l'œil pour glaner les derniers morceaux. © *Olivier Duriez pour A, et Bruno Berthemy pour B, C, D.*

laquelle chaque individu engloutit le plus de viande possible en un minimum de temps (Figure I.5B,C). Pour une carcasse de brebis, il faut seulement 20 minutes à une cinquantaine de vautours pour ne laisser que les os à curer (Duriez et al., 2012). Bien que les carcasses soient grosses et partageables, au fur et à mesure de l'arrivé de nouveaux individus (jusqu'à 100-120 individus, Bosè et al., 2012; Moreno-Opo et al., 2015) autour de celles-ci, les taux d'alimentation individuels diminuent en raison d'un accès réduit à la viande, de l'épuisement de la ressource par les concurrents et de l'augmentation des interactions agonistiques (Figure I.5D, Bosè et al., 2012). La hiérarchie de dominance semble jouer un rôle important dans l'accès à la nourriture chez les vautours. Les « pionniers », les tout premiers individus à se poser et à se nourrir sur les carcasses, sont majoritairement des individus de bas rang et sont rapidement évincés par les individus de haut rang qui arrivent par la suite (Bosè et al., 2012). Hormis ces quelques subordonnés qui arrivent à tirer leur épingle du jeu, la majorité des individus de bas rang devront attendre la fin de la curée avant de pouvoir récupérer quelques

restes. D'autre part, l'alimentation en groupe possède certains avantages, comme la détection précoce de perturbations ou de potentiels prédateurs (« many-eyes hypothesis », Guillemain et al., 2002; Pulliam, 1973; Sirot, 2006; Zarus, 1978) mais aussi de se nourrir plus vite et donc de retourner plus tôt dans une zone sûre, à savoir le ciel.

La compétition autour de la carcasse est relativement forte entre individus de la même espèce, mais relativement réduite entre espèces. En effet, les vautours de l'Ancien Monde qui ont évolué conjointement avec les grands mammifères herbivores dont ils consommaient les carcasses (Campbell, 2015; Ruxton & Houston, 2004) ont dû progressivement spécialiser leur régime alimentaire sur des parties différentes du cadavre afin de réduire la compétition. Trois groupes de vautours sont ainsi distinguables (Hertel, 1994), les « tireurs fouilleurs » dont le vautour fauve fait partie, spécialiste de la consommation des tissus mous. Les « déchireurs » se nourrissant des tissus coriaces : peau, cartilages et tendons. En Europe c'est le vautour moine qui s'en occupe. Enfin, les « picoreurs » comme le vautour percnoptère (*Neophron percnopterus*), ramassent les morceaux qui restent et sont bien plus opportunistes dans leur régime alimentaire. Le gypaète barbu quant à lui n'entre dans aucun des groupes de part son régime alimentaire essentiellement composé d'os : il intervient après le passage des trois autres espèces. Ces spécificités entre espèces réduisent la compétition inter-spécifique et permettent leur coexistence en Europe grâce au partage des ressources trophiques (Cortés-Avizanda et al., 2012, 2014). Ces trois groupes interviennent ainsi successivement dans l'élimination des cadavres, on parle cummunément de la « guilde des vautours ».

I.3.3. Une guilde utile et pourtant menacée

La rapidité d'action de la guilde des vautours couplée à l'acidité de leurs sucs gastriques assure une destruction rapide des pathogènes présents dans les carcasses (Plaza et al., 2020), limitant ainsi les risques d'épidémie en particulier celles liées aux ongulés sauvages et domestiques (D. L. Ogada, Keesing, et al., 2012). En assurant le rôle d'équarrisseur naturels, les vautours participent activement au recyclage de la matière organique (Olea et al., 2019). Cette faculté est mise à profit en Europe et permet une diminution drastique des coûts financiers et des émissions de CO_2 inhérents à l'équarrissage industriel (Dupont et al., 2012; Morales-Reyes et al., 2015). Dans d'autres cultures, notamment indienne et tibétaine, les vautours ont une valeur religieuse et spirituelle importante de par leur implication dans certains rites funéraires (*e.g.* funérailles célestes dans les tours du silence chez les Parsis), où ils sont censés permettre l'ascension au ciel de l'âme des défunts (MaMing et al., 2016; Markandya et al., 2008).

Malgré l'importance de leur rôle dans nos écosystèmes et leur place dans les sociétés humaines (Morales-Reyes et al., 2015), c'est bien à cause de l'homme que la guilde des vautours a été élevée au rang de guilde fonctionnelle aviaire la plus menacée à l'échelle mondiale (Buechley & Şekercioğlu, 2016; McClure et al., 2018). Avec 69% des espèces classées comme étant menacées d'extinction par la liste rouge de l'UICN et 81% des espèces toujours en déclin (McClure et al., 2018), la situation des vautours de l'Ancien monde est

particulièrement préoccupante car leur disparition aurait – et a déjà eu – des conséquences dramatiques pour nos sociétés.

Prenons pour s'en convaincre l'exemple tristement célèbre de la quasi-disparition de trois espèces de vautours (*Gyps bengalensis, Gyps tenuirostris* et *Gyps indicus*) en Inde due à un empoisonnement involontaire mais massif (Cuthbert et al., 2014; Green et al., 2004). Alors que ces espèces étaient considérées comme les plus abondante du monde, avec pas loin de 14 millions de couples nicheurs, seulement 1% du bétail traité au diclofénac, un anti-inflammatoire non-stéroïdien employé dans la médecine humaine et vétérinaire provoquant un blocage du système urinaire chez les vautours, aura suffit à décimer 97% des populations de ces trois espèces en 15 ans (1990 à 2005) (Cuthbert et al., 2014; Green et al., 2004). Dans ce pays, où le système d'équarrissage industriel était inexistant, les conséquences ne se sont pas fait attendre. L'accumulation des cadavres de bétail non consommé par les vautours (en particulier les vaches sacrées) a entraîné l'explosion démographique d'animaux nécrophage facultatif comme les rats et les chiens errants devenus alors porteurs d'agents pathogènes et vecteurs de maladies transmissibles à l'homme comme la rage, l'anthrax ou la peste (Markandya et al., 2008). Entre 1993 et 2006, près de 50 000 personnes en sont mortes, et 34 milliards de dollars ont été dépensés dans les institutions hospitalières mais aussi dans la stérilisation et l'abattage massif des chiens errants (Markandya et al., 2008). En Afrique, où la situation des vautours prend la même trajectoire, les conséquences pourraient être relativement proches (D. Ogada et al., 2016). Des études montrent que les mammifères charognards non exclusifs comme les hyènes et les chacals ne sont pas aussi efficaces que les vautours pour éliminer les carcasses, ainsi leur absence entraînerait un délai favorisant la propagation de maladies (D. L. Ogada, Torchin, et al., 2012). À cela s'ajoute la contamination des carcasses par les métaux lourds, notamment le plomb des munitions de chasse, qui a failli causer la disparition du condor de Californie (*Gymnogyps californianus*, Cade, 2007; Finkelstein et al., 2012; Hunt et al., 2009) et dont souffrent encore nombre de vautours européens (Berny et al., 2015).

À ces empoisonnements indirects s'ajoutent des persécutions directes comme le tir (Mingozzi & Estève, 1997). Ces persécutions sont principalement motivées par des superstitions et une méconnaissance des comportements naturels des vautours : hypothétique pouvoir de vision dans l'au-delà après la consommation de chair de vautour en Afrique (D. Ogada et al., 2016) et crainte d'attaque sur bétail vivant en Europe (Duriez et al., 2019; Lambertucci et al., 2021; Margalida et al., 2014).

De nouvelles menaces pèsent sur les vautours, les collisions avec les lignes électriques et les centrales éoliennes (de Lucas et al., 2012). En Espagne, Sebastián-González et al., (2018) constatent que sur les 10 700 carcasses retrouvées au pied des turbines dans les 39 centrales éoliennes suivies, 25% étaient des vautours fauves. Plusieurs paramètres morphologiques tels que le poids et la surface des ailes, qui définissent la charge alaire, ont été identifiés comme déterminants pour les risques de collision (Janss, 2000). Les oiseaux ayant une charge alaire élevée, tels que les vautours et les grands aigles, sont plus sujets aux collisions que d'autres rapaces ayant une charge alaire plus faible, tels que la buse variable

(*Buteo buteo*) ou le circaète Jean-le-Blanc (*Circaetus gallicus*) (Barrios & Rodríguez, 2004; de Lucas et al., 2008). Alors que les espèces à faible charge alaire sont plus manoeuvrables et peuvent facilement éviter les éoliennes situées à quelques mètres devant elles (Schaub et al., 2020), les grands planeurs rencontrent beaucoup plus de difficultés de par leur plus faible manoeuvrabilité et leur utilisation des ascendances qui limitent leurs déplacements (de Lucas et al., 2008; Shepard, 2022). Le poids des vautours fauves les contraint à voler plus vite que les autres espèces de vautour pendant les planés, aux alentours de 55 km/h contre 49 km/h en moyenne chez le vautour moine (Fluhr et al., in prep), ce qui réduit encore leurs capacités à changer brusquement de direction. Bien que ce soit possible, une tentative de fuite de dernière minute pour les vautours exige qu'ils passent au vol battu, un mode de vol qu'ils ne peuvent pas maintenir longtemps en raison de l'augmentation drastique des coûts énergétiques (Duriez et al., 2014). Ces caractéristiques rendent le vautour fauve probablement plus vulnérable que les autres espèces face au risque de collision. Actuellement, les connaissances sur leurs capacités à éviter ces structures restent très lacunaires alors que ces mortalités additionnelles non naturelles pourraient menacer à termes la viabilité des populations. En effet, toutes ces menaces peuvent fortement peser sur la démographie du vautour fauve car c'est une espèce avec une maturité sexuelle tardive (4 ans) et une reproduction lente (ne produit qu'un seul jeune par an au maximum, Cramp & Simmons, 1982; Thiollay, 1994). Cette maturité sexuelle tardive et cette faible fécondité sont compensées par une grande longévité des adultes, des traits d'histoire de vie décrits classiquement comme de type K (Chantepie et al., 2016). Le taux de croissance de ces populations étant plus sensible à la probabilité de survie des adultes, chaque mortalité additionnelle d'adultes peut avoir un impact négatif important sur la dynamique de ces populations, même si celles-ci sont en croissance (Duriez, Pilard, et al., 2022).

Chez les vautours, les maladies infectieuses représentent la troisième cause de mortalité après l'empoisonnement et les traumatismes, ces derniers englobant les collisions et les tirs (Ives et al., 2022). De par leur régime alimentaire, les vautours sont régulièrement en contact avec de nombreux micro-organismes potentiellement pathogènes (Plaza et al., 2020). Certaines bactéries comme les *Mycoplasma sp.* ont provoqué de l'arthrite chez des urubus noirs (*Coragyps atratus*, Ruder et al., 2009), des difficultés respiratoires pour le vautour fauve (Lecis et al., 2010; Poveda et al., 1990), et même un arrêt des déplacements (Spiegel et al., 2022). Des champignons, notamment les *Aspergillus sp.*, ont entraîné des cas de pneumonie chez des vautours moines et des vautours de l'Himalaya (*Gyps himalayensis,* Barathidasan et al., 2013; Jung et al., 2009). Enfin, parmi les virus pouvant impacter les oiseaux de manière générale, ceux de l'influenza aviaire sont bien connus, mais n'ont que très rarement été identifiés chez les vautours. Le virus de l'influenza aviaire (spécifiquement la souche hautement pathogène H5N1) a été détecté chez les vautours à capuchon (*Necrosyrtes monachus*) en 2006 au Burkina Faso, entraînant de nombreux signes neurologiques : troubles de la coordination des mouvements, de l'équilibre et une atteinte oculaire aboutissant à la mort de certains individus (Ducatez et al., 2007; Tarnagda et al., 2011). Entre 2020 et 2023, une panzootie d'influenza aviaire hautement pathogène a touché des centaines de milliers d'oiseaux à travers le monde (Alexandrou et al., 2022; Lane et al., 2023; Stokstad, 2022; Wille & Barr, 2022). Alors que les vautours n'avaient été que marginalement affectés jusque

là, un nouveau foyer a été identifié en 2022 en Amérique du Nord chez des urubus noirs (Stokstad, 2022) et des condors de Californie (US Fish and Wildlife Service, 2023). Cette épidémie représente alors une nouvelle menace pouvant aussi affecter les vautours fauves.

I.4. Objectifs et questionnements de la thèse

Le premier objectif de ma thèse est d'évaluer l'influence de la socialité sur les comportements de vol des vautours fauves à différentes échelles : du prochain « pas » lors des déplaçements, jusqu'à la stratégie de recherche alimentaire. Les vautours fauves sont des oiseaux contraints à chercher inlassablement dans leur environnement deux ressources particulièrement imprévisibles et éphémères : des courants ascendants pour se déplacer et des carcasses pour se nourrir. Face à ce défi, et parce que ce sont des oiseaux grégaires, ils peuvent tirer profit de la présence de congénères dans l'espace aérien pour récolter de l'information sociale et ainsi réduire leur incertitude quant à la disponibilité des ressources recherchées. Utiliser cette information sociale peut aussi engendrer des coûts, notamment si elle est utilisée pour trouver une ressource épuisable et/ou monopolisable. Ainsi les individus devraient optimiser l'importance qu'ils donnent aux informations personnelles et sociales afin d'optimiser le compromis coûts/bénéfices à l'utilisation de ces informations lors des déplacements.

À plus grande échelle, cette utilisation de l'information sociale peut aboutir à la formation de stratégies collectives de recherche alimentaire. Les ornithologues ont depuis longtemps fait l'hypothèse que les vautours profitent d'un réseau de recherche alimentaire expliquant leur efficacité à détecter et à s'agréger autour des carcasses (Deygout et al., 2010; Houston, 1974; Tristram, 1859). Si tel est le cas, ils devraient être distribués dans l'espace de façon à maintenir un contact visuel avec d'autres individus cherchant aussi des carcasses. Le nombre d'oiseaux en prospection simultanément étant fini, les distances entre individus (ou groupes d'individus), garantes de ces transferts d'information, structureraient leur distribution spatiale en motifs agrégés. Chez les oiseaux marins en prospection au-dessus de l'océan par exemple, les individus s'organisent en groupes, espacés d'environ 2 km les uns des autres en moyenne, formant des clusters ayant un diamètre pouvant aller jusqu'à 6 km (Assali et al., 2017). Ces clusters sont eux même distants de 2 à 27,8 km les uns des autres. Puisque les distances de recrutement mesurées chez les oiseaux marins, comme chez les fous du Cap, peuvent atteindre près de 40 km pour un oiseau en vol réagissant à un grand groupe (100-150 fous, Porter & Sealy, 1982; Thiebault, Mullers, Pistorius, & Tremblay, 2014), il est probable que l'ensemble des oiseaux composant un cluster soient en vue les uns des autres et qu'ils puissent même potentiellement détecter des changements dans le comportement de groupes d'autre cluster. À l'inverse des oiseaux marins, les vautours sont beaucoup plus contraints dans leurs déplacements par la nécessité d'utiliser les courants ascendants. Ainsi, nous pourrions supposer que s'il existe un réseau chez les vautours fauves, il devrait être beaucoup plus contraint par le paysage que ce que l'on observe chez les oiseaux marins.

Le second objectif de cette thèse est beaucoup plus appliqué. Il repose sur le constat qu'au cours de la dernière décennie, les vautours fauves doivent faire face à de nouvelles

menaces. D'une part, avec la demande croissante d'énergie renouvelable, le nombre d'éoliennes a considérablement augmenté (IPCC, 2022; Tabassum-Abbasi et al., 2014). En France, par exemple, une étude gouvernementale montre que la proportion d'énergie éolienne terrestre pourrait être multipliée par au moins 2,5 et jusqu'à 4 d'ici 2050 (Veyrenc & Houvenagel, 2021). Si le constat de la vulnérabilité des vautours fauves aux collisions ne fait plus de doute (de Lucas et al., 2008), en revanche, les facteurs provoquant ces collisions sont méconnus. À ce jour, nous ne savons pas si les vautours cherchent à éviter les éoliennes, ce qui impliquerait que les collisions observées seraient des accidents liés à des conditions particulières, ou s'ils n'évitent absolument pas ces structures. D'autre part, la panzootie d'influenza aviaire hautement pathogène faisant rage durant ma période de thèse, a frappé de manière inattendue, des vautours fauves en France. Nous avons donc eu l'occasion d'étudier l'impact de cette maladie sur une espèce commensale de l'homme, à grande capacité de déplacement, et dont la contamination a pu être facilitée par son fort grégarisme.

Ce travail de thèse vise à répondre aux questions suivantes :

1) Quelle est l'importance relative attribuée par les vautours aux informations personnelles et sociales lorsqu'ils sélectionnent les courants ascendants thermiques nécessaires à leurs déplacements ? Quels sont les facteurs faisant varier l'utilisation de ces sources d'informations ?

2) La distribution des vautours en prospection renseigne-t-elle sur l'occurrence d'un réseau de recherche alimentaire contraint par le paysage ?

3) Les vautours évitent-ils les centrales éoliennes ? Si oui, à quelle échelle : la centrale dans son ensemble, les éoliennes spécifiquement mais de manière anticipée ou par réflexe au dernier instant ?

4) Quelles sont les conséquences de l'influenza aviaire hautement pathogène sur les déplacements et la survie des vautours ?

J'aborderai ces questions dans le même ordre, au travers du plan suivant :

Dans le chapitre III, je me suis intéressé aux facteurs influençant l'utilisation des différentes sources d'information dans les décisions de déplacement des vautours fauves. Pour cela, j'ai collecté les données de déplacements de l'ensemble d'un groupe de huit vautours de la fauconnerie du Rocher des Aigles (Rocamadour, France), relâchés pour des vols libres dans des conditions naturelles de vol. J'ai exploré l'influence de facteurs tels que la hiérarchie de dominance, les affinités sociales ou encore les conditions météorologiques sur l'utilisation de l'information personnelle ou sociale lors du choix du prochain courant ascendant thermique.

Le chapitre IV présente une analyse préliminaire pour élucider le mystère de la formation d'un réseau par les vautours en recherche de carcasse. Pour ce faire, j'ai utilisé les images d'un radar dédié à l'observation des comportements d'oiseaux placés à plusieurs endroits dans les Grands Causses (France). Les images radar fournissent une visualisation inédite de la distribution instantanée de la communauté d'oiseaux en vol dans les 6 km autour du radar. Ce chapitre reporte les résultats préliminaires de l'exploration de ces données et notamment les patrons de déplacement coordonnés ainsi que les phénomènes d'aggregations observés.

Dans le chapitre V, j'ai utilisé des données de déplacement de vautours fauves sauvages des Grands Causses afin d'explorer l'existence de comportements d'évitement des centrales éoliennes chez ces oiseaux. Dans cette région où le nombre de vautours ainsi que le nombre d'éoliennes augmentent, cette question devient de plus en plus prégnante. En combinant le suivi GPS à haute résolution des vautours autour des centrales éoliennes, avec des modélisations agent-centrées, j'ai quantifié les comportements d'évitements à différentes échelles : macro (> 1 km), meso (< 1 km) et micro-échelle (< 200 m).

Le chapitre VI, réalisé en étroite collaboration avec Olivier Duriez, montre l'impact de l'influenza aviaire sur les comportements et la survie des vautours fauves. Nous avons combiné les données issues du suivi long terme par GPS des vautours fauves sauvages des Grands Causses avec celles du suivi démographique effectué sur le terrain, par la Ligue de Protection des Oiseaux et les gestionnaires d'espaces naturels, pour estimer l'impact de cette maladie sur la survie des jeunes et des adultes, ainsi que sur les déplacements des adultes.

En préambule des chapitres III à VI, écrits en anglais sous la forme d'articles scientifiques indépendants, le lecteur trouvera un résumé en français du chapitre. Enfin, après une synthèse des résultats, la discussion portera sur les avantages et les coûts potentiels de la socialité chez les vautours, avec d'une part la réduction de l'incertitude autour de la disponibilité d'une ressource imprévisible, et de l'autre la compétition autour de la resource, la propagation de maladie et le manque d'attention envers des structures anthropiques représentant un risque pour eux.

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II. Sites d'étude et méthode de suivi des vautours

II.1. Sites d'étude

Ce travail repose sur des données collectées dans deux sites en France (Figure II.1A). D'une part, le site des Grands Causses où j'ai pu bénéficier de données issues d'un suivi télémétrique à long terme de vautours fauves sauvages. Et d'autre part, le Rocher des Aigles à Rocamadour, dans lequel j'ai mené des expériences sur un groupe de vautours captifs.

II.1.1. Grands Causses

Les Grands Causses, situés au sud du Massif central (France), regroupent un ensemble de hauts plateaux calcaires ayant une altitude moyenne de 1000 m, séparés par des cours d'eau, notamment le Tarn, la Dourbie et la Jonte, qui ont, au fil du temps, creusé des gorges et des vallées profondes (300 - 500 m, Figure II.1B). Malgré un sol sec et une végétation clairsemée, ces plateaux aux allures de steppe (Figure II.1C) sont exploités par l'homme depuis le Néolithique. Les dolines, des dépressions humides dans lesquelles se sont accumulés des sédiments lors du Jurassique, sont utilisées par les agriculteurs pour la production de fourrage et de céréales. Les vastes étendues de pelouses sèches quant à elles, permettent un pastoralisme extensif ovin dirigé vers la production de fromage (Roquefort) et de viande (race Lacaune).

Le climat des Grands Causses se trouve à l'interface entre influences méditerranéennes et montagnardes (Cohen & Lecompte, 1985) créant des étés dans lesquels épisodes de sécheresse et déficits hydriques sont fréquents. En effet, toute l'eau s'infiltre rapidement au travers de la roche calcaire, ne permettant pas le maintien de cours d'eau permanents sur les plateaux. Les influences montagnardes permettent tout de même une

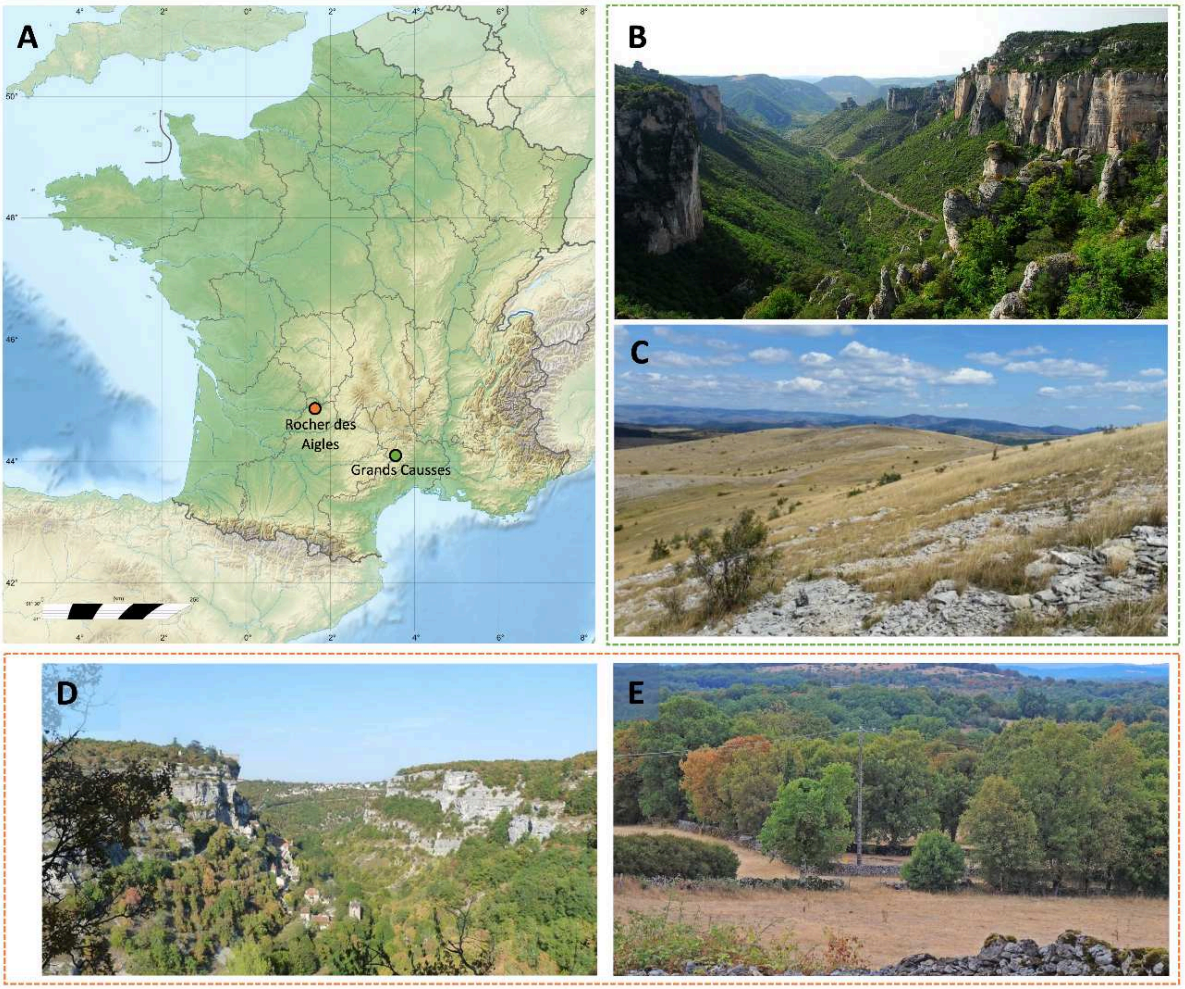

Figure II.1 : Sites d'étude. (A) Deux sites d'étude des vautours fauves dans la moitié sud de la France. (B) et (C) se situent dans les Grands Causses, et montrent respectivement les gorges de la Jonte où nichent les vautours fauves sauvages et une pelouse steppiques du Causse Méjean où pâturent des troupeaux d'ovins. (D) et (E) sont localisés dans les Causses du Quercy, précisément sur le Causse de Gramat, et illustrent respectivement le canyon de l'Alzou avec Rocamadour sur sa gauche, et les pelouses sèches, un peu plus arborées, dans lesquelles pâturent aussi des ovins. © *Michel Seguret, Gorges de la Jonte. PNR Les Causses du Quercy, Canyon de l'Alzou.*

pluviométrie plus étalée sur l'année qu'en plaine méditerranéenne. Cette saisonnalité marquée, combinée à la configuration du paysage, produisent une aérologie particulièrement favorable aux grands oiseaux planeurs. L'été, le soleil chauffe abondamment la surface des plateaux, créant de nombreuses et puissantes ascendances thermiques. Le paysage aérologique des Causses est complété par de nombreuses ascendances orographiques. Celles-ci résultent de la déviation du vent lors de sa rencontre avec les pentes et obstacles que constituent la topographie des gorges.

La combinaison entre un pastoralisme extensif, un paysage fournissant ascendances thermiques et orographiques, ainsi que des falaises (comme zones de reproduction) en abondance à proximité est favorable à la présence de vautours. Ces derniers ont disparu de cette région dans les années 1940, exterminés par l'homme à la suite de tirs volontaires, d'empoisonnement et d'un manque de ressource alimentaire. Entre 1981 et 1986, le vautour fauve a fait l'objet d'un programme de réintroduction (Terrasse et al., 1994). Dès lors, un premier site d'équarrissage collectif, aussi appelé « charnier collectif » a été mis en place à Cassagne, par les gestionnaires du Parc National des Cévennes (PNC) et de la Ligue de Protection des Oiseaux (LPO), pour soutenir les individus relâchés. Ce site concentre les carcasses collectées dans les fermes alentour trois fois par semaine. Il est désormais complété par un réseau de 113 placettes individuelles de recyclage naturel, nommées communément « placettes éleveurs », dispersées sur l'ensemble des Causses. Ces placettes se trouvent à proximité de fermes et sont gérées par les éleveurs qui y déposent les mortalités de leurs cheptels. Alors que le premier dispositif (charnier collectif) procure une ressource alimentaire abondante et relativement prévisible dans le temps et l'espace, le second (placettes éleveurs), par la nature occasionnelle des dépôts, rend la ressource imprévisible dans le temps et dispersée dans le paysage. La disponibilité alimentaire varie aussi avec les saisons, subissant une forte augmentation pendant la principale période d'agnelage (de janvier à avril, Bosè & Sarrazin, 2007). En 2020, c'est au total 157 tonnes de ressource alimentaire qui ont été mises à disposition des vautours via le réseau d'équarrissage naturel des Grands Causses (132 tonnes pour les placettes éleveurs et 25 tonnes pour le charnier, Comité interdépartemental Vautour et Activités d'Élevage massif Central, 2020).

L'ensemble de ces conditions ont permis à la réintroduction des vautours fauves dans cette zone de connaître un franc succès : la population atteignait plus de 820 couples nicheurs en 2021, 905 en 2022 (LPO, com. pers.). Malgré la relative prévisibilité des dépôts de nourriture sur le charnier collectif, ainsi que la prévisibilité spatiale des dépôts au sein des placettes éleveurs, les vautours ne semblent pas avoir développé un comportement stéréotypé de vérification systématique des placettes les unes après les autres (« traplining », voir introduction, Fluhr et al., 2017). De plus, 50% des comportements de nourrissage s'effectuent hors des placettes, sur des carcasses de faune sauvage, des déchets de chasse, ou des carcasses de bétail mort en nature et non retrouvé par les éleveurs (Duriez, Gregory, et al., 2022). Ainsi les comportements de vol et de recherche alimentaire semblent très peu impactés par ces dispositifs, et demeurent relativement fidèles aux comportements naturels pouvant être observés dans des zones n'ayant pas ces dispositifs d'équarrissage (*e.g.* Vallée d'Ossau, France, Fluhr et al., 2021).

Bien que la population de vautours fauves des Causses croît de manière régulière, elle fait face à de nouvelles menaces, en particulier le développement de centrales éoliennes. Il y a actuellement dans cette région du sud du Massif Central (Aveyron et Hérault) dix centrales éoliennes en activité (comptant 130 éoliennes) et neuf sont en projet (ajout de 91 éoliennes). Les éoliennes se situent entre 18 km et 52 km du centre de la colonie de vautours (en prenant comme référence les volières de réintroduction à Cassagne), une distance relativement faible pour des oiseaux parcourant plus de 80 km en moyenne par jour en été (Fluhr et al., 2021).

Bien que la majorité des vols se concentre dans un rayon d'une trentaine de kilomètres autour du centre de la colonie (Fluhr et al., 2021; Harel et al., 2016), ces éoliennes ont déjà causé la mort de 42 vautours fauves entre 2011 et 2022 (LPO France site Grands Causses/DREAL Occitanie, non publié). Ce constat et l'urgence de mieux comprendre l'impact des éoliennes ont orienté mon étude sur la quantification des comportements d'évitement des éoliennes par les vautours fauves, présentée dans le chapitre V.

II.1.2. Rocher des Aigles, Rocamadour

Le Rocher des Aigles est un parc zoologique, orienté vers les oiseaux, situé à Rocamadour (France) (Figure II.1A), accueillant près d'une soixantaine d'espèces de perroquets et de rapaces, dont des vautours. Créé en 1977, ce parc zoologique utilise des techniques de fauconnerie pour atteindre son objectif principal de sensibilisation du grand public à la protection des rapaces par l'intermédiaire d'un spectacle de vol libre. Des oiseaux lâchés, partant voler librement en plein ciel dans les alentours de Rocamadour, forment l'identité du Rocher des Aigles.

Bien qu'un peu plus arborée que les Grands Causses, le Rocher des Aigles est implanté dans un paysage possédant les mêmes caractéristiques géologiques et géomorphologiques (Figure II.1D,E). Situé dans les causses du Quercy (altitude moyenne 300 m), où les brebis et les chèvres sont nombreuses pour la production de fromage (Rocamadour), les plateaux calcaires séparés par des gorges offrent des conditions aérologiques particulièrement favorables au vol des rapaces. Le parc se trouve à l'aplomb du canyon de l'Alzou, profond de 120 m, dans lequel les oiseaux s'engouffrent à la recherche d'ascendances thermiques et orographiques lorsqu'ils sont lâchés pour les spectacles. Pendant la période estivale (avril à septembre), les oiseaux sont maintenus sur des perchoirs en bois (appelés « blocs ») à l'aide de longes (équivalent d'une laisse) ou dans des volières individuelles. Ils sont lâchés trois fois par jour (à 11h00, 14h30 et 16h00) pour des vols d'une trentaine de minutes en moyenne. Au cours de ces vols, les oiseaux atteignent régulièrement des altitudes de plus de 1000 m, le record étant attribué à un vautour de Rüppell (*Gyps rueppellii*) et un vautour de l'Himalaya, qui ont franchi la barre des 1800 m d'altitude (H. J. Williams, Duriez, et al., 2018). Ces oiseaux captifs, bien que nourris quotidiennement, trouvent et se nourrissent parfois sur des carcasses de brebis ou de chèvre dans les élevages alentours (observations personnelles). De plus, la fréquentation de la zone par des vautours fauves sauvages s'est intensifiée ces dernières années (information rapportée par le chef animalier - Basile Nouzières). Cet ensemble d'information laisse donc penser que les vols effectués par les vautours du Rocher des Aigles sont relativement comparables aux vols naturels des vautours sauvages.

Le reste de l'année (octobre à mars), les vautours sont placés en groupe (6 individus maximum) dans de grandes volières (6,7 x 6 x 6 m). Ces volières sont équipées de quatre perchoirs : trois mesurant 3,10 m placés respectivement à 1,7 m, 2,6 m et 3,5 m du sol et un

dernier de la longueur de la volière placé à 4 m de hauteur. Le nombre et la disposition de ces perchoirs offrent aux oiseaux la liberté de se placer où ils le souhaitent, de se mettre à proximité ou au contraire de s'éloigner de certains de leurs congénères. Durant cette période, les vautours sont nourris quotidiennement avec des petits morceaux de viande afin d'éviter les conflits. Cependant, une fois par semaine après un jour de jeûne, les soigneurs fournissent aux oiseaux une carcasse de boucherie afin de recréer le comportement de nourrissage naturel des vautours, la curée.

Le Rocher des Aigles offre l'opportunité de travailler avec un groupe de vautour entraîné à revenir à la fauconnerie après les vols et ayant l'habitude d'être manipulé. Étant captifs, j'ai eu accès à des informations précieuses sur ces oiseaux : age, sexe, masse, mais j'ai pu aussi estimer leurs affinités sociales et la hierarchie au sein du groupe. Ceci m'a permis notamment de conduire des expériences afin d'étudier l'influence de différentes sources d'information dans la prise de décision en vol chez les vautours, présentées dans le chapitre III.

II.2. Techniques utilisées pour le suivi des vautours

II.2.1. Suivi télémétrique

II.2.1.1. La biotélémetrie dans l'étude du comportement animal

La télémétrie, ou « mesure à distance », aussi appelée « bio-logging » par emprunt de la formule anglaise, implique de placer sur des êtres vivants des capteurs permettant de mesurer, suivre et enregistrer des données géolocalisées, physiologiques (*e.g.* fréquence cardiaque, Bevan et al., 1994), comportementales (*e.g.* position, accélération, Wilson et al., 2006) et/ou environnementales (*e.g.* pression, température ambiante, Tremblay & Cherel, 2000). Cette technologie offre la possibilité de recueillir à distance des données précises et relativement fréquentes sur des animaux sauvages difficilement observables dans leur milieu naturel, tout en minimisant le dérangement. Par exemple, le bio-logging permet de suivre le trajet migratoire de la sterne arctique (*Sterna paradisaea*) sur près de 35 000 km d'un pôle à l'autre du globe (Egevang et al., 2010), de comprendre les stratégies de plongée chez les gorfous sauteurs (*Eudyptes chrysocome*) à 35 m de profondeur dans l'océan glacial sub-antarctique (Tremblay & Cherel, 2003) ou encore l'utilisation de l'espace et les préférences d'habitat chez les phoques gris (*Halichoerus grypus*) sur les côtes Écossaises (Aarts et al., 2008).

Depuis les années 1980, la miniaturisation de l'électronique, le développement de balises satellitaires GPS (Global Positioning System) ainsi que l'amélioration de leur autonomie par l'ajout de panneaux solaires embarqués ont révolutionné le monde de l'écologie du déplacement. Ces balises, qui sont en fait des récepteurs, captent et identifient les ondes radio émises par des satellites du système NAVSTAR-GPS (NAVigation System with Time And Ranging - Global Positioning System). La triangulation des signaux détectés

par la balise permet de calculer sa position en trois dimensions (*i.e.* latitude, longitude et altitude avec une précision relativement bonne, <10 m en latitude/longitude et <50 m en altitude) ainsi que sa vitesse. Ces balises enregistrent les déplacements d'individus à différentes échelles temporelles et spatiales et cela potentiellement sur de longues durées (Benhamou, 2014). Désormais, dans la même balise, il est aussi possible d'intégrer de nouveaux capteurs tels que des magnétomètres ou encore des accéléromètres permettant d'inférer les comportements de l'individu portant la balise (Brown et al., 2013; Nathan et al., 2012).

II.2.1.2. Capture des oiseaux et pose des balises GPS

Dans le cadre de cette thèse, j'ai tiré profit de cette technologie pour étudier les prises de décisions en vol de vautours captifs (chapitre III), les comportements d'évitement des centrales éoliennes chez des individus sauvages (chapitre V) ainsi que l'impact de la grippe aviaire sur leurs déplacements (chapitre VI).

Au Rocher des Aigles, les vautours sont habitués à être manipulés par leurs soigneurs et entraînés à revenir sur l'esplanade du spectacle après leurs vols libres, garantissant de récupérer le matériel fixé aux animaux. Les vautours sont équipés d'un harnais composé d'une plaque en aluminium (6,7 x 8,5 cm) recouverte d'un côté d'une mousse de 3 mm d'épaisseur et de l'autre par du velcro, reliée par des rubans élastiques encapsulé dans une gaine de téflon. Ce harnais est fixé au dos de l'oiseau à la manière d'un baudrier d'escalade, en passant les lanières autour des jambes (Figure II.2A,C, Anderson et al., 2020; Longarini et al., 2023). Pour suivre les déplacements de l'ensemble des vautours lors des vols, j'ai bénéficié de balises de différents modèles : Gipsy 1, Gipsy 5 et Axy-trek, (Technosmart, Italy). Ces balises, accrochées sur le velcro en début de journée, enregistrent et stockent en mémoire la position en 3 dimensions des oiseaux à une fréquence de 4 points par seconde (4 Hz). Les balises sont récupérées à la fin de la journée, après les différents vols, et les données transférées vers un ordinateur. Le dispositif dans son ensemble (*i.e.* balise et harnais) pèse environ 90 g avec les balises Gipsy 1 (modèle le plus ancien et le plus lourd, Longarini et al., 2023) soit environ 1% de la masse corporelle moyenne d'un vautour fauve.

Le suivi de vautours fauves sauvages dans les Grands Causses est plus complexe et nécessite des moyens de capture spécifiques. À Cassagne, subsistent encore les volières qui ont abrité la colonie captive au moment de la réintroduction. Ces volières ont été modifiées pour y ajouter une porte coulissante pouvant être fermée à distance, après avoir attiré les oiseaux à l'intérieur avec un appât dans le but de les capturer afin de les baguer et/ou de les équiper de balises GPS. Une fois capturés, les oiseaux sont équipés de balises OrniTrack-50 (marque Ornitela) attachées également à la manière d'un baudrier à l'aide d'un câble de silicone élastique inséré dans une gaine de téflon (Figure II.2B, ~ 50g). Ces balises utilisent le réseau mobile (GPRS via le réseau 3G ou 4G) pour la transmission des données et sont alimentées par des panneaux solaires permettant le suivi des oiseaux sur de longues périodes (>5 ans). La résolution temporelle est ajustable en fonction du niveau de charge de la batterie,

Figure II.2 : Balises GPS pour le suivi des vautours fauves. L'encadré (A) montre l'équipement relatif aux vautours captifs. Dans sa partie gauche, le boitier noir est une balise GPS Technosmart modèle Gipsy 1, accrochée sur une plaque d'aluminium, attachée en baudrier sur le dos de l'oiseau ((C) pour la visualisation du positionnement du harnais sur l'oiseau), par l'intermédiaire des cordons en téflon. Dans la gaine transparente se trouve une balise GPS Technosmart modèle Gipsy 5. La partie de droite montre un oiseau lâché pour un vol libre dans le canyon de l'Alzou à Rocamadour, avec sur son dos une balise. L'encadré (B) montre l'équipement des vautours sauvages. La balise OrniTrack-50 (Ornitela) possède 2 panneaux solaires permettant de recharger la batterie. Ces balises sont posées en baudrier. En illustration, un poussin de vautour fauves équipé au nid peu avant son envol. © *Olivier Duriez, Germain Besson pour la photographie du poussin au nid et (C) extrait de Longarini et al. 2023.*

d'un point toutes les 2 minutes en été jusqu'à un point toutes les 30 minutes en hiver lorsque les niveaux de batterie sont faibles, dûs à une recharge plus difficile par les panneaux solaires. Ces balises offrent aussi la possibilité de créer des zones virtuelles géolocalisées (« geofences », Figure II.3) dans lesquelles les paramètres de la balise changent automatiquement vers un suivi à haute résolution (1 Hz). J'ai placé des géofences autour des centrales éoliennes afin d'obtenir un suivi haute résolution autour des éoliennes, exploité dans le chapitre V.

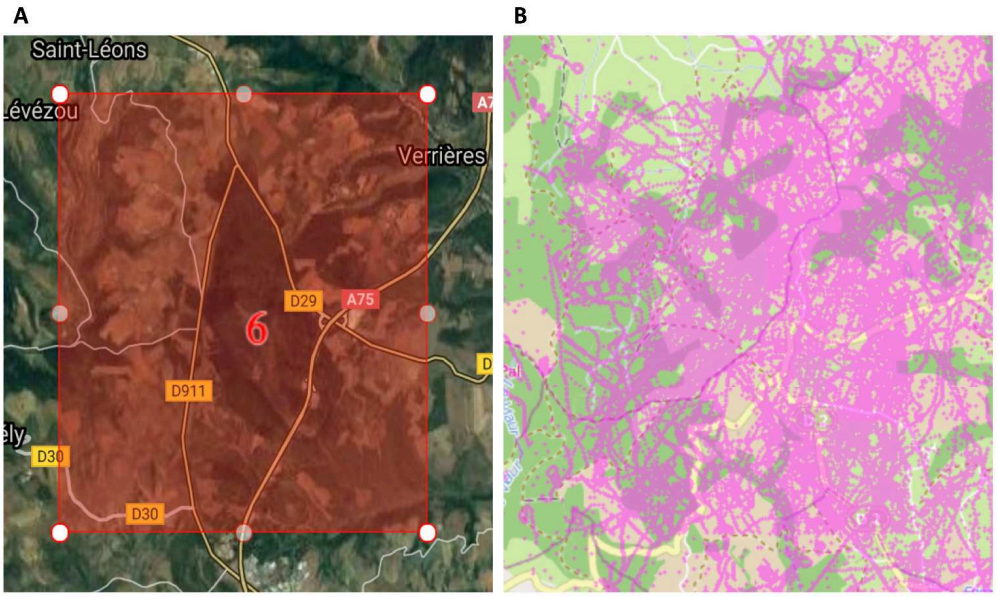

Figure II.3 : Les « geofences » des balises GPS Ornitela. (A) visualisation de la 6ème zone virtuelle géolocalisée (« geofence ») configurée pour les balises déployées sur les vautours sauvages des Causses. (B) montre les trajets effectués par l'ensemble des oiseaux suivi dans la zone de l'image: la délimitation de la geofence apparaît nettement à la suite de l' accumulation de point dans la zone de la geofence due au changement de programmation des balises (une position par seconde) une fois à l'intérieur.

II.2.2. Suivi radar

II.2.2.1. Développement des radar et utilisation en écologie

Le radar, acronyme de « RAdio Detection And Ranging » (Détection et Localisation Radio), est une technologie d'émission-réception d'ondes électromagnétiques destinée à détecter et localiser des objets à distance, lesquels réfléchissent ces ondes émises sous forme d'échos. L'histoire de la technologie radar remonte aux premières expérimentations menées par Heinrich Rudolf Hertz dans les années 1880 qui met en évidence l'existence de ces ondes électro-magnétiques non visibles. Cependant, les développements significatifs de cette technologie n'ont eu lieu qu'à l'aube de la Seconde Guerre mondiale, notamment en 1935, lorsque Sir Robert Watson-Watt a démontré avec succès la possibilité de détecter et localiser un avion ennemi en utilisant des ondes radio (onde électromagnétique avec une fréquence < 300 GHz).

Après la guerre, lorsque cette technologie militaire a été révélée au grand public, Lack & Varley, (1945) ont utilisés ces échos radar d'oiseaux, auparavant interprétés comme des hétérogénéités atmosphériques, pour enregistrer les plus longues trajectoires d'oiseaux migrateurs jusqu'alors - un vol d'oies à bec court (*Anser brachyrhynchus*) suivi pendant 1h39. Les premières applications du radar en ornithologie ont été principalement tournées vers l'étude des déplacements d'oiseaux migrateurs aussi bien sur terre (Mascher et al., 1962) qu'en mer (Casement, 1966). L'avantage clé de l'utilisation du radar en écologie réside dans sa capacité à fournir des données à grande échelle et en continu d'un écosystème méconnu et difficile d'accès : les basses couches de l'atmosphère, aussi nommée l'aérosphère (Chilson et al., 2012; Kunz et al., 2008). L'étude de la manière dont les formes de vie aériennes utilisent les autres composants biotiques et abiotiques de l'atmosphère et interagissent avec eux a donné naissance à une nouvelle discipline scientifique: l'aéroécologie (Chilson et al., 2012; Kunz et al., 2008).

Dans le cadre des études en aéroécologie, trois types de radars sont privilégiés : les radars de poursuite, les radars Doppler et les radars de surveillance qui se différencient principalement par leurs caractéristiques techniques (en particulier leur mode de fonctionnement et la fréquence d'onde utilisée). Actuellement, les radars utilisés pour le suivi des oiseaux, mais aussi pour l'étude d'autres taxons comme les chauves-souris (Horn & Kunz, 2008) ou encore les insectes (Drake & Reynolds, 2012; Noskov et al., 2021), n'ont pas été développés dans le but premier de détecter ces cibles. Ainsi, par un jeu de modification des réglages du radar, la détection de l'objet d'étude peut être « optimisée » mais ne sera pas exclusive (présence d'échos parasites).

Les radars de poursuite, initialement conçus à des fins militaires, sont capables de suivre avec précision les déplacements des cibles en trois dimensions. Ils peuvent détecter la fréquence des battements d'ailes (d'oiseaux *e.g.* Bruderer et al., 2010, ou de chauves-souris *e.g.* Bruderer & Popa-Lisseanu, 2005) créant une signature radar qui permet d'identifier

l'espèce ou un groupe d'espèces (T. C. Williams & Williams, 1980). Ces radars, bien que coûteux, sont de plus en plus utilisés dans les études de risque de collision d'oiseaux avec les centrales éoliennes (*e.g.* Erp et al., 2023). Les radars Doppler détectent le mouvement des cibles en mesurant le changement de fréquence du signal réfléchi par l'objet en déplacement. Ils sont très utilisés à fine échelle afin de déterminer la vitesse des véhicules (quelques dizaines de mètres dans le cas des radars de contrôles routiers), mais aussi à très large échelle (~200 km) dans le cas des prévisions météorologiques. L'avantage des radars météorologiques réside principalement dans leurs capacités à offrir une visualisation de tous les oiseaux en vol sur une très large zone (> 50 km de rayon autour du radar). En utilisant le réseau de radar au travers des États-Unis et des différents pays Européens, les ornithologues ont pu visualiser et même prédire les grands flux migratoires d'oiseaux (Dokter et al., 2018; Farnsworth et al., 2014; Gauthreaux & Belser, 2003; Nilsson et al., 2019; Shamoun-Baranes et al., 2014; Van Doren & Horton, 2018). En revanche, ces radars possèdent une résolution temporelle relativement faible (une image toutes les 15 min) ne permettant pas un suivi fin du comportement des oiseaux. Enfin, les radars de surveillance (maritime, aérienne) sont conçus pour détecter et surveiller des objets sur une large zone par l'émission régulière d'ondes à quelques secondes d'intervalle. Ces radars, en particulier les radars de navigation, sont très répandus car ils offrent un vaste éventail de réglages possibles (*e.g.* élargissement des échos, affichage des échos précédents) permettant de facilement optimiser la visualisation des oiseaux en vol (Cooper et al., 1991; T. C. Williams, 1984). Par conséquent, de nombreuses questions appliquées ont pu être explorées avec ces radars de surveillance, comme les risques de collisions avec les éoliennes et la mise en place de comportement d'évitement de ces structures par les oiseaux (Plonczkier & Simms, 2012) ou encore l'effet d'attraction des sources de lumière artificielles sur les oiseaux nocturnes (Van Doren et al., 2017). Récemment, ces radars ont été utilisés dans des contextes plus fondamentaux, par exemple pour étudier les stratégies collectives de recherche alimentaire chez les oiseaux marins (Assali et al., 2017, 2020). L'identification des espèces avec ces radars est possible, mais elle nécessite une phase d'apprentissage dans laquelle les échos radars doivent être annotés avec des observations visuelles ou acoustiques (Reynolds et al., 1997).

II.2.2.2. Fonctionnement du radar

Le radar dont proviennent les données utilisées dans cette thèse est un radar Furuno FAR-2127 (bande X, 25 kW). Ce radar est un radar de navigation maritime, à balayage horizontal, adapté pour l'observation des oiseaux. Il fonctionne de manière similaire à un radar de navigation maritime classique, mais avec des paramètres et des réglages adaptés pour détecter et suivre les oiseaux en vol dans un rayon de 6 km. Voici les étapes principales du fonctionnement de ce radar :

1 - **Émission du signal** : Le radar émet des impulsions d'ondes radio à travers son antenne émettrice (période de rotation = 2,5 s) qui les concentrent dans un faisceau de dimensions 1,23° (en horizontal) x 20° (en vertical). Ces ondes radio se propagent dans l'atmosphère à la vitesse de la lumière (3.10^9 m/s). L'élargissement du faisceau avec la distance au radar permet de balayer une gamme d'altitude de plus en plus

élevée lorsque la distance au radar augmente (1058 m à 6 km, Figure II.4). Cela permet de scanner un volume total de 239 km^3 sur une surface de 113 km^2 autour du radar.

2 - Interaction avec les cibles : Lorsque les ondes radio rencontrent un objet, tel qu'un avion, du relief, ou encore des oiseaux en vol (Figure II.4A,B), une partie de l'énergie de l'onde est réfléchie vers l'antenne réceptrice du radar. L'intensité de l'énergie réfléchie par la cible est influencée par sa forme, la matière dont elle est composée, son orientation par rapport au radar et par sa vitesse de déplacement. Ainsi, l'intensité de l'écho sera maximale pour une surface plane et réfléchissante (*e.g.* matériau métallique), perpendiculaire au radar et se déplaçant doucement afin de recevoir beaucoup d'émissions à chaque rotation de l'antenne radar.

3 - Réception de l'écho : L'antenne réceptrice capte les échos radar réfléchis par les cibles. Les signaux radar reçus sont généralement de faible puissance pour les oiseaux car ce sont de petites cibles, de formes irrégulières, avec une orientation changeante et une surface réfléchissante relativement limitée par rapport à de plus gros objets comme des avions. De plus, deux cibles alignées ne pourront être individualisées que si le signal réfléchi parvient au récepteur avec un décalage suffisant pour identifier deux échos. De la même manière, deux cibles proches, se trouvant à la même distance du radar, ne pourront être individualisées qu'à condition que la distance les séparant soit supérieure à la largeur du faisceau, sans quoi un seul et même écho sera détecté.

4 - Traitement du signal : Les signaux radar reçus sont amplifiés et filtrés pour éliminer le bruit indésirable. Le radar est configuré pour être sensible aux petits échos, afin de détecter les oiseaux en vol. Le gain est l'un des paramètres par exemple qui permet de régler la sensibilité du récepteur.

5 - Affichage des données : Les échos sont généralement affichés sur un écran radar (Figure II.5), semblable à celui utilisé pour la navigation maritime. Cependant, les réglages peuvent être ajustés pour rendre les échos d'oiseaux plus visibles et différenciables des autres échos tels que les précipitations ou dans notre cas des nuées d'insectes.

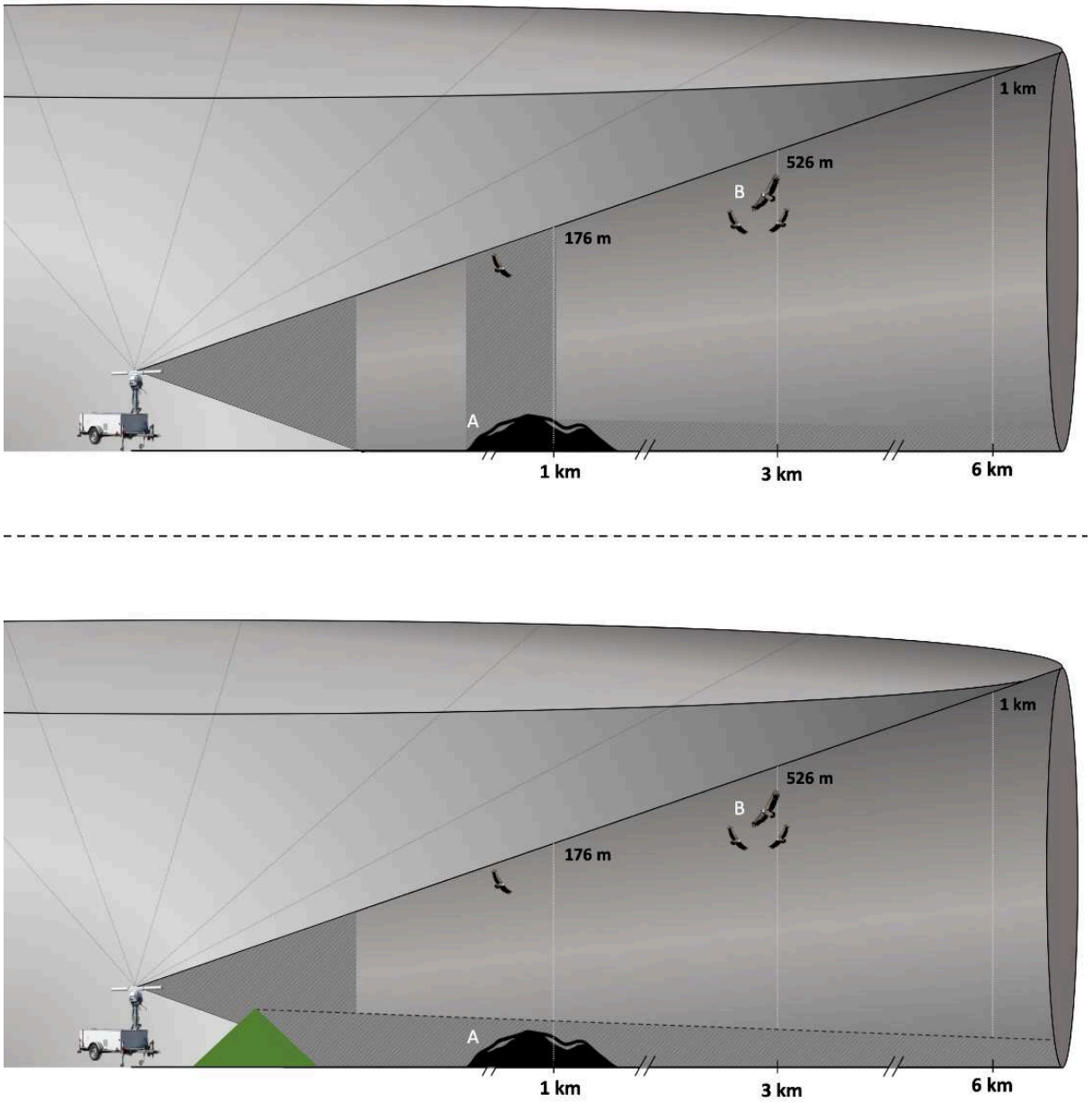

Figure II.4 : Schéma illustrant la section verticale scannée par le faisceau du radar. Les panneaux diffèrent par la présence des bords d'une cuvette, ou d'une haie basse (triangle vert) jouant le rôle de filtre des écho parasites due aux reliefs. Plus on s'éloigne du radar, plus l'altitude scannée augmente. (A) est un relief, qui réfléchit une grande quantité de l'onde émise par le radar, provoquant une saturation du signal (*i.e.* un masque, voir Figure II.5A) empêchant la visualisation d'éventuels oiseaux le survolant (*e.g.* panneau du haut). (B) représente un groupe de vautour en vol, se trouvant dans le faisceau, qui pourront être détectés et visualisés sur l'écran radar (voir Figure II.5B). Le radar monté sur une remorque appartient à Biotope, Mèze. Ce graphique n'est pas à l'échelle, seule la relation entre distance au radar et altitude scannée est exacte. La zone hachurée délimite la portion non détectée par le radar car dans la « zone aveugle » près du radar, masquée par le relief A, ou par les bords de la cuvette / haie.

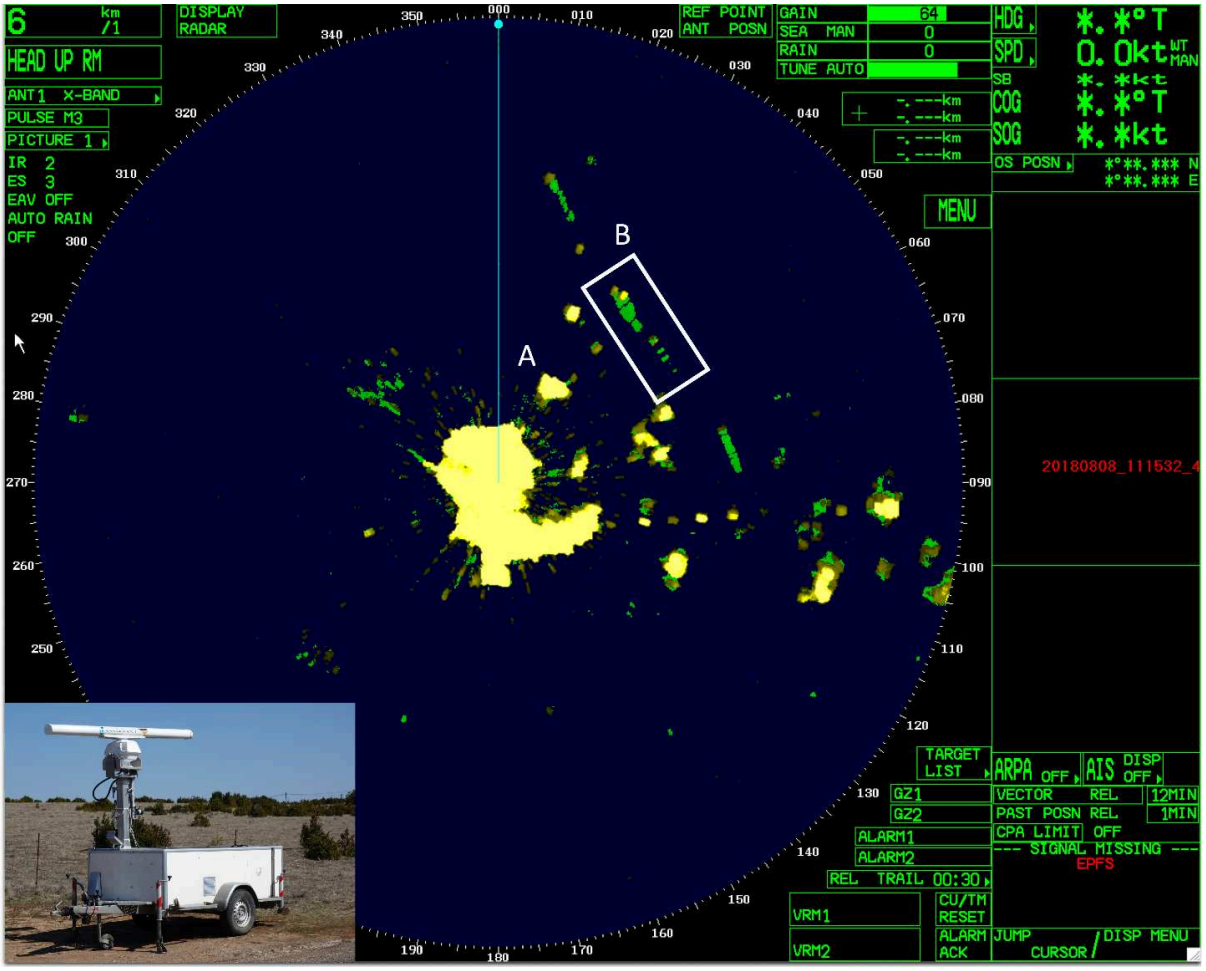

Figure II.5 : Visualisation d'une image radar brute – 08/08/2018. Le radar se trouve au centre, avec la ligne bleu indiquant le nord pour le radar. Le rayon d'observation est de 6 km (indiqué dans la case en haut à gauche). La couleur jaune vif dans le cercle radar (zone bleu foncé) indique de fort niveau de réflexion de l'onde du radar. La zone de forte intensité au centre est la « zone aveugle ». (A) est un masque dû à la présence d'un relief qui renvoie constamment une grande quantité de l'onde émise par le radar (relief A dans Figure II.4). Un oiseau passant au-dessus de ce relief, même si détecté, sera invisible car son écho est noyé dans celui du masque. (B) montre la visualisation d'un groupe de vautour en vol. Les points jaunes et marrons sont les échos au moment de l'image alors que les traces vertes représentent la position des échos sur les images précédentes (visualisation sur 30 s).
© Olivier Duriez et Biotope, Mèze.

Le radar permet donc de détecter tous les oiseaux en vol simultanément, dans un rayon de 6 km avec une résolution temporelle de 2,5 s. Cependant, autour du radar, une zone pseudo-circulaire apparaît saturée lors de la visualisation des données radar (voir Figure II.5). Cette zone, également appelée « zone aveugle », est un phénomène courant dans les radars et résulte de la réflexion du signal émis par des structures à proximité immédiate de l'antenne

(*e.g.* remorque, sol). Par ailleurs, les reliefs et pentes inclus dans le cercle radar renvoient également des échos parasites permanents, qui masquent les oiseaux qui se déplacent au-dessus de ces reliefs (*e.g.* vautour au-dessus du relief A dans Figure II.4). Le choix du site pour positionner le radar s'avère très délicat. Le placement idéal est au centre d'une petite cuvette (ou entouré d'une haie basse), située au sommet d'une colline, émergeant d'une zone relativement plate. De cette manière, les bordures de la cuvette (ou de la haie) bloquent les échos provenant du relief, rendant visible les cibles éloignées et dans une gamme de hauteur maximale, même au-dessus du relief (voir Figure II.4 et Figure II.5 pour la visualisation).

II.2.2.3. Acquisition des données

Les données radar utilisées dans cette thèse proviennent de captures d'écran du radar à oiseaux utilisé par le bureau d'étude Biotope à Mèze (France) lors de quatre semaines d'observation sur quatre sites dans les Grands Causses (total de 582 h de suivi, Figure II.6). L'acquisition des données consiste en une capture automatisée de la visualisation du signal radar à l'écran (toutes les 2,5 s). Pour cela, nous utilisons la seconde sortie vidéo du système radar pour y relier, par l'intermédiaire d'une carte vidéo (DVI2USB frame grabber, EPIPHAN), un ordinateur possédant un code de capture automatique de l'écran radar. Les images sont enregistrées (en format *.png, total de 838 675 images brutes) et stockées sur un disque externe (total de 100 GB de données). Lors de la prise de données radar, un ornithologue (Vincent Liebault, Biotope), a manuellement annoté les échos produits par 43 espèces d'oiseaux mais aussi par des activitées humaines ou des phénomènes météorologiques (*e.g.* avions, parapentes, hélicoptères, pluie, etc.). Pour cela, lorsqu'une espèce visible avec les moyens optiques classiques (*i.e.* jumelles et longues-vues) était détectée par le radar, il a associé à l'écho produit l'espèce identifiée, sa hauteur de vol, ainsi que le nombre d'individus visibles. Ces annotations m'ont permis par la suite d'entraîner un algorithme capable de différencier les trajectoires provenant d'espèces différentes (voir chapitre IV).

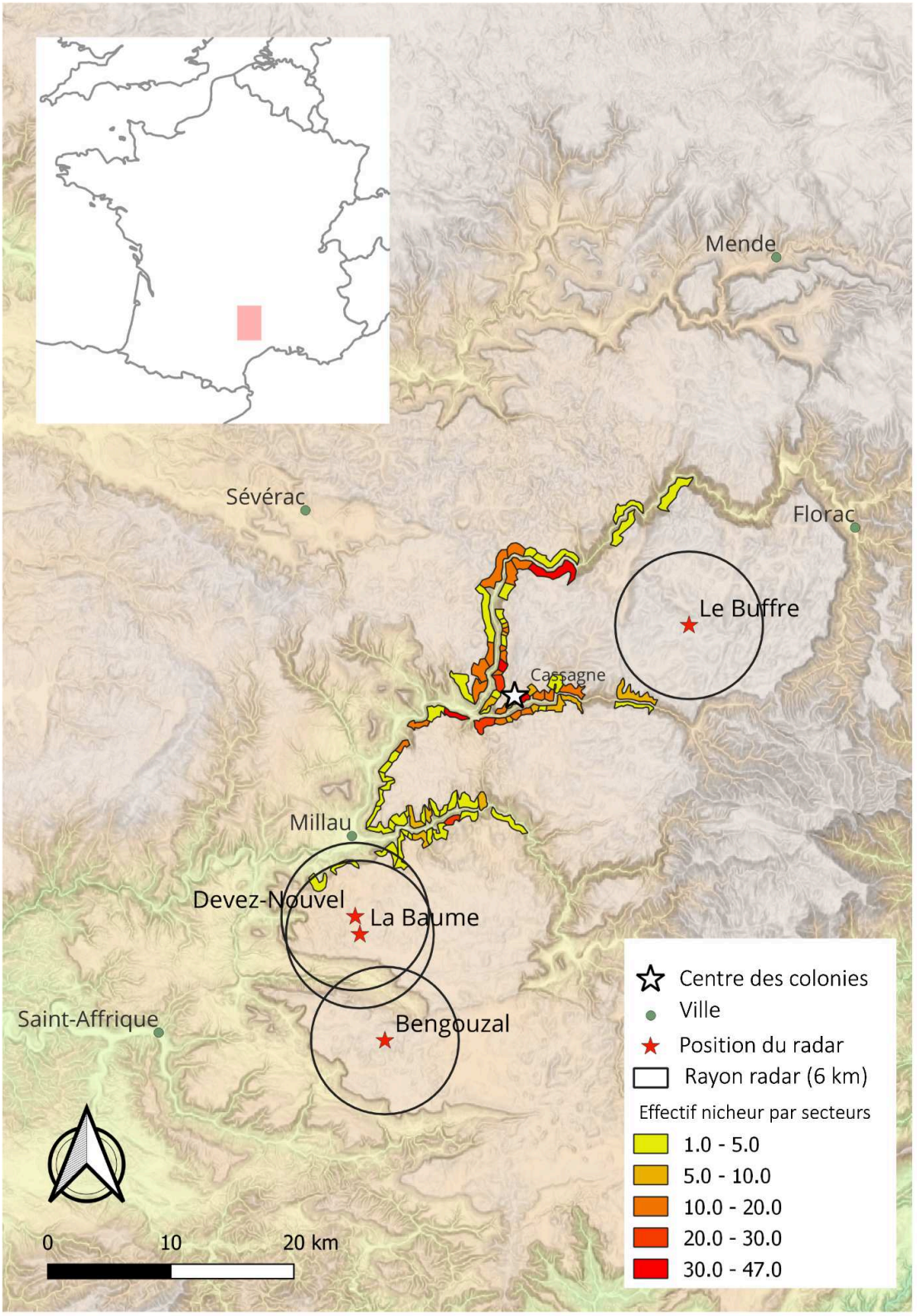

Figure II.6 : Sites de suivi radar dans les Grands Causses. Chacun des sites se trouve sur un plateau, relativement loin du centre de la colonie, afin d'enregistrer les vautours en prospection alimentaire, tout en maximisant la qualité des données récupérées (réduction des masques).

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III. L'utilisation de l'information sociale dans les prises de décision en vol chez les vautours

Ce chapitre s'intéresse aux facteurs influençant l'importance attribuée par les vautours aux différentes sources d'information dans les décisions de déplacement. Pour cela, j'ai suivi les interactions sociales (par l'intermédiaire de caméras et pièges photographiques) de l'ensemble d'un groupe de vautours de la fauconnerie du Rocher des Aigles (Rocamadour, France) afin de définir les affinités et les relations de hiérarchie au sein du groupe. Par la suite, j'ai collecté les données de déplacements à haute résolution de l'ensemble du groupe lorsqu'ils étaient relâchés pour les spectacles de vol libre dans le canyon de l'Alzou, offrant des conditions naturelles de vol. J'ai pu finalement explorer l'influence de la hiérarchie de dominance, des affinités sociales ou encore des conditions météorologiques sur l'utilisation de l'information personnelle (découverte d'une ascendance thermique) ou sociale (utilisation d'une ascendance thermique préalablement découverte par un congénère) lors du choix de leur prochaine ascendance thermique.

Note au lecteur :
- Le preprint est disponible ici: https://doi.org/10.1101/2023.07.26.550671
- L'article est en révision dans la revue Proceedings of the Royal Society B.
- Les annexes de l'article sont disponibles en annexe 1 du présent manuscrit p 181.

The use of social information in vulture flight decisions

Sassi Yohan [a,*], Nouzières Basile [b], Scacco Martina [c,d], Tremblay Yann [e], Duriez Olivier [a,§], Robira Benjamin [f,§]

a: CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
b: Rocher des Aigles, Rocamadour, France
c: Max Planck Institute of Animal Behavior, Department of Migration, Am Obstberg 1, 78315, Radolfzell, Germany
d: Department of Biology, University of Konstanz, Universitätsstraße 10, 78464, Konstanz, Germany
e: Marine Biodiversity Exploitation and Conservation (MARBEC), University of Montpellier, CNRS, Ifremer, IRD, 34203 Sète, France
f: Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy

* Corresponding author: yohan.sassi@cefe.cnrs.fr, CEFE, 1919 Routes de Mende, 34293 Montpellier cedex 5, France.
[§] Co-last authors

III. Abstract

Animals rely on a balance of personal and social information to decide when and where to move next in order to access a desired resource, such as food. The benefits from cueing on conspecifics to reduce uncertainty about resources availability can be rapidly overcome by the risks of within-group competition, often exacerbated toward low-ranked individuals. Being obligate soarers, relying on thermal updrafts to search for carcasses around which competition can be fierce, vultures represent ideal models to investigate the balance between personal and social information during foraging movements. Linking dominance hierarchy, social affinities and meteorological conditions to movement decisions of eight captive vultures, *Gyps spp*., released for free flights in natural-like soaring conditions, we found that they relied on social information (i.e. other vultures using/having used the thermals) to find the next thermal updraft, especially in unfavourable flight conditions. Low-ranked individuals were more likely to disregard social cues when deciding where to go next, possibly to minimise the competitive risk of social aggregation. These results exemplify the architecture of decision-making during flight in social birds. It suggests that the environmental context, the context of risk and the social system as a whole calibrate the balance between personal and social information use.

Key-words: griffon vulture, hierarchy, movement decision, landscape exploration, social information, unpredictable resource

III.1. Introduction

Animals must constantly decide where and when to move next in order to find resources such as food, water, shelter, or a mate, necessary for life. To make these decisions, they can rely on two sources of information: personal information and social information. Personal information includes knowledge of the spatiotemporal patterns of resource distribution that individuals may perceive or have memorised from previous encounters [1]. For example, food-storing birds are able to return to locations where they stored or saw food in the past, based on prior expectation of the resource availability [2]. Social information, on the other hand, is obtained by observing the behaviour of others [3–5]. Feeding, fleeing, or mating individuals provide discrete information about the availability and locations of food, predators, or potential mates.

For resources that are heterogeneously distributed in the environment, ephemeral and unpredictable, using only personal information for movement decisions may be prone to inaccuracies [6]. In such conditions, social animals may benefit from companions' knowledge and may follow the dominant or oldest individual(s) considered as knowledgeable (e.g. homing pigeons, *Columba livia*, or elephants, *Loxodonta africana*, [7,8]), follow the largest group through shared decision-making [9], or stay with preferred affiliates [10–12]. Because using social information can considerably reduce uncertainty in finding resources, individuals should favour this source of information to achieve cost-efficient movement [13–15]. However, relying heavily on social information can also lead individuals to aggregate on resources, potentially inducing competition by exploitation or interference if the resource is monopolizable and depletable [16]. Since both social and personal information are often available to social animals [1], they need to balance their relative importance, depending on the availability and predictability of the resource. When deciding on the next movement step, social animals must trade-off the decreased uncertainty of locating a resource through social information, with the potential increase in competition risk. Such a balance may be dictated by the immediate needs of the individual and its risk sensitivity [17] but also by the group social organisation. For example, low-ranked individuals are known to suffer more from within-group competition compared to high-ranked individuals [18] and should therefore be more reluctant to engage into social information use, which could eventually trigger proximity to despotic individuals [19].

Vultures rely on two unpredictable resources: carcasses to feed and thermal updrafts to move. During foraging flights, these large soaring birds gain altitude by circling into thermal updrafts (i.e. masses of hot air rising from heated surfaces) and glide across the landscape to the next updraft while scanning the ground for carcasses [20]. Although some topographic features are clearly favourable to updrafts presence [21], at the individual level, challenging local meteorological conditions (e.g. high wind speed, low temperature, high cloudiness) can make thermal locations and availability hard to predict [22]. If they fail to detect an updraft, vultures may be forced to switch to flapping flight, or worse to land and take-off again, significantly increasing their energy expenditure [23,24]. While both thermals and carcasses are relatively unpredictable, thermals are not depletable contrary to carcasses.

When a vulture discovers a carcass, its sharp drop in altitude while circling before landing is used as a signal by conspecifics, dragging tens of individuals to the food source in a few minutes [25,26]. As the number of vultures around the carcass increases (up to 100-120 individuals, [27,28]), individual feeding rates decrease due to reduced access to the resource, resource depletion by competitors and increased agonistic interactions [27]. Therefore, in these social birds, individuals should balance the advantage of conspecific presence to locate thermal updrafts [29] with the ultimate cost of competition around the carcasses that can be fierce [30–33]. As such, vultures are ideal models to investigate the role of conspecifics in shaping their foraging movement decisions.

Using a group of captive but freely-flying 'griffon' vultures, *Gyps fulvus* and *Gyps rueppellii,* tagged with high-resolution GPS loggers, we studied how conspecifics' presence shapes individuals' movement decisions during soaring flights. Despite being trained birds released for public shows, these individuals sometimes detected and fed on carcasses at surrounding farms (BN and YS, pers. obs.). We therefore consider these flights comparable to natural foraging flights. Focusing on the movement steps from thermal to thermal, we first assessed when do individuals preferentially discover new thermals (i.e. use of personal information) compared to using thermals already discovered by conspecifics (i.e. use of social information). We expected that vultures would favour the use of social information when unfavourable meteorological conditions increased thermal unpredictability and when flight conditions (e.g. low altitude) increased risks of landing [1]. Furthermore, given the hierarchy in vulture groups, we expected low-ranked individuals to be more prone to use personal information than high-ranked individuals to try to find the food source first, in order to avoid large aggregation [34,35]. Second, we investigated the drivers underlying thermal selection when individuals had to choose between simultaneously available thermals. We expected individuals to select thermals providing the maximal positive vertical speed (i.e. climb rate) as it may provide a reliable proxy of the thermal current strength helping them maximise their height gain [29]. To decrease uncertainty about resource finding and risks mentioned above, we expect that individuals should favour thermals hosting the maximum number of individuals to maintain cohesion and secure the possibility to cue on as many conspecifics as possible [29]. Finally, social preferences may also influence decision, with individuals preferentially moving together with preferred affiliates [12,36,37], as it could reduce competition due to familiarity between individuals [38].

III.2. Materials and methods

III.2.1. Study site, vultures housing conditions and experimental settings

The study was carried out in 2021 and 2022 at the Rocher des Aigles falconry centre, Rocamadour, France, and divided between winter and summer periods each year. During winters, vultures were housed within an aviary (6.7 x 6 x 6 m) equipped with four perches: three of them measuring 3.10 m, placed at 1.7, 2.6 and 3.5 m from the ground, and one of the full width of the aviary at 4 m heigh. This setting was used to estimate vulture social bonds

(see Social bond estimation). In addition, besides being fed daily on small pieces of meat to prevent conflicts, five feeding events (one each week during a five-week period) were organised in the aviary on a butchery carcass occurring after a one-day fasting (to motivate feeding). These feeding events were used to assess dominance hierarchy within the group (see Hierarchy estimation). In summer, these trained vultures were kept perching on individual logs, released several times per day to execute free flight shows for the public within a landscape composed of plateaus interspaced by canyons, similar to "Causses" landscape typically used by french wild vultures [39]. The falconry centre is located near a 120 m-deep canyon and offers natural soaring conditions for raptors, making this study site a great place to investigate natural group flight behaviour (see Group flights), [24].

We used GPS data and visual observations to characterise the social and flight behaviour of eight captive vultures (7 Eurasian griffon vultures, *Gyps fulvus,* and 1 closely-related Rüppell's vulture, *Gyps rueppellii*), including five females and three males (Table S1). Each year, we conducted experiments on a group of six individuals (two griffon vultures were replaced in 2022, Table S1). Experiments followed the animal ethic guidelines of France and the Centre National de la Recherche Scientifique. Handling of birds to fit GPS loggers followed the protocol of telemetry study of vultures authorised in the Programme Personnel 961, coordinated by OD, under the supervision of the French ringing centre, CRBPO, Paris. Furthermore, experiments, observations, handling and flight events were systematically performed under the guidance of the head of animal caretakers, BN.

III.2.1.1. Social bond estimation

During five weeks in both years (December/January 2020-2021 and November/December 2021), we recorded pictures of vultures in the aviary from 8:00 to 19:00 (local time) at 5 minutes interval, using three camera traps (Wosport Big Eye D3 and Reconyx HyperFire HC600).

We identified birds using repeated colours on plastic rings and marks on the ruff and backhead feathers, using harmless colour sticks (Raidex GmbH, Figure 1A). We then processed recorded pictures to extract the individuals' ID and position (bill or head position), using a purpose-built image annotation program in Julia software, JuliaHub Inc., [39]. For subsequent analyses, we relied on R software (v 4.2.2, R software, 2022, [40]).

We considered the social bond between a dyad of individuals *i* and *j* based on spatial proximity following the Simple Ratio association Index (SRI, equation 1, [41,42])

Equation 1: $SRI_{i,j} = SRI_{j,i} = \frac{n_{tog}}{n_{tot}}$,

where n_{tog} is the number of pictures in which individuals *i* and *j* were on the same perch at a Euclidean distance of less than 1.55 m and n_{tot} is the total number of pictures in which

Figure 1. Data collection. (A) Perched vultures. Distance between vultures during perching events were used to estimate social-bond strength. (B) Feeding event around a butchery carcass. Agonistic interactions during those feeding events were used to estimate dominance hierarchy. (C) Flying vulture. Vultures were released for free flight into a 120-m canyon, equipped with high-resolution GPS loggers.

individuals *i* and *j* were both detected on the same perch. SRI values varied between 0 and 1, where 0 represented dyads that were never seen associated and 1 represented dyads that were always observed sitting at less than 1.55 m from each other. The distance of 1.55 m was chosen as matching to the mode of the inter-individual distances distribution (Figure S1). This was also consistent with the aviary setting, as it corresponded to half the length of most available perches. Our analyses were robust to other choices for this distance threshold (see Supplementary Material, ESM01).

III.2.1.2. Hierarchy estimation

Each winter, we estimated hierarchy within the vulture group by monitoring feeding interactions during the five carcass-based feeding events in the aviary (10 in total, Figure 1B) using a remotely-controlled video camera (GoPro Hero 4, GoPro Inc.) fixed at 2 m height on the aviary wall. These feeding events lasted on average 34 min (SD $\pm$ 4 min).

We computed individuals' rank relying on the randomised Elo-rating approach [43,44], which accounts for potential temporal instability of the rank using permutations in the agonistic interaction series ('elo_scores' function, *aniDom* package, [44,45]; using 1000 randomisations and fixing the rank adjustment speed along the series, K-factor, to 200). The interaction series consisted in identifying the "wins" and "losses" for a given individual in agonistic interactions [46] with other individuals in each video (annotated with BORIS video analysis software, [47]). We used the ethograms from Bose & Sarrazin (2007, [30]) and Valverde (1959, [48]) to characterise griffon vulture feeding behaviour and between-individual interactions. An individual won the interaction when it interrupted another individual's feeding bout (by pecking it, displacing it or engaging in a fight), and finally accessed the carcass before its opponent. In other cases, the interaction was considered

as a “loss” for the initiator. We assessed the reliability of the dominance hierarchy through individual Elo-rating repeatability (‘estimate_uncertainty_by_repeatability’ function, *aniDom* package, [44]).

III.2.1.3. Group flights

We recorded vulture flights decisions during 42 flight sessions (21 sessions each year) in the vicinity of the Rocher des Aigles. In general, birds were released for a flight session three times per day (in rare occasions from 2 to 4 times), at around 11:00, 14:30 and 16:00 (local time) for a mean duration of 26.03 min (SD $\pm$ 14.15 min) of flight. These captive vultures are trained to fly freely, searching for thermals, gaining altitude and coming back to their trainers (Supplementary Video 1). Vultures were equipped with a high-resolution GPS logger (4 Hz, TechnoSmart, models Gipsy 1, Gipsy 5 or Axytreck) positioned at their lower back using a Teflon leg-loop harness (Figure 1C, [49]). They were released in two groups, built according to social preferences with the three most socially-bonded birds together, at 2-min intervals. Release order alternated between consecutive days. For each flight session, we recorded and considered as stable the cloudiness (i.e. the proportion of clouds covering the sky, on a scale from 0 - no clouds - to 8 - sky fully covered by clouds), horizontal wind speed and temperature (all extracted from meteofrance.com based on local meteorological models).

To further investigate how vulture thermal choices were shaped by personal and social information, we pre-processed flight tracks in three consecutive steps. We subsampled individuals’ tracks from 4 to 1 GPS fix per second, and segmented their flight behaviour into gliding, linear soaring and circular soaring. We then created spatio-temporally dynamic maps of thermal availability based on the spatial clustering of individual’s circular soaring phases. Leaning on these maps, we retraced the history of thermal use/choice by individuals.

III.2.1.3.1. Thermal use identification

To segment vulture flight between circular soaring, linear soaring and gliding flight we first calculated turning angle and vertical speed between consecutive locations using the *move* R package [50]. We applied a moving window of 30 s to calculate the absolute cumulative sum of the turning angles (hereafter cumulative turning angle) and a moving window of 5 s to calculate the average vertical speed. We then applied a k-means approach (k = 2, ‘kmeans’ function, *stats* R package) on the smoothed vertical speed (positive speed when flying upwards) to distinguish between soaring (ascending flight) and gliding (descending flight, [51,52]). We further classified soaring locations into circular soaring (indicating use of thermal updrafts) and linear soaring (also called slope soaring, expected to occur outside of thermals), with circular soaring being associated with a cumulative turning angle $\geq$ 300 degrees. A result of segmentation is illustrated in Figure 2B. Finally, we inferred the use of a thermal when the individual engaged in circular soaring for more than 30 s, with no interruption of more than 5 s of gliding.

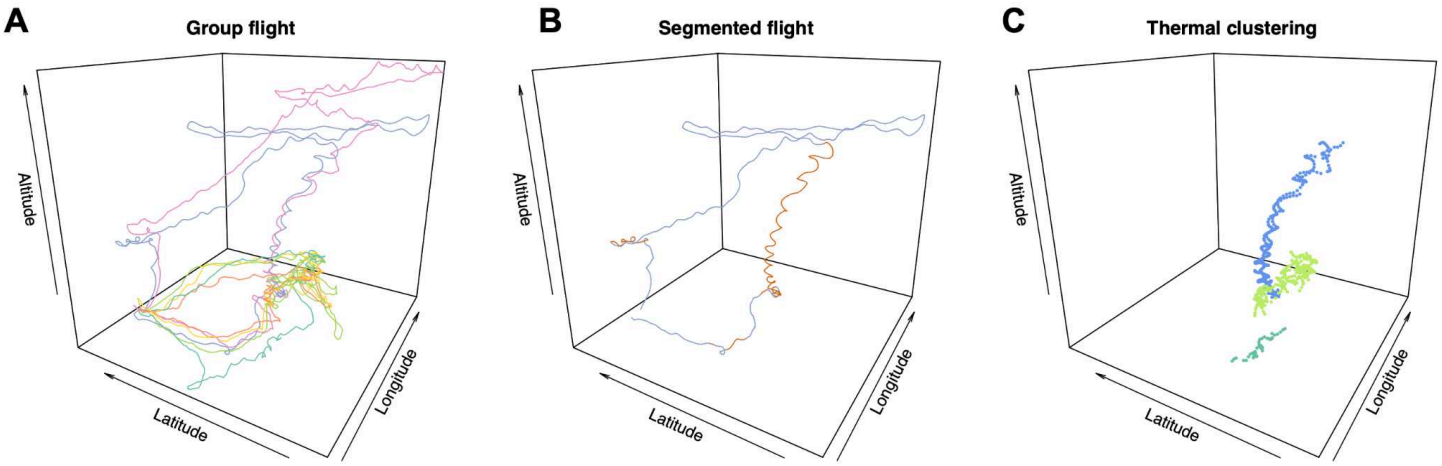

Figure 2. Flight data pre-processing. Pre-processing steps of group flight GPS data, example of one flight session. The altitude ranges from 200 m to 600 m. (A) shows a group flight (see Supplementary Video 1), with colours corresponding to each individual. (B) illustrates the segmentation of an individual's flight (blue individual in (A)), with the orange segments corresponding to circular soaring phases. (C) illustrates the 3D density-based spatial clustering of individuals circular soaring phases, with colours indicating the three thermals identified in this flight session.

III.2.1.3.2. Dynamic mapping of available thermals

Within each flight session, we created a dynamic map of thermals (Figure 3). First, we spatially clustered vulture circular soaring locations (reflecting the use of the same thermal updraft) independently of time by using a 3D density-based spatial clustering approach ('dbscan' function, *dbscan* R package, [53]). This algorithm relies on a spherical neighbourhood to perform density-based neighbour joining, i.e. clustering (Figure 2C). We assumed this neighbourhood to be of a 40-m radius, and a minimum number of five locations within this range for the algorithm to consider the neighbourhood further. This 40 m threshold corresponded to the largest 4-nearest-neighbour distance observed when considering locations attributed to thermal use only ('kNNdistplot' function, *dbscan* R package) and matched with empirical expectations of radius during circular soaring phases [54].

We then made those maps dynamic in time by considering the lifetime of each thermal. We considered a thermal as "available" from the moment when the first individual entered it until the last individual left it (Figure 3).

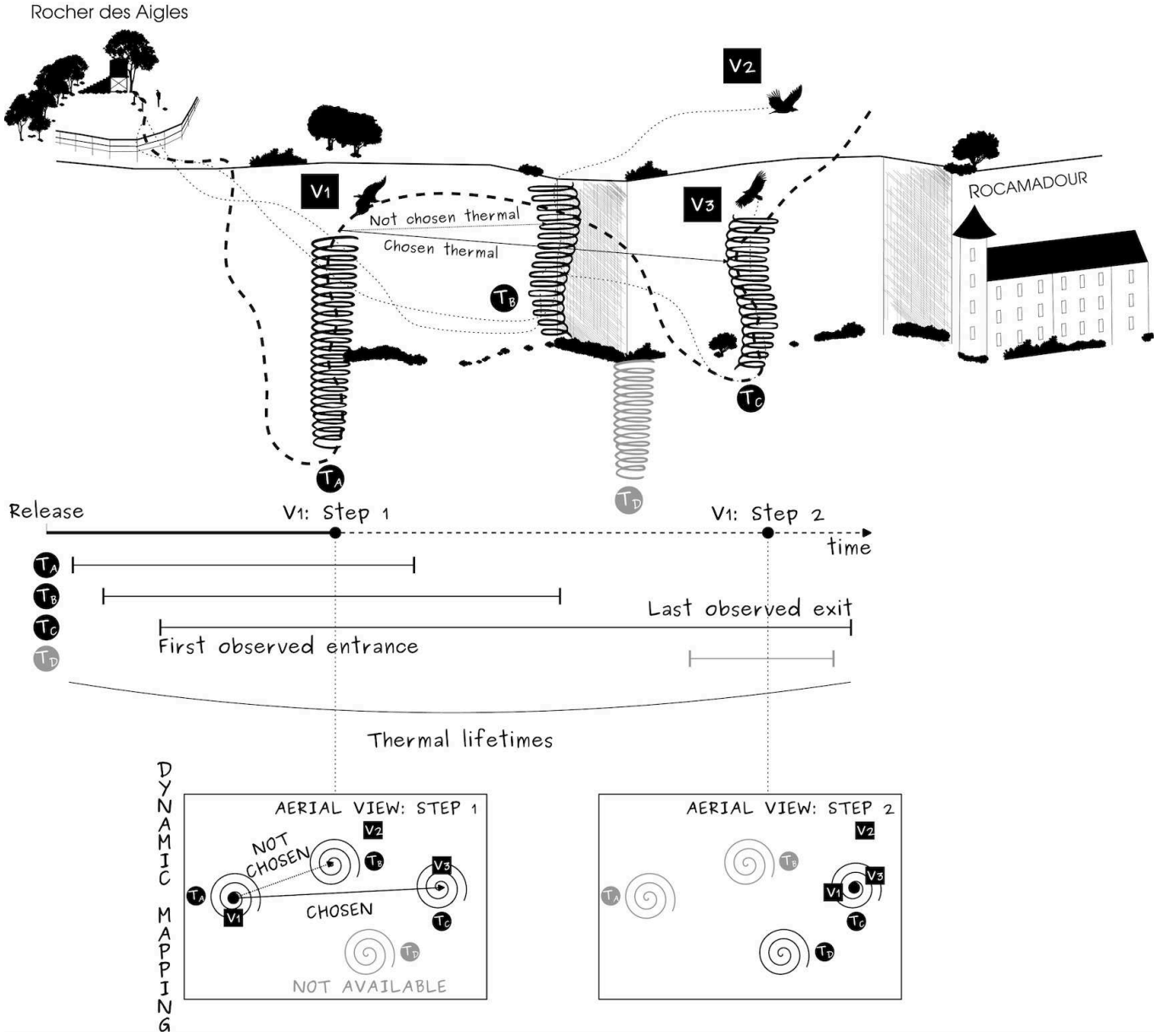

Figure 3. Illustration of the step selection framework used to investigate thermal selection. We focused on the movement of vultures released from the Rocher des Aigles when flying from thermal to thermal (i.e. a step). To do this, we mapped each thermal used during a flight session based on movement segmentation and clustering (see method section) to create dynamic maps of thermal availability over the flight session (as represented by the aerial views). The illustrated example focuses on the decision of a vulture (V_1; step 1) when leaving the thermal (T_A) and having to choose between two available thermals (T_B, close but not currently used by another vulture, and T_C, further away but currently used by another individual). T_D was not available until step 2, when it was discovered and used by another individual, and is therefore shown in grey at step 1. At step 2, V_1 joined V_3 in T_C and both thermals T_A and T_B were no longer available. A thermal was available from the moment when the first individual entered it until the last individual left it. Therefore, the number of available thermals could change during the flight session (see differences between maps in step 1 and 2).

III.2.2. Statistical analyses

We defined collective flight events as any time of a flight session when at least two individuals were flying. For each of these events, we first analysed the use of social information (the tendency to join thermals already discovered by conspecifics) as a function of external (meteorological) and internal drivers (individual traits). We then used step selection functions to define, at each movement step, which drivers determined the selection of the chosen next location (thermal updraft) relative to other potential locations.

III.2.2.1. Drivers of social information use

We investigated the effect of local meteorological context, individual traits and flight mechanics on the use of social information, defined here as the tendency to join thermals already discovered by conspecifics. We considered that an individual discovered a thermal when it was the first, among all individuals, to adopt circular soaring flight into it. For the analysis, we discarded the discovery of the first thermal in each flight session (as this thermal was necessarily discovered).

To investigate the drivers underlying the use of social information we modelled the probability to join a thermal already discovered by others using generalised linear mixed models (GLMMs) with binomial error structure and a logit link function [55]. Our full model contained the following ten fixed effects: **meteorological variables** with the (i) wind speed (categorical predictor), (ii) cloudiness and (iii) temperature (both continuous predictors); **social variables** with (iv) the age (continuous predictor) and (v) rank in the dominance hierarchy of the individual (ordinal categorical predictor), and variables related to the **mechanic of flight** with (vi) the glide-ratio (horizontal distance travelled during a 1-m altitude loss, only measured on glides with straightness > 0.95 in each flight), (vii) the altitude of and (iix) the 3D distance to the exit location from the previous thermal used (all continuous predictors). We also added (ix) the group in which individuals have been released (first or second group released for the flight) and (x) the time elapsed since the first individual take-off (continuous predictor) as control variables. Individual ID was considered as a random factor.

To compare the relative importance of the fixed effects we scaled all non-categorical variables to use their estimate as dimensionless effect size [56]. We examined the significance of each variable by comparing the goodness of fit of models with and without the variable of interest using a likelihood ratio test ('drop1' function, *stats* R package). Assumptions required for these statistical approaches (homoscedasticity, Gaussian distribution of residuals) were checked with plot diagnosis (histogram of residuals, residual Q-Q plot, distribution of residuals vs fitted values, *DHARMa* R package, [57]). We also tested for the presence of outliers, and calculated the variance inflation factor (VIF) to test for collinearity (VIF values ≥ 3 suggesting a strong collinearity [58]). We did not detect collinearity in our predictors ($VIF_{max} = 1.74$) (Figure S3). Furthermore, we extracted the

marginal coefficient of determination (R_m^2) and the conditional coefficient of determination (R_c^2) which describe, respectively, the proportion of variance explained by fixed effects and by the fixed and random effects combined [59]. Finally, as the flight time period, and the tested individuals differed, we cross-compared models fitting on the two years separately (see Supplementary Material ESM01).

III.2.2.2. Drivers of thermal updraft selection

To study the drivers underlying thermal selection, we embedded our work in the Step Selection framework [60]. We considered the series of thermals used by each individual. In that series, we focused on movement steps involving a flight to a thermal previously (or currently) used by a conspecific when other thermals were available. Using a conditional logistic regression, we compared the "chosen" thermal characteristics to those "available" but not chosen. The conditional logistic regression included seven predictors, respectively characterising the **thermal profitability** with (i) the distance to it and (ii) maximum vertical speed reached in the thermals by any individual since the focal individual has been released in the flight session (continuous predictors), **individual personal experience** considering whether (iii) the thermal was previously used by the focal individual (binary predictor), and **social information** with (iv) the presence of the focal individual's preferred affiliates in the thermal or not (binary predictor), (v) the number of individuals present in the thermal, (vi) the weighted mean (by the number of previous visits to the thermal) of the social bond with individuals that used the thermals, and (vii) the negative cubed difference of ranks between the focal individual and those in the thermals (all continuous predictors, set to 0 for the two latter if no individuals used it/were present). We used the negative cubed difference to consider an attraction-repulsion effect (high rank toward low rank and the opposite respectively) by translating a linear rank difference to a relative hierarchy scale which enhances large rank differences. For example, following the curve of the negative cube function, if the difference of rank was five (e.g. the focal individual is ranked 6th - a low rank, a conspecific in another thermal is ranked 1st - a high rank) the probability that the focal individual joined the conspecific should be drastically decreased, mimicking a repulsion effect.

Also for this model, we scaled all non-categorical variables to better compare their relative importance. We fitted the conditional regression considering all individuals together, yet considering data stratified at the individual-step level. We finally reported the relative selection strength (RSS) of significant variables which provides the magnitude of estimated selection coefficients, holding all other covariates fixed [61,62].

III.3. Results

Vulture dominance hierarchy was steep (Figure S2) and reliably inferred (individual Elo-rating repeatability = 0.82 and 0.83 in 2021 and 2022 respectively). The rank orders among individuals present in both years were relatively consistent and unrelated to sex or age

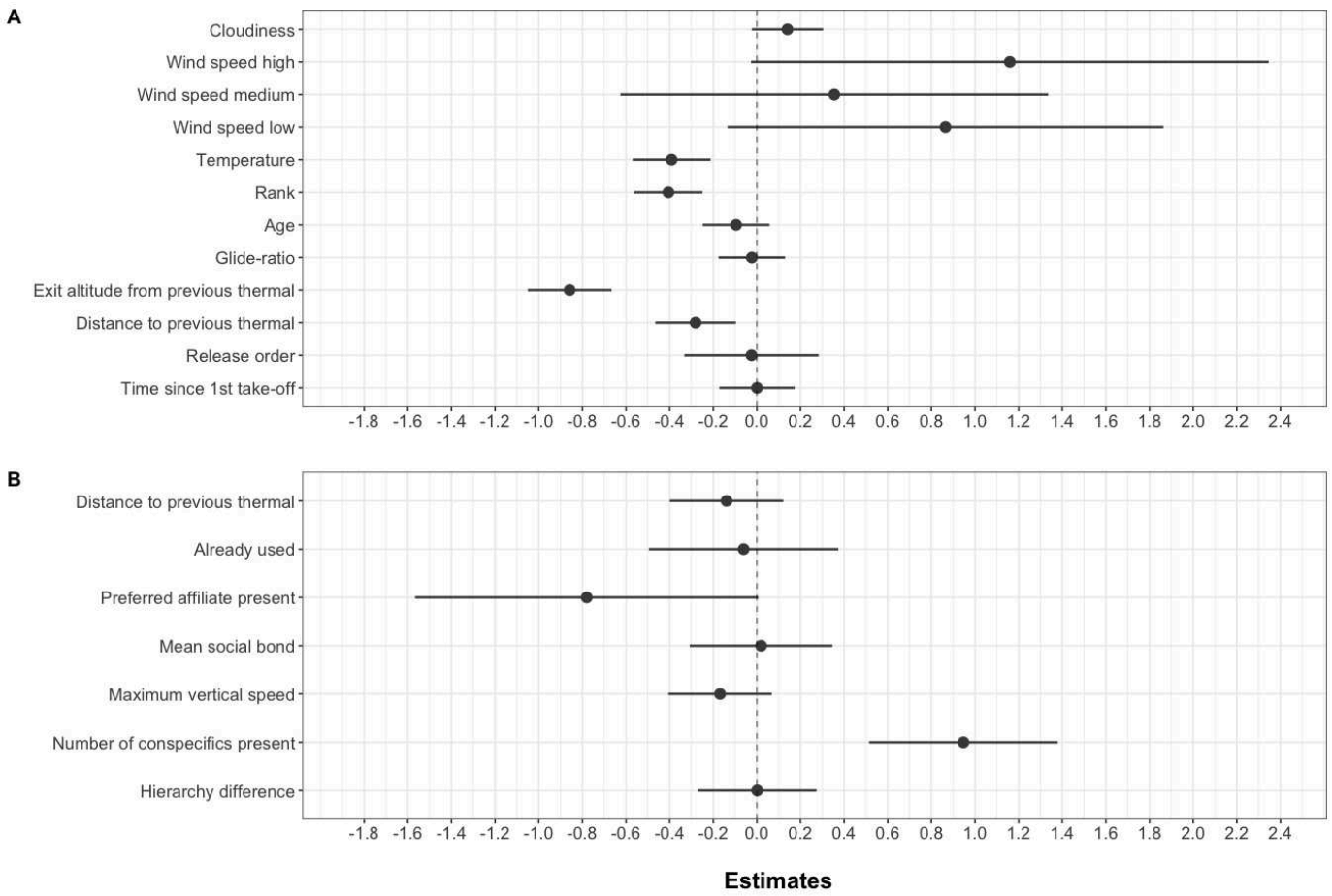

Figure 4. Estimates of models investigating the drivers of social information use (A) and thermal selection (B). Rows correspond to each predictor. Each point represents the standardised estimate value. Segments give the associated 95% confidence intervals.

(Table S1). During the 21 flight sessions performed each year, we identified a total of 520 and 578 thermalling events in 2021 and 2022. On average, 63% (SD ± 7%, Table S1) of these circular soaring behaviours took place in thermals discovered by a conspecific.

III.3.1. Flight risks and hierarchy shapes the use of social information

Our model was significantly better than the null model (considering only control effects; AIC = 1237.4 and 1412.7 respectively) and explained 30% of the variance (Table S2). The probability for an individual to use a thermal previously discovered by a conspecific decreased with temperature (from 0.74 at 17°C to 0.43 at 31°C, Figure 4A, Figure 5A, Table S2), but tended to increase with cloudiness and wind speed (Figure 4A, Table S2). This probability dropped also with the distance from the previous thermal and the altitude at which the bird left it (from 0.63 when being at a distance of 12 m from the last thermal used to 0.16 at a distance of 6776 m and from 0.76 when exiting the last thermal at an altitude of 195 m to 0.039 at 1574 m of altitude, Figure 4A, Figure 5B, C, Table S2). Individuals lower in the

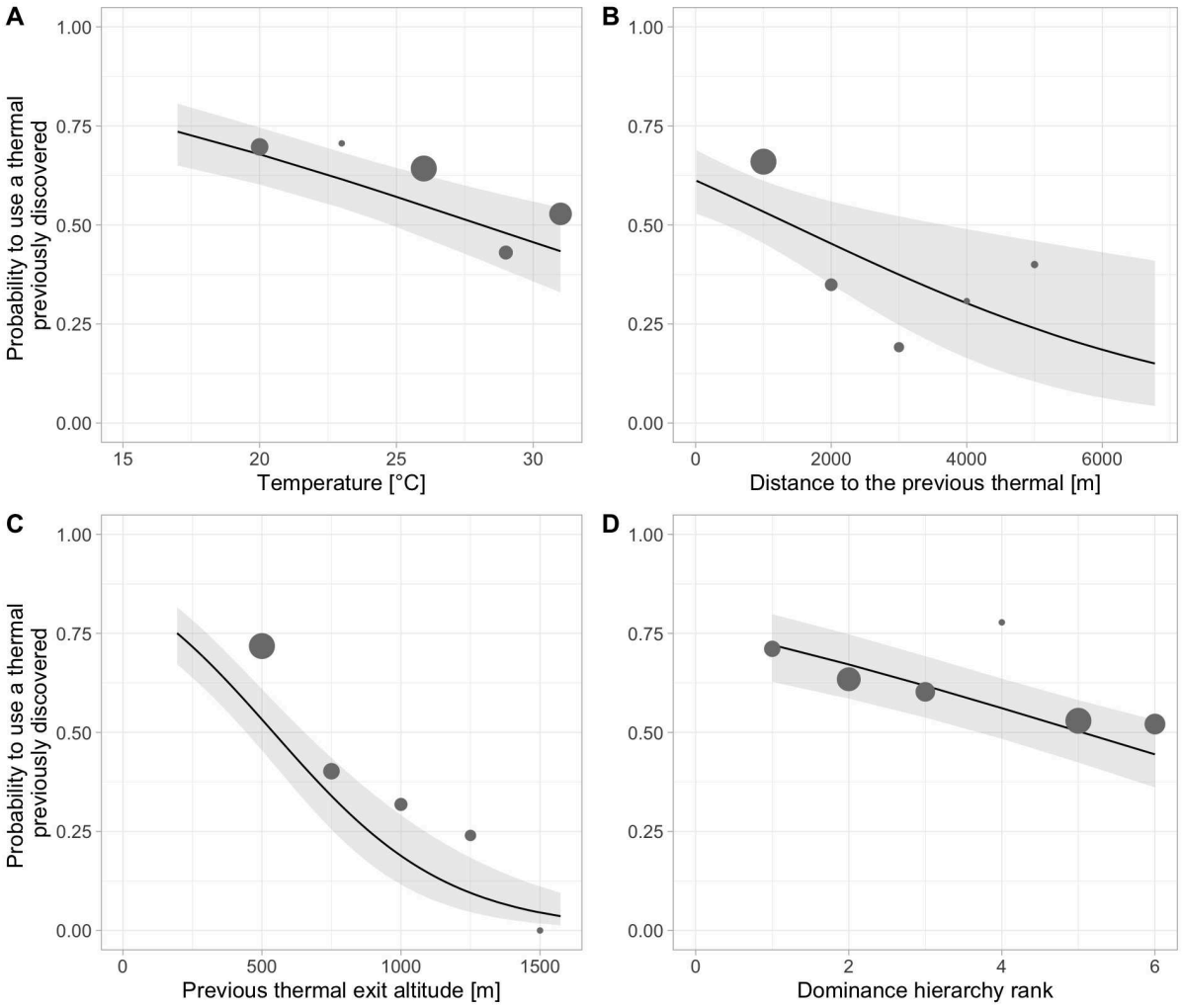

Figure 5. The probability to use a thermal already discovered by conspecifics decreases with temperature, distance to the thermal, flight altitude and hierarchy rank. Points represent the probability of using a thermal already discovered by a conspecific, estimated on the raw data. Their size is relative to the sample size. To do so, for (A), (B) and (C), predictors were binned. Black lines with grey shades show the GLMM estimated probability with its 95% confidence interval (N = 1098 thermals).

dominance hierarchy were approximately twice as likely to discover new thermals than high-ranked individuals (Figure 4A, Figure 5D). We did not detect significant effects of age and glide-ratio on the probability to use thermal previously discovered by conspecifics (Figure 4A, Table S2). Fitting the same model structure on 2021 and 2022 data separately yielded the same overall results, suggesting that the observed pattern was robust to changes in hierarchy and between-year conditions (Figure S4, Table S2).

III.3.2. Vultures select thermal updrafts hosting the most conspecifics

We identified 178 movement steps where an individual entered a thermal while at least one other thermal was available simultaneously. Individuals were significantly more likely to select thermals hosting the largest number of conspecifics at time of decision (Relative Selection Strength [95% confidence interval] = 27.94 [5.99, 131.63]; Figure 4B, Table S3). On the contrary, the probability to choose a thermal tended to decrease when the preferred affiliate was using it. The distance to the previous thermal and the maximal vertical speed reached in the thermal and whether individuals used this thermal in the past did not significantly affect thermal selection (Figure 4B, Table S3). At time of decision, the difference in dominance ranks as well as the presence of its preferred affiliate did not drive the individual's probability of selecting the thermal. This pattern was consistent when considering only movement steps where individuals had to choose between thermals used at time of decision (N = 61, Figure S5, Table S3). Furthermore, considering all decision events, the sensitivity analysis on the inter-individual distance threshold for the social bond strength estimation yielded the same results (i.e. 1.55 m, 1.30 m and 1 m; see Supplementary Material ESM01, Figure S6, Table S4).

III.4. Discussion

Using a combination of high-resolution tracking and social structure monitoring, we identified contextual drivers for the differential weighting of personal and social information in movement decisions. We showed that vultures' movement decisions predominantly relied on social information, especially in unfavourable flight conditions that increased thermal unpredictability or put individuals at risk of undesired landing. Overall, individuals preferentially joined thermals with the largest number of conspecifics. However, the use of social information depended on the individual social status: low-ranking individuals were more inclined to use personal information and discovered more thermals on their own than high-ranking individuals.

We found that low-ranked individuals, likely the ones suffering the most from interference competition, had higher probabilities of discovering new thermals, thus likely exploring their environment more intensively than the high-ranked individuals. Such flight strategy would enable subdominant individuals to reach carcasses first, or at least to arrive at the beginning of the feeding event when the rate of interference is lower [27] hence avoiding to loose opportunities due to conformity with conspecific behaviour [64]. From this may emerge a producer-scrounger dynamic [65,66] wherein the use of personal information from low-ranked individuals to arrive at food sources with lower competition levels would be exploited by dominant individuals to reduce their own searching effort [16,66,67]. This is coherent with previous observations of low-ranked vultures being "pioneers": the very first individuals to land and feed on the carcasses before being displaced by high-ranked individuals arriving afterwards [27]. This influence of dominance on foraging tactics where low-ranked individuals explore and find food while dominant profit has also been observed in other social bird species such as common cranes *grus grus*, oystercatcher *Haematopus ostralegus*, house sparrows, *Passer domesticus*, and barnacle goose, *Branta leucopsis*,

[18,67–69]. Eviction of subordinates from food patches has even recently been identified as a trigger for collective movements [70]. In contrast, in activities where individuals do not experience competition, such as tool-use learning in chimpanzees, naïve individuals will generally copy dominant (and knowledgeable) individuals [71]. Our study hence stands as a clear cut illustration of the “copy when asocial learning is costly" rule [72]: the vulture position in the dominance hierarchy, through the costs it imposes on access to food, seems to calibrate the balance between the use of personal and social information in foraging movements. In some cases, however, trading personal information in favour of social information is inevitable.

When the environment is largely unpredictable or whenever using error-prone personal knowledge can be energetically costly, individuals should tend to eavesdrop, and rely more on information provided by conspecifics to reduce uncertainty about resources availability [15,73]. Here, we evidenced both cases. First, vultures prioritised the use of social information when the temperature was low and tended to when cloudiness and wind speed increased. These weather conditions may translate into fewer and weaker thermals, drifting into the wind, making them less predictable [74–78]. Second, they also favoured social information when the altitude at which they left their previous thermal was low. When exiting a thermal at low altitude, individuals have limited time to glide to the next thermal before having to shift to flapping flight to stay aloft, or else landing in an undesired place, which both would add high energetic cost associated with flapping and take-off [23,24,79,80]. Reaching high altitudes quickly to avoid this risk may also explain why vultures used more thermals previously discovered by conspecifics if those were close to the last thermal they used. While vultures are able to cope with difficult flight conditions (e.g. turbulence and strong wind) by adjusting their banking angles [55], anticipating such risky events may remain the most efficient way to maximise the trade-off between time, energy and risk which largely dictates their flight strategy [81]. Adult individuals, through experience, are generally better at coping with difficult flight conditions [82], yet we did not evidence an effect of age relative to the use of social information, as observed in other group living species (e.g. [83]). More than age *per se,* the familiarity of individuals with a given situation might shape their tendency to rely or not on social knowledge (e.g. in spider monkeys, *Ateles geoffroyi*, during collective foraging [84]). The captive individuals tested in this experiment are all adults and fly in the same landscape every day since their birth, thus they are probably very familiar with the areas favourable to thermal emergence. This could explain why we did not detect any effect of age on the use of social information, but also indicates that the relative importance of this source of information is probably underestimated due to the birds' familiarity with the surroundings. An interesting complementary experiment (though technically difficult) to disentangle the effect of familiarity with the landscape would be to move the whole group and repeat the experiment in an unfamiliar area to better estimate the strength of personal versus social information use.

When faced with a choice between simultaneously available thermals, the previous experience of individuals (i.e. whether the thermal was used previously or not by the focal) or current expertise of the group (i.e., relative age/hierarchy difference) impacted very little

vulture movement decisions compared to other social cues, contrasting with previous findings from insects to mammals, including birds [85–89]. In the current system, ascending currents can be very ephemeral phenomena, sometimes only lasting a few minutes [90,91]. Certainly, a "live report" is therefore better provided by the accumulation of convergent information sources (i.e. numerous conspecifics, [92]) rather than relying on a unique individual source (i.e. the individual itself or one reference individual). In that line, and surprisingly, the presence of one preferred affiliate in a thermal tended to reduce the probability to join it. There is evidence that social bonds assessed "on the ground" are often unrelated to co-flight preferences [93]. It therefore questions whether collective flights might be used by vultures to strengthen initially weak social bonds. Maintaining in-flight bounds can indeed be important, as evidenced in the migratory behaviour of other soaring bird species to enable accurate collective mapping of the distribution of uplifts [94,95]. Furthermore, for soaring birds, the presence of conspecifics should provide not only information on the location and strength of updrafts [20,95] but could also indicate flight speed and circling radius needed to optimise climb rate, by remaining close to the centre of the thermal where uplift is highest [55]. Yet, the maximum speed reached by individuals using the thermal little affected vulture decision choices. Possibly, climb rate or individual speed are not as easy to assess at a distance, compared to the number of conspecifics. In other words, vultures tended to favour quantity signals (with the number of conspecifics) over quality signals (maximal vertical speed) [96]. The "power of the group" may indeed in turn drive cohesion, which could itself make social information even more profitable [96,97].

Altogether, our results provide insights into the architecture of decision-making during movement in a social bird. It highlighted the trade-offs between personal and social information these birds have to consider in order to optimise both their flying efficiency and their foraging success. As a first approximation, we considered social cues as coming from "conspecifics". Strictly speaking however, our study included two species, Griffon vulture and Rüppell's vulture, albeit phylogenetically close and with similar biology. The one Rüppell's vulture in fact, used social information provided by surrounding vultures and did not stand out as an outlier in its behaviour. It is known that even phylogenetically distant individuals could be an important source of social information, not only about the presence of carcasses [98], but also about the availability of thermals when sharing the same airspace (e.g. from black kites, *Milvus migrans,* or common swifts, *Apus apus,* [99,100]). Interactions with heterospecifics can indeed drastically affect animals' daily life [101], up to shaping the cognitive machinery underpinning their foraging decisions [102]. How heterospecific cues are used when foraging remains clearly overlooked. Future studies in this direction could provide valuable insights into understanding the fundamental rules dictating how animals decide where to go.

III. CRediT authors' contributions

Yohan Sassi: Conceptualization, Methodology, Software, Investigation, Formal Analysis, Visualization, Writing - original draft, Writing - Review & Editing
Basile Nousières: Investigation, Resources
Martina Scacco: Software, Writing - Review & Editing
Yann Tremblay: Conceptualization, Writing - Review & Editing
Olivier Duriez: Conceptualization, Investigation, Supervision, Writing - Review & Editing
Benjamin Robira: Conceptualization, Methodology, Software, Visualization, Validation, Supervision, Writing - original draft, Writing - Review & Editing

III. Declaration of competing interest

The authors declare to have no conflict of interest

III. Data availability

Scripts for review and supplementary video are available here:
https://github.com/YohanSassi/UpdraftsDecisions

A perennial storage of data and scripts will be provided after revision (e.g. Zenodo, Dryad)

III. Acknowledgment

We thank Dominique Maylin and Raphael Arnaud at Rocher des Aigles as well as all of the staff for their patience, help and enthusiasm for the project. GPS loggers were provided by Giacomo Dell'Omo. Camera traps and Gopro video cameras were provided by Aurélien Besnard, Samuel Caro and Samuel Perret. We also thank Samson Acoca-Pidolle for fruitful discussions about the statistical analyses.

III. Fundings

This work was supported by the GAIA doctoral school grant, University of Montpellier (YS) and the Gordon and Betty Moore Foundation (BR).

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IV. La stratégie de prospection alimentaire en réseau chez les vautours : une hypothèse centenaire étudiée par radar

Dans ce chapitre j'ai analysé les images d'un radar dédié à l'observation des comportements d'oiseaux, placé à quatre endroits dans les Grands Causses où niche la deuxième plus grande population de vautours fauves en France, afin de vérifier empiriquement l'hypothèse de la recherche en réseau chez les vautours.

Le traitement et l'analyse de ces données a représenté un énorme défi. En effet, les algorithmes de traitement automatique d'images radar développés auparavant pour des oiseaux marins ont dû être adapté pour être efficaces en milieu terrestre, du fait de la présence d'insectes volants, du relief entraînant la formation de masques, ainsi que de la difficulté de différencier les vautours fauves des autres espèces d'oiseaux et aéronefs. Après deux années de travail de prétraitement, j'ai finalement pu explorer, lors des 2 derniers mois de ma thèse, un jeu de données concernant 2 sites (sur 4) suivis pendant 10 jours de l'été 2018. Ce chapitre reporte les résultats préliminaires de l'exploration visuelle et manuelle de ce jeu de données. Il révèle déjà des phénomènes d'agrégations et des patrons de déplacement coordonnés jusqu'alors jamais observés chez une espèce terrestre.

Note au lecteur :
- L'article est toujours en préparation, il peut être amené à changer.
- Les annexes de l'article sont disponibles en annexe 2 du présent manuscrit p 195.

Vulture's foraging network: a century-old hypothesis investigated with radar

Sassi Yohan [a,*], Assali Camille [b], Liebault Vincent [b], Delcourt Vincent [b], Scacco Martina [c,d], Duriez Olivier [a], Tremblay Yann [e]

a: CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
b: Biotope, Mèze, France
c: Max Planck Institute of Animal Behavior, Department of Migration, Am Obstberg 1, 78315, Radolfzell, Germany
d: Department of Biology, University of Konstanz, Universitätsstraße 10, 78464, Konstanz, Germany
e: Marine Biodiversity Exploitation and Conservation (MARBEC), IRD - U. of Montpellier - CNRS - Ifremer, Sète, France

* Corresponding author: yohan.sassi@cefe.cnrs.fr, CEFE, 1919 Routes de Mende, 34293 Montpellier cedex 5, France, +33 6 59 06 16 52.

IV. Abstract

The fast aggregation of vultures around a carcass has been hypothesised to depend on two factors. First, local-enhancement is a social cue provided by a vulture's sudden loss of height that conspecifics can rely on to locate a carrion that he cannot see directly. Second, the use of a social foraging strategy in which individuals spatially disperse to forage while keeping an eye on their flying conspecifics, forming a network of observers. This network foraging strategy was first formulated by Tristram in 1867 and tested in computer simulations, but has never been measured empirically. We used a radar to track all birds flying simultaneously within a 6 km radius, at four different sites, for a total of 33 days. Our exploration of a subset of these data (only 2 sites and 10 days explored) provide empirical support for the local-enhancement effect, with vultures being drawn to carcass locations from distances of 7 km at least. We also discovered the existence of foraging groups, looking like small "trains" of vultures, organising themselves sometimes in parallel lines, which we termed "rails", spaced such that the visual fields of individuals projected onto the ground were juxtaposed. Overall, our preliminary results provide empirical support for the combination of the "group foraging network" strategy and local enhancement in vultures to explain their efficiency in finding and aggregating at carcasses.

Key-words: *Gyps fulvus*, foraging strategy, social information, group living, unpredictable resource

IV.1. Introduction

Foraging behaviour, especially searching strategy, largely depends on the nature of the exploited resource and its predictability in the ecosystem. When predictable, animals can rely on their personal information, memorised from previous encounters, to find the desired resource (Danchin et al., 2004). For instance, having learnt the filling temporal dynamics of nectar-bearing flowers, hummingbirds move routinely from flower to flower in a specific order to maximise their nectar consumption (called "traplining", Temeles et al., 2006). However, relying solely on personal information when searching ephemeral and unpredictable resources will result in imprecise decisions about where and when to find the resource of interest (Fawcett et al., 2014). In this case, using social information, acquired through the observation of conspecifics' behaviours (Dall et al., 2005; Danchin et al., 2004), is beneficial in that it may reduce the cost of individual searching (Rafacz & Templeton, 2003).

Vultures are renowned for their efficiency in locating carcasses, an ephemeral and unpredictable resource (Ostfeld et al., 2000). Although they are able to find carcasses on their own (using personal information; Cortés-Avizanda et al., 2010; Fluhr et al., 2017; Mundy et al., 1992), they are thought to rely heavily on social information when foraging, which may explain the rapid arrival of numerous vultures at carcasses. Field studies based on vulture counts at roosting sites yielded unclear conclusions about a possible role of roosts as "information centre", where individual vultures would collect information in the evening about the successful foragers of the day, and then follow those individuals on the next day (Buckley, 1996; Prior & Weatherhead, 1991; Rabenold, 1987). Only one telemetry study empirically showed the existence of an information centre at roost in griffon vultures in Israel (Harel et al., 2017). This is particularly relevant in areas where vultures feed on very large carcasses (e.g. cows, camels) which take several days to be consumed, hence potentially stay available on several consecutive days, increasing the probability for a vulture that fed the previous day, to leave the colony in the morning flying to the carcass left-overs. In areas where vultures mainly feed on sheep carcasses or other medium size mammals, typically fully consumed in a few hours (Duriez et al., 2012), this strategy is less likely to be at play. In these conditions, vultures should use instead a strategy based on information collected directly in flight or memorised from previous encounters with the ressource.

Theoretical studies have examined different foraging strategies to better understand the information used by vultures and what explains their efficiency (Cortés-Avizanda et al., 2014; Deygout et al., 2010; Jackson et al., 2008). First, Cortès-Avizanda et al. (2014) investigated a "non-social" strategy where vultures only use personal information when foraging. Second, they tested the ''local enhancement'' as a foraging strategy in itself, in which the rapid and direct descent of vultures, after a short circling, is used as a signal that a carcass has been found, and triggers the aggregation near the carcass of individuals from a distance to a particular site (Houston, 1974; Mundy et al., 1992; Pennycuick, 1972; Tucker, 1988). In Deygout et al. (2010), the phenomenon of local enhancement was included in both the random search strategy and the traplining. The latter assumed that vultures could also use

previously acquired personal information about the location of resources to repeatedly visit these specific sites. Third, both Deygout et al. (2010) and Cortès-Avizanda et al. (2014) simulated social foraging strategies based on the assumption that vultures that start to follow another vulture could in turn be followed by other conspecifics, resulting in an information cascade that could potentially lead vultures to a carcass from distances where they could not see it. This hypothesis has first been formulated by Tristram in 1867 when it speculated (cited in Houston, 1974): ‘‘The process is probably this: The griffon-vulture, who first detects the quarry, descends from his elevation at once. Another, sweeping the horizon at a still greater distance, observes his neighbor’s movements, and follows his course. A third, still farther removed, follows the flight of the second; he is traced by another, and thus a perpetual succession is kept up, so long as a morsel of flesh remains over which to consort.’’. The “chains of vulture” strategy described in Cortés-Avizanda et al. (2014) considered that individuals can join the chain indefinitely and eventually land near the carcass. Their results indicated that this strategy tended to consistently overestimate the number of individuals arriving at the carcass compared with what they counted in the field. On the contrary, simulations of local enhancement tended to produce estimates relatively close to those observed empirically. In the “group foraging network” strategy of Deygout et al. (2010) they assumed that foraging vultures were able to form groups with other individuals, flying parallel to each other to maintain visual contact in order to maximise the acquisition of social information about conspecific success (Buckley, 1996). For these authors, the local enhancement effect is not a searching strategy by itself, but the final step of any foraging strategy (random, traplining or network). Their results suggested that the “group foraging network” strategy became particularly valuable when the resource was largely unpredictable or when population size was very large. Overall, these simulation studies had concordant conclusions that the random search strategy, but also strategies based on personal information alone, generally performed worse than social strategies when searching for carcasses. Exceptions were made for traplining, where carcasses were made more predictable by feeding stations, although traplining strategy has been shown empirically to be used only marginally by vultures (Fluhr et al., 2017).

Social foraging strategies have been hypothesised in vultures more than 150 years ago (Houston, 1974; Tristram, 1867), studied theoretically and by simulations (Cortés-Avizanda et al., 2014; Deygout et al., 2010; Jackson et al., 2008), but have never been empirically observed. This is probably due to the technical difficulty of simultaneously recording the positions of several dozen vultures flying at high altitude. Indeed, foraging vultures tend to fly at an average height of 300 m (Harel et al., 2016), and cover hundreds of kilometres per day in their vast home ranges (more than 1000 km^2 and up to 8000 km^2, Duriez et al., 2019; Fluhr et al., 2021), making it very difficult to detect social foraging strategies by direct observation from the ground. In addition, these birds are colonial, making the study of social foraging strategy by GPS tracking impossible without tagging the entire population, which is only feasible in small populations where captures are efficient (Harel et al., 2017). To overcome this challenge in our study area where more than 2000 vultures live, we used a marine surveillance radar to track all birds flying simultaneously within a 6 km radius, at four different sites in the Causses, France, for a total of 33 days. After reconstructing the vultures'

tracks from radar images, we looked for patterns that supported the existence of a social foraging strategy, and whether this was matching a "chain of vulture" or a "group foraging network" strategy. Under the “chain of vultures” hypothesis we predict to observe vultures following each other, one behind the other, from side to side of the radar disk, and converging to carcasses from a few directions. Conversely, under the “group foraging network” we may observe some spatial structuration due to foraging birds organised in small groups, flying parallel to each other, and converging to carcasses from every direction as predicted by the local enhancement effect.

IV.2. Materials and methods

IV.2.1. Data collection

We used a marine surveillance radar (model FAR-2127, X-band, 25 kW, Furuno) with settings adapted to the detection of birds. Radar screen captures were collected by the means of an external video-card (DVI2USB frame-grabber, Epiphan System Inc., Ottawa, Canada) and saved onto a laptop computer every ~2.5 s, corresponding to the time needed for the antenna to perform a full rotation. This radar scanned a circular area of 6 km radius around it. Images were saved as *.png files (Portable Network Graphic, i.e. lossless compression format) and analysed after the survey.

We collected data in 4 different sites in the Grands Causses (see Figure II.6 in the manuscript): Devez Nouvel (2, 3, 4, 23 and 24 July 2018), La Baume (25 to 29 September 2018, 16 to 21 December 2018 and 11 to 16 April 2019), Bengouzal (25 and 26 July 2018, 6 to 8 August 2018) and Le Buffre (5, 6, 17, 18 and 19 July 2018). This region is characterised by limestone plateaux interspersed by valleys where a population of 900 breeding pairs of griffon vultures live (census 2022, LPO). Valleys offer conditions for orographic updrafts that vultures can use to soar efficiently. Away from the valleys, vultures patrol the open landscapes, relying on thermal updrafts to gain height, looking for mortality in herds of grazing livestocks. We placed the radar on plateaux, at a mean distance of 22.62 km ± 5.99 km from the centre of the colony. During the 33 days, we collected 838 675 radar images corresponding to 582 hours of observation.

IV.2.2. Data Processing

Data processing mostly followed the methodology described in Assali et al. (2017, 2020). Briefly, the echoes were distinguished based on their colours (which depicts echo strength or intensity). Each echo thus consisted of a set of adjacent pixels from which we extracted the maximum and mean echo intensity, the weighted centroid location and the size (number of pixels). In some cases, distinct echoes may be too close to be accurately separated. To overcome this issue, we used a watershed algorithm (Meyer, 1994), which allowed for the detection of dividing lines between echoes. However, the watershed transform was done using pixel intensity values, not with a “distance transform” as commonly done.

Radars have a blind zone at close distances. This resulted in a permanent large and almost circular fake echo around the radar. Other large echoes resulted from the landforms (we tried to reduce this by placing the radar in a basin on plateaux) or meteorological factors such as rainfalls. To filter out echoes created by the flickering signal reverberating on landforms or around the blind zone, we summed, over all images in a recording session, matrices of echo presence (0 or 1). This produced very high numbers where echoes were consistently found, typically for echoes from landforms and radar's blind zone and from which we can determine masks specific to each session. Echoes which centroid fell into these masks were removed.

Specific to this dataset, we had to overcome the issue of the occasional rise of insect swarms occurring on the Causses plateau in summer, which produced a multitude of very small echoes. The insect swarm echo filter was based on echo local density. For each echo, the number of neighbour echoes in a 60 pixel radius was calculated. Echoes with more than 80 neighbours were deleted. This threshold was empirically determined and was efficient in removing most "insect noise", as well as some "rain noise". Apart from echoes from insect swarms or rain that were deleted, remaining echoes could then stand for birds or human aircrafts (e.g. planes, paragliders, helicopters), and were identified and separated by a procedure further described (see Classification of tracks section).

All remaining echoes' centroïds in the image were converted into latitudes and longitudes, knowing the location of the radar both in the image (in the centre of the radar disk) and in space (latitude and longitude coordinates), the observation range (radius of the radar disk) and the angle of the radar axis (top of image) with respect to true north. Date and hour of each echo was obtained from images' recording time.

The observation of flying birds by radar could be biased as the signal received was attenuated when the distance to the radar increased. This was automatically corrected by signal processing inside the radar box before visualisation on the screen, but some birds might be missed when they are close to the radar disk edge or the echo lost. In order to select echoes that had temporal and spatial consistency in subsequent images (i.e. to favour iterative detections of a coherent object, like birds), we conducted a tracking procedure of echoes, adapted from Tinevez (2011), constrained by (i) a maximum linking speed of 120 km/h between echoes' centroids of successive images, (ii) a maximum gap closing (maximum number of images in which an echo might temporarily disappear) of 3, which corresponded to ~8 s. All echoes that were not members of tracks of at least 6 points (i.e appearing during 6 images), were considered too inconsistent and classified as noisy echoes. Because rainfalls echoes, and echoes remaining from noise around landforms were very densely distributed, some consistency could be randomly obtained. To distinguish tracks of bird-echoes from different species, rainfalls, and those from human activities we conducted a supervised classification of tracks (see Classification of tracks section).

Tracks' properties were obtained either from echoes' position over time (e.g. averaged speed, sinuosity, averaged distance to the radar), or from echoes' properties along tracks (e.g. area, intensity).

IV.2.3. Classification of tracks

During the radar data collection, V. L. manually annotated 2440 echoes from 43 bird species as well as from human aircrafts or meteorological phenomena (e.g. planes, paragliders, helicopters, rainfalls, etc.). We matched the location and time of the annotated echoe to the closest track among the 8,465,962 tracks obtained for the 33 days of data. All these annotated tracks were visualised, and manually attributed a score from 1 to 5. One was for a track that was obviously wrong (e.g. a track annotated as a bird while right in the middle of an extremely noisy area), and five was for a track on which we were sure that it corresponded to the annotation (e.g. a track annotated as a bird, not surrounded by multiple noisy tracks and not spiky). Tracks granted 2 to 4 were for intermediate degrees of truthfulness based on the track characteristics and its surrounding context. In addition, we randomly selected and visualised many tracks, and manually classified them as “valid” or “noise”. Noisy tracks were relatively easy to spot, as they typically lack spatial consistency and are anomalously spiky. We arbitrarily stopped this selection after having obtained a total of 1849 “noise” tracks.

A random forest classification procedure (Breiman, 2001; Cutler et al., 2007) was applied on annotated tracks being “noise” or having annotated confidence score ≥ 3 (2420 tracks), with 24 track descriptive features (listed in ESM01). We used 80 % of tracks of each category for training procedure, with categories being “Vulture” and “Not Vulture” (irrespective of classification). The number of grown trees was set to 500. The selected model was then tested on the remaining 20% of tracks. During the prediction process, a confidence score ([0 - 1]) was computed for each observation. We kept only predictions with a score ≥ 0.8 (77% of them). The confusion matrix indicated that 95.45% of these predictions were correctly identified as “Vulture” or “Not Vulture”. Among the 4.55% of errors, 88% were “Vultures” not recognised as such. When the model recognized a “Vulture”, it was true in 91.3% of the cases. The selected model was therefore conservative and robust in recognizing “Vultures”, providing we only kept good confidence predictions. This model and associated score selection were then applied to our > 8 million tracks dataset in order to identify tracks of vultures. Field observations indicated that the vast majority (96.4%) of visually identified vultures were griffon vultures (*Gyps fulvus*). Note that three other vulture species breed in the area (30 pairs of cinereous vulture (*Aegypius monachus*), 2 pairs of egyptian vulture (*Neophron percnopterus*) and a pair of bearded vultures *Gypaetus barbatus*) but griffon vultures (with > 900 pairs) greatly outnumber the three other species and we therefore considered the other species as negligible for this study.

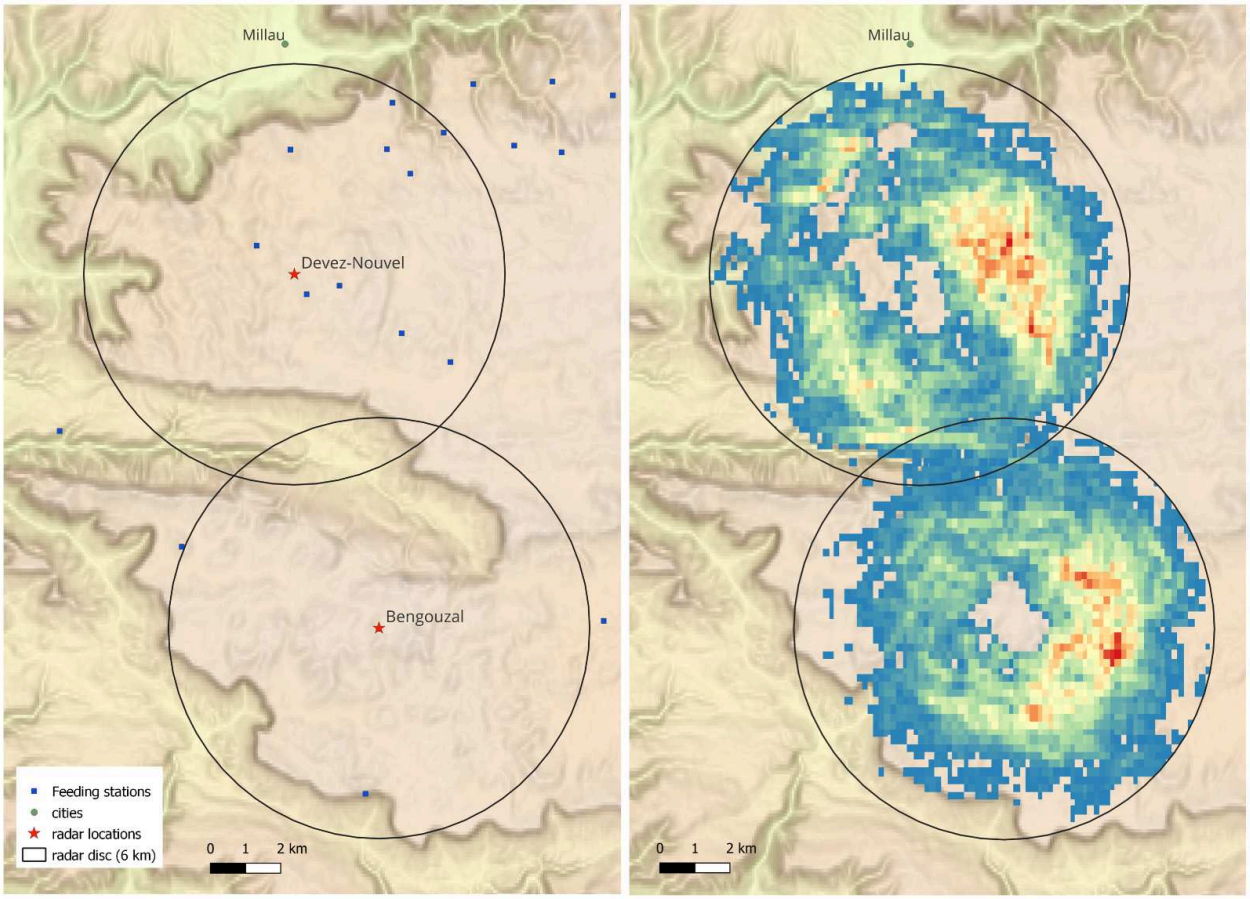

Figure 1 : Topography and vulture space use in the study sites. In the right panel, the density is estimated based on the number of tracks crossing each 200 x 200 m cells of the raster in the radar disk, with blue to red gradient indicating increasing use intensity.

IV.2.4. Data exploration and selection of patterns

In this preliminary version of the chapter, only the data collected at Devez Nouvel and Bengouzal will be presented (10 days, Figure 1). We first started at large scale to investigate whether vultures preferentially used specific areas by creating density maps at each site. We divided the radar disk area into grid cells of 200 m x 200 m. In each cell, we estimated the proportion of tracks crossing that cell over the total number of vulture tracks recorded at the site.

Then, three types of patterns of interest were visually detected as evident organised movements of several vulture-echoes. First, we detected “rails” which correspond to aligned tracks (or “trains”) forming temporary and simultaneous parallel straight lines across the landscape. These rails could be formed by 2 or 3 lines in which most of the echoes have the same direction, referred respectively as "2-lines rails" (Figure 2) and "3-lines rails" (Figure 3). Second, we observed “trains” resulting from the temporary alignment of tracks (≥ 3), one after the other, heading in the same direction (Figure 4). These "trains" were the "finite" version of the similar "infinite" pattern that could form as a result of the "chains of vultures"

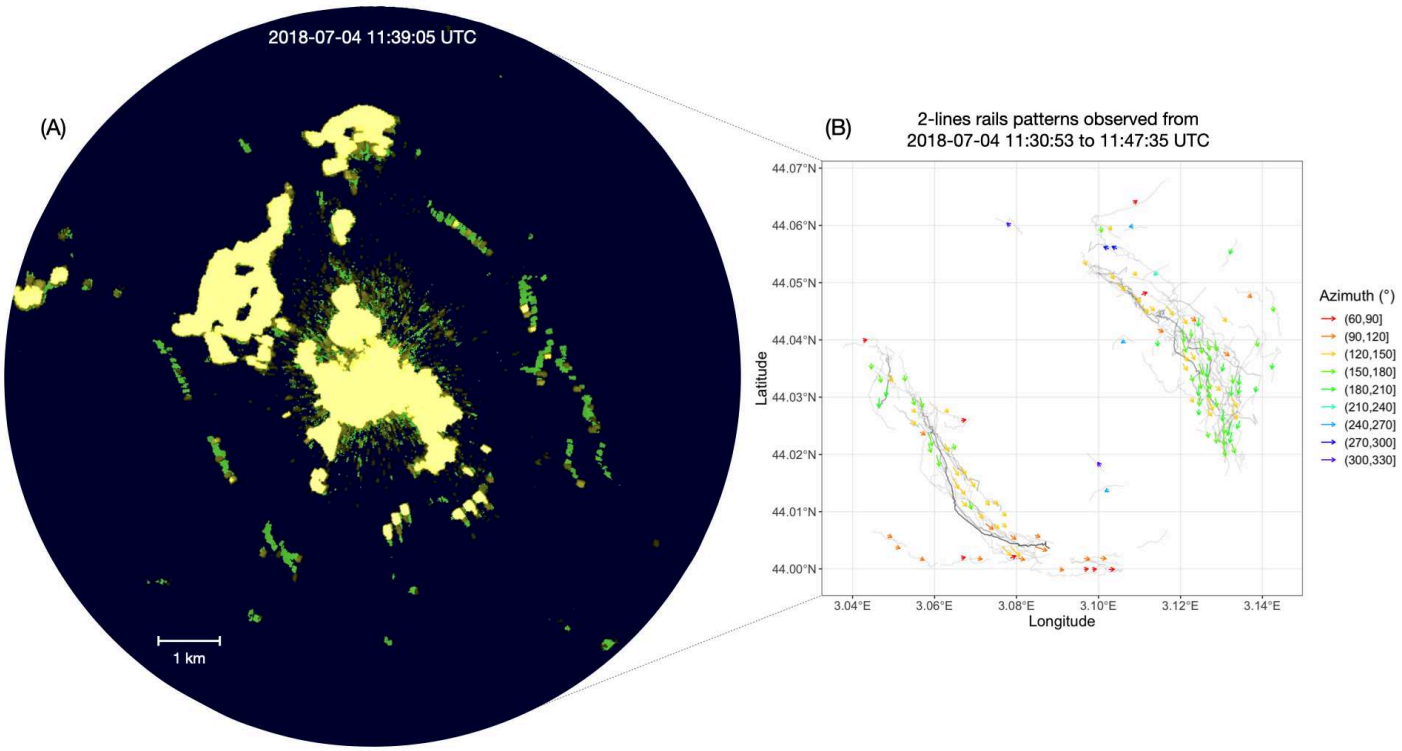

Figure 2 : Vultures in a 2-lines rail at Devez Nouvel. (A) represents a raw radar image in which brown/yellow spots are bird-echoes, followed by a green trail showing the location of the echoes in the last 30 s. Bright yellow indicates high level of intensity reflected by targets, with large yellow shapes in centre and top of the image being respectively due to the saturated (blind) zone around the radar and landforms. (B) show the averaged azimuth of vulture tracks occurring during the time period when the 2-lines rail was observed. Averaged azimuth was estimated on tracks crossing 200 m x 200 m cells, represented with an arrow starting from the cell containing the barycentre of the tracks and with a length proportional to the number of tracks crossing that cell.

strategy described by Cortes-Avizanda et al. (2014). And third, we observed “aggregations” corresponding to temporary and massive convergence of tracks towards specific locations (Figure 5).

All of these patterns were visually selected given that (i) they were observed on more than 30 consecutive images and (ii) they were conspicuously different from the movements of other vultures observed on the radar disk. While moving, vulture-echoes were not systematically involved in organised and coordinated movements such as the patterns of focus (Figure 6). Radar images were visualised and time periods of pattern occurrence were stored, with the radar image where most echoes were visible being extracted (except for aggregations where we extracted the image containing the furthest echoes attracted). Patterns that were not clearly formed or that occurred in a confusing high density of echoes in the image were not selected, even if they were suspected. Consequently, the 13 rails, 41 trains

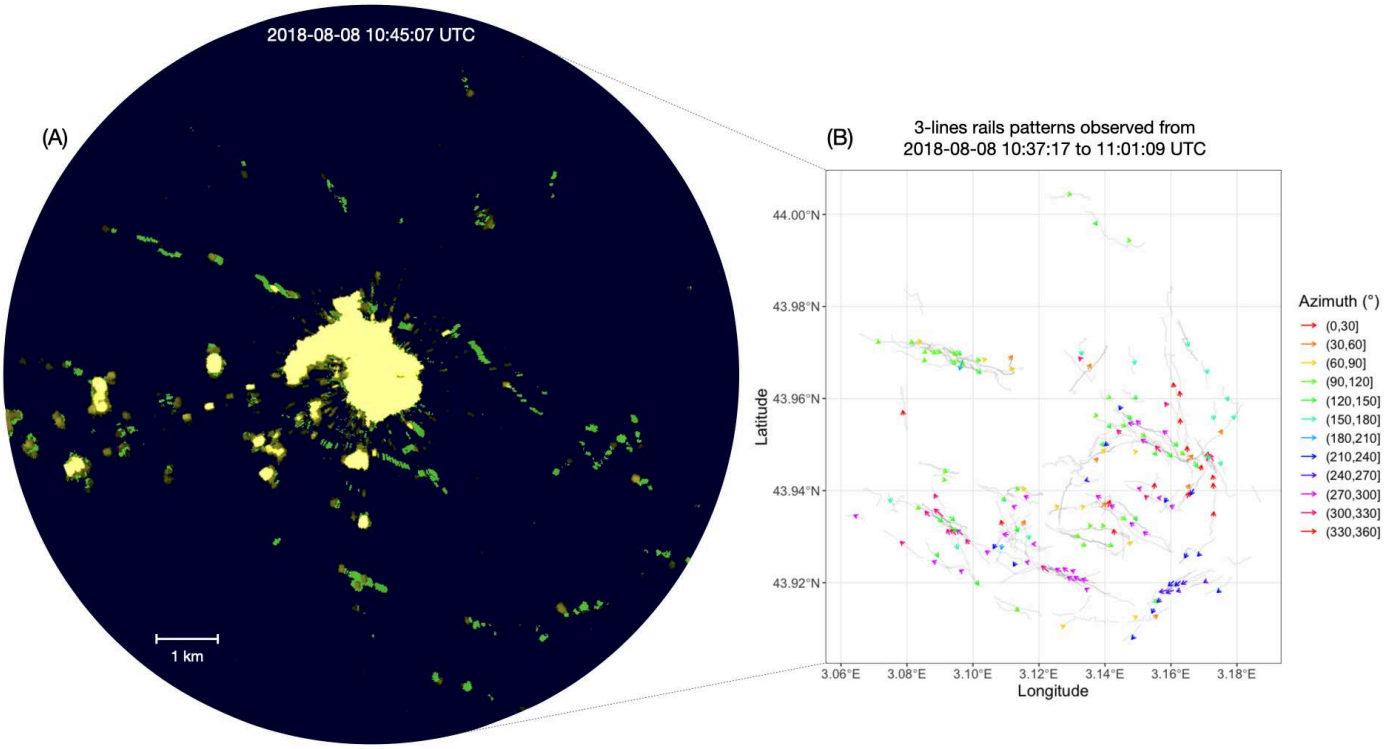

Figure 3 : Vultures in a 3-lines rail at Bengouzal. (A) represents a raw radar image in which brown/yellow spots are bird-echoes, followed by a green trail showing the location of the echo in the last 30 s. Bright yellow indicates high level of intensity reflected by targets, with large yellow shapes in centre and left of the image being respectively due to the saturated (blind) zone around the radar and landforms. (B) show the averaged azimuth of vulture tracks occurring during the time period when the 3-lines rail was observed. Averaged azimuth was estimated on tracks crossing 200 m x 200 m cells, represented with an arrow starting from the cell containing the barycentre of the tracks and with a length proportional to the number of tracks crossing that cell.

and the 2 aggregations selected in the 10 days of data represented the less noisy observations and not an exhaustive census of such patterns. The aggregation and rail patterns retained a fairly similar appearance across patterns, with only the location changing. This was not the case for trains, where we observed clear initiations by vulture groups splitting up (large static echoe, probably due to the use of a thermal, Figure 4 B_1-B_3) and starting to fly synchronously in the same direction one behind the other, or vultures forming trains and then converging so as to finally disappear in one or more points (Figure 4 B_4). On the contrary, the observation of trains could be limited because of vultures flying out of the radar circle or approaching its edge (Figure 4, C_4) or already deployed when they got detected by the radar (Figure 4, A_1). As a result, reported trains may not have been recorded during their entire "lifetime".

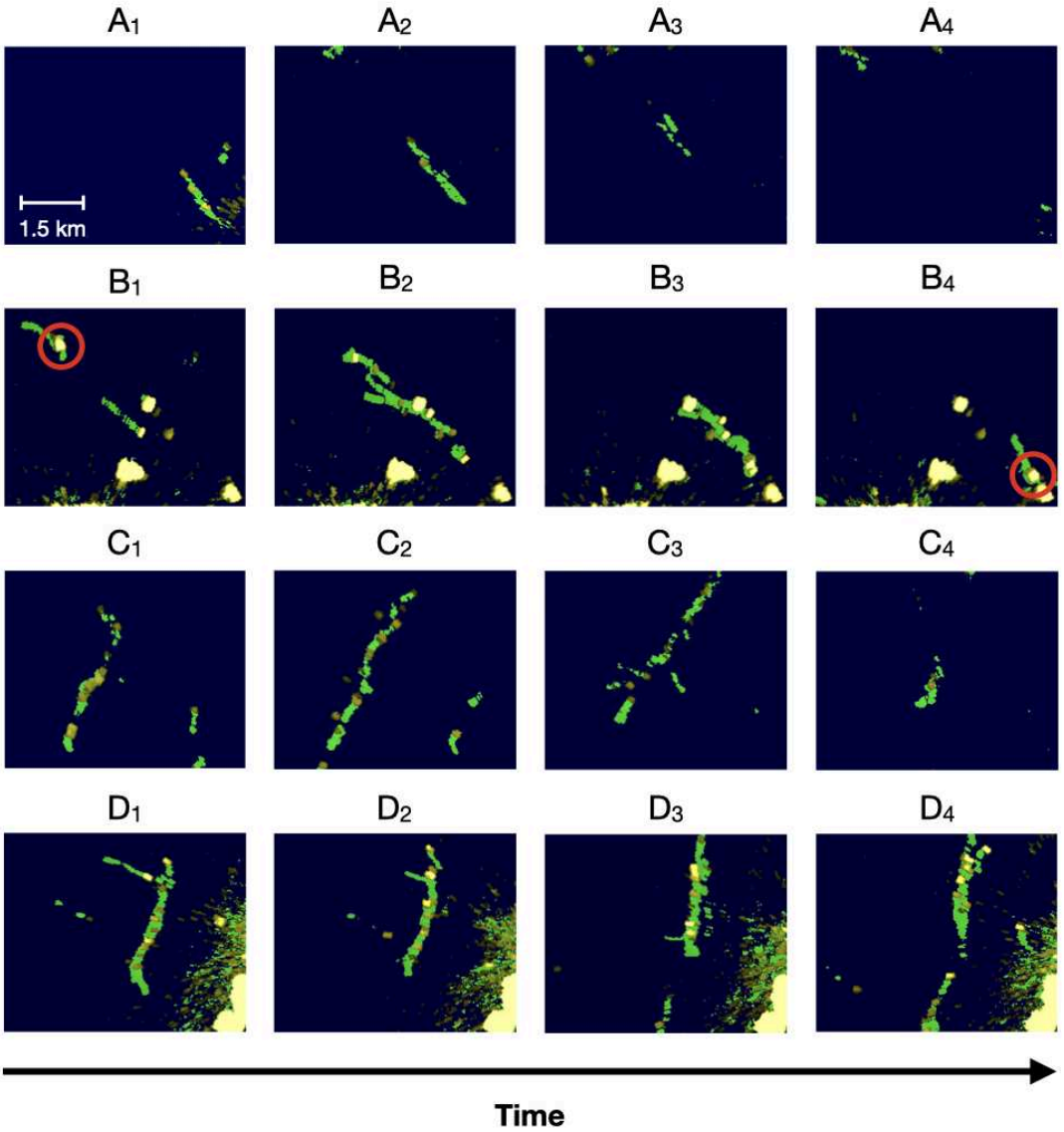

Figure 4 : Four examples highlighting the dynamic of vulture flights in trains, observed in radar images. The row (A) shows a train deployed during its all recording time, with echoes lost after A_3. The row (B) represents a train initiation by splitting echoes (red circle in B_1), its full deployment and its disappearance because vultures converged and merged into a single echoe (red circle in B_4). In this row, the stable yellow shape in the bottom centre of panels is due to landform. (C) highlights the train disappearance due to echoes' detection lost when approaching the radar disk edge. The row (D) documents the joining of two vultures to the train (D_1, D_2, D_3). In D_4 another train connects to the first. The stable yellow shape, with flickering green spots, in the bottom right corner of panels is due to the saturated (blind) zone around the radar. The scale indicated in A_1 is the same for all panels. Time gaps between panels are not regular and consistent among rows, the respective durations between first and last panel of each row are 3:20 min, 5:02 min, 3:59 min and 1:28 min.

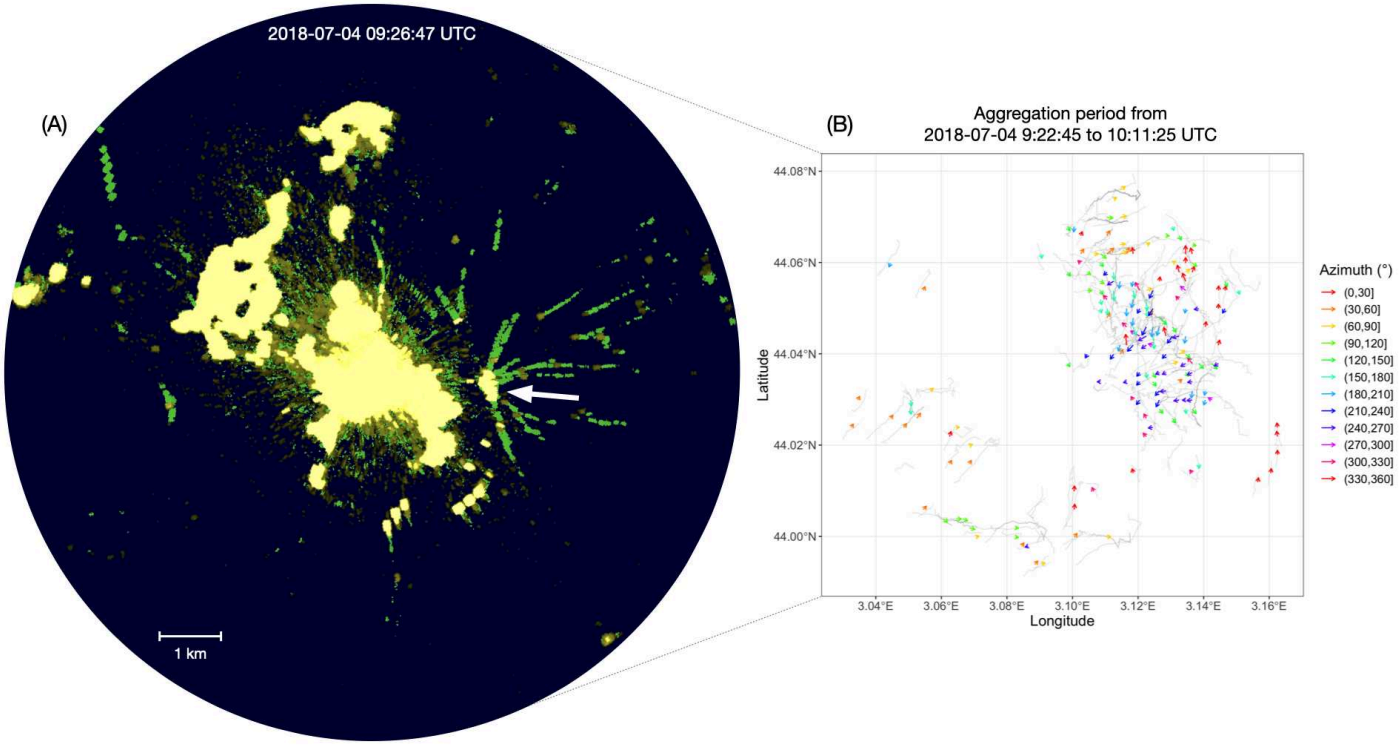

Figure 5 : Vulture aggregation event at Devez Nouvel. (A) represents a raw radar image in which brown/yellow spots are bird-echoes, followed by a green trail showing the location of the echo in the last 30 s. Bright yellow indicates high level of intensity reflected by targets, with large yellow shapes in centre and top of the image being respectively due to the saturated (blind) zone around the radar and landforms, while the aggregation location (highlighted by the white arrow) appears yellow because of the large number of birds aggregating. (B) show the averaged azimuth of vulture tracks during the aggregation period. Averaged azimuth were estimated on tracks crossing 200 m x 200 m cells, represented with an arrow starting from the cell containing the barycentre of the tracks and with a length proportional to the number of tracks crossing that cell.

IV.2.5. Calculation of patterns properties

For rails, we estimated the minimum distance between parallel lines and the duration during which the pattern was observed. For each train, we retrieved from the extracted image the number of echoes involved, the distances between the nearest neighbours, and the length of the trains (maximum distance between echoes within the train). We defined the duration of trains as the time sequence in which 3 or more echoes participated in the coordinated, aligned flight.

An aggregation started when at least 5 echoes from different directions converged linearly and at high speed to a specific location where they finally merged. An aggregation stopped when no more echoes were moving linearly and at high speed towards that point.

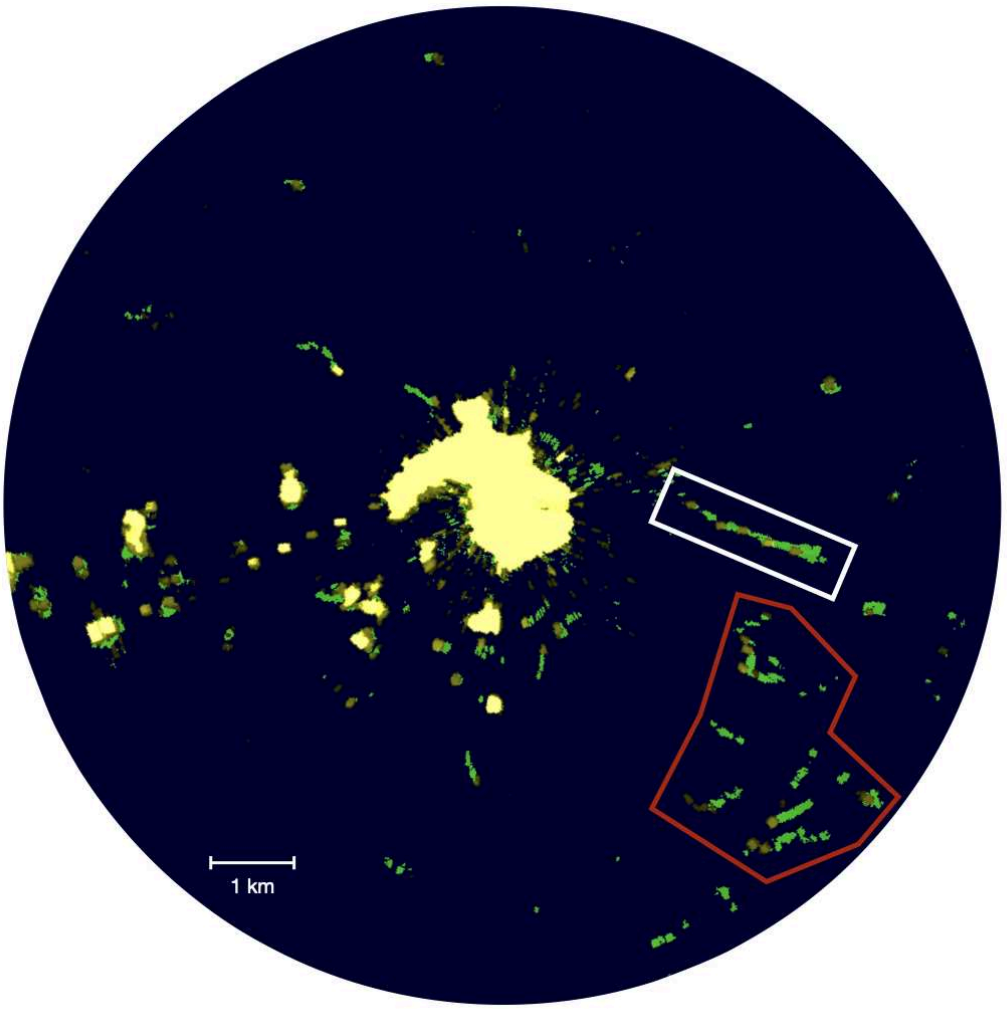

Figure 6 : Different bird flights observed in radar images at Bengouzal. Brown/yellow spots are bird-echoes, followed by a green trail showing the location of the echo in the last 30 s. The white rectangle shows a train of 5 vultures-echoes, occuring at the same time as uncoordinated flights of a dozen of vultures/echoes (in red polygon). Bright yellow indicates high level of intensity reflected by targets, with large yellow shapes in centre and left of the image being respectively due to the saturated (blind) zone around the radar and landforms.

This allowed us to estimate the duration of attraction to this aggregation point. We estimated the distance between the aggregation site and the farthest observed echoes attracted to it. In addition, with the mean cross-country speed of griffon vultures estimated at 27.67 km/h in this area (Fluhr et al., 2021) and considering that the last attracted individuals targeted this location since the beginning of the aggregation, we could estimate the theoretical maximum distance of attraction.

Differences between pattern characteristics were investigated with the Cohen's *d* effect size, and bootstrapped 1000 times to estimate the 95% confidence interval (Cohen,

1988). Hence, a confidence interval not overlapping with zero indicates a significant difference. When not specified, results are presented as mean ± standard deviation.

IV.3. Results

At both sites, we observed a non-homogeneous use of space by vultures (Figure 1). At Devez Nouvel, most of the cells that reached high levels of track density were located on the plateau, on the east part of the radar disk. We detected two lines (from 3.06°E; 44.00°N to 3.11°E; 44.00°N and from 3.05°E; 44.06°N to 3.07°E; 44.08°N in Figure 1) of cells with high density overlapping with valley edges. Except for these two lines, the general pattern of high density cells in this site suggested mostly North West - South East movements. At Bengouzal, almost all cells that reached a high level of density were clumped on the plateau as well, however movements seemed directed North - South, slightly tilted North East - South West.

IV.3.1. Description of rails

We observed 13 rails (8 2-lines rails, and 5 3-lines rails) occurring in 6 out of the 10 days period (in 2 days at Devez Nouvel and in 4 days at Bengouzal). While 90% of the 3-lines rails were observed in Bengouzal, 2-lines rails were found in equal proportion at both sites. In those rails, most echoes were moving in the same direction but movements were not as synchronised as in trains (movie S1, Figure 2 and 3).

No differences in mean duration of 2-lines and 3-lines rails have been detected (Cohen's d [95% CI] = 0.89 [-0.24; 2.41]), as they respectively lasted 12 ± 6 min (range 2 - 22 min) and 20 ± 12 min (range 7 - 39 min). Among the 2-lines rails however, those occurring in Bengouzal were on average shorter in time (8 ± 4 min) than those observed at Devez Nouvel (16 ± 5 min; Cohen's d = -1.88 [-5.96; -0.78]). The distance between parallel lines forming these rails was significantly shorter in 3-lines rails (2.63 ± 0.90 km; range 1.48 - 4.67 km) compared to 2-lines rails (5.42 ± 2.09 km, range 2.94 - 7.76 km, ; Cohen's d = -1.85 [-3.82; -1.01]). For 2-lines rails, no differences on the average distance between parallel lines were detected between sites (Devez Nouvel : 4.48 ± 1.63 km, Bengouzal : 6.36 ± 2.27 km; Cohen's d = 0.95 [-0.39; 5.92])

3.2. Description of train dynamic and spatial characteristics

In the 10 days of data inspected, between 1 and 10 trains were detected each day (4.1 ± 3.2). In total 41 trains were observed during this period, equally distributed between sites (21 in Devez Nouvel, 20 in Bengouzal).

While trains could appear steadily developed during their entire recording time (Figure 4, A_1-A_4), some initiations and endings have been observed too. Initiations were characterised by vulture groups splitting, individuals adopting the same direction and following one another in line (Figure 4, A_1-A_3 ,B_1-B_3 ,C_1-C_3). Trains could end for several reasons: crossing the central saturated zone around the radar, occurring in the last kilometre

close to the radar disk edge (Figure 4, C_4), but also because of vulture groups converging and merging (Figure 4, B_4), or, on the contrary, diverging and splitting. This convergence could involve all individuals or only a part of them. Finally, trains did not systematically involve the same vultures during their entire "lifetime", because some individuals (and even other trains) could join the train (Figure 4, D_1-D_4), or leave it independently from other participants.

When trains were fully "deployed", they involved 3 to 19 vulture-echoes. At Bengouzal, the trains involved slightly less echoes on average than at Devez Nouvel (6.55 ± 2.70 and 8.67 ± 4.23 respectively; Cohen's d = -0.59 [-1.24; -0.02]). The distance between nearest neighbours within trains ranged from 73.13 m to 1.45 km (389.05 ± 243.26 m; median = 329 m), with 75 % of them less or equal to 525 m and 47.8 % between 200 and 500 m. The mean distance between nearest neighbours did not differ significantly between sites (Cohen's d = 0.12 [-0.11; 0.39]).

The duration of trains lasted in average ~8 ± 4 min (range 2 - 18 min). The distance between the farthest echoes involved in the train (corresponding to the train length) varied from 465.99 m to 8.13 km (2.58 ± 1.48 km). The mean duration and length of trains did not differ significantly between sites (Cohen's d = -0.28 [-0.86; 0.30] and -0.43 [-1.02; 0.18] respectively).

IV.3.3. Description of aggregation events

One of the observed aggregations was congruent with a known feeding event that attracted more than 150 vultures, among which around 110 landed around the carcasse (movie S2). We saw the carcass disposal at a recycling station for vultures by a farmer (2018-07-04 at 9:24:00 UTC) at approximately 2 km East from the radar location at Devez Nouvel. For this certified feeding event, we observed on the radar data two consecutive rapid and massive aggregations of vulture-echoes at the feeding station location, followed by the disappearance of most of the echoes (because birds were no longer detected once on the ground) between 2018-07-04 9:22:45 and 10:11:25 UTC (movie S2, Figure 5). We also observed another event with relatively similar characteristics (not certified by field visit). The echoes converged from 2018-07-24 9:15:07 to 9:50:35 UTC, close to a valley before disappearing, in the direction of a feeding station down in the valley, located about 5 km from the aggregation location (but outside the radar disk). Echoes converged toward the aggregation location during 48 min and 45 min respectively, with furthest echoes attracted from 6.43 km and 9.76 km (note that the maximal distance possible in the radar disk was 12 km). We estimated a maximum distance of attraction of 20.75 km to 22.14 km.

IV.4. Discussion

To our knowledge, this is the first study to describe the instantaneous distribution of dozens to hundreds of vultures in the field. The temporal and spatial scales of the patterns

described prevented both direct observation in the field and detection within individual tracking data (unless the whole population was monitored). Using radar, we observed patterns of movements and spatial structures that revealed spatial and temporal consistency at various scales, as well as some level of synchronisation. This indicates that vultures do organise themselves in a specific manner while foraging, implying group coordination.

At a large temporal scale, when building density maps from the concatenation of all observation days per site, no clear pattern emerged. It suggested however that the distribution of foraging vultures was not homogenous in the landscape. So far, only analysis of tracks at a short temporal scale revealed conspicuous patterns.

In 60% of the days investigated, we observed groups of vultures aligning themselves, ultimately forming rails. While 3-lines rails were found almost exclusively at Bengouzal, 2-lines rails were found in equal numbers at each site. These rails tended to form repeatedly over several days in similar areas, with trajectories maintaining the feeding stations in between the parallel lines. In the case of 2-lines rails, vultures within a line were about 5.4 km apart, but in the case of 3-lines rails they were twice as close together (i.e. 2.6 km on average). This consistency in spacing suggests an underlying mechanism, possibly associated with vision abilities and group foraging strategies. Indeed, we hypothesised that parallel lines may correspond to optimization of carcass searching by visually covering the largest ground area, as it was proposed in seabirds (Assali et al., 2020). Griffon vultures, as all other Old-world vultures, are predominantly visual foragers (Potier, 2020), hence we expected any optimization strategy to be related to visual abilities. With this in mind, we attempted to project on the ground the field of view of griffon vultures (Martin et al., 2012). However, their field of view is so wide that they can virtually see almost all the ground around them, rendering the projection impossible. We therefore projected some specific areas of the field of view. Studies on other diurnal bird species having only one fovea found that their fovea was aligned with their eye axis (Tyrrell et al., 2013). In the short-toed eagle (*Circaetus gallicus*), the eye axis was measured at 55° from the sagittal axis and corresponds with the angle formed by the mediatrice of the eye opening from the skull (Figure S1). The same angle matches closely the eye openings of the griffon vultures' skull (Figure S1) so we assumed that 55° was likely close to the eye axis angle, around which acuity should be at the highest resolution on the retina (Potier et al., 2017). Further, we also projected the middle of the lateral field of view as a reference point. On the vertical axis, we projected the 80° angle corresponding to the angle at which some part of the vision includes binocular vision (see Figure 7A for visual explanation, Martin et al., 2012). It is unclear at which angle vultures tilt their head when foraging. Based on few direct observations, Martin et al (2012) suggested that the eye-bill axis would be tilted down by at least 60°, which should correspond to at least 40° for the vertical visual axis. Using successive trials, we found that a 48° tilt of the visual axis leads to a junction in covered space by the eye-axis projected lines, between two vultures 5.4 km away, at 300 m height (Harel et al., 2016) and looking in the same direction (Figure 7B).

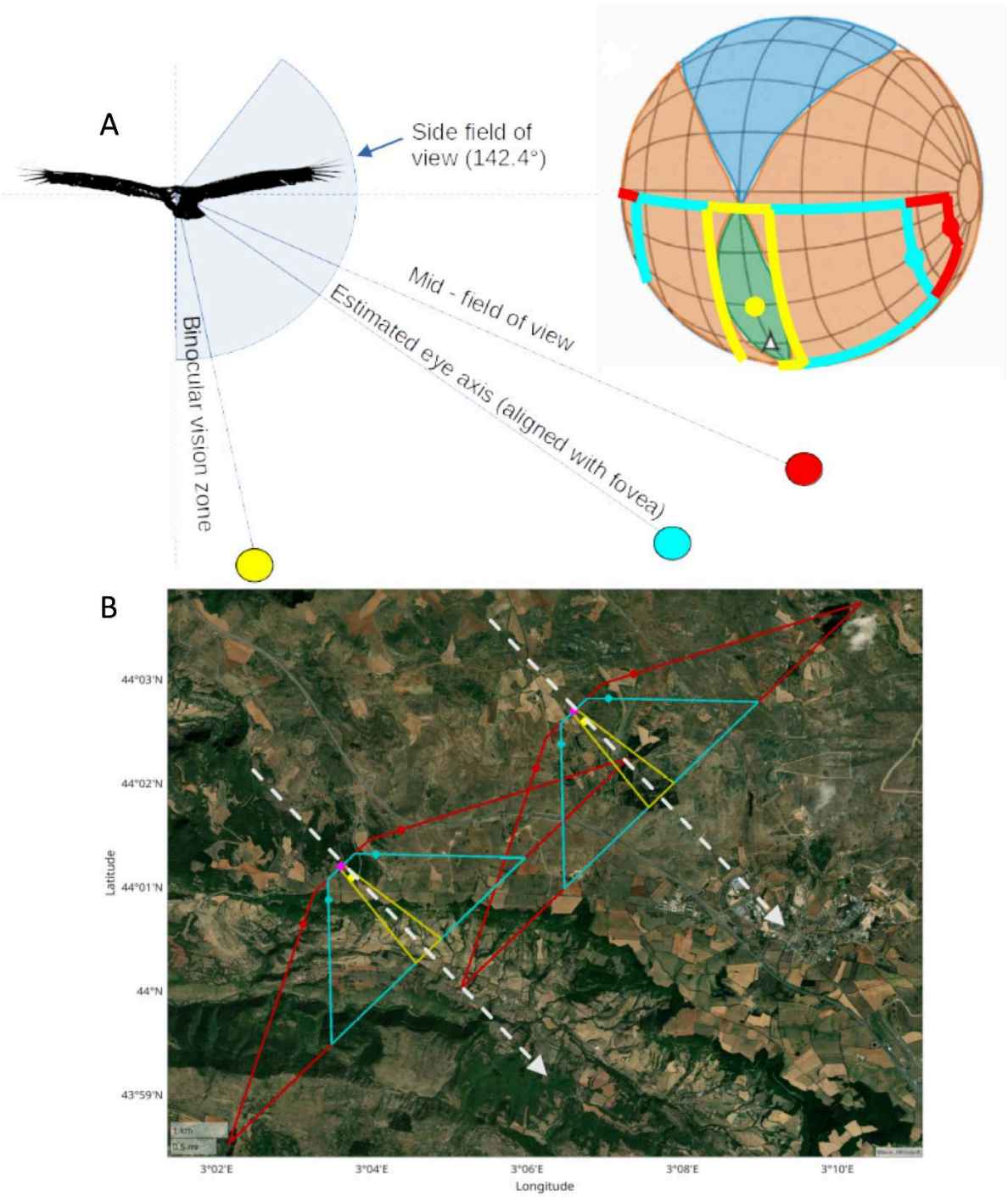

Figure 7 : Vultures' projected areas of the field of view in flight. (A left) definition of angles projected onto the ground in (B). (A right) perspective view of orthographic projections of the visual field : green, binocular sector; blue, blind sector (from Martin et al. 2012) on which is indicated the binocular zone in yellow, the eye axis projection in cyan, and the middle of the lateral field of view in red. (B) projected field of view on the ground, from vulture positions taken within the 2-lines rails shown in Figure 4, spaced 5 km apart, assuming 300 m of flight height and a tilt of the vertical eye axis of 48° below the horizontal.

Without additional data on griffon vultures' visual system, these calculations remain speculative but they suggest that the hypothesis that griffon vultures have a good visual ability at this angle (in the middle of the 2 rails) is far from unrealistic. Two foraging vultures flying in rails at 300 m above ground, should then see very well all the area between the rails. We hypothesise that there exists a compromise between flight height, distance from eye to ground and distance between rails that maintains sufficient ground resolution for carcass detection under a group foraging organisation that optimises collective ground coverage. Knowledge about griffon vulture visual fields show that they see the world more laterally than vertically, which once projected on the ground, resulted in a thin but wide ground strip zone (Martin, 2011 and see figure 7). A thicker area could possibly be too difficult to process by the brain, as finding a carcass does not only involve seeing but also detecting and recognizing (Harmening & Wagner, 2011; Martin, 2011). Vultures' searching strategy could work in a similar way to flatbed scanners, with the entire surface covered by the progressive movement of the long scanning strip. By adding parallel rails to this scheme, vultures would then further collectively increase their scanning efficiency. It is important to note that the field of view of vultures is so wide that they probably can see each other between rails, thus allowing collective flight adjustments. Under those assumptions, the closer 3-rails pattern is likely to allow for a higher resolution scan (i.e. closer distance, less difference with optical axis, higher cone resolution on the retina, and observation right below the neighbouring bird).

In Old-world vultures, food is located mainly by vision. However it is likely that individuals have imperfect carcass's detection ability, and in this case, forming foraging groups to search for an unpredictable resource becomes particularly valuable (Rafacz & Templeton, 2003). We observed vultures forming trains every day, up to 10 times a day. Such coordinated flights generally lasted about 8 min and involved about 7 echoes, on average 389 m apart (with rather small variation, coefficient of variation = 0.6), ruling out the possibility of random events. Although this train formation may seem suboptimal, as each member of the train is prospecting the same area, this repetition may compensate for the imperfect detection by each individual. This, combined with the prospection carried out by members of parallel lines (in rails), would allow groups of vultures to efficiently scan a huge area with a very low probability of missing a carcass. As an example, a 2-lines rail travelling in formation for 1 km will scan an area of 10.8 km^2 in about 2 min.

Despite finding a carcass lying on the ground could be tricky, it is likely that multiple vultures falling from the sky to land near a carcass is a conspicuous pattern, even from afar. In the radar disk, the farthest echoes attracted to aggregation sites (likely related to feeding events) ranged from 6.43 km to 9.76 km. These distances were consistent with the attraction distances used in several studies simulating vulture foraging strategies. (i.e. 4 and 10 km in Jackson et al., 2008, 7 km in Cortés-Avizanda et al., 2014). It also matched the observed distances at which seabirds showed behavioural changes to converge on predator aggregation sites (10 km in Haney et al., 1992; Thiebault et al., 2014). Theoretically, we estimated a maximum attraction distance of about 21 km, which was within a plausible distance range, as seabirds seemed to be attracted to boats up to 30 km away (Collet et al., 2015) while having lower visual acuity than raptors. Although boats are large conspicuous structures that should

contrast well with the surrounding in the open sea, it is likely that dozens of vultures, birds with a wingspan of 2.6 metres, falling from the sky at high speed to land near a carcass is a phenomenon visible from a great distance, especially to birds with visual acuity among the highest recorded in the avian class (Mitkus et al., 2018). Furthermore, when the tracks converged, they ended up forming a pattern (Figure 2) similar to that obtained by Cortés-Avizanda et al. (2014) when simulating the local enhancement strategy, providing empirical support for the existence of such phenomenon in vultures (proposed long ago by Buckley, 1996; Houston, 1974 and present in all foraging strategies of Deygout et al., 2010).

The measured attraction distances, combined with the juxtaposition of the visual fields, suggest that vultures were able to detect a sharp drop in height, the signal for the discovery of a carcass, from individuals in the other lines of a rail, while optimising the area searched. These lines were observed for an average of 15 minutes and occurred on plateaux where vultures usually search for carcasses (Fluhr et al., 2017; Monsarrat et al., 2013). Our results could actually suggest a collective foraging strategy used by vultures until now not even considered : a combination between the “group foraging network” and the “chain of vulture” strategy coupled to local enhancement effect. Indeed, the simulations of the “chains of vultures” strategy (Cortés-Avizanda et al., 2014) concluded that the number of vultures landing at the carcass was overestimated. Authors speculated that if this is actually the strategy used by vulture, a mechanism preventing illimited arrival should exist. They proposed a way of estimating the number of conspecifics already feeding and thus their chances of accessing food when circling above the carcass. Our observations show that vultures could form chains, but of finite number of individuals, that we named “trains”, which could act as the limiting mechanism missing in those simulations. Moreover, it appears here that it is groups of individuals that are flying in parallel, heading to the same direction in order to maintain visual contact with each other, rather than individuals of the same group as proposed in the “group foraging network” (Deygout et al., 2010). Ultimately, individuals in each line of the rails would benefit from social information about a discovery through local enhancement.

Finally, the frequency of the observed patterns is likely to be underestimated, as we have only examined a subset of the data and selected only the less noisy patterns. Nevertheless, our preliminary exploration revealed patterns that have never been observed empirically before. Vultures formed coordinated groups that aligned themselves as they scanned plateaux. This formation of rails supports the “group foraging network” hypothesis, in which vultures forage in groups to optimise both spatial exploration and the acquisition of social information. We also demonstrated empirically the pattern of local enhancement. Overall, our results suggest a combination of the “group foraging network” to search for carcasses, in which groups take the form of trains, and local enhancement to explain the rapid aggregation of large numbers of vultures around a newly discovered carcass.

IV. CRediT authors' contributions

Yohan Sassi: Conceptualization, Methodology, Software, Investigation, Formal Analysis, Visualization, Writing - original draft, Writing - Review & Editing
Camille Assali: Methodology, Software
Martina Scacco, Vincent Liebault & Vincent Delcourt: Resources, Data curation
Olivier Duriez: Conceptualization, Visualization, Supervision, Funding acquisition, Writing - Review & Editing
Yann Tremblay: Conceptualization, Methodology, Software, Investigation, Formal Analysis, Visualization, Supervision, Writing - original draft, Writing - Review & Editing

IV. Acknowledgment

We thank particularly Simon Potier for fruitful conversation about vulture vision abilities.

IV. Fundings

This work was supported by the GAIA doctoral school grant, University of Montpellier (YS). Fieldwork and part of the data analysis was funded by a PEPS-TOHMIS grant (project Radarapaces) attributed to OD.

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V. Analyse des comportements d'évitement des vautours face aux éoliennes en combinant des données empiriques et des données de simulation

Ce chapitre analyse si les vautours fauves sauvages des Grands Causses présentent des comportements d'évitement des centrales éoliennes, et ce à différentes échelles. Existe t'il un évitement de la centrale éolienne dans son intégralité (macro-échelle, > 1 km) ? Un évitement anticipé des éoliennes isolées (méso-échelle, < 1 km) ? Ou bien un évitement réflexe au dernier instant (micro-échelle, < 200 m). Pour cela j'ai combiné des données de déplacement provenant de 25 vautours adultes, notamment le suivi GPS à haute résolution collecté dans les 2 km entourant les centrales éoliennes, à des modélisations agent-centrées. Le modèle agent-centré, en contrôlant les paramètres simulant le comportement d'un vautour virtuel face aux éoliennes, permet d'étudier les mécanismes comportementaux sous-jacents des patrons observés sur les données provenant d'individus sauvages.

Note au lecteur :
- Le preprint est disponible ici: https://doi.org/10.1101/2023.07.26.550651
- L'article est en révision dans la revue Ornithological Applications.
- Les annexes de l'article sont disponibles en annexe 3 du présent manuscrit p 199.

Unravelling vulture avoidance tactic of wind turbines combining empirical and simulation data

Sassi Yohan [1,*], Ziletti Noémie [2], Duriez Olivier [1,†], Robira Benjamin [3,†]

1: CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
2: LPO France site Grands Causses, Le Bourg, Peyreleau, France
3: Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy

* Corresponding author: yoh.sassi22@gmail.com , CEFE, 1919 Routes de Mende, 34293 Montpellier cedex 5, France.
† These authors contributed equally.

V. Abstract

The increase of wind turbine installations to limit climate change may affect bird populations because of collisions with rotor blades. Birds may respond to wind turbine presence along a gradient of behavioural changes: avoiding the wind farm (macro-scale) or only the wind turbines either by anticipating wind turbine locations (meso-scale) or engaging into last-minute flee attempts after late perception (micro-scale). We investigated the flight response at these three spatial scales of 25 adult griffon vultures (*Gyps fulvus*) equipped with GPS tags over three years when flying in an area including ten wind farms in the Causses, France. At macro-scale, the population foraging range and habitat use revealed that vultures did not avoid wind farms. To investigate avoidance at meso- and micro-scales we focused on the four mostly visited wind farms. We compared vulture flights to null movement models, based on a method allowing us to keep the correlation between flights and topography while creating movement independent of wind turbine locations. At most sites, vultures did not show avoidance behaviour. Yet, simulations from our agent-based model highlighted that the avoidance pattern detected at one wind farm matched with an anticipated avoidance of turbines, probably linked to the presence of a ridge nearby. Overall, our results suggest wind farm-specific responses by soaring birds as a function of the landscape topography. Thus, stakeholders should carefully consider the wind farm location for siting and designing preventive measures (e.g. improve detection of species not able to avoid turbines in switching off on-demand technologies) to reduce collision risk of soaring birds.

Key-words: *Gyps fulvus,* renewable energy, collision risk, agent-based model, avoidance behaviour, GPS telemetry

V.1. Introduction

Wind turbines are a solution to produce electricity with limited CO_2 emissions, although their impact on wildlife raise some concerns about the large-scale deployment of this technology. Meanwhile wind-power generation worldwide has grown dramatically during the last two decades (e.g. by 70% from 2015 to 2019; IPCC, 2022), mortality due to collisions with the rotor blades have been frequently reported in bats and birds (Schuster et al., 2015; Thaxter et al., 2017). Among birds, diurnal raptors are considered as one of the most vulnerable taxa (Thaxter et al., 2017) because of their slow pace of life which makes population viabilities particularly sensitive to additional adult mortality (Bellebaum et al., 2013; Carrete et al., 2009; Dahl et al., 2012; Duriez et al., 2022).

In response to wind turbine occurrence, birds can develop avoidance mechanisms at three spatial scales: macro-scale, meso-scale and micro-scale (May, 2015). Macro-scale avoidance refers to an avoidance of the wind farm as a whole (e.g. in Cabrera-Cruz & Villegas-Patraca, 2016; Plonczkier & Simms, 2012). Meso-scale avoidance describes an avoidance of the wind turbines several hundred to thousands of metres ahead (e.g. in Garvin et al., 2011; Santos et al., 2022; Schaub et al., 2020). Micro-scale avoidance stands for a last-second flee attempt of the rotor blades (typically < 200 m ahead) (May, 2015).

The avoidance tactic employed may be influenced by birds' perception abilities, but also and largely by their morphology and flight capacities (Bevanger, 1998; Marques et al., 2014; Pennycuick, 2008). Several morphological parameters such as weight and wing area, which define wing loading, have been identified as determinants for collision risks (Janss, 2000). Birds with high wing loading, such as vultures and large eagles, have been shown to be more collision-prone than other raptors with lower wing loading such as common buzzard (*Buteo buteo*) or short-toed eagles (*Circaetus gallicus*) (Barrios & Rodríguez, 2004; de Lucas et al., 2008). The most likely reason for this pattern is that high wing-loading influences flight type (Shepard, 2022) and is associated with lower flight manoeuvrability (de Lucas et al., 2008). Unlike birds using flapping flight, large raptors use a soaring-gliding technique based on thermal and orographic updrafts to gain altitude effortlessly (Duriez et al., 2014; Shepard, 2022). Thermal and orographic updrafts, which are respectively masses of hot rising air emanating from heated surfaces and deviated wind onto topographical obstacles, constrain soaring birds in their displacement (Pennycuick, 1998). Thus, landscape features can also play an important role in the susceptibility of birds to collisions (de Lucas et al., 2012). While species with low wing loading could easily avoid wind turbines a few metres ahead (Schaub et al., 2020), those with high wing loading such as vultures will face much more difficulties. Despite being possible, a last minute flee attempt for large soaring birds requires them to switch to flapping flight, a flight mode they can not hold for long because of increased energetic costs (Duriez et al., 2014). Hence, if avoidance behaviour exists in these birds, we could expect an anticipated avoidance (meso-scale) allowing them to glide to their next updraft. This should particularly be true if the landscape favours thermal updraft or orographic uplift due to the surrounding topography.

Up to now, studies on wind turbines avoidance behaviours focused mainly on medium-sized birds with low wing loading such as black kites (*Milvus migrans;* Marques et al., 2020; Santos et al., 2022) or Montagu's harrier (*Circus pygargus;* Schaub et al., 2020) which flight is relatively independent of landscape features. In this study, we adapted new methods to study avoidance behaviour in griffon vultures (*Gyps fulvus*), large soaring birds which depend largely on topography for their movements (Scacco et al., 2023). We investigated whether vultures actively avoided wind farms (macro-scale avoidance) and/or wind turbines (meso-/micro-scale avoidance). In the latter case, we aimed to characterise what was the flight response to wind turbines (i.e. progressive long-distance avoidance or last-minute flee attempt). Because of the dependence of their flight on the landscape, as well as their low flight manoeuvrability, we expected vultures to prioritise long-distance anticipated avoidance of wind turbines. Such in-depth investigations could particularly support stakeholder decisions by providing applied knowledge on where to site wind farms and how far to detect birds to shut down wind turbines in time to prevent collisions (McClure et al., 2021).

We used high-resolution GPS tracking of 25 adult individuals that ranged over 10 wind farms of the Causses region, France, over three years. To investigate macro-scale avoidance, we estimated vulture space utilisation distribution to determine whether vultures excluded wind farms from their ranging area. We coupled this with a habitat selection analysis to estimate in-flight selection of wind farms. To investigate meso- and micro-scale avoidance, we studied vulture movements within the four most intensively used wind farms and compared them to a null model of expected movements if independent of wind turbines location, obtained by rotating wind turbine locations. Furthermore, we compared true flights within wind farms to those simulated with an agent-based model to have a mechanistic understanding of the wind turbine avoidance manoeuvre (see Fig. 1 for framework).

V.2. Materials and methods

V.2.1. Study system

This study took place in the Causses region, France (Fig. 2), where a population of ca. 820 breeding pairs of griffon vultures live (census 2021, LPO). This region is characterised by limestone plateaux interspersed by valleys. Valleys offer conditions for orographic updrafts that vultures can use to soar efficiently. Away from the valleys, vultures patrol the open landscapes, relying on thermal updrafts to gain height, looking for mortality in herds of grazing livestocks. In recent years, both the number of vultures and the number of wind turbines have increased. There are nowadays 10 operating wind farms (totalling 130 turbines) and nine additional are planned (projects totalling 91 turbines, Fig. 2), in a region where at least 30 vultures have been found dead due to collisions between 2012 and 2022 (including 10 casualties at the four focal wind farms cited below) (LPO/DREAL Occitanie, unpublished). These wind farms are located between 18 km and 52 km from Cassagne, the

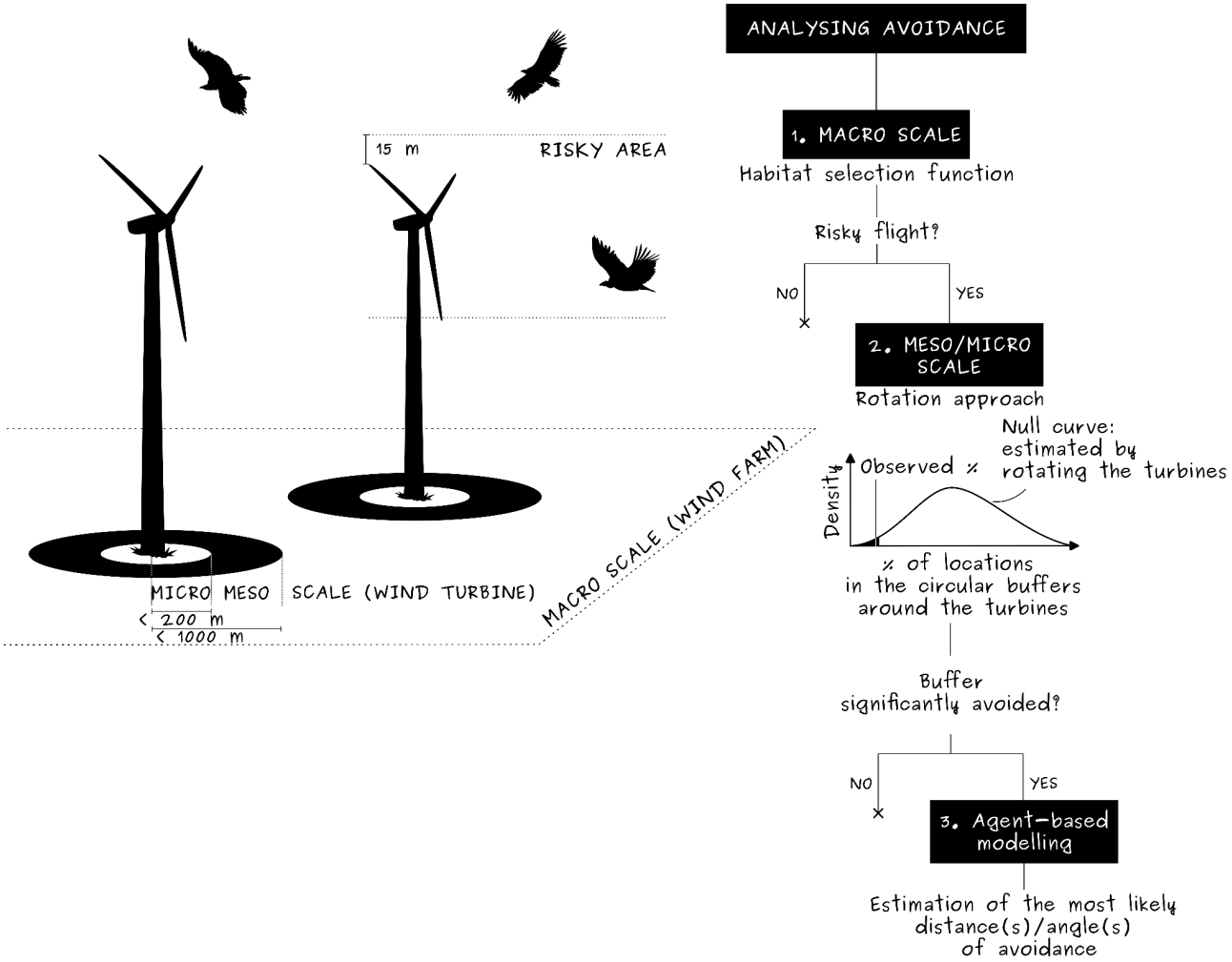

Fig. 1. Illustration of the methodological framework used to investigate wind turbine avoidance in vultures. Avoidance tactics were studied at the macro scale (avoidance of the entire wind farm) or at the micro/meso scale (avoidance of wind turbines, from a hundred to a thousand metres) (left). We used a top-down approach from the largest to the smallest scale (right) combining empirical and simulation data.

geographical centre of the breeding colony where a collective natural recycling station with vultures stands (44°12'N, 3°15'E, Fig. 2, Duriez et al., 2021).

We used tracking data spanning 3 years (from 1st January 2019 to 31st December 2021) from 25 vultures (Table S1) that had been captured in 2018 at Cassagne carcasses recycling station, and equipped with 50 g solar-powered GPS-GSM tags (Ornitrack-50, Ornitela), in a leg-loop harness configuration (Anderson et al., 2020). GPS tags were set to record location, speed and altitude at intervals of 2-15 min depending on battery levels and season (generally lower battery levels in winter). To study avoidance behaviour of operating wind turbines by vultures, we defined rectangular geofences (virtual barriers) placed at 2 km from the most outlying turbines in each wind farm. Within these geofences, GPS tags automatically shifted to high resolution recording (1 Hz) of individuals' location, speed and

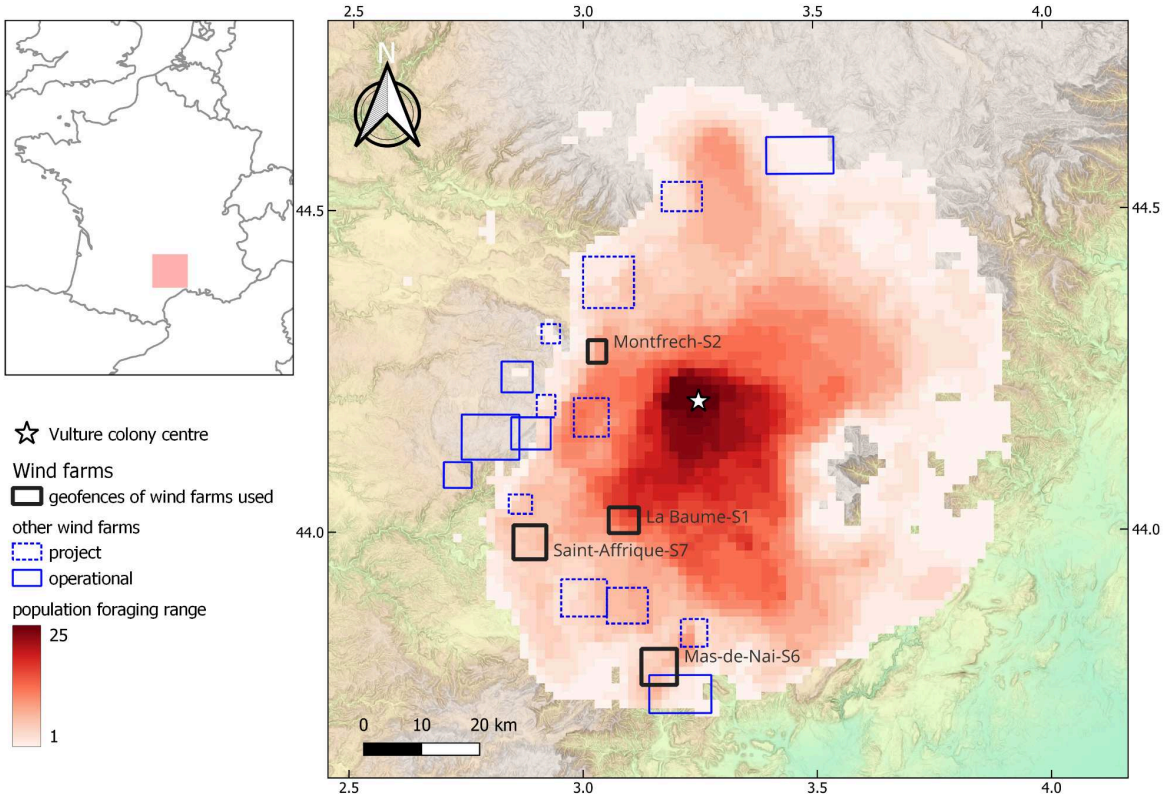

Fig. 2. Global vulture population foraging range in the Causses region, France. The darker the colour of the red raster, the higher the number of individual in-flight 95% utilisation distributions that overlap the given cell. Additional rectangles represent geofences around wind farms (black: study wind farms, plain blue: operational wind farms; dotted blue: project of construction). The star is the geographical centre of the nesting colony, Cassagne, where vultures have been reintroduced, are tagged and where a carcasse recycling station is located.

altitude. This 2 km threshold was defined based on a compromise between the need of time for the tags to switch to high resolution before entering the 1 km meso-scale buffer, and the need to prevent battery discharge by recording at high resolution in areas that we were not interested in. To retain only accurate in-flight GPS locations, we filtered the GPS locations of each individual by their groundspeed (> 4 m/s) and their horizontal dilution of precision index (HDOP < 4) (Martin-Díaz et al., 2020; Nathan et al., 2012). Data cleaning, processing and analysis were performed with *R* (version 4.2.2, R Core Team, 2022).

V.2.2. Data analysis

V.2.2.1. Macro-scale avoidance

To find out whether vultures expressed a macro-scale avoidance of wind farms, we computed an in-flight utilisation distribution (UD) and an habitat selection function for each

individual. First, we resampled flights every 10 min to homogenise the sampling frequencies ("track_resample" function, *amt* R package, Signer et al., 2019). Then, we focused on movements that were at a distance < 55 km of the colony centre. This distance enabled the inclusion of all wind farms of the region while focusing on vultures' daily flights (mean daily displacement from Cassagne by local birds equals 26 km (SD ± 10 km), Fig. S1, Fluhr et al., 2021). Individuals' UDs were estimated on these flights using brownian random bridge-based kernels (Benhamou, 2011, *adehabitatHR* R package (Calenge, 2006), see supplementary materials ESM01 for details). We then estimated a "population foraging range" as the layering of the 95% isopleth of individual UDs where each cell value corresponded to the number of individual UDs overlapping that cell (Duriez et al., 2019).

To estimate if vultures tended to fly further from wind turbines than expected by chance we computed an habitat selection function (HSF; Fieberg et al., 2021). To do so, for each individual we subsampled its daily datasets at three locations per day, evenly spaced during the main activity period of vultures and not temporally autocorrelated (at 10:00, 12:00, 14:00; Fluhr et al., 2021). This allowed us to categorise the locations "used" by individuals. In parallel, as the tracked vultures are central place foragers (Monsarrat et al., 2013), we sampled 10-fold more locations following a bivariate exponential distribution ("available locations", Benhamou & Courbin, 2023). We restricted these locations within a distance of 55 km from the colony centre. We fitted a HSF for each individual, using the distance to the closest operational wind turbine as the only predictor. Each HSF corresponded to a generalised linear mixed model with a binomial error structure (available: 0, used: 1) and a weighted logit link function considering a weight of 5000 for available locations, and 1 for used locations. The exponential of the unique slope estimate indicates whether vultures show no preference (≈ 1), favour wind farms (> 1) or avoid wind farms (< 1) (Fieberg et al., 2021).

V.2.2.2. Meso- and micro-scale avoidance

To investigate meso- and micro-scale avoidance behaviour we focused on four wind farms: La Baume, Montfrech, Mas de Naï and Saint Affrique. These wind farms were among the closest to the centre of the vultures' colony and were the most visited ones by vultures (Fig. 2, Table S2). Among the 25 vultures, 92% of them crossed at least once one of these four operating wind farms within the rotor swept zone during the three years considered (Table S1).

V.2.2.2.1. Use of topography within wind farm geofences

In the geofenced areas of these winds farms, orographic updrafts are generated by steep slopes associated to valleys, which are easily identifiable by a human eye in the coloured topography rasters presented in Fig. 3 (Digital Elevation Model, IGN BDTOPO, 25 m resolution). Hence, we estimated the central value of elevation among all pixels of the raster (i.e. $\frac{highest\ elevation\ value + lowest\ elevation\ value}{2}$) and we created an isoline of elevation at this value. Then, because orographic updrafts are generally drifted towards the upper part of

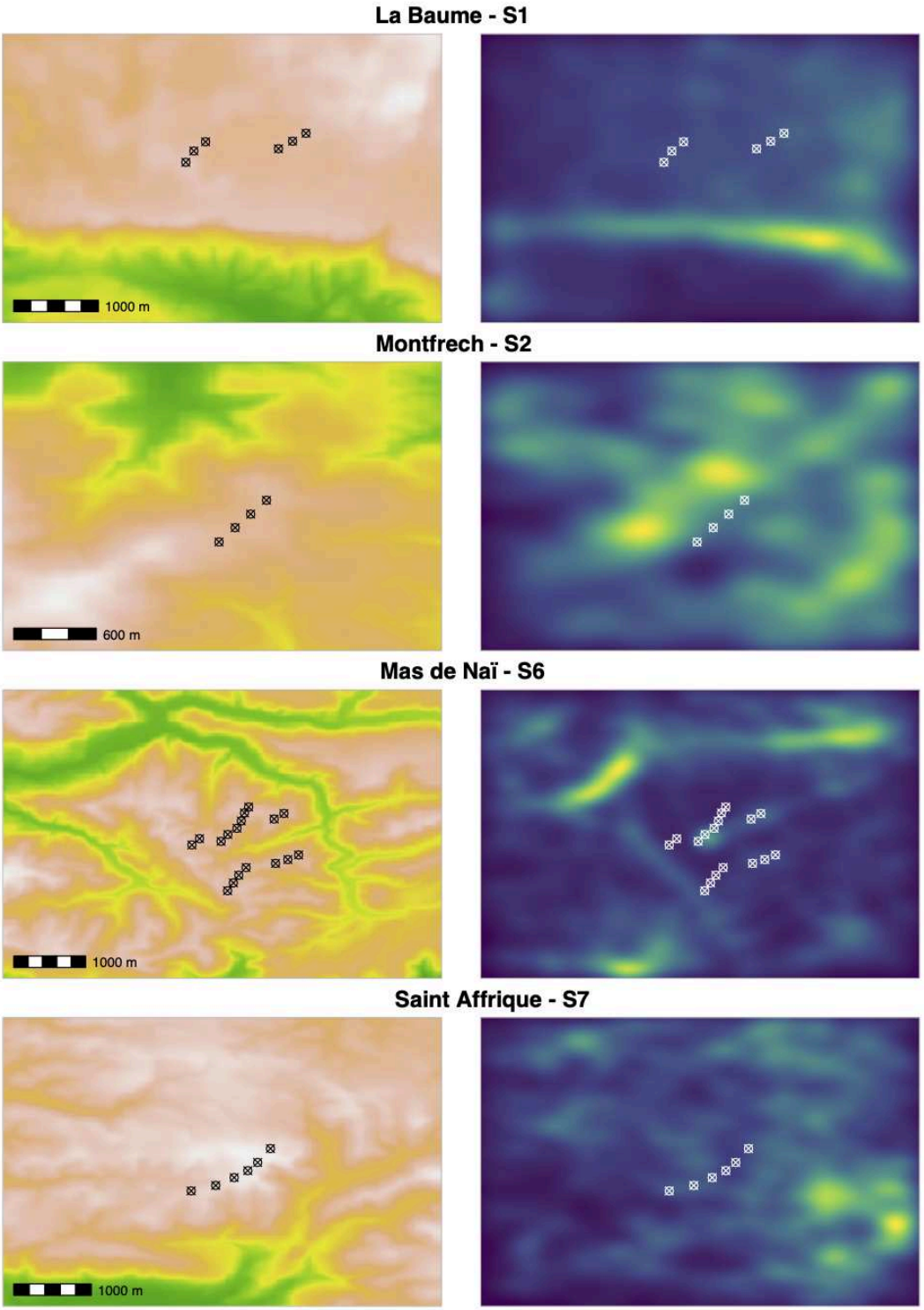

Fig. 3. Topography and vulture space utilisation distribution in the studied wind farms. Topography distribution (left column; green to white gradient indicating increasing altitude) and the weighted mean utilisation distribution (right column, blue to green gradient indicating increasing use intensity). See supplementary materials ESM01 for details on the estimation of the mean utilisation distribution.

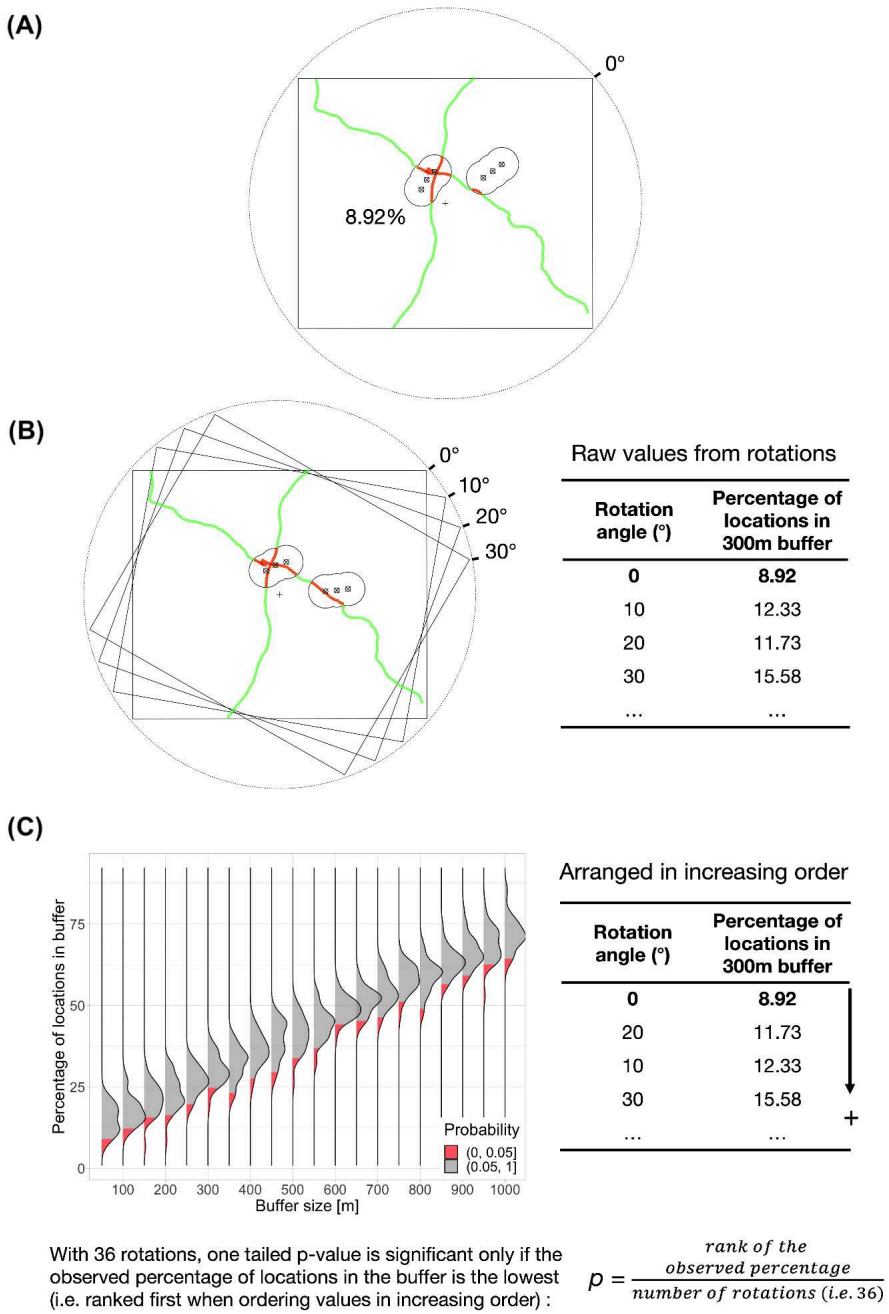

Fig. 4. Visual guide of the rotational approach used to estimate vulture turbine avoidance. (A) The geofence is represented by the rectangle around the wind farm (e.g. La Baume here). Wind turbines are indicated by the crossed circles and are surrounded by a specific buffer zone (e.g. 300 m here), the merged limits of which are shown by the solid black line. Two vulture flights are represented by the green and red lines (outside or inside buffers, respectively). For the original (true) wind turbine positions (0° of rotation), the percentage of vulture locations observed in the buffer was estimated. (B) A null model was constructed by rotating the wind turbines around the wind farm barycentre from 10° to 350° by steps of 10°. For each rotation the percentage of vulture locations in the considered buffer was calculated, giving 36 values of percentage per buffer size (1 observed and 35 theoretical values). (C) This method was applied to buffers from 50 m to 1000 m by steps of 50 m

around wind turbines, providing a null distribution of expected percentage for each buffer size. An avoidance should be detected if the truly observed percentage of locations in the buffer (i.e. for rotation angle = 0°) fell into the red part of the distribution. Hence, for each buffer size the percentages of locations were ranked by increasing order and we estimated the one-tailed p-value by dividing the rank of the truly observed percentage in the arranged distribution by the total number of rotations. Thus, the observed percentage of locations in the buffer was significantly lower than expected if it was ranked first in the distribution: $p = 1/36 = 0.028$. (These are simulated data for illustration)

the ridge we empirically used a 300 m buffer to geographically define the area (hereafter called "slopes") most likely to generate orographic updrafts. To estimate how topography constrained vulture flight we computed another HSF. Here we empirically found that subsampling 30% of the GPS locations composing each vulture track in the considered geofenced area gave robust results while reducing autocorrelation between locations. The locations "available" to vultures were randomly sampled within the geofenced area. The HSF used to estimate the preference for slopes over other areas followed the same structure as mentioned above with a dummy variable indicating whether the location was within a slope (1) or not (0) as a unique predictor.

V.2.2.2.2. Wind farm rotation to create null model

To investigate whether vultures anticipated wind turbine locations to start manoeuvring at long distance and/or whether they performed short-distance reflex manoeuvre to avoid them, we separated flights for which vultures flew within the rotor-swept zone of wind turbines (i.e. between the minimum rotor tip height and 15 m above the maximum rotor tip height, see Table S2 for wind farms' specific values) and those for which vultures flew above the rotor-swept zone. These flights were rediscretised at constant step length (50 m), to remove bias due to speed differences within and between the tracks but also to reduce location aggregation due to circular soaring phases compared to rectilinear gliding phases. Vultures can also fly below the rotor swept zone, yet, these events are rare (3.5 % of the locations are below the rotor swept zone in our study), thus we did not consider that case.

We defined avoidance behaviour as a use of an area containing wind turbines lower than expected if vulture flew independently of the wind turbine positions. To do so, we first estimated the percentage of locations occuring within a given range of turbines (buffer zone) at their original positions (e.g. 8.92% of the observed locations are within a 300 m buffer around wind turbines in the example shown in Fig. 4A). Then we compared this observed percentage to a null distribution expected if turbines were not avoided. We created this null distribution by recalculating the percentage of locations included into the same buffer zone when the geofenced area containing the wind farm was rotated around its barycenter from 10° to 350° with a 10° step (e.g. 12.33% of locations were included into the 300 m buffer with a 10° rotation in the example shown in Fig. 4B). Rotating the wind farm, instead of the flight tracks, allowed us to preserve correlations between flights and topography, a necessary

condition for the null model to be biologically meaningful (Martin et al., 2008). This process, repeated over buffers ranging from 50 to 1000 m from each turbine (with 50 m steps), provided a null distribution associated with each buffer size.

For each buffer, we defined it as avoided when the observed proportion of locations was significantly lower than expected through the null distribution. For this purpose, we ranked, by increasing order, the 36 percentage values obtained for the considered buffer (the observed value, at rotation = 0°, plus the 35 values from the rotations). We estimated the one-tailed probability (hereafter p) by dividing the observed proportion rank by the total number of values (i.e. 36; Fig. 4C). A significant avoidance of the buffer was detected ($p < 0.05$) when the observed percentage was ranked as the lowest (i.e. $p = 1/36 = 0.028$). We applied this procedure for both flights within and above the rotor swept zone separately. We checked that this rotation approach could adequately identify avoided buffers in each wind farm when simulating different avoidance scenarii with our agent-based model described in the following section (supplementary materials ESM02 and Fig. S2).

V.2.2.2.3. Agent-based model simulations

When a significant avoidance pattern was identified with the above-mentioned procedure, we aimed at determining whether this pattern fitted with a long-distance anticipated avoidance or a last-minute flee attempt. We built an agent-based model (DeAngelis & Mooij, 2005; Grimm & Railsback, 2005) simulating the behaviour of a virtual vulture able to perceive a turbine (and start manoeuvring) at a distance d, and able to adjust its heading (known as turning angle) of $\alpha°$ every 5 m. This 5 m step was meant to be as small as possible to mimic continuous movement, but sufficiently reasonable due to computational limits. The environment, in which a virtual vulture flew, contained wind turbines whose positions matched the true configuration of the studied wind farms.

Each simulation followed the subsequent flow:

1) A starting location was randomly selected on a side of the considered geofenced area and the target location (reached only through strict ballistic movement) was defined on the mirroring side, such that the target direction was θ.
2) The virtual vulture started moving in the direction of the target location, following a biased random walk (Codling et al., 2008). This biased random walk consisted of movement steps of 5 m in the direction θ' sampled in a Von Mises distribution of mean θ ("rvm" function of the *CircularDDM* package; Lin et al., 2018), and of persistence value κ (estimated based on the true vulture tracks occurring at wind farms of comparison, rediscretised at a 5 m interval, using the "est.kappa" function of the *CircStats* package, Lund & Agostinelli, 2018).
3) If the virtual vulture arrived at a defined distance of d metres from a wind turbine, it engaged in an avoidance behaviour which consisted in maintaining a turning angle of $\alpha°$ opposite to the turbine location (e. g. left if the turbine was initially located right with respect to the heading at start of avoidance, and *vice versa*) at each step.

4) If the virtual vulture was avoiding a turbine, avoidance behaviour stopped as soon as the distance to the turbine started to increase. It then resumed its biased random walk (heading to the last direction after avoidance), and would return into avoidance behaviour whenever a new turbine was perceived.
5) The simulation stopped when the agent flew out of the geofenced area.

We tested jointly for several values of α (0° to 14° by steps of 1°; 14° representing the maximum angle a griffon vulture can turn within a thermal; Williams et al., 2018) and d (50 m to 1000 m by a step of 50 m, similar to the rotation procedure), repeating the simulations 10 000 for each set of parameters. A small α and a large d would mimic long-distance anticipated avoidance, while a large α and a small d would mimic last-minute flee attempt.

To understand the movements rules underpinning vultures' avoidance behaviour, we focused on buffer sizes detected as avoided, and compared the absolute fit of the simulations with the empirical data. The absolute fit corresponded to the square of the difference between the percentage of locations obtained by simulations and the one observed on empirical data (ϑ). In simulations mimicking avoidance (d and $\alpha > 0$), we removed the ones for which the fit with empirical data was worse than for cases with no avoidance ($\vartheta/\vartheta_{null} < 1$ where ϑ_{null} is the percent of location obtained in the buffer when simulating no avoidance). For the remaining cases, we defined the fit quality between empirical and simulated percentage of location with a buffer as $f = 1 - \vartheta/\vartheta_{null}$. A perfect fit (i.e. the combination of α and d that correctly mimicked the observed vulture avoidance behaviour in the considered buffer) would give $f = 1$.

V.3. Results

V.3.1. Avoidance behaviour of wind farms at macro-scale

The population foraging range overlapped with 100% of the wind farm projects and 60% of the operating wind farms (Fig. 2). The turbines of the furthest wind farm from the colony centre, Mas de Naï, was included into the in-flight utilisation range of five vultures while one of the closest wind farm, La Baume, cut off the airspace used by 18 individuals (Fig. 2). In addition, the mean exponential of the HSF estimate associated with the closest distance to operational wind turbines was extremely close to 1 ($0.99 \pm$ SD 4.82×10^{-5}) suggesting no preferences toward large distances from wind turbines.

V.3.2. Avoidance behaviour of wind turbines at meso-/micro-scale

V.3.2.1. Importance of the topography when flying in the wind farms

Vultures crossed the wind farms several times during these three years (all individuals pooled, [min,max] = [207, 1793] in Montfrech and La Baume, respectively - Table S1 and

S2). The proportions of tracks that entered the rotor swept zone of these wind farms were not negligible ([min,max] = [32.84%, 50.28%] in Montfrech and Mas de Naï, respectively).

In the area defined by the geofences, 15.3% of La Baume, 51.5% of Montfrech, 80.5% of Mas de Naï and 19.7% of Saint Affrique, were represented by slopes (Fig. 3). While flying in these areas, vultures significantly favoured these slopes (exponential of HSF estimate associated to slope use [95% confidence interval]; La Baume: 1.807 [1.767,1.848], $p < 0.001$; Montfrech: 1.193 [1.106,1.287], $p < 0.001$; Mas de Naï: 1.306 [1.246,1.370], $p < 0.001$; Saint Affrique: 1.143 [1.088,1.200], $p < 0.001$).

V.3.2.2. Detection of active avoidance of wind turbines

In three wind farms (La Baume, Mas de Naï, and Saint Affrique), no avoidance behaviour was detected either for flights above or within the rotor swept zone (Fig. S3). In Montfrech, we did not detect avoidance when focusing on flights above the rotor swept zone (Fig. 5A). However, for flights within this risky zone, we observed a significantly lower proportion of GPS locations than expected for buffers from 50 m to 450 m (Fig. 5B). This suggests a significant avoidance in this range of distances, matching with the availability of steep slopes nearby (Fig. 5C).

V.3.2.3. Characterisation of meso- and micro-scale avoidance tactic

We further scrutinised flights in Montfrech, by comparing the amount of vulture locations observed within buffers around wind turbines, where avoidance was detected, to the amount obtained with agent-based simulations. Simulations with large distances of detection and low turning angles yielded best matches with observations for most of the buffers highlighting a predominant long-distance avoidance tactic (Fig. 5D). However, for the smallest buffers the best fit ($f > 0.95$) between simulated and observed data could be obtained for both low and large turning angle values, suggesting potential last-minute flee attempts (e.g. the observed avoidance of the 200 m buffer is well simulated with both sets of parameters: $d = 500$ m with $\alpha = 1°$ and $d = 250$ m with $\alpha = 6°$, Fig. 5D).

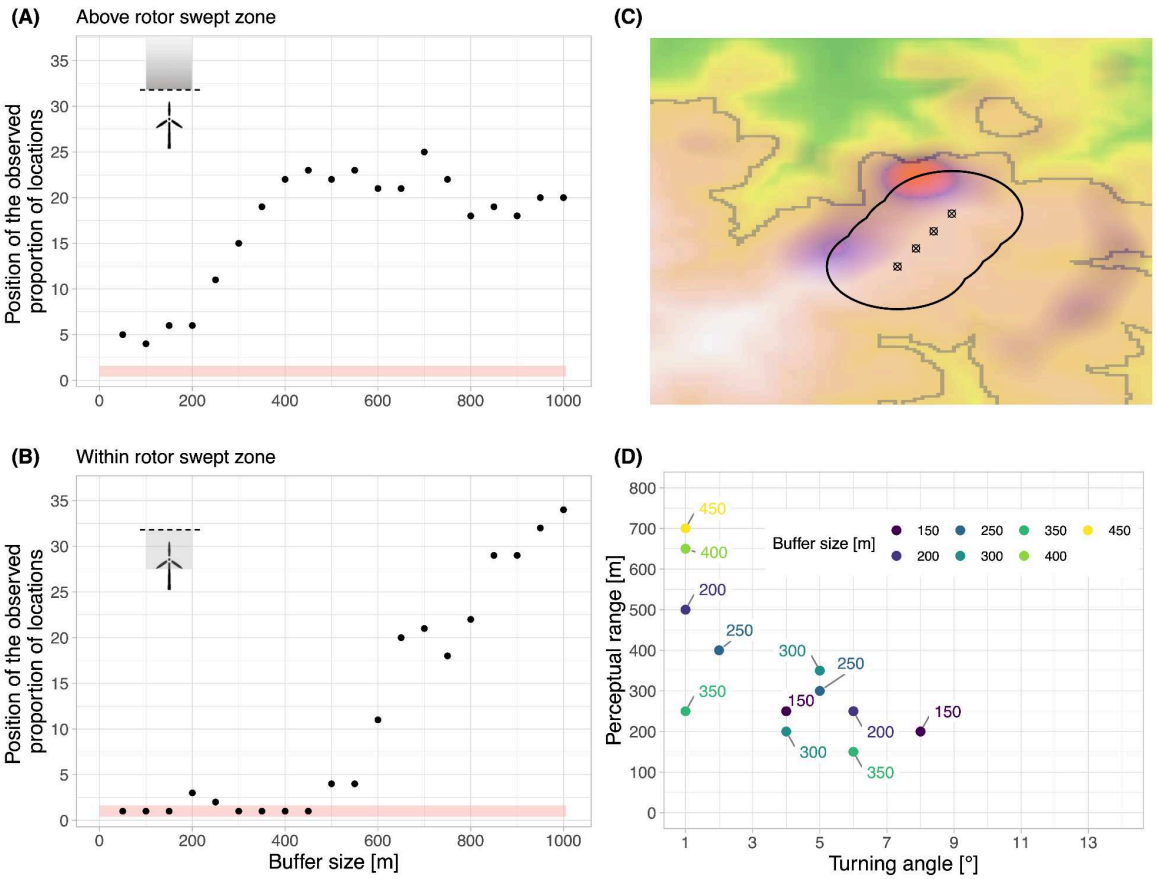

Fig. 5. Turbines avoidance in Montfrech wind farm. Results of the rotation analysis conducted on vultures' flights above (A) and within (B) the rotor swept zone: dots represent the position of the observed percentage of location, among the 36 estimated values (*y*-axis) during the rotational analysis, within a given circular buffer around wind turbines (*x*-axis). The red rectangle highlights buffers for which the amount of locations observed is significantly lower than randomly expected. (C) illustrates the overlap between topography (green to white gradient indicating increasing altitude) and utilisation distribution (purple to red gradient indicating increasing use intensity) of the Montfrech wind farm. The solid black line represents the limits of merged 450-m buffers around wind turbines. (D) shows the combination of parameters (perceptual range and turning angle) used in the agent-based model to simulate vulture flights yielding the best fits between simulations and observations ($f > 0.95$).

V.4. Discussion

Combining high-resolution GPS tracking data from 25 adult griffon vultures across four wind farms and simulations from an agent-based model revealed that wind turbine avoidance seems relatively limited in this species, possibly with specific responses in each wind farm strongly associated with landscape topography. The landscape surrounding wind farms thus appears of prime importance and should thus prevail for deciding wind farm sitting.

Our exploration of the population foraging range coupled with the habitat selection analysis highlighted that wind farm areas were still exploited by vultures. Precisely, we demonstrated that griffon vultures did not exhibit a macro-scale avoidance of the wind farms. This reminds of former results on other large raptors such as white-tailed eagles (*Haliaeetus albicilla*; Dahl et al., 2013) but contradicts results of macro-scale avoidance in medium-size birds such as migrating raptors at onshore wind farms (Cabrera-Cruz & Villegas-Patraca, 2016) and aquatic birds at offshore wind farms (e.g. in Plonczkier & Simms, 2012).

At meso-scale, we observed signs of avoidance behaviour, up to 450 m, only at one wind farm (Montfrech) among four commonly crossed by vultures. Unlike other wind farms, Montfrech turbines were located at about 500 m from steep slopes that were significantly selected by vultures for their foraging and commuting movements. Such a site-specific response could be explained by the topography of Montfrech, where vultures could reach slopes to take advantage of orographic uplift and fly parallel to the row of turbines (like black kites in Santos et al., 2022). Since it only requires positioning themselves over windward slopes to benefit from the deviated wind above canyons' ridges and slopes, the predictability of orographic updrafts make them easier to exploit compared to thermals (Katzner et al., 2012; Shepard, 2022). As such, the avoidance of wind turbines identified by our analyses could be "passive", as a by-product of topography, rather than an active avoidance due to a perceived threat. Indeed, as the strength of the slope uplift decreases with height above ground level (Shepard, 2022), vultures flying above 200 m over ground would no longer be able to rely on this source of uplift (Duerr et al., 2019). This framed consistently with the lack of avoidance when considering flights above the rotor swept zone at all wind farms, including Montfrech.

Far away from used slopes and ridges, as in the three remaining wind farms where we did not detect any avoidance, soaring birds may rely almost exclusively on thermals to gain altitude (Katzner et al., 2012). Péron et al. (2017) estimated that the probability for griffon vultures and other large raptors to fly above 200 m (i.e. above the rotor-swept zone) was significantly correlated to thermal uplift potential. Being constrained in their movements by such unpredictable resources may explain why soaring bird mortality by collision on wind turbines increases when thermals are less frequent or less powerful (e.g. during rainfall or during winter; Barrios & Rodríguez, 2004; Marques et al., 2014). The circling flight necessary to rise into thermal may be associated with a higher risk of collision than when using (linear) slope soaring due to repeated passages in the same area at increasing altitudes (Barrios & Rodríguez, 2004). This may also explain why many bird species that rely on the same flight tactics suffer heavy losses by collisions (Barrios & Rodríguez, 2004; de Lucas et al., 2008; Heuck et al., 2019; Katzner et al., 2012) and concur with a fairly low support for a last-minute flee attempt in our analyses. Such last-minute avoidance should require sharp turns, which are better achieved by birds with low wing-loading and elongated tails, which is not the case of *Gyps* vultures that possess a rather short tail and high wing loading (Balmford, 1995; Gillies et al., 2011). Such manoeuvre could still occur in rare cases of emergency but would result in a very rapid loss of altitude for the vultures. This picture, however, contrasts

partially with recent evidence on black kites and Montagu's harriers showing that flight behaviour was modified at a close range of wind turbines suggesting an active avoidance in these species (Santos et al., 2022; Schaub et al., 2020). These species, having a lower wind loading, are probably much less constrained by sources of uplift in their movements, giving them more room to adapt their flights according to perceived risks, likely explaining the observed differences in avoidance behaviour.

In this study we adapted a method consisting of rotating the locations of infrastructure to be avoided (here wind turbines) to construct null models distributions of space use independent of infrastructure locations. This method is similar in principle to the usual method to rotate tracks to create a null model (e.g. in Schaub et al., 2020) but it has the double advantage of saving the correlation between topography and animal flight, and also reducing the computation power (and time) needed to perform rotations of large amounts of tracks. This is particularly valuable for species heavily relying on topography to move through landscapes, whose rotated flight would become biologically unrealistic. In addition, the use of an agent-based model allowed us to highlight the robustness of our method and be confident in the pattern detected on empirical data. It is also a practical approach for understanding the processes underlying animal movements (Tang & Bennett, 2010), but is often overlooked for analysing collision and turbine avoidance by flying animals (but see in birds: Eichhorn et al., 2012, in bats: Ferreira et al., 2015). We have provided here a model that can be used as a framework for further investigation of the risk of collision with wind turbines. All together, our results revealed a new level of complexity in wind turbine avoidance behaviours as even among restricted groups such as soaring raptors, answer to turbine presence seem to be species- and site-specific.

V.5. Conclusion and management implications

The tragic conflict that we currently face is that soaring birds and wind energy developers are targeting the same resource: wind. The development of wind farms pose a major conservation problem for most large flying animals (Thaxter et al., 2017), as they can induce disturbance of the environment, leading to a decrease in local biodiversity, and can also lead to disruptions of population dynamics and stability through collision fatalities (Perrow, 2017). Here, we provided further evidence that the flight capabilities of some species may make them particularly sensitive to wind turbine collisions, and do not allow them to avoid wind turbines effectively. Yet, we detected an anticipated avoidance at one wind farm matching with the presence of slopes. Slopes aggregate soaring birds and may allow them to stay away from turbines, provided they are neither too close (high risk of collision using the slope uplift) nor too far away (high risk of collision using only thermal uplift; Péron et al., 2017). Taking into account distance from turbines to favourable conditions when sitting projects could help to reduce collision risk. However this would require further research to first understand what makes some slopes more attractive to soaring birds, as all slopes are not necessarily used. Furthermore, it would imply a better understanding of the distance which would be optimal to reduce collision risk. At already

operating sites it has become crucial to detect birds unable to avoid turbines well in advance to shutdown turbines in time to prevent collisions. Shutdown on-demand when animals at risk are detected is a potentially promising way to reduce collision mortality with a negligible reduction in energy production, yet automatic detection systems are costly and their efficiency is still debated (McClure et al., 2021; Tomé et al., 2017). Straightforwardly, to solve this green-green dilemma to reduce carbon emission and preserve biodiversity, it would be more efficient, and should be prioritised, to prevent siting the turbines at places where soaring birds are obliged to travel.

V. CRediT authorship contribution statement

Yohan Sassi: Conceptualization, Methodology, Software, Formal analysis, Visualisation, Writing - Original Draft, Writing - Review & Editing. **Noémie Ziletti**: Conceptualization, Funding acquisition, Writing - Review & Editing. **Olivier Duriez**: Conceptualization, Data curation, Visualisation, Writing - Review & Editing, Supervision. **Benjamin Robira**: Conceptualization, Methodology, Software, Formal analysis, Visualisation, Writing - Original Draft, Writing - Review & Editing, Supervision.

V. Declaration of competing interest

The authors declare to have no conflict of interest

V. Data availability

GPS telemetry data are stored in the www.movebank.org database in the study "Eurasian Griffon vulture in France (Grands Causses 2018) ID_PROG 961". Given the sensitive nature of tracking data for protected species, downloading permission should be asked through the platform to OD.

Scripts for review are available here: https://github.com/YohanSassi/windTurbinesAvoidance. A perennial storage will be provided after revision (e.g. Zenodo).

V. Acknowledgment

We thank the staff from the Grands Causses site of LPO France (T David, R Straughan, R Nadal L Giraud, P Lecuyer, B Descaves) for helping in capturing vultures for tagging. Telemetry study of vultures was authorised in the Programme Personnel 961, coordinated by O. Duriez, under the supervision of the French ringing centre, CRBPO, Paris. We also thank Patrick Boudarel (DREAL Occitanie, France) for fatalities data in the Occitanie region, France and Simon Benhamou for helpful discussions regarding data analyses.

V. Fundings

This work was supported by the GAIA doctoral school grant, University of Montpellier (YS), the Gordon and Betty Moore Foundation (BR). GPS tags were purchased with funds from the European Regional Development (2014-2020) "Conservation des rapaces nécrophages des milieux ouverts herbacés du Massif central" (NZ).

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VI. Effet de l'influenza aviaire hautement pathogène sur les déplacements et la reproduction des vautours

L'observation opportuniste d'arrêt du déplacement de plusieurs vautours fauves français suivi par GPS au moment de l'épidémie d'influenza aviaire en 2022 nous a interpellé. Ce chapitre révèle les résultats de notre investigation. Nous avons bénéficié d'un suivi à long terme par GPS des vautours fauves sauvages des Grands Causses, offrant la possibilité de comparer les déplacements sur plusieurs années consécutives. Ces analyses comportementales ont été couplées aux analyses sérologiques issues de prises de sang effectuées lors de l'épidémie en 2022. La combinaison de ces deux sources d'information a offert l'opportunité d'étudier les conséquences de l'influenza aviaire sur les comportements de ces oiseaux. De plus, le suivi démographique effectué sur le terrain, par la Ligue de Protection des Oiseaux et les gestionnaires d'espaces naturels, a permis de quantifier la survie des jeunes et des adultes face à une épidémie n'ayant jusqu'alors jamais été recensé chez cette espèce.

Note au lecteur :
- Article original publié dans la revue Current Biology.
- Les annexes de l'article sont disponibles en annexe 4 du présent manuscrit p 207.

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Report

Highly pathogenic avian influenza affects vultures' movements and breeding output

Olivier Duriez,[1,6,7,*] Yohan Sassi,[1,6] Chloé Le Gall-Ladevèze,[2] Léa Giraud,[3] Robert Straughan,[3] Lise Dauverné,[4] Anna Terras,[4] Thierry Boulinier,[1] Rémi Choquet,[1] Anne Van De Wiele,[5] Julien Hirschinger,[2] Jean-Luc Guérin,[2] and Guillaume Le Loc'h[2]

[1]CEFE, University of Montpellier, CNRS, EPHE, IRD, 1919 Route de Mende, 34293 Montpellier, France
[2]IHAP, ENVT, INRAE, Université de Toulouse, 23 chemin des Capelles, BP 87614, 31076 Toulouse Cedex 3, France
[3]LPO France - site Grands Causses, Le Bourg, 12720 Peyreleau, France
[4]LPO Occitanie DT Aude, Ecluse de Mandirac, 11100 Narbonne, France
[5]OFB, La Chapelle, 31800 Villeneuve-de-Rivière, France
[6]These authors contributed equally
[7]Lead contact
*Correspondence: olivier.duriez@cefe.cnrs.fr
https://doi.org/10.1016/j.cub.2023.07.061

SUMMARY

An exceptional highly pathogenic avian influenza (HPAI) outbreak due to H5N1 virus genotypes belonging to clade 2.3.4.4.b has been affecting birds worldwide since autumn 2021.[1–3] Mortality caused by viral infection has been well documented in poultry and more recently in wild birds, especially in seabird-breeding colonies.[4–6] However, there is a critical lack of knowledge about how terrestrial birds deal with HPAI virus infections in terms of behavior and space use, especially during the breeding season.[7–9] Understanding how birds move when they are infected could help evaluate the risk of spreading the virus at a distance among other populations of wild or domestic birds, this latter risk being especially important for commensal bird species. Through long-term GPS tracking, we described the changes in daily movement patterns of 31 adult griffon vultures *Gyps fulvus* in two French sites in 2022 compared with 3 previous years. In spring 2022, 21 vultures at both sites showed periods of immobility at the nest, during 5.6 days on average. Positive serological status of 2 individuals confirmed that they had been infected by HPAI viruses. Death was recorded for 3 of the 31 tracked individuals, whereas all others recovered and returned quickly to their foraging routine, although at least 9 birds failed breeding. Such immobility patterns and death rates were never observed in previous years and were not related to weather conditions. The high immobility behavior of infected birds could reduce the risks of transmission. The observed vulnerability to HPAI viruses questions the resistance of endangered vulture species worldwide if infected.

RESULTS

Highly pathogenic avian influenza (HPAI) viruses have become a major threat to poultry and wild bird health, mammalian health, and potentially human health.[10,11] Avian influenza viruses evolve continuously, and highly pathogenic lineages have recently been responsible for many large-scale outbreaks, mostly in domestic (poultry or duck farms) and wild (waterbirds, particularly the members of the Anatidae, seabirds, and raptors) avian populations.[12,13] Commensal (or synanthropic) birds that live near human settlements and livestock, sometimes sharing food resources and attending outdoor enclosures with poultry, can be exposed to HPAI viruses as well as represent potential vectors between wild and domestic birds.[14–16] For several millennia, vultures have behaved as commensals to extensive livestock and any organic wastes produced by humans.[17–19] Vultures provide crucial ecosystem services by consuming carcasses of mostly large ungulates, limiting environmental pathogen loads.[20,21] Surprisingly, despite this behavior, obligate scavengers such as vultures have only been marginally affected by HPAI viruses, with only two H5N1 outbreaks described, one in Hooded vultures (*Necrosyrtes monachus*) in 2006 in Burkina Faso after having fed on carcasses of infected poultry, and the second in black vultures (*Coragyps atratus*) and California condors (*Gymnogyps californianus*) in 2022 in North America.[3,22,23] On the contrary, other raptors from the order *Accipitriformes* like buzzards (*Buteo* sp.), sparrowhawks (*Accipiter* sp.), kites (*Milvus* sp.), and sea eagles (*Haliaeetus* sp.) are frequently victims of HPAI virus infections because of their diet, which includes live or dead birds.[24–26] On the other hand, given their large foraging range, commonly exceeding 1,000 km^2,[27–29] vultures can possibly spread avian pathogens over long distances, similarly to migratory birds that are sometimes hypothesized as being "super-spreaders" of infection.[30] It is therefore essential to understand how infected birds behave and move before, during, and after an outbreak. In the case of an outbreak, we could predict that some individuals would show dramatic changes in their behavior if infected with the pathogenic agent, before dying or recovering from the

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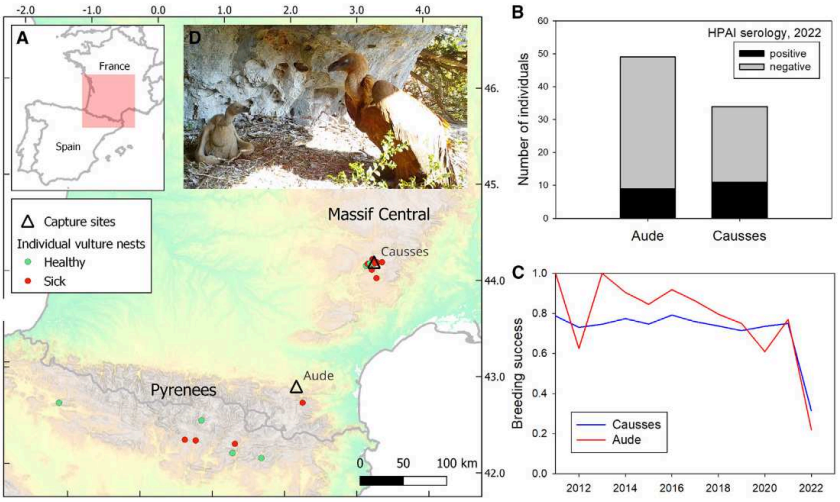

Figure 1. Griffon vulture infection at population level

(A) Map of the study sites, with capture sites (triangles) in proximity of nest sites of the GPS-tracked individual vultures, differentiating in red the nests belonging to individuals showing clinical signs of sickness in April and May 2022 (at least 3 days of immobility at nest, see results) and in green nests of apparently healthy individuals. Note that nests are concentrated within 20 km of the capture site in the Causses, whereas they were spread over 300 km along the Pyrenees range in Aude.

(B) Serological results (antibodies against HPAI H5) from 49 and 34 samples collected in July 2022 in Aude and Causses, respectively.

(C) Changes in overall breeding success (defined as the number of fledglings divided by the number of eggs laid) in Causses (blue) and Aude (red) between 2011 and 2022.

(D) Photograph of an adult griffon vulture showing clinical signs (eye closed) and staying immobile near its chick (that ultimately died) for several days (Photograph © C. Itty).

disease. This could be detected by tracking their movements through time and comparing them with those in years without an outbreak.[16,31] Studies on migratory animals hypothesized that pathogens could affect eco-epidemiological dynamics via an effect on the survival of the host ("migratory culling" hypothesis) and/or on its movement rates and phenology ("migratory separation" hypothesis).[32] Data on changes in the movement behavior of wild individuals as a function of their exposure to a disease agent could provide key information on this topic.

Since 2021, the emergence of H5N1 clade 2.3.4.4.b HPAI viruses has resulted in a panzootic, with massive outbreaks comprising hundreds of thousands of wild birds in Europe, the Middle East, Asia, and North America.[1,3,33] Here, we describe the impact of the HPAI (H5N1) outbreak of April–May 2022 on griffon vultures *Gyps fulvus* at two sites in France, both at the population level and at the individual level (GPS-tracked individuals). Through a long-term GPS-tracking program, we document changes in the foraging behavior of individuals that ultimately died or survived the outbreak. At one site (Causses), we could compare their behavior in 2022 with that observed in the 3 previous years. We hypothesized that one of the main manifestations of HPAI virus infection in vultures was a strong and long-lasting decrease in their daily distance traveled (DDT), as was observed in some duck species in winter and during migration.[8,34]

Vulture populations infected by HPAI virus

In Spain and France, hundreds of chicks and several adult griffon vultures were found dead in April–May 2022, among which 35 were confirmed as being infected by H5N1 HPAI virus. In the Causses (a long-term intensively studied site in south Massif Central, France) (Figure 1A), at least 59 chicks and 6 adults were dead in their nest in May 2022. All carcasses collected in May 2022 in the Causses (n = 8, 4 chicks and 4 adults including the GPS-tracked individual named "Bouffon"; see below) and Pyrenees (n = 2 adults) tested positive by real-time qPCR for HPAI virus (hereafter referred as "HPAI viro+"; STAR Methods).

To quantify the extent of exposure of live birds to HPAI virus, we captured 49 mature and 34 immature individuals (overall 50% adults and 50% immatures) in Aude (eastern Pyrenees, 22 July 2022) and Causses (25 July 2022), respectively, to collect blood samples for serological tests. In Aude, 18% (n = 9) of the vultures tested positive for antibodies against H5 HPAI virus, whereas in the Causses, the proportion of positive serological tests reached 33% (n = 11) (Figure 1B).

The consequence of the outbreak on vulture populations in both regions could also be measured via the overall breeding success (ratio between the number of fledglings and the number of breeding pairs; STAR Methods). In 2022, the overall breeding success was the lowest ever recorded since the start of monitoring (Figure 1C). In the Causses, the breeding success

averaged 0.71 ± SD 0.06 (range 0.57–0.80) between 1990 and 2021 and declined to 0.31 in 2022 (285 fledglings of 905 breeding pairs). Similarly, in Aude, the overall breeding success was 0.22 in 2022, whereas it averaged 0.82 ± SD 0.13 (range 0.61–1.00) between 2011 and 2021.

These results from the carcasses found in May 2022, blood sampling collected in July 2022, and the overall low breeding success confirm that the HPAI outbreak massively impacted populations at both sites.

Consequences of sickness on individual behavior

In the intensively monitored population of the Causses, we analyzed the behavior of all the GPS-tracked birds (n = 21) during that period of 2022 and in the 3 previous years and correlated it to individual breeding success (STAR Methods). In Aude, where the tracking program started in summer 2021 and where nests were distributed all over the Pyrenean range (Figure 1A), we could only study the behavior of 9 vultures in 2022 and were unable to assess with certainty individual breeding success. We focused the following analysis on the 45-day time period, between 15 April and 30 May, that encompassed the whole "vulture" outbreak in 2022 (all individuals positively tested by real-time qPCR had been collected between 3 and 19 May 2022). This study period corresponded with the nestling rearing phase, when most chicks are thermally emancipated and left alone in the nest, whereas both parents forage.[35]

In 2022, in the Causses, three breeding adult individuals died (diagnosed as dead by using GPS and accelerometer data; Figures 2A–2C) between 6 and 10 May 2022. One individual (named #Bouffon) was found dead near a trail and later diagnosed as HPAI viro+ by real-time qPCR. The body of the two other birds (#Goliath and #Claudine) could not be recovered from the cliffs. A visual inspection of the tracking data revealed that all three individuals showed a sharp decline in DDT (mean 2.9 ± SD 4.2 km [10% and 90%, respectively, 0.35–7.9 km], compared with 70.5 ± SD 47.9 km beforehand [10% and 90%, respectively, 13.1–136.9 km], assumed to be their usual mobility pattern) during the 5.0 ± SD 2.51 days before their death (Figures 2A–2C). Thus, we hypothesized that this prolonged reduction of movements (hereafter referred to as "immobility") at a threshold of DDT < 10 km could be a clinical sign of sickness.

Among the other 18 tracked individuals, 14 also displayed prolonged periods of immobility (>2 days with DDT < 10 km, on average, 5.64 ± SD 2.07 days). During these periods, DDT was significantly reduced (averaged 3.7 ± SD 4.0 km) as birds stayed at their nest or roost site, compared with the periods before and after, when DDT averaged, respectively, 66.5 ± SD 46.2 km and 60.1 ± SD 44.5 km (Table S1; Video S1). Three individuals even displayed 2 or 3 periods of immobility, interspaced by 6–22 days of reduced mobility where DDT averaged 35.7 ± SD 26.1 km. The number of days of immobility was significantly shorter in those birds with ongoing reproduction compared with the failed breeders and non-breeders (Table S1). However, for birds that showed prolonged periods of immobility, the total number of days of "sickness" did not differ according to breeding status (Table S1). In Aude, similar periods of immobility (mean DDT 2.7 ± SD 2.8 km) of 4.25 ± SD 2.50 days on average were detected in 4 of the 9 individuals in April–May 2022 (Figure S1). Overall, among individuals whose status was determined using behavior (GPS), the proportion of days of immobility was significantly larger in individuals determined as likely affected by HPAI (here referred to as "sick" for clarity) compared with those with usual DDTs (here referred to as "not sick" for clarity) ($\chi^2 = 24.26$, $p < 0.001$) (Table S3).

In the Causses, we confirmed that the nature of the pattern of DDT variations observed in 2022 was exceptional and potentially linked to the HPAI outbreak, by comparing the DDT recorded for the same 21 individuals in the 3 previous years. In 2019, 2020, and 2021, DDT averaged, respectively, 76.5 ± 52.2, 66.3 ± 51.8, and 77.1 ± SD 55.8 km and globally did not (or marginally) differ between breeders and non-breeders (respectively, $F_{1,916} = 4.001$, $p = 0.046$; $F_{2,963} = 2.245$, $p = 0.106$; and $F_{1,963} = 2.144$, $p = 0.143$). In 2019 and 2021, only one bird stayed immobile (DDT < 10 km) longer than 2 successive days (Figure 3). In 2020, however, almost all individuals displayed an immobility of 2–4 days, between 19 and 22 April, that perfectly matched a period of 5 days of rainfall (Figure 3). In those "control" years (2019–2021), most days of immobility corresponded with similar meteorological conditions that typically prevent efficient soaring-gliding flight for vultures,[29,36] and the number of immobile birds was correlated positively with rainfall (Table S3). In 2022, only the first period of immobility, between 20 and 24 April, seemed correlated with rainfall, whereas after this date, in May, the number of birds immobile no longer correlated with rainfall (Figure 3; Table S4). Indeed, May 2022 was among the hottest and driest ever recorded in France since 1900, which should have favored long-distance vulture flight.[37]

We were able to assess the exposure to HPAI virus in four GPS-tracked individuals that were luckily included among the sample of 34 individuals captured in the Causses on 25 May 2022. Two individuals tested positive for antibodies against H5 HPAI virus (#Millau and #Veto), both non-breeders that showed immobility periods (Figures 2F and 2G). For two individuals, antibodies against H5 HPAI virus were not detected: #Goulag did not display an immobility period and successfully raised a chick, and #Yucca failed breeding on 17 May 2022, after an immobility period (Figures 2D and 2E). The negative test of the later individual could be not only due to inter-individual variability in remanence time of AIV antibodies (samples collected more than 2 months after the outbreak), as described in other species but also due to technical issues (quality of the sample and sensitivity of the serological test)[38,39] or because this bird remained immobile for a reason not related to HPAI infection. However, overall, these results strengthened our hypothesis that the immobility period was highly correlated to the disease.

To confirm the association between immobility and HPAI infection, we developed a joint-modeling framework of movement pattern and infection, using a multi-event capture-recapture model (STAR Methods).[40,41] The model selection highlighted the behavioral similarity between individuals that tested HPAI positive and those inferred as sick by their spatial behavior, giving a stronger support when they were pooled into a single group as in model 3 (Table S5). From this model 3, the daily probability to get infected α_{HI} was twice as large for individuals from the *a priori* sick group compared with those from the *a priori* not sick group (0.06 versus 0.03), but the daily probability α_{IH} to recover from a previous day of state "infected" was much higher in the not sick group (0.734) than in the sick group (0.201)

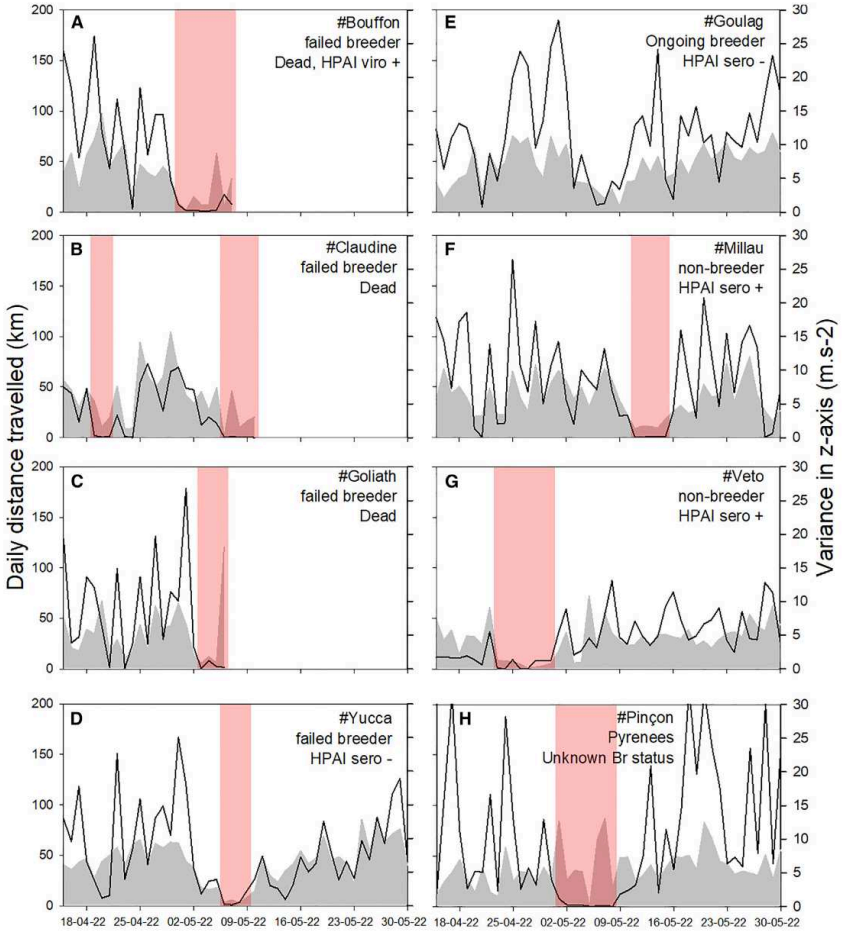

Figure 2. Consequences of sickness on individual behavior

Daily traveled distances (DDT) and overall activity recorded between 15 April and 30 May 2022 for 7 selected individuals in the Causses (A–G) and 1 individual in Pyrenees (H). Each panel indicates individual name (as referred to in the text and Figure S1), breeding status at the end of the period (not available for bird in H), fate and H5 serological status (distinguishing birds with virological tests [HPAI viro+], and birds with serological tests [HPAI sero+/−]; data not available for birds in B, C, and H). Periods of immobility, associated with clinical signs (DDT < 10 km), are highlighted in red. The overall daily activity (represented by the gray shading) was measured using the variance of the z axis of the accelerometer. The tracking maps of the 7 individuals from Causses can be visualized in Video S1.

(Table 1). From this value, we estimated the duration of sickness, using $1 - \alpha$ as the probability to remain in infected state, and using the esperance of a negative binomial law, as $(1 - \alpha)/(1 - (1 - \alpha))$; hence, duration = 0.80/0.20 = 4.0 days in the sick group (and 0.27/0.73 = 0.37 days in the not sick group). The probability $\beta_{H\text{-}IM}$ to display immobility for an *a priori* not sick individual was low (0.03), whereas for an *a priori* sick individual, the probability $\beta_{I\text{-}IM}$ to display immobility was very high (0.871). It was then possible to estimate the mean number of days of immobility for sick individuals in 2022 at 3.48 days by multiplying the duration of sickness (4 days) with this probability of displaying immobility (0.871). This model therefore statistically confirmed our hypothesis that sick birds have a much higher probability to display immobility for at least 3 days when considering a threshold of 10 km of DDT.

The consequence of the outbreak among the 21 GPS-tracked individuals in the Causses was a decrease in the overall breeding success (from 0.69 ± 0.10 SD on average between 2019 and

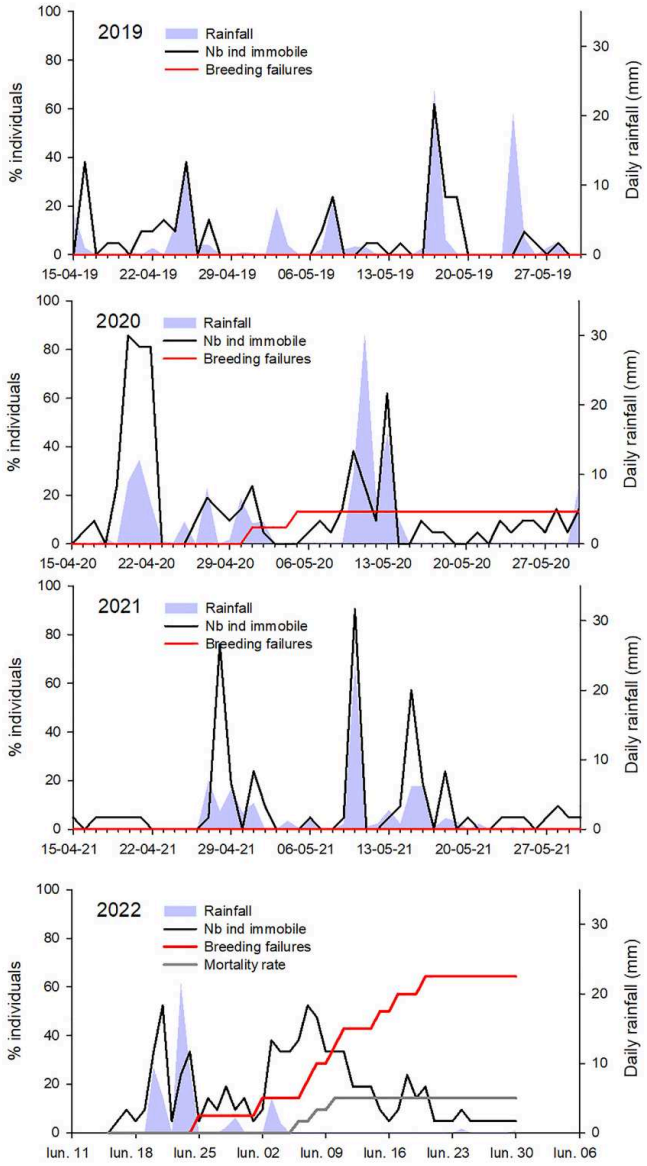

Figure 3. Temporal pattern of infection relative to weather conditions in the Causses

Distribution of days of immobility during the period 15 April–30 May during the years 2019–2022 for the same 21 adult vultures in the Causses. For each year, the proportions of individuals immobile (DDT < 10 km) each day (black line), of breeding failures (red line), and of dead individuals (gray line, only occurring in 2022) are shown in relation to the daily rainfall (blue shading).

See also Figure S1 and Tables S1, S2, and S4.

2021 to 0.27 in 2022). When focusing on the outbreak period (45-day period between 15 April and 30 May 2022), among the 14 birds who were active breeders at the start of the period, 9 birds failed breeding by the end of May (after having all displayed an immobility period), resulting in an "outbreak" breeding success of 0.36. Of the 5 birds that were still breeding at the end of May, only one (#Courage) had displayed an immobility period. Among the 38 birds cumulatively engaged in reproduction in April 2019, 2020, and 2021, only two failed breeding in early May 2020, after several days of bad weather (Figure 3).

DISCUSSION

This study is among the first to describe the effect of an HPAI outbreak on individual movement behavior in a relatively large sample of wild commensal species and among the first in raptors.[26] Furthermore, this study is among the first to occur during the breeding season, when individuals generally have the highest energy expenditure in their life cycle in order to provision their offspring in addition to their own maintenance needs.[42] The main finding was that all birds assumed to be sick displayed a period of immobility at their nest or roost, during 5.6 days on average, before dying or recovering. This immobility period, recorded at two distant sites, uncorrelated with weather conditions, and confirmed by serological investigations, could be used as an indirect method to estimate contamination of griffon vulture colonies.

Our results also add important elements to the documentation of the clinical signs of infection of animals in the wild.[31] Reduced movement has been described as a common sickness behavior.[43] To our knowledge, only four studies previously described how bird movement behavior, remotely monitored by satellite telemetry, could be affected by HPAI virus infections, yet only in very few non-breeding individuals and only in *Anseriformes*. The results were not congruent, with one study showing no apparent effect of infection on movements,[7] whereas two others

Table 1. Parameter estimates of the joint modeling

Parameter estimates from model 3	Group	Estimate ± SE	Lower 95% CI	Upper 95% CI
α_{HI} probability to get infected	sick	0.064 ± 0.014	0.0414	0.0966
	not sick	0.035 ± 0.022	0.0096	0.1161
α_{IH} probability to recover from infection	sick	0.201 ± 0.044	0.1292	0.3002
	not sick	0.734 ± 0.125	0.4396	0.9067
φ probability to survive	all birds	0.985 ± 0.009	0.9542	0.9952
$\beta_{H\text{-}IM}$ probability to remain immobile for healthy individual	sick	0.040 ± 0.013	0.0214	0.0733
	not sick	0.035 ± 0.023	0.0093	0.1213
$\beta_{I\text{-}IM}$ probability to remain immobile for infected individual	sick	0.871 ± 0.049	0.741	0.941
	not sick	–	–	–

From model 3, we estimated the daily probability α_{HI} to get infected and the probability α_{IH} to recover, the daily probability φ of survival, and the daily probability to remain immobile (with DDT < 10 km) when infected for individuals assigned as sick $\beta_{I\text{-}IM}$ or not sick $\beta_{H\text{-}IM}$ according to their spatial behavior. See also Tables S3 and S5.

found similar movements but with reduced speed.[8,9] The last one described reduced movements during 3 days before dying,[34] which recalls our results on griffon vultures. Although it may be premature to draw general conclusions about the way infected birds behave and potentially spread HPAI viruses, our results on vultures strengthen the hypothesis of reduced mobility, although patterns may vary between species and previous exposure to avian influenza viruses (especially low pathogenic strains). Our results show that both hypotheses of migratory culling (affecting survival) and migratory separation (affecting movements and their phenology)[32] could be somehow transposed to breeding birds.

The feeding method of vultures, when dozens of individuals pile on each other to feed on the same carcass,[44] provides little doubt about the opportunity of transmission of the virus among them and initially by eating a carcass of another infected bird. Some stakeholders feared that vultures would transmit domestic poultry with HPAI viruses, becoming super-spreaders of infection.[30] Given the large foraging range of vultures that can use several feeding sites per day,[29] this fear seems legitimate. However, considering the observed immobility of sick griffon vultures on inaccessible cliffs and their preferred mammalian carcasses diet, the risk of transmission from vultures to poultry seems unlikely. Although we assumed that virus excretion mostly occurred during the immobility period, which is supported by the absence of H5N1 virus detection on dead and live birds tested after May 2022 (unpublished data), it remains to be investigated as other studies found that the timing of virus excretion can be variable between species.[45,46] More work is needed to study how commensal species may interact with and infect livestock species of economic interest.[47,48]

Outbreaks of HPAI in vultures may have dramatic consequences for the conservation of vultures worldwide, as 85% of the species composing the *Gyps* genus are listed as endangered.[49] Griffon vultures, although their reproduction was heavily impacted by this outbreak, showed remarkable resilience to the disease, with most adult birds recovering quickly after showing clinical signs during 5–6 days. This contrasts with the massive die-off of colonial seabirds such as gannets (*Morus bassanus*) or great skuas (*Catharacta skua*), for which thousands of dead adults were found at the peak of the outbreak in summer 2022.[4] Although the Eurasian griffon vulture is not endangered worldwide, this gives hope that the critically endangered vulture species in Africa (*Gyps africanus*, *G. rueppelli*, and *G. coprotheres*), Asia (*G. bengalensis*, *G. indicus*, *G. tenuirostris*, and *G. himalayensis*), and America (*Gymnogyps californianus*) may be resistant and resilient if infected by HPAI viruses in the future; however, sister species may sometimes show very different sensitivity to HPAI.[50]

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.07.061.

ACKNOWLEDGMENTS

We thank the staff from LPOGC and LPO Occitanie for providing access to demographic data on griffon vulture population in Grands Causses, helping to capture vultures for tagging and collecting samples. Telemetry study of vultures was authorized in the Programme Personnel 961, coordinated by O.D., under the supervision of the French ringing centre, CRBPO, Paris. We thank staff from ENVT and CEFE for helping in collecting samples in the field and

analyzing the data. We thank all the stakeholders who made it possible to monitor the epidemiological monitoring of these birds (including SAGIR network and OFB). Viral and serological samples collected benefitted from special permission 2022-s-11 signed by the Prefecture de Lozère and DREAL Occitanie on 19 July 2022. GPS tags in the Causses were purchased thanks to Union through the European Regional Development (2014–2020) "Conservation des rapaces nécrophages des milieux ouverts herbacés du Massif central" (L.G. and R.S.). GPS tags in Aude were purchased as part of Life Gypconnect with European and Aude department fundings. Y.S. was funded via GAIA doctoral school grant. OSU OREME is acknowledged for long-term support for demography monitoring of Griffon vultures. ENVT participated in the framework of the "Chaire de Biosécurité et Santé Aviaires," funded by the Direction Generale de l'Alimentation, Ministère de l'Agriculture et de la Souveraineté Alimentaire, France.

AUTHOR CONTRIBUTIONS

Conceptualization, O.D., G.L.L., J.-L.G., and T.B.; resources, Y.S., R.S., C.L.G.-L., L.G., L.D., and A.T.; formal analysis, O.D., Y.S., C.L.G.-L., G.L.L., J.H., and R.C.; writing – original draft, O.D., Y.S., G.L.L., and T.B.; writing – review & editing, all; supervision, O.D. and G.L.L.; funding acquisition, L.G., L.D., A.V.D.W., and J.-L.G.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research. We worked to ensure sex balance in the selection of non-human subjects. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

Received: February 20, 2023
Revised: May 30, 2023
Accepted: July 27, 2023
Published: August 18, 2023

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Bacterial and virus strains		
AIV H5N8 A/decoyduck/France/161105a/2016	LDAR[24]	NF U 47 0-36-1 (French standard reference); NF U 47 0-36-2 (French standard reference)
Biological samples		
Cloacal and tracheal swabs	This paper	N/A
Serum samples	This paper	N/A
Critical commercial assays		
ID Screen Influenza H5 Antibody Competition	Innovative Diagnostics	FLUACH5-5P (kit reference)
ID Gene Mag Fast Extraction Kit	Innovative Diagnostics	MAGFAST-384 (kit reference)
Experimental models: Organisms/strains		
Eurasian griffon vulture *Gyps fulvus*	Wild	N/A
Deposited data		
GPS tracking data extracted from Movebank repository and derived capture-recapture data	This paper	Zenodo data: (DOI : 10.5281/zenodo.8021275)
A/vulture/France/22P018210/2022	Anses (Ploufragan-Plouzané)	EPI_ISL_14722960 (reference in GISAID database)
Software and algorithms		
R version 4.2.2.	The R Foundation for Statistical Computing	https://www.r-project.org/
E-SURGE	Choquet et al.[51]	https://www.cefe.cnrs.fr/fr/recherche/ee/eee/1037-desc/264-logiciels
QGIS version 3.22.12	N/A	https://www.qgis.org/en/site/
Other		
M and H5 PCR	N/A	Slomka et al.[52]
H5 2.3.4.4b PCR	N/A	Naguib et al.[53]

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Olivier Duriez (olivier.duriez@cefe.cnrs.fr).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Raw GPS telemetry data are stored in the https://www.movebank.org/ database in the studies "Eurasian Griffon vulture in France (Grands Causses 2018) ID_PROG 961" and "Eurasian Griffon vulture in France (Aude 2021) ID_PROG 961". Given the sensitive nature of tracking data for protected species, downloading permission should be sought from the lead contact. Telemetry data extracted from the above-mentioned Movebank studies and limited to the animals and period used in the paper are available in Zenodo repository. Additional dataset required for the capture-recapture joint modelling analysis are also included in Zenodo repository.
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Model species

Griffon vultures (family Accipitridae) are long-lived scavengers, with high annual adult survival probabilities (>0,95).[54] Highly social, vultures generally cover large distances daily (mean DDT of 91.7 km daily in spring for griffon vultures in the study area) to find ungulate carcasses, and once found, they tend to gather in large groups to feed (i.e. >100 individuals).[29,44] They nest in colonies in cliffs, laying a single egg per year in January, which hatches in March. The young is actively brooded by both parents alternatively until mid-April, then left alone at the nest while parents forage and feed it until in July.[35]

Study sites

In 2020, the population in France was c. 2800 pairs, including c. 800 pairs in the Massif Central (south-central France) and c. 1200 pairs in the French Pyrenees. We focused our study around two sites: the Causses (south Massif Central, 3.25°E, 42.20°N) and in Aude (eastern Pyrenees, 2.15°E, 42.91°N).

METHOD DETAILS

Demography and breeding parameters

At the population level, in the Causses, a detailed census of all breeding parameters is performed by LPO France (technical site of Grands Causses) every year (number of breeding pairs, numbers of eggs laid, laying and hatching dates, number of chicks fledged). In Aude, a similar census of breeding parameters is performed by LPO Occitanie, but limited to two colonies that gather c. 80 pairs in the area. The overall breeding success was defined at the population level as the number of chicks fledged divided by the number of eggs laid. Each year in the Causses a sample of 50 chicks are ringed at their nest.

At the individual level, the breeding status of tracked individuals was assessed only in the Causses by observations at nest sites. A bird was defined as "breeder" if it was actively and continuously caring for a chick during the 45-day study period (15 April - 30 May), and if this chick was still alive at the end of this period. A bird was defined as "failed-breeder" if the chick died or disappeared (nest empty) during the study period. A bird was defined as "non-breeder" if it didn't start breeding that year (no nest, no egg laid), or if it failed breeding before the outbreak (<15 April), generally during the egg stage.

GPS tracking

We captured vultures using walk-in traps, baited with sheep carcasses.[28] In the Causses, in September – November 2018, we selected a group of 21 adults (age ranging between 4 and 30 years old, including 11 males, 3 females and 7 unknown sex) that had been already ringed at the nest. In Aude, in July 2021, we trapped 9 adult individuals, of unknown age and sex. Each individual was fitted with a solar-powered, 50 g GPS-accelerometer tag (Ornitrack-50, Ornitela), attached with a teflon harness in a leg-loop configuration.[55]

Each tag could remotely send 3D position and body posture (using 3-axis accelerometer) data via GSM mobile phone network. The tags were set to collect position and posture data every 5 minutes.

Epidemiological survey

During the outbreak, all bird cadavers suspected to be infected with the HPAI virus were collected under the supervision of the SAGIR network, managed by the Office Français pour la Biodiversité, in accordance with French regulations. For each individual, cloacal and tracheal swabs were analysed for avian influenza virus M gene and H5 subtype: RNAs were extracted and tested by real-time RT-qPCR (rRT-PCR) for the M and H5 genes by approved laboratories and using validated primers and protocols.[52] The positive samples were then transferred to the National Reference Laboratory for Avian Influenza (LNR IA, Anses-Ploufragan-Plouzané-Niort) for specific rRT-PCR of the H5 gene of clade 2.3.4.4b[53] and if positive, genome sequencing was performed (for example: A/vulture/France/22P018210/2022 EPI_ISL_14722960 on GISAID - https://gisaid.org/). Individuals that tested positive and negative by RT-qPCR are thereafter referred to HPAI viro+ and HPAI viro-, respectively.

In July 2022, we organized special capture sessions, using the walk-in trap, to assess the prevalence of specific AIV antibodies in the Causses and Aude populations. Blood (1 mL) was collected from the brachial vein for the 34 and 49 birds captured respectively in Causses and Aude. Once extracted, serum was tested for AIV H5 subtypes antibodies using a commercial competition ELISA kit (ID Screen Influenza H5 Antibody Competition, Innovative Diagnostics, Grabels, France). Samples were considered positive for H5 when the competition percentage was less than or equal to 50%. H5 positive samples were then specifically tested by hemagglutination inhibition (HI) for antibodies against viruses belonging to clade 2.3.4.4b which group HPAIV viruses (HPAIV A/decoy duck/France/161105a/2016 antigen[56]). Individuals that tested positive and negative by HI are thereafter referred to positive or negative for antibodies against H5 HPAI virus in the text (and abbreviated as HPAI sero+ and HPAI sero-, respectively in figures).

QUANTIFICATION AND STATISTICAL ANALYSIS

Processing of tracking data

We exported all tracking data during the first 1.5 months of the chick rearing period (between 15 April and 30 May) in years 2019-2021 (used as 'control' years in the Causses) and in 2022 (used as an 'experimental' year both in Causses and Aude) for all individuals. We

subsampled the dataset at a 30-min interval in order to have comparable datasets between days and between individuals, and we calculated for each bird the daily distance travelled (hereafter DDT) as the cumulative distances between GPS fixes.

To estimate bird daily activity, we computed the variance of the z-axis (vertical axis "heave") of the accelerometer. We chose the z-axis because previous studies on vultures found that this vertical axis captured most of the variability in acceleration[29,57] and was well correlated to the commonly estimated Overall Dynamic Body Acceleration (we were unable to calculate ODBA here because acceleration data were not recorded at high temporal resolution bouts).[58]

Statistics for tracking data analyses

In the Causses only (that benefited from more intense monitoring of tracked birds in a small region), we investigated the DDT for the individuals that died in 2022, which allowed defining a DDT threshold of 10 km for "immobility" that was synonymous with "morbid status" (sickness). The differences in durations of sickness between breeding status were tested using non parametric Kruskal-Wallis tests. We also used χ^2 tests to compare the number of days of immobility and days with long trips (DDT>10km) between groups of birds defined as HPAI positive, negative, inferred as infected / healthy by behavior (see below).

In the Causses, where all nests of tracked birds are concentrated within 20 km from the capture site, the weather data (daily cumulative rainfall) were recorded at the weather station of Millau-Soulobre (Meteo-France). In the Pyrenees, where the nests of tracked birds are spread over 300 km along the mountain range, and mostly in Spain, we were unable to use weather data that would summarize conditions encountered for all individuals. To study how weather conditions affected vulture movements in the Causses, we used non-parametric Spearman correlations between the daily number of immobile birds and two weather parameters cited above (both dependent and independent variables being significantly different from normality; Kolmogorov-Smirnov tests, all $p < 0.001$).

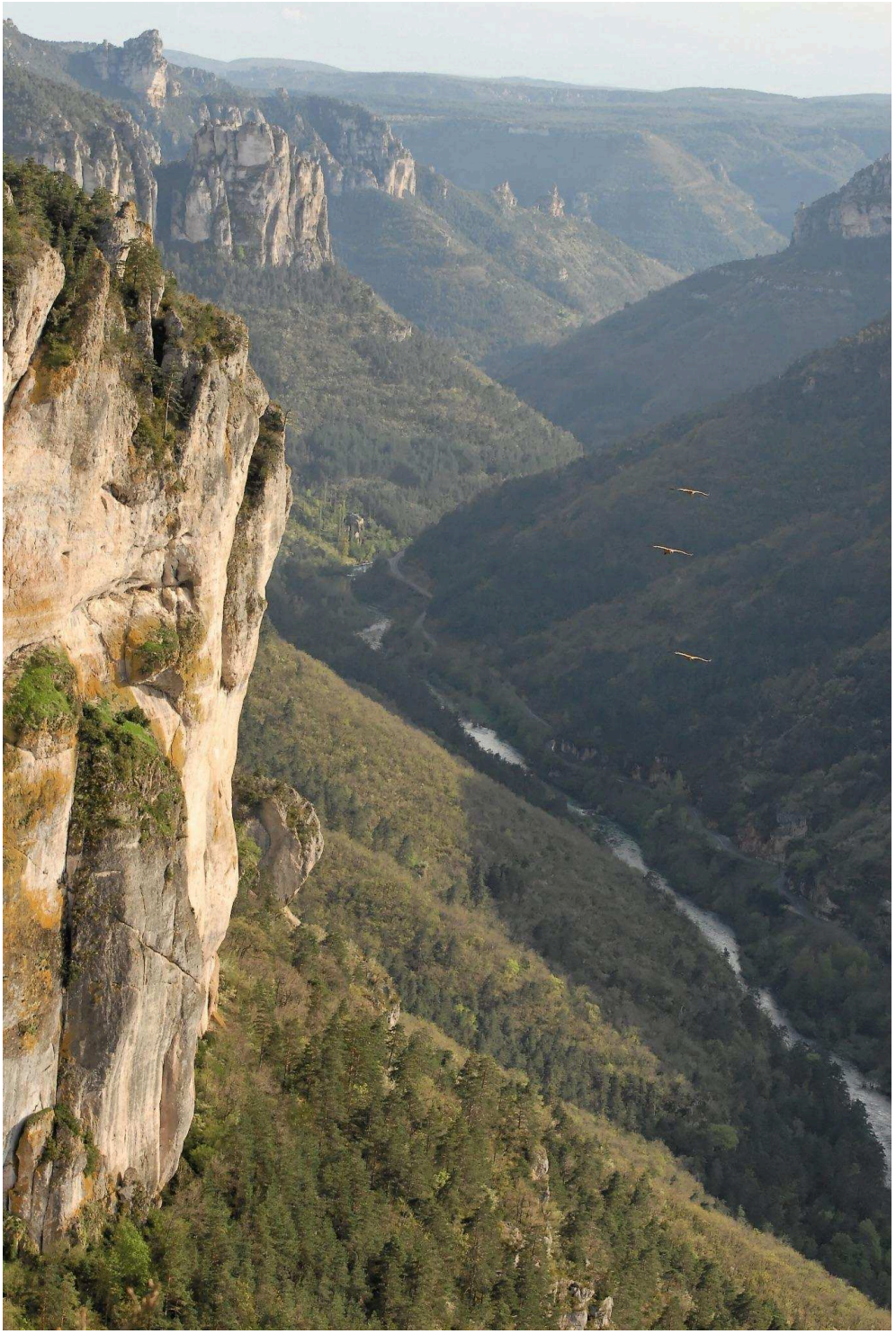
Joint modelling of movement pattern and infection

Based on the data recorded on the 3 dead birds and the birds that tested positive for HPAI virus by RT-qPCR, we complementarily investigated the reliability of our threshold of 10 km of DDT to assign a status as having been « Infected » or « Healthy » using only behavior from GPS data. To do so, we adapted a multi-event capture-recapture modelling approach[59] (hidden Markov model), generally used to study factors affecting survival probabilities, but recently adapted in eco-epidemiology.[40,41,60] Multi-event models were used to statistically estimate the probability of getting infected (as an uncertain state, based on behavioural data of reduced mobility at the 10 km threshold) and the probability to display immobility when infected. We based our analysis on the data recorded on 31 individuals tracked in 2022 in the Causses and in the Pyrenees (Aude).

We built the encounter history of each bird by including 4 events (types of observations). A living bird could be recorded as displaying usual mobility (UM : DDT>10 km), marked as event « 3 », or displaying Immobility (IM : DDT<10 km), hence marked as event « 2 »; a dead bird was marked as « 1 » on the day of its death, and marked as « 0 » in the following days. Four states were considered in the model: "alive and healthy", "alive and infected", "just dead" (the first day when it died) and "dead" (all the days after the observed death date; the reason to distinguish between the two dead states is explained in Schaub and Pradel,[61] and is common in models including dead recoveries). We computed individual encounter histories for 46 days (period 15 April to 30 May), with a daily time step. We further assigned each individual into one of the four groups based on their epidemiological status at the end of the period. An individual is assigned in group 1 if tested positive to HPAI (either with RT-qPCR or serological test); in group 2 if tested negative to HPAI (either with RT-qPCR or serological test); in group 3 if not tested but assigned as « sick » due to its spatial behavior (at least 3 consecutive days with DDT<10 km) and in group 4 if not tested but assigned as « not sick » due to its spatial behavior.

The multi-event model was structured using a vector for initial state, two transition matrices between states, one event matrix (see details in Figure S2). In brief, the initial state vector was set that all individuals started their history in a "Healthy" state, with probability $\pi = 1$. The first transition matrix (step 1) modeled the probability α of getting infected (i.e. the transition α_{HI} from state "Healthy" to state "Infected" and vice-versa α_{IH}) at every time step. The second transition matrix (step 2) modelled the survival probability φ (hence the transition from the state "Infected" to the state "Newly Dead", assuming that no individual from "Healthy" state could die in the dataset). The Event matrix estimated the probability β to observe an individual displaying immobility (IM, i.e. DDT<10 km) or usual mobility (UM; i.e. DDT>10 km), conditionally to its state ("Healthy" $\beta_{H\text{-}IM}$ or "Infected" $\beta_{I\text{-}IM}$).

We ran four simple models to test four hypotheses. In Model 1 we tested the hypothesis of equality between all treatment groups for probability α to get infected and probability β to display immobility. In Model 2 we tested the hypothesis that all 4 treatment groups were different for the same α and β parameters as Model 1. In Model 3, we tested the hypothesis of equality of α and β parameters between groups 1 and 3 (assumed to be 'sick', pooled) and between groups 2 and 4 (assumed to be 'not sick', pooled). In Model 4, we tested the hypothesis that the same α and β parameters were different for groups 1 and 2 (tested positive and negative respectively) but identical for groups 3 and 4 (individuals not tested and not behaviorally assigned as 'sick', pooled). Model selection was based on QAICc, with two models deemed to be significantly different if the difference in their QAICc value were larger than 2.



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VII. Discussion générale et conclusion

VII.1. Synthèse des résultats

Ce travail de doctorat alterne entre des questions de recherche fondamentale, et des questionnements plus appliqués. J'ai commencé par deux chapitres étudiant l'influence de la socialité sur les déplacements des vautours à l'échelle individuelle et collective. J'ai identifié certains facteurs internes (*i.e.* position dans la hiérarchie de dominance) et externes (*i.e.* météorologie et altitude de vol) influençant la part d'information personnelle et sociale utilisée lors des prises de décision des vautours en déplacement (Chapitre III). À plus large échelle, je montre que ces oiseaux semblent posséder une stratégie de prospection alimentaire collective, dans laquelle l'information sociale est primordiale, confortant les hypothèses de recrutement local et de réseau établies de longue date (Chapitre IV). Les deux chapitres suivants, ayant une visée plus appliquée, me permettent d'affirmer que les centrales éoliennes présentent un risque important pour les vautours, qui ne montrent pas de comportement d'évitement de ces structures, ou de manière marginale (Chapitre V). De plus, l'épidémie d'influenza aviaire hautement pathogène, ayant touché les vautours fauves pendant le printemps 2022, a entraîné des symptômes comportementaux observables chez cette espèce : un arrêt prolongé du déplacement (Chapitre VI). Par l'intermédiaire de ces travaux, je peux désormais apporter plusieurs éléments de réponse aux questions posées en introduction.

Quelle est l'importance relative attribuée par les vautours aux informations personnelles et sociales lorsqu'ils sélectionnent les courants ascendants thermiques nécessaires à leurs déplacements ? Quels sont les facteurs faisant varier l'utilisation de ces sources d'informations ?

Les expériences que j'ai mené sur les vautours captifs du Rocher des Aigles montrent que les décisions en vol des vautours s'appuient principalement sur des informations sociales, en particulier dans des conditions de vol défavorables qui augmentent l'imprévisibilité des ascendances thermiques ou qui exposent les individus à un risque d'atterrissage non désiré. En moyenne, 63% des ascendances thermiques utilisées par les individus ont été préalablement découvertes par un congénère. La décision de les rejoindre est donc issue de l'utilisation d'information sociale. Cependant, l'utilisation de ces informations sociales dépend largement de la position hiérarchique de l'individu. La probabilité qu'un individu utilise de l'information personnelle et découvre un thermique par lui-même est deux fois plus grande pour un individu en bas de la hiérarchie, comparé à un dominant. Autrement dit, les individus dominants ont tendance à suivre les dominés qui, eux, explorent le paysage et découvrent de nouveaux thermiques. Pour finir, les résultats montrent que, face à un choix entre plusieurs thermiques disponibles simultanément, les vautours privilégient les thermiques utilisés par le plus grand nombre de congénères.

La distribution des vautours en prospection renseigne-t-elle sur l'occurrence d'un réseau de recherche alimentaire contraint par le paysage ?

L'exploration préliminaire des données de suivi radar me permet de mettre en lumière des patrons de déplacement jusqu'alors jamais observés chez les vautours fauves. Ces oiseaux semblent parfois se déplacer en groupes, formant des chaînes d'une petite dizaine d'individus en moyenne, chacun espacés de 300 m environ. Ces chaînes s'organisent parfois en lignes parallèles (deux lignes, parfois trois), se déplaçant sur les plateaux de manière simultanée, dans une direction commune, et formant ce que j'ai appelé des « rails ». Ces rails sont espacés en moyenne de 5,4 et 2,6 km respectivement quand ils sont constitués par deux ou trois lignes parallèles. Les connaissances sur le champs visuels des vautours (Martin et al., 2012) m'ont permis de simuler la surface de sol « scannée » par chaque vautour en fonction de sa hauteur de vol, et il semblerait que cet espacement soit optimal pour que les champs visuels des oiseaux situés sur chaque ligne du rail soient exactement adjacents. Pour finir, j'ai observé l'agrégation rapide de vautours autour d'une carcasse et mesuré une distance d'attraction dépassant 6 km.

Les vautours évitent-ils les centrales éoliennes ? Si oui, à quelle échelle : la centrale dans son ensemble, les éoliennes spécifiquement mais de manière anticipée ou par réflexe au dernier instant ?

La combinaison entre données empiriques (suivi GPS haute résolution de 25 vautours fauves) et simulations informatiques (à l'aide d'un modèle agent-centré) m'a permis non seulement de quantifier l'évitement des centrales éoliennes par les vautours mais aussi de comprendre les mécanismes comportementaux sous-jacents, à différentes échelles. Notamment, j'ai adapté une méthode d'analyse afin d'étudier l'évitement des éoliennes tout en gardant la corrélation des trajets des vautours avec le paysage. Les résultats montrent que les vautours n'évitent pas les centrales éoliennes dans leur ensemble. Au sein des quatre centrales éoliennes les plus fréquentées par les vautours des Causses, je ne détecte un évitement que dans une seule des centrales, jusqu'à une distance de 450 m autour des éoliennes. Mon modèle agent-centré suggère que le comportement d'évitement observé dans cette centrale correspond à un évitement anticipé des éoliennes.

Quelles sont les conséquences de l'influenza aviaire hautement pathogène sur les déplacements et la survie des vautours ?

Grâce au suivi GPS à long terme sur les vautours français nous avons pu décrire les changements dans les déplacements quotidiens de 31 vautours en 2022, lors de l'épidémie d'influenza aviaire hautement pathogène (IAHP), par rapport aux trois années précédentes. Nos résultats montrent qu'au printemps 2022, 21 vautours présentaient des périodes d'immobilité au nid, pendant 5,6 jours en moyenne. Le statut sérologique de deux individus ayant présenté cet arrêt du déplacement confirme qu'ils avaient été infectés par le virus de l'IAHP. Parmi les 31 individus suivis, trois sont morts, tandis que tous les autres se sont rétablis et ont repris rapidement leur routine de prospection alimentaire. Cette épidémie, touchant les vautours en pleine période de reproduction, a aussi provoqué une mortalité sans précédent des jeunes au nid. De tels patrons d'immobilité et de taux de mortalité n'ont jamais

été observés au cours des années précédentes et ne sont pas liés aux conditions météorologiques.

VII.2. Discussion des résultats

Le vautour fauve, dès le départ de son nid et jusqu'à son retour, cherche inlassablement des ressources imprévisibles, d'abord pour se déplacer puis pour se nourrir. Où se trouve le prochain courant ascendant qui lui permettra de gagner de l'altitude sans efforts ? Mes résultats montrent que les vautours utilisent largement l'information sociale pour répondre à cette question, obtenue via les congénères avec lesquels ils partagent l'espace aérien, eux aussi à la recherche des mêmes ressources. Pour ces ressources éphémères, non épuisables par leur utilisation et partageables, la compétition intraspécifique dans leur exploitation doit être nulle, ou faible, favorisant ainsi l'utilisation d'information sociale. En revanche, au sein d'un vol, dans lequel un individu doit, de multiple fois, choisir le prochain courant ascendant qu'il va utiliser, la part d'information personnelle et sociale dans la décision peut varier. Les facteurs externes affectant directement la prévisibilité de la ressource, comme des basses températures qui réduisent le nombre de thermiques disponibles et les rendent relativement peu puissants, ou encore le vent qui les fait dériver (Bradbury, 1989; Kerlinger & Gauthreaux, 1984; Shamoun-Baranes et al., 2003, 2016; Shannon et al., 2002), tendent à augmenter l'utilisation d'information sociale. Dans ces conditions, un individu en vol, prenant de l'altitude en décrivant lui-même des cercles dans un courant ascendant, procure involontairement une information sur la présence d'un thermique à tout autre oiseau l'ayant dans son champ de perception. Utiliser cette information sociale est particulièrement efficace car elle réduit grandement l'incertitude autour de la disponibilité d'un thermique permettant de gagner de l'altitude (H. J. Williams & Safi, 2021). En plus des conditions environnementales, la situation de vol de l'individu peut elle aussi influer sur les sources d'information utilisées. Lorsque les oiseaux planeurs quittent un thermique à basse altitude, ils ne disposent que d'une distance limitée pour planer jusqu'au prochain thermique avant de devoir passer au vol battu pour rester en altitude, ou bien atterrir dans un endroit non désiré, ce qui, dans les deux cas, ajouterait un coût énergétique élevé associé au vol battu et au décollage (Duriez et al., 2014; Horvitz et al., 2014; Shepard, 2022; H. J. Williams et al., 2020). Dans ces conditions aussi l'utilisation d'information sociale est bénéfique pour garantir un déplacement peu coûteux. Ainsi, nos observations confortent la théorie prédisant que les individus devraient largement utiliser les informations sociales à leur portée car, en réduisant l'incertitude autour de la disponibilité de la ressource, elles permettent aux individus de réduire leurs coûts de déplacement et leur temps de recherche des ressources désirées (Riotte-Lambert & Matthiopoulos, 2020; H. J. Williams & Safi, 2021).

Mes résultats indiquent aussi une utilisation différentielle des informations sociales pour le choix des thermiques selon la position de l'individu dans la hiérarchie de dominance. Alors qu'il n'existe pas de compétition dans l'utilisation des thermiques, elle peut devenir relativement forte autour des carcasses, qui elles, bien que partageables peuvent être partiellement monopolisées par les dominants, et s'épuisent au fur et à mesure de leur exploitation (Bosè & Sarrazin, 2007; Donázar et al., 1999; Kirk & Houston, 1995; van

Overveld et al., 2018). En réponse, les individus de rang inférieur, en utilisant préférentiellement leurs informations personnelles pour découvrir de nouveaux thermiques et ainsi explorer leur environnement, pourraient atteindre les carcasses en premier, ou au moins arriver au début de la curée lorsque la compétition est encore faible (Bosè et al., 2012). Il pourrait s'agir d'un mécanisme expliquant que les « pionniers », les tout premiers vautours à se poser et se nourrir sur les carcasses, soient principalement des individus de bas rang, avant d'être évincés par les dominants (Bosè et al., 2012). Cette utilisation d'informations personnelles par des individus de rang inférieur pour arriver aux carcasses avec des niveaux de compétition plus faibles pourrait être exploitée par les individus dominants pour réduire leur propre effort de recherche des thermiques premièrement mais aussi de carcasses (Barta & Giraldeau, 1998; Lee et al., 2016; Stahl et al., 2001). Bien qu'il soit classique de penser que les leaders dans les déplacements collectifs sont souvent des individus dominants ou plus âgés, comme par exemple chez les pigeons voyageurs (*Columba livia,* Flack et al., 2012) ou les éléphants (*Loxodonta africana,* McComb et al., 2011), mes résultats montrent que ce rôle peut aussi être joué par les individus subordonnés avec relativement peu d'informations sur la disponibilité des ressources. Cette initiation des déplacements collectifs par les subordonnés, suivie par les dominants, a aussi récemment été découverte chez les pintades vulturines (*Acryllium vulturinum,* Papageorgiou & Farine, 2020). Ainsi, la position du vautour dans la hiérarchie de dominance, par les coûts qu'elle impose sur l'accès à la nourriture, semble calibrer le compromis entre l'utilisation d'informations personnelles et sociales dans le choix des thermiques, nécessaire lors des déplacements à la recherche de nourriture.

Cette dynamique entre vautours subordonnés et dominants lors de la recherche de thermique pourrait avoir un rôle, à plus grande échelle, dans la formation des chaînes de vautours observées lors de la prospection alimentaire. En effet, en initiant le mouvement pour explorer le paysage à la recherche de courants ascendants et de carcasses, les individus de bas rang pourraient être suivis par des individus de haut rang, créant ces patrons de déplacement en groupe, d'une petite dizaine d'individus, les uns derrière les autres espacé d'environ 300 m que j'ai appelé « trains ». J'ai aussi découvert que ces trains forment occasionnellement des lignes parallèles et aboutissent à la création de « rails », sur lesquels les oiseaux semblent s'organiser de sorte que leurs champs visuels projetés au sol soient adjacents.

Lors de la découverte d'une carcasse, la convergence et l'agrégation d'un grand nombre de vautours est clairement visible dans le suivi radar. L'ensemble de ces observations suggère une certaine coordination dans la distribution spatio-temporelle des vautours en prospection pour optimiser leur recherche alimentaire. Cela confirme l'existence du phénomène de recrutement local et renforce l'hypothèse d'une stratégie de prospection en réseau. Selon cette hypothèse, les groupes de vautours s'organisent de manière à inspecter méthodiquement la zone survolée, en la ratissant pour n'omettre aucun espace, tout en gardant leurs congénères dans leur champ de perception afin de les rejoindre en cas de découverte d'une carcasse. Cette stratégie n'aurait jamais été décrite chez des animaux terrestres bien que proposée de longue date pour les vautours (Houston, 1974; Tristram, 1867), testée par modélisation (Cortes-Avizanda et al., 2014; Deygout et al., 2010; Jackson et al., 2008), et récemment découverte chez les oiseaux marins (Assali et al., 2017, 2020). Chez

ces derniers, la participation à un réseau de recherche, ou même aux structures de recherche coordonnées (appelés « râteaux » par les auteurs, Assali et al., 2020) permet non seulement d'augmenter la probabilité de découvrir un banc de poissons mais surtout, par le phénomène de recrutement local, d'attirer une masse critique de congénères qui, par leurs attaques successives, empêchent le banc de se reconstituer, annihilant l'effet de dilution chez les proies, favorisant ainsi le taux de capture des oiseaux prédateurs (Thiebault et al., 2016; Thiebault, Mullers, Pistorius, & Tremblay, 2014). Chez les vautours, la participation à une stratégie en réseau permettant de s'agréger rapidement autour d'une carcasse pourrait finalement apporter des bénéfices proches de ceux observés chez les oiseaux marins, et ainsi surpasser la compétition induite par l'agrégation. Premièrement, la stratégie en réseau a été estimée comme étant particulièrement efficace en-deçà d'un certain seuil (20 %) de prévisibilité des ressources (Deygout et al., 2010), ainsi cette stratégie permettrait d'optimiser la découverte d'une ressource imprévisible. Ensuite, une fois autour de la carcasse, généralement bien plus grosse que les vautours, la présence de congénères peut leur permettre d'être plus efficace pour déchirer les cuirs en tirant la peau de toutes parts avec leurs becs acérés, et ainsi d'accéder rapidement aux organes internes et aux muscles des carcasses. Les vautours étant vulnérables au sol, la présence d'un groupe permet une détection précoce de perturbations ou de potentiels prédateurs (Guillemain et al., 2002; Pulliam, 1973; Sirot, 2006; Zarus, 1978) mais aussi de se nourrir plus vite pour regagner le ciel, une zone plus sûre pour eux. Pour que cette stratégie de recherche collective soit maintenue dans l'évolution, il est nécessaire que les bénéfices apportés soient supérieurs aux coûts subis. De ce fait, bien que la compétition intraspécifique puisse être féroce autour de la carcasse et qu'il ne soit pas rare de voir des vautours ne pouvant pas accéder à la nourriture durant la curée, il est probable que ces coûts soient surpassés par l'efficacité de la recherche en groupe et par le fait que ces carcasses soient, selon leur taille, en grande partie partageables. Par exemple, en considérant qu'un vautour peut consommer 1 kg de viande lors d'une curée (Mundy et al., 1992), une brebis qui pèse environ 40 kg, et une vache de plus de 200 kg, pourraient respectivement nourrir 40 et 200 vautours. L'occurrence d'une stratégie de recherche collective en réseau chez les oiseaux marins et les vautours pourrait donc être le fruit d'une convergence évolutive, une stratégie développée en réponses aux mêmes contraintes : trouver une source de nourriture imprévisible dans une vaste zone. On pourrait même s'attendre à retrouver des stratégies relativement similaires chez d'autres oiseaux marins comme les albatros et les pétrels géants (*Macronectes giganteus*), ayant un régime alimentaire plutôt charognard, que l'on appelle souvent « les vautours des mers » (Grémillet et al., 2012; Sakamoto et al., 2009; Weimerskirch et al., 2005).

Ce mode d'alimentation si particulier, où des dizaines de vautours s'empilent les uns sur les autres pour se nourrir sur la même carcasse (Figure I.5B,C, Bosè et al., 2012), laisse peu de doute sur son rôle dans la transmission de maladies, comme ce fut le cas au printemps 2022 lors de l'épidémie d'influenza aviaire hautement pathogène dont les vautours ont été victimes. La transmission de maladie compte parmi les coûts de la vie en groupe (Krause & Ruxton, 2002), en revanche c'est la première fois que cette maladie est identifiée chez les vautours fauves, laissant penser que cette maladie touche relativement rarement ces oiseaux, et qu'elle est peu coûteuse pour les individus adultes. En effet, l'un des symptômes de la

maladie est un arrêt du déplacement de 5 à 6 jours chez les individus adultes (Duriez, Sassi et al., 2023). Pour des oiseaux ayant des capacités de jeûnes pouvant durer jusqu'à trois semaines (Bahat, 1995), cet arrêt du déplacement empêchant l'individu adulte de se nourrir n'est sans doute pas problématique, pour peu qu'il ait participé à une curée dans les jours précédents. De plus, alors que près de 70% des jeunes au nid sont morts, parmi les adultes suivis ayant montré des symptômes de la maladie (21 individus), seulement trois sont morts, les autres ayant progressivement récupéré un comportement de prospection alimentaire normal. Pour une espèce longévive comme le vautour fauve, possédant des traits d'histoire de vie de type K, laquelle est surtout sensible à la survie des adultes, une mauvaise saison de reproduction n'est pas dramatique à condition que ce phénomène reste rare.

Si les vautours (adultes) semblent plutôt résistants face à l'influenza aviaire, ils le sont beaucoup moins face aux pales d'éoliennes. En Espagne, le vautour fauve est le rapace le plus souvent retrouvé mort au pied des éoliennes (Sebastián-González et al., 2018). Parmi nos sites d'étude, je détecte un évitement seulement dans une seule des centrales éoliennes, jusqu'à une distance de 450 m des éoliennes. Cette réponse, spécifique au site de Montfrech, pourrait s'expliquer par sa topographie où les vautours peuvent atteindre les pentes situées à environ 500 m des éoliennes, pour profiter des ascendances orographiques et ainsi voler parallèlement à la rangée d'éoliennes (comme les milans noirs, *Milvus migrans*, Santos et al., 2022). Puisqu'il suffit de se positionner au-dessus des pentes orientées face au vent pour bénéficier des ascendances orographiques, la prévisibilité de ce type d'ascendances les rend probablement plus faciles à exploiter que les thermiques (Katzner et al., 2012; Shepard, 2022). Ainsi, l'évitement des éoliennes identifié par nos analyses pourrait être « passive », en tant que sous-produit de la topographie, plutôt qu'un évitement actif dû à une menace perçue. Dans les autres sites où je ne détecte aucun évitement, les pentes et les crêtes utilisées par les vautours se trouvent relativement loin des éoliennes (> 1 km) et dans ces conditions, les vautours doivent compter presque exclusivement sur les thermiques pour gagner de l'altitude. Leurs caractéristiques morphologiques les rendant moins manoeuvrables et les contraignant à utiliser des ressources aussi imprévisibles que les thermiques pour se déplacer, peuvent expliquer pourquoi la mortalité des vautours par collision sur les éoliennes augmente lorsque les thermiques sont moins fréquents ou moins puissants (par exemple, lors de précipitations ou en hiver; Barrios & Rodríguez, 2004; Marques et al., 2014). De plus, le vol circulaire induit par l'utilisation d'un thermique peut être associé à un risque de collision plus élevé que lors d'un vol basé sur des ascendances orographiques (beaucoup plus linéaire) en raison des passages répétés dans la même zone à des altitudes croissantes (Barrios & Rodríguez, 2004). Ceci pourrait être une cause directe des nombreuses mortalités observées chez d'autres espèces d'oiseaux utilisant les mêmes stratégies de vol (Barrios & Rodríguez, 2004; de Lucas et al., 2008; Heuck et al., 2019; Katzner et al., 2012; Rushworth & Krüger, 2014; Sanz-Aguilar et al., 2015; Vasilakis et al., 2016).

Bien que les éoliennes soient une des solutions retenues par les gouvernements pour produire de l'électricité en limitant les émissions de CO_2, leur impact sur la faune et la flore soulève de nombreuses inquiétudes. Notamment, il serait intéressant de réduire l'impact de ces structures sur les populations de vautours, et les espèces nécrophages de manière plus

générale, puisque celles-ci permettent aussi une réduction drastique des émissions de CO_2 en évitant le recours au système d'équarrissage industriel (Dupont et al., 2012; Morales-Reyes et al., 2015). Il est malheureux de devoir avancer l'argument de service rendu par la biodiversité comme levier pour sa protection, mais c'est bien par celui-ci que les politiques pourraient apprécier le bénéfice apporté par les deux parties. Par exemple, sur le faucon crécerellette, *Falco naumanni*, autre espèce de rapace sociale et fréquemment victime des éoliennes (voir annexe 5) nous proposons un bridage adapté basé sur la prédiction de la probabilité de présence d'oiseaux à l'intérieur d'une centrale éolienne en fonction de différents facteurs (*e.g.* direction et force du vent, mais aussi saison). Les oiseaux ne se distribuant pas de la même manière dans la centrale éolienne selon ces facteurs, il est possible de prédire, suivant les conditions environnementales, les zones favorables à la présence d'oiseaux. Cela permet d'identifier les éoliennes entraînant un risque de collision dans chaque condition environnementale, et donc d'arrêter uniquement les turbines potentiellement accidentogènes. Une meilleure connaissance de l'utilisation du paysage par les vautours, mais plus généralement par l'ensemble des oiseaux sensibles aux collisions (Thaxter et al., 2017), offrirait l'opportunité de produire de l'électricité tout en réduisant les risques de collision pour les oiseaux. Cela pourrait passer par un bridage adapté dans les centrales déjà en activité, comme proposé dans l'étude sur les faucons crécerellettes. Mais surtout en amont, ces connaissances permettraient de favoriser l'installation de centrales éoliennes dans des secteurs à enjeu moindre pour les oiseaux.

VII.3. Limites et perspectives

Les résultats présentés dans ce travail de thèse confortent de nombreuses études précédentes sur les vautours de l'Ancien Monde (Cortes-Avizanda et al., 2014; Deygout et al., 2010; Jackson et al., 2008; H. J. Williams, King, et al., 2018) et du Nouveau Monde (Buckley, 1997; Prior & Weatherhead, 1991), montrant que ces oiseaux utilisent des informations transmises par leurs conspécifiques dans la recherche de courants ascendants et de carcasses. Or, dans la recherche de ces ressources, les individus peuvent aussi glaner de l'information sur des individus d'autres espèces, pouvant être taxonomiquement très différentes, du moment qu'ils utilisent les mêmes ressources (H. J. Williams & Safi, 2021). Par exemple, les vautours africains (*Gyps africanus*) et les vautours de Rüppell profitent des informations involontairement transmises par les aigles ravisseurs (*Aquila rapax*) et les aigles des steppes (*Aquila nipalensis*) pour localiser les carcasses dans la savane kenyane (Kane et al., 2014). En Espagne, ce sont les nécrophages facultatifs comme les grands corbeaux (*Corvus corax*) et les milans royaux (*Milvus milvus*) qui facilitent la détection des carcasses par les vautours (Cortes-Avizanda et al., 2013). Les vautours peuvent aussi se servir d'autres oiseaux utilisant les mêmes stratégies de vol, tels que les milans noirs (Santos et al., 2017) ou les cigognes blanches (Nagy et al., 2018), comme indicateur de la présence de courants ascendants. Ce type de transfert d'informations depuis des hétérospécifiques pourrait également opérer dans les régions françaises occupées par les vautours fauves puisqu'ils cohabitent avec de nombreuses espèces nécrophages facultatives (*i.e.* grand corbeau, milan royal et milan noir, aigle royal (*Aquila chrysaetos*)) et strictes (vautours moine, vautour

percnoptère et gypaète barbu), pouvant signaler involontairement la présence de courants ascendants et de carcasses par leurs comportements de vol. Pour intégrer ces sources d'informations dans mes études je pourrais envisager d'ajouter une caméra lors des expériences de vol sur les vautours captifs du Rocher des Aigles. Ainsi, en plus du suivi des déplacements par GPS de l'ensemble des oiseaux captifs, je verrais, au travers de la caméra, si et comment l'individu focal utilise des informations provenant d'oiseaux que je ne peux pas suivre dans sa recherche de courant ascendant (Figure VII.1). Il est donc probable que ma quantification de l'utilisation d'information sociale soit sous estimée, et une telle expérience permettrait d'avoir une estimation plus précise. Chez les oiseaux marins, la combinaison d'une balise GPS avec une caméra a permis de découvrir que les fous du Cap, lors de leurs prospections alimentaires, cherchent en priorité d'autres prédateurs tels que d'autres oiseaux, des dauphins et des bateaux, et non leurs proies, qui ne sont visées qu'au dernier moment (Tremblay et al., 2014). Dans mon étude des stratégies de prospection alimentaire par l'intermédiaire du radar, je pourrais aussi évaluer l'antériorité de trajectoires appartenant à d'autres espèces d'oiseaux vers les points d'agrégation comme un indice de l'utilisation des informations provenant d'hétérospécifiques dans la découverte de carcasse.

Mon exploration préliminaire des stratégies de recherche de carcasses par les vautours fauves s'est basée sur des données collectées durant l'été. À cette saison le bétail est dispersé sur l'ensemble des Causses, rendant la disponibilité en carcasse extrêmement imprévisible, et *de facto* la stratégie basée sur le partage d'information sociale devient particulièrement efficace (Deygout et al., 2010). En revanche, en hiver, les ressources alimentaires deviennent davantage prévisibles, notamment au cours de la période d'agnelage (janvier - avril), caractérisée par une hausse de la mortalité dans les cheptels. Les agriculteurs ont tendance, durant cette période, à approvisionner régulièrement les placettes individuelles de recyclage naturel proche des fermes. De plus, les conditions météorologiques durant cette période sont moins favorables aux vols de prospection alimentaire (Fluhr et al., 2021), ce qui pourrait expliquer la contraction des domaines vitaux des vautours autour de certains secteurs, avec une densité de placettes plus importante (Monsarrat et al., 2013). Selon la théorie et les études de simulation sur les stratégies de recherche, il serait plus avantageux pour un vautour d'utiliser sa mémoire et sa connaissance des placettes lorsque la prévisibilité des carcasses augmente (Deygout et al., 2010; Fluhr et al., 2017; Riotte-Lambert & Matthiopoulos, 2020). Ceci pourrait aboutir à des comportements beaucoup plus stéréotypés, de façon à minimiser la durée et la distance de leurs trajets quotidiens et maximiser leur probabilité de trouver des carcasses et donc d'augmenter leurs gains énergétiques. Ainsi, la poursuite de l'exploration des données radar en incluant la période hivernale me permettrait peut-être de quantifier une diminution de l'occurrence de la stratégie en réseau, qui pourrait être un indice de changement de comportement en fonction de la disponibilité alimentaire.

L'utilisation des sources d'information pour les prises de décision en vol, ainsi que les stratégies de recherche alimentaire, pourraient être influencée aussi par la personnalité des individus. La personnalité se définit au sens large comme des différences constantes et répétables entre individus dans un trait de comportement et impose ainsi des limites au comportement individuel (Dall et al., 2004). Classiquement, les études de personnalité

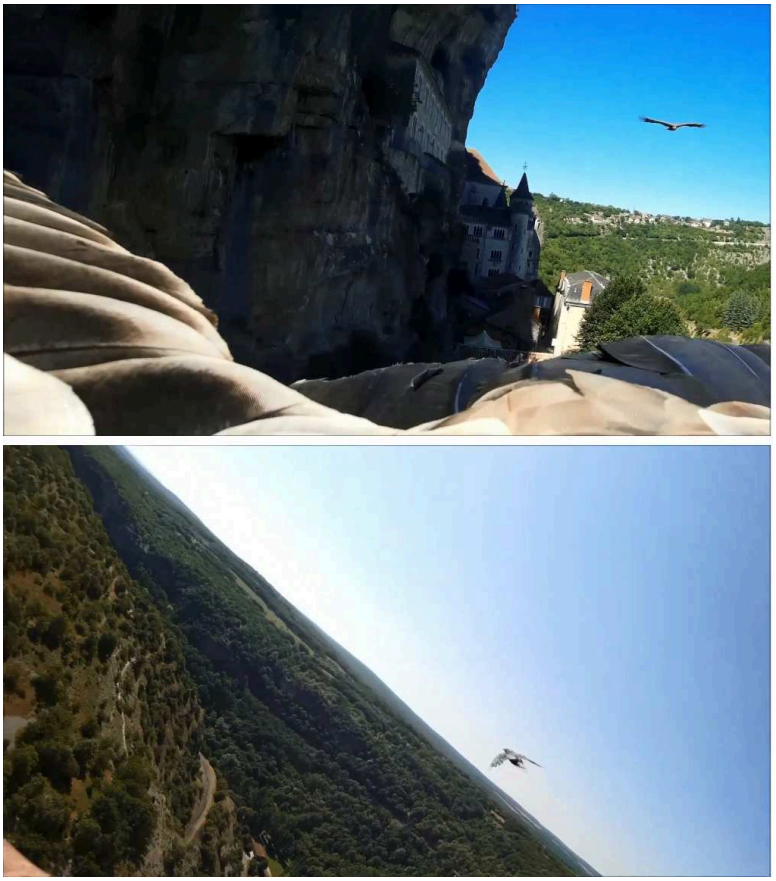

Figure VII.1: Images d'une caméra embarquée sur un vautour fauve du Rocher des Aigle. Dans la photographie du haut, l'individu qui porte la caméra est suivi par un congénère. Dans l'image du bas on observe un choucas des tours (*Coloeus monedula*).
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s'inscrivent dans un continuum de courageux à timide (« bold - shy »), dans lequel le courage, un trait de personnalité mesurant les réponses des animaux dans des contextes nouveaux (Sih et al., 2004; Sloan Wilson et al., 1994), est corrélé à de nombreux aspects du comportement. Par exemple, les animaux plus courageux prennent plus de risques (Montiglio et al., 2018; Réale et al., 2010), sont plus compétitifs (Patrick & Weimerskirch, 2014; Webster et al., 2009), ont tendance à mener le groupe lors des déplacements (Kurvers et al., 2009; Sasaki et al., 2018) et moins utiliser les informations sociales (Kurvers et al., 2010) que leurs homologues plus timides. Des observations chez les passereaux montrent que seuls les groupes contenant diverses personnalités présentaient à la fois une bonne cohésion de groupe et une exploration efficace du milieu à la recherche de nourriture (Aplin et al., 2014). Ainsi il semblerait qu'une mosaïque de personnalités soit nécessaire pour que l'ensemble bénéficie des avantages liés à la vie en groupe. Lors d'expérience d'exploration dans une volière inconnue, ou de test de néophobie (présentation d'un nouvel objet), j'ai constaté de nettes différences entre les individus du groupe de vautours captifs du Rocher des Aigles (voir annexe 6). En raison de l'épidémie d'influenza aviaire de 2022, je n'ai pas pu reproduire les expériences d'assez nombreuses fois pour estimer la répétabilité des différences

comportementales observées, comme indices d'une certaine personnalité, pour l'inclure dans mes analyses. Il serait intéressant de poursuivre cette voie afin de mieux comprendre comment la personnalité affecte les prises de décision en vol, l'exploration du paysage et potentiellement la découverte des carcasses chez les vautours.

Alors que la socialité est une caractéristique fondamentale du comportement de vol du vautour fauve, je n'ai pas pu prendre en compte cette caractéristique dans l'étude des comportements d'évitement des centrales éoliennes. Bien que l'avènement de balises GPS miniaturisées ait permis d'énormes progrès dans le suivi du déplacement des oiseaux, elles ne peuvent enregistrer que les comportements des individus sur lesquelles elles sont posées, et ignorent ainsi les comportements ou la présence de congénères alentour. Dans les Causses, où j'ai mené l'étude, une trentaine d'individus sont équipés de balises GPS, ce qui représente moins de 2% de la population de vautours fauves présente dans la région. Il est donc fort probable que les oiseaux dont j'ai récupéré les trajets au sein des centrales éoliennes étaient entourés d'autres individus sur lesquels je n'ai aucune information. L'attention portée aux congénères, notamment pour récupérer des indices de disponibilité de thermiques ou de carcasses, pourrait représenter un facteur de risque de collision supplémentaire. Dans les cas où la population est trop grande pour que l'ensemble des individus soient équipés de GPS, l'utilisation de radar faciliterait l'étude de l'influence de la socialité sur les comportements d'évitement. Il permettrait d'obtenir non seulement un suivi de l'ensemble des vautours en vol simultanément, mais plus largement de la communauté aviaire dans son ensemble et donc de mieux comprendre l'influence du comportements des individus alentour sur l'individu focal. L'utilisation de cette technologie radar pour des études d'évitement d'éolienne n'est pas nouvelle, par exemple chez les oies (Plonczkier & Simms, 2012), en revanche l'utilisation d'outil de machine learning pour différencier les espèces pourrait permettre d'étudier les réponses à l'échelle spécifique et ce depuis un unique jeu de donnée.

VII.4. Conclusion

À travers ce travail de thèse, il apparaît que les vautours fauves utilisent l'information sociale à différentes échelles : pour décider de leur prochain « pas » lors des déplacements, jusque dans leur stratégie de prospection alimentaire. Pour accéder à ces informations, au moment où celles-ci sont les plus pertinentes et utiles, il leur est nécessaire de maintenir une certaine cohésion avec leurs congénères créant *de facto* une barrière sociale empêchant les individus de trop s'éloigner (Armansin et al., 2020).

Étudier l'influence de la socialité sur les déplacements et les stratégies de prospection des vautours fauves nécessite de faire face à au moins deux grands défis : dans le monde des vautours, « pas trop s'éloigner » peut quand même se traduire par « plusieurs kilomètres », ce que nous humains ne sommes pas toujours capables de percevoir aisément, et « socialité » se traduit dans les Causses par des colonies regroupant plus de 2000 individus au total. Dans les différentes études présentées dans cette thèse, j'ai utilisé deux technologies, le suivi par GPS et par radar, et j'ai travaillé aussi bien avec des oiseaux captifs que sauvages, afin de répondre à ces problématiques. Alors que les ornithologues utilisent les radars depuis les années 1980,

essentiellement pour cartographier les voies migratoires des oiseaux (Gauthreaux & Belser, 2003), l'utilisation de cette technologie pour l'étude des comportements de recherche collectifs est relativement novatrice. Elle m'a permis notamment de révéler des patrons de déplacement qu'aucun outil à ce jour n'avait pu renseigner.

L'utilisation de balises GPS sur un groupe restreint d'oiseaux provenant d'un parc zoologique, leur offrant des conditions de vol libre en milieu naturel, m'a permis d'étudier l'effet de la présence de congénères sur les décisions de déplacement, une étude quasi-impossible à mener sur des vautours sauvages. Ces petits mouchards posés sur leurs dos, permettent aussi de mieux comprendre comment les oiseaux sauvages font face aux menaces présentes dans leur environnement. Et pour finir, c'est bien parce que nous pouvons suivre les déplacements des oiseaux, que nous pouvons détecter des arrêts anormaux de ces déplacements. C'est au départ cette observation opportuniste, rendue possible uniquement parce qu'il existe un programme de suivi GPS à long terme, que nous avons pu découvrir et quantifier les symptômes comportementaux de l'infection par la grippe aviaire chez les vautours. Ainsi, par l'ensemble de ce travail, je met en lumière la complémentarité des expériences en captivité, et de l'observation d'oiseaux sauvages, et ce à l'aide de technologies adaptées pour répondre à des questions tant fondamentales qu'appliquées.

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Annexes

Annexe 1. Informations supplémentaires : chapitre III

ESM01: Sensitivity analysis

To assess the robustness of our inference to variability in the social composition of the group and flight conditions between years and other "arbitrary" analytical decisions, we repeated the analysis based on different choices.

Drivers of social information used in movement decisions were investigated on all data combined to increase sample size. Yet, we evaluated the effect of years by refitting the full model structure on 2021 and 2022 data separately.

To study the drivers of thermal selection, we investigated the influence of social bond strength between individuals on thermal choice. Social bond strength was calculated considering spatial proximity on perches (≤ 1.55 m) between individuals as a sign for social bond. We repeated the model fit (see main text, Drivers of thermal updraft selection) using a distance threshold of 1.30 m (half the average wingspan of griffon vultures, [103]), and 1 m.

Furthermore, in the main text, to analyse thermal updraft choices, we considered all choices independently of whether vultures had to choose between thermals with and potentially without conspecifics. To verify whether the "presence" only of conspecifics influenced the choice, we repeated the analysis considering only choice events implying that currently available thermal updrafts were all used by conspecifics.

All these investigations revealed high robustness of our inference (Figure S5-7, Table S2-4). Therefore, we presented in main text the models which were the most complete and based on the most parsimonious rationale.

Supplementary Video 1 is accessible with scripts at :

https://github.com/YohanSassi/UpdraftsDecisions

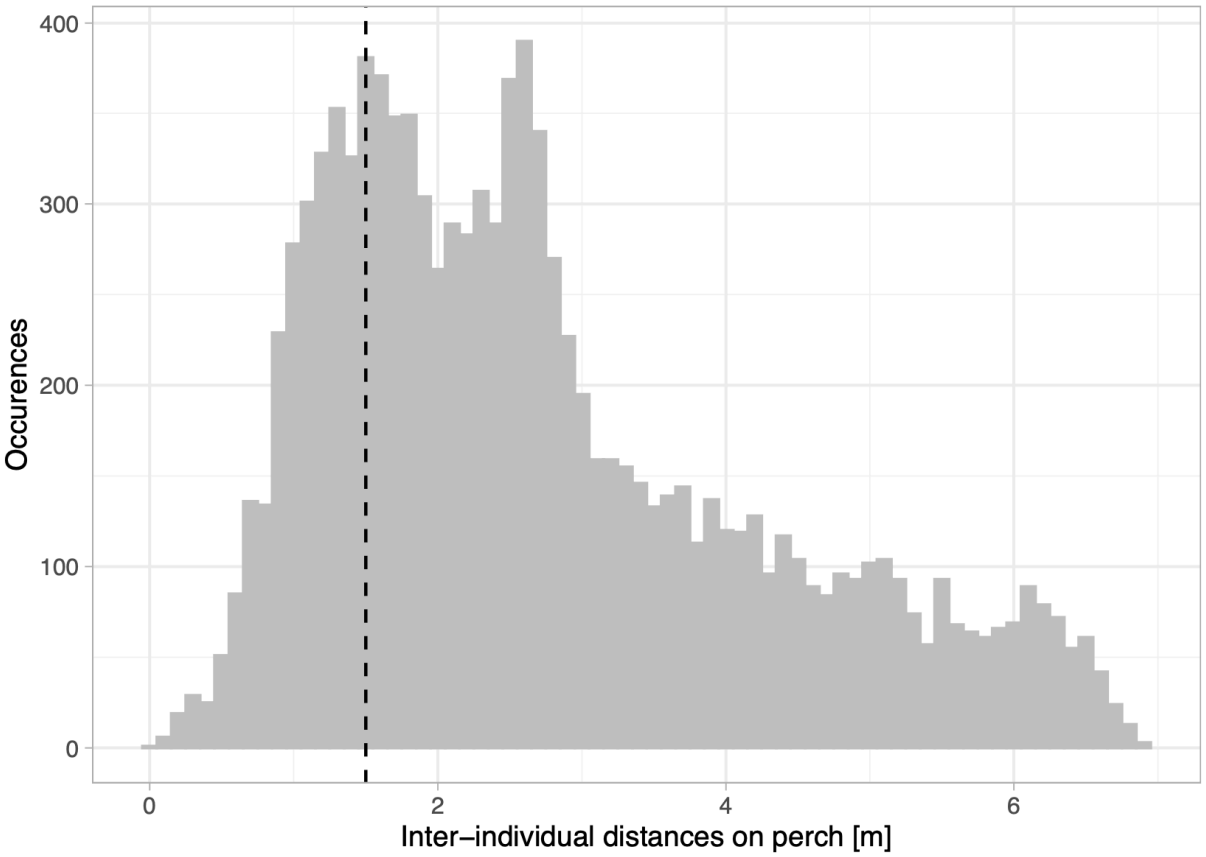


Figure S1. Distribution of the Euclidean inter-individual distances between birds on perches. Distances have been measured based on pictures taken in the wintering aviary. Every bin corresponds to 10 cm. The vertical black dotted line represents a distance of 1.55 m.

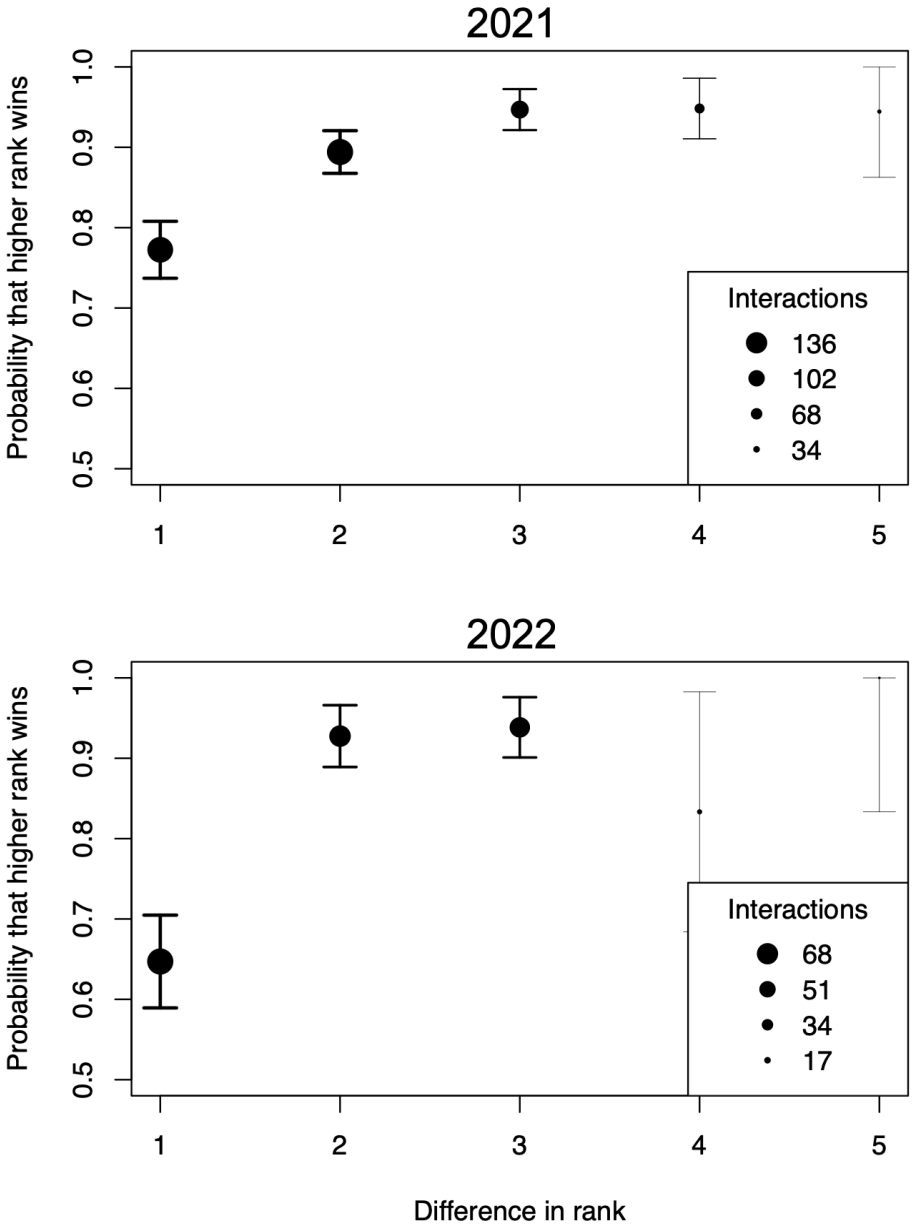


Figure S2. Dominance hierarchy steepness in vulture groups. Points represent the probability that the higher ranked individual wins an agonistic interaction as a function of the difference in rank. The size of the point is relative to the sample size. Segments give the 95% confidence interval.

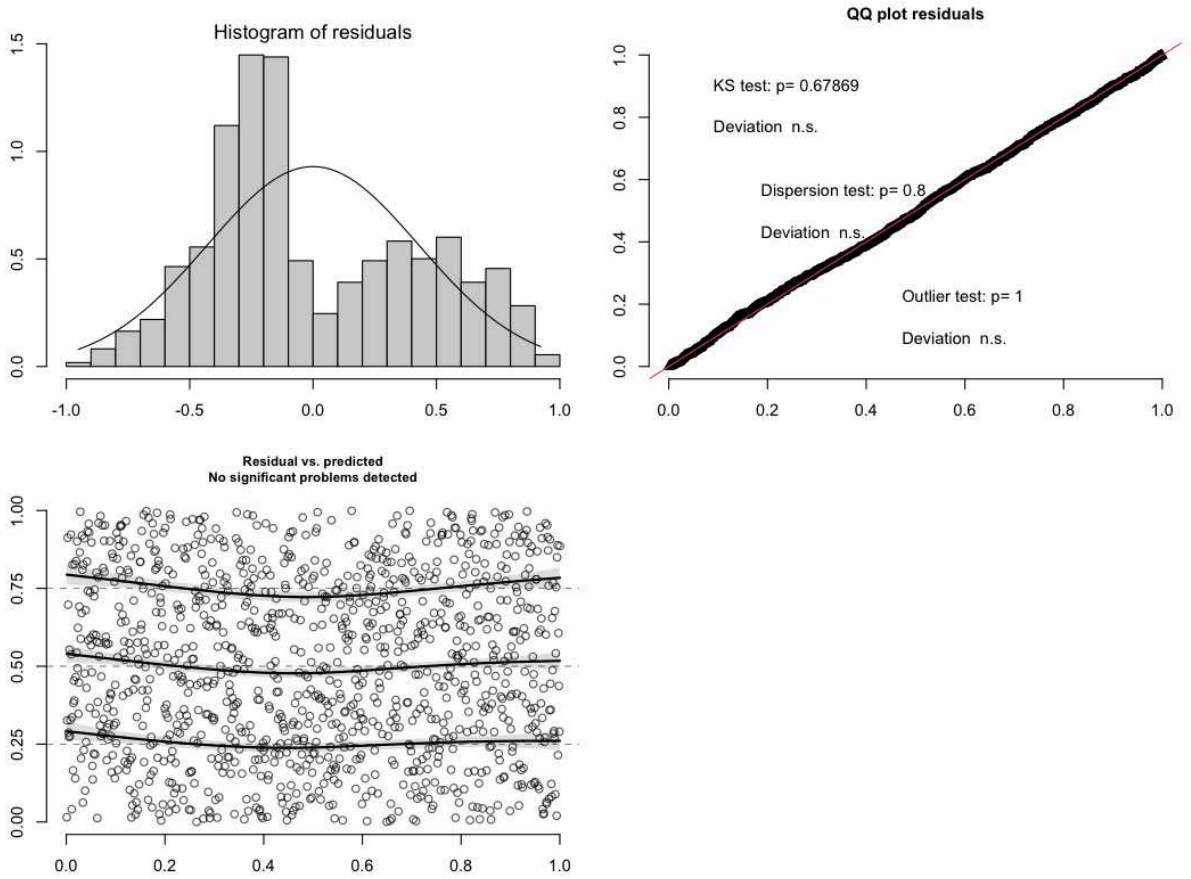


Figure S3. Diagnostic plot of the model investigating the drivers of social information use.

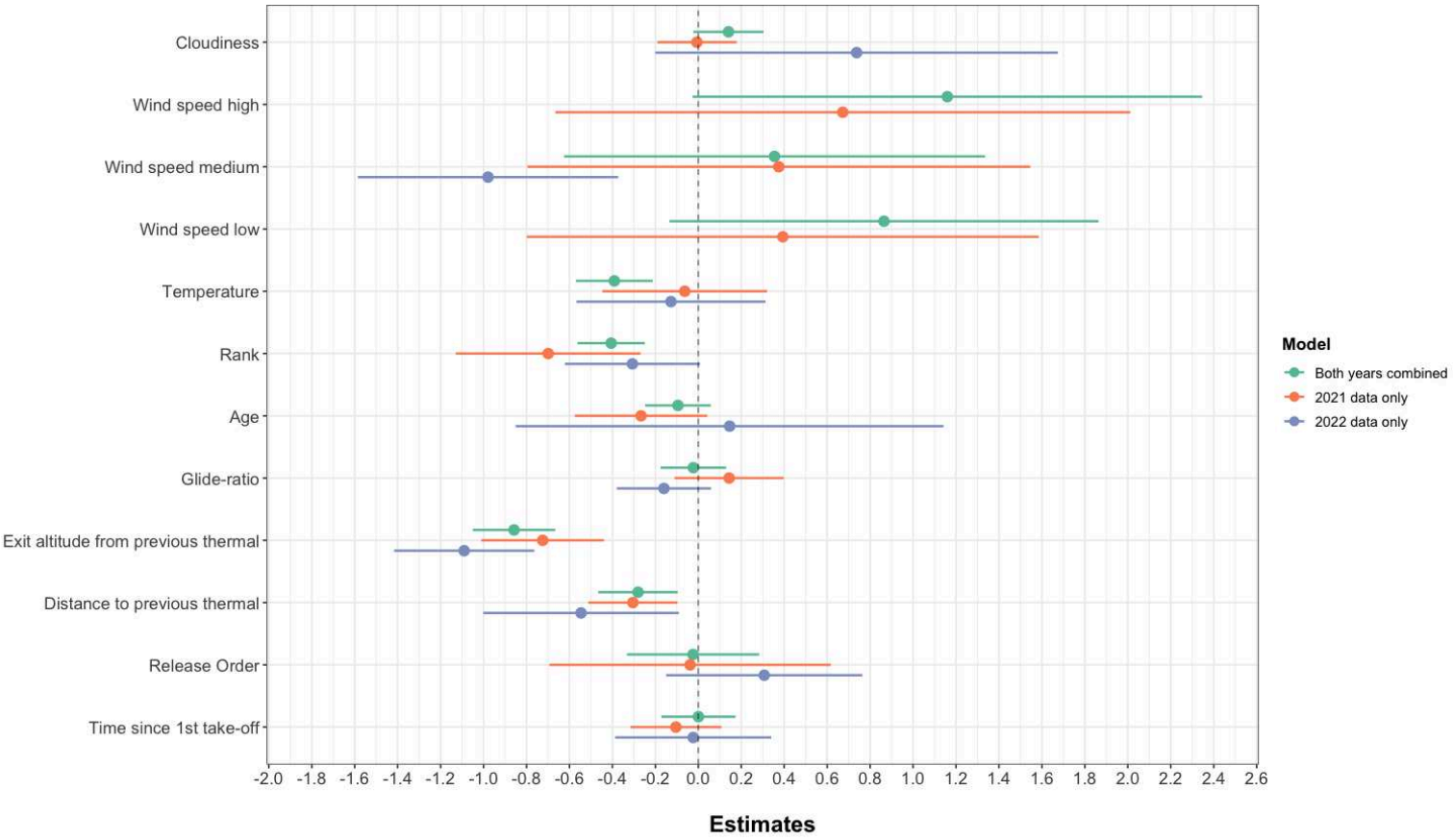


Figure S4. Estimates of models investigating the drivers of thermal discovery. Rows correspond to each predictor. Each point represents the (standardised) estimate value. Segments give the associated 95% confidence intervals. Models were fitted considering data of both years (green), only 2021 (orange) or only 2022 (blue).

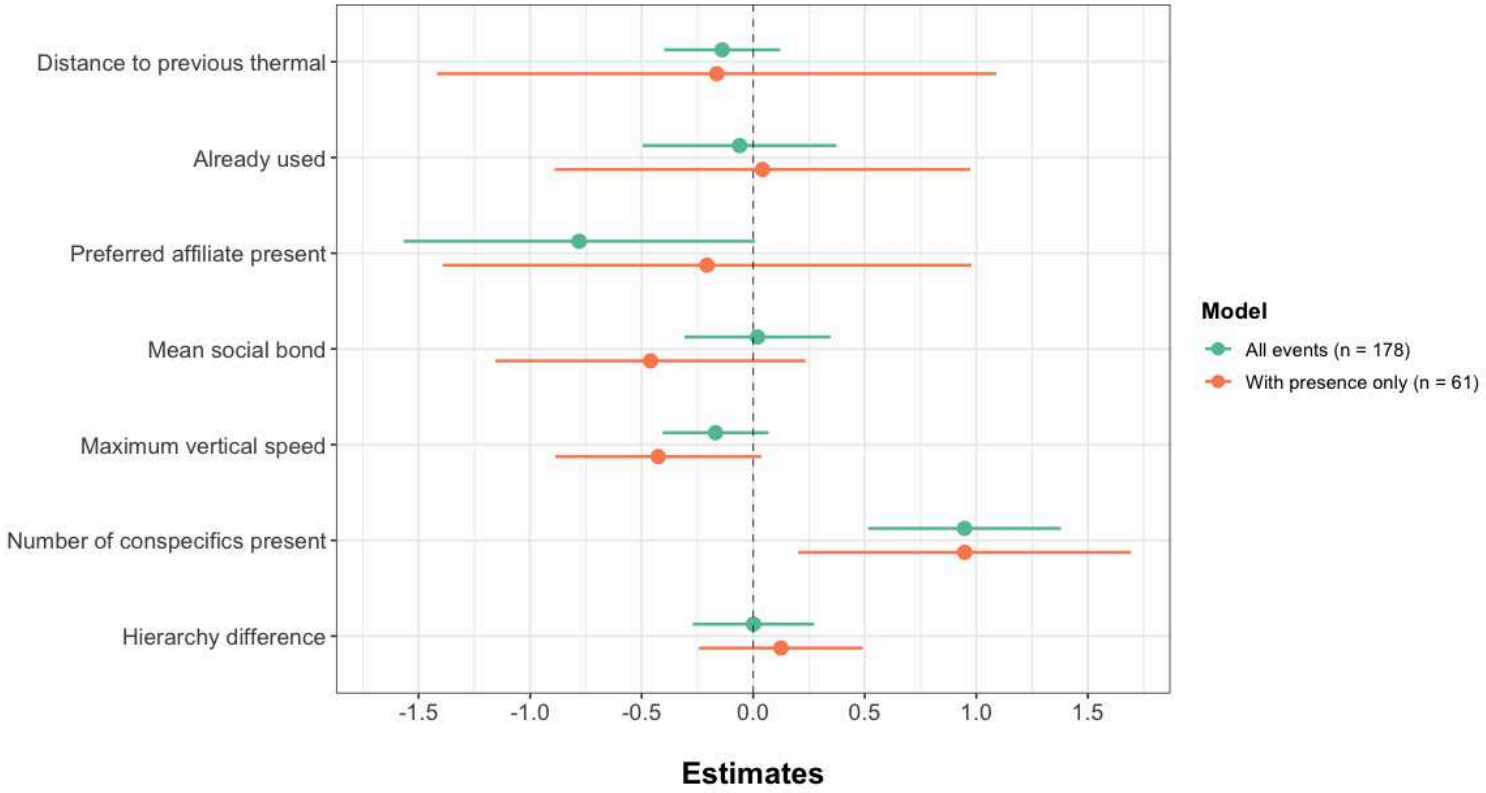


Figure S5. Estimates of models investigating the drivers of thermal selection. Rows correspond to each predictor. Each point represents the (standardised) estimate value. Segments give the associated 95% confidence intervals. "All events" refers to the model considering decision events where available thermals previously used but potentially empty at time of choice were considered. "With presence only" refers to the model focusing on decision events where vultures had to choose only between thermals currently used by conspecifics.

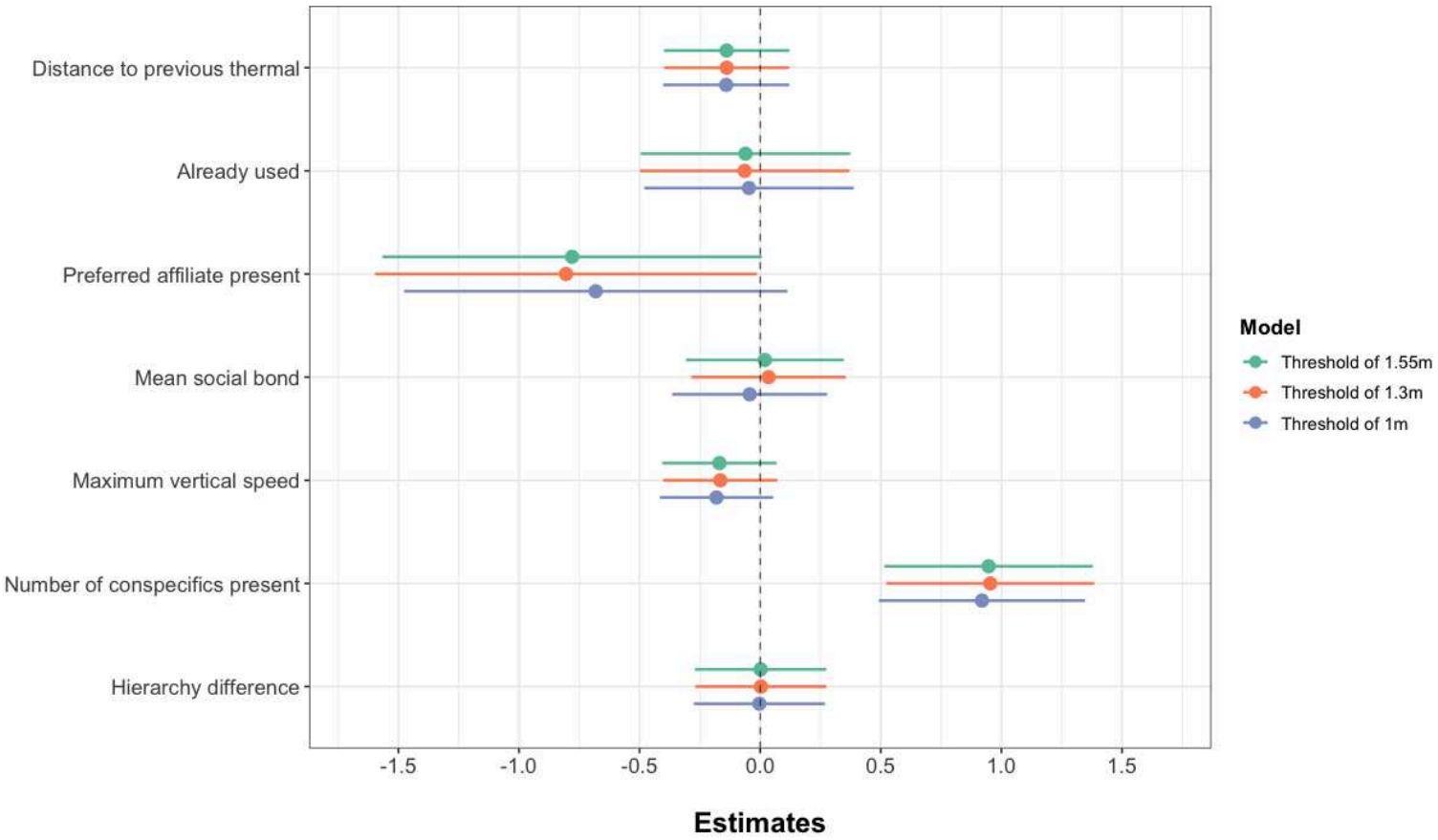


Figure S6. Estimates of models investigating the drivers of thermal selection. Rows correspond to each predictor. Each point represents the (standardised) estimate value. Segments give the associated 95% confidence intervals. “Threshold 1.55m" refers to the model considering an inter-individual distance threshold of 1.55m in the estimation of social bonds, which is the threshold considered in the analysis. The other levels are part of the sensitivity analysis.

Table S1. Summary table of vultures under study. For ranks, (-) means that for the considered year the rank of the individual was not estimated. The frequency of socially informed thermal use corresponds to the percentage of thermals used by each individual that was previously discovered by a conspecific.

Individuals	Species	Sex	Age	Year of presence	Rank (in 2021 / 2022)	Frequency of socially informed thermal use	Number of thermalling events
Henry	*G. fulvus*	F	25	2021	3 / -	0.654	78
Gregoire	*G. fulvus*	M	11	2021	1 / -	0.716	81
Hercule	*G. fulvus*	F	10	2022	- / 4	0.667	27
Kazimir	*G. fulvus*	M	8	2021 / 2022	6 / 6	0.521	190
Bulma	*G. fulvus*	F	8	2021 / 2022	4 / 3	0.652	138
Kirikou	*G. rueppelli*	F	8	2021 / 2022	5 / 5	0.529	291
Leon	*G. fulvus*	M	6	2021 / 2022	2 / 2	0.634	246
Mathilda	*G. fulvus*	F	4	2022	- / 1	0.702	47

Table S2. Outputs of models investigating the drivers of social information use. Estimates for continuous variables are scaled and provided with their 95% confidence intervals (95% CI), hence can be used as a dimensionless effect size. For the categorical predictor wind speed, the level without wind (i.e. wind speed null) is included in the intercept. ID gives the percentage of variance explained by the individual names (random effect), with N_{ID} the number of individuals considered. (-) indicates missing data preventing estimation of the considered parameters. Scaled variables are indicated by an asterisk.

	Use of already discovered thermal								
	Both year combined			*2021 data*			*2022 data*		
Predictors	*Estimates*	*95% CI*	*p*	*Estimates*	*95% CI*	*p*	*Estimates*	*95% CI*	*p*
(Intercept)	-0.24	[-1.18, 0.71]	-	0.61	[-0.54, 1.77]	-	0.52	[-0.40, 1.44]	-
Cloudiness *	0.14	[-0.02, 0.30]	0.089	-0.01	[-0.19, 0.18]	0.947	0.74	[-0.20, 1.67]	0.120
Wind speed high	1.16	[-0.03, 2.35]		0.67	[-0.67, 2.01]		-	-	
Wind speed medium	0.35	[-0.63, 1.34]	**0.011**	0.37	[-0.80, 1.55]	0.792	-0.98	[-1.59, -0.37]	**0.001**
Wind speed low	0.86	[-0.13, 1.86]		0.39	[-0.80, 1.59]		-	-	
Temperature *	-0.39	[-0.57, -0.21]	**<0.001**	-0.06	[-0.45, 0.32]	0.747	-0.13	[-0.57, 0.31]	0.570
Dominance rank *	-0.41	[-0.56, -0.25]	**0.003**	-0.70	[-1.13, -0.27]	**0.017**	-0.31	[-0.62, 0.01]	0.054
Age *	-0.09	[-0.25, 0.06]	0.247	-0.27	[-0.58, 0.04]	0.134	0.15	[-0.85, 1.14]	0.774
Glide-ratio *	-0.02	[-0.18, 0.13]	0.767	0.14	[-0.11, 0.40]	0.266	-0.16	[-0.38, 0.06]	0.158

Exit altitude from previous thermal *	-0.86	[-1.06, -0.66]	**<0.001**	-0.72	[-1.01, -0.44]	**<0.001**	-1.09	[-1.42, -0.76]	**<0.001**
Distance to previous thermal *	-0.28	[-0.47, -0.10]	**0.002**	-0.30	[-0.51, -0.10]	**0.003**	-0.55	[-1.00, -0.09]	**0.012**
Release order [2]	-0.02	[-0.33, 0.28]	0.875	-0.04	[-0.69, 0.62]	0.908	0.31	[-0.15, 0.76]	0.186
Time since 1st take-off	0.00	[0.17, 0.17]	0.994	-0.10	[-0.32, 0.11]	0.339	-0.02	[-0.39, 0.34]	0.898
Random Effects									
ID	0.00			0.18			0.00		
N_{ID}	8			6			6		
Observations	1098			520			578		
Marginal R^2 / Conditional R^2	0.304 / -			0.269 / 0.308			0.406 / -		
** Mean + SD prior to scaling*									
Cloudiness	1.07 + 1.73			1.98 + 2.13			0.24 + 0.43		
Temperature	25.43 + 4.14			22.00 + 2.86			28.50 + 2.22		
Dominance rank	3.66 + 1.72			3.55 + 1.76			3.75 + 1.67		
Age	8.86 + 4.71			10.60 + 6.23			7.28 + 1.40		
Glide-ratio	11.68 + 4.05			12.40 + 4.21			11.10 + 3.80		
Exit altitude from previous thermal	463.81 + 250.78			448.13 + 241.39			477.91 + 258.33		
Distance to previous thermal	653.11 + 932.68			683.40 + 1070.37			625.86 + 788.52		

Table S3. Outputs of models investigating the drivers thermal selection. Estimates for continuous variables are scaled and provided with their 95% confidence intervals (95% CI), hence can be used as a dimensionless effect size. "All events" refers to the model considering decision events where available thermals previously used but potentially empty at time of choice while "Presence only" indicates the model focusing on decision events where vultures had to choose only between thermals currently used by conspecifics, with their respective sample size in brackets. Scaled variables are indicated by an asterisk.

	All events (N = 178)			*Presence only (N = 61)*		
Predictors	*Estimates*	*95% CI*	*p*	*Estimates*	*95% CI*	*p*
Distance to previous thermal *	-0.14	[-0.40, 0.12]	0.295	-0.16	[-1.42, 1.08]	0.798
Thermal already used	-0.06	[-0.49, 0.37]	0.784	0.04	[-0.90, 0.96]	0.931
Preferred affiliate present	-0.78	[-1.56, 0.007]	0.052	-0.21	[-1.37, 1.00]	0.732
Mean social bond *	0.02	[-0.31, 0.35]	0.907	-0.46	[-1.14, 0.24]	0.194
Maximum vertical speed *	-0.17	[-0.40, 0.07]	0.163	-0.42	[-0.87, 0.05]	0.071
Number of conspecific present *	0.95	[0.51, 1.38]	**<0.001**	0.95	[0.20, 1.68]	**0.013**
Hierarchy difference *	-0.001	[-0.27, 0.27]	0.991	0.12	[-0.25, 0.48]	0.506
** Mean + SD prior to scaling*						
Distance to previous thermal	754.81 + 1220.90			562.49 + 991.70		
Mean social bond	0.13 + 0.09			0.13 + 0.09		
Maximum vertical speed	2.57 + 0.94			2.42 + 0.91		
Group size	0.73 + 0.83			1.16 + 0.79		
Hierarchy difference	- 2.34 + 27.78			- 3.03 + 39.93		

Table S4. Outputs of models investigating the drivers of social information use. Estimates for continuous variables are scaled and provided with their 95% confidence intervals (95% CI), hence can be used as a dimensionless effect size. Scaled variables are indicated by an asterisk

	Threshold of 1.55 m			*Threshold of 1.30 m*			*Threshold of 1 m*		
Predictors	*Estimates*	*95% CI*	*p*	*Estimates*	*95% CI*	*p*	*Estimates*	*95% CI*	*p*
Distance to previous thermal *	-0.14	[-0.40, 0.12]	0.295	-0.14	[-0.40, 0.12]	0.294	-0.14	[-0.40, 0.12]	0.290
Thermal already used	-0.06	[-0.49, 0.37]	0.784	-0.06	[-0.50, 0.37]	0.770	-0.04	[-0.48, 0.39]	0.833
Preferred affiliate present	-0.78	[-1.56, 0.007]	0.052	-0.80	[-1.59, -0.01]	**0.046**	-0.68	[-1.48, 0.11]	0.093
Mean social bond *	0.02	[-0.31, 0.35]	0.907	0.03	[-0.28, 0.35]	0.831	-0.04	[-0.36, 0.28]	0.791
Maximum vertical speed *	-0.17	[-0.40, 0.07]	0.163	-0.16	[-0.40, 0.07]	0.172	-0.18	[-0.42, 0.05]	0.130
Group size *	0.95	[0.51, 1.38]	**<0.001**	0.95	[0.52, 1.38]	**<0.001**	0.92	[0.49, 1.34]	**<0.001**
Hierarchy difference *	-0.001	[-0.27, 0.27]	0.991	0.003	[-0.27, 0.27]	0.984	-0.003	[-0.27, 0.27]	0.980
** Mean + SD prior to scaling*									
Distance to previous thermal	754.81 + 1220.90			754.81 + 1220.90			754.81 + 1220.90		
Mean social bond	0.13 + 0.09			0.13 + 0.10			0.12 + 0.10		
Maximum vertical speed	2.57 + 0.94			2.57 + 0.94			2.57 + 0.94		
Group size	0.73 + 0.83			0.73 + 0.83			0.73 + 0.83		
Hierarchy difference	- 2.34 + 27.78			- 2.34 + 27.78			- 2.34 + 27.78		

Annexe 2. Informations supplémentaires : chapitre IV

ESM01 : List of track characteristics used for random forest classification procedure

The starting time, the track duration, the proportion of missing points, the total number of point, the cumulative distance, the distance between first and last point, the ratio of cumulative distance over absolute distance between starting and ending points of the track (i.e. sinuosity), the total angle turned, the number of loop to the left, to the right, the proportion between both and the total number of loop detected in the track. The minimum, maximum, median, mean and standard deviation of tracks' ground-speed, as well as the speed between first and last point of the track. In addition, we used the mean with the standard deviation of : averaged echoes' area, averaged distance to the radar, averaged echoes' intensity and the averaged maximal echoes' intensity.

Note that we transformed the starting time in order to account for the diel cycle. Time was transformed between 0 and 1, the interval [0 0.5] being for night hours, and between [0.5 and 1] for daytimes irrespective of Day and night duration. Thus, this new time is not affected by the season and varying day length.

Movies could be found in the repository "VulturesRadar" of my GitHub account (YohanSassi) : https://github.com/YohanSassi/VulturesRadar

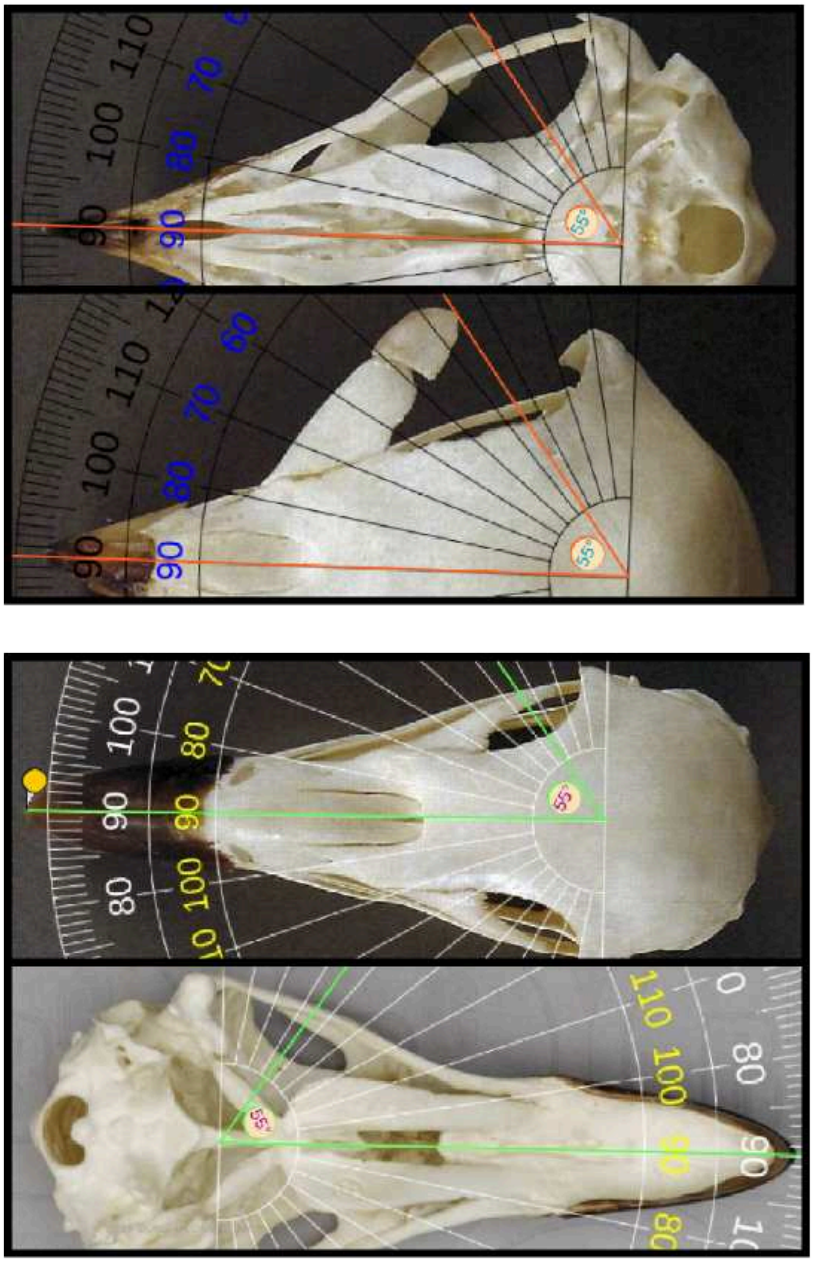


Figure S1 : Estimation of optical axis angle. The upper part shows the estimation of the optical axis angle on a skull of a Short-toed eagle (*Circaetus gallicus*). The lower part is similar, but on a skull of eurasian griffon vulture (*Gyps fulvus*). (source of image : SkullSite)

Annexe 3. Informations supplémentaires : chapitre V

ESM01 : Additional methods for utilisation distribution

To explore the space used by vultures at macro-scale we computed an in-flight utilisation distribution (UD). UDs were estimated using brownian random bridge-based kernels (Benhamou, 2011) using the ”BRB.D” function (to first estimate the coefficient of diffusion) and the “BRB" function (to estimate the UD) of the *adehabitatHR* R package (Calenge, 2006). Because of vultures’ mean flight speed of 50 km/h (Williams et al., 2018), we considered locations as independent (i.e. no inference of a bridge) when the time interval exceeded 1 h (parameter T_{max}). We considered static phases when vultures travelled a distance < 20 m during the 10 min interval (i.e. higher than GPS precision, parameter L_{min}) and used a smoothing parameter (h_{min}) of 500 m.

To explore the space used by vultures in wind farm geofences, we used the same method as described above but on rediscretised individual flights (with a constant step of 50 m). We changed the parameters as follows. We considered locations as independent (i.e. no inference of a bridge) when the time interval exceeded 30 s (parameter T_{max}) due to the high resolution tracking. We considered static phases when vultures travelled a distance < 20 m (i.e. higher than GPS precision, parameter L_{min}) and used a smoothing parameter (h_{min}) of 150 m. As the number of flights in the wind farms varied greatly between vultures (Table S1), the population UD was obtained here by previously weighting each individual 95% UD by the number of flights in the wind farm of interest.

ESM02: additional methods to assess validity of the rotational approach

The rotational procedure identified avoidance patterns accurately when we simulated 1000 tracks, each time with the following combination of parameters: a perceptual range (d) of 450 m and a turning angle (α) of 0°, 1° or 5° for the three first scenarios, respectively and d = 50 m with α = 5° for the last scenario. Specifically, for the two first scenarios in Montfrech, it did not detect any avoidance when α = 0°, but as soon as we simulated an avoidance with α = 1°, it accurately detected a significantly lower proportion of locations in buffers up to 450 m.

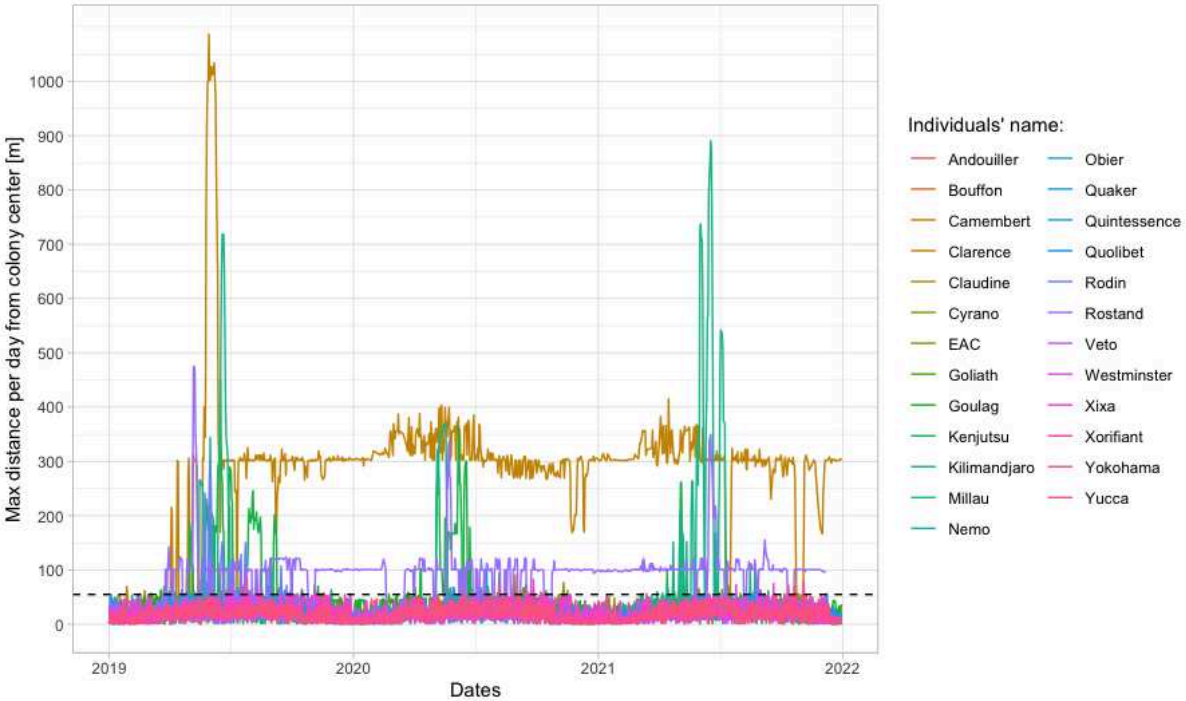


Fig. S1. Maximum daily distances from the centre of the colony reached by vultures between 2019 and 2021. A threshold of 55 km from the centre of the colony is highlighted by the horizontal black dotted line. Two individuals, Clarence and Rostand, mostly settled in Pyrenees and Ardeche respectively, > 100 km from the Causses, France and were discarded in the estimation of the mean maximum displacement from the centre colony reached daily by vultures.

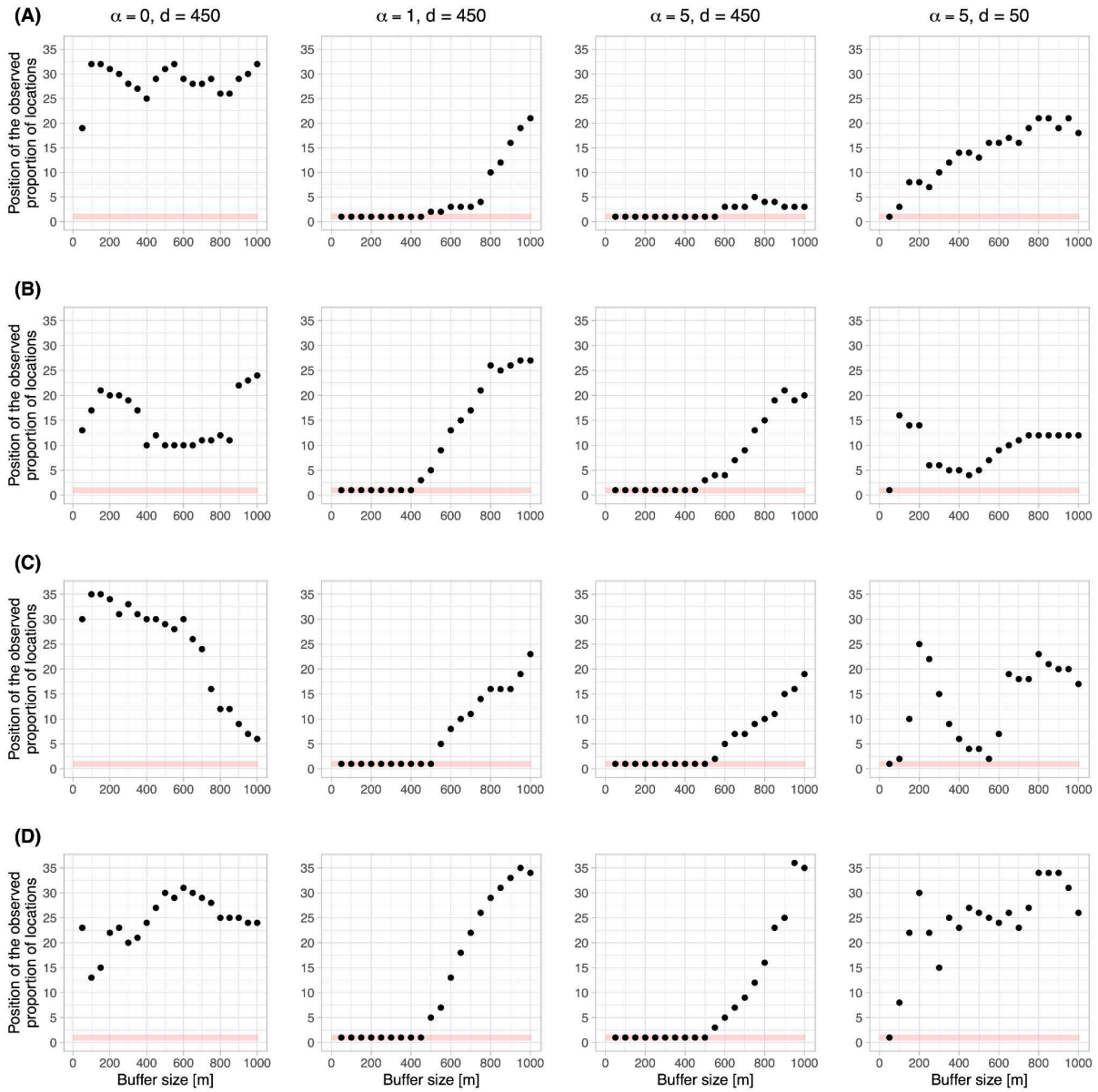


Fig. S2. Rotation analysis results on simulated tracks under four avoidance behaviour scenarii. Results are based on 1000 simulated tracks, each column representing a combination of turning angle (α) and perceptual range (*d*). Rows refers to simulations done in different wind farms (hence with different wind turbine locations and configuration): La Baume (A), Montfrech (B), Mas de Naï (C) and Saint Affrique (D). Dots represent the position of the observed percentage of location, among the 36 estimated values (*y*-axis) during the rotational analysis, for a given circular buffer around wind turbines (*x*-axis). The red rectangle highlights buffers for which the amount of locations observed is significantly lower than randomly expected.

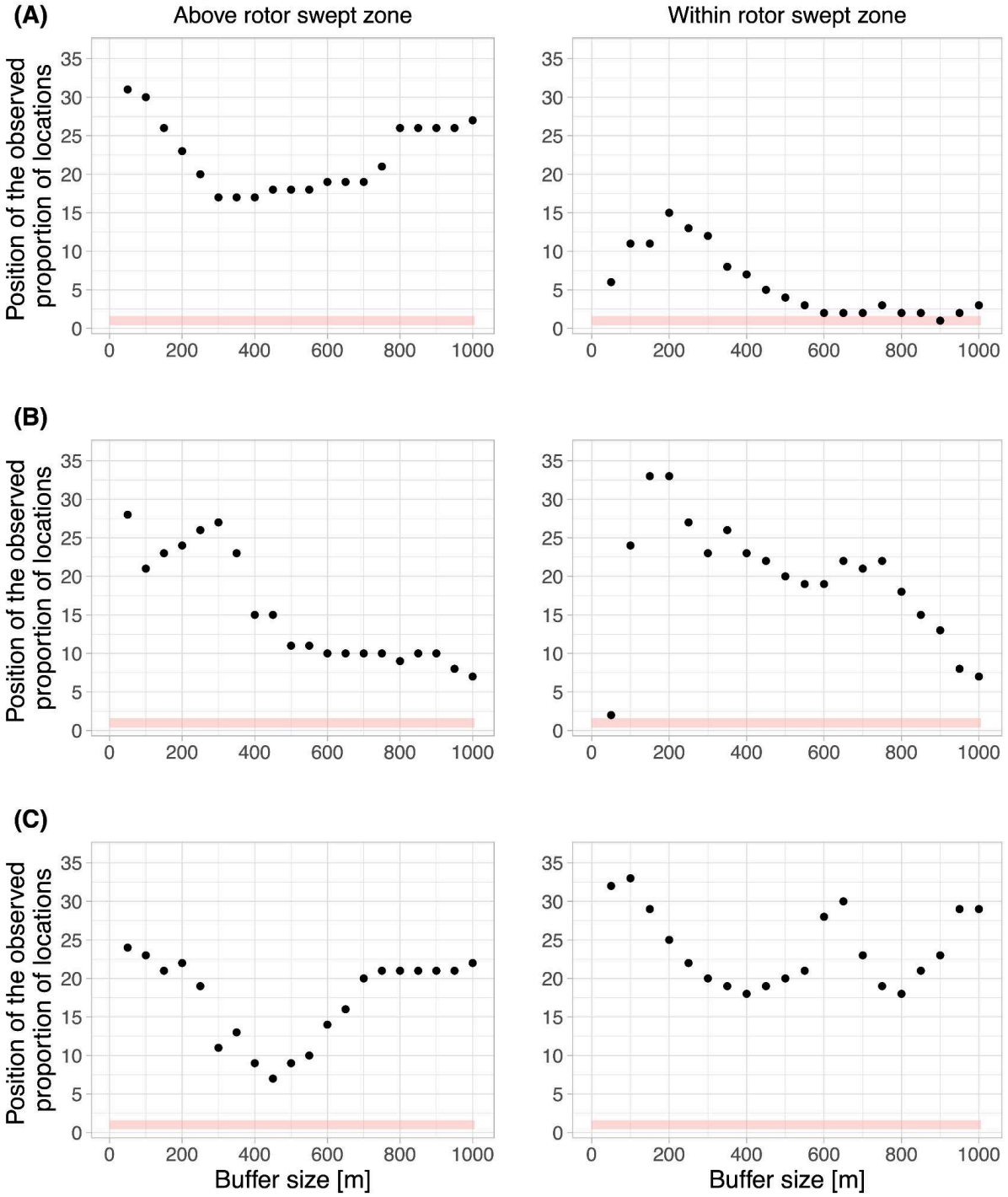


Fig. S3. Rotation analysis results for vulture flights above (left) or within (right) the rotor swept zone of La Baume (A), Mas de Naï (B) and Saint Affrique (C) wind farms. Dots represent the position of the observed percentage of location, among the 36 estimated values (*y*-axis) during the rotational analysis, for a given circular buffer around wind turbines (*x*-axis). The red rectangle highlights buffers for which the amount of locations observed is significantly lower than randomly expected.

Table S1. Vulture-level data collection summary. "Nb days of tracking" refers to the total number of days in which we had GPS data. The last four columns give the total number of flights that each individual did in each wind farm's geofence. These four wind farms were considered for meso-scale and micro-scale avoidance analysis (flights retained only if >10 consecutive GPS locations). Numbers in between brackets highlight the number of flights that entered the rotor swept zone. A "-" indicates that the individual did not cross the considered wind farm.

Vulture names	Nb days of tracking	Nb flights in La Baume	Nb flights in Montfrech	Nb flights in Mas de Naï	Nb flights in Saint Affrique
Andouiller	1095	15 (9)	-	1 (0)	-
Bouffon	1095	36 (19)	1 (0)	33 (6)	1 (0)
Camembert	681	-	16 (5)	-	-
Clarence	1095	5 (2)	1 (1)	4 (3)	-
Claudine	1095	46 (16)	67 (21)	3 (1)	45 (15)
Cyrano	1095	270 (127)	30 (7)	107 (46)	91 (42)
EAC	1095	311 (111)	36 (14)	80 (44)	74 (33)
Goliath	1095	9 (3)	5 (2)	-	1 (0)
Goulag	1095	45 (24)	-	88 (55)	-
Kilimandjaro	341	1 (0)	1 (0)	-	-
Millau	1095	11 (3)	4 (0)	11 (5)	1 (1)
Nemo	1095	90 (53)	-	17 (9)	18 (8)
Obier	870	3 (1)	-	-	-
Quaker	1095	108 (60)	-	4 (3)	-
Quintessence	1095	527 (252)	10 (5)	5 (3)	111 (55)
Quolibet	1095	99 (61)	1 (0)	16 (7)	-
Rodin	365	4 (1)	7 (4)	2 (1)	7 (1)
Rostand	1072	21 (6)	4 (0)	1 (0)	6 (1)
Veto	1095	2 (2)	-	-	-
Westminster	1095	-	2 (1)	1 (1)	-
Xixa	1095	80 (31)	21 (7)	89 (50)	98 (34)
Xorifiant	1095	81 (37)	-	17 (10)	2 (0)
Yokohama	1095	1 (0)	-	-	-
Yucca	1095	9 (5)	-	46 (20)	-
Kenjutsu	1095	19 (13)	1 (0)	4 (1)	1 (1)

Table S2. Wind farm-level data collection summary. “Max” and “Min rotor height” columns refer to the distance (in metres) between the ground and the tip of wind turbine blades. “Nb tot flights” column gives the total number of flights (flights retained only if > to 10 consecutive GPS locations) detected within the wind farm geofence. “Percentage of flights crossing the rotor-swept zone” counts the number of flights that happened (at least partially) in the rotor swept zone (i.e. between Min rotor height and Max rotor height + 15 m). “Percentage of locations above the rotor swept zone” informs about the percentage of GPS locations that were above the rotor swept zone.

Wind farm names	Nb turbines	Min rotor height	Max rotor height	Nb tot flights	Percentage of flights crossing the rotor swept zone	Percentage of locations above the rotor swept zone
La Baume - S1	6	25	125	1793	46.80	82.55
Montfrech - S2	4	30	110	207	32.84	84.70
Mas de Naï - S6	17	30	90	529	50.28	85.49
Saint Affrique - S7	6	35	125	456	42.07	86.80

Annexe 4. Informations supplémentaires : chapitre VI

Figure S1: Distribution of days of immobility of individual vultures during the years 2022, 2021, 2020 and 2019, related to Figure 3.

Each line represents the timeline (period 15 April to 30 May) for each individual, highlighting in red the periods of immobility (DDT < 10km longer than 2 consecutive days), assumed to be related to sickness or rainy weather. Data are from the same 21 adult vultures in the Causses and for 9 individuals in Aude in 2022 (highlighted in green). Shorter periods of immobility (1 or 2 days) are coloured in yellow. For each individual, the total number of days of immobility (Total immob. Days) and the breeding status on 30 May 2022 (O: ongoing in green; F: failed in red; NB: non-breeder in white) are indicated in the extreme right columns. Names of individuals who died during the period are in bold, identified with an asterisk and a grey line on the timeline after their death. The result of the HPAI test is indicated at the right of each individual concerned.

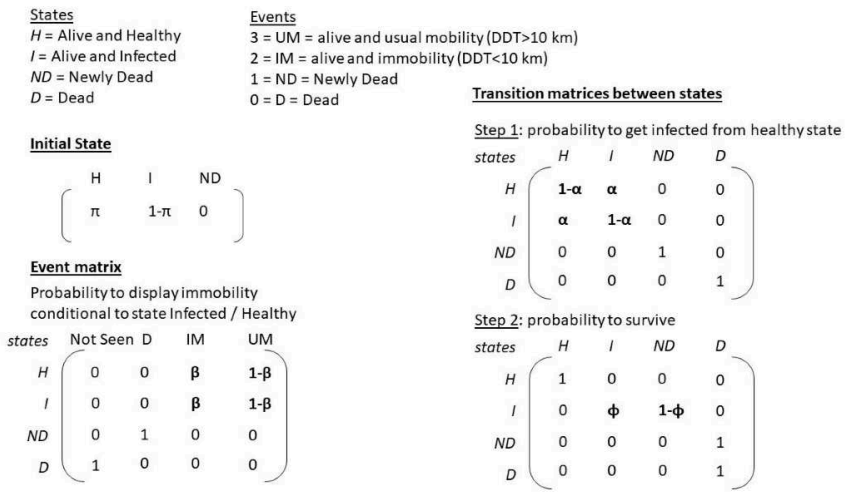


Figure S2: Description of the matrices of the multi-event model, related to STAR methods.

The initial state vector was set that all individuals started their history in a "Healthy" state, with probability $\pi = 1$. The first transition matrix (step 1) modelled the probability α of getting infected (i.e. the transition α_{HI} from state "Healthy" to state "Infected" and vice-versa α_{IH}) at every time step. The second transition matrix (step 2) modelled the survival probability φ (hence the transition from the state "Infected" to the state "Newly Dead", assuming that no individual from "Healthy" state could die in the dataset). The Event matrix estimated the probability β to observe an individual displaying immobility (IM, i.e. DDT<10 km) or usual mobility (UM; i.e. DDT>10 km), conditionally to its state ("Healthy" $\beta_{H\text{-}IM}$ or "Infected" $\beta_{I\text{-}IM}$).

		Breeding status			Comparison between breeding status		
Total number of days of	Overall	Ongoing reproduction	Failed breeder	Non-breeder	Kruskal-Wallis test	df	p
Immobility	7.95 ± 5.39 (21)	2.8 ± 2.39 (5)	7.56 ± 2.07 (9)	12.14 ± 6.67 (7)	10.27	2	0.006
Sickness	5.48 ± 4.26 (21)	5.0 ± 0.0 (1)	5.67 ± 2.0 (9)	8.43 ± 4.99 (7)	1.074	2	0.584

Table S1: Total number of days of immobility and sickness symptoms of vultures in the Causses in 2022, related to Figure 3

Summary statistics are reported as mean ± SD. Sickness symptoms are defined as periods of immobility lasting more than 2 days. The breeding status was estimated after the HPAI outbreak on 30 May 2022. At the right of the table, Kruskal-Wallis tests compare values between the three classes of breeding status. Sample size (number of individuals concerned) are indicated in brackets (note that for total number of days of sickness, there was only one bird with ongoing reproduction that showed symptoms of sickness, hence no SD for this category).

			Breeding status			Comparison between breeding status		
		overall	Ongoing reproduction	failed breeder	Non-breeder	fixed effects F test	df	p
	sample size (individuals)	21	5	9	7			
DDT (km)	before sickness	66.51 ± 46.24	75.79 ± 45.07	62.61 ± 47.46	54.73 ± 43.03	7.944	2,463	<0.001
	during sickness	3.71 ± 3.99	5.89 ± 3.71	3.91 ± 4.76	3.28 ± 3.13	1.48	2,113	0.232
	between sickness	35.71 ± 26.08	NA	36.29 ± 25.34	35.51 ± 26.63	0.009	1,53	0.925
	after sickness	60.07 ± 44.52	80.12 ± 43.00	59.56 ± 46.25	56.22 ± 45.65	3.274	2,259	0.039

Table S2: Daily travelled distance (DDT) according to period (before, during, between and after sickness) in the Causses in 2022, related to Figure 3

Summary statistics are reported as mean ± SD. The breeding status was estimated after the HPAI outbreak on 30 May 2022. At the right of the table, statistical tests compare values between the three classes of breeding status. At the bottom of the table, fixed effects tests from GLMM compare DDT values between each period and Bonferroni tests compare DDT before and during sickness.

type of determination	status	n individuals	n days in usual mobility (DDT>10 km)	n days of immobility (DDT<10 km)	total
RT-qPCR / serology	negative	2	84	8	92
	positive	3	47	24	71
behaviour (GPS)	not sick	3	133	5	138
	sick	13	469	129	598

Table S3: Comparison of the number of days of immobility (using threshold of DDT<10 km) and number of days with usual mobility (UM), between individuals in the Causses that had been tested positive or negative for HPAI (either using RT-qPCR or via antibody against H5 HPAI), and individuals that had been assigned as "sick" or "not sick" using their behaviour and prolonged immobility, related to Table 1

Among the individuals that could be tested using PCR or serology, the proportion of days of immobility was significantly larger in individuals with positive tests compared to those with negative tests ($Chi^2 = 16.01$, $p < 0.001$). Among individuals whose status was determined using behaviour (GPS), the proportion of days of immobility was significantly larger in individuals determined as sick ($Chi^2 = 24.26$, $p < 0.001$). These proportions were not different when comparing individuals determined as not sick by behaviour and negative test ($Chi^2 = 2.66$, $p = 0.103$), but significantly different also when comparing individuals determined as sick by behaviour and positive test ($Chi^2 = 5.38$, $p=0.025$).

Year	Daily cumulative rainfall	
	r	p
2019 April-May	0.350	0.017
2020 April-May	0.461	<0.001
2021 April-May	0.377	0.010
2022 April-May	0.349	0.017
2019 May	0.408	0.025
2020 May	0.515	0.004
2021 May	0.401	0.028
2022 May	**0.134**	**0.481**

Table S4 Correlations between the daily number of individuals immobile (defined as days where daily distance travelled <10 km) and daily cumulative rainfall (in mm) in the Causses, related to Figure 3

We studied correlations using non-parametric Spearman Rho tests for each year separately (between 2019 and 2022) during the period 15 April and 31 May (n = 46 days each year) and during the period 01-31 May (n = 31 days).

Model description	N param.	Deviance	QAIC	QAICc
Model 3 : 2 groups: sick vs not sick	9	961.890	979.890	980.028
Model 2 : 4 groups separated	15	956.661	986.661	987.030
Model 1 : all groups equals	5	983.287	993.287	993.332
Model 4 : 3 groups : test+, test- and not tested pooled	11	975.269	997.269	997.471

Table S5: Model selection of the joint-modelling, related to Table 1

Model selection based on QAICc determined a stronger support for model 3, where individuals tested HPAI positive (viro + and sero+) and individuals behaviourally inferred as sick were considered as belonging to one single group, and compared to another group that combined individuals tested HPAI negative and individuals behaviourally inferred as not sick.

Annexe 5. Vers un bridage des éoliennes sélectif et adapté en fonction des probabilités de présence des oiseaux ?

This is a manuscript still in preparation, likely to change substantially

The use of orographic updraft explains the occurrence of lesser kestrel in a wind power plant

Bartholus Lise [1]*, Sassi Yohan [1]*, Garcia Matthieu [2], Saulnier Nicolas [3], Pilard Philippe [4], Duriez Olivier [1]

1. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
2. Micro Entreprise Matthieu Garcia, Saint Pargoire, France
3. LPO Occitanie, Villeveyrac, France
4. LPO mission rapaces, Arles, France

* both authors contributed equally to the article

Abstract

While wind energy is being developed internationally as a way to reduce atmospheric carbon emissions, numerous studies show the negative impacts of such installations on biodiversity. Raptors following updrafts trajectories to glide and reduce their energy expenditure are among the main victims of wind turbine collisions. In this study, we examined what are the factors driving the use of a wind farm by lesser kestrels, frequent victims of collisions at this wind farm since 2006. As the Lesser Kestrel uses hovering and wind updrafts to locate its prey, we hypothesized that the falcons would be distributed accordingly to the distribution of orographic updrafts. Using telemetry tracking data collected since 2017 on 26 individuals, we built models explaining their use of the wind farm and predicting their presence on the site based on the availability of orographic updrafts, falcon's phenology and distance to turbines. We found that kestrel's presence was driven by the availability of orographic updrafts and the attractiveness of the wind farm was higher in May than in June or July. Orographic updrafts were good predictors for estimating kestrel probabilities inside the wind farm. These results allow identifying turbines where kestrel presence was more likely under certain wind conditions, in order to organize a selective curtailment of these turbines in order to prevent collisions.

Key-words: *Falco naumanni*; telemetry; collisions; wind farms; orographic updraft; hovering flight; spatial model; RSF; mitigation

1. Introduction

Renewable energies are massively deployed around the world and one of the most common is wind energy. However, wind turbines can have serious drawbacks: through collisions with rotor blades, or because of the displacement effect induced, wind turbines can negatively impact biodiversity and especially bats and birds (De Lucas & Perrow, 2017; Thaxter et al., 2017). While 13% of the bird species are threatened and their status are deteriorating in Europe (Birdlife International, 2022), a large-scale deployment of this technology is particularly concerning. In bats, mitigation measures commonly applied consist in a selective curtailment of turbines as soon as wind speed and air temperatures reach certain thresholds (Arnett & May, 2016; Richardson et al., 2021). In birds, so far, curtailment mostly consisted in stopping turbines during the period when a species of concern was present in the wind farm area, generally detected by an automated detection system (eg (McClure et al., 2018). For migratory species, the curtailment period could be the whole period of presence of the species (e.g. the breeding or migratory seasons) but its efficiency in reducing fatalities is debated (Smallwood & Bell, 2020). However such long-term curtailment is difficult to negotiate with wind farm operators because they lose money during all that period. More selective methods for curtailing turbines must be found for birds.

Raptors are among the main victims of collisions with wind turbines. Because of their slow demographic strategy, these additional adult mortalities can largely affect population dynamics (De Lucas & Perrow, 2017; Duriez et al., 2023; Eichhorn et al., 2012; Marques et al., 2014). Different parameters linked to their morphology, life-history traits and ecology can explain their vulnerability to collisions with rotor blades (Thaxter et al., 2017). Specifically, soaring-gliding raptors rely on wind assistance and updrafts to minimize energy costs of movements (Bohrer et al., 2012; Duerr et al., 2015; Shepard et al., 2013). The species-specific wing morphologies influence their ability to exploit such updrafts (Pennycuick, 2008; Videler, 2005). Because both soaring-gliding birds and wind developers look for the same resource, wind, conflicts arise when they exploit the same areas and come into contact. This is particularly true when wind farms are sited close to migratory bottlenecks or breeding colonies, creating aggregation sites (Martín et al., 2018; Villegas-Patraca et al., 2014).

Predicting bird space use is an important component for developing management and conservation strategies to limit collisions (Barrios & Rodríguez, 2004; Eichhorn et al., 2012; Hanssen et al., 2020). Modeling wind updrafts could allow us to identify where birds are more likely to occur and thus, to mitigate the risks of collision. Raptors can use two types of updrafts. Modeling their occurrence and strength remains challenging given the high temporal and spatial resolution of weather data needed and the high number of parameters influencing updraft occurrence and strength. Thermal updrafts are generated by solar radiations heating the surface, making bubbles of hot air to rise. Thermal updrafts thus depend on solar radiation, on the surface reflectance and on air density. These updrafts tend to form over flat terrain and are most efficiently used by birds when wind conditions are

weak (Akos et al., 2010; Leshem & Yom-Tov, 1996; Shamoun-Baranes et al., 2003). Orographic updrafts are formed when horizontal wind encounters a slope and is deviated upwards (Bohrer et al., 2012; Pennycuick, 2008). Orographic updrafts thus depend on wind angle (direction), wind speed and on the topography (slope and aspect) of the landscape deflecting wind upwards. They are more frequently used by birds at high wind speed and necessitate obstacles or significant slopes to be generated (Duerr et al., 2015; Shepard et al., 2013, 2016).

A method to map orographic updrafts according to Digital Elevation Models (DEM) had been developed to predict the migratory path that golden eagles (*Aquila chrysaetos)* that would preferentially choose to benefit from those updrafts and travel more efficiently (Brandes & Ombalski, 2004). This approach had been improved by adding the estimates of thermal updrafts, thus simulating the two sources of orographic and thermal updrafts (Bohrer et al., 2012). These estimates have been used efficiently to inform movement patterns of a range of soaring species such as the white stork (*Ciconia Ciconia)*, osprey (*Pandion haliaetus*), Western marsh harrier (*Circus aeruginosus*), Egyptian vulture (*Neophron percnopterus*) and short-toed eagle (*Circaetus gallicus*) (Flack et al., 2016; Mellone et al., 2012). In white-tailed eagles (*Haliaeetus albicilla)*, such modeling approach could efficiently predict the distribution of birds tracked by telemetry, based on the spatio-temporal distribution of updrafts, and map high-traffic areas of eagle in order to elaborate micrositing strategy of wind turbine settlement to reduce collision risks (Hanssen et al., 2020).

The lesser kestrel (*Falco naumanni),* a small soaring raptor, is known as one of the species most vulnerable to collisions with wind turbines (De Lucas et al., 2007; Duriez et al., 2023; Thaxter et al., 2017). Its hunting behavior, using hovering flight to locate prey, sometimes with the help of the wind to reduce their energy cost (Roselaar, 1980; Videler, 2005), could be a reason for this high collision rate. The largest French sub-population of lesser kestrel, located near Montpellier is living close to the Causse d'Aumelas, an area of scrubland rich in large insects, the main prey of lesser kestrels, and so, constitutes an important foraging area for this falcon (Pilard et al., 2021). In this area, a wind farm had been built between 2006 and 2014. As a result, 64 falcon corpses had been found at the bottom of wind turbines between 2011 and 2022. This high collision rate is directly responsible for the reduction in population growth rate (Duriez et al., 2023). Even after the deployment of Automatic Detection Systems (ADS) at all turbines in 2017 onwards, 5.8 ± 3.5 collisions are still recorded every year. It is therefore urgent to find alternative ways to strongly reduce this source of mortality.

Here we aimed at determining the environmental factors driving the use of the Aumelas Causse and the wind farm by lesser kestrels, in order to predict their spatio-temporal distribution. Such predictions would allow us to determine if particular environmental conditions may likely generate high collision risk. If this is true, mitigation strategies such as curtailing the wind turbines under specific conditions could be implemented, as is commonly done for bats (Arnett & May, 2016).

Lesser kestrels are known to regularly use thermal updrafts to commute between breeding and hunting areas, commonly reaching flight height of 150m above ground (Hernández-Pliego et al., 2015). Since lesser kestrels forage using hovering flight at height of 10 to 20 m above ground, they are likely rather search for orographic updrafts allowing birds to soar at a fairly low and stable altitude (Hernández-Pliego et al., 2017; Roselaar, 1980). Other wind hovering birds such as the common kestrel (*Falco tinnunculus)* have been observed reacting to changing winds to stay in a stable position (head and eyes on a steadily position to detect prey) and compensate for wind deviations or speed increase (Videler, 2005; Videler et al., 1983). Therefore, as the thermals are stronger and more unpredictable than orographic updrafts (Harel et al., 2016; Reddy et al., 2016), we hypothesized that thermals would be less suitable for wind hovering flight. Thus, we predict that lesser kestrels will favor foraging areas where and when orographic updrafts occur. We also tested whether kestrels would be repulsed by wind turbines when they use the wind farm. We analyzed GPS tracking data recorded on 26 falcons and meteorological data measured at the wind farm. We built a first model depicting the attractiveness of the Causse for kestrels and which factors drive the individual movements across the breeding season and according to the nesting colony. Second, we built a spatially-explicit resource selection model within the wind farm area to estimate the probabilities of occurrence of falcons in order to identify the situations at risk around each wind turbine.

2. Materials and Methods

2.1. Model species

The Lesser kestrel is a small colonial and migratory falcon, mainly wintering in the Sahelian region and breeding along the Mediterranean basin and Asia (Roselaar, 1980; White et al., 1994). The species suffered a major decline in western Europe in the 20th century, and the French population almost collapsed with only one remaining pair in the 1980s. Still classified as “vulnerable” in France since 2011, it is now fully protected and has been subject to national and global action plans for its conservation (Pilard et al., 2021). In 2021, the national population had partially recovered, numbering 626 pairs.

The species is present in France on the breeding grounds from March to July, followed by a post-nuptial dispersal until the end of September and the start of post-nuptial migration (Pilard et al., 2021). The breeding season is concentrated in 3 months. In May, the female is laying 4-5 eggs. The female handles most of the incubation duty, staying at the nest or near the colony, while being provisioned by the male (Pilard et al., 2021). The chick rearing period starts in June, with the female guarding the chicks during the first week after hatching, while the male provides food to the nest. Progressively both parents forage independently and feed the nestlings at the nest. In July, the chicks fledge but are still fed by their parents near the nest.

2.2. Study area and wind farm

We focused our study on the central sub-population from “Hérault”, where 243 pairs bred in 13 colonies in 2021. Lesser kestrels install their nest in the roofs (under tiles) of old houses. Falcons firstly colonized the village of Saint-Pons-de-Mauchiens (SPM), and later extended breeding colonies into other villages nearby : Saint Pargoire (SP) and Villeveyrac (V) (Pilard et al., 2021). These three villages are located at the western edge of the Aumelas Causse, at a short distance from the wind farm: less than 4 km for V and about 6 km for SPM and SP (Fig 1). The three villages have similar surrounded-habitat types, all mainly composed of fields (vineyards), scrubland, forest, grassland and natural pastures.

The Aumelas Causse is a limestone plateau, with a mean altitude of c.200m. This wild area of 15,000 hectares of scrubland includes two Natura 2000 sites: "Montagne de la Moure et causse d'Aumelas", FR9101393 (2006) (including three priority habitat types: wet meadows, temporary Mediterranean ponds and steppes) and "Garrigues de la Moure et d'Aumelas", FR9112037 (2016) (a special protection area for birds, partly overlapping with the first site). The vegetation is abundant on the Causse, as well as the falcons’ favorite food: insects, orthopterans, small mammals (Roselaar, 1980).

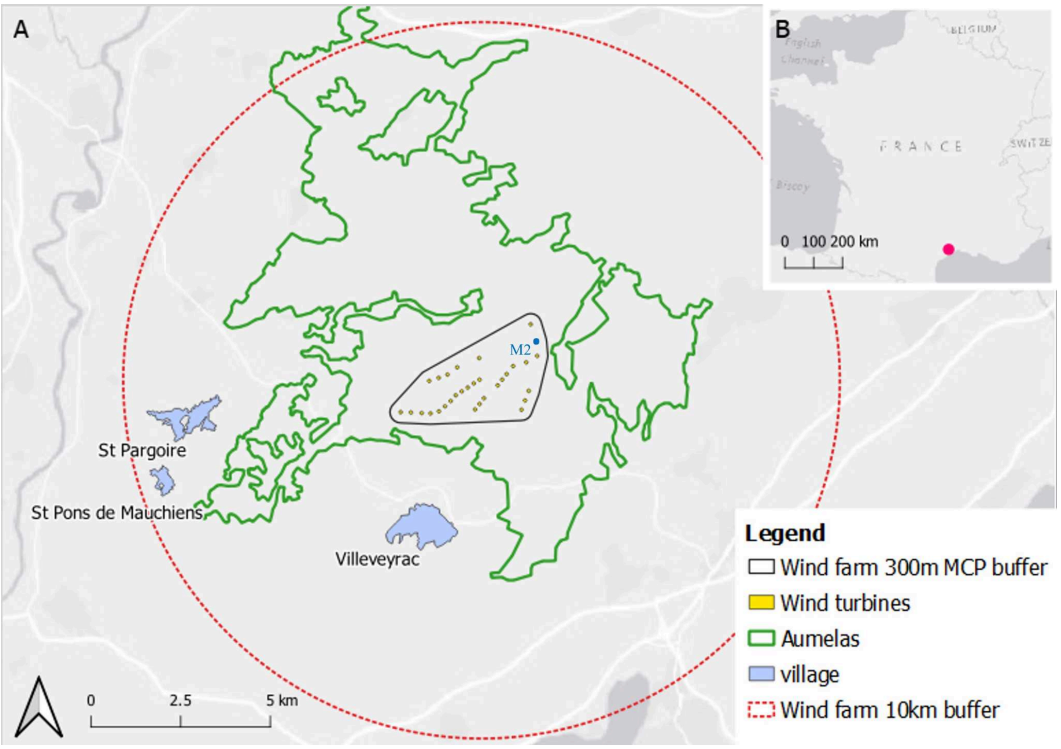
The Aumelas wind farm was composed of 31 turbines, built between 2006 and 2014: 14 turbines with a pole height of 56 m and blade length of 41 m, 11 turbines with a pole height of 65 m and blade length of 35 m and 6 turbines with a pole height of 78 m and blade length of 41 m. We defined a risk area around the wind farm by estimating a Minimum Convex polygon (hereafter named “WF-MCP”) from the 300 meter buffer around each wind turbine. This 300 m buffer corresponded to the distance a lesser kestrel is able to travel in about 40 s, the time required in this wind farm to shutdown wind turbines after a bird being detected by the Automatic Detection System (Fluhr et al., submitted)

2.3. Meteorological variables and updraft estimation

In this region, the winds show well-defined and relatively constant patterns (see table 1). The two dominant winds in the region are the “sea breeze”, blowing from the south-east, at daytime, and the "tramontane", a turbulent wind coming from north-west, from the Atlantic and along the Pyrenees. The latter is the strongest wind and dominates most of the time, day and night. Two other winds, minor in occurrence and strength compared to sea breeze and tramontane, are the north-eastern winds, blowing mainly at night, and the south-western wind, appearing from the middle of the day.

Meteorological data (wind speed and wind angle, temperature, pressure and humidity) were automatically recorded every 10 min, from a weather station located on the wind turbine #M2, Northeast of the wind farm, and provided by EDF. We attributed to each kestrel location its corresponding values of meteorological variables .

To estimate the orographic updrafts strength, we used the function of horizontal wind speed and topography (Bohrer et al., 2012; Brandes & Ombalski, 2004; Hanssen et al., 2020). This estimates the orographic updraft velocity W0 (equation 1):



<u>Figure 1</u> : Map of the study site (A) and its location in France (B). The map (A) shows the 31 wind turbine locations (yellow) surrounded by a 300m buffer zone (solid black line) present on the Aumelas Causse (borders in green). The M2 turbine from which weather data have been collected is highlighted in blue. The 3 villages hosting lesser kestrels colonies are represented by blue shapes, all encompassed in a 10 km buffer zone around the wind farm (red dotted line).

$$\text{(eq. 1) } W0 = v \,.\, C\alpha$$

Where v is the wind speed (m.s^{-1}) and $C\alpha$ is the updraft coefficient, defined as the product of the sine of the slope angle (θ) by the cosine of the angle between the wind direction (α) and the terrain aspect (β) (equation 2) :

$$\text{(eq. 2) } C\alpha = sin\,(\theta)\ .\ cos(\alpha - \beta)$$

Because the slope is always positive, $sin\,(\theta)$ is always positive, as well as for the wind speed, the sign of W0 depends on the cosine. When (α – β) gives an angle between [-90° ; 90°], the cosine is positive, so W0 is positive. It means that when the wind is blowing against the slope up to an angle of 90°, an orographic updraft is generated, whose intensity is proportional to the wind-speed. Conversely, when (α – β) gives an angle > 90°, the cosine is negative, so the W0 is negative. It means that when the wind comes from behind the slope there is no orographic updraft (downdraft air current).

To each GPS location, we associated slopes and aspects values derived from the DEM "BD ALTI®" (25 m resolution, IGN 2015) and estimated the corresponding W0.

Table 1: Average ± SD statistics of wind regimes in the Aumelas plateau from May to July, during the period 2017-2021, during the time period 9:00 - 20:00 CET when kestrels are foraging.

Wind name and orientation	Orientation (°)	Wind speed (m.s-1)	% of total time of occurrence	% days of occurrence	Annual mean number of days of occurrence	Overall nycthemeral occurrence
Tramontane (NW)	302 +/- 23.7	8.84 +/- 4.17	29.3	73.0	67.2 +/- 6.43	all day and night
Sea breeze (SE)	132 +/-25.7	5.19 +/- 2.02	26.2	64.1	59.0 +/- 6.26	mostly by day
Land breeze (NE)	52 +/-24.8	4.85+/-2.19	20.2	65.6	60.3 +/- 8.85	mostly by night
Labé (SW)	240+/-26.8	7.34+/-3.73	24.4	65.9	60.7+/- 6.15	mostly in evening

2.4. GPS tracking and data processing

We captured 43 adult lesser kestrels (34 males and 9 females) in the vicinity of the three villages of SPM, SP and V in April 2017-2021. The sex bias in the captures is likely due to male being more responsive to traps than females which spend more time at the nest during the capture period (Roselaar, 1980). We used Bal Chatri traps composed of a compartment for the bait (living domestic mouse) on top of which a clapnet was attached. We weighted every individual and kept only those with body mass > 250 g to ensure that total equipment weight (7.81 g for rings, harness and GPS tag) stayed 3% of body mass to minimize disturbance of birds behaviors (Barron et al., 2010; Bodey et al., 2017). We fitted the selected individuals with GPS tags (model "PICA", ECOTONE), attached with a pelvic (leg-loop) harness made of 2-mm teflon ribbon. These solar-powered tags record bird location in 2D (1-m horizontal accuracy) as well as the instantaneous speed every 5 to 10 minutes (depending on battery levels). Data was transferred via UHF signal, collected with a unidirectional receiving antenna at distances >500 m.

We kept tracking data within a perimeter of 10 km around the wind farm (our site of interest), encompassing the Causse and the 3 villages where kestrels breed (Fig 1). Because kestrels are impacted by wind turbines when they are foraging, we specifically focused on foraging movements and foraging behavior, i.e. commuting flights and hovering flights. We thus excluded all locations recorded within 200 m buffers around the villages, nesting sites and known roosts. We focused on data collected from May to July each year (the core of the breeding season), and subsampled them to a GPS location every 10 minutes during falcons

activity time (i.e. from 09:00 to 20:00 CET). Finally, we used only the data from individuals who visited the wind farm (26 individuals out of 43 tracked in total, 60%).

2.5. Statistical analyses

All the statistical analyses have been performed using R version 4.3.1 (2023).

2.5.1. Modeling wind farm attractiveness

To identify variables driving kestrel presence within the wind farm, we modeled the probability of presence within the MCP using generalized linear mixed models (GLMM), with binomial error structure and a logit link function (Bolker et al., 2009; Zuur et al., 2009). Our full model contained the following fixed effects: orographic updraft velocities (W0, continuous variable), the village of origin (colony, categorical variable) and the months (month, categorical variable). The village of origin was used to investigate the effect of the differences in their distance to the WF-MCP while month gives information on the effect of breeding phases on the probability to visit the WF-MCP. Individuals' identity was used as random effects. We centered and scaled W0 for the model to converge.

We fitted our model using glmmTMB package (Brooks et al., 2017) with Laplace Approximation for the maximum likelihood estimation (Bolker et al., 2009). We investigated the significance of variables with the '*drop1*' function (Chambers & Hastie, 1992) using a $\chi 2$ test and the Akaike's Information Criterion (AIC) to select the most parsimonious model (Zuur et al., 2009). Finally, we tested residuals normality, dispersion and the presence of outliers with the DHARMa package (Hartig, 2020)(ESM01).

2.5.2. Modeling kestrel presence within the windfarm

To estimate where lesser kestrels were more likely to forage within the wind farm we built a Resource Selection Function (RSF), based on the explanatory variables from the previously selected model (Fieberg et al., 2021). To do so, all locations of individuals within the WF-MCP were categorized as "used" by individuals. For each location of an individual, we sampled 10-fold more locations within the WF-MCP guaranteeing having the same timestamp while representing "available" locations. Having the same timestamp allowed us to associate meteorological variables and calculate W0 at each "available" location. Moreover, we hypothesized that strong orographic updrafts may become unfavorable for kestrel hovering flight as the kestrel needs to fly at a slightly higher velocity than the horizontal wind speed to perform hovering flight, making high speed wind unfavorable for saving energy (Videler et al., 1983). Thus, we hypothesized that the W0-kestrel occurrence relationship may not be linear and we included a quadratic effect on W0 in the model. We also computed the distance of each location to the nearest wind turbine (DTurbine) to investigate potential wind turbine avoidance behaviors. Here again, we scaled all the

continuous variables (W0, W02, DTurbine). The RSF corresponded to a generalized linear mixed model with a binomial error structure (available: 0, used: 1) and a weighted logit link function considering a weight of 5000 for available locations, and 1 for used locations (Fieberg et al., 2021). However, the resulting random effect has zero variance (ESM02), so we reduced the model to build a weighted RSF with a simple generalized linear model (*glm*). We tested the relative importance of each variable using the '*drop1*' function with a $\chi 2$ test and selected the most parsimonious model based on the Akaike's Information Criterion (AIC).

We computed predictions for the probabilities of presence of kestrels in the WF-MCP using W0 values from 0 to 7 (the maximum W0 associated with kestrel data in the WF-MCP being 5.68 ± 1.00) with a step of 0.01 (taking into account quadratic W0 effects in the estimates of the model) to visualize the shape of the relationship between kestrel presence probabilities in the MCP and orographic updrafts. We also calculated the 95% confidence interval around those predictions with a bootstrap (Fig 3).

2.5.3. Predictions and model validation

From the RSF, we predicted the kestrel probability of presence within the wind farm for the two main wind regimes NW (Tramontane) and SE (Sea breeze; see above). We used the mean speed and the mean angle of wind regimes to compute W0 in each pixel of the raster covering the WF-MCP. We computed the minimum distance to a wind turbine for each pixel of the raster ("*distanceFromPoints"* function, *raster* package). We finally predicted over the raster the probability of presence (*predict* function) (Chambers & Hastie, 1992).

To test the performance and validate our RSF models, we applied a cross-validation approach (Boyce et al., 2002; Hanssen et al., 2020; Thurfjell et al., 2014). We conducted a 10-fold cross-validation and used the AUC as the model performance criterion. Additionally, we divided the data into a training set with 80% of the data and a test set with 20% of the data to perform a visual validation of the model. We graphically visualized the presence points of observed falcons in conditions of Tramontane or Sea breeze, on prediction maps made under corresponding conditions, providing an overview of the model's validity.

Wind turbines having a pixel with a probability of presence > 0.5 or 0.75 in less than 100 m around were considered as provoking respectively moderate and high levels of collision risks for kestrels.

3. Results

We used a total of 54,309 GPS locations recorded from 2017 to 2021 by 26 falcons, evenly distributed between May and July in the 10 km buffer defining the study area. A total of 3278 locations have been recorded within the WF-MCP. In May, 47.67% of the locations were recorded at the Causse including 8.9% within the WF-MCP, while these proportions

were reduced to 30.11% and 5.57% respectively in June, and 19.25% and 1.37% respectively in July.

Compared to our full model, the model predicting the probability for a location to be in the WF-MCP without considering colony got a better support (Table 2) The positive estimate for W0 shows that the kestrel's occurrence in the wind farm increased with velocity of orographic updrafts (Table 3). The negative estimates of the months of June and July compared to May (intercept, Table 3) show a decreasing occurrence in the wind farm during these months (Fig 2). Consequently, the W0 threshold to have a presence probability >0.5 was 5.82, 6.41 and 9.59 m.s-1 for respectively May, June and July. The colony had no significant effect to explain the falcon's occurrence in the wind farm.

Table 2 : Selection table of the GLMM describing the wind farm attractiveness (presence in/out the windfarm 300m MCP as a function of the orographic updrafts W0, Month and Colony and with individuals as random factor). The selection is made with a stepwise deletion of variables, dropping all possible single terms and testing the changes in fit of each degraded model. The df, AIC and chi-squared value of each model are given.

Model	df	AIC	*P*
1) int+W0+Month+Colony		19150	
2) int+Month+Colony	1	19616	< 0.001
3) int+W0+Colony	2	20239	< 0.001
4) int+W0+Month	2	19147	0.5903

The reference full model 1 of the RSF had the best statistical support (Table 4). This final RSF model (cross-validation AUC = 0.688 ± 0.008 S.E) revealed significant effects of the orographic updraft velocity but also of the distance to the nearest turbine, on the lesser kestrel probability of presence in the WF-MCP (Table 5). Notably, W0 shows positive linear effect but also a quadratic effect with a negative W02 coefficient, depicting a non linear change and decreasing probability of presence for high W0 values and so, highlighting the existence of a maximum optimal W0 value at c. 1.5 m.s-1 (Fig. 3). Kestrel presence also appeared as positively correlated with the distance to wind turbines (Table 5).

Table 3 : Estimates and confidence intervals at 95% of the final most parsimonious model 4 (without Colony) selected with the model selection (Table 2). This GLMM includes the orographic updraft velocity estimate (W0) and the months (May, June and July) as fixed effects and the individuals (Individual local identifiers) as a random effect. It also shows the residual variance σ2 of the random effect (or the within-subject variance), the random intercept variance τ00 (or between-subject variance) and the intraclass correlation coefficient of the random effect (ICC).

Predictors	Estimate	CI	*P*
Intercept	-2.82	-3.26 – -2.37	< 0.001
W0	0.36	0.33 – 0.39	< 0.001
Month [6]	-0.32	-0.40 – -0.24	< 0.001
Month [7]	-2.04	-2.18 – -1.89	< 0.001
Random Effect			
ID	1.28		
ICC	0.28		
$N_{individual.local.indentifier}$	26		
Observations	54309		
Marginal R^2 /Conditional R^2	0.170/0.402		

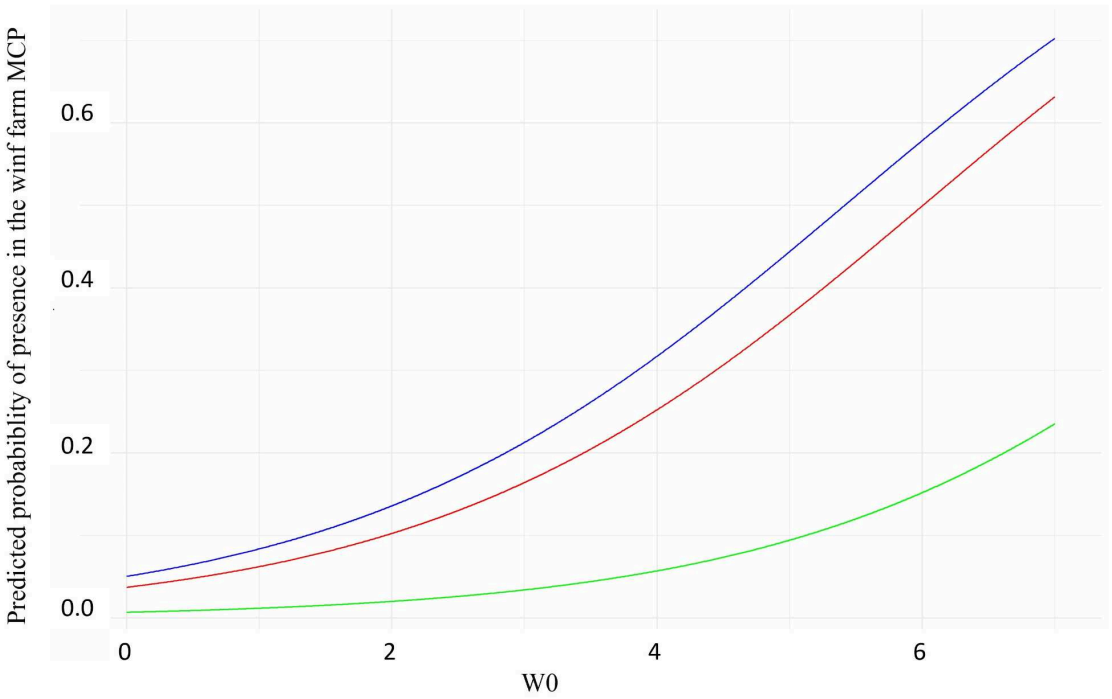


Figure 2 : Probability of presence of lesser kestrels in the wind farm MCP, according to month (May in blue, June in red, July in green), issued from model 4 in table 2.

Table 4 : Selection table of the RSF modeling the use of the wind farm MCP by the lesser kestrel (use/available locations in the WF-MCP as a function of the orographic updrafts (W0), a quadratic W0 (W02) and the distance to the nearest turbine (DTurbine)). The selection was made with a stepwise deletion of variables, dropping all possible single terms and testing the changes in fit of each degraded model. The df, AIC and chi-squared value of each model are given.

Model	df	AIC	*P*
1) int+W0+W02+DTurbine		69161	
2) int+W02+DTurbine	1	70071	< 0.001
3) int+W0+DTurbine	1	69373	< 0.001
4) int+W0+W02	1	69261	< 0.001

Table 5 : Estimates and confidence intervals at 95% of the final RSF model predicting kestrel presence in the wind farm MCP. This GLM included the orographic updraft velocity estimate (W0) as a linear and quadratic predictor and the distance to the nearest wind turbine (DTurbine).

Predictors	Estimate	CI	P
Intercept	-11.03	-11.08 – -10.99	< 0.001
W0	0.96	0.89 – 1.04	< 0.001
$W0^2$	-0.32	-0.37 – -0.27	< 0.001
DTurbine	0.17	0.14 – 0.21	< 0.001
Observations	32780		

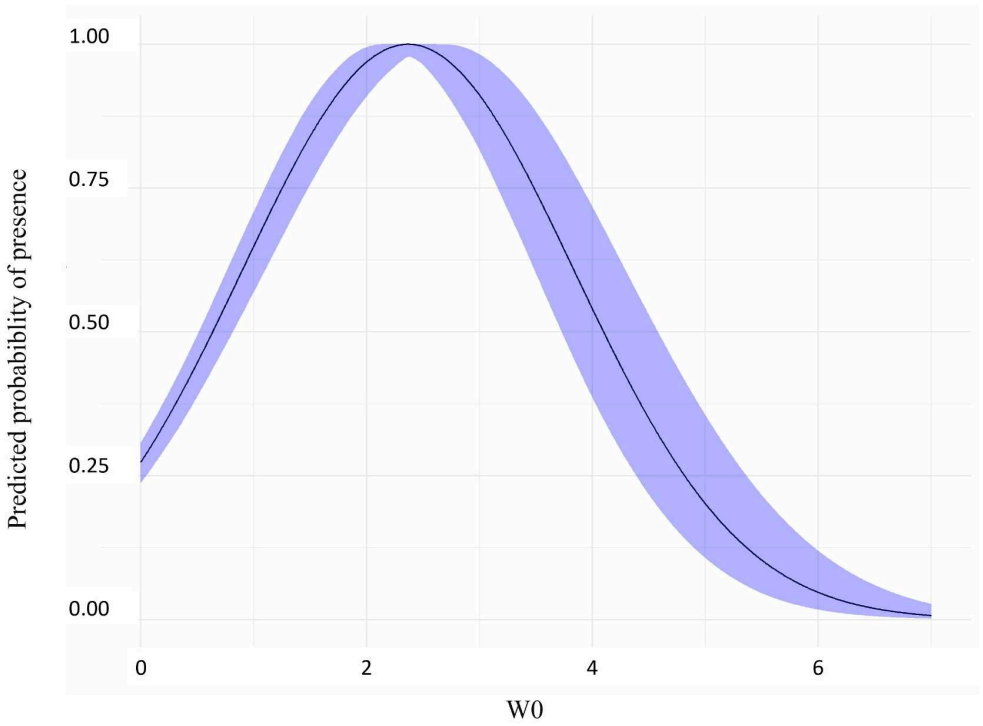


Figure 3 : Changes of the presence probabilities of the lesser kestrel in the WF-MCP and their 95% confidence interval (shaded area) as a function of the orographic gradients W0 (m.s-1), built with the RSF model.

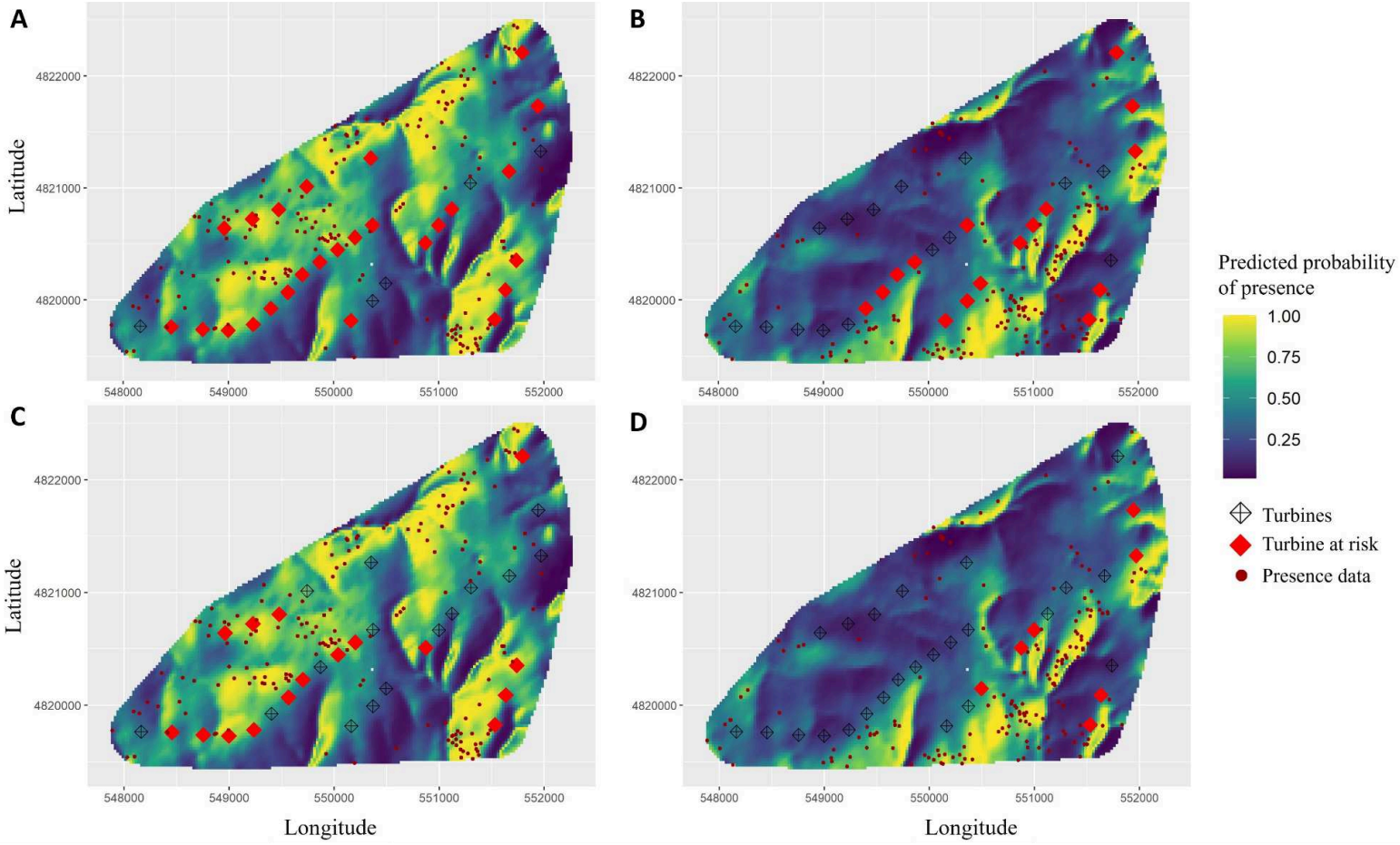


Figure 4 : Predictions of Lesser Kestrel presence probabilities in the 300m buffer zone of the Aumelas wind farm. Predictions and risk identification are carried out under north-westerly (Tramontane) (A, C) and south-easterly (Sea breeze) (B, D) wind conditions. All wind turbines are shown either in black (risk P<0.5) or in red when identified as being at risk for P>0.5 (A, B) and P>0.75 (C, D). Kestrel locations extracted from a 'test set' of 20% of the data and under Tramontane or Sea breeze conditions have been plotted over the prediction maps

Figure 4 displays the prediction map of the lesser kestrel presence probabilities according to wind regime. Under average Tramontane conditions, a large proportion (55%) of the WF-MCP area yielded presence probabilities >0.5 (Fig 4A). Under average Sea breeze conditions, only 26% of the WF-MCP yielded presence probabilities >0.5 (Fig 4B). In addition, 26% and 12% of the WF-MCP show probabilities higher than 0.75 under Tramontane or Sea breeze wind conditions, respectively (Fig 4 C, D). When applying a buffer of 100m around each turbine, under Tramontane regime, 16 turbines (52%) and 26 turbines (84%) have a kestrel presence probability higher than 0.75 and 0.5 respectively (ESM03). Under the Sea breeze regime, 7 turbines (23%) and 16 turbines (52%) have a kestrel presence probability of 0.75 and 0.5 respectively (Fig 4; ESM03).

4. Discussion

The aim of this study was to identify the factors driving the use of Aumelas wind farm by lesser kestrels, in order to predict their presence according to the environmental conditions. We first found that kestrel presence was correlated with wind conditions generating orographic updrafts and differed between months. Second, at a fine scale, kestrels selected sectors of the wind farm where they could find higher orographic updraft velocity coefficients (W0) and the selection was also correlated to the distance to the nearest turbine. The final goal was to identify turbines at risks that kestrels may approach when wind conditions are favorable for generating orographic updraft, in order to propose a novel method of selective curtailment.

In a first analysis, we found that lesser kestrels were actively using the wind farm MCP relative to the rest of the study area early in the season and when prevailing winds generate orographic updrafts. This seasonal pattern may be explained by the breeding phenology. In May, while the female mostly stays at the nest to incubate (Pilard et al., 2021), the male should have more time to travel long distances (>5 km) to forage towards the Causse d'Aumelas and in the WF-MCP. Indeed, in this population, lesser kestrels display larger home ranges during the incubation period than during installation and rearing periods (Pilard et al., 2021). However in Spain, in different agricultural contexts, female lesser kestrels performed longer and more distant foraging trips than males (Hernandez-Pliego et al., 2017). On the other hand, in June and July, when both parents must provision nestlings several times per day, time may be limited to forage at the Causse d'Aumelas and parents may concentrate their foraging activity in the agricultural landscape closer to the colony. Furthermore, in June-July, high temperatures may favor an increase in the abundance of insect prey in agricultural habitats closer to the breeding colonies (Pescador et al., 2019; Rodríguez et al., 2010). Interestingly, we found no significant effect of the breeding colony on the probability to use the WF-MCP. The "colony" factor was used as a categorical proxy for the commuting distance between the nest (i.e. the central place) and hunting grounds. Therefore, birds from all colonies had the same probability to use the Causse d'Aumelas, further strengthening our hypothesis that this place should be a high quality hunting ground, encouraging birds to come from all directions whenever hunting conditions are favorable. In

Italy and Spain, unfavorable habitats near colonies forced lesser kestrels to commute to distant hunting grounds where prey quality and quantity were higher, and in turn resulted in elongated home ranges (Gustin et al., 2017; Hernández-Pliego et al., 2015).

The most important factor explaining kestrel presence in the wind farm MCP compared to the study area was the orographic updraft potential W0, further confirmed by the second analysis, using resource selection function at small scale within the wind farm. Given the attractiveness of the causse as a resource area by foraging lesser kestrels, we assumed that hunting was the reason why kestrels commuted to the causse. When hovering and hunting insects, lesser kestrels typically fly between 10 and 20 m height, continually turning into wind to hover, generally with less wing-flapping than Common kestrels (Roselaar, 1980). We thus hypothesized that lesser kestrels would prefer moderate but predictable updrafts. Thermal updrafts can be typically strong (vertical speed between 1 and 4 m.s-1), only occurring at the warmest hours of the day, and spatially poorly predictable (Westbrook & Eyster, 2018; Williams et al., 2018). Technically, estimating and mapping thermal updrafts at small scale is also highly difficult because of the chaotic nature of the turbulences (Reddy et al., 2016). On the other hand, orographic updrafts can occur at any time of the day, depending directly on wind speed and direction, and are thus spatially more predictable. We therefore considered that thermal updrafts would be a less suitable source of updraft than orographic updrafts for lesser kestrels practicing hovering flight to hunt (Videler, 2005; Videler et al., 1983) and we focused our analysis on mapping orographic updrafts. Nevertheless, thermals are known to be used by lesser kestrels when they commute between breeding and hunting grounds, notably when they need to cross unfavorable habitat for hunting (Hernández-Pliego et al., 2015). Furthermore, lesser kestrels are known to align their foraging trip departure direction with the dominant wind, to benefit from tailwind support (Hernández-Pliego et al., 2014). During Tramontane (NW) episodes, the Causse d'Aumelas, located globally at the east of the colonies, may then have a double avantage to be in the direction of the prevailing wind when departing for efficient commuting flights, and to provide abundant orographic updrafts for efficient hunting hovering flights.

With the RSF analysis, we confirmed a linear and a quadratic effect of W0 to explain lesser kestrel presence in the wind farm. According to our results, the optimal (vertical) orographic updraft velocity for kestrels would be at 2.35 m.s-1. The glide polar curve generated for lesser kestrel, using Flight program (Pennycuick, 2008), showed that the sink rate at the best glide speed was 0.368 m.s-1 (ESM04). Therefore lesser kestrels need to find updrafts >0.368 m.s-1 to compensate for their sink rate (i.e. negative vertical speed) and therefore practice hovering stationary flight at minimal energy cost. Previous studies on common kestrels found that windhovering behavior was only possible at horizontal wind speeds between 3 and 13 m.s-1, and the optimal horizontal wind speed for minimizing energy expenditure was around 7 m.s-1 (Videler et al., 1983). Such optimal values for W0 (>0.368 m.s-1) and horizontal wind speeds (around 7 m.s-1) are commonly encountered during Tramontane and Sea breeze conditions at the Causse d'Aumelas and in the wind farm area. As a consequence, we found that lesser kestrels presence probability was >0.5 for 55% and 26% of the wind farm MCP area under respectively Tramontane and Sea breeze

conditions. Similarly, in both Norway and Spain, strong winds generated important orographic updrafts at specific places that white-tailed eagles and black kites *Milvus migrans* preferred to use (Hanssen et al., 2020; Santos et al., 2017).

The resource selection function also highlighted a positive effect of the distance to the nearest turbine on the probability of presence of lesser kestrels. This result is opposite to our prediction that kestrels would be repulsed by giant turbines on the hunting grounds, as has been observed in several species of raptors and migratory birds (Hötker, 2017; Marques et al., 2020; Santos et al., 2022). Such counterintuitive attraction to wind turbines may have several explanations. First, wind turbines had been sited on ridges or on slopes that provide orographic updrafts, that lesser kestrels seek (Drewitt & Langston, 2008). Second the vegetation around each mast is regularly mown by wind farm managers, potentially making insect prey detection easier than in the surrounding matorral shrubs. A similar pattern had been observed in Spain, where an experiment of tilling the ground around masts, eliminating any vegetation, resulted in decrease in insect abundance, and consequently reduced attraction of lesser kestrels in the subsequent weeks (Pescador et al., 2019). At the scale of the wind farm, we did not consider any land cover factor in the resource selection function, because the shrubland matorral vegetation was homogeneously distributed across in wind farm MCP, representing 97% of the total area, except for the few patches of grassland around each turbine and a few trees.

The final step was to generate maps giving the probability of presence at 25 m resolution in order to identify areas and wind turbines at risk under specific wind conditions. Such maps could be used to elaborate conservation plans such as selective curtailing of the turbines. Even though rotor radius was 35 to 41 m (depending on the turbines), we chose a buffer of 100 m around each turbine, to account for the likely turbulence generated by the turbine that can possibly perturbate kestrel hunting flight. Thus we overall considered that kestrels were at risk when they were at distances <100 m from a turbine. Under the Tramontane wind regime, 84% of turbines had a presence probability >0.5 and 16 turbines out of 31 had a kestrel presence probability >0.75, i.e. with high collision risk. The situation was not so dramatic under the Sea breeze regime, yet 7 turbines were considered at high collision risk. However we are currently unable to ascertain that mortalities recorded at specific turbines occurred during Tramontane or Sea breeze regime, because corpses can be found several days after the mortality event, so we can not know the exact wind conditions prevailing when the bird collided. Nevertheless, using a precautionary principle, it should be possible to define a novel type of selective curtailment, based on lesser kestrel presence probability according to wind direction. By selectively curtailling 16 turbines under Tramontane and 7 other turbines under Sea breeze, the collision risk would be strongly reduced for lesser kestrels at this wind farm, at limited costs for wind farm operators compared to an overall curtailment of the entire wind farm during the months of presence of kestrels.

In lesser kestrels, it is too early to assume that this pattern of presence related to orographic updrafts observed at Aumelas is a common feature of the species everywhere else in the distribution range. It would be necessary to replicate this study at other sites, with and

without wind turbines to strengthen our conclusions. It would be also necessary to extend this analysis to juvenile birds that were not tagged as part of this study, yet juveniles constitute the bulk of collision cases in Aumelas wind farm in summer. Therefore the seasonal pattern of decreasing occurrence in the wind farm by adults that we found may be counterbalanced by an increasing occurrence by fledglings in summer. Once our results will be confirmed at other sites and all age and sex classes, then we could map lesser kestrel presence probability at all wind farms in the distribution range (breeding sites, wintering sites and migratory flyways), and potentially propose selective curtailment at a large scale.

Studying and mapping thermal and orographic updrafts seems to be a promising tool to understand bird occurrence at fine scale. This had been performed on several migratory species such as black kites at the migratory corridor of Gibraltar Strait (Santos et al., 2017), Golden eagles *Aquila chrysaetos* in eastern USA (Duerr et al., 2015) or white Storks *Ciconia ciconia* in Europe (Scacco et al., 2018). Hanssen et al (2020) used a similar approach to map white-tailed eagle presence probability in an island, according to thermal and orographic updraft probability, to inform micro-sitting of future wind turbines, so as to prevent future collision risks. This approach could probably be extended to other species and sites.

CRediT authors' contributions

Bartholus Lise: data processing, data analysis, writing

Sassi Yohan: conception, data analysis, writing

Garcia Matthieu: field data collection, data processing

Saulnier Nicolas: conception, field data collection

Pilard Philippe: field data collection

Duriez Olivier: conception, writing

Acknowledgments

We thank all the people involved in the field work of catching and tagging lesser kestrels: M Bouzin, J.F. Blanc, A Bea. We thank Patrick Boudarel and the board of the plan National d'Action pour le faucon crécerelette for their support and useful discussions. GPS tags and associated fieldwork were funded by EDF. We thank the SO ECOPOP, as part of OSU-OREME, for funding demographic studies of lesser kestrels.

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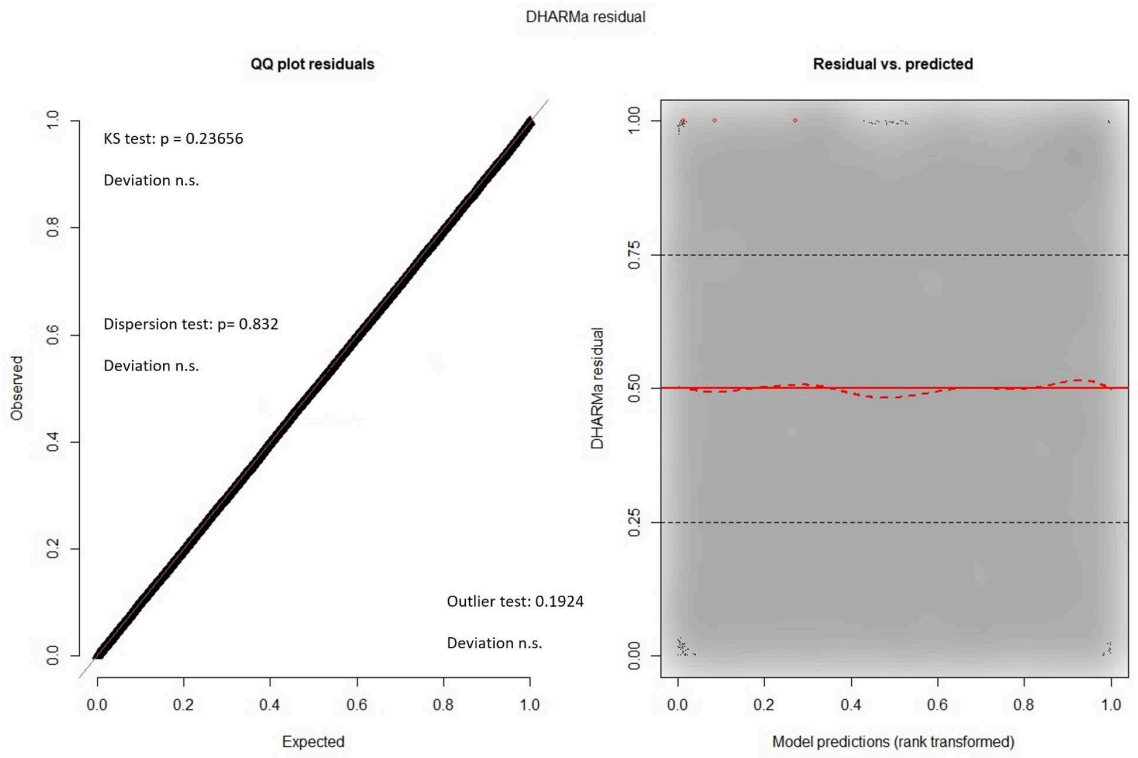
Electronic Supplementary material

ESM01: Residual diagnostics for the final most parsimonious GLMM model.

This GLMM includes the orographic updraft velocity estimate (W0) and the months (May, June and July) as fixed effects and the individuals (Individual local identifiers) as a random effect. Tests showed no dispersion, no outliers and no trend in the residuals.



ESM02: Summary of the first RSF model built with individuals ID as a mixed effect.

GLMM includes the orographic updraft velocity estimate (W0) and the distance to the closest rotor as fixed effects.The table shows the summary of the fixed effects and of the random effect variances with the residual variance σ2 of the random effect and the random intercept variance τ00.

Predictors	Estimate	CI	P
Intercept	-11.03	-11.08 – -10.99	< 0.001
W0	0.96	0.89 – 1.04	< 0.001
W02	-0.32	-0.37 – -0.27	< 0.001
DTurbine	0.17	0.14 – 0.21	< 0.001
Random Effect			
σ2	3.29		
$\tau 00_{individual.local.indentifier}$	0.00		
$N_{individual.local.indentifier}$	26		
Observations	32780		

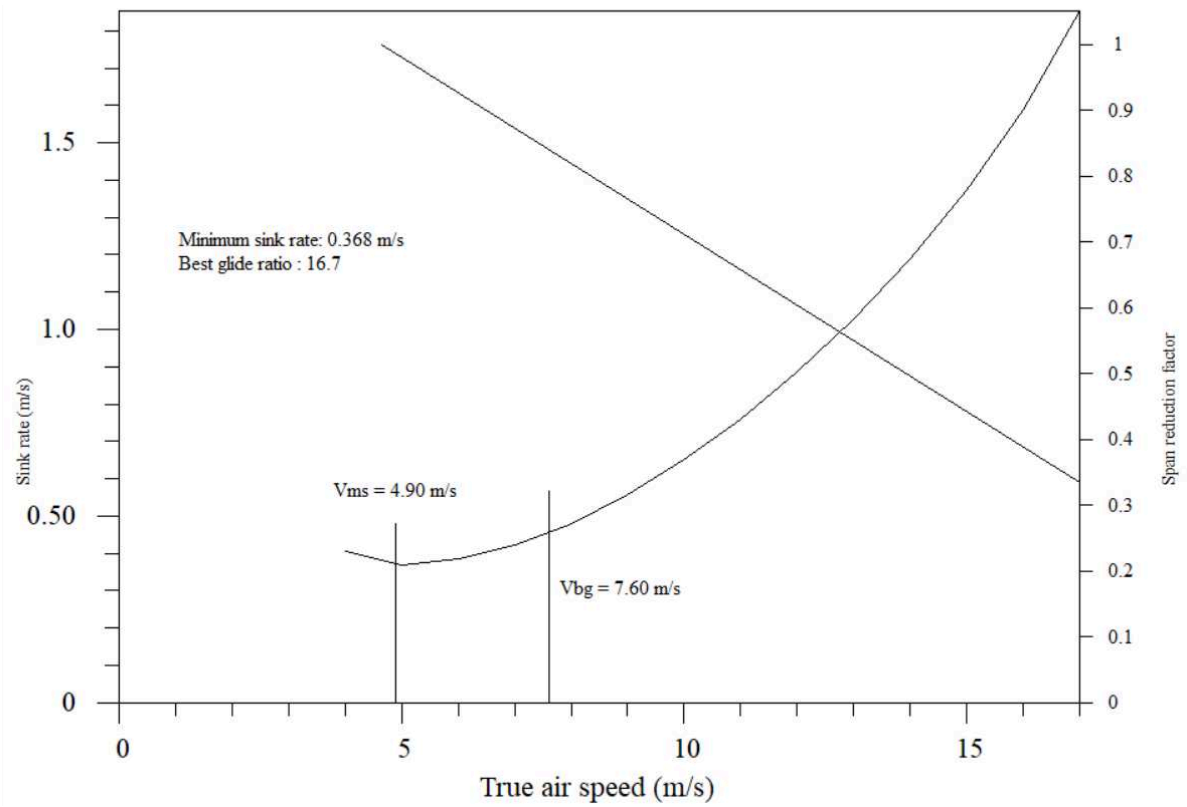
ESM03: Summary table of turbines at risk under prevailing wind regimes

For each turbine, we reported the number of collisions recorded (i.e. number of lesser kestrels corpses found) between 2011 and 2022 (Data DEAL Occitanie), the maximum probability of presence (P_{max}) and the class of collision risk under Tramontane (NW) wind regime and Sea breeze (SE) wind regime. The collision risk was estimated with the probability of presence of lesser kestrels (P >0.5 for moderate risk and P > 0.75 for high risk) within a 100m-buffer, issued from RSF model 1 and fig 4. Turbines with highest collision risk, in any wind conditions, are highlighted in red.

		Tramontane		Sea breeze	
# wind turbine	n collisions	P_{max}	Risk	P_{max}	Risk
A1	0	0.89	High	0.46	
A2	4	0.98	High	0.16	
A3	3	0.90	High	0.28	
A4	0	0.74	Moderate	0.28	
A5	2	0.73	Moderate	0.41	
A6	0	0.47		0.41	
A7	3	0.64	Moderate	0.48	
E1	0	0.78	High	0.54	Moderate
E2	1	0.62	Moderate	0.57	Moderate
E3	4	0.91	High	0.29	
E4	0	0.91	High	0.25	
E5	0	0.72	Moderate	0.63	Moderate
E6	3	0.59	Moderate	0.54	Moderate
E7	3	0.48		0.70	Moderate
E8	1	0.40		0.79	High
E9	3	0.89	High	0.91	High
E10	1	0.72	Moderate	0.99	High
E11	1	0.64	Moderate	0.75	Moderate
M1	1	0.98	High	0.59	Moderate
M2	3	0.54	Moderate	0.87	High

M3	4	0.35		0.97	High
P1	1	0.98	High	0.20	
P2	1	0.92	High	0.80	High
P3	1	0.96	High	0.99	High
V1	3	0.46		0.47	
V2	3	0.81	High	0.45	
V3	8	0.81	High	0.40	
V4	3	0.98	High	0.24	
V5	3	0.87	High	0.47	
V6	3	0.69	Moderate	0.50	1
V7	1	0.76	High	0.53	1
Total	64		26		16

ESM04: Theoretical flight performances of lesser kestrels



Glide polar curve for lesser kestrel *Falco naumanni* generated on Flight program (Pennycuick, 2008) according to lesser kestrel morphology and with an air density of 1.20 $kg.m^{-3}$. The graph shows a minimum sinking (vertical) speed (rate) of 0.368 $m.s^{-1}$ for a true air speed of 4.90 $m.s^{-1}$ and a best Glide ratio of 16.7 (16.7 m glided for 1 m of altitude lost) for a true air speed of 7.60 $m.s^{-1}$.

Annexe 6. Premier essai d'identification de la personnalité chez les vautours

First attempt to describe vulture personalities

When I designed the experiments to study vultures' decision-making in flight at the Rochers des Aigles, I thought about ways of testing the repeatability of individuals' behaviour when faced with different tests. The idea was to discriminate between bolder and shyer individuals, so as to be able to control for any difference in the propensity of individuals to seek thermals on their own or to follow their conspecifics. To do so, I used two classical tests (Carter et al., 2013): the exploration of an unknown area and the presentation of a new object (neophobia).

- **Exploration of an unknown area :**

For this test, I used a specific aviary (6 x 6 x 4 m) in which none of the vultures to be tested ever entered. Each perch was removed (except for one which I could not remove but on which I placed a black plastic container) to prevent the birds from perching and remaining immobile on that perch for the duration of the test. A remote-controlled camera was attached to the ceiling of the aviary, in the middle of the aviary, facing downwards, to film the entire area of the aviary from above. One bird from the group was then captured in its wintering aviary and placed in a box at the entrance of the test aviary, in the dark, for 10 minutes to calm down. After this period, I opened the door so that it would enter the aviary. At the same time, I started recording with the camera and left the area for 30 minutes. When the test was complete, I returned the bird to its wintering aviary with its conspecifics.

I developed an algorithm to add a grid of 2 x 2 m cells to each frame of the video. It allows me to estimate the number of cells crossed during the test by the bird. Each individual was tested twice, with an interval of one month in December 2021 and January 2022. The original plan was to repeat these tests the following winter (2022-2023) to obtain 4 exploration values per individual. However, highly pathogenic avian influenza affected some of the birds in the park and the manipulation of birds was banned by veterinarian authorities, preventing the tests from being repeated.

Knowing that I would not be able to obtain a robust estimate of repeatability due to the lack of per-individual measurements, I did not perform robust analyses of these data, but only quickly screened the videos. However, I did observe interesting differences in behaviour between individuals. For example, some individuals tended to run from side to side, while others walked calmly (Figure A6.1A) and even took time out to sunbathe (Figure A6.1B). It is also important to note that every single individual has tried at least once to escape by taking off and crashing in the net-wall (Figure A6.1C). Without repeating these tests it is difficult to know if the observed differences in "exploratory" behaviour among individuals denotes a real personality.

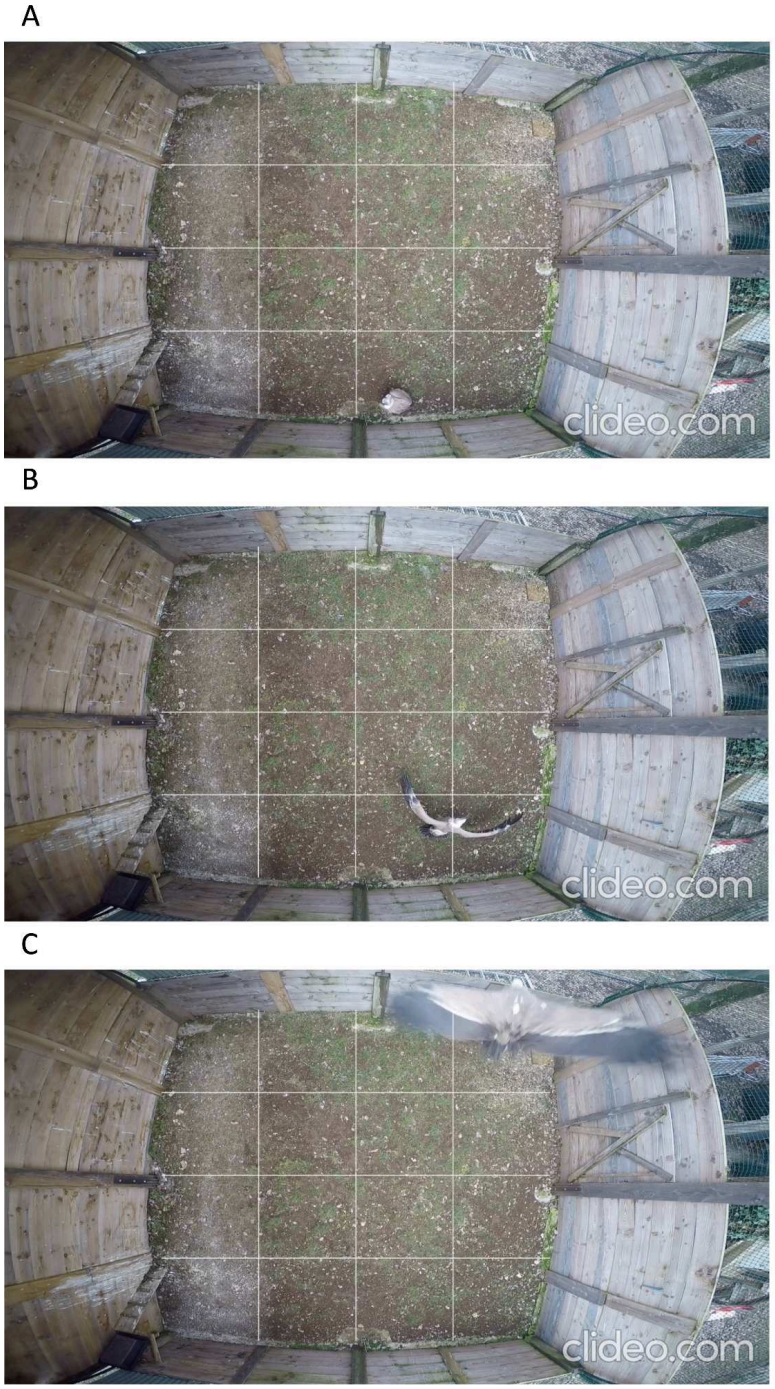


Figure A6.1: Exploration test

- **Neophobia test :**

Being frightened by a new object in the environment, or conversely being intrigued by it, could also be used as a discriminative factor to assess an animal's personality. I tried to investigate neophobia in vultures with a two-step experiment.

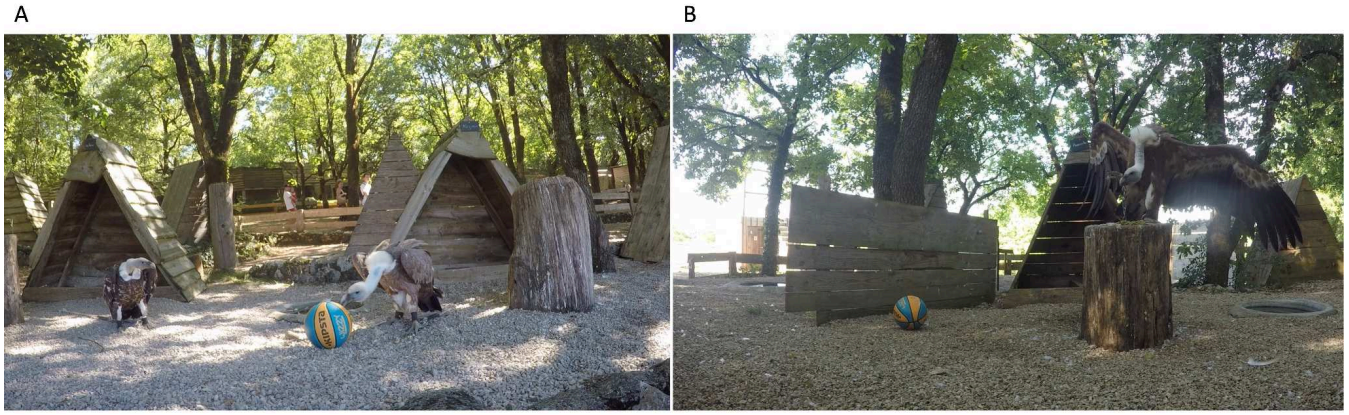


Figure A6.2: Neophobia test

First, I placed a piece of meat 1m away from the vulture's individual perching-logs and left it for 10 minutes. Then I came back and repeated the process, but this time I also placed a blue-and-orange basketball 10 cm from the piece of meat and between the vulture's log and the food. I left for another 10 minutes before stopping the experiment. I recorded the experiment with a camera and the goal was to estimate the differences in latency to take the food in the presence or absence of this new object, that birds never saw before in their life. The experiments were carried out in June-July 2021, in the morning, before the first flight of the day, when there were no visitors (or just a few) in the park and mainly to ensure that all birds had the same level of satiety (individuals receive food when they return from their flight).

We observed contrasting responses to this new object. Some individuals were not affected at all and immediately jumped on the food in both conditions, even interacting with the ball sometimes (Figure A6.2A). On the other hand, other individuals, who initially ate the food quickly, but did not approach the food in the presence of the ball. They did not eat the meat at all for the entire duration of the test with the object (the food was then removed). Finally, we observed individuals in between, who jumped at the food without the ball and hesitated to approach in the presence of the ball. These individuals eventually took the food from the tip of the bill, stretching their neck to the maximum, and immediately climbed up their log and began an intimidating posture (e.g. paw parade - Figure A6.2B).

These experiments of neophobia with basketball seemed promising and highly discriminating among individual personalities. However, as 2 individuals were breeding we had to replace these individuals with 2 other vultures in the summer 2022. This resulted in a dataset in which 4 individuals were tested 4 times and the remaining 4 individuals were tested only twice. From my personal feelings, this test of neophobia is more discriminant than the test of “exploration”, in which I believe that we are more quantifying response to stress than exploratory behaviour.

Both experiments are first attempts and should be replicated and refined. This is an interesting avenue but limited so far to captive birds.

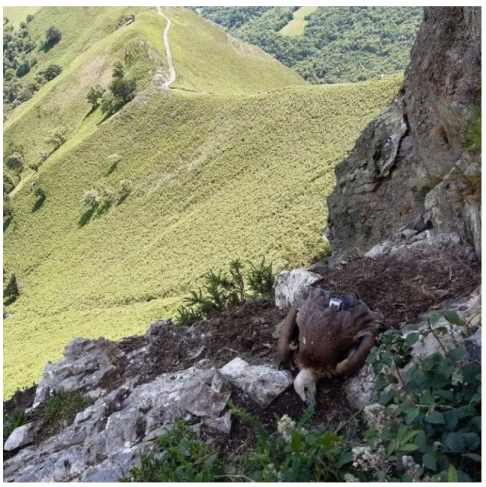
Annexe 7. La thèse c'est aussi …

… des captures qui ne fonctionnent pas …

Travailler sur les déplacements des vautours implique aussi de les équiper de balise GPS, et d'abord de les capturer. Et là ça se complique. Bien que nous, avec l'ensemble des collaborateurs sur le terrain qui reconnaîtront les situations au travers de ces lignes, soyons ingénieux, capturer des vautours n'est jamais une mince affaire. Cage avec fermeture à distance du toit et de la porte simultanément dans l'Aude, cage de capture passive avec des barreaux permettant théoriquement aux oiseaux de rentrer dans la cage mais pas d'en sortir au Pays Basque, et pourtant toujours le même résultat sur l'ensemble des tentatives de captures auxquelles j'ai participé dans ma première année de thèse. Beaucoup de temps à attendre pour zéro oiseau capturé. Pas de vautour à équiper ? Qu'à cela ne tienne, la première leçon de pose de balise GPS en baudrier se fera sur … une dinde royale ! La formation avant tout, puis bon, une dinde royale quand même, pas si différente d'un vautour en termes de taille, poids et structure de corps !

… mais avec un peu de persévérance on y arrive !

Deuxième année de thèse : puisque les vautours n'avaient visiblement pas envie de venir à nous, nous avons décidé d'aller à eux, en visant prioritairement ceux qui ne peuvent pas s'échapper : les jeunes au nid. J'ai pu participer à la pose de balises GPS sur les premiers poussins de vautours fauves équipés au nid en France, un programme de recherche initié par Olivier Duriez. N'oublions pas que c'est une espèce qui niche dans des falaises, ainsi ce qui semble facile nécessite tout de même de descendre en rappel dans les nids. En parallèle, nous avons persévéré dans la tentative de capture d'adulte, on a fini par réussir ! Et ça se fête !




… des expériences au Rocher des Aigles, Rocamadour

Travailler avec des vautours captifs possède un sacré avantage, on est sûr de les capturer à tous les coups. Enfin presque… parce que quand ils partent du Rocher des Aigles en vol libre, et bien, ils rentrent quand ils le veulent. « Force est de constater que nous n'avons pas tous le même sens du timing » disait souvent Oriane, lorsque les vautours ne montraient aucun signe de retour vers l'esplanade pendant l'animation du spectacle au parc. Il est arrivé plusieurs fois lors de mes expériences de vol que les oiseaux ne rentrent pas à la fin du dernier spectacle de la journée, il fallait donc aller les chercher sur les falaises du canyon de l'Alzou. Alors que le chef animalier, Basile, craignait pour la sécurité des oiseaux, je dois avouer que moi je m'inquiétais plutôt pour le matériel. Ces oiseaux cassent tout ! Être posé sur une falaise loin de mon regard leur laisse pas mal de temps pour malmener le matériel, et potentiellement détruire mes données de thèse... J'en profite pour remercier à nouveau Basile, une motivation sans faille pour m'aider à mener à bien mes expériences, et qui m'a toujours autorisé à le suivre dans ses virées à la recherche des vautours retardataires.

… des cours

J'ai eu la chance d'arriver en thèse lors du passage au LMD 5. Si les enseignants-chercheurs vous diront que ces changements dans les programmes les fatiguent quelque peu, de mon côté ça m'a permis d'intégrer l'équipe enseignante et de créer avec eux une nouvelle unité d'enseignement (UE) sur le comportement animal. Dans cette UE, destinée aux étudiants de 1ère et de 3ème année de licence, j'ai construit 2 cours magistraux (CM), 1 travail dirigé (TD) et 2 travaux pratiques (TP) sur les thèmes suivants :

- CM : Comportements sociaux
- CM : Cognition animale
- TD : Apport de l'étude du comportement animal
- TP : Estimation de la hiérarchie chez les vautours par l'analyse de vidéos collectées au Rocher des Aigles.

- TP : Théorie des jeux et biais de décision

Par ailleurs, j'ai pu intervenir dans d'autres UE notamment en écologie fonctionnelle, écologie évolutive et biologie intégrative. J'ai eu aussi l'opportunité d'assister aux sorties terrain pour les UE naturalistes et de biologie marine. Je remercie encore une fois Aurélie Célérier, Arnaud Grégoire et Olivier Duriez pour m'avoir fait confiance dans la création des cours en comportement animal. Ainsi que les directeurs des autres UEs dans lesquelles j'ai pu intervenir.

… et des conférences (scientifique et grand public).

Au cours de la thèse, j'ai eu la possibilité de participer aux évènements suivants :

- Sassi,Y., Nouzière, B., Sacco, M., Tremblay, Y., Duriez, O., Robira, B. (2022) Poster : The relative importance of contextual drivers in flight decision making of a soaring raptor. European Conference on Behavioral Biology 2022 - Groningen, Pays-Bas.

- Sassi, Y., Ziletti, N., Duriez, O., Robira. B. (2022) Présentation orale : Do vultures display avoidance behaviours in front of wind turbines? 28ème Rencontres Vautours - Rennes-le-Chateau, France.

- Sassi, Y., Ziletti, N., Duriez, O., Robira. B. (2022) Présentation orale : Do vultures display avoidance behaviours in front of wind turbines? Conference on Wind energy and Wildlife impacts 2022 - Egmond Aan Zee, Pays-Bas.

- Invité à présenter mon projet de thèse lors d'un café-débat sur les vautours, Le Kairn, Vallée d'Ossau, France (11th November 2021).

Résumé

Pour un animal, trouver les ressources nécessaires pour maintenir ses fonctions vitales, sa survie et sa reproduction peut s'avérer difficile lorsque celles-ci sont imprévisibles et distribuées de manière hétérogène dans l'environnement. Les vautours fauves bénéficient d'information sociale, glanée lors de l'interaction de leurs congénères avec l'environnement, en plus de leur information personnelle, acquise à travers leur propre expérience de cet environnement. Par des expériences réalisées en fauconnerie, je montre que certains facteurs internes (*i.e.* position dans la hiérarchie de dominance) et externes (*e.g.* météorologie) façonnent l'équilibre dans l'utilisation d'information personnelle et sociale dans la recherche de courants ascendants, nécessaires aux déplacements des vautours. L'information sociale semble aussi capitale dans leur recherche de carcasse, car j'ai mis en lumière au travers de suivis radar une stratégie de prospection alimentaire dans laquelle des groupes de vautours s'organisent dans l'espace de sorte à prospecter, de manière coordonnée, les zones d'alimentation tout en gardant leurs congénères en vue. Ces comportements augmentent l'efficacité de recherche de carcasses et permettent l'agrégation rapide de nombreux vautours pour la consommer. En revanche, ces rassemblements peuvent favoriser la propagation de maladies comme l'influenza aviaire hautement pathogène qui a touché des vautours fauves en 2022. En réponse à l'infection, je montre grâce à des suivis télémétriques un arrêt prolongé du déplacement des vautours, avant leur mort ou leur récupération progressive. Par ailleurs, face aux turbines des centrales éoliennes, je montre que les vautours ne présentent pas de comportement d'évitement anticipé, ce qui les rend particulièrement vulnérables aux collisions. Ainsi, bien que la vie en groupe procure des avantages, elle peut aussi entraîner des coûts tels que la compétition ou encore la propagation de maladies, nécessitant un ajustement constant du compromis entre l'utilisation des différentes sources d'information lors de la prise de décision.

Abstract

It can be difficult for an animal to find the resources it needs to maintain its vital functions, survival and reproduction when these resources are unpredictable and heterogeneously distributed in the environment. Griffon vultures benefit from social information gained from the interaction of their conspecifics with the environment, in addition to personal information acquired through their own experience of this environment. Using experiments on captive vultures, I show that some internal factors (i.e. position in the dominance hierarchy) and external factors (e.g. meteorology) shape the trade-off between the use of personal and social information in the search for updrafts necessary for vulture movement. Social information also seems to be crucial in their search for carcasses, as I have highlighted, through radar tracking, a foraging strategy in which groups of vultures organise themselves so that they can scan foraging areas in a coordinated way, while keeping their conspecifics in sight. This behaviour increases the efficiency in finding carcasses and enables large numbers of vultures to gather quickly to consume the carcass. On the other hand, these gatherings can facilitate the spread of diseases such as highly pathogenic avian influenza, which struck griffon vultures in 2022. Using telemetry monitoring, I show a prolonged interruption in vulture's movements, before their death or gradual recovery. In addition, I show that vultures do not show any anticipatory avoidance behaviour of wind turbines, which makes them particularly vulnerable to collisions. So, although group living brings benefits, it can also have costs such as competition or the spread of disease, requiring constant adjustment of the trade-off between the use of different sources of information when making decisions.