



**HAL**  
open science

# Stratégies de repos en milieu anthropisé, cas d'étude du sanglier (*Sus scrofa*)

Gustave Fradin

► **To cite this version:**

Gustave Fradin. Stratégies de repos en milieu anthropisé, cas d'étude du sanglier (*Sus scrofa*). Ecologie, Environnement. Université de Montpellier, 2023. Français. NNT: 2023UMONG028 . tel-04868693

**HAL Id: tel-04868693**

**<https://theses.hal.science/tel-04868693v1>**

Submitted on 6 Jan 2025

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

En Ecologie et Biodiversité

École doctorale GAIA

Unité de recherche CEFE - UMR 5175

## Stratégies de repos en milieu anthropisé, cas d'étude du sanglier (*Sus scrofa*)

Présentée par **Gustave FRADIN**  
Le 06 décembre 2023

Sous la direction de **Simon Chamailé-Jammes**

### Devant le jury composé de

**Francesca CAGNACCI**, Professeure, Fondation Edmund Mach, Trente, Italie

**Anne LOISON**, Directrice de recherche CNRS, Laboratoire d'Écologie Alpine, Chambéry, France

**Ferran JORI MASSANAS**, Chercheur Senior Cirad, UMR ASTRE, Montpellier, France

**Paul-Antoine LIBOUREL**, Ingénieur de recherche, CRNL, Bron, France

**Kévin MORELLE**, Ingénieur de recherche, Max Planck institute of animal behavior, Radolfzell, Allemagne

**Simon CHAMAILLÉ-JAMMES**, Directeur de recherche CNRS, CEFE, Montpellier, France

**Rapporteuse**

**Rapporteuse**

**Président du jury**

**Examineur**

**Membre invité**

**Directeur de thèse**



UNIVERSITÉ  
DE MONTPELLIER



À ma grand-mère,  
qui depuis trois ans se demande  
ce qui peut bien m'intéresser chez le sanglier...



# Remerciements

Déjà en Master à Lyon, je me projetais un peu au CEFÉ, et pourtant c'est presque par hasard que j'y ai débarqué. Après mon stage, c'était l'évidence : si je devais me lancer dans une thèse un jour, ce serait ici. Finalement, la pandémie de Covid m'a ramené à Montpellier plus tôt que prévu, et j'ai eu la chance incroyable d'être à nouveau accueilli par Simon. Bien sûr au début, les conditions n'étaient pas les plus confortables : c'était l'après-Covid, Sofia était à Lyon... mais il y avait du soleil, de jolis oiseaux, et surtout des personnes géniales, qui m'ont accompagné et soutenu tout au long de cette aventure Montpelliéraine, aussi bien dans la sphère professionnelle qu'en dehors. C'est le moment pour moi de leur adresser mes remerciements, en essayant de n'oublier personne.

\*\*\*

Tout d'abord, un grand merci aux personnes qui ont accepté d'évaluer mon travail : mes deux rapportrices, **Anne Loison** et **Francesca Cagnacci** (qui a gentiment accepté de me lire en français, merci beaucoup pour ça Francesca), ainsi que **Ferran Jori** et **Paul-Antoine Libourel**. Merci aussi à **Kévin Morelle**, pour avoir accepté de faire partie du jury, et pour ta réactivité, à chaque fois que j'avais besoin d'aide avec les données Euroboar. Je remercie également les membres de mon comité de thèse **Daniel Cornélis**, **Aurélié Coulon**, **Vincent Devictor**, **Arnaud Grégoire** et **Marion Valeix**.

Merci aussi aux photographes dont les clichés illustrent ce manuscrit, et en particulier un immense merci à **Daniel Maillard** sans qui les pages suivantes seraient bien ternes, et manqueraient cruellement de sangliers (si vous aimez la photographie animalière, n'hésitez pas à aller faire un tour par-là : [www.danielmaillard.com](http://www.danielmaillard.com)).

**Simon**, merci pour tout. Depuis mon stage en 2019 jusqu'à la fin de ma thèse, j'ai pu compter sur un directeur attentif et bienveillant. Merci de m'avoir fait confiance, et de m'avoir soutenu quand le moral était un peu bas. Dans ces moments difficiles, en particulier au début de la 2<sup>e</sup> année, j'avais au ralenti mais tu ne m'as jamais fait sentir la moindre pression, et je veux te remercier pour ça. Merci pour tes conseils pertinents, pour nos longues discussions qui m'ont aidé à avancer dans la bonne direction quand j'étais un peu perdu, et pour ta réactivité, en particulier en fin de thèse, quand je ne te laissais pas toujours beaucoup de temps pour relire mes manuscrits. Merci aussi pour les bons moments passés sur le terrain, avec ou sans sangliers, et en conf, à Barcelone et à Rome. Ce sont ces moments-là, hors du cadre du labo, qui m'ont permis de mieux te connaître, et qui me feront les meilleurs souvenirs. Pour tout ça, et pour les autres choses que j'oublie, merci.

Merci à toutes les personnes qui m'ont accompagné sur le terrain pour capturer des sangliers. Evidemment, c'était la partie la plus marrante, mais pas toujours une mince affaire. C'est qu'ils sont malins les bougres. D'abord, merci à **Sam**, toujours à fond ! C'était à la fois un plaisir et une expérience formatrice de passer du temps sur le terrain avec toi. On pourra dire qu'on a chassé quelques cochons ensemble, même s'il y a eu une ou deux sessions infructueuses, en particulier dans les Ecrins. Mais même à défaut de cochons, je me réjouis d'avoir eu l'occasion de passer ces moments avec toi. Merci aussi aux personnels du **Syndicat Mixte des Gorges du Gardon**, et du **Parc National des Ecrins** qui ont versé quelques gouttes de sueur pour nous aider avec les captures. Je pense en particulier à **Guillaume** et **Jérémy** pour le SMGG et à **Emmanuel, Baki** et **Samy** pour le PNE. Merci aussi aux personnes qui ont accepté que l'on pose des cages sur leur terrain. Un grand merci à toutes les personnes qui m'ont aidé à capturer les cochons : il y a eu **Deborah, Jules**, et quelques autres... Mention spéciale pour **Paul**, qui ne s'est jamais trop moqué de moi pour l'histoire des clés du Kangoo. En parlant de ça, merci aux membres de l'équipe du TE, qui eux n'ont généralement pas hésité à se moquer. Bien sûr, un grand merci à **David**, toujours souriant et prêt à filer un coup de main, avec une efficacité redoutable ! Enfin, merci pour leur patience aux partenaires des piégeurs de sangliers, qui subissent le réveil à 6h tous les matins dans l'hypothèse (parfois improbable) d'un sanglier pris au piège quelque part.

Merci à celles et ceux, académiques ou non, qui contribuent à faire du CEFE un lieu de travail si agréable. Merci à mes collègues de l'équipe MAD. **Yves, Aurélie, Olivier, Nico, Louise, David**, merci de faire de notre équipe un environnement sain et encourageant. **Simon B** merci de te préoccuper régulièrement de mon sommeil, je vais beaucoup mieux dormir maintenant. Un merci tout particulier à **Ana** et **Marion**, à qui la bonne ambiance qui règne à notre étage doit beaucoup.

Merci **Marie, Antoine, Edouard**, vous qui m'avez tellement bien accueilli au CEFE à mon arrivée en stage. A nos pauses café et à nos hurlements de rire !

Merci à ceux qui ont supporté l'épreuve de partager mon bureau... Merci **Paul, Sara** et **Gio** pour les longues discussions et les bonnes rigolades. **Ben** aussi. On peut presque dire que tu en fais partie. Merci pour la façon dont tu vis et fais vivre la musique.

Merci aux stagiaires, doctorants et doctorantes, et autres précaires de la recherche dont j'ai croisé la route au CEFE. Merci aux basketteurs et basketteuses, merci aux coincheuses et coincheurs. **Adé, Noa, Samson**, je pense à vous. **Romain** aussi. Merci de m'avoir emmené au foot, c'est un grand regret de ne pas t'y avoir suivi plus tôt. **Jan**, merci pour ton soutien et pour tes plans dictatoriaux. **Fanny, Nico, Lilian** qu'est-ce qu'on a pu se marrer... Merci pour les grosses clés. Enfin **Yohan**, compagnon de thèse, on aura grimpé dans quelques arbres, et bien charbonné ensemble. Merci pour la machine à café. Plus globalement merci aux jeunes de MAD, HAIR et NCS

avec qui j'ai partagé le 3<sup>e</sup> : **João, Ninon, Thibaut, Maud, Oksana, Javi, Tristan...** et bien d'autres encore. **Gilles** tu fais partie de cette clique-là, merci pour le grain de folie et pour le schlaglier. J'oublie certainement du monde, ne m'en voulez pas...

En dehors du labo, merci aux vieux de la vieille, **Basile, Simon, Paul, Manue, Cyril, Alice, Sophie, Constant.** Si j'en suis ici aujourd'hui, c'est en grande partie grâce à vous. Merci aussi pour m'avoir si bien préparé à cette thèse. Tout ce que j'ai appris auprès des sangliers, je l'avais déjà appris auprès de vous. **Emma** je ne sais plus trop où te mettre dans ces remerciements. J'ai adoré partager ces années avec toi à Montpellier, je crois qu'on est faits pour être voisins donc c'est peut-être pas fini, qui sait !

Merci aux collemboles indépendants, **Mamou, Carole, la Gonelle, Windy, Julia, Léo, Nico,** je vous aime. Où que l'on soit, il y aura une place pour les squatteurs (qui se reconnaîtront). **Val...** merci pour tout. La thèse aurait été bien différente sans toi. Je t'enverrai les squatteurs en trop. **Marsouille, Thib, Jim, Alexis** malgré la distance, je vous oublie pas.

Merci à **Alice et Bastien** pour l'open-space Guillestrois. Merci aussi à **Jérôme, Cyrille et Man,** qui m'ont laissé entrevoir un après-thèse rassurant auquel me raccrocher.

Merci aux Montpelliérains, **Stan & Marie, Asli Begüm Guy, Witold & Iris, Fanny & Seba, Manon & Morgan,** pour les bons moments passés ensemble, à Montpellier et aux alentours.

Bien sûr, un immense merci à **mes parents,** qui m'ont soutenu tout au long de mon parcours. Merci d'avoir toujours été derrière nous, dans les projets qu'on a eus au cours de la thèse, avec **Soffia.** Et puis aussi désolé pour l'histoire du tricycle. Merci à mes frères, et à ma sœur. **Etienne, Cyp et Colombine,** vous avez survécu à une enfance avec moi, c'est déjà un gage de qualité. Merci de m'avoir supporté pendant toutes ces années, et désolé pour les crasses que j'ai pu vous faire. Merci aussi à **Mamie** pour ton soutien, même si j'ai l'impression que mon sujet d'étude ne t'a jamais trop enchanté...

Le dernier remerciement est pour toi **Soffia.** Merci de m'avoir soutenu pendant ces trois années, alors même que souvent tu en avais au moins autant besoin que moi. Merci pour ce mois de mai 2023 qui restera pour toujours une parenthèse en suspens. Merci, surtout, de me donner une direction dans laquelle regarder. En plus de tout le reste, il faut bien que je te le dise : merci pour les fruits coupés.

\*\*\*

Enfin, à celles et ceux qui se posent encore la grande question éternelle, ne vous en faites plus :

**Les sangliers vont bien.**





# Table des matières

<b>INTRODUCTION GÉNÉRALE</b> .....	<b>11</b>
1. Le comportement animal face à l'anthropisation .....	11
2. Le repos face à l'anthropisation .....	15
3. Objectifs de la thèse .....	16
<b>RÉFÉRENCES</b> .....	<b>19</b>
<b>PREMIER AXE : L'ÉCOLOGIE DU REPOS DANS UN MONDE ANTHROPIsé</b> .....	<b>25</b>
<b>CHAPITRE 1</b> .....	<b>27</b>
1. Introduction .....	29
2. What is resting? .....	31
3. Why resting? .....	36
4. How to rest? .....	41
5. Unknown effects of anthropization .....	45
6. Conclusions .....	51
<b>RÉFÉRENCES</b> .....	<b>53</b>
<b>SECOND AXE : CAS D'ÉTUDE DU SANGLIER</b> .....	<b>73</b>
<b>INTRODUCTION</b> .....	<b>75</b>
1. Une espèce charismatique de la faune Européenne .....	75
2. Un animal controversé .....	77
3. La flexibilité comportementale du sanglier .....	78
4. Un modèle pour étudier le repos en milieu anthropisé .....	81
5. Objectifs du second axe .....	84
<b>MATÉRIEL &amp; MÉTHODES</b> .....	<b>87</b>
1. Sites d'étude .....	87
2. Captures .....	89
3. Suivi télémétrique .....	93
4. Réalisations annexes .....	99
<b>CHAPITRE 2</b> .....	<b>101</b>
1. Introduction .....	103
2. Materials & methods .....	105
3. Results .....	111
4. Discussion .....	117
Appendices .....	122
<b>CHAPITRE 3</b> .....	<b>131</b>
1. Introduction .....	133
2. Materials & methods .....	135
3. Results .....	140
4. Discussion .....	143
Appendices .....	148
<b>RÉFÉRENCES</b> .....	<b>163</b>
<b>DISCUSSION GÉNÉRALE</b> .....	<b>175</b>
1. Résumé des chapitres et résultats .....	175
2. Perspectives .....	181
3. Conclusion .....	185
<b>RÉFÉRENCES</b> .....	<b>187</b>





# Introduction générale

## 1 Le comportement animal face à l'anthropisation

### 1.1 Un monde en rapide changement

Depuis la révolution industrielle, les écosystèmes terrestres font face à une série de bouleversements sans précédent. Partout, les paysages, les communautés vivantes et les conditions climatiques se transforment. A l'échelle globale, les écosystèmes se détériorent à un rythme inédit. La principale cause de ces dégradations sont les activités humaines qui, depuis la révolution industrielle, n'ont cessé d'augmenter leur impact sur la biodiversité (Purvis et al. 2019). Nous sommes entrés dans la sixième extinction de masse, ce qui signifie que les espèces vivantes disparaissent aujourd'hui à un rythme rarement atteint—si ce n'est jamais—au cours des quelques 3,5 Milliards d'années d'existence de la vie sur Terre (Ceballos et al. 2017; Cowie et al. 2022). Dans ce contexte, l'avenir de la biodiversité est plus qu'incertain (Shin et al. 2019).

Parmi les facteurs les plus décisifs dans cette érosion de la biodiversité, comptent la dégradation des paysages et la disparition des habitats, qui touchent tous les milieux (Brook et al. 2008; Davison et al. 2021). En 1700, environ 50% des écosystèmes terrestres étaient encore vierges de toute altération d'origine anthropique, et 45% demeuraient dans un état semi-naturel, légèrement impactés par l'agriculture. En l'an 2000, seuls 25% et 20% des écosystèmes terrestres persistaient dans des états respectivement naturel, et semi-naturel (Ellis et al. 2010). La majorité de la surface terrestre émergée est aujourd'hui couverte de paysages fortement structurés par les activités humaines, qu'ils soient agricoles, urbains ou péri-urbains. Ainsi, l'expansion des paysages anthropiques de 5% à 55% de la surface terrestre s'est produite en seulement 300 ans. L'extrême rapidité de ce bouleversement global est d'autant plus frappante que la majeure partie de cette transformation a eu lieu au cours du 20<sup>e</sup> siècle, et continue aujourd'hui à un rythme effréné.

L'agriculture représente le plus puissant vecteur de dégradation des paysages. L'espace dédié à la production agricole s'étend année après année, fractionnant les régions où l'emprise humaine est encore réduite (Foley et al. 2011; Tilman et al. 2011). Il représente aujourd'hui plus d'un tiers de la surface terrestre (Balvanera et al. 2019). Les terres cultivées s'étendaient à elles-seules sur 12,2% des terres en 2015, alors qu'elles n'en occupaient que 2,2% en 1700 (Klein Goldewijk et al. 2017). De la même façon, les surfaces dévolues à l'élevage ont connu une expansion fulgurante. Les pâturages intensifs, notamment, se sont étendus de 1,1% à 6% de la surface terrestre entre 1700 et 2015. Cette expansion s'est produite en grande partie aux dépens des forêts tropicales, riches en biodiversité, à travers la déforestation (FAO 2016). L'expansion des terres agricoles conduit à la disparition des habitats de nombreuses espèces, et produit des paysages fragmentés, dans lesquelles les dynamiques écologiques sont profondément altérées. A l'échelle globale, la fragmentation des espaces naturels, c'est-à-dire la discontinuité spatiale des ressources et des conditions environnementales, est considérable (Fahrig 2003). Haddad et al. (2015) ont estimé que 70% de la surface forestière globale était située à moins de 1 km d'une lisière.

L'urbanisation, qui correspond à une artificialisation généralisée des sols dans une enceinte donnée, a doublé entre 1992 et 2015 (Balvanera et al. 2019). Les surfaces urbanisées représentent une proportion relativement faible de la surface terrestre (0,5 % des terres en 2015; Klein Goldewijk et al. 2017), mais l'urbanisation a un impact fort sur les espaces naturels environnants. Ceux-ci sont généralement liés à la pollution chimique (Lee et al. 2006), sonore (Marín-Gómez and MacGregor-Fors 2021), lumineuse (Raap et al. 2015), et entre autres, au développement d'infrastructures de transport (Venter et al. 2016), qui constituent d'importantes barrières physiques pour de nombreuses espèces (Bennett 2017).

Les paysages anthropisés sont également caractérisés par la présence humaine, qui n'a cessé d'augmenter avec la croissance démographique humaine, l'augmentation des prélèvements directs liés à la chasse, la pêche et l'exploitation forestière, ainsi que la popularisation des loisirs de plein air (Balvanera et al. 2019). La présence humaine a un effet sur la faune qui diffère de celui du taux d'anthropisation de l'habitat, car elle façonne un paysage de la peur très contraignant pour de nombreuses espèces (Nickel et al. 2020; Corradini et al. 2021). Ceci est vrai dans les milieux densément peuplés mais aussi dans des régions où les densités de peuplement humain sont faibles, notamment via la chasse (Ripple et al. 2016) et les autres activités récréatives (Naylor et al. 2009; Marzano and Dandy 2012). Les dérangements anthropiques sont ainsi associés au déclin de nombreuses espèces (Beale and Monaghan 2004).

Enfin, il est difficile de parler des changements globaux auxquels fait face la biodiversité sans mentionner le dérèglement du climat, et les invasions biologiques qui, bien qu'ils ne seront que

peu abordés dans cette thèse, représentent deux menaces majeures pour la biodiversité à l'échelle globale (Hogue and Breon 2022).

Ainsi, dans la plupart des milieux, les animaux sont aujourd'hui confrontés à des contextes radicalement différents de ceux qui prévalaient jusque quelques décennies auparavant. Une grande partie des habitats naturels ont disparu, et ceux qui persistent sont pour la plupart fortement fragmentés, et soumis à la fréquentation humaine. De nombreuses espèces sont ainsi contraintes à faire face à des conditions nouvelles, incohérentes avec leur histoire évolutive.

## **1.2 La biodiversité face aux pressions anthropiques**

Face à la rapidité des transformations que subit l'environnement, la plupart des mécanismes classiques par lesquels le vivant s'adapte au changement sont peu efficaces (Parmesan 2006). En effet, l'évolution des espèces vivantes vers des formes adaptées à leur environnement repose en grande partie sur la sélection naturelle. Celle-ci agit sur des différences interindividuelles survenues aléatoirement au sein des populations, au gré de mutations, recombinaisons, et autres évènements stochastiques inhérents au maintien et à la reproduction de l'information génétique.

La sélection de phénotypes mieux adaptés à des conditions nouvelles peut être rapide. C'est ainsi que l'on a observé chez certaines espèces, suite à la mise en place par l'être humain de pressions de chasse extrêmes, la généralisation de traits opposés à ceux recherchés par les chasseurs (Otto 2018). C'est par exemple le cas de la réduction de la taille des défenses chez les éléphants d'Afrique, liée au commerce de l'ivoire (Chiyo et al. 2015; Campbell-Staton et al. 2021), ou du déclin du morphe argenté, très prisé par les trappeurs, chez les renards Nord-Américains (Haldane 1942). De la même façon, la pêche industrielle a entraîné une réduction de la taille et de l'âge de la maturité sexuelle chez de nombreuses espèces commerciales de poissons (Sharpe and Hendry 2009). En revanche, si de nombreux traits (anatomiques, ontogénétiques, physiologiques, etc.) présentent une variabilité naturelle au sein des populations, sur laquelle la sélection peut agir, cette variabilité est souvent insuffisante pour permettre une réponse proportionnée aux modifications rapides de l'environnement. Lorsque les modifications des conditions environnementales sont trop marquées, de nombreuses espèces ne peuvent pas persister dans les paysages altérés. Ainsi, les changements globaux conduisent de nombreuses espèces, incapables de s'adapter aux nouvelles conditions, à modifier leur répartition pour retrouver des conditions environnementales pour lesquelles elles sont adaptées, où à disparaître (Parmesan 2006; Wong and Candolin 2015).

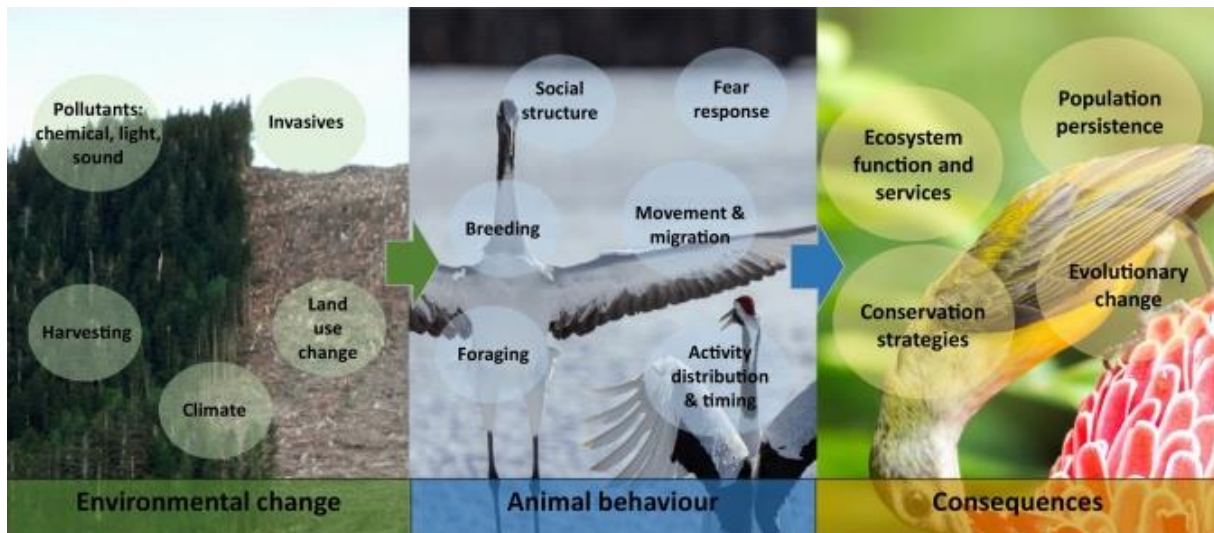
## **1.3 Une réponse possible : l'ajustement du comportement**

Les animaux qui persistent dans des environnements anthropisés répondent souvent aux altérations de leur milieu par l'ajustement de leur comportement (*Figure 1*; Candolin et al. 2023).

Parmi les exemples bien documentés figurent la phénologie de la migration et de la reproduction de nombreuses espèces, qui sont affectées par les altérations du climat (Inouye 2022), ou encore les patrons journaliers d'activité, qui varient en fonction de la pression liée à la présence humaine dans les espaces naturels (Gilbert et al. 2023). Un même individu peut adopter des comportements différents, en réponse à des stimuli contrastés. Ces ajustements comportementaux dépendent des conditions extérieures mais aussi de la motivation de l'individu. La variabilité intra-individuelle du comportement représente un mécanisme d'ajustement particulièrement efficace car elle permet aux animaux de réagir à des situations nouvelles à l'échelle de leur vie (Melin et al. 2008), comme à l'échelle de l'histoire évolutive de leur espèce, et donc de persister dans des environnements où les conditions ont été fortement altérées.

Par ailleurs, différents individus peuvent adopter des comportements différents face à une même situation. C'est la variabilité inter-individuelle du comportement. Si une tendance comportementale est stable dans un intervalle de temps, on parle de stratégie comportementale. Différentes populations appartenant à une même espèce peuvent présenter des stratégies comportementales différentes en fonction du niveau de pression anthropique perçu (Samia et al. 2015). Ainsi par exemple, il a été montré que chez de nombreuses espèces, les individus issus de populations urbaines sont généralement moins prudents et craintifs que leurs congénères des milieux ruraux (Miranda et al. 2013). La flexibilité inter-individuelle du comportement d'une espèce est donc un atout pour persister dans des paysages contrastés (Tuomainen and Candolin 2011).

La variabilité du comportement dans une population a une base génétique, et certains traits comportementaux sont héréditaires (Dochtermann et al. 2015), mais elle est également influencée par l'expérience de vie des individus (Jones et al. 2021). Chez certaines espèces, la transmission de stratégies comportementales aux congénères ou aux descendants a été démontrée (Seppänen et al. 2010). Ainsi, les comportements adaptés à de nouvelles conditions de vie peuvent, par plusieurs mécanismes, être transmis à la génération suivante, et fournir un moyen d'adaptation aux populations. La flexibilité du comportement est donc un outil précieux dans la réponse des animaux aux altérations anthropiques de leur environnement. Le comportement peut notamment permettre un ajustement à des changements rapides, là où les autres mécanismes d'adaptations sont souvent trop lents pour permettre la persistance d'une espèce.



*Figure 1. Conséquences des effets des changements environnementaux sur le comportement animal. Adapté de Candolin et al. (2023).*

## 2 Le repos face à l'anthropisation

### 2.1 La face cachée du comportement animal

Dans une édition spéciale intitulée « Special issue: Animal behaviour in a changing world » publiée en avril 2023, la revue « Trends in Ecology and Evolution » propose de démontrer l'importance des réponses comportementales dans le devenir de la biodiversité, face aux changements globaux. De multiples mécanismes d'ajustement sont présentés, et les comportements concernés sont résumés dans un schéma conceptuel publié dans l'édito (*Figure 1*; Candolin et al. 2023). Cependant, un aspect essentiel du comportement animal semble manquer à ce schéma, ainsi qu'à l'édition spéciale toute entière : le repos. Cette absence illustre le peu d'attention que les écologues accordent généralement aux comportements inactifs, probablement en raison de l'absence de mouvements associés. Malgré leur caractère essentiel, ils sont le plus souvent laissés pour compte dans les études qui traitent du comportement face aux changements globaux (Tuomainen and Candolin 2011; Wong and Candolin 2015; Gunn et al. 2022).

Pourtant, pour vivre dans un habitat donné, un animal doit être en mesure d'y trouver des refuges adéquats pour se reposer, ou bien de se déplacer régulièrement pour se reposer ailleurs. Par ailleurs, les animaux consacrent chaque jour un temps considérable aux comportements inactifs. Les stratégies de repos employées par les animaux sont façonnées par des contraintes non seulement physiologiques, mais aussi écologiques (Lima et al. 2005; Siegel 2009), qui sont susceptibles d'entrer en conflit avec celles imposées par les activités humaines (Aulsebrook et al. 2018; Mohanty et al. 2022). Face aux pressions anthropiques toujours grandissantes, le repos



animal est bien sûr affecté, mais les mécanismes de ces perturbations sont mal connus, et leurs effets mal anticipés.

### **2.2 Un potentiel d'ajustement**

Le repos présente une vulnérabilité importante aux changements globaux, avec des implications majeures pour l'équilibre énergétique, les performances cognitives, la thermorégulation, l'évitement de la prédation, et l'utilisation de l'espace et du temps. Pour se reposer, les animaux dépendent de la disponibilité de sites de repos, qui tendent à disparaître dans certains paysages fragmentés ou modifiés par l'activité humaine. Le repos peut également rendre vulnérable à la prédation et aux dérangements, ce qui est parfois incompatible avec l'augmentation du risque de dérangements anthropiques. Par de multiples mécanismes, l'anthropisation est donc susceptible d'influencer les lieux, les moments et les conditions dans lesquelles les animaux sont en mesure de se reposer. Il est aisé d'imaginer que dans certains cas, ces pressions sur le comportement de repos peuvent affecter les performances des individus, et l'abondance et la distribution des espèces. Pourtant jusqu'ici, les écologues n'ont montré que très peu d'intérêts pour ces processus.

L'ajustement des stratégies de repos peut contribuer à la persistance ou au succès des espèces capables de flexibilité dans les espaces les plus anthropisés. Par exemple, la transition de certaines espèces vers des modes de vie nocturnes dans les milieux anthropisés est un mécanisme d'ajustement bien documenté, qui repose sur une modification de la stratégie de repos (Gaynor et al. 2018). Pourtant, les études abordant cette question la traitent systématiquement sous l'angle de l'activité, et ne mentionnent que rarement les phases inactives (Gilbert et al. 2023). En devenant nocturne en milieu anthropisé, un animal évite les rencontres avec l'être humain lorsqu'il est actif, mais il soumet ses phases de repos, alors diurnes, à un risque de dérangement plus élevé. Il peut donc être contraint à également modifier la façon dont il sélectionne ses sites de repos, pour réduire le risque de dérangement. Pourtant, la façon dont les activités humaines influencent la sélection des sites de repos par les animaux est peu documentée. Cet exemple illustre à la fois l'importance de l'ajustement du comportement de repos pour la persistance des espèces animales dans les milieux anthropisés, et le peu de connaissances disponibles à ce jour sur ce sujet.

## **3 Objectifs de la thèse**

Cette thèse est divisée en deux axes. Le premier axe propose un cadre théorique à l'étude des effets de l'anthropisation sur le comportement de repos, en écologie. Le second axe constitue un cas d'étude.

### 3.1 Objectifs du premier axe

Dans le premier axe, je présente une revue de littérature traitant du comportement de repos chez les vertébrés terrestres, avec un regard issu du domaine de l'écologie. Les objectifs sont multiples :

- (1) Proposer une définition opérationnelle du repos pour les écologues.
- (2) Établir l'état des connaissances au sujet des stratégies de repos, et des mécanismes par lesquelles elles sont affectées par les activités humaines.
- (3) Souligner le déficit de connaissances existant à ce jour dans ce domaine.

Dans cette revue de littérature, je présente les stratégies de repos utilisées par les vertébrés terrestres et leurs implications écologiques. J'y discute des fonctions des différentes composantes du repos, qui sont diverses et pour certaines très débattues, ainsi que les raisons qui poussent les animaux à se reposer. Je résume la diversité des stratégies de repos utilisées par les vertébrés terrestres, et notamment où, quand, combien de temps, et avec qui les espèces animales choisissent de se reposer. Enfin, je détaille les mécanismes par lesquels les perturbations d'origines anthropiques peuvent interférer avec ces stratégies.

### 3.2 Objectifs du second axe

Dans le second axe de cette thèse, j'utilise les concepts développés dans le premier axe pour explorer les impacts des activités humaines sur la stratégie de repos d'un grand mammifère des milieux anthropisés : le sanglier. Cette espèce est connue pour sa flexibilité comportementale et est soumise à des pressions anthropiques diverses, incluant les modifications du paysage et les dérangements directs (dont la chasse). Elle constitue un objet d'étude intéressant pour analyser l'influence de l'anthropisation sur les stratégies de repos.

Cet axe est composé de deux études indépendantes, mais toutes deux s'intéressent tout particulièrement à l'aspect spatial de la stratégie de repos du sanglier, en relation avec les modifications du paysage et les dérangements directs liés aux activités humaines. Les objectifs de cet axe peuvent être résumés de la façon suivante :

- (1) Décrire la dynamique spatiale d'utilisation des sites de repos par le sanglier, afin d'identifier les paramètres qui influencent la stratégie de repos chez cette espèce.
- (2) Identifier en particulier les effets de l'anthropisation sur les aspects spatiaux de la stratégie de repos du sanglier.
- (3) Questionner l'efficacité de la stratégie d'ajustement utilisée en estimant la fréquence des dérangements subis par les sangliers pendant leur phase de repos.

## INTRODUCTION GÉNÉRALE

---

(4) Explorer l'influence de la stratégie spatiale de repos sur l'ensemble des déplacements effectués par le sanglier.

Les détails de ces objectifs, et la façon dont ces questions sont abordées dans les deux études qui composent le second axe de cette thèse sont présentés de façon plus élaborée en introduction de l'axe en question.



## Références

Aulsebrook AE, Jones TM, Mulder RA, Lesku JA. 2018. Impacts of artificial light at night on sleep: A review and prospectus. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*. 329(8–9):409–418. doi:10.1002/jez.2189.

Balvanera P, Pfaff A, Viña A, Garcia Frapolli E, Hussain SA, Merino L, Minang PA, Nagabhatla N, Sidorovich A. 2019. Chapter 2.1 Status and Trends –Drivers of Change. Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Brondízio, E. S., Settele, J., Díaz, S., Ngo, H. T. (eds). IPBES secretariat, Bonn, Germany. doi:10.5281/zenodo.5517423.

Beale CM, Monaghan P. 2004. Human disturbance: people as predation-free predators? *Journal of Applied Ecology*. 41(2):335–343. doi:10.1111/j.0021-8901.2004.00900.x.

Bennett VJ. 2017. Effects of Road Density and Pattern on the Conservation of Species and Biodiversity. *Curr Landscape Ecol Rep*. 2(1):1–11. doi:10.1007/s40823-017-0020-6.

Brook BW, Sodhi NS, Bradshaw CJA. 2008. Synergies among extinction drivers under global change. *Trends Ecol Evol*. 23(8):453–460. doi:10.1016/j.tree.2008.03.011.

Campbell-Staton SC, Arnold BJ, Gonçalves D, Granli P, Poole J, Long RA, Pringle RM. 2021. Ivory poaching and the rapid evolution of tusklessness in African elephants. *Science*. 374(6566):483–487. doi:10.1126/science.abe7389.

Candolin U, Fletcher RJ, Stephens AEA. 2023. Animal behaviour in a changing world. *Trends in Ecology & Evolution*. 38(4):313–315. doi:10.1016/j.tree.2023.02.006.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*. 114(30):E6089–E6096. doi:10.1073/pnas.1704949114.

Chiyo PI, Obanda V, Korir DK. 2015. Illegal tusk harvest and the decline of tusk size in the African elephant. *Ecology and Evolution*. 5(22):5216–5229. doi:10.1002/ece3.1769.

Corradini A, Randles M, Pedrotti L, van Loon E, Passoni G, Oberosler V, Rovero F, Tattoni C, Ciolli M, Cagnacci F. 2021. Effects of cumulated outdoor activity on wildlife habitat use. *Biological Conservation*. 253:108818. doi:10.1016/j.biocon.2020.108818.

Cowie RH, Bouchet P, Fontaine B. 2022. The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews*. 97(2):640–663. doi:10.1111/brv.12816.

Davison CW, Rahbek C, Morueta-Holme N. 2021. Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. *Global Change Biology*. 27(21):5414–5429. doi:10.1111/gcb.15846.

Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*. 282(1798):20142201. doi:10.1098/rspb.2014.2201.

Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, Ramankutty N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*. 19(5):589–606. doi:10.1111/j.1466-8238.2010.00540.x.

Fahrig L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*. 34(1):487–515. doi:10.1146/annurev.ecolsys.34.011802.132419.

FAO. 2016. State of the World's Forests 2016. Forests and Agriculture: Land-Use Challenges and Opportunities. Rome, Italy: FAO. <https://www.fao.org/3/a-i5588e.pdf>.

Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PC, et al. 2011. Solutions for a cultivated planet. *Nature*. 478(7369):337–342. doi:10.1038/nature10452.

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. *Science*. 360(6394):1232–1235. doi:10.1126/science.aar7121.

Gilbert NA, McGinn KA, Nunes LA, Shipley AA, Bernath-Plaisted J, Clare JDJ, Murphy PW, Keyser SR, Thompson KL, Nelson SBM, et al. 2023. Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution*. 38(4):324–336. doi:10.1016/j.tree.2022.10.008.

Gunn RL, Hartley IR, Algar AC, Niemelä PT, Keith SA. 2022. Understanding behavioural responses to human-induced rapid environmental change: a meta-analysis. *Oikos*. 2022(4):e08366. doi:10.1111/oik.08366.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*. 1(2):e1500052. doi:10.1126/sciadv.1500052.

Haldane JBS. 1942. The selective elimination of silver foxes in Eastern Canada. *Journ of Genetics*. 44(2):296–304. doi:10.1007/BF02982833.

Hogue AS, Breon K. 2022. The greatest threats to species. *Conservation Science and Practice*. 4(5):e12670. doi:10.1111/csp2.12670.

Inouye DW. 2022. Climate change and phenology. *WIREs Climate Change*. 13(3):e764. doi:10.1002/wcc.764.

Jones NAR, Spence-Jones HC, Webster M, Rendell L. 2021. Individual behavioural traits not social context affects learning about novel objects in archerfish. *Behav Ecol Sociobiol*. 75(3):58. doi:10.1007/s00265-021-02996-4.

Klein Goldewijk K, Beusen A, Doelman J, Stehfest E. 2017. Anthropogenic land use estimates for the Holocene – HYDE 3.2. *Earth System Science Data*. 9(2):927–953. doi:10.5194/essd-9-927-2017.

Lee SY, Dunn RJK, Young RA, Connolly RM, Dale PER, Dehayr R, Lemckert CJ, Mckinnon S, Powell B, Teasdale PR, et al. 2006. Impact of urbanization on coastal wetland structure and function. *Austral Ecology*. 31(2):149–163. doi:10.1111/j.1442-9993.2006.01581.x.

Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ. 2005. Sleeping under the risk of predation. *Animal Behaviour*. 70(4):723–736. doi:10.1016/j.anbehav.2005.01.008.

Marín-Gómez OH, MacGregor-Fors I. 2021. A global synthesis of the impacts of urbanization on bird dawn choruses. *Ibis*. 163(4):1133–1154. doi:10.1111/ibi.12949.

Marzano M, Dandy N. 2012. Recreationist behaviour in forests and the disturbance of wildlife. *Biodivers Conserv*. 21(11):2967–2986. doi:10.1007/s10531-012-0350-y.

Melin SR, DeLong RL, Siniff DB. 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Can J Zool*. 86(3):192–206. doi:10.1139/Z07-132.

Miranda AC, Schielzeth H, Sonntag T, Partecke J. 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*. 19(9):2634–2644. doi:10.1111/gcb.12258.

Mohanty NP, Wagener C, Herrel A, Thaker M. 2022. The ecology of sleep in non-avian reptiles. *Biological Reviews*. 97(2):505–526. doi:10.1111/brv.12808.

Naylor LM, Wisdom MJ, Anthony RG. 2009. Behavioral Responses of North American Elk to Recreational Activity. *The Journal of Wildlife Management*. 73(3):328–338. doi:10.2193/2008-102.

Nickel BA, Suraci JP, Allen ML, Wilmers CC. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*. 241:108383. doi:10.1016/j.biocon.2019.108383.

Otto SP. 2018. Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences*. 285(1891):20182047. doi:10.1098/rspb.2018.2047.

Parmesan C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*. 37(1):637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.

Purvis A, Molnár Z, Obura D, Ichii K, Willis K, Chettri N, Dulloo M, Hendry A, Gabrielyan B, Gutt J, et al. 2019. Chapter 2.2 Status and Trends –Nature. Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Brondízio, E. S., Settele, J., Díaz, S., Ngo, H. T. (eds). IPBES secretariat, Bonn, Germany. doi:10.5281/zenodo.5517457.

Raap T, Pinxten R, Eens M. 2015. Light pollution disrupts sleep in free-living animals. *Sci Rep*. 5(1):13557. doi:10.1038/srep13557.

Ripple WJ, Abernethy K, Betts MG, Chapron G, Dirzo R, Galetti M, Levi T, Lindsey PA, Macdonald DW, Machovina B, et al. 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*. 3(10):160498. doi:10.1098/rsos.160498.

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT. 2015. Increased tolerance to humans among disturbed wildlife. *Nat Commun*. 6(1):8877. doi:10.1038/ncomms9877.

Seppänen J-T, Forsman JT, Mönkkönen M, Krams I, Salmi T. 2010. New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B: Biological Sciences*. 278(1712):1736–1741. doi:10.1098/rspb.2010.1610.

Sharpe DMT, Hendry AP. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol Appl*. 2(3):260–275. doi:10.1111/j.1752-4571.2009.00080.x.

Shin Y-J, Arneth A, Chowdhury RR, Midgley GF, Bukvareva E, Heinimann A, Horcea-Milcu AI, Kolb M, Leadley P, Oberdorff T, et al. 2019. Chapter 4. Plausible futures of nature, its contributions to people and their good quality of life. Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Brondízio, E. S., Settele, J., Díaz, S., Ngo, H. T. (eds). IPBES secretariat, Bonn, Germany. doi: 10.5281/zenodo.5656910

Siegel JM. 2009. Sleep viewed as a state of adaptive inactivity. *Nature Reviews Neuroscience*. 10(10):747–753. doi:10.1038/nrn2697.

Tilman D, Balzer C, Hill J, Befort BL. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*. 108(50):20260–20264. doi:10.1073/pnas.1116437108.

Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced environmental change. *Biol Rev Camb Philos Soc*. 86(3):640–657. doi:10.1111/j.1469-185X.2010.00164.x.

Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, Fekete BM, et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun*. 7(1):12558. doi:10.1038/ncomms12558.

Wong BBM, Candolin U. 2015. Behavioral responses to changing environments. *Behavioral Ecology*. 26(3):665–673. doi:10.1093/beheco/aru183.





# Premier Axe



L'écologie du repos  
dans un monde anthropisé



# Chapitre 1



**Résumé :** L'inactivité constitue un aspect prépondérant de la vie des animaux, et représente généralement une part importante de leur budget temps. Les conditions dans lesquelles les comportements inactifs ont lieu sont donc susceptibles d'avoir des effets importants sur la valeur sélective des individus. Pourtant, les études portant sur les conséquences écologiques des perturbations des comportements inactifs sont rares, et en particulier celles traitant des effets de l'anthropisation. Dans cette revue de littérature, nous proposons de regrouper plusieurs états comportementaux, et en particulier l'éveil calme, le sommeil et la torpeur journalière, sous le terme de « repos » afin de faciliter l'étude de l'inactivité dans les contextes naturels. Nous détaillons les déterminants physiologiques et environnementaux qui stimulent les comportements qui composent le repos, ainsi que leurs conséquences écologiques. Nous montrons en quoi la diversité des comportements de repos peut permettre une certaine flexibilité dans les réponses comportementales aux contraintes liées au métabolisme, à la disponibilité des ressources, au risque de prédation, et à la thermorégulation. Nous détaillons comment le lieu, le moment, et le contexte social dans lesquels se produit le repos, définissent ensemble une stratégie de repos qui peut être ajustée à des conditions environnementales changeantes. Enfin, nous explorons les mécanismes par lesquels l'anthropisation peut affecter les stratégies de repos à travers l'augmentation du risque de dérangement direct, l'altération des habitats et des communautés, et les effets du changement climatique.

**Mots clés :** activités humaines, ajustements comportementaux, inactivité, sommeil

# The ecology of resting behavior, and the unknown effects of anthropization

Gustave Fradin<sup>1</sup>, Andrew Sih<sup>2</sup>, Aurélie Coulon<sup>1,3</sup>, Paul-Antoine Libourel<sup>4</sup>,  
Adrian M. Shrader<sup>5</sup>, Bianca Teseling<sup>5</sup>, Marion Valeix<sup>1</sup>,  
Simon Chamailé-Jammes<sup>1,5</sup>

1. CEFÉ, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France
2. Department of Environmental Science and Policy, University of California, Davis, USA
3. CESCO, MNHN, CNRS, Sorbonne University, Paris, Concarneau, France
4. CRNL, CNRS, INSERM, Université Claude Bernard Lyon 1, Bron, France
5. Mammal Research Institute, University of Pretoria, Pretoria, South Africa

**Abstract:** Inactive behaviors are a preponderant component of animals' lives, generally representing important proportions of time budgets. The conditions in which they occur are thus likely to have important effects on individuals' fitness. Yet, little research focuses on the ecological consequences of the disruptions of inactive behaviors. In particular, the effects of anthropization on inactivity are largely unexplored. In this review, we propose to bring quiet wake, sleep, and daily torpor together under the term of "resting", in order to facilitate the study of inactivity in wild settings. We detail the shared physiological and environmental drivers of resting behaviors, as well as their ecological outcomes. We suggest that together, the diversity of resting behaviors provide a toolkit that may enable flexible responses to constraints linked with metabolism, resource availability, predation risk and thermoregulation. We detail how the location in space, the timing, duration, and the social context in which resting occurs, shape a resting strategy that may be adjusted to changing environmental conditions. Finally, we explore how anthropisation may affect resting strategies through the increase in direct disturbances, the alterations of habitats and communities, and the effects of climate change.

**Keywords:** behavioral adjustments, human activity, inactivity, sleep

## 1 Introduction

An animal's life is a sequence of behavioral states, whose timing and duration are adjusted in response to physiological and environmental challenges, in a way that is assumed to be shaped by natural selection (Levitis et al. 2009; Baum 2013; Gunn et al. 2022). A coarse, yet obvious and striking classification of these behavioral states can be made between active and inactive ones. The costs and benefits of active states (e.g., moving, foraging, mating) are usually well understood, and often quantified (Kacelnik and Houston 1984; Pyke 2019). Conversely, costs and benefits of inactive states remain much less understood (Lesku and Schmidt 2022; Mohanty et al. 2022) and are debated (Lesku and Rattenborg 2022). Inactive states, which range from long-lasting dormant states (e.g., hibernation) to daily sleep and quiet wake, are neither associated with direct reproductive output nor energy intake. Yet, they always represent important proportions of time budgets, often spanning more than half of the 24-h period (Campbell and Tobler, 1984; Herbers, 1981). The significance of inactivity in time budgets suggests that the timing and conditions under which it occurs will have an effect on individual fitness. Disruptions of inactive behavioral states are thus likely to result in substantial ecological outcomes.

Inactivity is sometimes enforced by physiological constraints. Ectotherms, for instance, are typically bound to remain inactive when their internal temperature drops. More generally, all animals need to sleep on a regular basis to fulfill various metabolic, restorative or developmental processes, both at the cerebral and whole-body levels (Tononi and Cirelli, 2014). As a number of metabolic and neurophysiological functions are specifically performed during this state, the time required for sleeping each day is usually constrained internally (Schmidt 2014; Anafi et al. 2019). However, these functions alone cannot explain the diversity of sleeping patterns observed across species, nor their intra-species and intra-individual variations (Siegel 2009; Ungurean et al. 2020). Sleep occurs in a variety of ways, and often in alternation with quiet wake, thus forming consolidated inactive phases. The timing, duration and location in space of daily inactive phases are highly adaptable traits that together define resting strategies, which animals fine-tune to tackle ecological challenges. Animals stay inactive to maintain their energetic balance (Walker and Berger 1980; Dasilva 1993; Korstjens et al. 2010), for thermoregulation (Sato 2012; Davimes et al. 2018; Li et al. 2020), predator avoidance (Lima et al. 2005; Bonnot et al. 2020; Burger et al. 2020), and even to maintain social bonds (Silk et al. 2003). These functions shape highly variable inactivity patterns between species, and drive important intra-species and intra-individual variations, notably across environmental gradients (Gaynor et al. 2018).

As the anthropization of ecosystems increases, disruptions of animal behavior are becoming more common and widespread, and are expected to have significant ecological consequences

(Candolin et al. 2023; Gilbert et al. 2023). The impact of land use changes, species introduction, climate change, and other anthropic disturbances on habitat use and foraging behaviors have been well described, but the mechanisms involved in the anthropic disruptions of inactive behaviors remain poorly studied (Berger-Tal et al. 2011; Tougeron and Abram 2017; Candolin et al. 2023). Yet, anthropization could affect animals' inactivity in a variety of ways, and this in turn has the potential to modify individual fitness and species interactions. Animals disturbed during resting might become exposed to unfavorable conditions, or suffer from sleep deprivation. Direct disturbances of inactive behavior by people may lead to reactive behavioral adjustments involving flight (Price 2008; Stankowich 2008) or increased vigilance (McBlain et al. 2020), which can ultimately lead to long lasting effects on animal behavior, landscape use, and fitness (e.g. in Ordiz et al. 2013). Indirect effects of anthropization, like climate change, landscape artificialization (Bradsworth et al. 2021) and simplification, light pollution (Dominoni et al. 2014; Aulsebrook et al. 2018), species introduction, and predator depletion are also all likely to influence where, when, and how long animals remain inactive. Understanding animal resting strategies is thus essential to understand how human activities might affect animal behavior and activity patterns.

In this review, we point out the importance of inactive behaviors from an ecological perspective, and explore how human activities may interfere with them. The different inactive states (sleep, quiet wake, and dormant states) may look similar from the outside, but they correspond to very distinct physiological states (Heller and Ruby 2004), and are generally impossible to tell apart in practice, under natural conditions (Rattenborg et al. 2017). To overcome this problem, we propose to pool all inactive behaviors with a daily cyclicity under the term "resting", thus excluding seasonal dormancies. This concept offers a straightforward framework to study inactive behaviors in natural settings, thus facilitating the study of the ecological processes related to inactivity. In this manuscript, we first provide a detailed behavioral definition of resting, and point out how recent technological advances make it easier to study than ever. We then review previous work on why animals rest, and describe how ecological constraints shape how they do it. Finally, we explore the current knowledge on how anthropic disturbances might affect resting behavior, and we assess the potential consequences. We tried, as much as possible, to broaden our thinking to any form of resting, although much of the literature on daily inactivity focuses on sleep, thus generating an unavoidable bias. We focused our review on terrestrial vertebrate species, and intended to be as inclusive as possible in terms of taxa. However, most studies about resting behaviors focused on mammals, and to a lesser extent on birds, which inevitably biased our review to relate particularly to these clades.

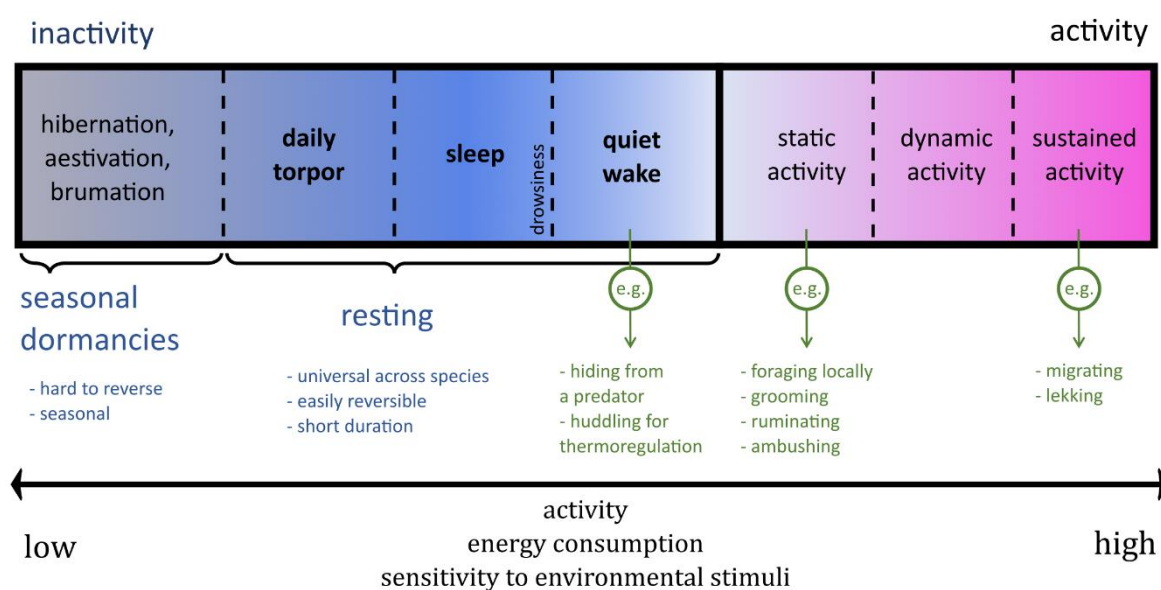
Nonetheless, we expect a wide range of diverse species to be concerned by the ecological implications of resting described in this review.

## 2 What is resting?

### 2.1 A behavioral definition of resting

#### 2.1.1 A behavioral continuum

The dichotomy between active and inactive behavioral states may be useful, but behaviors are best seen as fitting along a gradient ranging from low to high levels of activity (Siegel 2009; Rial et al. 2010; Lesku and Schmidt 2022). This continuum reflects the level of energy consumption associated with each behavior, the degree of consciousness of the surrounding environment, as well as the range of activity levels existing within each behavioral state (e.g., deeper to shallower stages of sleep; *Figure 1*). It also fits transitioning states, like drowsiness. Our definition of “resting” brings together all inactive behaviors occurring on a daily basis. On the continuum presented in *Figure 1*, this corresponds to a continuous interval excluding active behavioral states and seasonal dormancies. In that context, resting can be defined behaviorally by: i) a low level of general activity, with little motion, ii) a specific relaxed posture, and iii) a duration and cyclicity comprised within the 24-h cycle. This definition fits three main resting stages: quiet wake, sleep, and daily torpor.



*Figure 1. The situation of resting behavior on a continuum ranging from energy efficient to energy demanding behaviors.*



### 2.1.2 *Quiet wake*

Quiet wake is given a variety of names in the literature : *motionlessness*, *loafing*, or even *resting* (Herbers 1981; Das 2001; Henson et al. 2004). This state is associated with a behavioral quiescence and a relaxed posture, but does not correspond to a standard neurological state, with a simple electroencephalographic signature. It is easy to distinguish from active wake based on electromyography or accelerometry, but requires both electromyography and electroencephalography (EEG) to be discriminated from sleep (Bagur et al. 2018). Among all resting states, it has the lowest arousal threshold—the level of stimulus required to trigger a reaction—and allows for the highest level of vigilance (Lima et al. 2005; Rattenborg et al. 2017). Eyelids can be open or closed during quiet wake, making this resting state particularly hard to tell apart from sleep with behavioral criteria only (Kortekaas and Kotrschal, 2019). Despite reaching high proportions of daily awake time in many species (Herbers 1981; Das 2001; Mohanty et al. 2022), quiet wake has received very little attention from ecologists. Animals are generally quietly awake before and after sleep, which leads to long-lasting contiguous resting phases.

### 2.1.3 *Sleep*

Of all resting states, sleep has received the most attention from researchers. It is a reversible state of low responsiveness and awareness of the environment. Just like quiet wake, it corresponds to behavioral quiescence, but with an increased arousal threshold and usually a more specific relaxed posture. Sleep is quickly reversible to wakefulness after arousal (Campbell and Tobler, 1984). Sleep deprivation is generally followed by a compensatory increase in sleep behavior called *sleep rebound* (Lesku and Rattenborg 2022). This homeostatic regulation constitute an important specificity of sleep compared to other resting states. Most behavioral criteria used to define sleep, however, are impossible to test without altering the behavior displayed. This is why electrophysiological correlates are often needed to reliably identify sleep, which is associated with specific EEG profiles (Cirelli and Tononi, 2008). Sleep comprises deeper and shallower stages, associated with a variety of distinct functions (Lima et al. 2005; Mignot, 2008). In mammals and birds, EEG enables the distinction of two main sleep stages: rapid eye movement (REM) sleep and non-REM sleep, also called slow-wave sleep (SWS). SWS is characterized by high amplitudes and slow frequencies of the EEG, and occurs in a variety of depths or intensity (Rodriguez et al. 2016). Many animals—notably among birds—are also able to perform unihemispheric SWS, in which one cerebral hemisphere is awake while the other sleeps (Rattenborg et al. 2000). REM sleep is associated with a wake-like EEG, the inhibition of the thermoregulation mechanisms, and the loss of muscle tone (except muscular twitches and rapid movements of the eyes), which often implies a postural change (Blumberg et al. 2020). As

a result, REM sleep is sometimes recognizable based on behavioral criteria. In most cases however, EEG is required to differentiate REM sleep from SWS with certainty (Rattenborg et al. 2017). Sleep has received the most attention from the fields of physiology and neurology, but interest from ecologists is growing. A vast majority of studies have focused on humans and rodents (Rattenborg et al. 2017). However, sleep has been described in a wide range of species (including all the investigated vertebrate species; Campbell and Tobler 1984; Libourel and Barrillot 2020; Mohanty et al. 2022). While most studies have been conducted under laboratory conditions, there is a growing recognition that sleep patterns of wild animals must be investigated under natural conditions, in which they differ greatly (Rattenborg et al. 2017). For instance, sloths (*Bradypus variegatus*) have been documented to sleep six hours less in the wild than what was recorded in captivity (Rattenborg et al. 2008). Under natural conditions sleeping patterns are also highly variable within species and enable behavioral flexibility (Ungurean et al. 2020).

#### 2.1.4 *Daily torpor*

Daily torpor is practiced by many small mammals and birds, called daily heterotherms (Withers and Cooper 2010; Geiser 2013), and is entered through sleep (Berger 1984; Heller and Ruby 2004). It is characterized by a strong reduction of body temperature, energy expenditure, and a deep behavioral quiescence (Geiser, 2013). Daily heterotherms alternate on a daily basis between normothermic phases, when they maintain high body temperature, and heterothermic torpid phases, when they drastically reduce their metabolic rate, and let their body temperature drop (Ruf and Geiser, 2015). These physiological changes are driven by environmental and physiological conditions. Heterothermy is considered as the best physiological energy conservation strategy available to endotherms (Geiser, 2013; Ruf and Geiser, 2015). However, it does not allow for the neurophysiological functions of sleep to take place, and is thus usually followed by compensatory sleep rebounds (Blumberg and Rattenborg, 2017; Schmidt, 2014).

## 2.2 A practical and relevant construct

### 2.2.1 *The difficulty of direct observations*

Defining resting as the concatenation of quiet wake, sleep and daily torpor is particularly useful in ecology, as it provides a tool to study wild animals' daily inactive phases that is both practical and relevant. In a wild setting, assessing whether an animal is asleep or quietly awake is difficult, and often impossible. Inactive animals usually remain out-of-sight or hidden. Burrowers for instance, may stay in their den for great lengths of time, and split their time underground between all kinds of inactive behaviors. In such situations, observations are obviously complicated, and assessing which behaviors are displayed using direct observations is usually impossible. Even when an animal is visible, the determination of its neurological and physiological state is not an easy task. In most cases, sleep and quiet wake cannot be told apart

based on behavioral criteria only (Heller and Ruby, 2004; Rattenborg et al. 2017), and ecologists rarely have access to neurological records from wild animals. Daily torpor is equally complicated to tell apart from sleep, based on behavioral criteria. As a matter of fact, its mere existence was only discovered in the sixties (Geiser, 2013).

### 2.2.2 *New tools to study resting*

The study of animal behavior and activity patterns has long relied on direct observation, which can be biased and inaccurate (Wilmers et al. 2015). However, the fast-developing methods of biologging have marked the beginning of a new era in the study of wild animals, simplifying research on wild animals, with the study of inactive behaviors being no exception. Automated data logging is a crucial advantage when resting phases last uninterrupted for many hours, and include night-time, when observations are particularly difficult. In addition to that, biologging allows continuous monitoring of cryptic resting animals, even within burrows, cavities, or dense vegetation. Finally, animals (even habituated) are known to modify their behavior if they feel observed, and can become reluctant to rest (Rattenborg et al. 2017). Biologging methods are thus particularly adapted to studying animals' resting. As on-board recording devices are getting more and more diversified, efficient, and miniaturized, and as their costs drop, these methods become applicable to a whole new range of species and situations.

### 2.2.3 *Accelerometry as a simple measure of resting*

The wide diversity of sensors available enables to log information about many physiological and behavioral traits. However, only a single tool is usually necessary to study resting: an accelerometer (Brown et al. 2013). An accelerometer is a spring-like piezoelectric sensor that measures acceleration in its own instantaneous rest frame. Accelerometers are usually very small, battery efficient, and affordable. They can be fit to both large and small species (Wilmers et al. 2015). The accelerometric signature of resting usually differs greatly from that of active behaviors, and it is generally very easy to divide an animal's time budget between active and inactive behaviors based only on an accelerometric record (Brivio et al. 2021). Sometimes the accelerometric record allows distinction to go farther than between active and inactive states, by giving insights into an animal's posture (Brown et al. 2013). Animals' posture can sometimes be used as a proxy to differentiate quiet wake, sleeping, and even possibly different sleeping stages such as SWS and REM sleep (Gravett et al. 2017; Burger et al. 2020). In combination with other devices, accelerometers can provide even more detailed information on animal behavior.

### 2.2.4 *Other available sensors*

There exists a wide range of other bio-logging devices that can be of some use for the study of resting. For example, GPS tracking is essential to understand the movement's decision related to

resting. The selection of resting sites is a critical aspect of resting behavior, and this decision-making process can be studied through GPS tracking. More specific physiological bio-loggers are useful to assess an animal's resting stage (daily torpor, SWS, REM sleep, etc.). For example, heart rate and temperature loggers (e.g., subcutaneous thermometer) allow the identification of different resting stages. Daily torpor, in particular, is associated with drastic changes in heart rate and body temperature, and can be easily monitored this way. Sleep is also associated with physiological changes but is best tracked by neurological records. Using EEG loggers, sleep stages have been studied in some birds during flight, suggesting such loggers are light enough to be used in a variety of different settings (Rattenborg et al. 2017). However, although the technology is improving, such specialized sensors are not always practicable in the field, as they can be energy demanding, heavy, expensive, or difficult to fit on some species (see Libourel 2022). Some loggers also require invasive practices such as surgery to be fit on animals, which raises important ethical questions (Reinhardt 2020). However, it is almost always possible to fit an animal with a simple accelerometer, which is more than enough to quantify resting as defined in this review (Nuijten et al. 2020). In fact, many datasets already exist, with data about resting readily available, but which have not been studied as such.

### 2.2.5 *Ambiguous behaviors*

Of course, this concept of resting bears some limits. In some cases, the behavioral definition of resting may fail to include some unusual sleeping behaviors. For example, birds that sleep during flight using unihemispheric SWS can hardly be considered behaviorally quiescent, even though they are technically asleep (Rattenborg et al. 2016). More generally, behavioral states in the transition zone between inactivity and activity are difficult to classify. Non-resting, motionless behaviors are challenging to account for when they are long-lasting, related with reproduction or food acquisition, and associated with a null accelerometric signal (e.g., rumination, egg incubation, ambushing). Depending on the set of behaviors expected from a given species, resting should be described cautiously and with flexibility. Although it seems difficult or impossible to find a universal definition of resting, we expect the behavioral definition proposed here to facilitate the study of resting patterns.

### 2.2.6 *A relevant concept for studies in ecology*

The concept of resting is relevant to tackle a variety of ecological questions. All the behavioral states that we have pooled as “resting” behaviors share similar functions (energy management, thermoregulation, predation avoidance), are often displayed contiguously, and many of their ecological outcomes are identical (prolonged immobility, reduced responsiveness, shaping of space-use). The selection of a resting site, for example, has long-lasting implications and is thus of prime importance. In order to rest, animals select specific sites, which may not be distributed

evenly in the landscape. This can set restrictions on how they are able to use their home range, because resting sites may be distant to good-quality foraging sites. Many species re-use previously visited resting sites, and the dynamics of such visitations constrain landscape use, territorial defense, and predictability (Génin 2010; Janmaat et al. 2014). Resting also enables predation avoidance through hiding, and the different resting states allow different levels of vigilance (Lima et al. 2005). Animals may switch between resting states (quiet wake and sleep for instance) to adjust to the predation risk, as part of an anti-predator strategy (Capellini et al. 2009). Similarly, resting states have variable thermal efficiencies, but they all (except REM sleep) offer some thermoregulatory benefits (Terrien et al. 2011). Together, they provide a behavioral toolkit to respond to stressful thermal conditions. Seasonal dormancies being out of the scope of resting behaviors, the process of decision making relative to where, when, and how long to rest takes place on a regular basis. It thus implies frequent, yet critical choices. As a result, the construct of resting that we propose provides a framework to understand how animals use inactivity to adjust to challenging environmental conditions, on a daily basis. Understanding when and under which conditions animals use resting has the potential to give insights into how tolerant animals are to environmental pressures. Understanding how much animals get disturbed while at rest, and what are the consequences of such disruptions, should be a crucial concern in conservation biology.

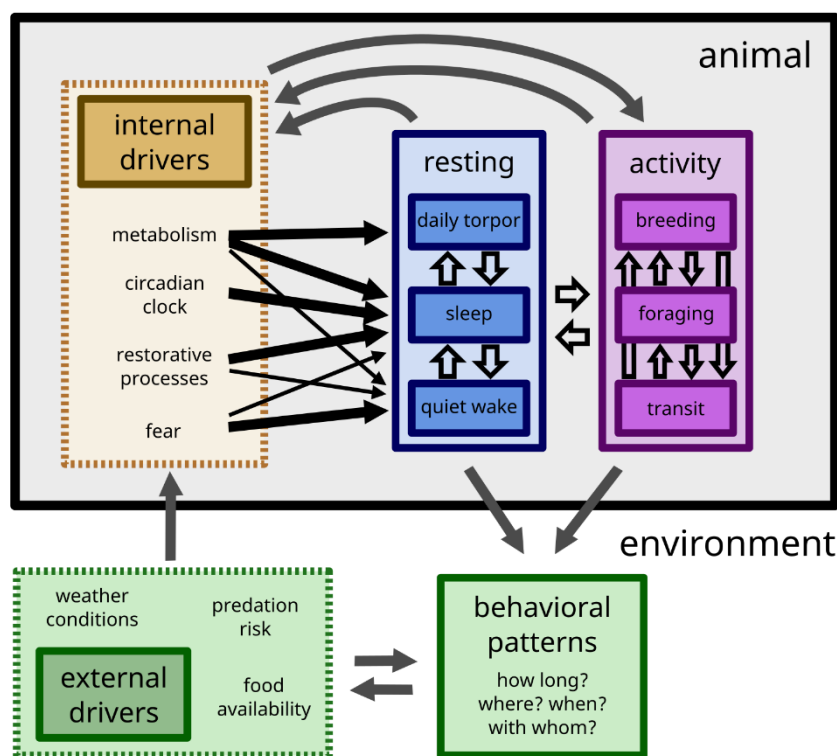
### 3 Why resting?

#### 3.1 Intrinsic drivers of resting

##### 3.1.1 *The need for sleep*

All animals need to rest at some point to maintain the homeostatic balance of their body. The most striking example of such intrinsic drivers of resting is the need for sleep. Although it has been found in phyla as diverse as cnidarian, insects, nematodes and vertebrates, suggesting an ancestral and vital shared function (Schmidt, 2014), the functions of sleep are still debated (Schmidt 2014; Libourel and Barrillot 2020), and whether sleep has one fundamental underlying function remains unclear (Freiberg 2020). Sleep is required on a regular basis in all terrestrial vertebrates, and is most often submitted to a circadian regulation (Borbély et al. 2016). It has been linked to a diversity of essential restorative processes, ranging from energy homeostasis to synaptic plasticity, memory consolidation, and maintenance of the immune function (Mignot 2008; Imeri and Opp 2009; Tononi and Cirelli 2014; Zielinski et al. 2016; Schmidt et al. 2017). It also enables energy savings (Lesku and Schmidt 2022) and predator avoidance (Lima et al. 2005; [Figure 2](#)). The energy allocation theory states that some necessary biological functions are downregulated during wake and upregulated during sleep, to optimize overall daily energy consumption. This means that some sleep helps to accomplish some restorative functions

efficiently. Sleep loss is usually followed by adverse effects on cognition and behavioral performance (Lesku et al. 2012; Lesku and Rattenborg 2022). In laboratory conditions, sleep deprivation is often followed by a compensatory increase in sleep behavior called ‘rebound’ (Marinesco et al. 1999; Raap et al. 2016). Similar patterns are often assumed to exist in the wild as well, but experimental data is very limited (Reinhardt 2020). On the other end, there are examples of long-term sleep deprivation without subsequent rebound (Lesku and Rattenborg 2022). These examples generally correspond to demanding situations in which sustained activity is highly beneficial, like long-distance travels, or competition for reproduction (Rattenborg et al. 2004; Lesku et al. 2012; Lyamin et al. 2018; Lesku and Rattenborg 2022). However, despite the internal need for sleep, sleep patterns are largely influenced by ecological factors (Blumberg and Rattenborg, 2017; Schmidt, 2014).



**Figure 2.** Effects of internal and external drivers on the components of resting and active behaviors. Solid arrows represent direct effects. The thickness of the black solid arrows indicates the importance of the effects. Empty arrows indicate shifts in behavioural states.

### 3.1.2 Other physiological drivers of resting

Physiological constraints also impose resting as a homeostatic reaction to specific active behaviors. Activity can lead to muscle fatigue or thermal stresses, which in some instances call for immediate compensatory resting. The need for post-effort recuperation is particularly important for ectotherms, due to their low aerobic capacity (Wagner and Gleeson, 1997). It is also

common for both ectotherms (Huey 1991; Parlin et al. 2020) and endotherms (Huey et al. 2012) to need some rest for thermic recuperation, after having suffered thermal stresses caused by activity out of their thermal neutral zone. In some cases, digestive needs also enforce some resting between foraging bouts. The energetic requirements of digestion, however, strongly depend on the strategy used and the nature of the food consumed (Guillemette, 1998; Korstjens et al. 2010). Animals relying on low-digestibility food sometimes need to allocate specific time for their digestive tracks to process it, and often need to rest before they can resume activity (Guillemette 1998; Masi et al. 2009).

## 3.2 Extrinsic drivers of resting

Extrinsic constraints linked with the daily fluctuations of environmental conditions (temperature, light intensity), and to the activity patterns of other species (potential prey, predators), make portions of the 24-h cycle more suitable for activity than others, and impose an important proportion of animals' daily rest (*Figure 2*). In addition to its neurophysiological functions, sleep does enable energy savings when activity is unprofitable or risky. Consequently, sleeping patterns are greatly influenced by extrinsic parameters (Ungurean et al. 2020; van Hasselt 2021; Mohanty et al. 2022). Similarly, daily torpor is used to cope with periods of unfavorable environmental conditions, as an energy conservation strategy similar to hibernation, but with a 24-h cyclicity (Ruf and Geiser 2015).

### 3.2.1 Resource availability and detectability

The efficiency of resource acquisition depends on environmental conditions, so that for most animals, the foraging phases are bounded in time by fluctuating abiotic factors. Species that rely on eyesight for instance have their foraging efficiency governed by the dark-light cycle. Likewise, coastal foragers depend on tidal cycles for feeding site availability. For these species, part of the 24-h period is unsuitable for resource acquisition. In that context, resting can be used to reduce energy consumption when foraging efficiency is low. In many shorebirds, the time spent resting correlates with the times of day when feeding grounds are inaccessible (Fasola and Biddau 1997; Dominguez 2003). Likewise, the resting patterns of predatory species may be driven by the activity patterns of their prey, that defines their availability. For example, insectivorous bats tune their activity with the daily peaks in insect catchability, and spend much of the remaining time at roosting sites, to reduce energy consumption and predation risk (Erkert 1982).

### 3.2.2 Thermic constraints

Both ectotherms and endotherms use behavioral adjustments to address thermoregulation issues. Among those, switching between activity and resting is effective to deal with fluctuating ambient temperatures. Resting is commonly used to avoid both too cold and too hot conditions.

Often, only resting allows the retreat to thermally buffered sites, such as burrows or shaded areas, as well as the use of social thermoregulation (Brodsky and Weatherhead 1984; Gestich et al. 2014; Mohanty et al. 2022). Furthermore, many thermoregulatory behaviors and postures, such as basking and ball-like postures, are not compatible with activity (Terrien et al. 2011). Daily torpor is used by some mammals and birds to reduce their energy expenditure when the daily fluctuation of environmental conditions make the maintenance of body temperature too costly (Geiser, 2013; Hetem et al. 2016). All resting states enable thermoregulation, and animals may use them alternatively to keep a thermal equilibrium while dealing with other constraints at the same time. A notable exception, however, is REM sleep, as it imposes to shut thermic defenses off (Schmidt 2014; Blumberg et al. 2020). REM sleep is essential for mammals and birds, but it is incompatible with internal heat production. It may be expressed specifically by endotherms at times when the need for thermoregulatory defense is low (Komagata et al. 2019).

### 3.2.3 *Predation risk*

Resting allows to select safe areas, retreat to inaccessible refuges, and enables concealment through immobilization (Lima et al. 2005). It thus can constitute an efficient anti-predator strategy. When perceived as high, predation risk thus often promotes resting, influencing both its timing and duration (Monterroso et al. 2013; Stuber et al. 2014; Bidner et al. 2018). However, resting implies a null energy intake, and animals using resting as an anti-predator strategy have a special interest in spending as little energy as possible. On the other hand, they need to be aware of their environment to be able to react to danger and assess predation risk. Resting states range from energy-efficient, low-vigilance states to energy-demanding vigilant states. Torpid animals are most vulnerable, as they are unable to react to external stimuli. However, such energy-efficient strategy can enable them to remain hidden for longer, or even to trade efficiency for safety when foraging, due to lower energetic needs (Turbill and Stojanovski, 2018). Quiet wake allows for efficient responses to predator encounters, but is more energy consuming. Although sleep is often viewed as a vulnerable state, it is a compromise between those two extremes. It permits some energy savings but remains quickly reversible, and allows some processing of sensory information (Lima et al. 2005; Siegel, 2009). Quiet wake and sleep often alternate when predation risk is high (Lesku et al. 2008; Burger et al. 2020). Depending on the perceived predation risk, animals are thus expected not only to adjust the timing and duration of resting, but also their level of consciousness, and thus the form of resting involved.

### 3.2.4 *A toolkit for unfavorable conditions*

Animals mitigate the costs of activity, such as energy expenditure or predator encounter risk, by switching to resting when environmental conditions are not optimal. The diversity of available resting states provides a way to adjust several potentially conflicting parameters like the energy



conservation rate, the awareness of the surroundings and the ability to answer external stimuli (Ferretti et al. 2019). Due to a high rate of genetic control on its homeostatic regulation, sleep likely presents less flexibility than quiet wake. However, the integration of those distinct inactive states in a global resting strategy may offer more flexibility in the behavioral responses of animals to environmental fluctuations. More generally, the energy savings enabled by resting can be used not only to cope with climatic conditions, but to answer any kind of energetic stress. For instance, some birds use daily torpor to meet energetic balance during stages of high energy requirements such as migration, development, pregnancy, or lactation (Geiser, 2013).

### **3.3 How long to keep resting?**

#### *3.3.1 Balancing time budgets*

All animals rest for important proportions of their time budgets. Even species that are famous for their low amount of sleeping, like large ungulates and elephants, spend at least 20% of their time at rest (Gravett et al. 2017; Guy, 1976; Owen-Smith and Goodall, 2014). Total resting time is constrained by ecological and physiological characteristics such as habitat, diet, trophic level, and ecological niche (Capellini et al. 2009; Dunbar et al. 2009). It is however also variable within species and individuals, and is influenced by several factors including weather conditions, food availability, predation risk, and generally, by on how time-consuming daily maintenance activities are (Lima et al. 2005; Lesku et al. 2008; Korstjens et al. 2010). The time needed to gather sufficient food can vary considerably according to the quality, accessibility, and distribution of food, and to predation risk levels on the foraging sites. In addition, the distance between foraging and resting sites determines how much travel time is needed each time the animal switches between foraging and resting phases. When more time is needed for active behaviors, animals adjust their time budgets by reducing resting time, sometimes resting more 'intensely' (using more energy efficient resting states) to compensate for the loss of resting time (Turbill and Stojanovski 2018). Animals rest for shorter bouts when food is scarce (McFarland et al. 2014), but also when competition for reproduction is intense, or when migrating or dispersing (Rattenborg et al. 2004; Lesku et al. 2012). Some studies of sleep in animals facing situations in which staying active is strongly selected have shown that in some instances at least, sleep can be drastically reduced, or even suppressed altogether without subsequent rebound, suggesting that the amount of enforced resting might also be variable (Lesku et al. 2012; Rattenborg et al. 2016; Lesku and Rattenborg 2022). It is also noteworthy that the amount of rest needed strongly depends on life stage, early developmental stages demanding more resting time (Jouvet-Mounier et al. 1970; Frank and Heller 2003; Frank 2020). REM sleep for example is more predominant during development than during adult life (Blumberg et al. 2020).

### 3.3.2 Laziness

Part of the time animals spend resting is not enforced by ecological or physiological factors, and has been referred to as 'laziness' (Herbers 1981). In accordance with the satisficing theory of foraging, animals tend to rest when they have met their daily energetic requirements, even when no specific hazard urges them to do so. Such uncommitted resting, has been evidenced in primates (Korstjens et al. 2010) and is also commonly observed in captive animals (Fureix and Meagher 2015). This means that resting can stretch for longer than needed for obligate functions of resting to be complete. The allocation to resting of any spare time left after the achievement of obligate daily tasks may allow energetic savings. However, as time is a precious and limited resource, uncommitted resting most importantly constitutes a time capital, available to be allocated to other behaviors whenever needed. In most cases, it is complicated to measure how much time an animal spends in uncommitted resting, as part of resting is enforced. Such a measurement would provide an interesting insight into how time pressured a population actually is (Dunbar et al. 2009).

## 4 How to rest?

Given the universality of resting and the variety of its drivers, it is not surprising that resting strategies are extremely diversified. Parameters like the timing, duration, the spatial organization, and the social context of resting are key to understanding the effects of the extrinsic pressures faced by animals.

### 4.1 When to rest?

#### 4.1.1 Monophasic rhythms

Animals may engage in resting at any time. Short bouts of resting are sometimes embedded within longer bouts of activity. However, most of the resting displayed by animals occurs within consolidated bouts, usually several hours long, alternating cyclically with similarly long phases of activity. Animals are called monophasic when they display a single daily alternation between an active phase and a resting phase every 24 h. When resting phases happen within the 24-h cycle is variable across species. The temporal organization of resting results from the need to meet physiological balance and energetic requirements, while dealing with the temporal variations of environmental conditions, food availability and predation risk. It is driven by both endogenous rhythms (like the circadian clock) and exogenous zeitgebers (environmental rhythms like solar cycle, tides, and food availability) (Aulsebrook et al. 2021; Hazlerigg and Tyler, 2019). Since most terrestrial habitats usually undergo strong daily fluctuations of temperature, relative humidity, and luminosity across the day-night cycle, many animals rest in one single consolidated bout, either diurnally or nocturnally (Riede et al. 2017). Mean ambient temperature is usually lower

than animals' optimal body temperature. Because resting enables to withdraw from colder environmental conditions, nocturnal resting is usually an efficient strategy for the maintenance of thermal balance (Hazlerigg and Tyler, 2019). Besides, resting at night is imposed for many species that rely heavily on eyesight, like most birds for instance (Daan, 1981). When and where water availability is a limiting factor (in arid habitats, during the dry season, or for species vulnerable to dehydration, like many amphibians), diurnal resting is often preferred to minimize water loss during the day (Daan, 1981).

#### 4.1.2 *Crepuscular and polyphasic rhythms*

Resting in one consolidated bout each day, however, is not the only strategy (Halle 2006). Many species are rather crepuscular, and thus spend most of both day and night at rest. Other species rest for shorter bouts, spread throughout the day and night periods, in alternation with activity (Bloch et al. 2013; Hazlerigg and Tyler 2019). These animals are called polyphasic. In polar environments, daily environmental rhythms are extremely seasonal, and disappear altogether for most of the year. In these conditions, animals adapt the timing of their resting phases to physiological constraints and biotic external parameters. They often use polyphasic patterns of activity (Bloch et al. 2013). Another driver of polyphasic activity is metabolism. Herbivores using microbial fermentation, like voles and some ungulates, as well as small endotherms, like shrews, require frequent bouts of foraging to meet their metabolic requirements, and cannot afford to interrupt foraging for more than a few hours. They thus spread short bouts of resting throughout the day and night (Hazlerigg and Tyler, 2019).

## 4.2 **Where to rest?**

### 4.2.1 *Resting site selection*

Animals choose their resting sites according to their physical properties. They precisely select habitat types, depending on species-specific requirements, and often use particular structures such as burrows and cavities, sometimes creating these structures themselves. Resting sites are notably characterized by their anti-predator and thermoregulatory properties (Larroque et al. 2015; Tisdale et al. 2018; Courbin et al. 2019). The amount of structural cover (Mysterud and Ims 1998), the possibility to sense approaching predators (Mohanty et al. 2022), the thermal properties (Baghli and Verhagen 2005; Glass et al. 2021; Mohanty et al. 2022) and the density of parasites (Hausfater and Meade 1982; Schneider et al. 2013) are commonly assessed by animals when selecting a resting site. As a result, the utilization of the habitat is commonly very different between the active and the resting phases. For example, a surprising number of squamate species select unstable perches specifically for sleeping, as an early warning system to detect approaching predators, although they do not use these perches when active (Mohanty et al. 2022). Trade-offs emerge from the diversity of constraints to resting site selection. Animals typically need to

balance predator avoidance and thermoregulation when choosing where to rest. For example, an Australian gecko (*Oedura lesueurii*) has been shown to trade thermal efficiency for safety (Downes and Shine 1998), while wolverines (*Gulo gulo*) are willing to rest in more risky sites, to gain a thermoregulatory benefit (Glass et al. 2021). For many species, the availability and quality of resting sites are seasonally variable. When suitable resting sites are a limited resource, memorizing their location can be advantageous to minimize travelling costs (Fei et al. 2022). While the choice of a resting site is highly constrained for some species, it has fewer implications for others, which can afford to be less selective, and animals with low thermal sensitivity and low risk of being predated should be less specific in their choices. For example, ducks and shorebirds, which have a good thermal insulation and ability to detect predators while at rest, thanks to group resting and unihemispheric SWS, usually rest in relatively exposed conditions, both in terms of thermal stresses and predation risk (Rattenborg et al. 2000; Dominguez 2003; Lima et al. 2005).

#### 4.2.2 Fidelity to resting sites

Many animals re-use the same resting sites over time. Such fidelity to a resting site may be useful when resting sites are rare, scattered, unpredictable, or when their quality is difficult to assess. Resting site fidelity is expected to be enhanced when resting sites' quality is stable over time (Gerber et al. 2019; Kaiser and Kaiser 2021). When the availability of suitable resting sites is low, competition may arise over high quality sites (Markham et al. 2016) and animals may have to fight to maintain their fidelity to resting sites (Kondo and Downes 2007). On the other hand, resting site fidelity enhances predictability, which might come at a cost in terms of predation risk (Smith et al. 2007). The anti-predator quality of a resting site may thus decrease with increased utilization rate (Markham et al. 2016).

#### 4.2.3 Where to rest within the home range?

The choice of a resting site is always constrained by its connectivity with sites that enable efficient activity, which is necessary for maintenance and survival. In particular, it may be constrained by the distance to foraging sites (Génin 2010; Burger et al. 2020; Hočevár et al. 2021). Animals with a strong dependency on specific foraging sites, must adjust their resting site selection accordingly (Chapman et al. 1989; Janmaat et al. 2014), decrease their selectivity over resting sites (Génin 2010), or travel more distance to commute between resting and foraging sites (Courbin et al. 2019). For these species, resting site selection should be influenced by landscape patchiness and resource distribution. Conversely, when resting sites are a limited resource, their availability may determine the range of animal movements and distribution (Anderson 2000; Barnett et al. 2012; Larroque et al. 2015). Considering resting and foraging in a framework of landscape complementation (Dunning et al. 1992) would help to improve our understanding of animals' resting strategies, and how they affect landscape utilization and species distribution.

Finally, territoriality influences where in its home range an animal should rest. Resting on the edge of the defended area could help territorial defense through improved detection of neighboring rivals or early access contested sites (Day and Elwood 1999; Singhal et al. 2007; Mohanty et al. 2022), while resting near the core of the defended area could be beneficial by allowing exclusive use of spatially aggregated resources (Smith et al. 2007).

#### 4.2.4 *Resting site selection and activity patterns*

Animals spend important proportions of the 24-h cycle at rest, but their daily resting time is either aggregated in one consolidated bout, or shared between many short bout (Bloch et al. 2013; Hazlerigg and Tyler 2019). As resting implies immobility, the choice of a resting site has implications that last until the end of the resting phase. Therefore, the selection of a resting site is a decision with long-lasting implications for monophasic animals, and is required frequently for polyphasic species. Monophasic species must choose a single resting site each day, and remain at this location for several hours, while environmental conditions such as temperature, weather, and predation risk fluctuate. When they select a resting site, they must thus anticipate changing environmental conditions, like weather conditions and predation risk. If a monophasic animal selects a resting site with high risk of predator encounter, the risk it faces will be set high for a long period. For monophasic species, resting site selection is a daily choice with crucial implications that last for hours. On the other hand, polyphasic species organize their activity pattern as an alternation of bouts of activity and resting throughout the 24-h cycle. These species must select resting sites several times a day. Each of these choices should be less critical than in monophasic species, due to the lesser time spent at rest in each occasion. However, the selection of a resting site may be spatially more constrained in polyphasic species, as their pattern of activity allows less time to travel between resting sites and foraging grounds. These species should thus depend on reliable and accessible resting sites. This might be particularly true for small polyphasic animals like shrews, for which high metabolic needs likely increase the need to find good quality, thermally efficient resting sites (Halle 2006). The influence of activity patterns on resting site selection has, however, not been thoroughly investigated so far.

### 4.3 **With whom?**

#### 4.3.1 *The benefits of resting in groups*

Gregarious animals do not rest independently of each other: many tune when and where they rest to benefit from resting together. Social resting is frequently used for thermoregulation, in both endotherms (Gilbert et al. 2010; Eppley et al. 2017) and ectotherms (Mohanty et al. 2022), as huddling reduces heat loss. Resting in a group also has the potential to reduce predation risk through predation dilution effect (Lima et al. 2005), and increased vigilance (Gauthier-Clerc et al. 1998; Lanham and Bull 2004). In addition, the potential for asynchronous vigilance enables less

individual vigilance when resting aggregations are larger (Bidner et al. 2018; McBlain et al. 2020), which may benefit mixed-species groups too. Resting in groups thus increases both the quantity of resting time, and its quality, through a reduced need for vigilance, and increased thermal defenses. The outcome of social resting, however, might yield unequal benefits for individuals in the group, depending on their position within the resting aggregation (Dominguez 2003).

#### 4.3.2 *Social aspects of resting*

Social dynamics also continue during resting periods, and influence when and where animals rest (Smeltzer et al. 2022). The time spent resting along with conspecifics affects social bonds (Silk et al. 2003). Social animals thus invest resting time to enhance their social relationships and hierarchical situation, which may indirectly improve their reproductive success and survival. The social dynamics during resting times are getting more and more attention from ecologists as it is now possible to track several individuals from a social group at the same time (Loftus et al. 2022). Social parameters influence details about how animals sleep, such as the spatial location within the group, and the social status of neighbors. These fine-scale parameters also have the potential to affect safety, thermic conditions, and the risk of being disturbed while at rest, which in turn affect the quantity and quality of resting (Anderson, 1998; Loftus et al. 2022). The influences of sociality on resting behavior are multiple and complex, and would require a specific focus to be treated properly (see Smeltzer et al. 2022), which is why they are not discussed further in this review.

## 5 **Unknown effects of anthropization**

The globally increasing pressure humans put on ecosystems affects animal behavior through a variety of pathways. Animals respond to direct disturbance, habitat destruction, landscape fragmentation, light and noise pollution, alteration of communities' compositions, and increased temperature by modifying their behavior. Obviously, just like any other behavior, resting is concerned. In general, however, very little is known about how anthropic pressures affect how animals rest, and what consequences this may have on individual fitness, and species abundance and distributions. The effects of anthropization on resting are likely to interact between each other and with their effects on other behaviors. As a result, making predictions on the consequences of the anthropic disruptions of resting is certainly challenging. Nevertheless, here, we explore some of the pathways through which human activity, at local or global scales, may interfere with animals' resting behavior.

## 5.1 Direct anthropic disturbances

### 5.1.1 Shifts in vigilance levels

As human presence in all landscapes increases, animals are ever more likely to be disturbed by people while at rest. Obviously, animals resting in areas relatively accessible to people are most at risk. Direct anthropic disturbances disrupt resting by increasing vigilance level. McBlain et al. (2020) described how oystercatcher (*Haematopus ostralegus*) reduce sleeping time and increase vigilance in the presence of people, and even more when along with dogs. Human presence near animals' resting sites stimulates high-awareness resting behaviors such as quiet wake, at the expense of sleep, thus potentially initiating sleep debt. In the case of persistent disturbances, this might have important drawbacks on performance during subsequent activity (Kolbe et al. 2021). A disturbed animal may decide to abandon its resting site, either because the disturbance is perceived as a true threat, or because maintaining an elevated vigilance level would be too costly (Dukas and Clark 1995; Gauthier-Clerc et al. 1998; Tworkowski and Lesku 2019). Such a reaction can have lasting effects, as demonstrated with experimental disturbances on resting bears (*Ursus arctos*), which altered their behavior for several days after an encounter with humans at the resting site (Ordiz et al. 2013). The costs of flights from resting sites include increased energy expenditure, predation and thermal risk, and displacement away from sites suitable with subsequent activity. In addition, animals giving up on resting time following anthropic disturbance are not necessarily able to compensate with delayed resting, which may induce more costs, related to sleep deprivation (Kaburu et al. 2019).

### 5.1.2 Shifts in activity patterns

Some animals proactively adjust when they rest to reduce the risk of direct anthropic disturbances. As human activity is most intense during daytime, an efficient way for animal to reduce disturbance when resting would be to rest at night. However, it is well established that the opposite most often occurs, as animals prefer to reduce human encounters during their phase of activity (Gaynor et al. 2018), and therefore expose their resting to human disturbance. This kind of adjustment has been observed in a number of large herbivores and predator species (Shukla et al. 2021). Resting is indeed an efficient anti-predator strategy, as it reduces the risk of human encounter. Animals preferentially exposing their resting phase to human disturbance highlights that the effective cost of anthropic disturbance (accounting for the rate at which they occur) is generally lower for resting than for active behaviors. Nonetheless, for animals that are generally active diurnally in the absence of anthropic pressure, daytime resting may have physiological consequences related to increased vigilance and altered thermic balance. These effects, however, remain largely unexplored.

### 5.1.3 *Spatial avoidance*

Animals usually adjust their temporal patterns of activity to reduce the costs of anthropic disturbances of active phases. To lower the risk they face of encountering people while resting, animals may modify the spatial organization of their resting phases. The fear of the human super-predator leads to spatial avoidance in general (Nickel et al. 2020; Corradini et al. 2021), and the location of resting sites are commonly impacted (Wam et al. 2012; Wittemyer et al. 2017; Belotti et al. 2018; Suraci et al. 2019; Weinberger et al. 2019). If areas free of disturbances become too rare, the lack of quiet and safe resting sites could drive population decline, even in landscapes where food is available, and movements are unrestricted (Beale 2007).

## 5.2 **Landscape modification and fragmentation**

### 5.2.1 *Availability of resting habitat*

Besides increasing the risk of disturbance at resting sites, anthropization also affects the availability of resting sites altogether, through habitat destruction. Numerous microhabitats and structures that are needed by animals for resting are rare or absent in anthropized landscapes, many species struggle to find where to rest (Weinberger et al. 2019; Torretta et al. 2022). A good example of such a constraint imposed by anthropization on resting behavior is the global decline of tree cavities and hollows due to deforestation, forest management, and urbanization (Remm and Löhmus 2011; Le Roux et al. 2014). These structures represent a limited resource, and are essential to many birds, mammals and reptiles not only to breed, but also to rest on a daily basis (Blakely et al. 2008; Lutermann et al. 2010), thus shaping home range sizes and species distribution (Martin and Martin 2007; Manning et al. 2013). In managed forests, agricultural lands, and urban environment, species that depend on tree cavities for resting are expected either to restrict their distribution to the areas with most resting sites, or to increase home range sizes, thus increasing energetic costs. Where suitable resting sites are lacking, animals may use alternative sites of lower quality, if possible. For example, while many lizards favor unstable perches for resting to increase their chances to sense approaching predators (Mohanty et al. 2022), such perches lack in some agricultural landscapes, thus forcing them to use riskier perches (Bors et al. 2020). The lack of suitable structure for resting has been shown to affect population sizes (Taylor et al. 2016), and could be an important constraint on species persistence in anthropized landscapes (Weinberger et al. 2019). For non-territorial species, competition over resting sites might also arise from limited availability (Markham et al. 2016).

The disappearance of potential shelters in anthropized landscapes is well described, and studies generally acknowledge that it may affect species distribution by compromising both reproduction and resting. However, almost all the examples cited in the literature focus on reproduction (Lowry et al. 2013; Manning et al. 2013; Sarkar and Bhadra 2022). The



consequences of the reduction of resting sites' on species abundance and distribution, however, is almost never studied in details. In contrast to most anthropized landscapes, urban environments provide unusually high densities of suitable resting sites to some species (Sarkar and Bhadra 2022). Medium-sized carnivores like stone martens (*Martes foina*), raccoons (*Procyon lotor*), and opossums (*Didelphis virginianus*) use manmade structures to rest even in densely populated cities (Bateman and Fleming 2012), which favors their expansion into urbanized areas. Reptiles also make use of artificial structures to find shelter in urban areas (Koenig et al. 2001), and their abundance in cities may depend on the availability of such structures (de Andrade 2020). In some cases, urban environments may support unusually high densities of certain species, due to the profusion of resting sites (Lowry et al. 2013; de Andrade 2020). However, the disparity in resting site availability to different species may alter community structures in anthropized landscapes.

### 5.2.2 Constraints on movements

The need to rest is susceptible to constrain importantly the movements of animals living in fragmented landscapes. In areas where the spatial layout of habitats used for foraging and resting is altered, animals may be compelled to landscape complementation (Dunning et al. 1992), and their need to move may increase. In fragmented anthropized landscapes, many animals are forced to travel more to get to foraging sites (Podgórski et al. 2013; Torretta et al. 2022), with increased energetic costs, and risks linked with transit (like collisions with vehicles). This adds to the many constraints imposed by anthropization on animal movement (Tucker et al. 2018). Increased commuting time linked with landscape fragmentation is expected to lead to a reduction of resting time. This of course should have drawbacks that remain poorly understood. Polyphasic species might be particularly at risk as they need to travel more often from foraging grounds to resting sites.

## 5.3 Noise and light pollution

### 5.3.1 Light pollution

Artificial lights at night (ALAN) are an important characteristic of anthropization in populated areas, but also in industrial complexes and along some roads. Their effects may extend well away from the light sources, notably through the effect of skyglow (Gaston and Sánchez de Miguel 2022). ALAN are susceptible of affecting how animals rest through a variety of pathways. In nocturnally resting birds and reptiles, exposure to ALAN has been linked with sleep disruption (Aulsebrook et al. 2021; Mohanty et al. 2022), sometimes leading to impaired performances during wake (Taufique and Kumar 2016; Kolbe et al. 2021). Raap et al. (2016) described sleep disruption by ALAN in great tits (*Parus major*), followed a sleep rebound. Kolbe et al. (2021) observed a lower arousal threshold and impaired performance during subsequent activity in

*Anolis* lizards exposed to ALAN, compared to animals sleeping in dark conditions (Kolbe et al. 2021). For many animals moonlight increases the risk of predation (Prugh and Golden 2014). ALAN could thus decrease the anti-predator quality of artificially lit resting sites, thus stressing animals to select more secure, darker resting sites. If ALAN reduces the quality of resting sites, animals might be expected to avoid resting in exposed areas (Dominoni et al. 2014). However, such a behavioral adjustment could drastically reduce the availability of resting sites, with potentially cascading effects on other behaviors. Besides, avoiding ALAN exposure during resting might simply be impossible to some animals, due to the wide spread of anthropic lightings. The decline of resting quality might thus be unavoidable to some animals living close to people, with unknown effects on their fitness. In addition, it seems some animals are unable to adjust their resting sites selection to ALAN (Kolbe et al. 2021), or even preferentially select artificially lit roosts (Ulgezen et al. 2019), despite physiological costs. These effects illustrate the fact that ALAN are a new feature in most animals' environments, and predictions on their effects on animals' resting behavior are hard to make.

### 5.3.2 Noise pollution

Anthropized landscapes are also characterized by anthropogenic noise pollution. Ambient noise levels have been shown to alter activity patterns in some urban populations (Fuller et al. 2007; Dominoni et al. 2020), and are thus expected to influence resting behavior to some extent. Besides, exposure to environmental noise impairs sleep quality, with potential physiological drawbacks (Kight and Swaddle 2011; Grunst et al. 2023). Animals are expected to exhibit increased vigilance when exposed to anthropogenic noise, and particularly so if those noises are sudden and unexpected, or associated to a real threat (e.g. dog barks). Many animals certainly able to easily habituate to noise pollution, especially when sounds are heard continuously and not associated to any threat (see Fradin and Chamailé-Jammes 2023), but even background noise, harmless in itself, may decrease the chances to hear an approaching threat, thus decreasing the quality of a resting site (Bojarska et al. 2021). As a consequence, animals should generally account for the anthropogenic soundscape when selecting resting sites, and avoid noisy areas. The effects of noise pollution on resting, however, are mostly unknown and are likely to interact with ALAN and direct disturbances, to contribute to a general pattern (Dominoni et al. 2020): animals living closest to human settlements are more likely to suffer from a low availability of good quality resting sites, and frequent disruption of resting behavior. Species that are able to adjust their behavior, by finding alternative resting sites or habituating to these constraints are likely to be favored in these contexts (Lowry et al. 2013).

## 5.4 Alterations of communities

### 5.4.1 Introduction of predators and competitors

Anthropized landscapes are associated with altered animal communities, with important effects on animals' resting behavior. In some cases, the introduction of exotic species generates intense competition over resting site (Cole et al. 2005). For example, the rose-ringed parakeet (*Psittacula krameri*) which is invasive across Western Europe, competes over tree cavities with a number of native birds and bats, that use them both for nesting and resting (Mori et al. 2017). The extent to which this affects species abundances however is unknown. Extreme predator densities occurring in cities is also susceptible of affecting how animals rest in urban landscapes. Duarte and Young (2011) have shown that urban marmosets (*Callithrix penicillata*) strongly modify their selection of resting site accordingly to the density of cats in the neighborhood. Similar adjustments could be expected from many small urban animals.

### 5.4.2 Predator depletion

Besides, human-dominated landscapes are often characterized by the lack of large predators (Woodroffe 2000). Prey species that, as a consequence, experience a reduced predation pressure could therefore afford to be less selective on safe resting sites, which may possibly compensate the lack of available resting sites in these landscapes. In addition, the release of predation pressure could allow prey species that normally time their activity to avoid predation to shift their activity pattern (Shores et al. 2019). That, however, would require habituation to human presence from them.

## 5.5 Increased temperature

Resting is often used in response to adverse environmental conditions, which include harsh temperatures. Consequently, global warming is certainly expected to disrupt animals' resting patterns. Ambient temperature affects the quality of sleep (Harding et al. 2019), as well as when and where animals rest (Rattenborg et al. 2017; Mohanty et al. 2022), and the total amount of time spent at rest (Dewasmes et al. 2001). Levy et al. (2019) and DeGregorio et al. (2015) have proposed that some diurnal animals might adjust to increased summer temperatures by shifting to a nocturnal activity pattern. While changes in activity patterns in response to environmental stimuli have been documented in a wide diversity of species (Levy et al. 2019), such a shift would imply resting under the hottest conditions, with costs that are currently unknown and should be investigated. Animals with the ability to rest in thermally buffered sites (e.g. burrows) could be the most likely to express such behavioral shift (Moore et al. 2018). An increase in the selection of cool resting sites under increased temperatures should be observed in a number of species, and has been described in reindeer (*Rangifer tarandus*) in Svalbard (Williamson et al. 2019). Such

adjustments could produce more competition over resting sites, especially where suitable resting sites are already low. Warmer temperatures may directly affect the quality of resting time in some animals. Flesch, Rosen, and Holm (2017) predict that increased temperatures due to global warming should lead to metabolic costs in resting ectotherms, with important drawbacks on subsequent activity. As temperatures keep increasing, animals' ability to cope with change through behavioral adjustments will decrease. Extreme weather events should become the most important pathways through which temperature could affect resting behavior. During heatwaves, animals should increase resting time, possibly at the expense of other activities. Species capable of using daily torpor flexibly in response to unpredictable and severe weather events are predicted to stand better chances of survival during extreme events (Geiser and Turbill 2009; Nowack et al. 2017). However, most of the effects that climate change might have on animals through the disruption of resting remain unknown.

## 6 Conclusions

(1) Resting often represents substantial proportions of animals' time budgets and yet has received little attention from ecologists.

(2) Resting strategies are highly variable between species and individuals, and often show a great plasticity, although they are shaped by a diversity of constraints.

(3) Decision making related to resting behavior has crucial implications for energy balance, thermoregulation, predator avoidance, and use of the landscape.

(4) Anthropization greatly influences where, when, and how animals rest, which could have important consequences on individual fitness, and species abundance and distribution

(5) To date, the effects of anthropization on resting behavior seem to have been overlooked by ecologists.

(6) Considering all inactive behaviors occurring on a daily basis together under the term of "resting" would enable facilitated large-scale monitoring through accelerometry.

**Author contributions:** **Gustave Fradin:** Conceptualization (equal); investigation (lead); writing – original draft (lead); writing – review and editing (lead). **Simon Chamailé-Jammes:** Conceptualization (equal); investigation (supporting); supervision (lead); writing – review and editing (supporting). **Andy Sih, Aurélie Coulon, Paul-Antoine Libourel, Adrian M. Shrader, Bianca Teseling, and Marion Valeix:** writing – review and editing (supporting).

**Conflict of interest statement:** The authors declare no conflict of interest

## Références du premier axe

Anafi RC, Kayser MS, Raizen DM. 2019. Exploring phylogeny to find the function of sleep. *Nat Rev Neurosci.* 20(2):109–116. doi:10.1038/s41583-018-0098-9.

Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am J Primatol.* 46(1):63–75. doi:10.1002/(SICI)1098-2345(1998)46:1<63::AID-AJP5>3.0.CO;2-T.

Anderson JR. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Med Rev.* 4(4):355–373. doi:10.1053/smr.2000.0105.

de Andrade AC. 2020. Metropolitan lizards? Urbanization gradient and the density of lagartixas (*Tropidurus hispidus*) in a tropical city. *Ecology and Evolution.* 10(4):1740–1750. doi:10.1002/ece3.5518.

Aulsebrook AE, Johnsson RD, Lesku JA. 2021. Light, Sleep and Performance in Diurnal Birds. *Clocks & Sleep.* 3(1):115–131. doi:10.3390/clockssleep3010008.

Aulsebrook AE, Jones TM, Mulder RA, Lesku JA. 2018. Impacts of artificial light at night on sleep: A review and prospectus. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology.* 329(8–9):409–418. doi:10.1002/jez.2189.

Baghli A, Verhagen R. 2005. Activity patterns and use of resting sites by polecats in an endangered population. *Mammal Review.* 69(2):211–222. doi:10.1515/mamm.2005.018.

Bagur S, Lacroix MM, Lavilléon G de, Lefort JM, Geoffroy H, Benchenane K. 2018. Harnessing olfactory bulb oscillations to perform fully brain-based sleep-scoring and real-time monitoring of anaesthesia depth. *PLOS Biology.* 16(11):e2005458. doi:10.1371/journal.pbio.2005458.

Barnett AA, Shaw P, Spironello WR, MacLarnon A, Ross C. 2012. Sleeping site selection by golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian flooded forests. *Primates.* 53(3):273–285. doi:10.1007/s10329-012-0296-4.

Bateman PW, Fleming PA. 2012. Big city life: carnivores in urban environments. *Journal of Zoology.* 287(1):1–23. doi:10.1111/j.1469-7998.2011.00887.x.

Baum WM. 2013. What Counts as Behavior? The Molar Multiscale View. *Behav Anal.* 36(2):283–293.

Beale CM. 2007. The Behavioral Ecology of Disturbance Responses. *International Journal of Comparative Psychology*. 20(2). doi:10.46867/ijcp.2007.20.02.13.

Belotti E, Mayer K, Kreisinger J, Heurich M, Bufka L. 2018. Recreational activities affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*). *Hystrix It J Mamm*. 29(2):181–189. doi:10.4404/hystrix-00053-2018.

Berger RJ. 1984. Slow wave sleep, shallow torpor and hibernation: Homologous states of diminished metabolism and body temperature. *Biological Psychology*. 19(3):305–326. doi:10.1016/0301-0511(84)90045-0.

Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*. 22(2):236–239. doi:10.1093/beheco/arq224.

Bidner LR, Matsumoto-Oda A, Isbell LA. 2018. The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *American Journal of Primatology*. 80(12):e22932. doi:10.1002/ajp.22932.

Blakely TJ, Jellyman PG, Holdaway RJ, Young L, Burrows B, Duncan P, Thirkettle D, Simpson J, Ewers RM, Didham RK. 2008. The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand. *Austral Ecology*. 33(8):963–974. doi:10.1111/j.1442-9993.2008.01867.x.

Bloch G, Barnes BM, Gerkema MP, Helm B. 2013. Animal activity around the clock with no overt circadian rhythms: patterns, mechanisms and adaptive value. *Proc Biol Sci*. 280(1765):20130019. doi:10.1098/rspb.2013.0019.

Blumberg M, Rattenborg N. 2017. Decomposing the Evolution of Sleep: Comparative and Developmental Approaches. p. 523–545. doi: 10.1016/B978-0-12-804042-3.00100-7

Blumberg MS, Lesku JA, Libourel P-A, Schmidt MH, Rattenborg NC. 2020. What Is REM Sleep? *Curr Biol*. 30(1):R38–R49. doi:10.1016/j.cub.2019.11.045.

Bojarska K, Maugeri L, Kuehn R, Król W, Theuerkauf J, Okarma H, Gula R. 2021. Wolves under cover: The importance of human-related factors in resting site selection in a commercial forest. *Forest Ecology and Management*. 497(119511). doi:10.1016/j.foreco.2021.119511.

Bonnot NC, Couriot O, Berger A, Cagnacci F, Ciuti S, Groeve JED, Gehr B, Heurich M, Kjellander P, Kröschel M, et al. 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology*. 89(1):132–145. doi:10.1111/1365-2656.13161.

Borbély AA, Daan S, Wirz-Justice A, Deboer T. 2016. The two-process model of sleep regulation: a reappraisal. *J Sleep Res.* 25(2):131–143. doi:10.1111/jsr.12371.

Bors M, Mohanty NP, Gowri Shankar P. 2020. Anti-predatory sleep strategies are conserved in the agamid lizard *Monilesaurus rouxii*. *Behav Ecol Sociobiol.* 74(10):121. doi:10.1007/s00265-020-02905-1.

Bradsworth N, White JG, Rendall AR, Carter N, Cooke R. 2021. Where to sleep in the city? How urbanisation impacts roosting habitat availability for an apex predator. *Global Ecology and Conservation.* 26:e01494. doi:10.1016/j.gecco.2021.e01494.

Brivio F, Bertolucci C, Marcon A, Cotza A, Apollonio M, Grignolio S. 2021. Dealing with intra-individual variability in the analysis of activity patterns from accelerometer data. *Hystrix It J Mamm.* 32(1):41–47. doi:10.4404/hystrix-00391-2020.

Brodsky LM, Weatherhead PJ. 1984. Behavioural thermoregulation in wintering black ducks: roosting and resting. *Can J Zool.* 62(7):1223–1226. doi:10.1139/z84-177.

Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry.* 1(1):20. doi:10.1186/2050-3385-1-20.

Burger AL, Fennessy J, Fennessy S, Dierkes PW. 2020. Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. *Ecol Evol.* 10(6):2917–2927. doi:10.1002/ece3.6106.

Campbell SS, Tobler I. 1984. Animal sleep: A review of sleep duration across phylogeny. *Neuroscience & Biobehavioral Reviews.* 8(3):269–300. doi: 10.1016/0149-7634(84)90054-X.

Candolin U, Fletcher RJ, Stephens AEA. 2023. Animal behaviour in a changing world. *Trends in Ecology & Evolution.* 38(4):313–315. doi:10.1016/j.tree.2023.02.006.

Capellini I, Preston B, McNamara P, Barton R, Nunn C. 2009. Ecological constraints on mammalian sleep architecture. In: *Evolution of Sleep: Phylogenetic and Functional Perspectives.* Cambridge University Press. doi:10.1017/CBO9780511642074.002

Chapman CA, Chapman LJ, Melaughlin RL. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia.* 79:506–511. doi:10.1007/BF00378668

Cirelli C, Tononi G. 2008. Is Sleep Essential? *PLOS Biology.* 6(8):e216. doi:10.1371/journal.pbio.0060216.



Cole NC, Jones CG, Harris S. 2005. The need for enemy-free space: The impact of an invasive gecko on island endemics. *Biological Conservation*. 125(4):467–474. doi:10.1016/j.biocon.2005.04.017.

Corradini A, Randles M, Pedrotti L, van Loon E, Passoni G, Oberosler V, Rovero F, Tattoni C, Ciolli M, Cagnacci F. 2021. Effects of cumulated outdoor activity on wildlife habitat use. *Biological Conservation*. 253:108818. doi:10.1016/j.biocon.2020.108818.

Courbin N, Loveridge AJ, Fritz H, Macdonald DW, Patin R, Valeix M, Chamaillé-Jammes S. 2019. Zebra diel migrations reduce encounter risk with lions at night. *Journal of Animal Ecology*. 88(1):92–101. doi:10.1111/1365-2656.12910.

Daan S. 1981. Adaptive Daily Strategies in Behavior. In: Aschoff J, editor. *Biological Rhythms*. Boston, MA: Springer US. p. 275–298. doi:10.1007/978-1-4615-6552-9\_15.

Das N. 2001. Factors influencing the inactive behaviours of stall-fed sheep under experimental conditions. *Small Ruminant Research*. 42(1):39–47. doi:10.1016/S0921-4488(01)00225-5.

Dasilva GL. 1993. Postural changes and behavioural thermoregulation in *Colobus polykomos*: the effect of climate and diet. *African Journal of Ecology*. 31(3):226–241. doi:10.1111/j.1365-2028.1993.tb00536.x.

Davimes JG, Alagaili AN, Bhagwandin A, Bertelsen MF, Mohammed OB, Bennett NC, Manger PR, Gravett N. 2018. Seasonal variations in sleep of free-ranging Arabian oryx (*Oryx leucoryx*) under natural hyperarid conditions. *Sleep*. 41(5). doi:10.1093/sleep/zsy038.

Day RT, Elwood RW. 1999. Sleeping Site Selection by the Golden-handed Tamarin *Saguinus midas midas*: The Role of Predation Risk, Proximity to Feeding Sites, and Territorial Defence. *Ethology*. 105(12):1035–1051. doi:10.1046/j.1439-0310.1999.10512492.x.

DeGregorio BA, Westervelt JD, Weatherhead PJ, Sperry JH. 2015. Indirect effect of climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation. *Ecological Modelling*. 312:239–246. doi:10.1016/j.ecolmodel.2015.05.031.

Dewasmes G, Côté S, Le Maho Y, Groscolas R, Robin J, Vardon G, Libert J. 2001. Effects of weather on activity and sleep in brooding king penguins (*Aptenodytes patagonicus*). *Polar Biol*. 24(7):508–511. doi:10.1007/s003000100249.

Dominguez J. 2003. Sleeping and vigilance in Black-tailed Godwit. *J Ethol*. 21(1):57–60. doi:10.1007/s10164-002-0074-7.

Dominoni D, Smit JAH, Visser ME, Halfwerk W. 2020. Multisensory pollution: Artificial light at night and anthropogenic noise have interactive effects on activity patterns of great tits (*Parus major*). *Environmental Pollution*. 256:113314. doi:10.1016/j.envpol.2019.113314.

Dominoni DM, Carmona-Wagner EO, Hofmann M, Kranstauber B, Partecke J. 2014. Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *J Anim Ecol*. 83(3):681–692. doi:10.1111/1365-2656.12150.

Downes S, Shine R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Animal Behaviour*. 55(5):1387–1396. doi:10.1006/anbe.1997.0705.

Duarte MHL, Young RJ. 2011. Sleeping Site Selection by Urban Marmosets (*Callithrix penicillata*) Under Conditions of Exceptionally High Predator Density. *Int J Primatol*. 32(2):329–334. doi:10.1007/s10764-010-9468-5.

Dukas R, Clark CW. 1995. Sustained vigilance and animal performance. *Animal Behaviour*. 49(5):1259–1267. doi:10.1006/anbe.1995.0158.

Dunbar RIM, Korstjens AH, Lehmann J. 2009. Time as an ecological constraint. *Biological Reviews*. 84(3):413–429. doi:10.1111/j.1469-185X.2009.00080.x.

Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological Processes That Affect Populations in Complex Landscapes. *Oikos*. 65(1):169–175. doi:10.2307/3544901.

Eppley TM, Watzek J, Dausmann KH, Ganzhorn JU, Donati G. 2017. Huddling is more important than rest site selection for thermoregulation in southern bamboo lemurs. *Animal Behaviour*. 127:153–161. doi:10.1016/j.anbehav.2017.03.019.

Erkert HG. 1982. Ecological Aspects of Bat Activity Rhythms. In: Kunz TH, editor. *Ecology of Bats*. Boston, MA: Springer US. p. 201–242. doi:10.1007/978-1-4613-3421-7\_5.

Fasola M, Biddau L. 1997. An assemblage of wintering waders in coastal Kenya: activity budget and habitat use. *African Journal of Ecology*. 35(4):339–350. doi:10.1111/j.1365-2028.1997.087-89087.x.

Fei H, de Guinea M, Yang L, Chapman CA, Fan P. 2022. Where to sleep next? Evidence for spatial memory associated with sleeping sites in Skywalker gibbons (*Hoolock tianxing*). *Anim Cogn*. 25(4):891–903. doi:10.1007/s10071-022-01600-0.

Ferretti A, Rattenborg NC, Ruf T, McWilliams SR, Cardinale M, Fusani L. 2019. Sleeping Unsafely Tucked in to Conserve Energy in a Nocturnal Migratory Songbird. *Current Biology*. 29(16):2766-2772.e4. doi:10.1016/j.cub.2019.07.028.

Flesch AD, Rosen PC, Holm P. 2017. Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation. *Glob Chang Biol*. 23(12):5492-5508. doi:10.1111/gcb.13813.

Fradin G, Chamaille-Jammes S. 2023. Hogs sleep like logs: Wild boars reduce the risk of anthropic disturbance by adjusting where they rest. *Ecol Evol*. 13(7):e10336. doi:10.1002/ece3.10336.

Frank MG. 2020. The Ontogenesis of Mammalian Sleep: Form and Function. *Curr Sleep Medicine Rep*. 6(4):267-279. doi:10.1007/s40675-020-00190-y.

Frank MG, Heller HC. 2003. The ontogeny of mammalian sleep: a reappraisal of alternative hypotheses. *J Sleep Res*. 12(1):25-34. doi:10.1046/j.1365-2869.2003.00339.x.

Freiberg A. 2020. Why We Sleep: A Hypothesis for an Ultimate or Evolutionary Origin for Sleep and Other Physiological Rhythms. *Journal of Circadian Rhythms*. 18. doi:10.5334/jcr.189.

Fuller RA, Warren PH, Gaston KJ. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biol Lett*. 3(4):368-370. doi:10.1098/rsbl.2007.0134.

Fureix C, Meagher RK. 2015. What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. *Applied Animal Behaviour Science*. 171:8-24. doi:10.1016/j.applanim.2015.08.036.

Gaston KJ, Sánchez de Miguel A. 2022. Environmental Impacts of Artificial Light at Night. *Annual Review of Environment and Resources*. 47(1):373-398. doi:10.1146/annurev-environ-112420-014438.

Gauthier-Clerc M, Tamisier A, Cezilly F. 1998. Sleep-vigilance trade-off in Green-winged Teals (*Anas crecca crecca*). *Can J Zool*. 76(12):2214-2218. doi:10.1139/z98-166.

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. *Science*. 360(6394):1232-1235. doi: 10.1126/science.aar7121.

Geiser F. 2013. Hibernation. *Current Biology*. 23(5):R188-R193. doi:10.1016/j.cub.2013.01.062.

Geiser F, Turbill C. 2009. Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften*. 96(10):1235-1240. doi:10.1007/s00114-009-0583-0.

- Génin F. 2010. Who sleeps with whom? Sleeping association and socio-territoriality in *Microcebus griseorufus*. *Journal of Mammalogy*. 91(4):942–951. doi:10.1644/09-MAMM-A-239.1.
- Gerber BD, Hooten MB, Peck CP, Rice MB, Gammonley JH, Apa AD, Davis AJ. 2019. Extreme site fidelity as an optimal strategy in an unpredictable and homogeneous environment. *Functional Ecology*. 33(9):1695–1707. doi:10.1111/1365-2435.13390.
- Gestich CC, Caselli CB, Setz EZF. 2014. Behavioural Thermoregulation in a Small Neotropical Primate. *Ethology*. 120(4):331–339. doi:10.1111/eth.12203.
- Gilbert C, McCafferty D, Le Maho Y, Martrette J-M, Giroud S, Blanc S, Ancel A. 2010. One for all and all for one: the energetic benefits of huddling in endotherms. *Biological Reviews*. 85(3):545–569. doi:10.1111/j.1469-185X.2009.00115.x.
- Gilbert NA, McGinn KA, Nunes LA, Shipley AA, Bernath-Plaisted J, Clare JDJ, Murphy PW, Keyser SR, Thompson KL, Nelson SBM, et al. 2023. Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution*. 38(4):324–336. doi:10.1016/j.tree.2022.10.008.
- Glass TW, Breed GA, Robards MD, Williams CT, Kielland K. 2021. Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*. 175:163–174. doi:10.1016/j.anbehav.2021.02.017.
- Gravett N, Bhagwandin A, Sutcliffe R, Landen K, Chase MJ, Lyamin OI, Siegel JM, Manger PR. 2017. Inactivity/sleep in two wild free-roaming African elephant matriarchs – Does large body size make elephants the shortest mammalian sleepers? *PLOS ONE*. 12(3):e0171903. doi:10.1371/journal.pone.0171903.
- Grunst AS, Grunst ML, Raap T, Pinxten R, Eens M. 2023. Anthropogenic noise and light pollution additively affect sleep behaviour in free-living birds in sex- and season-dependent fashions. *Environmental Pollution*. 316:120426. doi:10.1016/j.envpol.2022.120426.
- Guillemette M. 1998. The effect of time and digestion constraints in Common Eiders while feeding and diving over Blue Mussel beds. *Functional Ecology*. 12(1):123–131. doi:10.1046/j.1365-2435.1998.00164.x.
- Gunn RL, Hartley IR, Algar AC, Niemelä PT, Keith SA. 2022. Understanding behavioural responses to human-induced rapid environmental change: a meta-analysis. *Oikos*. 2022(4):e08366. doi:10.1111/oik.08366.
- Guy PR. 1976. Diurnal activity patterns of elephant in the Sengwa Area, Rhodesia. *African Journal of Ecology*. 14(4):285–295. doi:10.1111/j.1365-2028.1976.tb00243.x.

Halle S. 2006. Polyphasic activity patterns in small mammals. *Folia Primatol (Basel)*. 77(1-2):15-26. doi:10.1159/000089693.

Harding EC, Franks NP, Wisden W. 2019. The Temperature Dependence of Sleep. *Frontiers in Neuroscience*. 13. doi:10.3389/fnins.2019.00336.

van Hasselt SJ. 2021. Studies on sleep patterns and sleep homeostasis in birds: An ecological approach. [Thesis fully internal (DIV), University of Groningen]. University of Groningen. doi:10.33612/diss.182116715

Hausfater G, Meade BJ. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates*. 23(2):287-297. doi:10.1007/BF02381167.

Hazlerigg DG, Tyler NJC. 2019. Activity patterns in mammals: Circadian dominance challenged. *PLOS Biology*. 17(7):e3000360. doi:10.1371/journal.pbio.3000360.

Heller HC, Ruby NF. 2004. Sleep and Circadian Rhythms in Mammalian Torpor. *Annual Review of Physiology*. 66(1):275-289. doi:10.1146/annurev.physiol.66.032102.115313.

Henson SM, Hayward JL, Burden CM, Logan CJ, Galusha JG. 2004. Predicting Dynamics of Aggregate Loafing Behavior in Glaucous-Winged Gulls (*Larus Glaucescens*) at a Washington Colony. *The Auk*. 121(2):380-390. doi:10.1093/auk/121.2.380.

Herbers JM. 1981. Time resources and laziness in animals. *Oecologia*. 49(2):252-262. doi:10.1007/BF00349198.

Hetem RS, Maloney SK, Fuller A, Mitchell D. 2016. Heterothermy in large mammals: inevitable or implemented? *Biological Reviews*. 91(1):187-205. doi:10.1111/brv.12166.

Hočevar L, Oliveira T, Krofel M. 2021. Felid bedrooms with a panoramic view: selection of resting sites by Eurasian lynx (*Lynx lynx*) in a karstic landscape. *Behav Ecol Sociobiol*. 75(2):34. doi:10.1007/s00265-021-02977-7.

Huey RB. 1991. Physiological Consequences of Habitat Selection. *The American Naturalist*. 137:S91-S115. doi:10.1086/285141

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 367(1596):1665-1679. doi:10.1098/rstb.2012.0005.

Imeri L, Opp MR. 2009. How (and why) the immune system makes us sleep. *Nat Rev Neurosci*. 10(3):199–210. doi:10.1038/nrn2576.

Janmaat KRL, Polansky L, Ban SD, Boesch C. 2014. Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences*. 111(46):16343–16348. doi:10.1073/pnas.1407524111.

Jouvet-Mounier D, Astic L, Lacote D. 1970. Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. *Dev Psychobiol*. 2(4):216–239. doi:10.1002/dev.420020407.

Kaburu SSK, Beisner B, Balasubramaniam KN, Marty PR, Bliss-Moreau E, Mohan L, Rattan SK, Arlet ME, Atwill ER, McCowan B. 2019. Interactions with humans impose time constraints on urban-dwelling rhesus macaques (*Macaca mulatta*). *Behav*. 156(12):1255–1282. doi:10.1163/1568539X-00003565.

Kacelnik A, Houston AI. 1984. Some effects of energy costs on foraging strategies. *Animal Behaviour*. 32(2):609–614. doi:10.1016/S0003-3472(84)80298-5.

Kaiser C, Kaiser H. 2021. Coming home to roost: comments on individual sleep-site fidelity, sleep-site choice, and sleeping positions in *Anolis (Norops) leditzigorum* in Costa Rica (Squamata: Dactyloidae). *Herpetology Notes*. 14:375–378.

Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*. 14(10):1052–1061. doi:10.1111/j.1461-0248.2011.01664.x.

Koenig J, Shine R, Shea G. 2001. The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? *Wildlife Research*. 28(3):215–227. doi:10.1071/WR00068.

Kolbe JJ, Moniz HA, Lapiedra O, Thawley CJ. 2021. Bright lights, big city: an experimental assessment of short-term behavioral and performance effects of artificial light at night on *Anolis* lizards. *Urban Ecosyst*. 24(5):1035–1045. doi:10.1007/s11252-021-01098-3.

Komagata N, Latifi B, Rusterholz T, Bassetti CLA, Adamantidis A, Schmidt MH. 2019. Dynamic REM Sleep Modulation by Ambient Temperature and the Critical Role of the Melanin-Concentrating Hormone System. *Curr Biol*. 29(12):1976–1987.e4. doi:10.1016/j.cub.2019.05.009.

Kondo J, Downes SJ. 2007. Does social behaviour reliably reflect temperature-dependent physiological capacity in geckos? *Animal Behaviour*. 74(4):873–880. doi:10.1016/j.anbehav.2006.10.030.

Korstjens AH, Lehmann J, Dunbar RIM. 2010. Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*. 79(2):361–374. doi:10.1016/j.anbehav.2009.11.012.

Kortekaas K, Kotrschal K. 2019. Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes*. 166:103877. doi:10.1016/j.beproc.2019.05.024.

Lanham EJ, Bull CM. 2004. Enhanced vigilance in groups in *Egernia stokesii*, a lizard with stable social aggregations. *Journal of Zoology*. 263(1):95–99. doi:10.1017/S0952836904004923.

Larroque J, Ruetten S, Vandel J-M, Devillard S. 2015. Where to sleep in a rural landscape? A comparative study of resting sites pattern in two syntopic *Martes* species. *Ecography*. 38(11):1129–1140. doi:10.1111/ecog.01133.

Le Roux DS, Ikin K, Lindenmayer DB, Blanchard W, Manning AD, Gibbons P. 2014. Reduced availability of habitat structures in urban landscapes: Implications for policy and practice. *Landscape and Urban Planning*. 125:57–64. doi:10.1016/j.landurbplan.2014.01.015.

Lesku JA, Bark RJ, Martinez-Gonzalez D, Rattenborg NC, Amlaner CJ, Lima SL. 2008. Predator-induced plasticity in sleep architecture in wild-caught Norway rats (*Rattus norvegicus*). *Behavioural Brain Research*. 189(2):298–305. doi:10.1016/j.bbr.2008.01.006.

Lesku JA, Rattenborg NC. 2022. The missing cost of ecological sleep loss. *SLEEP Advances*. 3(1):zpac036. doi:10.1093/sleepadvances/zpac036.

Lesku JA, Rattenborg NC, Valcu M, Vyssotski AL, Kuhn S, Kuemmeth F, Heidrich W, Kempenaers B. 2012. Adaptive Sleep Loss in Polygynous Pectoral Sandpipers. *Science*. 337(6102):1654–1658. doi:10.1126/science.1220939.

Lesku JA, Schmidt MH. 2022. Energetic costs and benefits of sleep. *Curr Biol*. 32(12):R656–R661. doi:10.1016/j.cub.2022.04.004.

Levitis DA, Lidicker WZ, Freund G. 2009. Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*. 78(1):103–110. doi:10.1016/j.anbehav.2009.03.018.

Levy O, Dayan T, Porter WP, Kronfeld-Schor N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecological Monographs*. 89(1):e01334. doi:10.1002/ecm.1334.

Li Y, Huang X, Huang Z. 2020. Behavioral adjustments and support use of François' langur in limestone habitat in Fusui, China: Implications for behavioral thermoregulation. *Ecology and Evolution*. 10(11):4956–4967. doi:10.1002/ece3.6249.

Libourel P-A. 2022. Chapter 9 - Wireless vigilance state monitoring. In: Murillo-Rodriguez E, editor. *Methodological Approaches for Sleep and Vigilance Research*. Academic Press. p. 171–189. doi:10.1016/B978-0-323-85235-7.00009-0

Libourel P-A, Barrillot B. 2020. Is there REM sleep in reptiles? A key question, but still unanswered. *Current Opinion in Physiology*. 15:134–142. doi:10.1016/j.cophys.2020.01.001.

Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ. 2005. Sleeping under the risk of predation. *Animal Behaviour*. 70(4):723–736. doi:10.1016/j.anbehav.2005.01.008.

Loftus JC, Harel R, Núñez CL, Crofoot MC. 2022. Ecological and social pressures interfere with homeostatic sleep regulation in the wild. Watanabe YY, Rutz C, Watanabe YY, editors. *eLife*. 11:e73695. doi:10.7554/eLife.73695.

Lowry H, Lill A, Wong BBM. 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews*. 88(3):537–549. doi:10.1111/brv.12012.

Lutermann H, Verburgt L, Rendigs A. 2010. Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*. 79(6):1211–1219. doi:10.1016/j.anbehav.2010.02.017.

Lyamin OI, Kosenko PO, Korneva SM, Vyssotski AL, Mukhametov LM, Siegel JM. 2018. Fur Seals Suppress REM Sleep for Very Long Periods without Subsequent Rebound. *Curr Biol*. 28(12):2000–2005.e2. doi:10.1016/j.cub.2018.05.022.

Manning AD, Gibbons P, Fischer J, Oliver DL, Lindenmayer DB. 2013. Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation*. 16(4):395–403. doi:10.1111/acv.12006.

Marinesco S, Bonnet C, Cespuglio R. 1999. Influence of stress duration on the sleep rebound induced by immobilization in the rat: a possible role for corticosterone. *Neuroscience*. 92(3):921–933. doi:10.1016/s0306-4522(99)00045-7.

Markham AC, Alberts SC, Altmann J. 2016. Haven for the night: sleeping site selection in a wild primate. *Behavioral Ecology*. 27(1):29–35. doi:10.1093/beheco/arv118.



Martin JK, Martin AA. 2007. Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*: Marsupialia). *Oecologia*. 154(1):227–236. doi:10.1007/s00442-007-0823-y.

Masi S, Cipolletta C, Robbins MM. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *Am J Primatol*. 71(2):91–100. doi:10.1002/ajp.20629.

McBlain M, Jones KA, Shannon G. 2020. Sleeping Eurasian oystercatchers adjust their vigilance in response to the behaviour of neighbours, human disturbance and environmental conditions. *Journal of Zoology*. doi:10.1111/jzo.12812.

McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP. 2014. Behavioral flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology*. 154(3):357–364. doi:10.1002/ajpa.22518.

Mignot E. 2008. Why We Sleep: The Temporal Organization of Recovery. *PLOS Biology*. 6(4):e106. doi:10.1371/journal.pbio.0060106.

Mohanty NP, Wagener C, Herrel A, Thaker M. 2022. The ecology of sleep in non-avian reptiles. *Biological Reviews*. 97(2):505–526. doi:10.1111/brv.12808.

Monterroso P, Alves PC, Ferreras P. 2013. Catch Me If You Can: Diel Activity Patterns of Mammalian Prey and Predators. *Ethology*. 119(12):1044–1056. doi:10.1111/eth.12156.

Moore D, Stow A, Kearney MR. 2018. Under the weather?—The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology*. 87(3):660–671. doi:10.1111/1365-2656.12812.

Mori E, Ancillotto L, Menchetti M, Strubbe D. 2017. ‘The early bird catches the nest’: possible competition between scops owls and ring-necked parakeets. *Animal Conservation*. 20(5):463–470. doi:10.1111/acv.12334.

Mysterud A, Ims RA. 1998. Functional Responses in Habitat Use: Availability Influences Relative Use in Trade-Off Situations. *Ecology*. 79(4):1435–1441. doi:10.1890/0012-9658(1998)079[1435:FRIHUA]2.0.CO;2.

Nickel BA, Suraci JP, Allen ML, Wilmers CC. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*. 241:108383. doi:10.1016/j.biocon.2019.108383.

Nowack J, Stawski C, Geiser F. 2017. More functions of torpor and their roles in a changing world. *J Comp Physiol B*. 187(5):889–897. doi:10.1007/s00360-017-1100-y.

Nuijten RJM, Gerrits T, Shamoun-Baranes J, Nolet BA. 2020. Less is more: On-board lossy compression of accelerometer data increases biologging capacity. *Journal of Animal Ecology*. 89(1):237–247. doi:10.1111/1365-2656.13164.

Ordiz A, Støen O-G, Sæbø S, Sahlén V, Pedersen BE, Kindberg J, Swenson JE. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*. 50(2):306–314. doi:10.1111/1365-2664.12047.

Owen-Smith N, Goodall V. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *Journal of Zoology*. 293(3):181–191. doi:10.1111/jzo.12132.

Parlin AF, Schaeffer PJ, Jezkova T. 2020. Modelling the effect of environmental temperatures, microhabitat and behavioural thermoregulation on predicted activity patterns in a desert lizard across its thermally diverse distribution. *Journal of Biogeography*. 47(11):2315–2327. doi:10.1111/jbi.13936.

Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śniezko S, Jędrzejewski W, Okarma H. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*. 94(1):109–119. doi:10.1644/12-MAMM-A-038.1.

Price M. 2008. The impact of human disturbance on birds: a selective review. In: Lunney D, Munn A, and Meikle W (eds). *Too close for comfort: contentious issues in human–wildlife encounters*. Royal Zoological Society of New South Wales. p163–196. doi:10.7882/FS.2008.023.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*. 83(2):504–514. doi:10.1111/1365-2656.12148.

Pyke GH. 2019. Animal Movements – An Optimal Foraging Theory Approach. In: Choe JC, editor. *Encyclopedia of Animal Behavior (Second Edition)*. Oxford: Academic Press. p. 149–156. doi:10.1016/B978-0-12-809633-8.90160-2

Raap T, Pinxten R, Eens M. 2016. Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution*. 215:125–134. doi:10.1016/j.envpol.2016.04.100.

Rattenborg N, Mandt BH, Obermeyer W, Winsauer P, Huber R, Wikelski M, Benca R. 2004. Migratory Sleeplessness in the White-Crowned Sparrow (*Zonotrichia leucophrys gambelii*). *PLoS biology*. doi:10.1371/journal.pbio.0020212.

Rattenborg NC, Amlaner CJ, Lima SL. 2000. Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neuroscience & Biobehavioral Reviews*. 24(8):817–842. doi:10.1016/S0149-7634(00)00039-7.

Rattenborg NC, de la Iglesia HO, Kempnaers B, Lesku JA, Meerlo P, Scriba MF. 2017. Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 372(1734):20160251. doi:10.1098/rstb.2016.0251.

Rattenborg NC, Voirin B, Cruz SM, Tisdale R, Dell’Omo G, Lipp H-P, Wikelski M, Vyssotski AL. 2016. Evidence that birds sleep in mid-flight. *Nature Communications*. 7(1):12468. doi:10.1038/ncomms12468.

Rattenborg NC, Voirin B, Vyssotski AL, Kays RW, Spoelstra K, Kuemmeth F, Heidrich W, Wikelski M. 2008. Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biol Lett*. 4(4):402–405. doi:10.1098/rsbl.2008.0203.

Reinhardt KD. 2020. Wild primate sleep: understanding sleep in an ecological context. *Current Opinion in Physiology*. 15:238–244. doi:10.1016/j.cophys.2020.04.002.

Remm J, Lõhmus A. 2011. Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*. 262(4):579–585. doi:10.1016/j.foreco.2011.04.028.

Rial RV, Akaârir M, Gamundí A, Nicolau C, Garau C, Aparicio S, Tejada S, Gené L, González J, De Vera LM, et al. 2010. Evolution of wakefulness, sleep and hibernation: From reptiles to mammals. *Neuroscience & Biobehavioral Reviews*. 34(8):1144–1160. doi:10.1016/j.neubiorev.2010.01.008.

Riede SJ, van der Vinne V, Hut RA. 2017. The flexible clock: predictive and reactive homeostasis, energy balance and the circadian regulation of sleep-wake timing. *Journal of Experimental Biology*. 220(5):738–749. doi:10.1242/jeb.130757.

Rodriguez AV, Funk CM, Vyazovskiy VV, Nir Y, Tononi G, Cirelli C. 2016. Why Does Sleep Slow-Wave Activity Increase After Extended Wake? Assessing the Effects of Increased Cortical Firing During Wake and Sleep. *J Neurosci*. 36(49):12436–12447. doi:10.1523/JNEUROSCI.1614-16.2016.

Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. *Biological Reviews*. 90(3):891–926. doi:10.1111/brv.12137.

Sarkar R, Bhadra A. 2022. How do animals navigate the urban jungle? A review of cognition in urban-adapted animals. *Current Opinion in Behavioral Sciences*. 46:101177. doi:10.1016/j.cobeha.2022.101177.

Sato H. 2012. Diurnal resting in brown lemurs in a dry deciduous forest, northwestern Madagascar: implications for seasonal thermoregulation. *Primates*. 53(3):255–263. doi:10.1007/s10329-012-0301-y.

Schmidt MH. 2014. The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience & Biobehavioral Reviews*. 47:122–153. doi:10.1016/j.neubiorev.2014.08.001.

Schmidt MH, Swang TW, Hamilton IM, Best JA. 2017. State-dependent metabolic partitioning and energy conservation: A theoretical framework for understanding the function of sleep. *PLOS ONE*. 12(10):e0185746. doi:10.1371/journal.pone.0185746.

Schneider TC, Kowalczyk R, Köhler M. 2013. Resting site selection by large herbivores – The case of European bison (*Bison bonasus*) in Białowieża Primeval Forest. *Mamm Biol*. 78(6):438–445. doi:10.1016/j.mambio.2013.06.002.

Shores CR, Dellinger JA, Newkirk ES, Kachel SM, Wirsing AJ. 2019. Mesopredators change temporal activity in response to a recolonizing apex predator. *Behavioral Ecology*. 30(5):1324–1335. doi:10.1093/beheco/arz080.

Shukla I, Kilpatrick AM, Beltran RS. 2021. Variation in resting strategies across trophic levels and habitats in mammals. *Ecology and Evolution*. 11(21):14405–14415. doi:10.1002/ece3.8073.

Siegel JM. 2009. Sleep viewed as a state of adaptive inactivity. *Nature Reviews Neuroscience*. 10(10):747–753. doi:10.1038/nrn2697.

Silk JB, Alberts SC, Altmann J. 2003. Social Bonds of Female Baboons Enhance Infant Survival. *Science*. 302(5648):1231–1234. doi:10.1126/science.1088580.

Singhal S, Johnson MA, Ladner JT. 2007. The Behavioral Ecology of Sleep: Natural Sleeping Site Choice in Three Anolis Lizard Species. *Behaviour*. 144(9):1033–1052.

Smeltzer EA, Stead SM, Li MF, Samson D, Kumpan LT, Teichroeb JA. 2022. Social sleepers: The effects of social status on sleep in terrestrial mammals. *Hormones and Behavior*. 143:105181. doi:10.1016/j.yhbeh.2022.105181.

Smith AC, Knogge C, Huck M, Löttker P, Buchanan-Smith HM, Heymann EW. 2007. Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*): Effects of foraging, thermoregulation, predation, and resource defense constraints. *American Journal of Physical Anthropology*. 134(3):340–353. doi:10.1002/ajpa.20676.

Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*. 141(9):2159–2173. doi:10.1016/j.biocon.2008.06.026.

Stuber EF, Grobis MM, Abbey-Lee R, Kempenaers B, Mueller JC, Dingemanse NJ. 2014. Perceived predation risk affects sleep behaviour in free-living great tits, *Parus major*. *Animal Behaviour*. 98:157–165. doi:10.1016/j.anbehav.2014.10.010.

Suraci JP, Clinchy M, Zanette LY, Wilmers CC. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*. 22(10):1578–1586. doi:10.1111/ele.13344.

Taufique SKT, Kumar V. 2016. Differential activation and tyrosine hydroxylase distribution in the hippocampal, pallial and midbrain brain regions in response to cognitive performance in Indian house crows exposed to abrupt light environment. *Behav Brain Res*. 314:21–29. doi:10.1016/j.bbr.2016.07.046.

Taylor D, Daniels CB, Johnston G. 2016. Habitat selection by an arboreal lizard in an urban parkland: not just any tree will do. *Urban Ecosyst*. 19(1):243–255. doi:10.1007/s11252-015-0480-6.

Terrien J, Perret M, Aujard F. 2011. Behavioral thermoregulation in mammals: a review. *Front Biosci (Landmark Ed)*. 16(4):1428–1444. doi:10.2741/3797.

Tisdale RK, Lesku JA, Beckers GJL, Vyssotski AL, Rattenborg NC. 2018. The low-down on sleeping down low: pigeons shift to lighter forms of sleep when sleeping near the ground. *Journal of Experimental Biology*. 221(19):jeb182634. doi:10.1242/jeb.182634.

Tononi G, Cirelli C. 2014. Sleep and the Price of Plasticity: From Synaptic and Cellular Homeostasis to Memory Consolidation and Integration. *Neuron*. 81(1):12–34. doi:10.1016/j.neuron.2013.12.025.

Torretta E, Corradini A, Pedrotti L, Bani L, Bisi F, Dondina O. 2022. Hide-and-Seek in a Highly Human-Dominated Landscape: Insights into Movement Patterns and Selection of Resting Sites of Rehabilitated Wolves (*Canis lupus*) in Northern Italy. *Animals (Basel)*. 13(1):46. doi:10.3390/ani13010046.

Tougeron K, Abram PK. 2017. An Ecological Perspective on Sleep Disruption. *The American Naturalist*. 190(3):E55–E66. doi:10.1086/692604.

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*. 359(6374):466–469. doi:10.1126/science.aam9712.

Turbill C, Stojanovski L. 2018. Torpor reduces predation risk by compensating for the energetic cost of antipredator foraging behaviours. *Proceedings of the Royal Society B: Biological Sciences*. 285(1893):20182370. doi:10.1098/rspb.2018.2370.

Tworkowski L, Lesku JA. 2019. Behavioural Ecology: Sleeping Safely Carries Energetic Costs. *Current Biology*. 29(16):R801–R803. doi:10.1016/j.cub.2019.07.024.

Ulgezen ZN, Käpylä T, Meerlo P, Spoelstra K, Visser ME, Dominoni DM. 2019. The preference and costs of sleeping under light at night in forest and urban great tits. *Proceedings of the Royal Society B: Biological Sciences*. 286(1905):20190872. doi:10.1098/rspb.2019.0872.

Ungurean G, van der Meij J, Rattenborg NC, Lesku JA. 2020. Evolution and plasticity of sleep. *Current Opinion in Physiology*. 15:111–119. doi:10.1016/j.cophys.2019.12.013.

Wagner EL, Gleeson TT. 1997. The influence of thermoregulation on behavioural recovery from exercise in a lizard. *Functional Ecology*. 11(6):723–728. doi:10.1046/j.1365-2435.1997.00146.x.

Walker JM, Berger RJ. 1980. Sleep as an Adaptation for Energy Conservation Functionally Related to Hibernation and Shallow Torpor. In: McConnell PS, Boer GJ, Romijn HJ, Van De Poll NE, Corner MA, editors. *Progress in Brain Research*. Vol. 53. Elsevier. p. 255–278. doi:10.1016/S0079-6123(08)60068-0

Wam HK, Eldegard K, Hjeljord O. 2012. From overlooking to concealed: predator avoidance in an apex carnivore. *Eur J Wildl Res*. 58(6):1001–1003. doi:10.1007/s10344-012-0670-y.

Weinberger IC, Muff S, Kranz A, Bontadina F. 2019. Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape. *Mamm Biol*. 98(1):179–187. doi:10.1016/j.mambio.2019.09.001.

Williamson L, Pigeon G, Myrsterud A, Stien A, Forchhammer M, Loe LE. 2019. Keeping cool in the warming Arctic: thermoregulatory behaviour by Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Can J Zool*. 97(12):1177–1185. doi:10.1139/cjz-2019-0090.

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*. 96(7):1741–1753. doi:10.1890/14-1401.1.

Withers PC, Cooper CE. 2010. Metabolic Depression: A Historical Perspective. In: Arturo Navas C, Carvalho JE, editors. *Aestivation: Molecular and Physiological Aspects*. Berlin, Heidelberg: Springer. (Progress in Molecular and Subcellular Biology). p. 1–23. doi:10.1007/978-3-642-02421-4\_1.

Wittemyer G, Keating LM, Vollrath F, Douglas-Hamilton I. 2017. Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography*. 40(5):598–605. doi:10.1111/ecog.02379.

Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*. 3(2):165–173. doi:10.1111/j.1469-1795.2000.tb00241.x.

Zielinski MR, McKenna JT, McCarley RW. 2016. Functions and Mechanisms of Sleep. *AIMS Neurosci*. 3(1):67–104. doi:10.3934/Neuroscience.2016.1.67.







# Second Axe



## Cas d'étude du sanglier





# Introduction

## 1 Une espèce charismatique de la faune Européenne

Le sanglier (*Sus scrofa*) est natif de la zone paléarctique, où il est largement répandu dans une grande diversité d'environnements : forêt boréales, garrigue Méditerranéenne, haute montagne, etc. (Figure 1). En Europe tempérée, il figure parmi les plus grands animaux terrestres. Le sanglier présente un dimorphisme sexuel important, avec un poids compris entre 50 et 130 kg pour les mâles, et entre 30 et 80 kg pour les femelles (appelées « laies »). La taille du sanglier est très variable selon les régions et les conditions environnementales.

C'est une espèce opportuniste et omnivore, dont le régime alimentaire, remarquablement variable selon les saisons et les environnements, est très largement déterminé par la disponibilité alimentaire (Schley and Roper 2003; Ballari and Barrios-García 2014). Le sanglier consomme des éléments végétaux variés (fruits, feuilles et racines), des champignons, et une grande diversité de proies animales (lombrics, arthropodes, reptiles et amphibiens, petits oiseaux et mammifères, etc.), ainsi que des œufs et des charognes. La base de son alimentation comprend toujours un élément végétal riche en énergie, et disponible en grande quantité (Schley and Roper 2003). Il s'agit généralement de fruits forestiers (glands, faînes, noisettes), mais dans les zones agricoles, ceux-ci peuvent être complétés ou remplacés par une grande diversité de plantes cultivées (céréales, légumineuses, pommes de terre, etc.) (Schley and Roper 2003; Herrero et al. 2006; Fournier-Chambrillon et al. 2014). La consommation de produits agricoles est fortement influencée par la disponibilité des fruits forestiers, qui fluctue selon les saisons, et selon un cycle pluriannuel de fructification de masse (glandées, fainées). Dans certains cas, les dégâts agricoles occasionnés par les sangliers peuvent être importants (Schley and Roper 2003; Barrios-Garcia and Ballari 2012).



**Figure 1.** Le sanglier, un animal omniprésent. (a) Carte de la répartition du sanglier dans le monde, adapté de Lewis et al. (2017) et Barrios-Garcia et Ballari (2012). (b) La diversité des habitats où vit le sanglier : montagnes, marais, forêts tempérées, garrigues méditerranéennes, etc.

Le sanglier est un animal social. Les femelles vivent en groupes matrilineaires composés d'une laie dite meneuse, accompagnée d'autres femelles adultes et de jeunes des deux sexes (Kaminski et al. 2005; Poteaux et al. 2009). Les mâles sont solitaires pendant la majeure partie de l'année et

rejoignent les groupes familiaux en automne pour la période du rut (Maselli et al. 2014). Les traits d'histoire de vie des sangliers sont surprenants pour des mammifères de leur taille : une laie peut se reproduire pour la première fois dès la première année (Servanty et al. 2009), et produit en moyenne entre quatre et six petits par portée (Focardi et al. 2008). A titre de comparaison, une femelle d'ongulé (non-suidé) de taille similaire produit moins de trois petits par portée, à partir de sa deuxième ou troisième année (Focardi et al. 2008; Servanty et al. 2009). Même si les marcassins naissent généralement à la fin de l'hiver, ou au printemps, des mises bas sont régulièrement observées à toutes les périodes de l'année (Malmsten et al. 2017).

## 2 Un animal controversé

Le sanglier génère aujourd'hui de fortes tensions sociales et suscite de nombreux débats. Ceux-ci concernent en particulier les dégâts matériels occasionnés par les sangliers (dégâts agricoles, collisions routières, dégradation des espaces verts publics et privés...), et les risques sanitaires qu'ils peuvent représenter pour l'être humain et pour les animaux domestiques. Il existe aussi d'importantes controverses autour des moyens mis en œuvre pour limiter les populations de sangliers : chasse, piégeage pour destruction, etc.

Les tensions liées au sanglier sont exacerbées par la récente croissance démographique de l'espèce sur l'ensemble de son aire de répartition. Entre 1960 et 1980, les populations Européennes de sangliers ont connu une forte augmentation, supérieure à 100% (Sáez-Royuela and Tellería 1986), et leur croissance continue depuis les années 80 (Massei et al. 2015). L'espèce a également recolonisé certains pays d'où elle avait disparu, comme le Royaume-Uni, la Suède, la Finlande et l'Estonie (Veeroja and Männil 2013; Wilson 2013; Markov et al. 2022). Cette explosion démographique spectaculaire, permise par la fécondité exceptionnelle du sanglier et ses capacités de dispersion, a été déclenchée par une combinaison de facteurs externes. La déprise agricole et le reboisement dans certaines régions, l'intensification de l'agriculture dans d'autres, le nourrissage artificiel, et l'augmentation de la fréquence des glandées exceptionnelles liée au changement climatique ont simultanément augmenté la disponibilité des ressources alimentaires (Massei et al. 2015; Touzot et al. 2020). Par ailleurs, la mortalité de l'espèce, et en particulier des jeunes individus, a été réduite par le manque de prédateurs naturels (en particulier le loup gris, *Canis lupus*), la prévalence des hivers doux, et certaines pratiques conservatrices de gestion, comme par exemple le tir sélectif des mâles (Bieber and Ruf 2005; Vetter et al. 2020). L'importance de ces différents facteurs dans l'augmentation des populations de sangliers est en revanche difficile à évaluer. Cette dynamique démographique s'est accompagnée de l'expansion de l'aire de répartition du sanglier (Apollonio et al. 2010), ainsi que de la colonisation de nouveaux habitats où cette espèce était rare ou absente, et en particulier de paysages fortement

urbanisés ou dominés par l'agriculture (Cahill and Llimona 2004; Keuling et al. 2009; Podgórski et al. 2013). Naturellement, l'augmentation des populations de sanglier s'est aussi accompagnée d'une augmentation des dégâts agricoles (Massei et al. 2011), qui sont localement devenus considérables (Bobek et al. 2017). En France, par exemple, les compensations financières pour les dégâts agricoles liés au sanglier sont passées de 2,5 à 32,5 millions d'euros par an entre 1973 et 2008 (Massei et al. 2015). Il y a donc un appel à urgemment diminuer les densités de sangliers (Barrios-Garcia and Ballari 2012; Keuling et al. 2016), et ce dans un contexte où les chasseurs sont de moins en moins nombreux, et la chasse elle-même est de plus en plus critiquée et questionnée (Mathevet and Bondon 2022; Vajas et al. 2023). La chasse récréative représente le facteur de mortalité le plus important pour les sangliers en Europe (Massei et al. 2015; Quirós-Fernández et al. 2017). Dans les pays du Sud de l'Europe, et en particulier dans les régions Méditerranéennes, le sanglier est chassé lors de battues, ou des « piqueurs », avec l'aide des chiens, rabattent les sangliers vers l'extérieur d'une enceinte, autour de laquelle sont postés les « tireurs ». Plus au Nord, la chasse à l'affut ou à l'approche est souvent privilégiée.

### **3 La flexibilité comportementale du sanglier**

Le sanglier fait preuve d'une grande flexibilité dans son comportement spatial (Keuling et al. 2008a). Son aptitude à effectuer des déplacements importants à l'échelle du paysage lui confère une grande capacité d'ajustement aux conditions environnementales. Les connaissances concernant le comportement spatial du sanglier ont été synthétisées par Morelle et al. (2015), selon le cadre de l'écologie du mouvement proposé par Nathan et al. (2008). Selon Nathan et al., le déplacement d'un organisme dans l'espace résulte de l'interaction entre une série de facteurs intrinsèques à l'organisme et les conditions environnementales. Les facteurs intrinsèques influençant le déplacement d'un animal peuvent être décomposés entre les capacités de navigation, les capacités motrices, et la motivation (qui est influencée par des facteurs physiologiques et psychologiques, comme la faim et la peur).

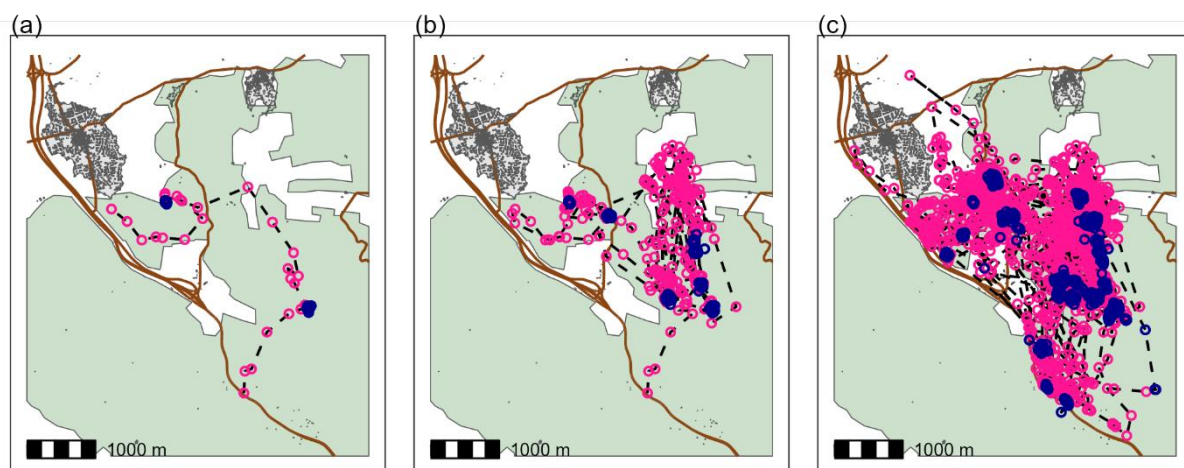
#### **3.1 Navigation**

La navigation dans l'espace chez le sanglier dépend largement de son excellent sens de l'olfaction (Cronney et al. 2003; Morelle et al. 2015), ainsi que d'une bonne mémoire spatiale (Mendl et al. 2010; Gieling et al. 2011). Ainsi, le sanglier utilise des points de repères paysagers et apprend auprès de ses congénères pour créer une carte mentale de son environnement (Dardaillon and Beugnon 1987; Morelle et al. 2015), et revisiter régulièrement les mêmes sites d'alimentation et de repos (Spitz and Janeau 1990; Spitz and Janeau 1995). Il semble tenir compte de signaux magnétiques pour l'orientation de son corps, ce qui suggère que le champ magnétique terrestre pourrait aussi contribuer à l'assemblage de cette carte mentale (Červený et al. 2017).

Lorsqu'il se déplace, le sanglier est donc capable de prendre en compte des éléments distants, qu'ils soient disponibles à sa perception ou stockés en mémoire, dans ses prises de décision.

### 3.2 Motricité

Le sanglier est un animal de grande taille dont les capacités motrices sont importantes (*Figure 2*). Il parcourt quotidiennement entre 2 et 17 km, avec des variations selon le sexe, la saison et la disponibilité alimentaire. Le déplacement quotidien moyen est d'environ 4 km (Spitz and Janeau 1990). Ses modes de déplacement sont de deux types : le mode de transit, rectiligne et rapide, et le mode de fourragement, plus sinueux et lent (Allwin et al. 2016). Le sanglier est assez sédentaire, et il parcourt quotidiennement une proportion importante de son domaine vital annuel (Podgórski et al. 2013; Morelle et al. 2015), qui couvre souvent plusieurs centaines d'hectares. L'étendue de ce domaine vital est influencée par la saison, l'âge, et la structure sociale (Keuling et al. 2008a), mais aussi par les perturbations anthropiques, et notamment la chasse (Boitani et al. 1994; Maillard and Fournier 1995; Calenge et al. 2002; Laguna et al. 2021). Le sanglier vit dans une grande diversité de paysages, et ajuste sa mobilité en fonction de son environnement. Par exemple, les sangliers vivant en milieu urbanisé ont tendance à occuper des domaines vitaux plus restreints, mais à se déplacer davantage chaque jour pour trouver leur nourriture (Podgórski et al. 2013). Le sanglier utilise les éléments paysagers linéaires, tels que les fossés, les haies, et les ripisylves, pour se déplacer sur de longues distances dans les paysages agricoles, tout en restant à couvert (Thurfjell et al. 2009).



**Figure 2.** Déplacements d'un sanglier dans son domaine vital des Gorges du Gardon, pendant (a) deux jours, (b) 15 jours, (c) 104 jours. Les cercles roses et bleus correspondent respectivement aux points GPS enregistrés pendant l'activité et le repos. La ligne pointillée représente le trajet de l'animal. Les bâtiments sont représentés en gris foncé, les villages en gris clair, les routes en brun, et les blocs forestiers en vert.



### 3.3 Motivation

Le sanglier se déplace pour se reproduire, s'alimenter, pour échapper à ses prédateurs et pour rejoindre les sites de repos favorables.

Son cycle reproductif influence différemment les déplacements des mâles et des femelles (Spitz and Janeau 1990). De manière générale, les mâles, qui sont solitaires, se déplacent plus que les femelles. Cette tendance est amplifiée entre l'automne et l'hiver, lors du rut (Cavazza et al. 2023). A cette période, les mâles cessent d'être solitaires, mais se déplacent davantage, et occupent des domaines vitaux plus grands, afin de côtoyer plusieurs groupes sociaux et augmenter leur succès reproducteur (Johann, Handschuh, Linderoth, Heurich, et al. 2020; Cavazza et al. 2023). A l'inverse, les femelles, qui vivent au sein des groupes sociaux toute l'année, réduisent leurs déplacements et la surface de leur domaine vital lorsqu'elles sont accompagnées de juvéniles (Iacolina et al. 2009; Cavazza et al. 2023).

Une autre préoccupation majeure du sanglier, et qui influence fortement ses déplacements, est l'acquisition de nourriture. Le sanglier alloue une proportion importante de son temps au fourragement. Du fait de son régime alimentaire opportuniste, il doit se déplacer plus ou moins en fonction de la disponibilité alimentaire. Certaines ressources, comme les fruits forestiers (glands, faînes, châtaignes), sont concentrées dans l'espace. D'autres modes de fourragement, comme l'exploitation des champs cultivés, impliquent davantage de déplacements (Keuling et al. 2009). La disponibilité de la ressource alimentaire la plus abondante dans un environnement donné et à une saison donnée affecte donc fortement la façon dont le sanglier utilise l'espace. On observe ainsi des déplacements saisonniers des domaines vitaux, liés à la disponibilité alimentaire. Par exemple, les sangliers fréquentent régulièrement les champs cultivés en été, lorsque les cultures sont à maturité, et retournent généralement dans les forêts en automne, pour profiter de la fructification des chênes, hêtres et autres arbres (Morelle et al. 2015). Bisi et al. (2018) ont montré que la taille du domaine vital des sangliers augmente fortement les années de faible production de fruits forestiers. Lorsqu'une ressource alimentaire est abondante localement à une période donnée, le sanglier peut l'exploiter intensément en adoptant un patron de déplacement stéréotypé, caractérisé par des aller-retours entre les sites de repos et d'alimentation (Keuling et al. 2009).

La volonté d'échapper aux prédateurs (ainsi qu'aux chasseurs) influence également les déplacements du sanglier. Par exemple, Gordigiani et al. (2021) ont constaté que le sanglier peut ajuster son activité au cycle lunaire, réduisant ses déplacements lors des nuits les plus claires, probablement pour réduire le risque de prédation par le loup gris (*Canis lupus*). Cependant, dans une grande partie de l'Europe, le loup gris, seul prédateur notable du sanglier, est absent, ou peu

abondant (Kuijper et al. 2014; Massei et al. 2015). C'est l'être humain, à travers la chasse, qui représente la principale cause de mortalité chez le sanglier (Toïgo et al. 2008; Keuling et al. 2013; Massei et al. 2015). Par ailleurs, l'être humain non-chasseur, bien qu'inoffensif pour le sanglier, est aussi à l'origine, par sa seule présence dans les espaces où vit l'animal, de perturbations fréquentes qui peuvent modifier son comportement (Stillfried et al. 2017; Olejarz et al. 2023). Ainsi, l'être humain façonne un paysage de la peur qui structure fortement les déplacements du sanglier (Tolon et al. 2009; Stillfried et al. 2017). Dans les habitats où la présence humaine est réduite, le sanglier est régulièrement actif de jour. Au contraire, lorsque la présence humaine est importante, il est exclusivement nocturne (Podgórski et al. 2013; Ohashi et al. 2014), et se déplace davantage. Ainsi, le sanglier est capable d'ajuster son rythme d'activité au risque de dérangement ou de prédation perçu. Le sanglier ajuste également son comportement aux périodes de chasse. De manière générale, il sélectionne des zones où la végétation est plus dense pendant la saison de chasse (Laguna et al. 2021). L'effet de la période de chasse sur les déplacements du sanglier dépend de nombreux facteurs, et notamment du type de chasse pratiqué. Certains auteurs ont documenté une augmentation des déplacements pendant les périodes chassées (Maillard and Fournier 1995; Laguna et al. 2021). D'autres au contraire, ont trouvé une réduction du domaine vital et des déplacements totaux (Tolon et al. 2009; Thurfjell et al. 2013).

## **4 Un modèle pour étudier le repos en milieu anthropisé**

### **4.1 Un modèle de flexibilité**

Le sanglier vit dans des environnements très contrastés. Il est rencontré tout le long du gradient d'anthropisation, depuis les hautes montagnes et les forêts les plus reculées, jusqu'aux grands bassins agricoles et aux zones péri-urbaines. Comme nous l'avons vu, sa flexibilité comportementale est un atout majeur pour occuper des milieux diversifiés, et persister dans les milieux les plus anthropisés. En effet, le sanglier est capable de comportements drastiquement différents en fonction des conditions : il peut modifier son régime alimentaire de façon spectaculaire en fonction de la disponibilité en ressources. Son rythme d'activité peut aussi changer du tout au tout, oscillant entre des patrons temporels radicalement différents : nocturne, crépusculaire ou diurne, en réponse aux variations du risque de prédation, ou de dérangement. De plus, il est capable d'ajuster ses modes de déplacement à la structure du paysage, et au niveau d'anthropisation. Ainsi, il peut parcourir des distances plus importantes, et plus rapidement, lorsque l'environnement présente à la fois une résistance au déplacement, et des ressources alimentaires diffuses, impliquant donc des déplacements plus efficaces, comme c'est le cas dans les milieux urbanisés.

Quotidiennement, le sanglier alterne entre une phase d'activité et une phase de repos. Cette dernière représente une proportion importante du temps journalier, et implique une série de prises de décisions, qui sont susceptibles de laisser place à de la flexibilité. Ainsi, des choix tels que celui de l'habitat utilisé lors de la sélection des sites de repos, celui de leur disposition dans le paysage, entre eux et par rapport aux sites d'alimentation, et celui de l'organisation temporelle des phases de repos, sont autant de paramètres qui peuvent permettre au sanglier de s'ajuster aux contraintes de son environnement. La flexibilité du comportement de repos pourrait ainsi participer à la persistance du sanglier dans des milieux particulièrement stressants, comme les zones urbanisées, ou fortement chassées. Le sanglier, vivant dans des environnements aux niveaux d'anthropisation variés, et présentant une stupéfiante capacité à ajuster son comportement aux contraintes de son environnement, présente des caractéristiques appropriées pour étudier les effets de l'anthropisation sur le comportement de repos.

## **4.2 Stratégie de repos du sanglier**

Le temps de sommeil journalier a été estimé à environ 7,8 h chez le porc domestique, et à 10,6 h chez le sanglier en milieu naturel (Campbell and Tobler 1984; Mortlock et al. 2022). La phase de repos complète, qui comprend les phases de sommeil ainsi que des phases de veille calme, occupe plus de la moitié du cycle journalier : entre 12 et 14 h de repos journaliers sont généralement rapportées (Sodeikat and Pohlmeier 2007; Podgórski et al. 2013). La durée totale du repos quotidien ne dépend pas du taux d'anthropisation (Podgórski et al. 2013; Olejarz et al. 2023). En revanche, le patron temporel d'alternance des phases de repos et d'activité présente des spécificités locales. De manière générale, on observe un patron d'activité monophasique, et peu affecté par la variation saisonnière et latitudinale de la durée du jour (Lemel et al. 2003; Brivio et al. 2017). Dans les milieux anthropisés, les sangliers sont exclusivement nocturnes, et n'entrent en activité qu'après que le coucher du soleil (Sodeikat and Pohlmeier 2007; Brivio et al. 2017). Dans les milieux plus naturels, le sanglier peut présenter des rythmes d'activité variés (Boitani et al. 1994; Russo et al. 1997; Podgórski et al. 2013; Ikeda et al. 2019). L'utilisation d'un rythme d'activité en particulier ne fixe pas seulement les conditions environnementales pour la phase active, mais expose également la phase de repos à des conditions spécifiques. En effet, les qualités d'un site de repos, en termes de thermorégulation, de risque de prédation et de dérangement, varient entre le jour et la nuit. Ainsi, par exemple, un sanglier actif de nuit expose sa phase de repos à des conditions diurnes, ce qui implique des températures plus élevées, un risque de dérangement par les activités humaines plus important, mais vraisemblablement un risque moindre de prédation naturelle. Le site de repos doit donc être choisi en fonction de ces conditions spécifiques.

En théorie, le sanglier connaît peu de contraintes spécifiques pour la sélection de ses sites de repos (Allwin et al. 2016). Pour se reposer, il s'allonge dans un lit qui consiste en une simple dépression creusée dans la terre, souvent au pied d'un arbre, ou d'un rocher. Il peut y ajouter des éléments végétaux qui en améliorent l'isolation thermique. Les lits sont généralement choisis dans les zones où la végétation est la plus dense possible (Maillard et al. 1995; Saïd et al. 2012). En dehors des zones forestières, le sanglier se repose dans les lieux où il trouve une végétation suffisamment dense, telles que les ripisylves et les roselières, mais aussi les haies, les parcs et les jardins, en particulier lorsque le sous-bois y est dense. En milieu agricole, les champs peuvent aussi être utilisés pour le repos (Keuling et al. 2009; Allwin et al. 2016). Les femelles et les jeunes se reposant ensemble, au sein des groupes familiaux, il est probable qu'ils aient besoin d'un espace plus conséquent pour se reposer, comparé à un mâle solitaire.

Un même lit peut ne servir qu'une seule fois, ou être réutilisé à de nombreuses reprises. Le sanglier garde en mémoire la localisation et les caractéristiques des sites de repos qu'il a déjà utilisé, et lorsqu'ils sont favorables, il revient régulièrement s'y reposer. Cette tendance à la réutilisation des sites de repos peut dans certains cas mener à des patrons d'activités stéréotypés, avec des allers-retours entre un site de repos et un ou plusieurs sites d'activité (Boitani et al. 1994; Morelle et al. 2015). La réutilisation d'un site de repos peut avoir lieu d'un jour sur l'autre, mais elle peut aussi tout à fait être différée à plusieurs mois d'intervalle. Les sangliers entretiennent donc de véritables réseaux de sites de repos qui quadrillent leur domaine vital. Parmi ces sites de repos, certains sont utilisés fréquemment, parfois de façon saisonnière, et d'autres sont occasionnels. Les facteurs qui poussent un sanglier à réutiliser ou non un site de repos sont certainement liés à ses qualités physiques, comme son potentiel de thermorégulation, mais aussi à sa localisation dans le paysage, qui influence le risque de dérangement, ainsi qu'à sa position par rapport aux sites d'alimentation utilisés (Sodeikat and Pohlmeier 2007). La chasse influence également la sélection des sites de repos par le sanglier. Ainsi, une augmentation de la distance entre sites de repos successifs est souvent observée pendant la saison de chasse (Maillard and Fournier 1995; Sodeikat and Pohlmeier 2007; Scillitani et al. 2010). Une telle réponse pourrait diminuer la prédictibilité de la position du sanglier, et ainsi agir comme une stratégie anti-prédation. Pourtant, en dehors de ces quelques effets liés à la chasse, la dynamique spatiotemporelle d'utilisation des sites de repos par le sanglier, et en particulier son interaction avec les activités humaines, reste mal connue. De manière générale, les facteurs qui influencent la prise de décision relative à la sélection des sites de repos par le sanglier demeurent, par de nombreux aspects, inexplorés.

## 5 Objectifs du second axe

Dans ce second axe de ma thèse, nous nous intéressons au sanglier comme objet d'étude, pour approfondir plusieurs questions relatives à l'influence de l'activité humaine sur le comportement de repos. Cette espèce présente des caractéristiques intéressantes pour étudier les effets de l'anthropisation sur le repos animal, et en particulier ceux liés au risque de dérangements directs et à l'altération du paysage. Les deux études suivantes (chapitres 2 et 3) s'appliquent à décrire la dynamique spatiale de l'utilisation des sites de repos par le sanglier à deux échelles différentes. Dans un premier temps, nous nous focalisons sur une échelle locale, celle de la région des Garrigues languedociennes, dans le Sud de la France, pour analyser la stratégie de repos du sanglier dans un contexte unique, homogène, et bien maîtrisé. Dans un second temps, nous prenons une perspective plus globale, en étudiant des populations de sanglier réparties à travers l'Europe entière. Dans les deux cas, l'objectif est de comprendre les mécanismes par lesquels l'anthropisation affecte l'aspect spatial de la stratégie de repos chez cette espèce.

### 5.1 Objectifs du chapitre 2

Dans le premier volet du second axe de cette thèse, nous cherchons à caractériser la stratégie de repos du sanglier en réponse au risque de dérangement par les activités humaines, et à évaluer l'efficacité. Pour cela, nous examinons l'utilisation du paysage par le sanglier lors du repos, avec pour objectif de caractériser l'influence du risque de dérangement par les activités humaines. Le comportement spatial du sanglier est bien sûr contraint par la chasse, mais dans les milieux fortement anthropisés, il peut également être influencé par la présence humaine non liée à la chasse. Nous cherchons à évaluer la fréquence des dérangements liés ou non à la chasse en fonction du type de site de repos sélectionné, afin d'estimer l'efficacité de la stratégie d'ajustement comportemental dans la réduction du risque de dérangement par les activités humaines. Enfin, nous tentons d'estimer l'importance des conséquences directes des perturbations du repos, en termes de distances parcourues lors des mouvements de fuite potentiels. Nous utilisons une méthode basée sur un suivi spatial et accélérométrique, complété par quelques enregistrements audios. Dans cette étude, nous nous cantonnons à deux populations de sangliers du Sud de la France, pour en décrire le comportement spatial à fine échelle.

### 5.2 Objectifs du chapitre 3

Dans le second volet du second axe de cette thèse, nous nous intéressons à l'interaction entre la sélection de l'habitat pour le repos et l'utilisation du paysage lors des phases actives. L'objectif est de comprendre comment la localisation des sites de repos dans le paysage peut contraindre l'utilisation de son domaine vital par un individu. En particulier, nous cherchons à caractériser

l'influence de l'anthropisation et du couvert forestier sur la capacité du sanglier à se déplacer de façon non contrainte entre les sites utilisés pour le repos et pour l'activité. Nous nous plaçons pour cela à une échelle spatiale plus globale, en étudiant des sangliers répartis à travers l'Europe entière, et appliquons une méthode utilisant une mesure de centralité issue du domaine de l'analyse des réseaux. Le comportement de repos n'a jamais été décrit chez le sanglier à une échelle aussi large. Nous profitons donc de cette opportunité pour estimer l'influence de l'anthropisation sur la stratégie spatiale de repos du sanglier, afin de participer à la caractérisation des mécanismes comportementaux qui permettent à cette espèce de persister avec un succès certain dans une grande diversité de milieux, anthropisés ou non.





# Matériel & méthodes

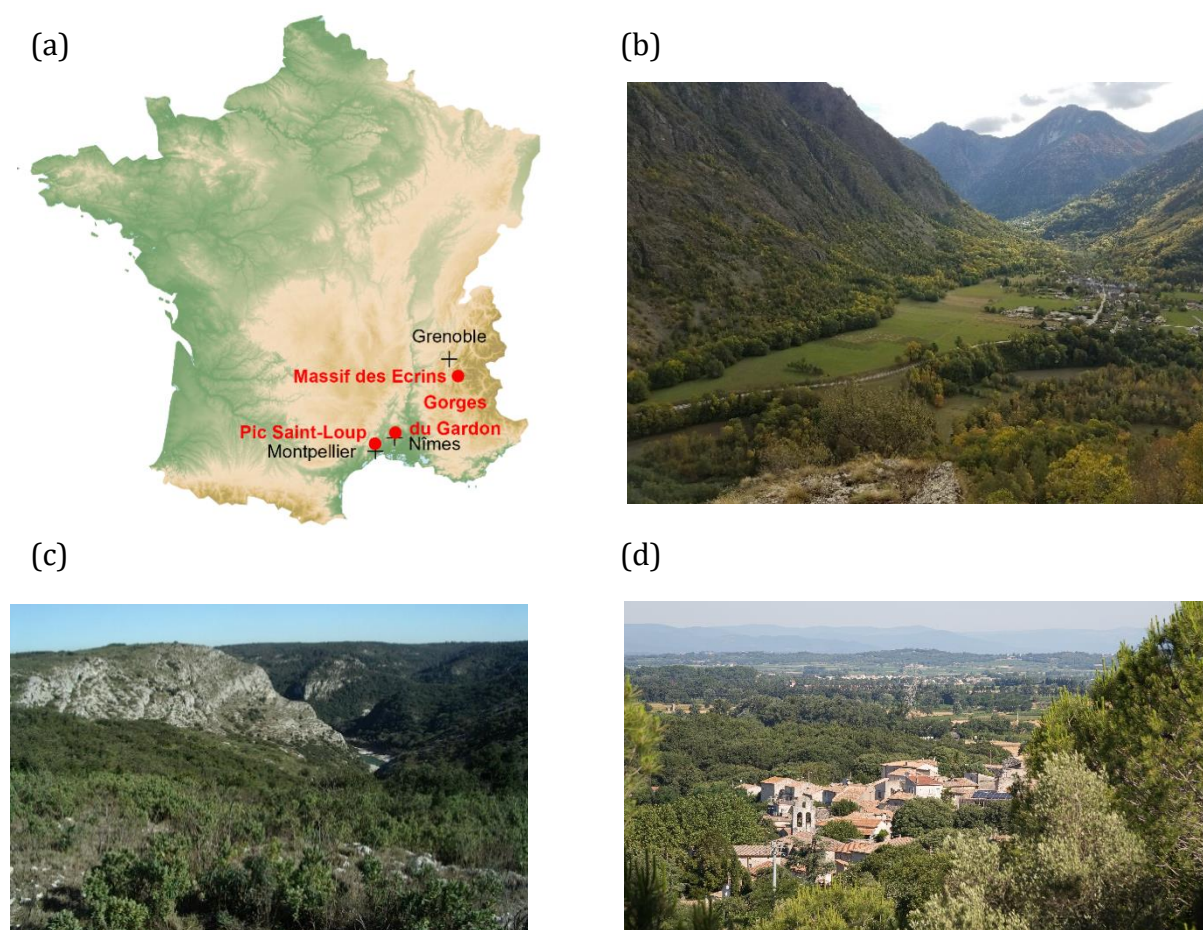
Dans les deux études qui composent le second axe de cette thèse (chapitres 2 et 3) nous nous intéressons au comportement de repos du sanglier, par une approche basée sur le suivi télémétrique d'animaux sauvages. Dans cette section matériel et méthodes, je présente le travail de terrain qui a été nécessaire à l'acquisition des données utilisées dans ces deux chapitres, je décris le contenu des données récoltées, et j'expose les méthodes générales qui ont été utilisées pour l'analyse.

## 1 Sites d'étude

Au cours de cette thèse, nous avons capturé des sangliers dans trois sites d'études distincts de la moitié sud de la France (*Figure 1*). Deux de ces sites font partie de la même unité géographique, et sont très similaires : les Gorges du Gardon (43.93°N ; 4.38°E) et la zone du Pic Saint-Loup (43.74°N ; 3.88°E). Chacun de ces deux sites est situé à une dizaine de kilomètres au nord d'une ville majeure (Nîmes, pour les Gorges du Gardon et Montpellier pour le Pic Saint-Loup), et constitue une zone rurale relativement peuplée. La densité de population moyenne y est de 280 habitants par km<sup>2</sup>, regroupés dans des villages et de petites villes. Coincés entre le massif des Cévennes et la mer Méditerranée, ces deux sites font partie de la région des « Garrigues languedociennes ». Cette région Méditerranéenne calcaire, aux étés chauds et secs et aux hivers doux, est caractérisée par une végétation xérophyte et par la culture de la vigne. Elle a été largement façonnée par le pastoralisme et l'agriculture, pratiqués par ses populations humaines depuis le Néolithique, puis par l'exploitation du bois (Martin 1987). Au cours des siècles, les forêts de chênes vert et de chênes blanc ont graduellement laissé place à une végétation arbustive très ouverte, appelée garrigue, d'où le sanglier est devenu rare ou absent (Martin 1987; Raynal 2020). Depuis la révolution industrielle, le pastoralisme et le déboisement ayant diminué, la forêt est en partie revenue, refermant la garrigue, et favorisant le retour du sanglier (Maillard et al. 1995).



Dans les Gorges du Gardon comme la zone du Pic Saint-Loup, l'abondance des sangliers est aujourd'hui fortement décriée en raison des dommages occasionnés, en particulier sur la vigne. Les battues au sanglier y sont pratiquées de façon intense, et la saison de chasse y est régulièrement allongée par arrêtés préfectoraux. Par ailleurs, la croissance démographique récente et le peuplement des zones rurales périphériques aux villes y ont accentué les conflits entre humains et sangliers.



**Figure 1.** *Présentation des sites d'étude. (a) Situation géographique des trois sites d'étude en France, les villes de Montpellier, Nîmes, et Grenoble étant signalées pour indication. (b) Vallée encaissée typique du site du Massif des Ecrins. (c & d) Paysages naturel et agricole de la région des Garrigues languedociennes, représentatifs des sites du Pic Saint-Loup et des Gorges du Gardon.*

Le troisième site, le Massif des Ecrins (44.90°N ; 5.95°E), situé dans les Alpes, est très différent des deux premiers. Comprenant les vallées de la Bonne et de la Malsanne, dans le Valbonnais, en Isère, il est à cheval sur la zone cœur du Parc National des Ecrins. Son point le plus bas est situé à 800 mètres au-dessus du niveau de la mer, et les montagnes avoisinantes, aux versants abruptes, culminent au-delà de 3000 mètres. Le climat, montagnard, est caractérisé par des hivers froids et

longs, avec d'importants épisodes neigeux, et des étés doux. La densité de population y est faible (environ 21 habitants par km<sup>2</sup>) et l'agriculture très réduite, mais les alpages y sont nombreux. La cohabitation avec le sanglier dans le Valbonnais est conflictuelle en raison des dégâts agricoles occasionnés par cet animal, et de la présence du Parc National des Ecrins, au cœur duquel la chasse est interdite, et qui est accusé de constituer une zone refuge où les sangliers se multiplient (Mounet 2007). Hors de la zone cœur du Parc National, la chasse en battue est pratiquée sur ce site, mais de façon réduite en comparaison de la situation des deux sites du Sud de la France.

Les sangliers du Massif des Ecrins et des Gorges du Gardon, étaient depuis 2018 l'objet d'un projet de recherche qui questionnait l'utilisation de l'espace par cette espèce dans un contexte de lisière entre zones chassée et non-chassée. En effet, la chasse est interdite toute l'année dans la zone cœur du Parc National des Ecrins, et au printemps dans trois zones distribuées le long du Gardon, et concernées par des arrêtés préfectoraux de protection de biotope, dans les Gorges du Gardon. Des captures de sangliers étaient donc déjà pratiquées dans ces deux sites d'étude, et une certaine quantité de données était déjà disponible dès le début de cette thèse. C'est la raison pour laquelle ces deux sites ont été sélectionnés pour le travail de terrain à réaliser, bien que ma thèse s'inscrive dans un cadre différent de celui du projet qui y était initialement mené. Le troisième site d'étude, le Pic Saint-Loup, a été sélectionné pour ses similitudes avec celui des Gorges du Gardon, permettant d'analyser les données des deux sites de façon simultanée, ainsi que pour la proximité géographique avec la ville de Montpellier, facilitant la logistique des captures.

## 2 Captures

Sur les trois sites d'études, les sangliers ont été capturés dans des cages-pièges (*Encadré 1*). Les cages étaient montées à des emplacements stratégiques, choisis pour leur isolement par rapport aux routes et aux lieux fréquentés par les passants, et où le passage de sangliers était avéré. Il s'agissait le plus souvent de terrains privés, avec l'accord du propriétaire. Nous avons utilisé du goudron végétal pour attirer les sangliers, et du maïs sec pour les inciter à entrer dans les cages. Chaque session de captures était organisée sur une semaine complète, au niveau d'un site d'étude (parfois deux simultanément). Lors de ces sessions, entre une et six cages étaient armées le lundi, et refermée le vendredi. Chaque matin, les cages étaient inspectées soit par le passage d'un agent, soit par l'intermédiaire d'un piège photographique, pour vérifier la présence d'un animal.

**Encadré 1. Cages de capture et de contention.**

Nous avons utilisé des cages de deux formats : les plus grandes (a) avaient une surface au sol de 7 m<sup>2</sup> pour 2 m de haut, et une porte de type battante. Les plus petites (b), de dimensions variables (souvent 2 m<sup>2</sup> au sol pour 1 m de haut) étaient équipée d'une porte tombante.

(a)



(b)



(c)



(d)



Les cages de plus petit format avaient un succès de capture plus faible que les grandes, mais laissaient moins d'espace à l'animal capturé pour prendre de l'élan et frapper les parois. C'est la raison pour laquelle nous les avons progressivement privilégiées. Pour réduire le stress de l'animal et le risque de blessure, en particulier dans les grandes cages, un filet de camouflage pouvait être accolé aux parois, et un buisson ou autre obstacle naturel être positionné à l'intérieur de la cage. Une cage de contention (c) était parfois utilisée pour manipuler l'animal (d), lorsqu'il ne dépassait pas 60 kg.

Comme pour d'autres projets de suivis télémétriques de sangliers (Torres-Blas et al. 2020), le succès de capture était relativement bas (voir les détails des captures réalisées dans le [Tableau 1](#)). Bien que l'effort de capture n'ait pas été formellement quantifié, plusieurs sessions d'une semaine étaient souvent nécessaires à la pose d'un collier. Cela était au moins en partie dû au caractère méfiant des sangliers, qui consommaient le maïs laissé à l'extérieur des cages, mais sans y entrer. Par ailleurs, en de nombreuses occasions révélées par piège photographique, les laies se montraient vigilantes aux abords de la cage et reniflaient l'air pendant que les marcassins s'alimentaient et se faisaient piéger. Les marcassins étant trop petits pour recevoir un collier, ces déclenchements qu'ils occasionnaient réduisaient fortement l'efficacité de nos sessions de capture. Ce comportement observé lors des visites par des groupes familiaux pourrait expliquer le léger biais observé vers les mâles dans nos captures (63%). En effet, les mâles étant le plus souvent solitaires, ils pouvaient être piégés sans que des marcassins ne déclenchent la fermeture prématurée de la cage. Dans le massif des Ecrins, le succès de capture était particulièrement faible, probablement pour des raisons liées à la démographie du sanglier dans la région, à la disponibilité alimentaire, ainsi qu'à l'espacement temporel entre les sessions de captures, imposé par les contraintes logistiques, et qui ne permettait pas une habitude des sangliers à l'agrainage.

Une fois en cage, les sangliers visuellement estimés à au moins 40 kg étaient équipés d'une boucle auriculaire d'identification et d'un collier de suivi télémétrique, suivant l'une des deux méthodes suivantes : lorsque cela était possible, l'animal était transféré dans une cage de contention, et le collier lui était passé directement, à travers les barreaux ([Encadré 1](#)). Cette méthode était surtout efficace pour des individus ne dépassant pas 60 kg. Lorsque la méthode par contention était impossible, ou jugée trop difficile, une anesthésie était réalisée, au moyen d'un mélange de tiletamine (3 mg/kg), de zolazepam (3 mg/kg) et de xylazine (0.3 mg/kg), administré directement dans la cage de capture au moyen d'un pistolet hypodermique à air comprimé. Après la manipulation, l'effet de la xylazine était inversé par l'administration d'une dose d'atipamezol (0.03 mg/kg). Cette méthode, plus risquée pour l'animal (trois cas de mortalité), n'était réalisée qu'en cas de nécessité. Dans tous les cas, le temps de manipulation était réduit au maximum afin de limiter le stress de l'animal.

Les colliers étaient équipés d'un système de relargage automatique, programmé pour faire tomber le collier de l'animal après une période de deux, trois, six, ou quatorze mois, selon le modèle. Nous pouvions ainsi ajuster la durée du suivi télémétrique selon la taille de l'animal, prévenant ainsi tout risque de lésion cutanée ou d'étouffement liés à la croissance de l'animal porteur d'un collier. Un signal VHF émis par le collier permettait sa localisation et récupération après son relargage. Les sociétés de chasses locales étaient tenues au courant de nos activités. Il

n'était pas demandé aux chasseurs de se comporter différemment en présence d'un animal porteur de collier. De fait, douze colliers sur les 36 déployés ont été récupérés par l'intermédiaires de chasseurs, après le tir de l'animal étudié. Par ailleurs, deux colliers ont été récupérés à suite de la collision de l'animal avec un véhicule, et un autre après le décès inexpliqué de l'animal. Parmi les autres colliers, onze se sont décrochés automatiquement par le déclenchement du système de relargage, cinq sont tombés prématurément, et deux ont cessé de fonctionner et n'ont jamais été retrouvés.

Le tableau suivant (*Tableau 1*) synthétise le résultat des activités de terrain effectuées, en recensant les individus équipés de colliers GPS avant, et au cours de la thèse. Les individus dont le suivi n'a pas dépassé une durée d'un mois sont signalés indépendamment, car les données correspondantes sont souvent trop laconiques pour être utilisées dans les analyses.

	Suivis disponible avant la thèse							
	Massif des Ecrins		Gorges du Gardon		Pic Saint-Loup		Tous sites	
	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois
avec activité	2	0	7	1	1	0	10	1
sans activité	0	1	2	2	0	2	2	5
	Suivis obtenus pendant la thèse							
	Massif des Ecrins		Gorges du Gardon		Pic Saint-Loup		Tous sites	
	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois
avec activité	2	0	6	1	5	1	13	2
sans activité	0	1	0	1	0	1	0	3
	Tous suivis disponibles							
	Massif des Ecrins		Gorges du Gardon		Pic Saint-Loup		Tous sites	
	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois	> 1mois	< 1 mois
avec activité	4	0	13	2	6	1	23	3
sans activité	0	2	2	3	0	3	2	8

*Tableau 1. Détail, par site d'étude et selon la durée du suivi, du nombre de sangliers équipés de colliers, avec ou sans accéléromètre. Les animaux de moins de 40 kg, qui n'ont pas reçu de collier GPS, ne sont pas comptabilisés.*

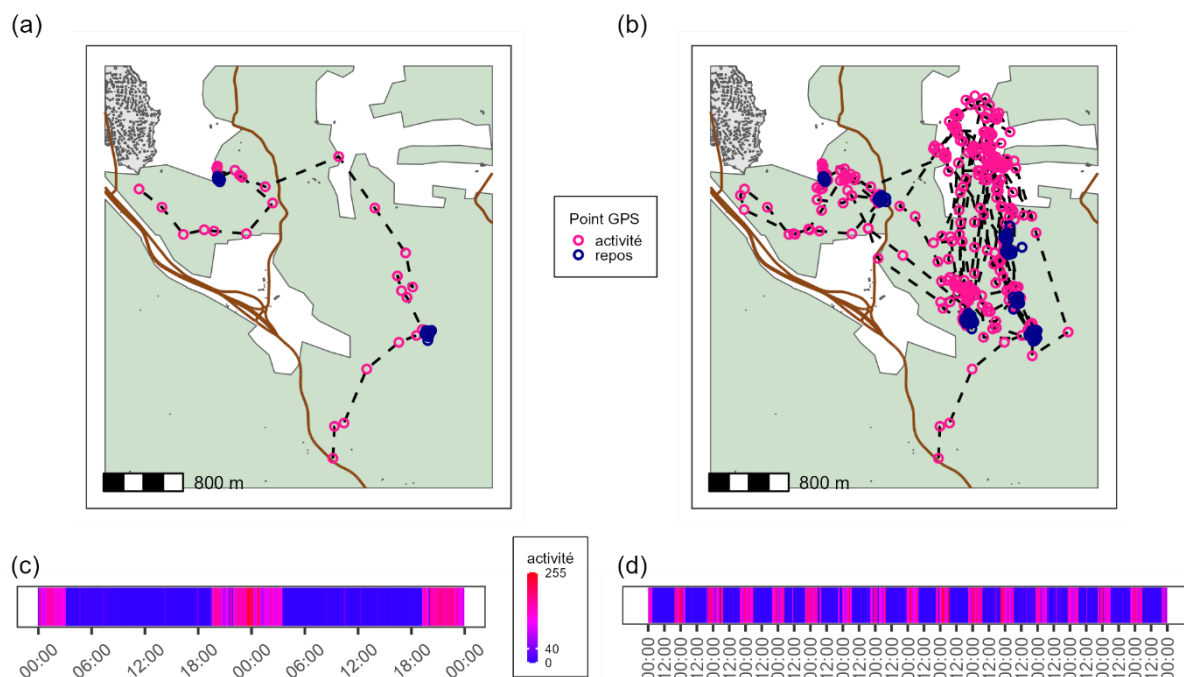
### 3 Suivi télémétrique

#### 3.1 Apport de la télémétrie à l'écologie

Comme nous l'avons vu dans le premier axe de la thèse, l'étude du comportement animal a connu une révolution lorsque l'avancée technologique a permis d'équiper des animaux avec des instruments de télémétrie (Wilmers et al. 2015). De nombreux comportements sont trop rares pour que l'on puisse espérer les étudier par observation directe. D'autres, au contraire, sont si fréquents, ou si étendus dans le temps, que leur quantification n'est rendue vraiment possible que par l'automatisation de la prise de données. Enfin, comme les animaux sauvages se déplacent, fréquentent souvent des lieux où il est impossible de les suivre, et modifient leur comportement lorsqu'ils se sentent observés, l'étude du comportement en milieu naturel par observations directes est, dans de nombreux cas, vouée à l'échec. C'est pourquoi le « bio-logging », c'est-à-dire le déploiement d'instruments de mesure autonomes directement sur des animaux vivants, est devenu un champ méthodologique incontournable dans l'étude du comportement animal dans des conditions naturelles. Pour étudier le comportement de repos chez le sanglier, cette approche semble indispensable.

#### 3.2 GPS

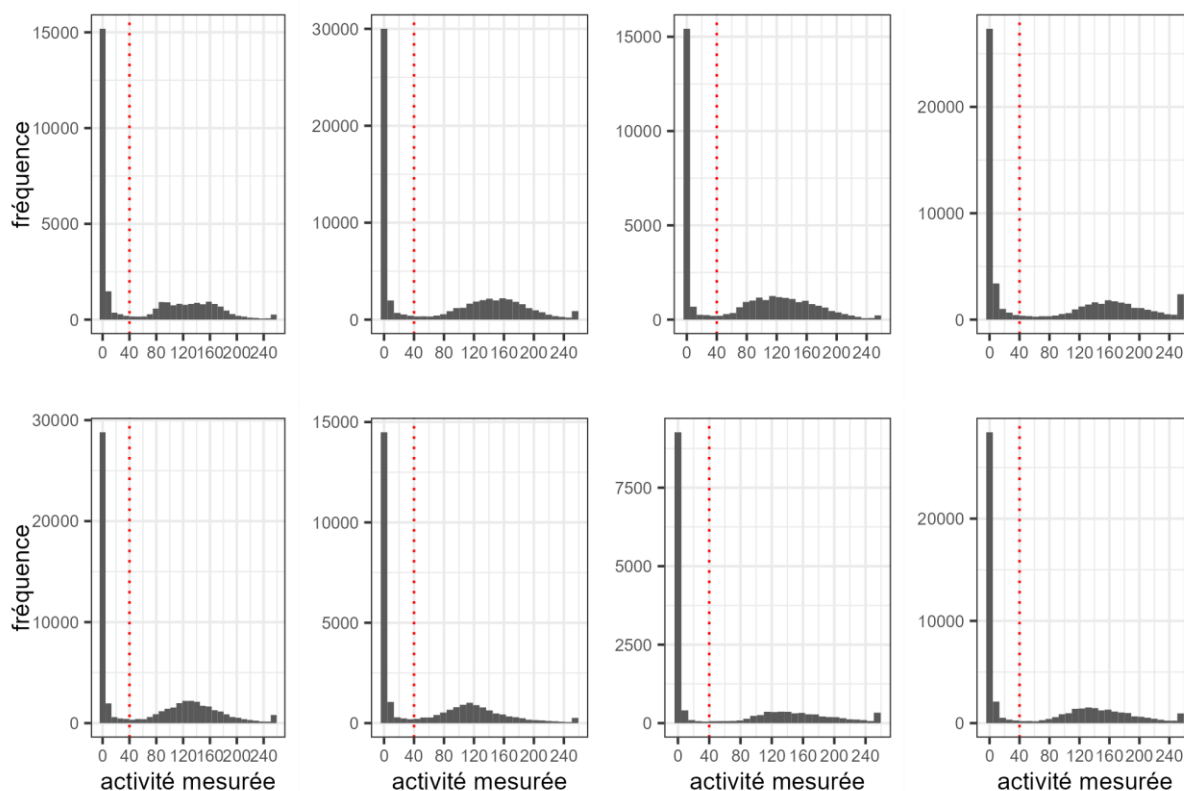
Nous avons déployé des colliers de suivi télémétriques utilisant le « Global Positioning System » (GPS), un système utilisant la trilatération de signaux émis par des satellites pour calculer avec précision une position à la surface de la Terre. Sur nos sites d'études du Pic Saint-Loup et des Gorges du Gardon, nous avons estimé que 95% des points GPS avaient une erreur GPS inférieure à 45 m (et inférieure à 13 m pour 50% des localisations). Dans le massif des Ecrins, l'erreur GPS observée était plus importante, car les hautes montagnes environnantes diminuaient le nombre de satellites visibles par les colliers, réduisant ainsi la précision des calculs de position. Néanmoins, la précision des localisations dans le Massif des Ecrins était aussi inférieure à 50m dans la majorité des cas, bien que les points aberrants étaient plus fréquents. Chaque collier GPS calculait une position toutes les 30 minutes. Etant donnée les échelles spatiales et temporelles qui correspondent aux déplacements des sangliers, la précision spatiale et la fréquence d'échantillonnage utilisées étaient largement suffisantes pour identifier avec finesse les sites de repos utilisés, et les lieux visités lors des phases d'activité (*Figure 2*).



**Figure 2.** (a & b) Déplacements d'un sanglier dans son domaine vital des Gorges du Gardon, pendant (a) deux jours, (b) 15 jours. Les cercles roses et bleus correspondent respectivement aux points GPS enregistrés pendant l'activité et le repos. La ligne pointillée représente le trajet de l'animal. Les bâtiments sont représentés en gris foncé, les villages en gris clair, les routes en brun, et les blocs forestiers en vert. (c & d) Activité mesurée sur les périodes considérées respectivement en (a) et en (b). Le patron d'activité monophasique et nocturne est clairement visible.

### 3.3 Activité

En plus du GPS, une proportion importante des colliers déployés étaient équipés d'un accéléromètre 3D. Celui-ci enregistre, toutes les cinq minutes et selon trois axes orthogonaux, une valeur correspondant à la moyenne de l'accélération du collier mesurée à une fréquence de 8 Hz. Cette mesure de l'activité du collier, donnée sur une échelle allant de 0 à 255, renseignait directement le taux de mouvement de l'animal, et ce indépendamment de sa trajectoire, et à une échelle temporelle bien plus fine que celle utilisée par le GPS. Un accéléromètre étant peu sujet aux erreurs de mesures, il constitue un outil extrêmement précis pour identifier les phases de repos et d'activité chez les mammifères (Brivio et al. 2017). Lorsqu'un animal était au repos complet sur un intervalle de temps de cinq minutes, la valeur d'activité correspondante était nulle, ou très faible. Au contraire, lorsque l'animal était en mouvement, l'activité mesurée était importante (supérieure à 80). Les valeurs d'activité intermédiaires (entre 40 et 80) étaient rares, ce qui permettait une distinction nette entre deux modes dans la distribution des valeurs d'activité (Figure 3). Les données d'activité permettaient ainsi une identification fiable de l'organisation temporelle du comportement de repos (exemple Figure 2).



*Figure 3. Distribution bimodale des valeurs d'activité mesurée pour huit individus suivis par télémétrie dans les Gorges du Gardon. Le seuil de 40, séparant les deux modes, est indiqué par une ligne rouge pointillée.*

### 3.4 Euroboar

Les données que nous avons récoltées sur les trois sites d'étude mentionnés plus haut ont été partagées à la communauté scientifique du réseau Euroboar. Cette initiative, qui fait partie de Euromammals (<https://euromammals.org/>, Urbano et al. 2021), est un projet collaboratif de partage des données issues de suivi télémétriques de sanglier en Europe entière, et qui est régulièrement augmenté par de nouvelles données. Au moment de l'écriture de cette thèse, Euroboar compte 51 institutions réparties entre 24 pays d'Europe (*Figure 4*).





*Figure 4. Carte des institutions participant au réseau Euroboar (Septembre 2023, carte réalisée par Kévin Morelle).*

Ce réseau centralise et maintient la plus grande la base de données spatiales concernant le sanglier : en ne considérant que les individus dont la durée du suivi télémétrique dépasse un mois, on comptabilise plus de 4,2 millions de points GPS issus de 520 sangliers, répartis entre 49 sites d'études, et 13 pays différents. Les fréquences d'échantillonnage utilisées par les collaborateurs impliqués dans Euroboar varient entre un point GPS toutes les 4 heures, et un point GPS toutes les 5 minutes. Cependant, environ 73% des données Euroboar correspondent à un échantillonnage d'au moins un point par heure, et environ 90% du jeu de données correspondent à un échantillonnage d'au moins un point toutes les deux heures (*Tableau 2*). Parmi ces sangliers, 205 ont été suivis pendant plus de six mois, et 103 pendant plus d'un an. En plus des données GPS, des données actimétriques structurées comme celles que nous avons récoltées dans nos trois sites d'étude (décrites plus haut, en 3.3) sont aussi disponibles à travers Euroboar, pour 157 individus.

Partager ses données avec Euroboar donne accès à l'ensemble des données disponibles à travers le réseau pour développer des analyses. Un tel jeu de données est un outil puissant pour étudier les tendances comportementales générales du sanglier, à l'échelle continentale. Bien sûr, étant donnée la disparité de sites d'études représentés dans Euroboar, chacun ayant ses

spécificités, ce jeu de données n'est pas adapté à toutes les questions de recherche concernant le comportement spatial du sanglier. Les réponses comportementales d'un animal à la structure de son habitat (et des activités humaines) à fine échelle, sont souvent mieux appréhendées à une échelle locale. En revanche, les données issues de Euroboar représentent une excellente opportunité d'étudier la façon dont le comportement du sanglier varie en fonction des gradients d'anthropisation à l'échelle de l'Europe.

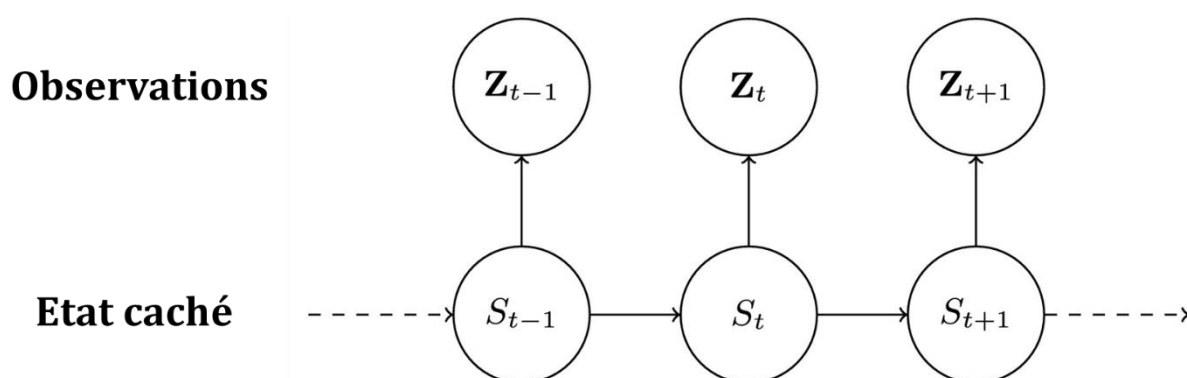
fréquence d'échantillonnage (minutes)	5	15	30	60	120	180	240	360	420	autres
pourcentage du suivi (tous individus confondus)	2	9	33	29	17	1	3	1	1	4

**Tableau 2.** Découpage du temps de suivi total (obtenu par concaténation des données GPS issues de Euroboar) en fonction de la fréquence d'échantillonnage utilisée. Les périodes de plus de 480 minutes (8 heures) sans point GPS sont exclues de ce calcul. La colonne « autres » réunit les fréquences d'échantillonnage inférieures à 480 minutes et représentant moins de 1% du jeu de données.

### 3.5 Méthodes de classification du comportement

Dans les deux chapitres du deuxième axe de cette thèse nous avons besoin d'identifier les sites de repos utilisés, chaque jour, par les sangliers. Grâce au GPS, nous avons accès à l'ensemble des lieux visités par les sangliers, et donc aux endroits précis où le repos avait eu lieu. Cependant pour pouvoir identifier les sites de repos, il était nécessaire de segmenter les trajets dans le temps, pour classer les localisations entre repos et activité. Il est possible, à partir des données GPS uniquement, d'avoir accès à la composante temporelle du repos : il faut pour cela utiliser un modèle de Markov caché (« hidden Markov model » ou HMM; voir McClintock and Michelot 2018). Appliqué au comportement animal, un HMM est un modèle selon lequel la vie d'un individu peut être découpée en un certain nombre de modes comportementaux, chacun caractérisé par la ou les distributions des valeurs d'une ou plusieurs variables observables (*Figure 5*). A chaque observation de l'animal, un certain nombre de métriques sont associées, et permettent de calculer les probabilités que l'individu soit dans chacun des états comportementaux possibles, en fonction de son état lors de l'observation précédente. Appliqué à un trajet GPS, l'approche standard par HMM considère chaque localisation comme une observation de l'animal, et utilise la distance parcourue lors du pas suivant, et l'angle imprimé entre les pas précédant et suivant, pour associer une probabilité que l'animal soit dans chaque état comportemental possible, à chaque observation. Le nombre d'états comportementaux possibles, et leur interprétation en termes de biologie, sont définis par l'utilisateur. Tant que la fréquence d'échantillonnage est suffisamment

élevée, les HMM sont généralement très efficaces pour identifier les phases de repos et d'activité sur le trajet d'un animal, car ces deux modes comportementaux présentent des caractéristiques très contrastées, en termes de disposition géométrique des points successifs. Le repos est associé à des distances parcourues très faibles, et à des angles aigus, car les points successifs lors d'une phase de repos sont disposés aléatoirement autour de la vraie position de l'animal, dans une zone définie par l'erreur du GPS. Les phases d'activité, elles, correspondent à des distances beaucoup plus grandes, et à des angles plus ouverts.



*Figure 5. Illustration du principe du HMM appliqué au comportement animal, adaptée de Michelot et al. (2016). Les états  $S$  représentent l'état comportemental dans lequel l'animal se trouve aux instants  $t-1$ ,  $t$  et  $t+1$ . L'animal étant impossible à observer en continu, son état comportemental ne peut être inféré que ponctuellement, au travers de métriques extraites lors des observations  $Z$ .*

Néanmoins les HMM présentent aussi des limites. D'abord, un comportement actif ayant lieu de manière très localisée peut être confondu avec le repos. Certains comportements actifs du sanglier sont stationnaires ou quasi-stationnaires (notamment lorsqu'il s'alimente ou se bauge), et ces comportements peuvent avoir lieu à proximité des sites de repos (Morelle et al. 2015). Il y a donc un risque que certaines positions GPS ne correspondant techniquement pas à du repos soient classifiées comme tel par un HMM. Par ailleurs, étant donné qu'un HMM utilise des métriques calculées à partir de positions successives chacune séparée de la précédente par 30 minutes, les phases comportementales courtes ne peuvent pas être détectées. Il est donc possible qu'un HMM identifie deux phases de repos distinctes, séparées par une période d'activité de moins de 30 min, et ayant eu lieu dans deux endroits différents, comme une seule. Inversement, une phase de repos ayant duré moins de 90 min, et donc représentée par deux points GPS seulement, connaît le risque de ne pas être identifiée correctement par un HMM. De même, les points GPS situés dans les périodes de transition entre les phases de repos et d'activité peuvent être mal identifiées par un HMM, biaisant ainsi l'estimation du temps total consacré au repos. La méthode de classification des localisations par HMM est donc une méthode simple et efficace,

particulièrement utile quand seul le trajet GPS de l'animal est disponible, mais elle peut manquer de précision pour décrire avec finesse le comportement de repos, et en particulier son aspect temporel.

## **4 Réalisations annexes**

### **4.1 Suivi acoustique**

Au cours de cette thèse, nous avons également déployé des microphones sur certains colliers GPS. L'objectif de ce suivi était de permettre l'identification d'évènements de chasse et d'autres perturbations d'origine anthropique subis par les sangliers lors du repos. Neuf sangliers ont reçu un microphone programmé pour enregistrer un signal acoustique continu sur une période d'un mois. Malheureusement, plusieurs de ces dispositifs ont cessé de fonctionner après seulement quelques jours, probablement à cause d'infiltrations d'eau dans les boîtiers. La durée des enregistrements récoltés ne nous a pas permis d'approfondir cet aspect autant que nous l'aurions voulu. Nous avons cependant utilisé les données disponibles pour tenter de déterminer les causes des relocalisations diurnes que nous avons identifiées grâce aux données GPS et actimétriques, dans le chapitre 2.

### **4.2 Dérangements expérimentaux**

En parallèle du suivi télémétrique, nous avons réalisé un protocole de dérangements expérimentaux sur les sangliers équipés de colliers GPS. L'objectif était de décrire les réactions possibles d'un sanglier à l'approche d'un être humain. Nous voulions notamment évaluer la distance parcourue lors d'une relocalisation provoquée par un dérangement non lié à la chasse, afin de mieux comprendre l'effet des perturbations humaines sur le comportement de repos du sanglier. Pour réaliser un dérangement expérimental, j'identifiais un sanglier au repos grâce aux données GPS transmises en direct par satellite, et je m'en approchais autant que possible, en signalant ma présence par la voix. Le dérangement était considéré comme valide si je parvenais à une distance inférieure à dix mètres de la position initiale du sanglier. Pour des raisons techniques et logistiques, je n'ai pas pu répéter ce protocole un nombre satisfaisant de fois (seulement 19 tentatives dont 13 dérangements valides, le sanglier ayant quitté le site de repos longtemps avant l'expérience dans six cas). Pourtant, cette expérience a contribué à me familiariser avec le comportement de repos du sanglier, et m'a aidé à concevoir les enjeux liés aux perturbations anthropiques du repos chez cette espèce.



## Chapitre 2



**Résumé :** Dans les milieux fortement impactés par les activités humaines, de nombreux animaux choisissent d'être actifs de nuit, afin d'éviter les dérangements. En adoptant cette stratégie, ils augmentent toutefois le risque d'être dérangés lorsqu'ils se reposent pendant la journée. Pour réduire ce risque, ces animaux pourraient augmenter leur sélectivité envers les lieux où ils se reposent. Grâce à un suivi spatial et actimétrique, nous avons étudié l'ajustement comportemental du sanglier (*Sus scrofa*), en termes de sélection et de réutilisation des sites de repos, en fonction du risque de dérangement par l'être humain. Nous avons évalué la probabilité qu'un sanglier change de site de repos en journée, afin d'évaluer l'efficacité de la stratégie de repos de ces animaux dans la réduction du risque de rencontre avec l'être humain, au cours du repos diurne. Nous avons tenté d'identifier la cause de certains de ces déplacements diurnes, à l'aide d'enregistrements audio. Nous avons constaté que, tant qu'ils avaient accès à un couvert végétal important, les sangliers n'évitaient pas spécifiquement de se reposer près des villages ou des routes, c'est-à-dire là où le risque de dérangement était le plus élevé. De manière générale, la probabilité pour un sanglier d'être dérangé lors du repos était faible, même proche des villages. Plus un site de repos était situé proche d'un village, plus il avait tendance à être visité de manière répétée. Ces résultats suggèrent que pour le sanglier, se concentrer sur quelques sites de repos familiers et sûrs est une stratégie efficace pour se reposer sans risque de dérangement dans les milieux anthropisés.

**Mots clés :** activités humaines, anthropisation, patrons d'activité, sélection de l'habitat, sommeil

# Hogs sleep like logs: wild boars reduce the risk of anthropic disturbance by adjusting where they rest

Gustave Fradin<sup>1</sup>, Simon Chamaille-Jammes<sup>1</sup>

1. CEFE, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France

## Original article published in *Ecology and Evolution*:

Fradin G, Chamaille-Jammes S. 2023. Hogs sleep like logs: Wild boars reduce the risk of anthropic disturbance by adjusting where they rest. *Ecol Evol.* 13(7):e10336. doi:10.1002/ece3.10336.

**Abstract:** Many animals living in anthropized landscapes try to avoid encountering people by being active at night. By doing so, however, they risk being disturbed while at rest during the day. To mitigate this risk, diurnally resting species may be highly selective about where they rest. Here, we used GPS and activity sensors to study how wild boars (*Sus scrofa*) might adjust their resting site selection and revisitation patterns to the risk of disturbance by people. We evaluated the probability of daytime relocation to assess the efficacy of wild boars' resting strategy in reducing the risk of human encounter while at rest. We attempted to identify the cause of some relocations using audio recordings. Generally, we found that wild boars did not specifically avoid resting near villages or roads, i.e. where the risk of encountering people is higher, if they could find sites with suitable vegetation cover. The risk of disturbance by people was low, even near villages. Resting sites located close to villages were visited more repeatedly than those located further away, suggesting that focusing on a few familiar and quiet resting sites was a successful strategy for resting undisturbed in an anthropized landscape.

**Keywords:** activity pattern, anthropization, habitat selection, human activities, sleep

## 1 Introduction

Resting is a crucial daily requirement for all animals. It serves various purposes such as energy conservation (Riede, van der Vinne, and Hut 2017; Glass et al. 2021), thermoregulation (Lutermann et al. 2010), and predator avoidance (Lima et al. 2005). Additionally, rest encompasses sleep, which is essential for neuro-physiological homeostasis (Schmidt 2014; Freiberg 2020). To meet physiological requirements and integrate ecological constraints, such as predation risk, animals allocate a significant proportion—often more than half—of their daily time budget to resting, which takes place at specific resting sites (Campbell and Tobler 1984; Siegel 2009; Ungurean et al. 2020). These sites may vary in quality, and in particular may offer different levels of safety (Markham, Alberts, and Altmann 2016; Burger et al. 2020). Thus, resting site selection can be fine-tuned to minimize the risk of predation or disturbance, and the need for daily rest is likely to have an important influence on how animals use the landscape.

In many environments, animals are facing increasing anthropic pressures that can impact their resting behavior (Gaynor et al. 2018; Wilson et al. 2020). It is well documented that many species modify their activity patterns in response to human pressures, and tend towards nocturnality to avoid being active during the day, when the intensity of human activity is highest (Gaynor et al. 2018). Such a response to anthropisation, however, exposes resting behavior to higher risks of disturbances by people. When at rest, animals may be subjected to both targeted (e.g., hunting) and untargeted (e.g., outdoor sports) disturbances, and could be expected to adjust their resting strategy—and in particular where they rest—to minimize the risk of being disturbed. Indeed, some species have been shown to fine-tune their selection of resting sites to the perceived level of risk of anthropic disturbances. For instance, wolves have been demonstrated to select more concealed resting sites after an encounter with people (Wam et al. 2012), and to proactively choose to rest farther from human infrastructures (Bojarska et al. 2021). Similarly, elephants have been observed returning more often to preferred resting sites, when ranging outside protected areas (Wittemyer et al. 2017). However, despite a few documented examples such as these, our overall understanding of adjustments of resting site selection and revisitation rate to the risk of disturbance by people remains limited. Additionally, we are not aware of any study having quantified the actual success of such adjustments in reducing the likelihood of being disturbed. Generally, there is very little information about how frequent anthropic disturbances of resting animals are in the wild.

One species that offers great opportunities to learn more about these adjustments is the wild boar (*Sus scrofa*). It is a widespread species that can be found to survive and exploit even the most anthropized landscapes (Stillfried et al. 2017). When living near people, wild boars could



naturally be subjected to non-targeted disturbances (e.g., by walkers and dogs being walked). Additionally, as a commonly favored game species, wild boars are subject to hunting. Wild boars are known for their great behavioral flexibility and are able to adjust their patterns of activity to various factors including the season, the food availability (Keuling et al. 2008b; Brivio et al. 2017), but also the risk of human encounter (Ohashi et al. 2014; Johann, Handschuh, Linderoth, Dormann, and Arnold 2020; Rosalino et al. 2022). Although they can be readily active during the day where human densities are low (Podgórski et al. 2013), they become more nocturnal when they live near people (Podgórski et al. 2013; Ikeda et al. 2019), and when they are hunted (Keuling et al. 2008b; Johann, Handschuh, Linderoth, Dormann, and Arnold 2020). Most outdoors activities—including recreational hunting—occur during the day. By switching to a predominantly nocturnal pattern of activity in human-dominated landscapes, wild boars chose to expose their resting phase to a higher risk of anthropic disturbance. This likely is a successful strategy for risk mitigation, as resting is a well-known and efficient anti-predator strategy (Lima et al. 2005). However, this also means that the daily choice of a resting site is critical for minimizing the risk of encountering people. When nocturnal, wild boars are monophasic sleepers, and usually remain at rest for the entire daytime period. This implies that the choice of a specific resting site, made in the early morning, determines the exposure of the animal to the risk of disturbance for the rest of the day. The decision-making process for choosing a resting site has several components, offering several opportunities to adjust to the risks imposed by people. For example, wild boars could adjust where they rest in the landscape (e.g., distance to infrastructures, habitat types), and how they use their network of potential resting sites, coming back to some more often. It is well known that anthropic pressures can shape the spatial behavior of wild boars (Tolon et al. 2009; Stillfried et al. 2017), and several studies have investigated how their use of resting sites varies with the risk of being hunted (Maillard and Fournier 1995; Sodeikat and Pohlmeier 2007; Scillitani, Monaco and Toso 2010; Saïd et al. 2012). However, studies rarely considered the risk of disturbances unrelated to hunting, despite their potential importance in anthropized landscapes (Marzano and Dandy 2012).

Here, we present a study of the resting strategy of wild boars living in a rural Mediterranean landscape in the South of France. Using activity and GPS data collected on collared animals, we examined how wild boars modify their resting site selection in response to the risk of anthropic disturbance. This includes the assessment of (i) the potential avoidance of areas where meeting people is more likely (i.e. close to villages and roads), and (ii) the selective re-use of previously visited sites, depending on their location in the landscape with regards to the risk of being disturbed. We also estimated, across the landscape, (iii) how frequently wild boars engaged in a significant and potentially costly relocation to a secondary site, and attempted, when possible, to

identify the cause of these relocations using audio recordings. Overall, our study provides insights into the effectiveness of behavioral adjustments in reducing the risk of disturbance of rest by animals living in anthropized landscapes.

## 2 Materials & methods

### 2.1 Study Sites

We studied wild boars in the *Gorges du Gardon* (43.93°N; 4.38°E) and the *Pic Saint-Loup* areas (43.74°N; 3.88°E), in southern France. Both sites are very similar, the landscape forming a mosaic of agricultural lands, densely vegetated patches (shrublands and forests), and villages, covering 38%, 48%, and 11% of the land in the *Gorges du Gardon* area, and 55%, 29%, and 12% in the *Pic Saint-Loup* area, respectively. The altitude is ~100m. Vineyards make up most of the agricultural lands. The natural vegetation patches are mostly Mediterranean *garrigues*, with thick understory and dominated by dense evergreen oak (*Quercus ilex*) or Aleppo pine (*Pinus halepensis*) tree stands. Villages have hundreds to a few thousand inhabitants, and the general population density is approximately 280 inhabitants/km<sup>2</sup>, with some isolated houses also spread throughout the landscape. Both sites are located about ten kilometers away from a large city (Nîmes for the *Gorges du Gardon* area, Montpellier for the *Pic Saint-Loup* area). Wild boars are mostly hunted in drive hunts involving an average of twenty hunters (usually between ten and forty) and about three to fifteen hounds. The open season for drive hunt lasts from the 15<sup>th</sup> of August to the end of February or March, depending on the year and the study area. In addition to the risk induced by hunting, wild boars could potentially be disturbed, at both study sites, by agricultural and recreational outdoors activities (e.g., biking, hiking, dog-walking, etc.). The lack of natural predators in the study areas guarantees that human activity represents the only potential risk of disturbance for resting wild boars. Part of the *Gorges du Gardon* area is a densely vegetated military zone where public access is denied, although recreational hunting of wild boars is allowed. The military activities, however, are likely to represent a source of disturbance for the wild boars, even though we could not evaluate how the level of human disturbance could differ within and out of the military zone.

### 2.2 Captures and tracking

From 2018 to 2022, we captured wild boars with corn-baited traps, using a protocol approved by the ethical committee of the French Ministry of Research (APAFIS#20279-2019041522576537v3). We immobilized them either with a small immobilization box, or through anesthesia, using a combination of tiletamine (3 mg/kg), zolazepam (3 mg/kg) and xylazine (0.3 mg/kg), and using atipamezol (0.03 mg/kg) to reverse xylazine at the end of the operations. We equipped 22 animals weighing more than 40kg with a GPS collar. The collars

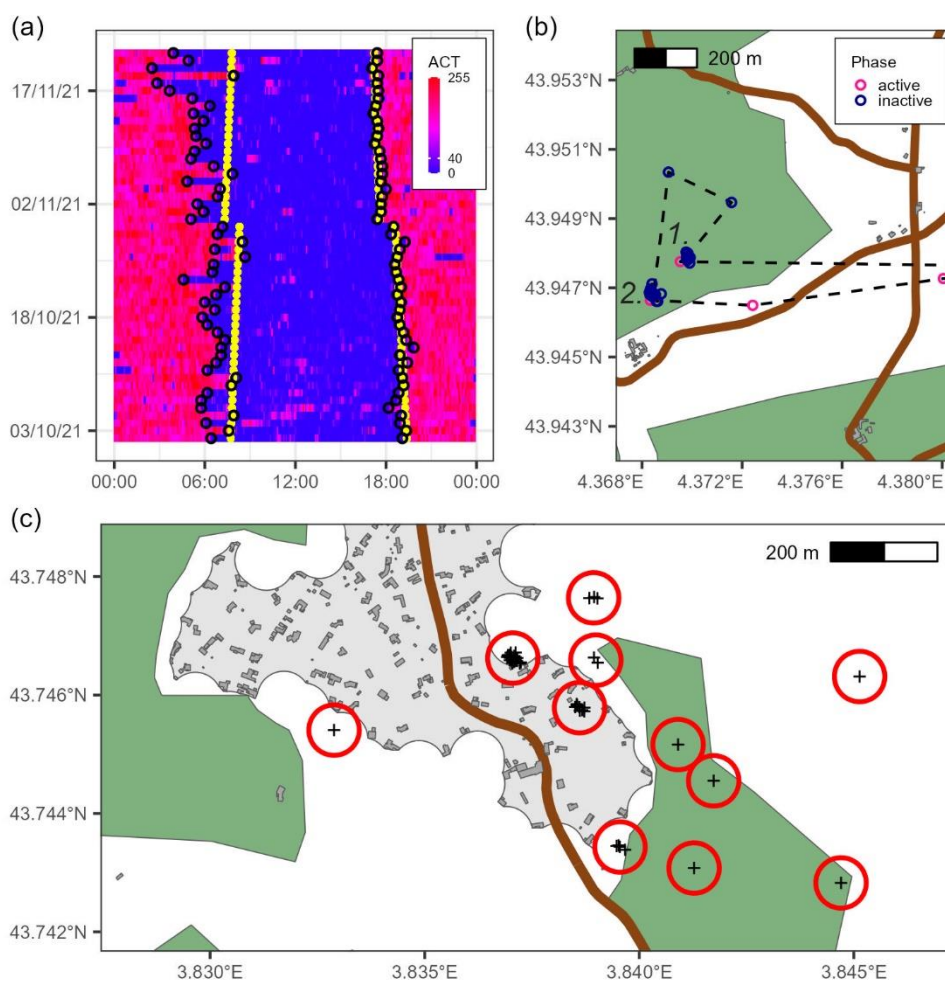
acquired a GPS location every 30 minutes, and a measure of activity level (hereafter ACT) every 5 minutes. ACT was calculated as the average of 8Hz acceleration measurements over three orthogonal axes, and was available to us on a dimensionless scale ranging from zero (indicating no movement of the collar over the 5-minute interval) to 255. As values were highly correlated between axes, we only used the ACT data corresponding to the anteroposterior axis. We recovered two collars after the animals had been killed by a collision with a vehicle, six after the animals had been shot by local hunters, nine through the activation of the collars' remote drop-off system, and five after they had fell off the animals prematurely. Out of these five collars, three dropped less than fifteen days after deployment and we excluded the corresponding animals from the study. After a capture, a wild boar can display reduced activity levels for several days (Brogi et al. 2019). After visual inspection of the patterns of activity, we chose to exclude the first three days following each capture from the analyses, which resulted in survey periods averaging 126 days long (SD=53). The activity profiles of the animals clearly showed that most of them were nocturnally active, and rested each day across the daylight hours, in one consolidated bout (example in [Figure 1a](#)). Only two animals were significantly active during the day during parts of their survey period and were excluded from the analysis to focus only on daytime resting strategies. Seventeen animals (twelve males and five females) remained in our final dataset. Two males and two females had been using extensively the military zone. No pair of collared animals moved together as part of the same sounder. Due to the very limited movement data from females, we excluded them from the analyses. As male and female wild boars generally have different spatial ecology (Saïd et al. 2012; Morelle et al. 2015), this avoided a possible bias in our analyses, which can be interpreted as describing the behavior of male wild boars. Note however that exploration of the female data did not suggest that their behavior differed largely from that of males, with regard to aspects investigated here (Appendix 1). Also, for brevity, we hereafter refer to the animals studied in the analyses as "wild boars," without specifying their sex each time.

## 2.3 Data preparation

### 2.3.1 *When did resting occur?*

To study where wild boars rested, we first needed to determine when they rested each day. Upon visually examining their activity patterns ([Figure 1a](#)), it was evident that wild boars consistently divided their 24-hour cycle between an inactive phase (primarily resting with some occasional activity) and an active phase (during which they could occasionally rest). To recover the start and end times of these inactive phases, we first classified each 5-minute period as "resting" ( $ACT \leq 40$ ) or "active" ( $ACT > 40$ ; see Appendix 2 for details). This allowed us to identify a continuous inactive phase spanning the daytime hours each day, separated from the previous and next inactive phases by an active phase. During this process, we disregarded the short bouts

of activity that occurred between long-lasting “resting” bouts, which were irrelevant for the description of the large-scale pattern of activity. The resulting patterns closely matched those anticipated based on visual inspection (see Appendix 2).



**Figure 1.** (a) Example of the activity pattern of a wild boar. The color codes for the value of the ACT variable (blue = low activity; red = high activity). The black circles indicate the start and end times of the inactive phases. The yellow dots indicate the times of sunrises and sunsets. (b) Example of a wild boar’s relocation during an inactive phase. The black dashed line represents the trajectory linking GPS fixes (pink and blue circles). The animal first rested in (1) and then relocated to spend the rest of the inactive phase in (2). (c) Example of the resting site revisitation pattern of a wild boar. The daily resting locations (black crosses) are clustered into resting sites (red circles). In (b) and (c), buildings are represented in dark grey, villages in light grey, roads in brown, and densely vegetated patches in dark green.

### 2.3.2 Where did resting occur?

We used the GPS data to determine where the wild boars rested during each inactive phase. Usually, the entire inactive phase was spent at a single location. On some occasions, however, the

wild boars would start resting in one place and then move to another location to spend the rest of the inactive phase (example in *Figure 1b*). To identify such relocations, we looked for any substantial movements recorded in the ACT data during the inactive phases. We compared the mean GPS position of the animal before and after the high ACT values, and if those locations were more than 100 meters apart, we considered that the animal had relocated. See Appendix 2 for more details.

Throughout their lives, wild boars tend to return to rest at sites where they have rested before. To test whether this behavior could be affected by where the animals rested in the landscape, we first had to identify where their resting sites (hereafter called RS, example in *Figure 1c*) were located. We did so by calculating the mean of the GPS positions of each inactive phase. We ignored in this process the GPS locations acquired after a relocation happened, so that the positions of the RSs reflected the choices made by the wild boars at the end of their active phase, to select a place where to settle for the day. We then performed a hierarchical clustering analysis on these mean GPS positions, using an average linkage, to define clusters that were more than 50 meters apart. All the locations that fell within the same cluster were considered to be revisitations of the same RS.

### 2.3.3 *Environmental variables*

Our study sites could be coarsely partitioned between villages, agricultural lands, and densely vegetated areas. Wild boars rarely rested inside villages, and when they did so, they always stayed at the outskirts, in the transitional zones between villages and agricultural lands. To simplify, we characterized the vegetation cover of each RS as a binary variable, indicating whether it was located within a densely vegetated patch or not, at a large scale. We used the CORINE Land Cover (2018) data to identify large patches of dense vegetation, that we distinguished from villages and agricultural lands scattered with small thickets and hedgerows. We considered that a wild boar could rest either inside, or outside densely vegetated patches. See Appendix 3 for more details.

Then, we used OpenStreetMap (OSM) to calculate the distance of each RS to two features associated with higher risks of human disturbance: villages and roads. We laid out the road network by combining the “motorway,” “trunk,” “primary,” “secondary,” and “tertiary” road categories from OSM. This way we excluded the residential roads, the roads with very low traffic, and the forest tracks, along which anthropic activity was infrequent. We also used OSM data to determine the edges of villages. To do so, we applied a buffer of 50 meters around OSM’s polygonal layer for buildings and merged the polygons that overlapped after this operation. This allowed us to identify villages as clusters of buildings closer together than 100 meters. We then shrunk the obtained polygons with a buffer of -50 meters, so that their edges matched the edges of the villages’ peripheral buildings. Any such polygon larger than 1.5 hectares was considered a

village and visual inspection confirmed the adequacy of this approach. We calculated the distances of each RS to the nearest road, and village edge (with negative distances indicating locations inside villages).

Finally, we associated each visit of a RS to the status of the hunting season the day it occurred. Drive hunting is the primary hunting technique for wild boars in the study areas, and the only one that targets resting animals. Therefore, we defined the hunting season (HS) based on the dates of the open season for drive hunting (see section 2.1). Drive hunts were only permitted on “hunting days” (Wednesdays, Saturdays, Sundays, and bank holidays). During the non-hunting season (NHS), drive hunts were prohibited, except with a specific authorization from the local authority, concerning a negligible number of hunts. We did not account for the Covid-19 lockdowns because they never affected the hunting patterns during the periods in which we monitored the animals. Although lockdowns may have reduced the probability of untargeted disturbances, in our study this only affected 28 days for four animals.

## 2.4 Data analysis

### 2.4.1 *Habitat selection for resting sites*

We investigated how the selection of RSs by wild boars varied with vegetation cover and proximity to villages and roads. We estimated this selection within the home ranges of the animals, defining the home range as the contour of the 90% utilization distribution, estimated with a standard kernel density approach, from GPS locations collected during the active phase. For each used RS of each wild boar, we drew one thousand random locations in the wild boar’s home range and considered these locations to be available RSs. For both used and available RSs, we extracted the dominant vegetation type (open = 0; densely vegetated = 1) and the distance to roads or villages. We then fit a standard resource selection function (RSF) using a generalized linear mixed model (GLMM), using the type of location (used vs. available) as response variable and a binomial distribution for errors. Predictor variables included an interaction between vegetation type and distance to roads and an interaction between vegetation type and distance to villages. We also included individual animal identities nested within study sites as random intercepts. We also expected the hunting season to influence how wild boars selected RSs. However, a non-negligible proportion of the RSs had been visited during both the HS and the NHS (10% of all RSs), so that we could not simply include the hunting season in the RSF as a predictor variable. We thus decided to run two separate models: one with the RSs visited at least once during the HS, and one with the RSs visited at least once during the NHS. We then calculated selection ratios as a metric of habitat selection following Chamaillé-Jammes (2020). A selection ratio above one indicates selection, and a value below one indicates avoidance. We estimated the fit of the RSF models using the now well-established k-fold cross-validation approach proposed

by Boyce et al. (2002). This approach uses the Spearman-rank's correlation as the model's performance metrics. For each model, we used 5 folds, 10 bins of RSF scores, replicated the calculations 20 times, and reported the average Spearman-rank correlation and its standard error. See Boyce et al. (2002) for details on the approach.

#### 2.4.2 *Resting sites' revisitation rate*

Some RSs were preferred and visited more often than others. We investigated how the proximity of villages and roads influenced the frequency of visits to RSs. We did so by fitting a GLMM on the number of visits to each RS, using a zero-truncated Poisson regression that contained the same predictors as our RSF analysis: the vegetation cover in interaction with the distances to roads, and to villages. The length of the survey period could naturally influence the number of times a RS was visited (but does not have to, as a wild boar could also use new RSs as the survey progresses), and we therefore included this variable (log-transformed to account for the link function of the Poisson regression) in the model as a control variable. Finally, we included individual animal identities, nested within study sites, as random intercepts. As for the habitat selection analysis, we fitted one model for the NHS and one for the HS. The marginal Nakagawa's  $R^2$  was used as a measure of model fit (Nakagawa and Schielzeth 2013).

#### 2.4.3 *Relocation events*

We used relocation events to gain insight into how often wild boars are disturbed while at rest. We modeled the probability of a wild boar to relocate as a binary (0 = no relocation; 1 = relocation) response variable using a binomial GLMM. The predictor variables were an interaction between vegetation type and the distance to roads, an interaction between vegetation type and the distance to villages, and a season variable accounting for the risk of being hunted. We expected that the relocation probability was influenced not only by the HS being open or closed, but also by whether the day was actually a hunting day or not. Therefore, we used a 3-category variable coding for "HS and hunting day," "HS and non-hunting day" and "NHS." This differed from the analysis of habitat selection of RSs above, in which we implicitly studied proactive adjustments of resting behavior to human activity and assumed that there could be a seasonality linked to hunting in wild boars' behavior, without accounting for hunting days. In addition to the predictor variables, we included individual animal identities, nested within study sites, as random intercepts. We also modeled the distance traveled between RSs each time a relocation event occurred using a similar model and the same predictor variables. The marginal Nakagawa's  $R^2$  was used as a measure of model fit.

#### 2.4.4 Audio data extraction and analysis

Six of the collars, deployed on four males and two females, had an audiologger (Latorre et al. 2021), i.e. an autonomous microphone, which recorded an average of 16 days (SD = 9) of continuous audio data after capture. We used this data to gain insight into what exactly happened right before relocations occurred. In particular, we looked for sounds that could attest disturbances by people. Even though the females were excluded from the main analysis, we considered the audio data from both sexes, because we did not expect sex to influence the nature of the possible causes of relocations, and because the amount of relocation events for which we had audio data was low. Nine relocation events occurred during a period with audio monitoring, with an average distance traveled of 170 meters (maximum = 317m). For each relocation event, we precisely identified the moment the wild boar stopped resting (a sharp rise in ACT) and extracted the audio from 40 minutes prior to this moment to 5 minutes after. This way, we ensured that the extract started while the wild boar was resting and quiet, and ended after it had started to relocate. For each of those “relocation” audio tracks, we also extracted one “control” track, recorded at the same time of day but on a different date. Tracks are available in Appendix 4. We randomly sorted all tracks, listened to them while viewing the corresponding spectrogram, and noted any sounds that could be identified, focusing specifically on sounds related to human activities (e.g., motor sounds, dog barks, human voices, gunshots) that could have interrupted the resting of wild boars. Of course, this approach might have missed some disturbances if they occurred silently or if the wild boars were able to detect danger and relocate before any sound could be picked up by the microphone. However, a sensitivity trial we conducted under realistic conditions suggested that the microphones were sensitive to even faint distant sounds: we placed a microphone in the vegetation, facing the ground, and spoke in a calm voice several meters away from it. We were able to identify normal speech both in the audio recording and in the spectrogram when the experimenter stood as far as 30m away from the microphone, facing it (20m when facing the opposite direction).

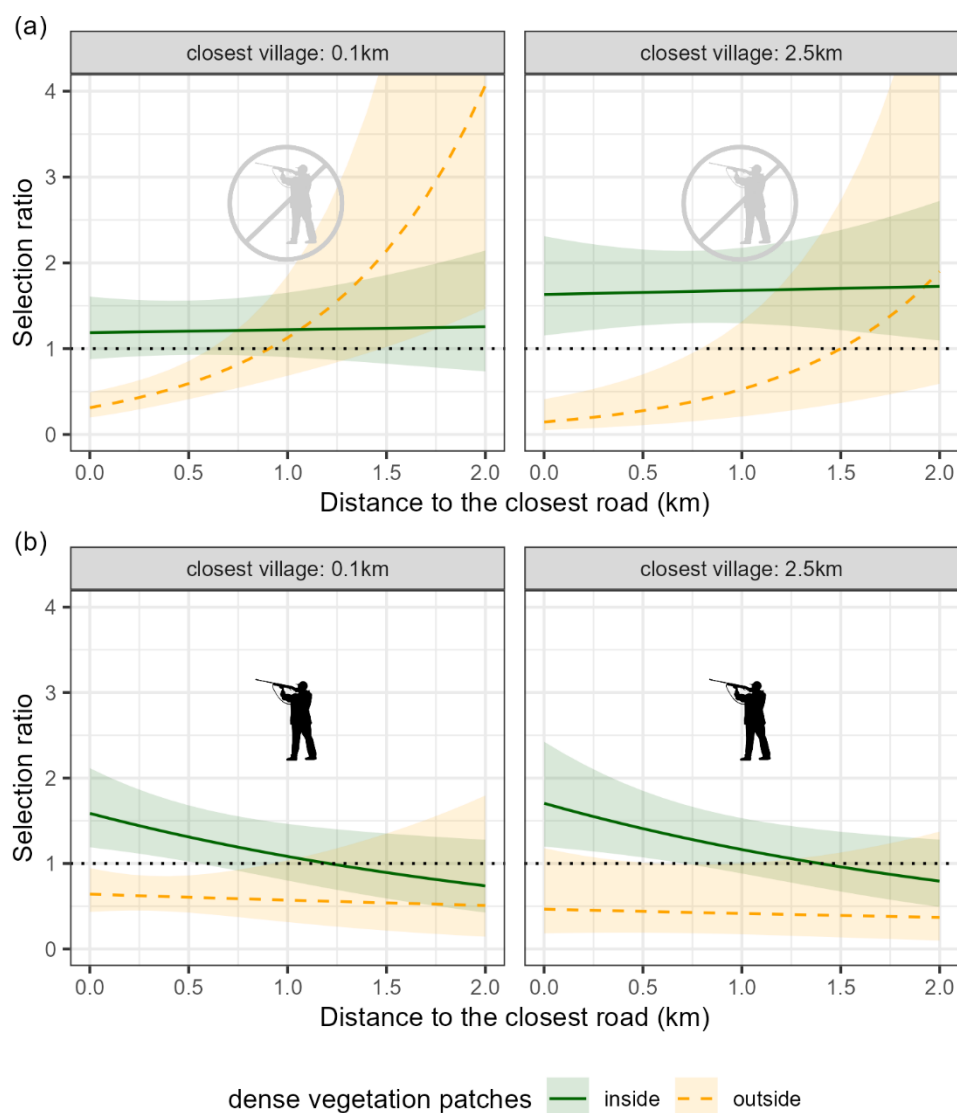
## 3 Results

### 3.1 Timing and duration of inactive phases

The wild boars studied spent most of their time at rest. On average, 58.5% (SD = 4.4) of their time budgets corresponded to the inactive phase, which typically started at the last hours of the night, and spanned throughout daytime (examples in [Figure 1a](#) and Appendix 2). Activity patterns were mostly synchronized with sunset times throughout the year. The end of the inactive phase occurred within 30 minutes around sunset in 44% of cases (and within 90 minutes in 80% of



cases), whereas it started within 30 minutes around sunrise in only 24% of cases (and within 90 minutes in only 53% of cases).



**Figure 2.** Estimation of the selection ratio for resting sites by wild boars during the non-hunting season (a) and the hunting season (b), for different distances to roads and villages. Selection for densely vegetated patches is represented in a dark green, solid line. Selection for non-densely vegetated patches is represented in a yellow, dashed line. A selection ratio above one indicates that sites are selected, and a selection ratio below one indicates that sites are avoided. Lightly-colored ribbons show the 95% confidence intervals.

Variable	B	SE	z-value	p-value
<b>Model: Selection ratio for resting sites during the non-hunting season</b>				
Intercept	-8.04	0.24	-33.20	<0.001
inside densely vegetated patches	1.29	0.29	4.45	<0.001
d(road)	1.28	0.31	4.10	<0.001
d(village)	-0.32	0.24	-1.34	0.18
inside densely vegetated patches x d(road)	-1.26	0.35	-3.58	<0.001
inside densely vegetated patches x d(village)	0.45	0.25	1.77	0.08
<b>Model: Selection ratio for resting sites during the hunting season</b>				
Intercept	-7.34	0.21	-35.44	<0.001
inside densely vegetated patches	0.89	0.26	3.46	<0.001
d(road)	-0.12	0.37	-0.31	0.75
d(village)	-0.13	0.21	-0.62	0.53
inside densely vegetated patches x d(road)	-0.27	0.40	-0.67	0.5
inside densely vegetated patches x d(village)	0.16	0.23	0.70	0.48

"d(village/road)" stands for "distance to the closest village/road."

**Table 1.** Parameters and statistics for the models estimating the selection ratio for resting sites during the non-hunting season and the hunting season. The 5-fold cross-validation performance scores (Spearman-rank correlations) of the models are respectively  $0.61 \pm 0.16$  s.e. and  $0.72 \pm 0.14$  s.e.

## 3.2 Patterns of resting site selection

### 3.2.1 Habitat selection for resting sites

As expected, wild boars favored resting in dense vegetation patches and generally avoided resting at sites that were in more open habitats (*Figure 2; Table 1*). During the NHS, the proximity of roads or villages had no effect on the selection of sites by wild boars, as long as they were in dense vegetation (*Figure 2a; Table 1*). Sites in more open vegetation were avoided when they were close to roads, but this avoidance disappeared, maybe shifting to a selection, when they were far from roads (*Figure 2a; Table 1*). Note however the large confidence intervals, caused by the fact that little data were available for those sites, that are rare in the landscape. During the HS, wild boars also did not adjust their selection to the distance to the closest village (*Figure 2b; Table 1*). In contrast to the NHS, they however did select more strongly sites located close to roads when they were in dense vegetation (*Figure 2b; Table 1*). The proximity of roads had no effect on the selection of sites in more open vegetation, and they were always avoided in this season (*Figure 2b; Table 1*).

### 3.2.2 Resting sites' revisitation rate

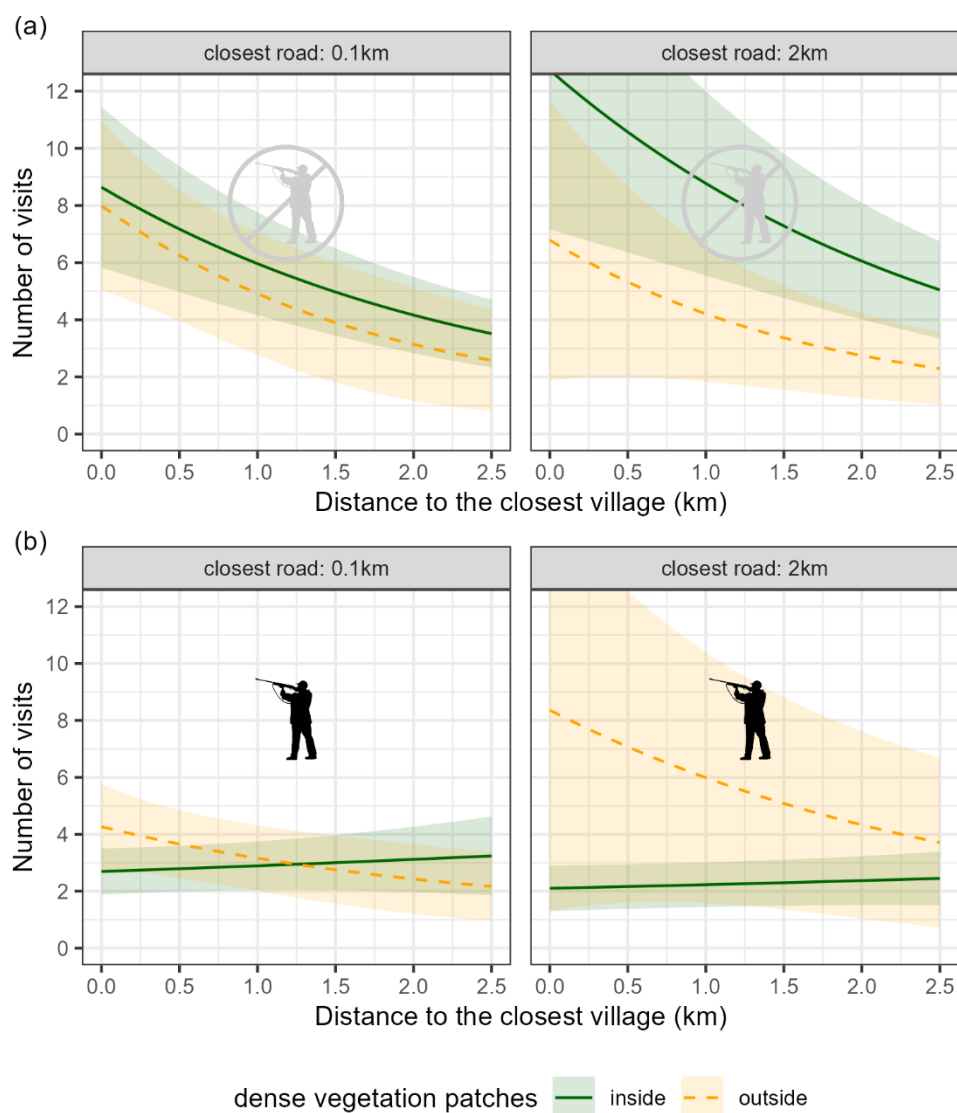
Wild boars regularly revisited RSs (51% were visited more than once), and some were visited more often than others (*Figure 1c*). RSs located close to villages were frequently revisited during

the NHS, and significantly more often than those located further away, irrespectively of whether they were in dense vegetation or not (*Figure 3a; Table 2*). Except the control variable of the length of the survey period, no other predictors were influential on the number of visits to RSs, during the NHS (*Table 2*). During the HS, we found significant effects of the type of vegetation—and its interactions with the distances to villages and roads—on the number of visits to RSs during the HS (*Table 2*). Note however that the predicted number of visits to RSs remained low during the HS, except far from roads and outside densely vegetated patches, where the confidence intervals are large, due to limited data and little availability of the habitat (*Figure 3b*).

Variable	$\beta$	SE	z-value	p-value
<b>Model: Number of visits to resting sites non-hunting season</b>				
Intercept	-1.17	0.73	-1.60	0.11
d(village)	-0.49	0.19	-2.57	0.01
d(road)	-0.09	0.20	-0.43	0.67
inside densely vegetated patches	0.05	0.15	0.32	0.75
log(length of the survey period)	0.63	0.16	3.88	<0.001
inside densely vegetated patches x d(village)	0.12	0.20	0.59	0.55
inside densely vegetated patches x d(road)	0.29	0.21	1.36	0.17
<b>Model: Number of visits to resting sites hunting season</b>				
Intercept	-0.40	0.64	-0.63	0.53
d(village)	-0.34	0.18	-1.85	0.06
d(road)	0.36	0.22	1.64	0.1
inside densely vegetated patches	-0.48	0.17	-2.77	<0.01
log(length of the survey period)	0.35	0.14	2.41	0.02
inside densely vegetated patches x d(village)	0.43	0.20	2.11	0.03
inside densely vegetated patches x d(road)	-0.55	0.26	-2.12	0.03

"d(village/road)" stands for "distance to the closest village/road."

**Table 2.** Parameters and statistics for the models estimating the number of visits to resting sites during the non-hunting season and the hunting season. The model's  $R^2$  are respectively 80% and 39%.



**Figure 3.** Estimation of the number of visits to resting sites over a 6-month period, during the non-hunting season (a) and the hunting season (b), for different distances to roads and villages. The estimation for the resting sites located inside densely vegetated patches is represented in a dark green, solid line. The estimation for the resting sites located outside those patches is represented in a yellow, dashed line. Lightly-colored ribbons show the 95% confidence intervals.

### 3.3 Relocations

The probability that a relocation occurred during the inactive phase was very low during the NHS (0.08; 95% CI [0.05-0.11]; *Figure 4a*; *Table 3*). Although the probability of relocation remained relatively low in the HS, it did increase two-fold during the hunting days of the HS (0.17; 95% CI [0.11-0.27]; *Figure 4a*; *Table 3*). Besides, when a relocation happened during the NHS, the distance traveled was virtually always less than 500 meters (*Figure 4b*). Indeed, almost all the few long-distance relocations (17 out of 21 of the relocations > 500 meters) happened during the

HS (*Figure 4b*). When the animal was initially resting in dense vegetation patches, neither the distance to the closest village, nor the distance to the closest road affected the probability of a relocation (*Figure 4c; Table 3*), or the distance traveled on relocations when they occurred (*Table 3*). When the animal was initially resting outside dense vegetation patches, there were a few significant effects of distance to the closest village or road on the probability of relocation and on the distance traveled, that were likely not biologically relevant (small effect or large confidence interval) and possibly caused by the low sample size in this condition (*Table 3*). Note however that the  $R^2$  of both models were very low (*Table 3*), indicating that a large part of the variability in both the probability of relocation and the distance travelled on relocations was not explained, neither by hunting, nor by the other variables considered in the models.

Variable	$\beta$	SE	z-value	p-value
<b>Model: Probability of relocation</b>				
Intercept	-2.96	0.34	-8.66	<0.001
d(village)	-0.15	0.41	-0.36	0.72
d(road)	1.20	0.44	2.69	<0.01
inside densely vegetated patches	0.29	0.37	0.77	0.44
during HS out of hunting days	0.51	0.25	2.08	0.04
during HS and hunting days	0.82	0.25	3.25	<0.01
inside densely vegetated patches x d(village)	0.46	0.43	1.07	0.29
inside densely vegetated patches x d(road)	-1.59	0.51	-3.09	<0.01
<b>Model: Distance of relocation (km)</b>				
Intercept	-1.44	0.25	-5.77	<0.001
d(village)	0.51	0.27	1.92	0.05
d(road)	-0.41	0.28	-1.48	0.14
inside densely vegetated patches	-0.23	0.25	-0.92	0.36
during HS out of hunting days	0.18	0.15	1.16	0.25
during HS and hunting days	0.54	0.17	3.22	<0.01
inside densely vegetated patches x d(village)	-0.42	0.28	-1.50	0.13
inside densely vegetated patches x d(road)	0.71	0.33	2.18	0.03

"d(village/road)" stands for "distance to the closest village/road."

**Table 3.** Parameters and statistics for the models estimating the probability and the distance of relocations. The models'  $R^2$  are respectively 6% and 16%.

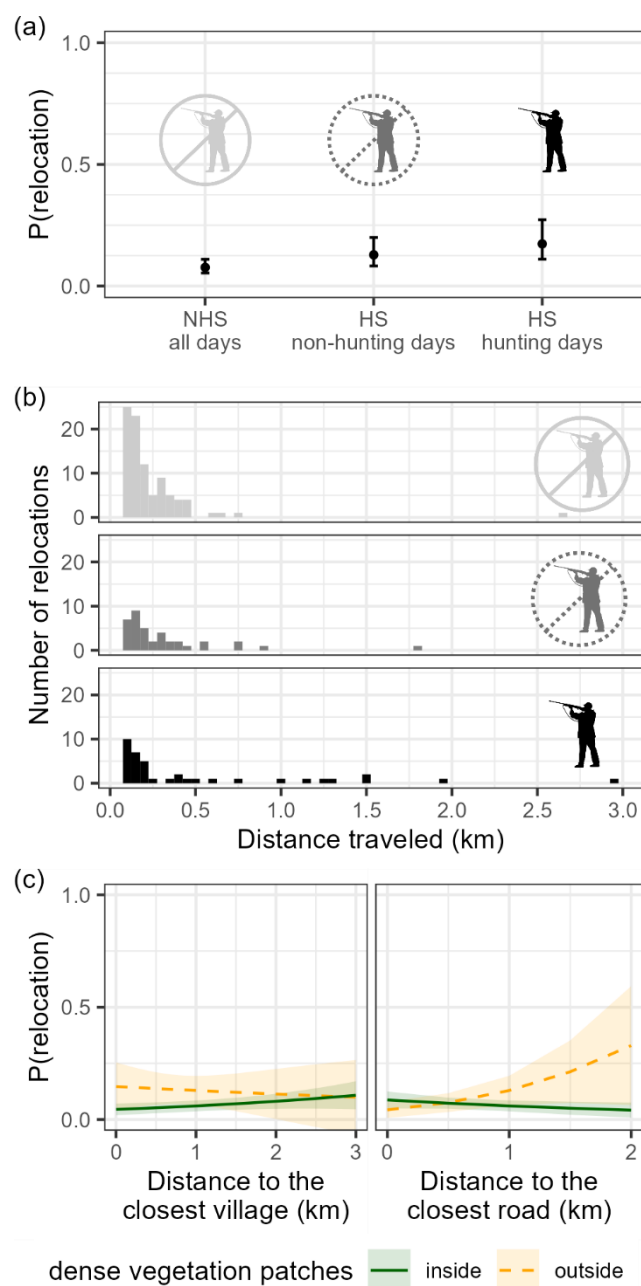
In all the nine audio tracks extracted from before relocations and the nine control tracks, the wild boars could be heard resting quietly, usually snoring, breathing calmly and grooming. Although we could hear vehicles passing at close distance in two control tracks, the wild boars did not seem to react to those sounds. In 8 extracts corresponding to a relocation, we could hear the wild boars walking away, without any disturbance being identifiable in the audio. In the ninth

extract, which was recorded on a Sunday during the HS, we could clearly identify a hunting event by the barks of a pack of dogs and a gunshot, right when the wild boar started to move away (Appendix 4). We did not hear any other potential disturbance linked to human activity in the selected extracts.

## 4 Discussion

Resting is an important part of an animal's life, both in duration and function. Yet, our knowledge of the flexibility of animals' resting behavior remains limited. In particular, we know little about how animals adjust their resting behavior to the risk of human disturbances, how often actual disruptions of resting phases occur, and how animals respond to them. The wild boars we studied allocated more than half of their time budget to resting, mostly during daytime, and thus preferred to be exposed to anthropic disturbances when resting compared to when foraging. This pattern has been observed in other populations of wild boars (Brivio et al. 2017; Johann, Handschuh, Linderoth, Dormann, and Arnold 2020; Rosalino et al. 2022) but also in a variety of other species (Gaynor et al. 2018) living in anthropized landscapes. We questioned whether wild boars tried to minimize the risk of being disturbed through resting site (RS) selection, and in such a case, whether they were successful.

As expected, wild boars always favored resting under the cover of densely vegetated patches, which is certainly the best way to reduce the risk of being disturbed. Additionally, we expected the selection of RSs to vary with the risk of encountering people. Surprisingly, however, we did not find any effect of the proximity of villages on the selection of RSs. As resting near villages is undoubtedly associated with costs and benefits, linked to both resource acquisition and safety, these must probably offset each other so that there is no net advantage of selecting to rest near or far from a village. The fact that the proximity of villages did not affect habitat selection for RSs however contrasted with the strong effect it had on the fidelity to RSs, during the NHS. When they were not at risk of being hunted, wild boars came back to rest at the same spot more often when it was close, or even within, a village. We tentatively suggest that predictably quiet places, suitable for resting, are rare near villages, and that wild boars rely heavily upon them. This effect disappeared during the HS, as revisitations of RSs were less frequent, maybe because wild boars avoid being predictable when they are actively being sought by hunters. Our study shows that the need to find suitable RSs does not prevent wild boars from exploiting areas with high degrees of proximity with people, as they can compensate a general increased probability of disturbance by selecting more intensely some specific RSs that they know are safe. This plasticity in wild boars' resting strategy is certainly critical to explain their success in subsisting, and sometimes thriving, in a wide diversity of habitats, even those heavily urbanized (Stillfried et al. 2017).



**Figure 4.** (a) Estimation of the probability of relocation during the hunting season and hunting days (Wednesdays, Saturdays, Sundays, and bank holidays), during the hunting season and non-hunting days, and during the non-hunting season. (b) Distribution of the distances traveled during relocations, according to hunting periods (same categories as in (a)). (c) Estimation of the probability of a relocation, during the non-hunting season, according to the distance to the closest village and to the closest road. The estimation for the resting sites located inside densely vegetated patches is represented in a dark green, solid line. The estimation for the resting sites located outside those patches is represented in a yellow, dashed line. Lightly-colored ribbons show the 95% confidence intervals

The effect of roads on wild boars' RS selection was more complex. During the NHS, wild boars selected to rest in densely vegetated patches irrespectively of their distance to roads. In contrast, wild boars avoided resting outside densely vegetated patches only close to roads, and they selected, or at least were neutral to, such sites if they were far from roads. This could be because the risk of being disturbed was lower there. However, note that areas outside densely vegetated patches and far from roads are rare in the landscape, leading to large confidence intervals that warrant caution in interpretation. Wild boars' response to the proximity of roads changed during the HS, as they selected densely vegetated sites more strongly when they were close to roads, and did not select sites in more open vegetation even far from roads. We argue that this could reflect a proactive strategy of wild boars to minimize hunting risk. Hunters tend to focus their effort away from main roads as they make hunting dangerous for people and dogs. Areas near roads are thus safer than elsewhere, and exposure in the open, far from roads is likely particularly unsafe for a wild boar during the HS.

Resting strategies that involve behavioral adjustments to the risk of disturbances by people, as demonstrated here for wild boars, have been documented before (Scillitani et al. 2010; Wittemyer et al. 2017; Bojarska et al. 2021). Previous studies however rarely evaluated how successful these adjustments were at reducing this risk. We addressed this gap by studying the probability of wild boars relocating during their resting phases, a possible indicator of disturbance, depending on the location of the RSs. Our results generally suggest that the RS selection strategy of wild boars was effective in keeping the probability of being disturbed low, even in places where chances of meeting people is high. Wild boars rested at all distances from villages, and yet the probability of them relocating during the inactive phase was just as low close to villages than several kilometers away from them. This supports our assertion that, close to villages, wild boars use particularly quiet spots where encounters with people are unlikely, and re-use them over time. They could thus rest in anthropized landscape with perhaps little cost.

Of course, not all disturbances may lead to a relocation. It is well known that wild boars may hide rather than flee when hunted (Scillitani et al. 2010; Thurfjell et al. 2013), and wild boars may sometimes be disturbed and not leave their RS. We actually observed this response in 62% (8 out of 13) of the experimental disturbances that we led on resting wild boars (personal observations). Although any disturbance can affect the 'quality' of resting (e.g., through sleep deprivation), keeping quiet in response to an untargeted disturbance is likely a good strategy, as it avoids the costs and risks associated with relocating. Besides, non-targeted disturbances are often short-lived, and will only reduce resting time marginally. Additionally, in our study, the wild boars remained inactive for 14 hours per day on average, which was longer than the total sleep time previously recorded in domestic pigs (7.8 hours) (Campbell and Tobler 1984) and in free-ranging



wild boars (10.6 hours) (Mortlock et al. 2022). This suggests that the wild boars were unlikely to suffer harmful reductions of resting time due to anthropic disturbances. In some cases, wild boars might not even respond to a stimulus that we would have assumed stressful for them. For instance, upon opportunistically listening to the rest of the audio data, we heard a dog barking from what seemed like a close distance, but the wild boar did not react and continued to snore calmly throughout the event (Appendix 4). This extract supports the hypothesis that resting wild boars show little sensitivity to untargeted disturbances. Given the low frequency of relocations, and the little impact expected from disturbances that do not entice relocations, it seems safe to conclude that wild boars, in our study area, are little affected by human activity during resting. Unsurprisingly though, this was less true during the hunting season as hunting is a significant source of targeted disturbance for wild boars in this landscape. The probability of relocation was highest during hunting days of the HS, and long-distance relocations (> 1km) were virtually only observed during these days. These could correspond to actual hunts, with dogs chasing the animal over large distances. The moderately greater probability of relocation in non-hunting days of the HS might reflect a higher responsiveness of wild boars to even non-targeted disturbances, during the HS. However, it is important to note that the low explanatory power of the models suggest that the fact that the hunting season was open did not substantially change the causes or consequences of relocations, and therefore the relocation patterns of wild boars. It likely only added the possibility that a hunting event would sometimes cause some long-distance relocation. Of course, not all relocations may have been a response to a disturbance. In 9 out of 10 audio extracts collected at the onset of a relocation, the animal could only be heard resting quietly and snoring, before leaving the area for no apparent reason. It is possible that we did not hear a person or a dog that was nearby, which the wild boar would have smelt, or heard, and reacted to. It is also possible that the wild boar simply woke up and left for a new area for a different reason (e.g., weather change). If such natural daily movement occur during the inactive phase, this would strengthen our general interpretation that people rarely disturb wild boars once they have selected a RS.

In conclusion, our study shows that wild boars are efficient at exploiting areas near people, while still finding suitable sites where to rest. They do so by selecting sites with high cover, by responding to the proximity of human presence in ways that can change with the hunting season, and by revisiting preferentially the safest sites near human settlements. It is apparently a successful strategy, as they rarely have to relocate far away in response to a disturbance, apart when targeted by hunting. As more and more habitats become subject to anthropisation, the need to find suitable sites where to rest is likely to become a constraint for a variety of animal species. In such circumstances, species with a high behavioral and ecological flexibility are likely to be

avored, in particular through the adjustment of their resting patterns. Although successful temporal adjustments of activity patterns in response to human pressure had been extensively described (Lowry et al. 2013; Gaynor et al. 2018) , our study shows that resting site selection is another efficient way for animals to avoid encounters with people.

**Acknowledgments:** This work was supported by the REPOS project through the I-site Montpellier Université d'Excellence (grant number ANR-16-IDEX-0006) and by the François Sommer foundation. We are indebted to the various landowners who permitted to work on their land, to S. Perret, D. Degueldre, G. Fréchet, J. Nicot for assistance with wild boar captures, and to R. Mathevet and J.-M. Chanabe for some aspects of project management. D. Cornelis kindly offered the first collars used in the study. L. Latorre and J. Miquel developed the audiloggers. M. Valeix kindly reviewed a draft of the manuscript. We also thank the OpenStreetMap contributors for the map data available from <https://www.openstreetmap.org>. An anonymous associate editor and two reviewers provided helpful comments that improved the manuscript.

**Author contributions:** **Gustave Fradin:** Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (supporting); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Simon Chamailé-Jammes:** Conceptualization (equal); formal analysis (supporting); investigation (lead); supervision (lead); funding acquisition (lead); project administration (lead); writing – review and editing (equal).

**Conflict of interest statement:** The authors declare no conflict of interest.

**Data accessibility statement:** GPS and activity data collected on wild boars are available at <https://doi.org/10.5061/dryad.3j9kd51qj>.

## Appendices

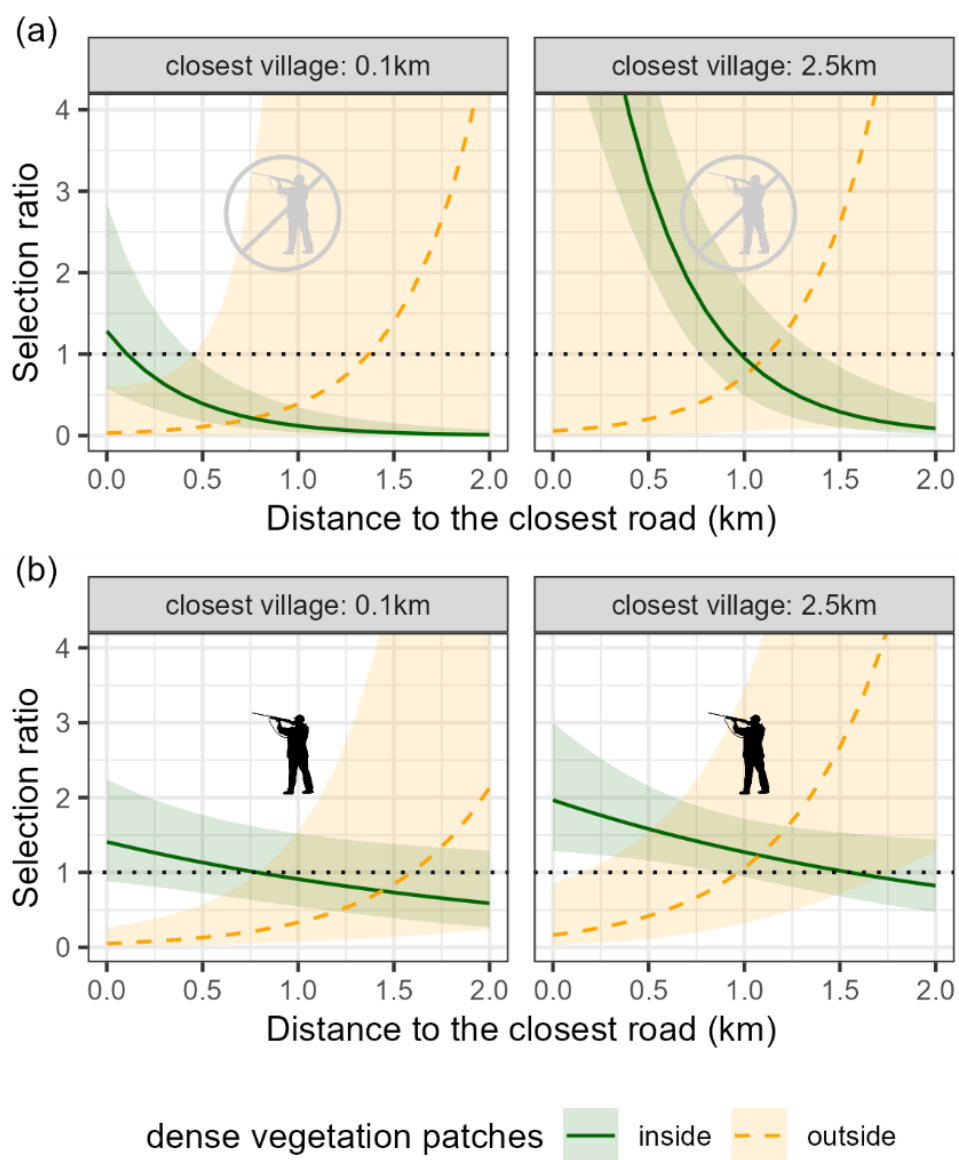
### Appendix 1. Selection of resting sites by the females

We could collect only very limited data from female wild boars. We tracked only five females, of which two did not provide data during the NHS. They rested mostly inside densely vegetated patches, and extremely few resting sites were located out of them: nine during the HS and two during the NHS. In addition, few resting sites were located far from a road or close to a village. It is well known that male and female wild boars generally differ in their use of space, habitats, and responses to anthropic pressures (Saïd et al. 2012; Morelle et al. 2015). Considering that, it did not seem relevant to include the females in the analysis without accounting for the effect of sex. Fitting models with the data from both sexes and considering sex as a fixed effect was impossible, due to the low amount of data from females. This is why we fitted models on the males' and the females' data separately. Here we provide information about the exploration of the females' data.

We used the method described in section 2.4.1 of the main text to fit a resource selection function (RSF) to the females' data. As with the males, we fitted a GLMM, using the type of resting site (used vs. available) as a response variable and a binomial distribution for errors. We used the vegetation cover (inside or outside densely vegetated patches) in interaction with the distances to roads and to villages as predictor variables. We also included individual animal identities nested within study sites as random intercepts. As with the males, we fitted this model independently for the HS and the NHS. Finally, we converted RSF scores into selection ratios for interpretability.

During the NHS, the lack of data made it impossible to draw any conclusion on the selection of resting sites by females. We fitted the model on only three individuals, with two resting sites observed outside densely vegetated patches and two observed further than a kilometer from a road. This explains the large confidence intervals outside densely vegetated patches, as well as the avoidance that we observed far from roads (*Figure S1a; Table S1*).

During the HS, more data was available, although the overall amount remained limited. The results were similar to those obtained for the males (*Figure S1b; Table S1*). The selection ratio for sites outside densely vegetated patches was globally similar to the one observed for the males. However, we found a significant effect of the interaction between the type of vegetation and the distance to roads, while it was not significant in males. Once again, however, the low amount of data for females outside densely vegetated patches made it complicated to interpret this result.



**Figure S1.** Estimation of the selection ratio for resting sites by female wild boars during the non-hunting season (a) and the hunting season (b), for different distances to roads and villages. Selection for densely vegetated patches is represented in a dark green, solid line. Selection for non-densely vegetated patches is represented in a yellow, dashed line. A selection ratio above one indicates that sites are selected, and a selection ratio below one indicates that sites are avoided. Lightly-colored ribbons show the 95% confidence intervals.

Variable	$\beta$	SE	z-value	p-value
<b>Model: Selection ratio for resting sites during the non-hunting season (females)</b>				
Intercept	-10.42	1.56	-6.70	<0.001
inside densely vegetated patches	3.68	1.61	2.28	0.02
d(road)	2.55	2.18	1.17	0.24
d(village)	0.26	1.00	0.26	0.79
inside densely vegetated patches x d(road)	-4.91	2.23	-2.20	0.03
inside densely vegetated patches x d(village)	0.60	1.02	0.59	0.56
<b>Model: Selection ratio for resting sites during the hunting season (females)</b>				
Intercept	-9.91	0.87	-11.45	<0.001
inside densely vegetated patches	3.33	0.90	3.70	<0.001
d(road)	1.85	0.58	3.18	<0.01
d(village)	0.48	0.50	0.97	0.33
inside densely vegetated patches x d(road)	-2.29	0.62	-3.71	<0.001
inside densely vegetated patches x d(village)	-0.34	0.51	-0.66	0.51

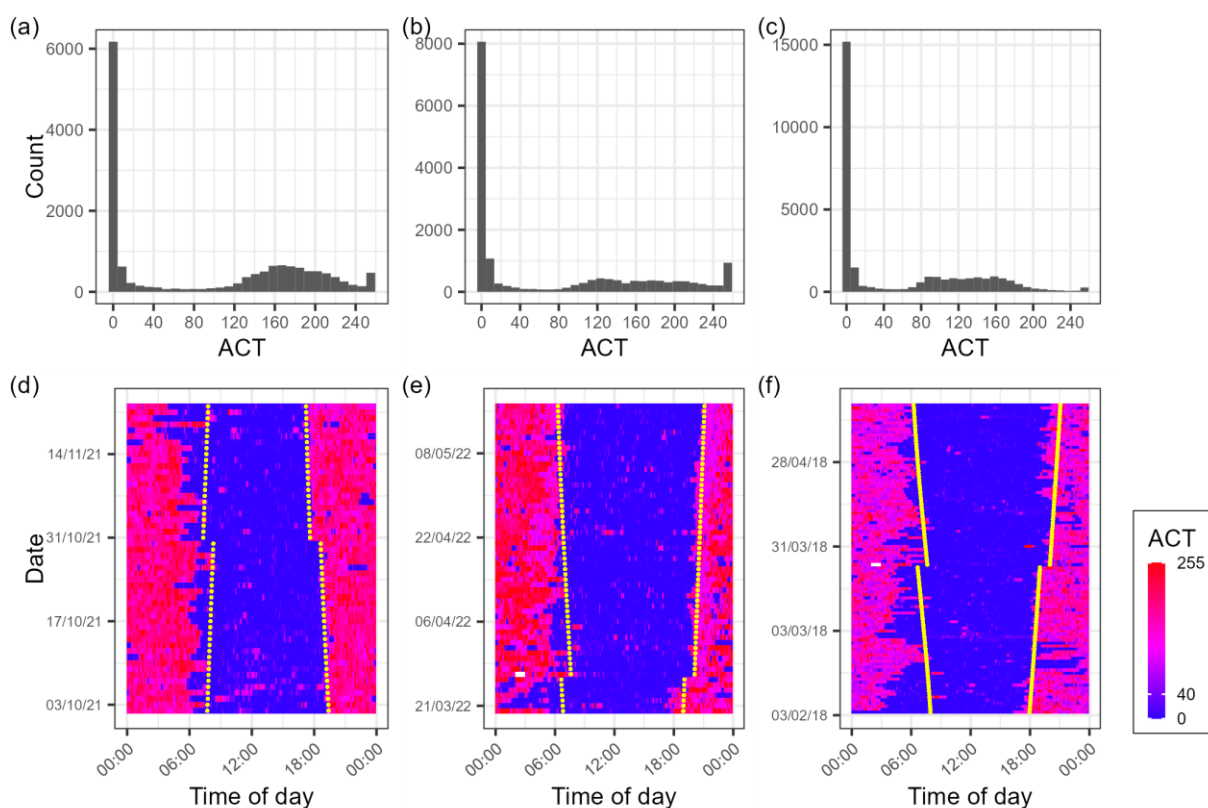
"d(village/road)" stands for "distance to the closest village/road."

**Table S1.** Parameters and statistics for the models estimating the selection ratio for resting sites by females, during the non-hunting season and the hunting season. The 5-fold cross-validation performance scores (Spearman-rank correlations) of the models are respectively  $0.58 \pm 0.18$  s.e. and  $0.53 \pm 0.13$  s.e.

## Appendix 2. Identification of resting patterns

### Identification of the inactive phases

From visual inspection of the activity data, we inferred that, in our study area, the wild boars were nocturnal. The distribution of activity values (ACT) was bimodal for all individuals, with one mode around zero - corresponding to resting - and one mode between 80 and 240 - corresponding to activity (three examples in [Figure S2a-b-c](#)). We chose a threshold value (ACT = 40) to separate those activity values in two groups such that the least frequent values of activity, i.e. those between 10 and 80, were mostly classified as "activity." We thus kept the "resting" category as constrained as possible. All the individuals considered in the analysis showed a clear nocturnal pattern of activity, with one sequence of low values of activity spanning throughout daytime - sometimes starting a little before sunrise - and one sequence of high values of activity spanning quite precisely from sunset to the start of the next sequence of inactivity, in the morning (three examples in [Figure S2d-e-f](#)).



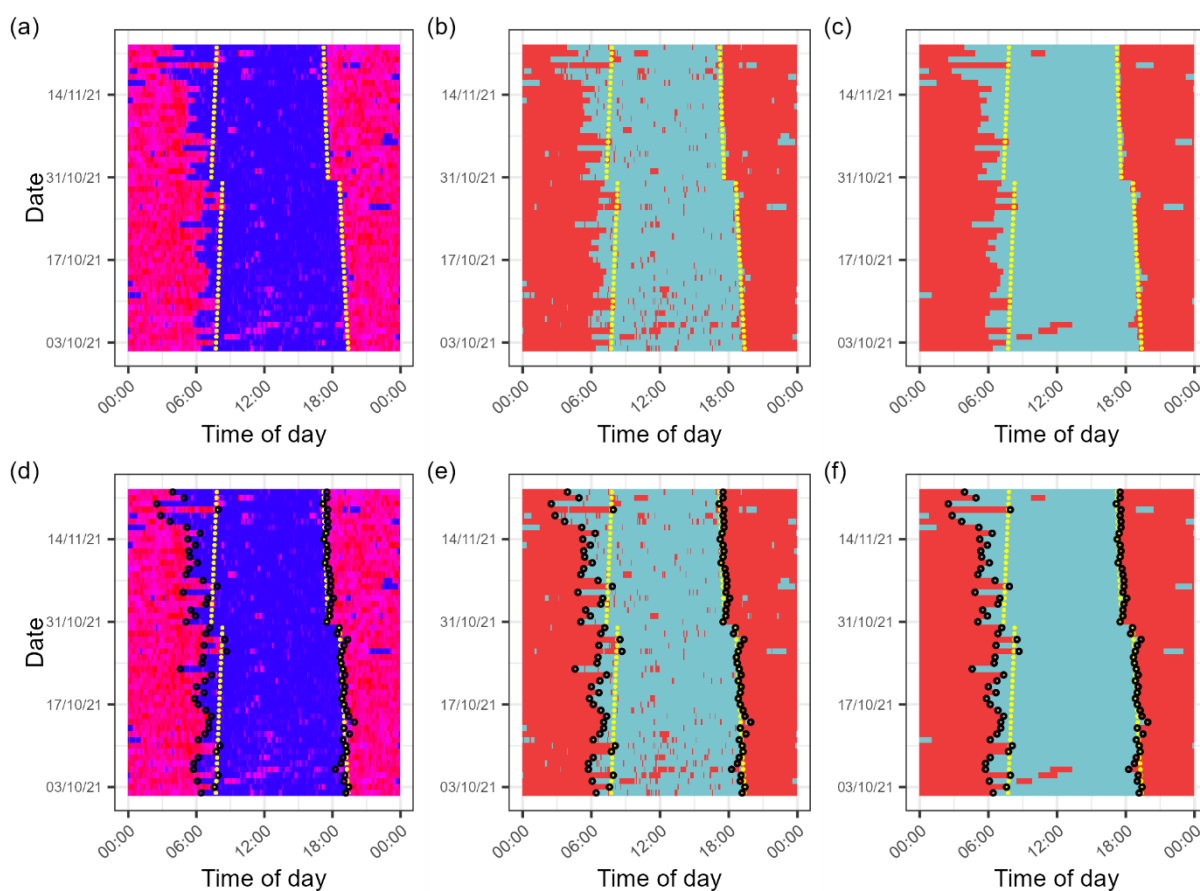
**Figure S2.** Patterns of activity of three wild boars. (a-b-c) Distribution of the raw ACT values, for three individuals from our study. (d-e-f) Temporal patterns of activity of the animals presented respectively in (a), (b) and (c). Each date (by rows) is divided into 5min slots that are colored according to their level of activity, ranging from blue ( $ACT = 0$ ) to red ( $ACT = 255$ ). The yellow dots indicate, for each date, the times of sunrise and sunset. Times are in local time, which includes daylight savings (note the discontinuities in sunrise and sunset times).

Based on the observed temporal patterns of activity, we considered that each 24-hour cycle could be divided into two continuous phases: the active and the inactive phase. We identified the time boundaries of these phases by applying the same treatment to each animal's activity data. We first applied a threshold on the raw activity data (one example in [Figure S3a](#)) to obtain a binary time series with values being either “active” ( $ACT > 40$ ) or “resting” ( $ACT \leq 40$ ) behavior, each value corresponding to a 5min time slot ([Figure S3b](#)). Many short sequences of “active” behavior were typically spread across what would be the inactive phase, i.e. during the day, and conversely, some short “resting” sequences existed within what would be the “active” phase, i.e. during the night. We therefore simplified the time series by smoothing out the short sequences that we considered irrelevant for the determination of the time boundaries of “active” and “inactive” phases. We did so by iteratively switching the category (“resting” or “active”) of the shortest sequence in the time series, until the shortest sequence in the entire time series was 1 hour long ([Figure S3c](#)). Five minutes time slots with intermediate activity values (between 10 and

80) were rarely consecutive. For that reason, the outcome of the last processing step was robust to the choice of a different threshold value to identify “active” and “resting” behaviors. Finally, we determined the times of the starting and ending of the “inactive” and “active” phases, so that they matched as closely as possible the pattern observed visually on the raw data (*Figure S3d-e-f*). We used the following three rules to attribute each sequence of the time series to one or the other phase: (i) All sequences of “resting” behavior overlapping daytime, and (ii) all sequences of “active” behavior spanning entirely within daytime were considered part of the inactive phase. In addition, (iii) whenever a sequence of “resting” behavior restricted to nighttime lasted more than 1.5h, and was separated from the rest of the “inactive” phase by an “active” sequence less than 1.5h long, both the “resting” and the “active” sequences were added to the “inactive” phase. The result of this last step closely matched the pattern expected by visual inspection of the raw data (*Figure S3d*).

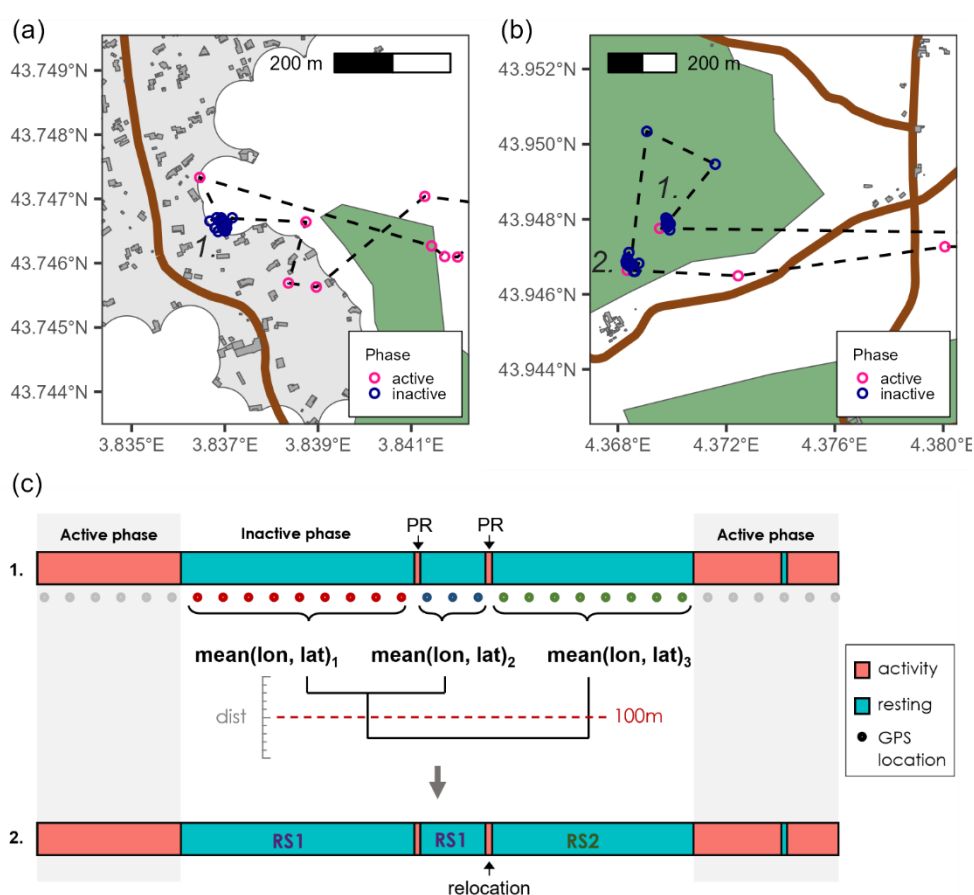
#### *Identification of the resting sites*

After having determined the start and end times of the daily inactive phases, we used GPS data to identify where resting had occurred each day. Often, resting occurred at a single resting site throughout the inactive phase (example in *Figure S4a*). In some instances, however, wild boars did move from an initial resting site, to settle in a secondary resting site, during the inactive phase, in what we called a “relocation” (example in *Figure S4b*). Relocations would obviously be associated with important values of ACT. To identify them, we compared the location of the animal before and after the bouts of activity that we considered sufficiently “active” to be considered a “possible relocation” (hereafter PR, see *Figure S4c*). We considered a PR whenever a continuous “active” bout reached a cumulative ACT value of at least 100. Between PRs, the ACT signal was too low for the animal to have possibly traveled from one resting site to another. We compared the mean GPS positions before and after the first PR of each inactive phase. If they were further apart than 100m, we considered that a relocation had occurred. If not, we discarded the PR and applied the same method to the next PR in the inactive phase. Once we had identified all the relocations, we estimated the exact location of the different resting sites to be the average of the GPS positions recorded during the inactive phase, between each relocation (*Figure S4c*).



**Figure S3.** Visual description of the steps taken to determine the timing of the “inactive” phases. (a) Temporal pattern of activity of one wild boar, as raw data. The scale used is the same as in Figure S2. (b) Result of the application of a threshold on the time series of raw data, to distinguish “active” ( $ACT > 40$ , in red) and “inactive” ( $ACT \leq 40$ , in light blue) behaviors. (c) Result of the smoothing processing step applied to the time series shown in (b). (d), (e) and (f) respectively show how the start and end times of the “active” and “inactive” phases (black circles) fit on the time series presented in (a), (b) and (c). The yellow dots indicate, for each date, the times of sunrise and sunset.





**Figure S4.** Identification of the relocations. (a) Trajectory of a wild boar (dashed line), including an inactive phase with no relocation, and thus a single resting site (1). (b) Trajectory of a wild boar (dashed line), including an inactive phase with a relocation, in which the animal traveled from a primary resting site (1) to a secondary resting site (2). In (a) and (b), buildings are represented in dark grey, villages in light grey, roads in brown, and densely vegetated patches in dark green. (c) Method of identification of the relocations. We focus on a theoretical trajectory, spanning across one inactive phase, and represented spatially in (1). The associated time series of “active” and “resting” bouts is represented in (2a). The colors of the dots indicate groups of GPS locations that were acquired during the same resting bout. During the inactive phase, between the potential relocations (PR), the distances (dist) between mean GPS positions ( $\text{mean}(\text{lon}, \text{lat})$ ) are calculated. Whenever dist exceeds 100m, we consider that the PR corresponds to a relocation. This method enables the identification of RS1 and RS2, two resting sites that were visited during the inactive phase (2). The first PR did not correspond to a relocation, but the second one did.

### **Appendix 3. Identification of densely vegetated patches**

We retrieved spatial information on vegetation cover from CORINE Land Cover 2018 (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>). The following list shows the categories that we included in the definition of “densely vegetated patches”, together with the percentage of the land they occupied in our study area:

- Broad-leaved forest (14.5%)
- Coniferous forest (2.4%)
- Mixed forest (4.4%)
- Sclerophyllous vegetation (12.7%)
- Transitional woodland-shrub (4.1%)
- Land principally occupied by agriculture, with significant areas of natural vegetation (3.6%)
- Natural grasslands (2.2%)
- Moors and heathland (0.3%)

Although usually associated with low vegetation, the “natural grasslands” and the “moors and heathland” categories corresponded, in our study area, to areas of regrowth, offering suitable vegetation cover for wild boars to hide. This is why we considered relevant to group them together with taller vegetation layers in this study.

### **Appendix 4. Sound extracts**

All the sound extracts mentioned in the paper are available for listening at the following address: <https://doi.org/10.5281/zenodo.7660803>. The tracks that were extracted from 40 minutes before to 5 minutes after a relocation was initiated are labelled as “relocation”. The tracks labelled as “control” were extracted at the same time of day as the “relocation” tracks, but on different dates, when relocations did not occur. We also make available an additional track, corresponding to a dog barking, with the wild boar not reacting to it. It was identified upon opportunistic listening of the dataset.



## Chapitre 3



**Résumé :** Pour de nombreuses espèces animales, le repos et l'activité se déroulent dans des lieux distincts, parfois éloignés entre eux. Les animaux étant limités dans la distance qu'ils peuvent parcourir chaque jour, la disposition des sites de repos et d'alimentation peut contraindre les individus dans leur utilisation du domaine vital. Dans les paysages anthropisés, les sites de repos adéquats sont souvent rares et dispersés, et les déplacements sont généralement restreints. Dans ce contexte, certains déplacements entre sites de repos peuvent devenir impossible à effectuer au cours d'une seule phase d'activité. Il est donc attendu que certains sites de repos deviennent centraux dans les patrons de déplacement, en servant d'étapes lors des déplacements dans le domaine vital. Dans cet article, nous avons testé cette hypothèse en étudiant les sites de repos et d'activité de sangliers (*Sus scrofa*) répartis à travers l'Europe entière. Nous avons construit des réseaux de déplacement pour étudier la contribution des sites de repos à la connectivité des domaines vitaux. Nous avons comparé la centralité des zones utilisées pour le repos et pour l'activité, afin de définir un indice de contribution des sites de repos à cette connectivité, et d'évaluer les effets du niveau d'anthropisation et de la couverture arborée sur la valeur de cet indice. Nous avons constaté que les sangliers vivant dans des domaines vitaux peu boisés structuraient davantage leurs déplacements en fonction de leurs sites de repos. L'effet du niveau d'anthropisation sur la centralité des sites de repos était plus difficile à interpréter. Cependant, le degré de colinéarité entre cette variable et la couverture arborée suggère que les sangliers vivant dans des paysages anthropisés dépendent davantage de quelques sites de repos importants pour circuler dans leur domaine vital. Dans les paysages anthropisés, où les sites de repos représentent souvent ressource limitée, leur disposition dans le paysage peut jouer un rôle crucial en influençant les capacités de déplacements des animaux.

**Mots clés :** couvert forestier, empreinte anthropique, patrons d'activité, réseaux de déplacement, sanglier, sommeil

# The contribution of resting sites to the connectivity of animals' movement networks along a gradient of anthropization

Gustave Fradin<sup>1</sup>, collaborators from Euroboar<sup>2</sup>, Simon Chamailé-Jammes<sup>1</sup>

1. CEFE, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France
2. Prospective coauthors who shared Euroboar datasets are listed at the end of the chapter

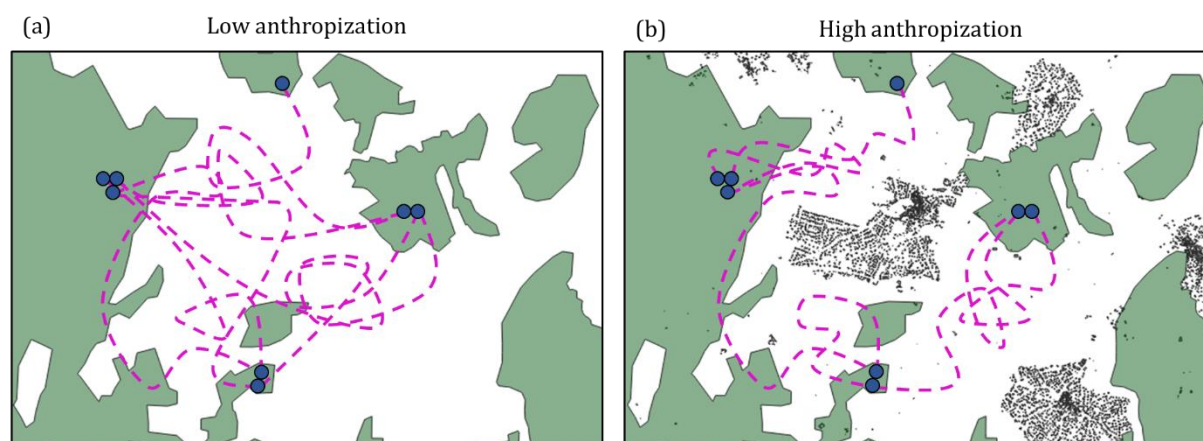
**Abstract:** For many animal species, resting and activity happen in distinct sites, that may be located far apart in the landscape. As animals are limited in how far they can travel each day between resting and foraging sites, the spatial layout of those sites may impose constraints on how animal may use their home range. In anthropized landscapes, suitable resting sites are often scarce and dispersed, and movements are generally more constrained than in natural landscapes. In this context, animals may not be able to travel between any pair of resting sites in one single phase of activity. Some resting sites may thus become central in animals' movement patterns, serving as "stepping-stones" to allow them to travel between different sectors of their home range. In this paper, we tested this hypothesis by investigating the resting site selection and movement patterns of wild boars (*Sus scrofa*) living across Europe, along a wide gradient of anthropization level. After a brief description of the patterns of utilization of resting sites by the wild boars, we constructed movement networks to investigate the contribution of resting sites to connecting different parts of the home ranges together. We calculated the ratio of betweenness centrality of the areas used for resting and for activity, and evaluated the effects of anthropization level and tree cover on that ratio. We found that wild boars living in little forested home ranges had movement patterns that were more structured around the sites that they used for resting. Although the effect of the anthropization level was not clear, the amount of collinearity between this variable and the amount of tree cover suggested that wild boars living in anthropized landscapes must be more reliant on a few important resting sites to move across their home range. In anthropized landscapes, where resting sites are sometimes a limited resource for many animals, their spatial layout may play a crucial role in allowing animal movements across the landscape.

**Keywords:** activity patterns, human footprint, movement networks, sleep, tree cover, wild boar

## 1 Introduction

The choice of a daily resting site is a crucial recurring decision for many animals. When they select a place where to rest, animals determine the risk of predation that they will face while in maybe their most vulnerable state (Lima et al. 2005), and usually for a long period of time (Campbell and Tobler 1984). In addition to the risk of being predated upon, the location of a resting site influences the probability of any disruption of resting—including anthropogenic ones—to occur. Therefore, it may set the level of vigilance required during the resting phase, which in turn may affect the quality of sleep, with potential physiological drawbacks (Tisdale et al. 2018; Olejarz et al. 2023). Equally importantly, animals are constrained, both in terms of motor skills and navigation, in their capacity to travel from one resting site to the next (Nathan et al. 2008). This means that the location of a resting site may impose restrictions on where the subsequent active phase may occur, and where the next resting site to be used may be (Génin 2010; Janmaat et al. 2014). Landscape characteristics, such as permeability to movement and resting sites' availability, are key drivers of the distances and path animals may move across, to go from one resting site to the next. Consequently, the resting sites and the areas used for activity, such as the preferred foraging grounds, are connected between each other, through movement, in ways that may depend on motion capacity and environmental features. Resting sites might thus bear a more or less important position in the whole movement patterns of animals, depending on how they connect activity sites with each other.

As anthropization increases and intensifies worldwide, suitable resting sites become rare in altered landscapes, and large and medium-sized animals increasingly struggle to find where to rest (Bateman and Fleming 2012; Weinberger et al. 2019). The risk of encountering people participates to the reduction of resting sites' suitability for these animals (Wam et al. 2012; Wittemyer et al. 2017; Bojarska et al. 2021). In addition, the spatial distribution of potential resting sites—i.e. how they are spatially laid out between each other and with the areas used during activity—may be altered in anthropized landscapes, compared to undisturbed ones. The capacity to find suitable resting sites, and to travel from them and to the foraging grounds, and vice-versa, constitutes an important constraint on how animals may use the landscape. Transit from resting sites to foraging sites is expected to prove harder in anthropized landscapes, where animals' movements in general are reduced (Tucker et al. 2018). Being able to adjust where to rest, and how to organize movement patterns between resting sites and activity sites, may thus be a crucial advantage for animals to live in human altered environments (Candolin et al. 2023; Gilbert et al. 2023). Yet, how animals move within their home ranges according to the spatial layout of their resting sites has, to our knowledge, never been investigated with respect to the level of anthropization.



**Figure 1.** Illustration of the expected movement pattern of an animal using one type of habitat for resting (blue circles), and another type of habitat for activity (pink dashed lines). The pattern of movements between resting sites is expected to be less structured in a little anthropized landscape (a), than in a highly anthropized landscape (b). Green and white patches represent two types of habitat, with green habitats being suitable for resting. Villages and isolated buildings are added in panel (b), compared to panel (a).

In this manuscript, we hypothesize that animals living in barely anthropized landscapes should be little constrained in their movements and selection of resting site, and thus should travel from and to resting sites in a rather unstructured way (as illustrated in *Figure 1a*). Conversely in anthropized landscape, where resting and foraging sites are rarer, and transit from one to the other is more constrained, resting sites should become important in connecting home ranges' sectors together (*Figure 1b*). We tested this prediction by studying the wild boar (*Sus scrofa*) as model species, at the scale of the European continent.

In Europe, wild boars occupy a wide diversity of landscapes, along the widest possible gradient of anthropization. They equally thrive in remote forests, swamps and mountains, across agricultural areas, at the fringes of cities and even within them (Massei et al. 2015). The success and current geographic and demographic expansion of this species is in great part attributed to its impressive behavioral flexibility, and capacity to adjust to environmental constraints. Wild boars have been shown to modify their displacement rate and home range size to the level of anthropization, and to the risk of anthropic human disturbance (Sodeikat and Pohlmeier 2007; Podgórski et al. 2013; Stillfried et al. 2017). They also adjust both their temporal patterns of activity (Podgórski et al. 2013; Johann, Handschuh, Linderoth, Dormann, and Arnold 2020) and where they rest (Maillard and Fournier 1995; Fradin and Chamaillé-Jammes 2023) to avoid encounters with human.

Specific needs in terms of resting site selection are low in wild boars, but sufficient vegetation cover is required for concealment (Spitz and Janeau 1995), and wild boars frequently revisit resting sites that they have previously visited (Boitani et al. 1994; Morelle et al. 2015). Their resting behavior is thus spatially structured, and is constrained by the availability and spatial distribution of the areas where resting is possible. In addition, the spatial layout of their resting sites in the landscape might also constrain their movement patterns. Wild boars frequently re-utilize the same path and areas for transit and foraging (Morelle et al. 2015), and their movement patterns may be structured by important resting sites, foraging sites and/or corridors used for transit. When anthropization is low, animals should be able to travel quickly and rather linearly between foraging areas. In this context, resting sites should only be selected for their intrinsic qualities, and in particular for their safety. As anthropization increases and constrains movements, animals should increasingly struggle to move from one foraging area to the next. Then, wild boars could select resting sites not only for their safety, but also to use them like “stepping-stones”, to move across their home range. The relative importance of the resting sites, compared with the sites used for activity, in the connectivity of the animals’ movement patterns might thus be affected by anthropization.

In this article, we studied wild boars’ behavior across the European continent to shed light on how wild boars utilize their resting sites and move between them, along a wide gradient of human activity levels. After studying how tree cover and anthropization levels affect resting site selection and revisitation patterns, we used the betweenness, a metric of centrality calculated from movement networks, to test whether the contribution of resting sites to the connectivity of animals’ movement patterns increases as anthropization increases.

## 2 Materials & methods

### 2.1 Data preparation

#### 2.1.1 GPS data preparation

Movement data sets were collected through Euroboar, the European collaborative initiative for research on wild boars’ movement ecology, as part of Euromammals (<https://euromammals.org/>; Urbano et al. 2021). These data were supplemented with additional tracking data collected by two local hunting federations from Southern France (Fédérations Départementales des Chasseurs du Tarn et de la Haute-Garonne), and by the CEFÉ-CNRS research unit, Montpellier, France. We subsampled the GPS tracks to a resolution of one location every 60 min and we linearly interpolated missing locations whenever data gaps were isolated and not exceeding 150 min. Some animals had been tracked only every 120 min for parts, or all, of their tracking period. Instead of interpolating these data every 60 min, we generated a second dataset,



with GPS locations subsampled to one location every 120 min, and linearly interpolated whenever data gaps did not exceed 150 min, to complement the data sampled every 60 min.

Many animals from Euroboar were part of the same social group and stayed together for parts, or all, of their tracking period. To ensure tracks' independence, we discarded one individual per dyad that had spent more than 10% of their tracking period in close proximity (50 m). Besides, studying the dynamics of resting sites' utilization only makes sense for stationary behavioral phases, over stable home ranges. We computed the net square displacement of each animal to identify any non-stationary use of the landscape, and trimmed the portions of the GPS tracks corresponding to the animal remaining more than 15 km from the first (or the last) location in the survey, always keeping the longest stationary phase available.

### 2.1.2 *When did the wild boars rest?*

Although most individuals were exclusively nocturnal, a non-negligible proportion of them was not. To identify when the wild boars were at rest each day, we classified the GPS data between two behavioral modes: activity and resting. To do so, we used the succession of step lengths and turning angles calculated from the GPS tracks to associate a behavioral mode to each GPS location, with a Hidden Markov Model (HMM; Michelot et al. 2016). We did this independently for the data sampled every 60 min, and for the data sampled every 120 min, so that whenever 60min-sampled data was lacking, we could use the categorization obtained from the 120 min sampled data to fill the gaps. The relevance of the categorization between behavioral states could be visually validated using actimetric data, which was available from Euroboar for 26% of the individuals (Appendix 1).

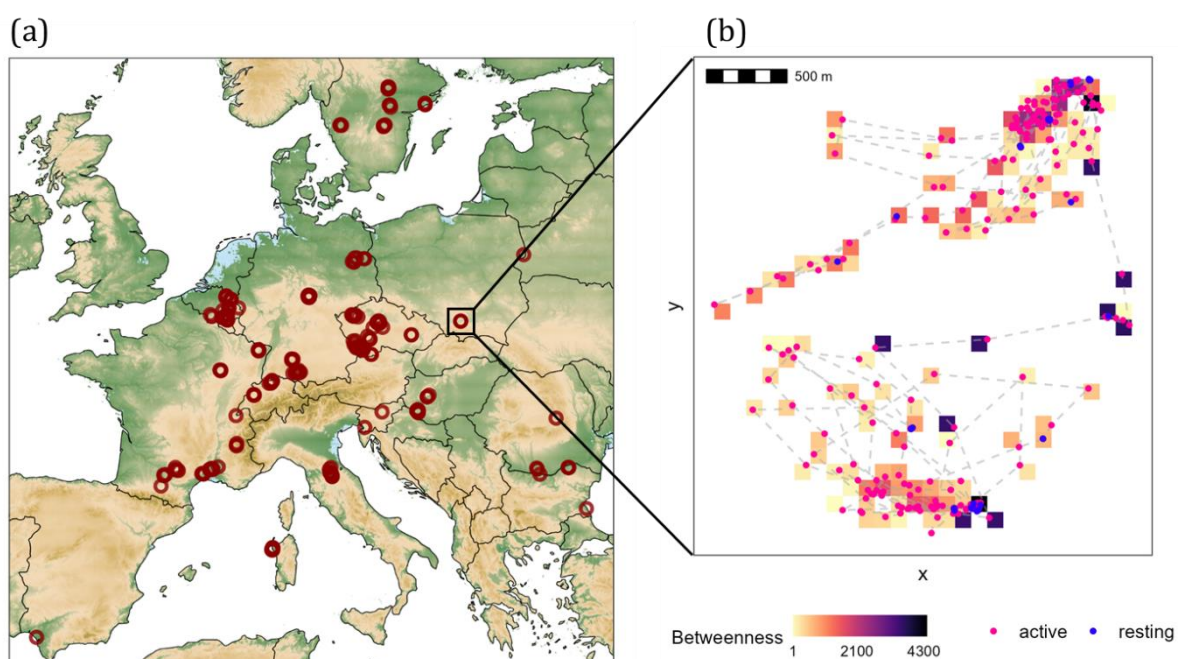
### 2.1.3 *Where did the wild boars rest?*

As revealed by both the HMMs' output and the actimetric data, the wild boars consistently exhibited monophasic activity patterns (Appendix 1). This means that they organized each 24-hour cycle between one active phase and one resting phase, although these phases could sometimes be scattered with short bouts of respectively inactivity and activity. For each animal and each date, we identified a single resting site (hereafter RS), that corresponded to the location where the animal had been spending most (if not all) of its resting phase. The method we followed is described in more detail in Appendix 1.

### 2.1.4 *Summary of the data available*

The survey periods available in the dataset were extremely variable (ranging from one month to three years). Animal movement networks' metrics being sensitive to the duration of the tracking period, we standardized the survey periods by splitting each wild boar's data by month. We thus considered separately each "individual-month", in the network analysis. Because some

gaps remained in the dataset despite the interpolation of the data, we could not identify a RS for every date. We excluded any individual-month for which a RS could not be identified every single day. We computed the monthly home ranges of each animal, defined as the contour of the 95% utilization distribution, using a standard kernel density approach, estimated from the active GPS locations. Four of them were disproportionately large, and obviously corresponded to non-stationary phases that we had failed to exclude in the data preparation stage. We removed the corresponding individual-months from the dataset. After this process, we were left with ~905,000 data points (~847,000 and 58,000 with the sampling frequencies of respectively 60 and 120 min) corresponding to 1340 individual-month. These corresponded to 275 wild boars (162 females and 113 males), distributed between 50 populations from 13 countries (*Figure 2a*). These data were collected between 2009 and 2022.



**Figure 2.** (a) Sampling location of the wild boars (red circles) considered in the study. (b) Example of a movement network corresponding to one individual wild boar's monthly movements. Blue dots represent resting sites' locations while pink dots represent the GPS locations corresponding to activity. The dashed grey line represents the animal's path. The tiles correspond to the nodes of the movement network obtained by laying the animal's trajectory over a 100-m resolution raster grid, as described in Bastille-Rousseau et al. (2018). The color of the tiles indicates their betweenness, calculated with the R package *moveNT* (Bastille-Rousseau, 2023).

### 2.1.5 Environmental variables

Forest patches and dense vegetation in general are known to be favorable for resting wild boars, and we thus expected tree cover to influence the spatial organization of the wild boars'

RSs. We used Copernicus' high-resolution layer on tree cover density (TCD; <https://land.copernicus.eu/pan-european/high-resolution-layers/forests>), a freely available geographic layer derived from satellite imagery, at the European scale. TCD gives a percentage of tree cover with a resolution of 100m, which allows taking into account even small patches of forest, where wild boars may select RSs (Salvatori et al. 2022). We used the TCD layers available for the years 2012, 2015 and 2018, to match more closely the conditions experienced by each wild boar. In addition, we described the level of human activity in the landscapes in which the wild boars rested, using the Human Footprint Index (HFI) map of 2009, downloaded from the NASA/SEDAC website (Venter et al. 2018). This global proxy of the cumulative human pressure on the environment, is given with a spatial resolution of 1 km<sup>2</sup> as a value ranging from 0 (untouched habitat) to 50 (heavily anthropized habitat), and accounts for multiple factors including human population density, infrastructures, and landscape modification by agriculture (Venter et al. 2016; Venter et al. 2018).

## 2.2 Spatial analysis of resting sites

### 2.2.1 Selection of resting sites

We first explored how the wild boars' selection of RSs was influenced by the TCD and the HFI. We used one RS and one randomly selected active GPS location per day to represent landscape use for respectively resting and activity. We simulated landscape availability by generating 10 random locations per used location, within the animals' monthly home range, which we enlarged with a 1 km buffer to include the habitats that were accessible but avoided by the wild boars. We then used a resource selection function (RSF), fitted using a generalized linear mixed model (GLMM) with a binomial distribution of errors. The response variable was the type of location (used vs. available) and the predictors were the HFI, the TCD, the behavioral state (resting or active), and the sex of the animal, all in interaction with each other. The individual's identity and the population were included as nested random intercepts. Selection ratios were then calculated, following Chamaillé-Jammes (2020), to quantify habitat selection (selection ratio above one) and avoidance (selection ratio below one). We used the k-fold cross-validation method described by Boyce et al. (2002) for model fit assessment. This method uses the Spearman-rank's correlation as the performance metric. We reported the average Spearman-rank correlation and standard error obtained for 20 model replications, with 5 folds, and 10 bins of RSF scores.

### 2.2.2 Number of visits to resting sites

Wild boars often revisit the same places over time for resting. For each animal-month, we evaluated how often the same area was used as a RS. We did so by laying out the RSs over a raster grid of a resolution of 100 m, and counting the number of RSs within each cell. This resolution fitted the scale of the RSs' clusters across individuals by visual assessment (see a full justification

of the choice of the raster grid resolution in Appendix 2). We explored the influence of HFI and TCD on the number of visits to RSs by fitting a GLMM, utilizing a zero-truncated Poisson regression. The response variable was the number of visits to a RS, and the predictors were the TCD, the HFI, and the animal's sex, all in interaction between each other. Individuals' identities nested within populations were incorporated as random intercepts. Model fit was evaluated using the marginal Nakagawa's  $R^2$  (Nakagawa and Schielzeth 2013).

## **2.3 Contribution of resting sites to the connectivity of movement networks**

### *2.3.1 Construction of the movement networks*

For each individual-month, we constructed a movement network using the framework developed by Bastille-Rousseau et al. (2018). We laid out the trajectories over raster grids of a resolution of 100 m, and considered each cell containing GPS location as a node in the movement network (see a justification of the choice of the raster grid resolution in Appendix 2). We considered two types of nodes: the resting nodes, containing at least one RS, and the activity nodes, not containing any RS. In these networks, the edges between nodes are defined by the steps between GPS locations in the tracking data (see one example in [Figure 2b](#)). We calculated the betweenness of each node by using the R package *moveNT*, developed by Bastille-Rousseau (2023). This node-level metric corresponds to the number of shortest paths between two nodes passing through a node of interest. It measures the importance of this node in the overall connectivity of the network (Jacoby et al. 2012). We assessed the relative importance of the RSs, compared with activity sites, in the movement networks' connectivity. To do this, we calculated the ratio of the mean betweenness of the resting nodes over the mean betweenness of the activity nodes, in each network. This resulted in an index of contribution of the RSs to movement networks' connectivity (hereafter called RSs' contribution to connectivity).

### *2.3.2 Analysis of the drivers of resting sites' contribution to connectivity*

We used a GLMM to evaluate the effect of landscape variables on the RSs' contribution to connectivity. As predictor variables, we used the overall levels of anthropization and tree cover experienced by each individual-month. These were expressed as the mean value of respectively HFI and TCD, within the monthly home range, which we enlarged with a 1 km buffer to account for the habitats that were accessible but avoided by the wild boars. We considered these two variables in interaction with the sex. Exploration of the data revealed that the home range size had a strong non-linear relationship with RSs' contribution to connectivity, so we incorporated it as an additive polynomial predictor in the model. Finally, we considered the population and individual identities as nested random intercepts. We evaluated the fit of the model by using the marginal Nakagawa's  $R^2$  (Nakagawa and Schielzeth 2013).

### 3 Results

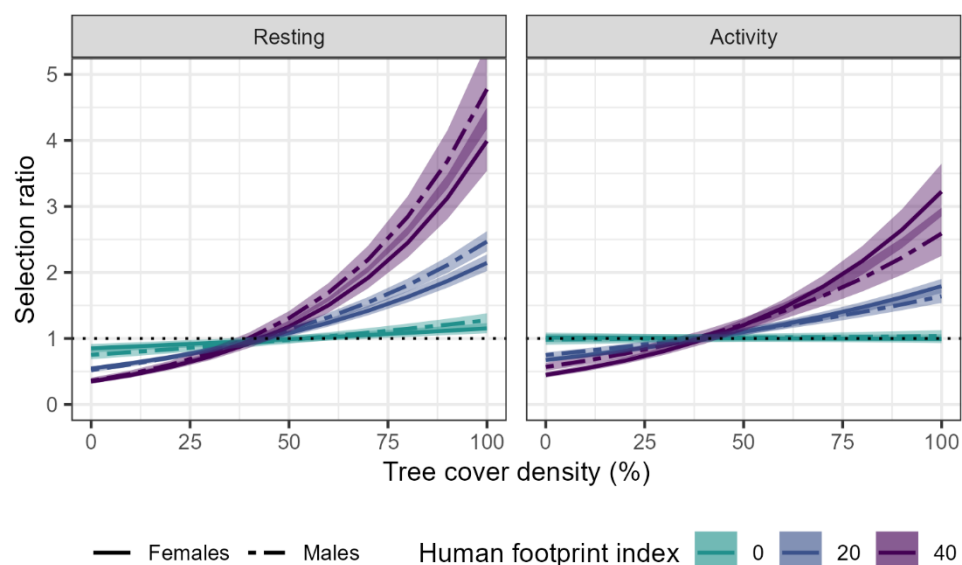
#### 3.1 Selection of resting sites

All the possible combinations of HFI and TCD were available within the dataset, and the animals made some use of this wide diversity of habitats, both for resting and activity (see details in Appendix 3). As expected, wild boars' sensitivity to TCD for habitat selection was highly dependent on the level of HFI (*Figure 3; Table 1*). At low HFI, wild boars showed virtually no selection for sites with greater cover (selection ratio  $\approx 1$ ), particularly during the active phase. During resting, wild boars slightly selected for higher TCD, and avoided low TCD, even in the least anthropized areas. At high HFI, during the active phase and even more during the resting phase, wild boars strongly selected for areas with high TCD, and strongly avoided areas with low TCD (*Figure 3; Table 1*). There was small but significant sex differences, selection for TCD being more sensitive to HFI in males than in females (*Figure 3; Table 1*).

Variable	$\beta$	SE	z-value	p-value
Intercept	-2.2898	0.0365	-62.7504	<0.001
Male	-0.0302	0.0492	-0.6138	0.54
Resting	-0.1747	0.0369	-4.7298	<0.001
HFI	-0.0204	0.0017	-12.2685	<0.001
TCD	-0.0002	0.0004	-0.4173	0.68
Male x Resting	-0.0935	0.0603	-1.5505	0.12
Male x HFI	0.0067	0.0027	2.5148	0.01
Resting x HFI	-0.0019	0.0020	-0.9321	0.35
Male x TCD	0.0007	0.0008	0.9678	0.33
Resting x TCD	0.0032	0.0006	5.5666	<0.001
HFI x TCD	0.0005	0.0000	17.1311	<0.001
Male x Resting x HFI	-0.0029	0.0033	-0.8988	0.37
Male x Resting x TCD	0.0015	0.0009	1.6101	0.11
Male x HFI x TCD	-0.0001	0.0000	-2.7457	<0.01
Resting x HFI x TCD	0.0000	0.0000	0.9305	0.35
Male x Resting x HFI x TCD	0.0001	0.0001	1.9372	0.05

'Female' and 'Active' are respectively the default sex and behavioral state. 'Male' and 'Resting' are the alternatives.

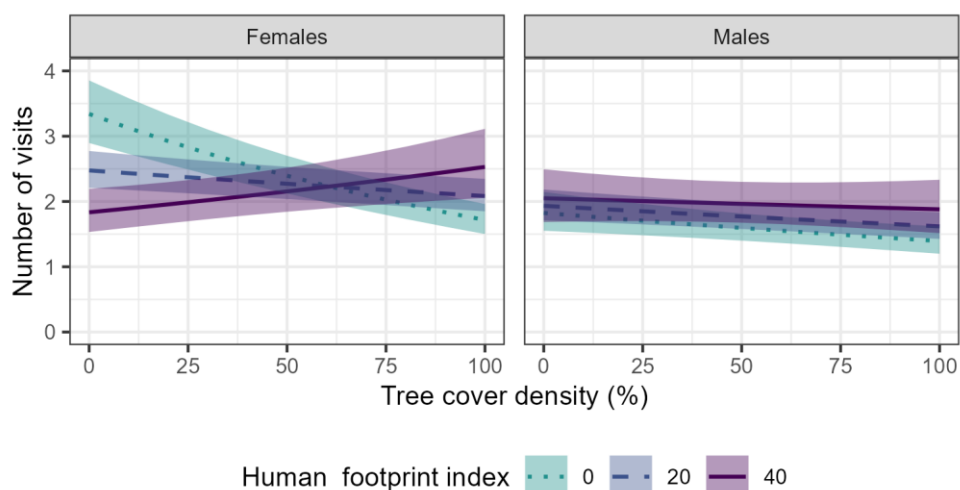
**Table 1.** Parameters and statistics of the model estimating the selection ratio for areas of varying levels of tree cover density (TCD) and human footprint index (HFI). The 5-fold cross-validation performance score (Spearman-rank correlation) of the model is  $0.98 \pm 0.03$  SE.



**Figure 3.** Selection ratio for areas of increasing tree cover density as a function of the human footprint index, for male and female wild boars, during resting and activity. Sites are selected for when the selection ratio is above one, avoided when it is below one. Color ribbons show the 95% confidence intervals.

### 3.2 Number of visits to a resting site

Over a month, the number of visits to a RS was dependent on the TCD and HFI at the site, and on the sex of the animal (Figure 4; Table 2). At low HFI, females mostly revisited the sites with the lowest TCD (Figure 4). This pattern was reversed at high HFI, when females revisited sites with high TCD more than those with lower cover (Figure 4). In contrast, the number visits to a RS by males was not affected by the TCD or HFI level of this site (Figure 4). Note however that the predictor variables included in the model (HFI, TCD and sex) poorly explained the variability observed (marginal  $R^2 = 0.06$ ; Table 2), which was mostly accounted for by individual's and population's factors (conditional  $R^2 = 0.6$ ; Table 2).



**Figure 4.** Number of visits to resting sites as a function of tree cover density and human footprint index, for male and female wild boars. Color ribbons show the 95% confidence intervals.

Variable	$\beta$	SE	z-value	p-value
Intercept	1.2063	0.0730	16.5353	<0.001
Male	-0.6049	0.0945	-6.4041	<0.001
HFI	-0.0150	0.0029	-5.0820	<0.001
TCD	-0.0067	0.0007	-9.5789	<0.001
Male x HFI	0.0179	0.0044	4.0232	<0.001
Male x TCD	0.0040	0.0011	3.5460	<0.001
HFI x TCD	0.0002	0.0000	5.6869	<0.001
Male x HFI x TCD	-0.0002	0.0001	-3.0091	<0.01

'Female' is the default sex. 'Male' is the alternative.

**Table 2.** Parameters and statistics of the model estimating the number of visits to resting sites with varying levels of tree cover density (TCD) and human footprint index (HFI). The conditional  $R^2$  is 0.6 and the marginal  $R^2$  is 0.06.

### 3.3 Contribution of the resting sites to movement network’s connectivity

The RSs’ contribution to connectivity was significantly lower for animals with large home ranges compared to animals with small home ranges (Figure 5; Table 3). It was however generally well above one, indicating that RSs serve as connectivity hotspots to move within the home range, more than sites of activity. This was particularly true in home ranges that had little tree cover, for which RS contribution to connectivity was greater (Figure 5; Table 3). An effect of the level of anthropization was only noticeable through a tendency of the RS contribution to connectivity to increase with HFI for females that had home ranges with important tree cover (Figure 5; Table 3). We note however that the lack of statistical significance (at alpha = 0.05) of this pattern could be

linked to the moderate correlation (Pearson's product-moment correlation = -0.59; Appendix 3) observed between TCD and HFI values, which lead to inflated standard errors of the estimates.

Variable	$\beta$	SE	z-value	p-value
Intercept	3.2684	0.4068	8.0349	<0.001
Male	-0.7537	0.5584	-1.3499	0.18
mean HFI	-0.0249	0.0203	-1.2286	0.22
mean TCD	-0.0180	0.0071	-2.5202	0.01
(Home range size) <sup>1</sup>	-12.3769	1.4219	-8.7046	<0.001
(Home range size) <sup>2</sup>	7.8101	1.2317	6.3409	<0.001
Male x mean HFI	0.0298	0.0305	0.9744	0.33
Male x mean TCD	0.0162	0.0111	1.4587	0.14
mean HFI x mean TCD	0.0008	0.0005	1.8375	0.07
Male x mean HFI x mean TCD	-0.0010	0.0008	-1.3176	0.19

<sup>1</sup>'Female' is the default sex. 'Male' is the alternative.

**Table 3.** Parameters and statistics of the model estimating the contribution of the resting sites' contribution to connectivity for home ranges of varying levels of tree cover density (TCD) and human footprint index (HFI). The conditional  $R^2$  is 0.3 and the marginal  $R^2$  is 0.11.

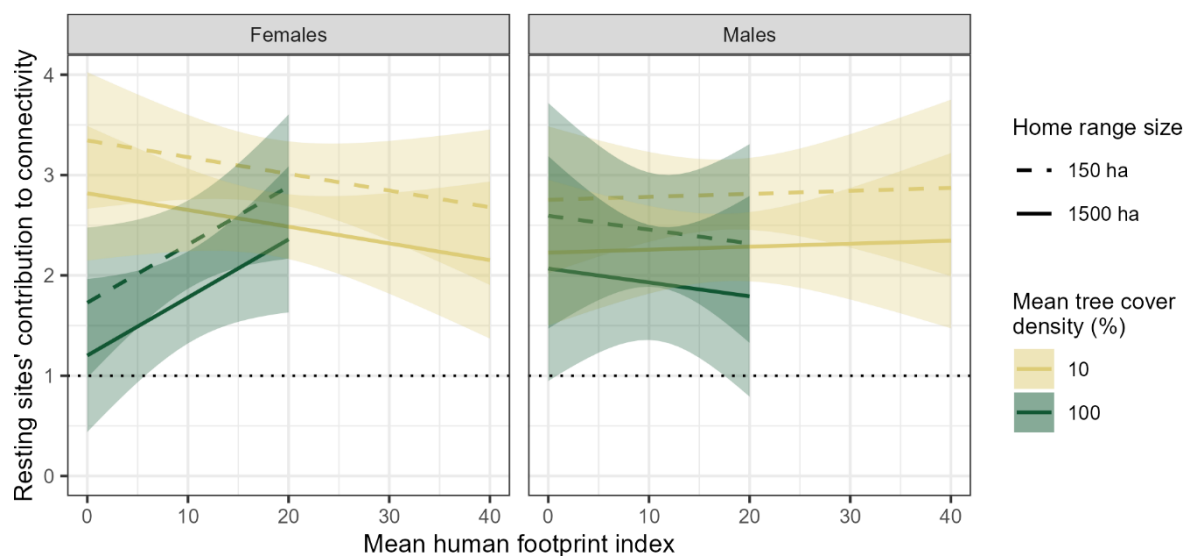
## 4 Discussion

For many animals, the decision about where to rest every day is constrained by the spatial layout of suitable resting sites (RSs). In addition, where resting occurs itself constrains the subsequent movements of an animal in the landscape. Anthropogenic pressures are susceptible of affecting both where animals may rest, and where they may be active (notably foraging and in transit) in the landscape, but overall tend to restrict daily movements (Tucker et al. 2018). This should thus change the contribution of daily RSs to the overall connectivity of movements within home ranges (*Figure 1*). Here we provided a test of this hypothesis, we believe for the first time. We did so by leveraging a continental-scale movement database of a species that is found to thrive across the full gradient of anthropization: the wild boar.

We first described how wild boars select their RSs according to the human footprint index (HFI) and tree cover density (TCD). Interestingly, we found that in the areas not impacted by human activity, while the wild boars slightly selected sites with higher TCD for resting, they used the available TCD at random for activity. This supports the hypothesis that wild boars under low anthropic pressure are little constrained in their use of the habitat and should be able to travel unrestrictedly from and to RSs (like in *Figure 1a*). Unsurprisingly, in areas with high HFI, wild boars strongly selected high TCD and avoided low TCD during activity, and even more strongly during resting. This confirms, on a scale never investigated before, that wild boars adjust to the



level of human pressure by seeking the cover of vegetation, and particularly so when they select where to rest. Vegetation cover being rarer and more fragmented where human pressure is high, wild boars are thus more constrained in how they can move around and where they can rest, in anthropized landscapes.



**Figure 5.** Resting sites' contribution to connectivity as a function of the mean human footprint index (HFI) and mean tree cover density (TCD) of the home ranges, for male and female wild boars. We did not make predictions for home ranges with high HFI and high TCD, these being virtually non-existent in the data.

Female wild boars were found to adjust their pattern of revisitation of RSs according to HFI and TCD. In low HFI and high TCD, where suitable RSs are presumably commonplace, they rarely revisited the same RSs. In low HFI and low TCD, where concealed spots are likely more sporadic, females frequently came back to previously visited sites for resting. Where HFI was high, female wild boars did not revisit frequently the sites with low TCD (that were avoided according to the RSF), but often revisited the same spots for resting, within high TCD areas. This pattern of RS revisitation suggests that where safe, concealed RSs are rare, female wild boars compensate this scarcity by targeting well-known RSs to reuse over time. The males showed a different pattern of RS revisitation, as they rarely came back to rest to previously visited RSs. This was probably related to the fact that male wild boars travel across greater distances and have larger home ranges compared to females, which means that they are more likely to come across new suitable RSs. However, the males' tendency to revisit RSs was not affected by HFI nor TCD, which cannot be explained by their movement patterns only. We hypothesized that being solitary, male wild boars may find concealment in even small patches of vegetation, where a female's sounder would simply not fit. This may explain how males, contrarily to females, manage to rest in areas with

either low vegetation cover or high human pressure without relying on a small number of frequently visited RSs. Nevertheless, male wild boars might adjust their RSs' revisit rate to anthropic pressure on a finer scale than the 1 km<sup>2</sup> resolution of HFI, as they do in Mediterranean France (Fradin and Chamaillé-Jammes 2023).

Wild boars manage to find RSs even in anthropized landscapes by selecting high TCD, and in the case of females, by revisiting the same RSs over time. This flexibility is surely key to the ability of this species to live across the widest gradient of anthropization. However, in anthropized landscapes, selecting a reduced number of RSs possibly scattered between few suitable patches surely increases the risk for the RSs spatial layout to constrain movement patterns. We used a movement networks' metric, the betweenness, to evaluate whether the importance of RSs in the utilization pattern of the landscape differed between home ranges with contrasted overall levels of anthropization. For each individual and each month, we compared the mean betweenness of the areas with and without RSs, among those where we had observed the animal. As the betweenness is an indicator of the importance of a given location in the overall connectivity of movement networks in sedentary animals (Jacoby et al. 2012), this allowed us to evaluate the importance of the areas used for resting in connecting, through the movements occurring between them, the different sectors of home ranges (Wittemyer et al. 2019). The obtained ratio (that we called RSs' contribution to connectivity), was highly variable between individuals, but always greater than one, indicating that the RSs were always more important to the connectivity of the whole movement patterns than the sites where wild boars were active.

The size of the home range showed a strong negative correlation with the RSs' contribution to connectivity. We hypothesize that this was an artefact due to some long-distance transits remaining in the dataset. Despite our efforts to exclude the individuals that we identified as non-stationary, some of the large home ranges considered probably resulted from long-distance transits that we failed to get rid of. Non-stationary use of the landscape should produce high modularity in movement networks, with extreme betweenness in the nodes connecting the modules together (López-Calderón et al. 2023). As these nodes are more likely to be frequented during the animal's movements, and thus to be active nodes, such movement patterns are expected to have low RSs' contribution to connectivity, and could explain the effect of home range size on RSs' contribution to connectivity.

We observed a slight but significant negative effect of the mean TCD on the RSs' contribution to connectivity. This means that for the wild boars living in highly forested landscapes, RSs were less important in connecting different sectors of the home range together, than for the wild boars living in landscapes with little forest. This result suggests that animals having access to enough vegetation cover are able to move between RSs and foraging areas quite unrestrictedly, not

requiring RSs to serve as “stepping-stones” to move across their home range. Conversely, when vegetation cover is limited, wild boars are more constrained to rest at specific places in order to connect, through their movement, different parts of the landscape. Such highly connected RSs may be seen as bottlenecks in the movement patterns of the animals (Wittemyer et al. 2019). One of the most important mechanisms through which anthropization affects the landscape is the destruction and fragmentation of natural habitats, including forests, which explains the non-negligible collinearity we observed between the mean TCD and mean HFI in the wild boars’ home ranges. This suggests that the sensitivity of RSs’ contribution to connectivity to the amount of tree cover in the landscape should be at least in part related to anthropic modifications of the landscape.

Aside this effect of the amount of tree cover, we did not observe the expected effect of the mean HFI on the RSs’ contribution to connectivity. Interestingly however, in females with highly forested home ranges, it seemed that the level of anthropization was positively correlated with the RSs’ contribution to connectivity. This trend suggests that the layout of females’ RSs may structure how they use the landscape in ways that change in response to anthropic factors unrelated with the amount of tree cover. This could maybe result from the effect of direct anthropic disturbances, as these are known to affect females’ habitat selection more than that of males (Saïd et al. 2012). The partial collinearity between mean TCD and mean HFI, which resulted in inflated standard errors, could explain the lack of statistical significance for this interaction. Besides, few individuals in the dataset had home ranges with high values of mean HFI, possibly participating to hide an existing effect.

Overall, our results suggest that the RSs’ contribution to connectivity is affected by the level of anthropization, mostly (but maybe not only) through the reduction of vegetation cover in anthropized landscapes. The RSs’ contribution to connectivity being affected by the mean TCD in the wild boars’ home ranges suggests that wild boars living in areas with little vegetation cover may be the most constrained in their use of the landscape. We believe that low mean TCD generally corresponds to fragmented habitats scattered with small patches of trees. In such fragmented environments, the permeability of the landscape to large animals’ movements is reduced (Gehring and Swihart 2003; Jayadevan et al. 2020; Mumme et al. 2023). Suitable RSs might also be more sporadic, due to the increased proximity of any site to a forest edge. In such conditions, the use of certain portions of the landscape could be restricted to the vicinity of suitable RSs and movements across the landscape could be constrained by the spatial layout of the RSs, which would act like “stepping-stones”.

Wild boars fine-tune their resting behavior in a variety of ways to adjust to the landscape they live in. When they select resting sites, they adjust to locally high levels of anthropization by

targeting patches with dense vegetation cover. Females also revisit suitable resting sites over time in low vegetated or in anthropic landscapes, and such adjustments to human pressure also probably occur in males, on a finer scale (Fradin and Chamaillé-Jammes 2023). Although we did not find definitive evidence that the importance of wild boars' resting sites in the connectivity of their overall movement patterns depends on the level of anthropization (as hypothesized in *Figure 1*), we have found that it is sensitive to the amount of vegetation cover in the home range. The spatial layout of their resting sites seems to constrain more the wild boars' movements when they live in overall poorly vegetated areas, than when they have access to extensive vegetation cover. As anthropization is often associated with a reduction of tree cover, it is however likely that human activity indirectly affects how resting sites' locations influence movement patterns, in wild boars. More generally, in anthropogenic landscapes, and in particular where dense vegetation is rare, the availability of suitable resting sites may be of crucial importance to allow animals to use the wholeness of the landscape.

**Acknowledgments:** This work was carried out with the support of the EUROMAMMALS/EUROBOAR collaborative project (<https://euromammals.org/euroboar/>). We are grateful to all members who supported this initiative, and to the numerous people who, over Europe, helped capturing, and tagging the animals studied in this manuscript. We also thank the people who contribute to the administration and animation of EUROMAMMALS and EUROBOAR. We are grateful to the Copernicus project, which provided the data on tree cover density (European Union, EEA - European Environment Agency).

**Author contributions:** **Gustave Fradin:** Conceptualization (equal); investigation (lead); writing – original draft (lead); writing – review and editing (lead). **Simon Chamaillé-Jammes:** Conceptualization (equal); investigation (supporting); supervision (lead); writing – review and editing (supporting).

**Tsvyatko Alexandrov, Marco Apollonio, Janosch Arnold, Grzegorz Baś, Joaquín Vicente Baños, Rudy Brogi, Eric Baubet, Jim Casaer, Simon Chamaillé-Jammes, Attila Farkas, Claude Fischer, József-Tamás Fodor, Justine Güldenpfennig, Marco Heurich, Klemen Jerina, Miloš Ježek, Petter Kjellander, Alisa Klamm, Stephanie Kramer-Schadt, Alain Licoppe, András Náhlik, Tomasz Podgórski, Sonia Saïd, Thomas Scheppers, Stefan Suter, and Tamás Tari** collected the data and shared them through the Euroboar initiative.

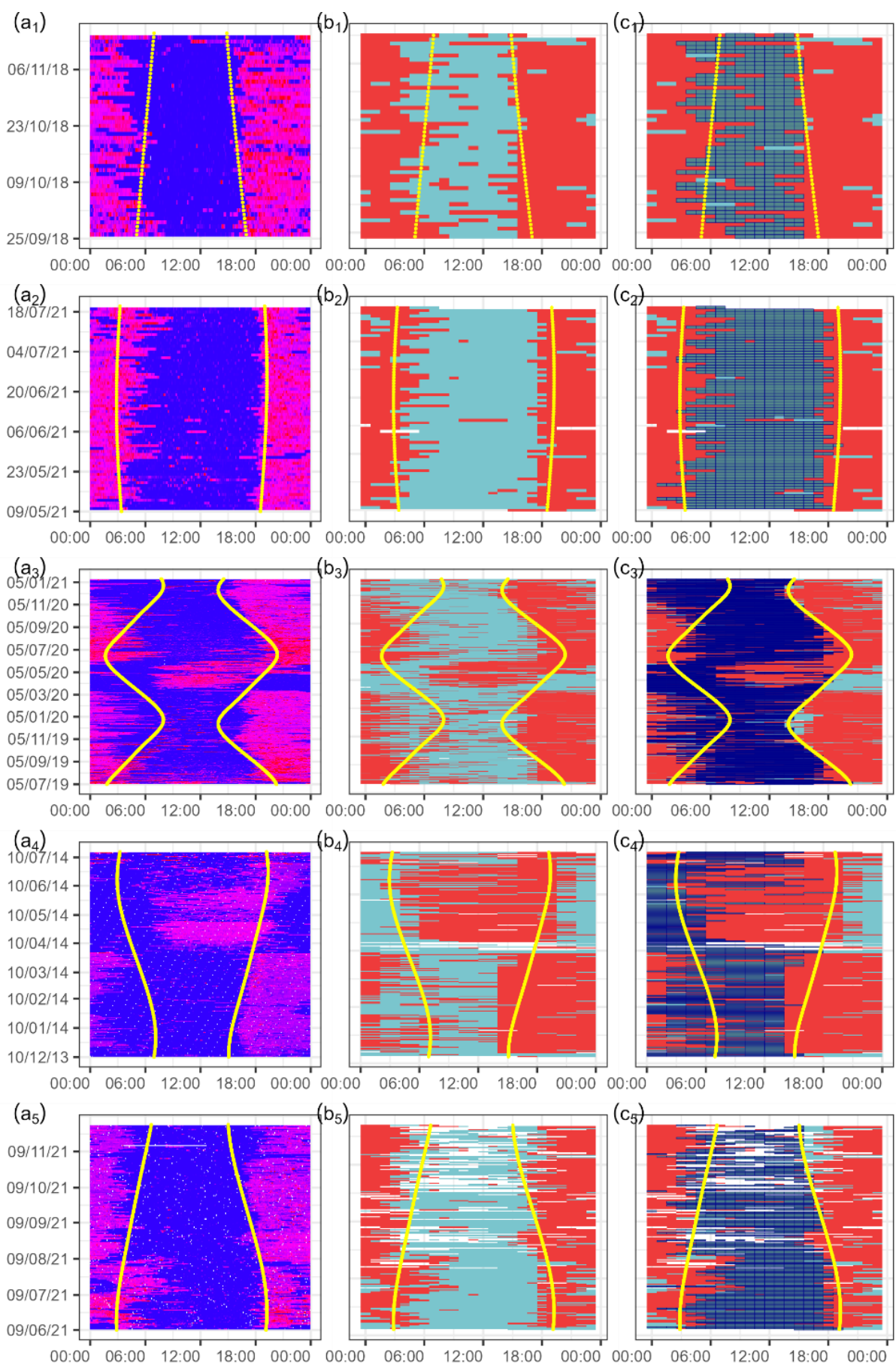
**Conflict of interest statement:** The authors declare no conflict of interest

## Appendices

### Appendix 1. Identification of resting sites

We used actimetric data, whenever they were available (26% of the wild boars), to visually validate the relevance of the output of the HMMs fitted to the GPS data (the examples for five individuals are provided in *Figure S1*). The level of similarities between the actograms (*Figure S1a<sub>1-5</sub>*) and the time series of behavioral modes identified by the HMMs (*Figure S1b<sub>1-5</sub>*) was always very high, even when GPS data was mostly sampled every 120 min (e.g., *Figure S1b<sub>4</sub>*) or patchy (e.g., *Figure S1b<sub>5</sub>*). For all the individuals, the pattern of activity was characterized by a clear monophasic pattern. Most wild boars were strictly nocturnal (*Figure S1a<sub>1,2,5</sub>*), but some exhibited a diurnal lifestyle for durations that varied from a few days to a few months (e.g., *Figure S1a<sub>4-5</sub>*). This monophasic nature of the activity patterns allowed us to identify a single resting site, every day, for each animal.

*Figure S1 (next page). Temporal patterns of activity of five wild boars, the individuals being given by rows (1-5). (a<sub>1-5</sub>) Patterns of activity observed from actimetric data. Each date (by rows) is divided into 5min slots that are colored according to their level of activity, ranging from blue (ACT = 0) to red (ACT = 255). (b<sub>1-5</sub>) Patterns of activity of the same individuals, resulting from HMMs performed on GPS data with a 60 min (sometimes 120min) sampling rate. Light blue indicates resting, and orange indicates activity. (c<sub>1-5</sub>) Same patterns as in (b<sub>1-5</sub>), with the GPS locations that were identified as part of the daily resting site highlighted with a dark blue frame. The yellow dots indicate, for each date, the times of sunrise and sunset. Times are in local time, which includes daylight savings (note the discontinuities in sunrise and sunset times).*

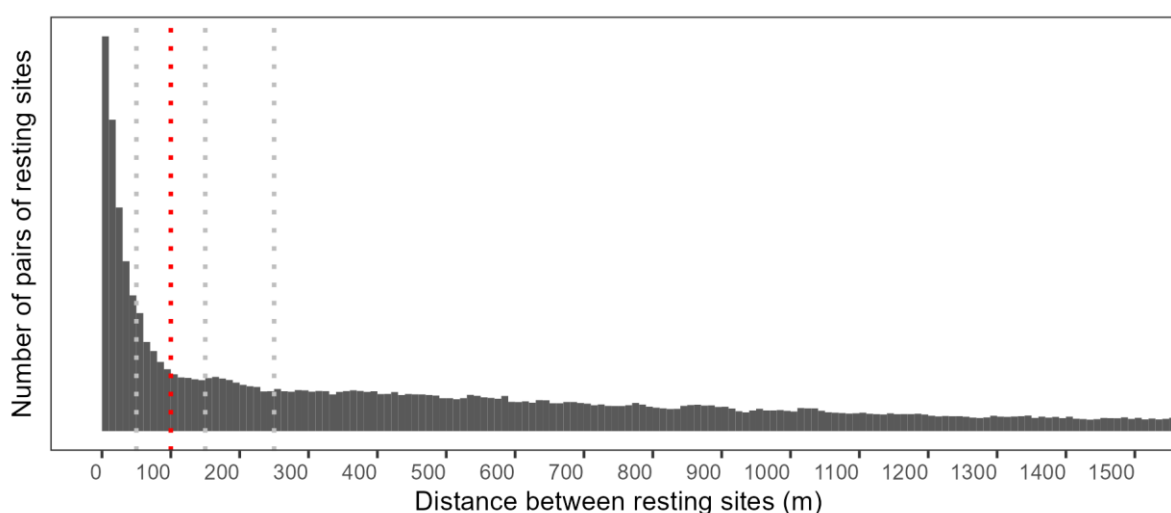


Given the important variability, both inter- and intra-individuals, in the timings of the transitions between active and resting phases, it was impossible to identify a time of the day that would always correspond to resting. Neither could we consider that the daily resting site was the place where most resting had occurred on each date, because this would have split any nocturnal resting phase between different dates. To overcome the challenge of automatically identifying daily resting sites, we had to use a more refined method. We observed that when the activity pattern was diurnal—and thus when resting occurred during the night—resting always lasted a few hours later than midnight (e.g., *Figure S1b<sub>3-4</sub>*). This ensured that the resting site used during a nocturnal resting phase could be identified from the GPS locations acquired after midnight only. This meant that the GPS locations acquired between the time of sunset and midnight were never necessary to the determination of the location of any resting site. For each individual and each date, to identify the daily resting site, we thus only considered the GPS locations labelled as resting, that had occurred between midnight and the time of sunset (*Figure S1c<sub>1-5</sub>*). We used a hierarchical clustering method with single linkage to classify them between clusters further apart than 50m. For each individual and each date, we considered that the centroid of the cluster with the most numerous GPS locations was the daily resting site.

## Appendix 2. Raster grid resolution

In this study, we laid out wild boars' movement path over a raster grid for two purposes: to quantify revisitations to resting sites, and to construct movement networks.

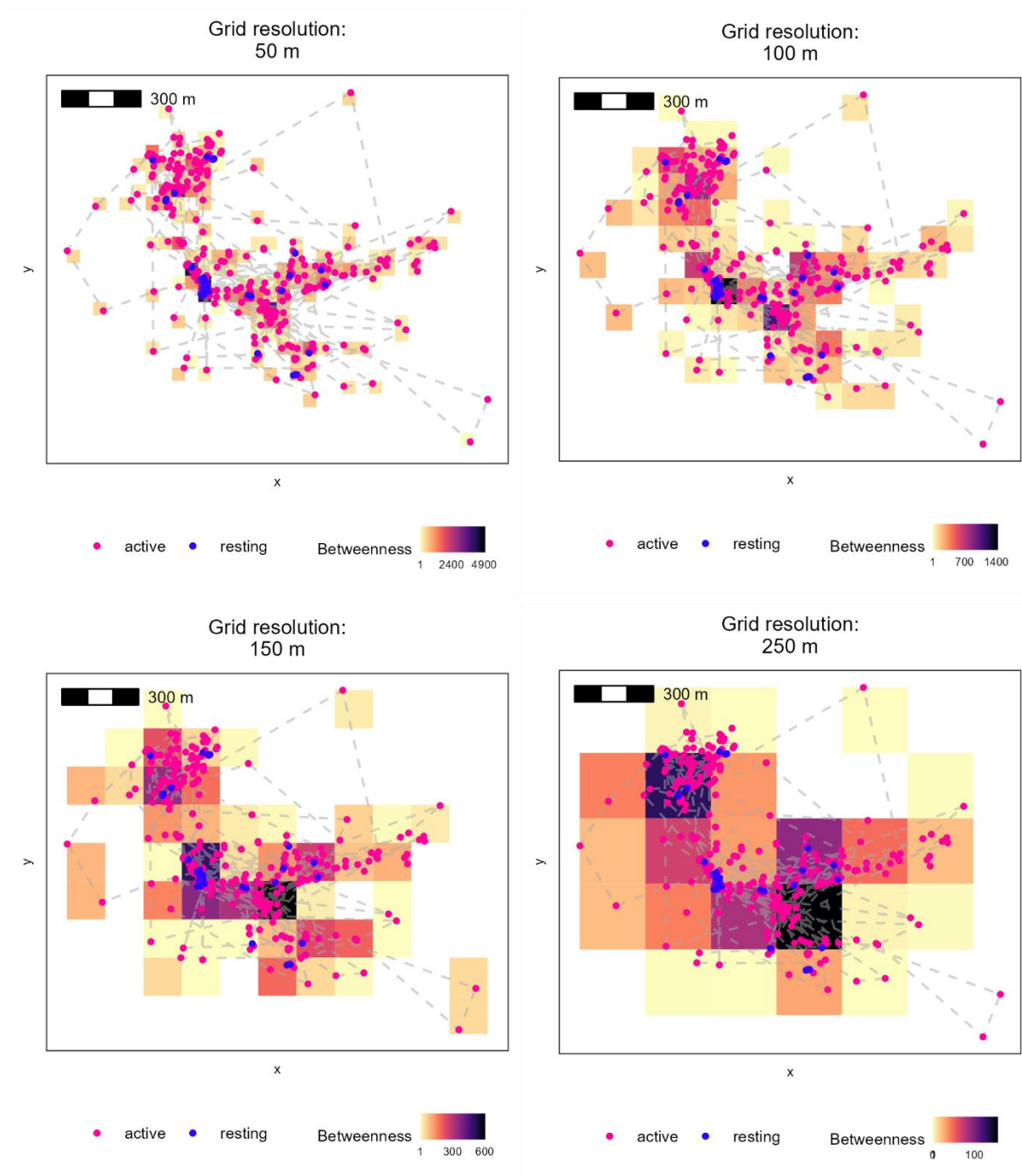
First, we evaluated how often an area was used for resting, based on the number of resting sites within each cell of a raster grid. The resolution of the grid to be used was defined according to the scale of aggregation of resting sites. This was variable between individuals. However, the distribution of the distances between the resting sites used by each wild boar showed a clear breakpoint around 100 m (*Figure S2*), suggesting that this was a biologically relevant threshold to define resting site revisitation.



*Figure S2. Distribution of the distances between resting sites used by each wild boar in the study. A red dotted line highlights the raster grid resolution used for the analysis. Grey dotted lines highlight the other resolutions we tested.*

We also used the raster grid to construct movement networks to calculate the betweenness centrality of the areas used for resting and for activity, following the method described in Bastille-Rousseau et al. (2018). The authors suggest that a relevant grid resolution to use is the median step length in the movement paths (which in our case is 170 m). However, they also point out that the network metrics are relatively stable to a variation in the raster grid resolution from the 25% to the 75% quantile of the distribution of step lengths (which in our case correspond to a resolution between 67 to 380 m). We therefore decided to use the same grid (resolution 100 m) for both analyses, i.e. to quantify the number of visits to resting sites and to construct movement networks. We checked that the results were not affected by the raster grid resolution by performing the analysis with grid resolutions of 50 m, 150 m and 250 m (illustrated in *Figure S3*).





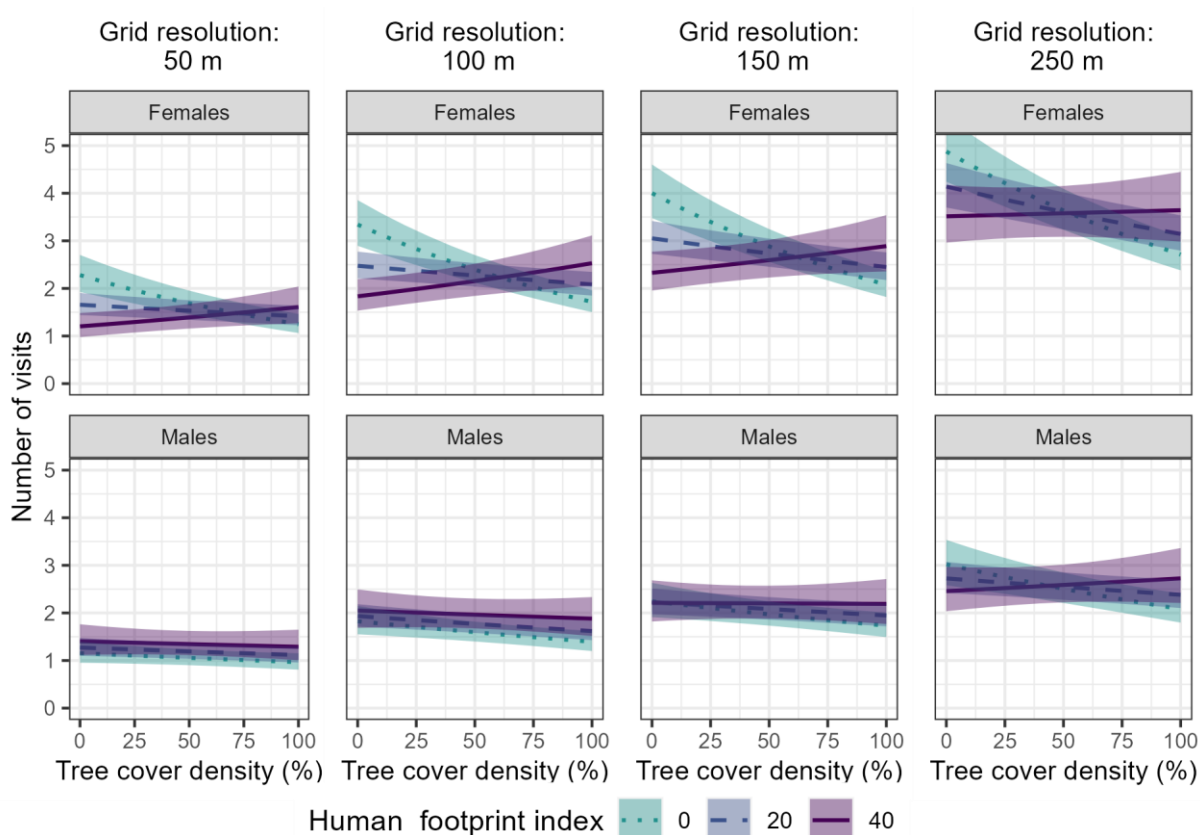
**Figure S3.** Movement network of an individual wild boar laid out over a raster grid of varying resolutions (50 m, 100 m, 150 m, and 250 m). Blue dots represent resting sites' locations while pink dots represent the GPS locations corresponding to activity. The dashed grey line represents the animal's path. The tiles correspond to the nodes in the movement network, as described in Bastille-Rousseau et al. (2018). The color of the tiles indicates their betweenness, calculated with the R package moveNT (Bastille-Rousseau, 2023).

Variable	$\beta$	SE	z-value	p-value
<b>Grid resolution: 50 m</b>				
Intercept	0.82	0.09	9.52	<0.001
Male	-0.68	0.11	-6.40	<0.001
HFI	-0.02	0.00	-4.84	<0.001
TCD	-0.01	0.00	-7.87	<0.001
Male x HFI	0.02	0.00	4.19	<0.001
Male x TCD	0.00	0.00	3.43	<0.001
HFI x TCD	0.00	0.00	4.70	<0.001
Male x HFI x TCD	-0.00	0.00	-2.73	<0.01
<b>Grid resolution: 100 m</b>				
Intercept	1.21	0.07	16.54	<0.001
Male	-0.60	0.09	-6.40	<0.001
HFI	-0.01	0.00	-5.08	<0.001
TCD	-0.01	0.00	-9.58	<0.001
Male x HFI	0.02	0.00	4.02	<0.001
Male x TCD	0.00	0.00	3.55	<0.001
HFI x TCD	0.00	0.00	5.69	<0.001
Male x HFI x TCD	-0.00	0.00	-3.01	<0.01
<b>Grid resolution: 150 m</b>				
Intercept	1.39	0.07	19.37	<0.001
Male	-0.58	0.09	-6.27	<0.001
HFI	-0.01	0.00	-4.79	<0.001
TCD	-0.01	0.00	-9.65	<0.001
Male x HFI	0.01	0.00	3.04	<0.01
Male x TCD	0.00	0.00	3.61	<0.001
HFI x TCD	0.00	0.00	5.12	<0.001
Male x HFI x TCD	-0.00	0.00	-2.34	0.02
<b>Grid resolution: 250 m</b>				
Intercept	1.58	0.07	22.32	<0.001
Male	-0.48	0.09	-5.31	<0.001
HFI	-0.01	0.00	-2.98	<0.01
TCD	-0.01	0.00	-8.76	<0.001
Male x HFI	0.00	0.00	0.72	0.47
Male x TCD	0.00	0.00	1.97	0.05
HFI x TCD	0.00	0.00	3.73	<0.001
Male x HFI x TCD	-0.00	0.00	-0.56	0.58

'Female' is the default sex. 'Male' is the alternative.

**Table S1.** Parameters and statistics of four models estimating the number of visits to resting sites with varying levels of tree cover density (TCD) and human footprint index (HFI), at four spatial resolutions (50 m, 100 m, 150 m and 250 m). The conditional  $R^2$  are respectively 0.52, 0.6, 0.68 and 0.78. The marginal  $R^2$  are respectively 0.04, 0.06, 0.07 and 0.11.

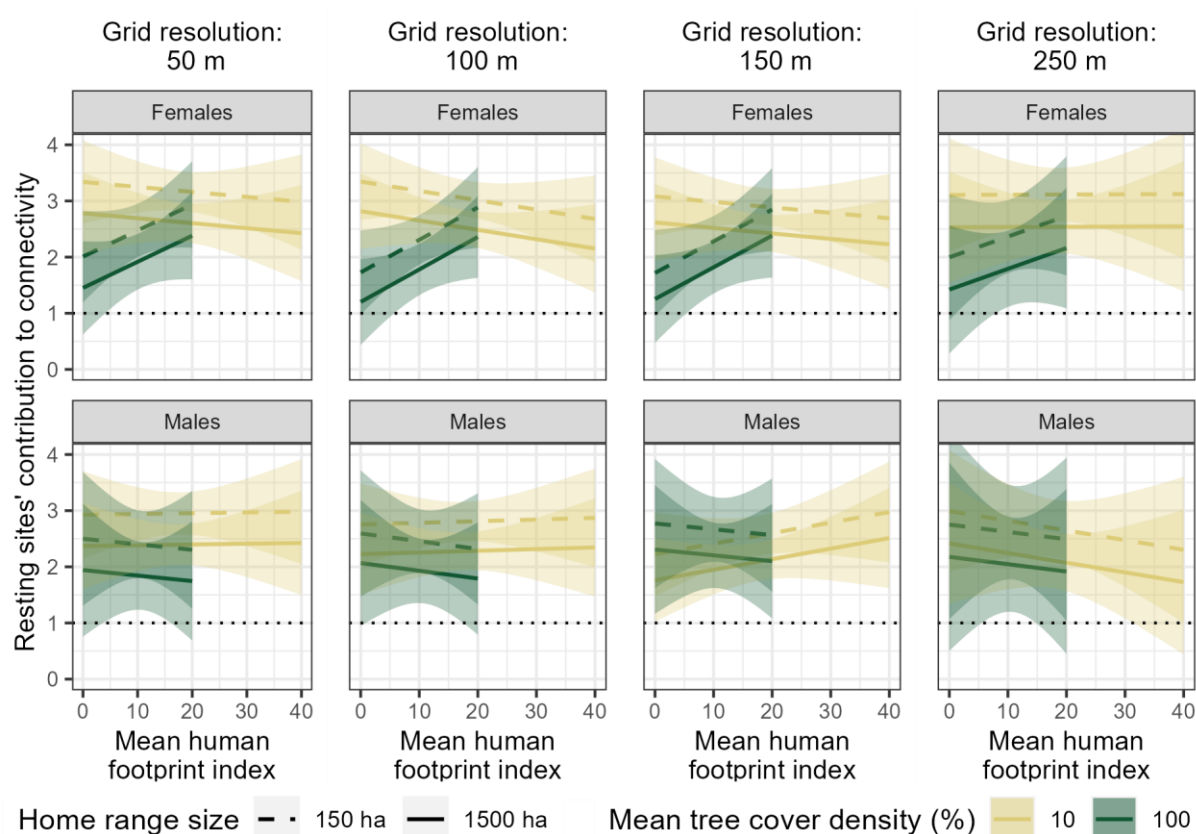
The total number of visits to resting sites increased constantly with increasing raster grid resolution, which was expected by construction. However, the effects of sex, human footprint index and tree cover density were identical for raster grid resolutions of 50 m, 100 m, and 150 m (*Figure S4; Table S1*). In the case of males, model predictions suggested that when using a resolution of 250 m, an effect of the interaction between the human footprint index and the tree cover density could emerge. This effect, however, is similar to that observed in females and does not change our interpretation of the results. These results show that a raster grid resolution of 100 m does not produce specific results compared to resolutions between 50 m and 250 m. Given the distribution presented in *Figure S2*, 100 m seems like a relevant raster grid resolution to use to quantify the number of visits to resting sites.



**Figure S4.** Number of visits to resting sites as a function of tree cover density and human footprint index, for male and female wild boars, calculated as the number of resting sites within each cell of raster grids of varying resolutions (50 m, 100 m, 150 m, and 250 m). Color ribbons show the 95% confidence intervals.

The results of the models on RSs' contribution to connectivity suggest that, as in the sensitivity analysis performed by Bastille-Rousseau et al. (2018), the value of a node's betweenness centrality (which was used to calculate RSs' contribution to connectivity) was little affected by the raster grid resolution (*Figure S5; Table S2*). The predictions of the models were similar when using raster grid resolutions of 50m, 100 m and 150m, with significant negative effects of home

range size and mean tree cover density. The effect of the mean tree cover density is not significant anymore with a raster grid resolution of 250 m, but the trends in the model predictions are similar, with a potential interaction between HFI and TCD in the females. Predictions for the males are only slightly different with resolutions of 150 m and 250 m, but the results are overall similar. These results show that constructing movement networks using a raster grid resolution of 100 m does not produce specific results compared to resolutions between 50 m and 250 m. We decided to stick to a resolution of 100 m for more coherence with the analysis on the quantification of the number of visits to resting sites.



**Figure S5.** Resting sites' contribution to connectivity as a function of the mean human footprint index (HFI) and mean tree cover density (TCD) of the home ranges, for male and female wild boars, calculated from movement networks constructed with raster grids of varying resolutions (50 m, 100 m, 150 m, and 250 m). We did not make predictions for home ranges with high HFI and high TCD, these being virtually non-existent in the data.

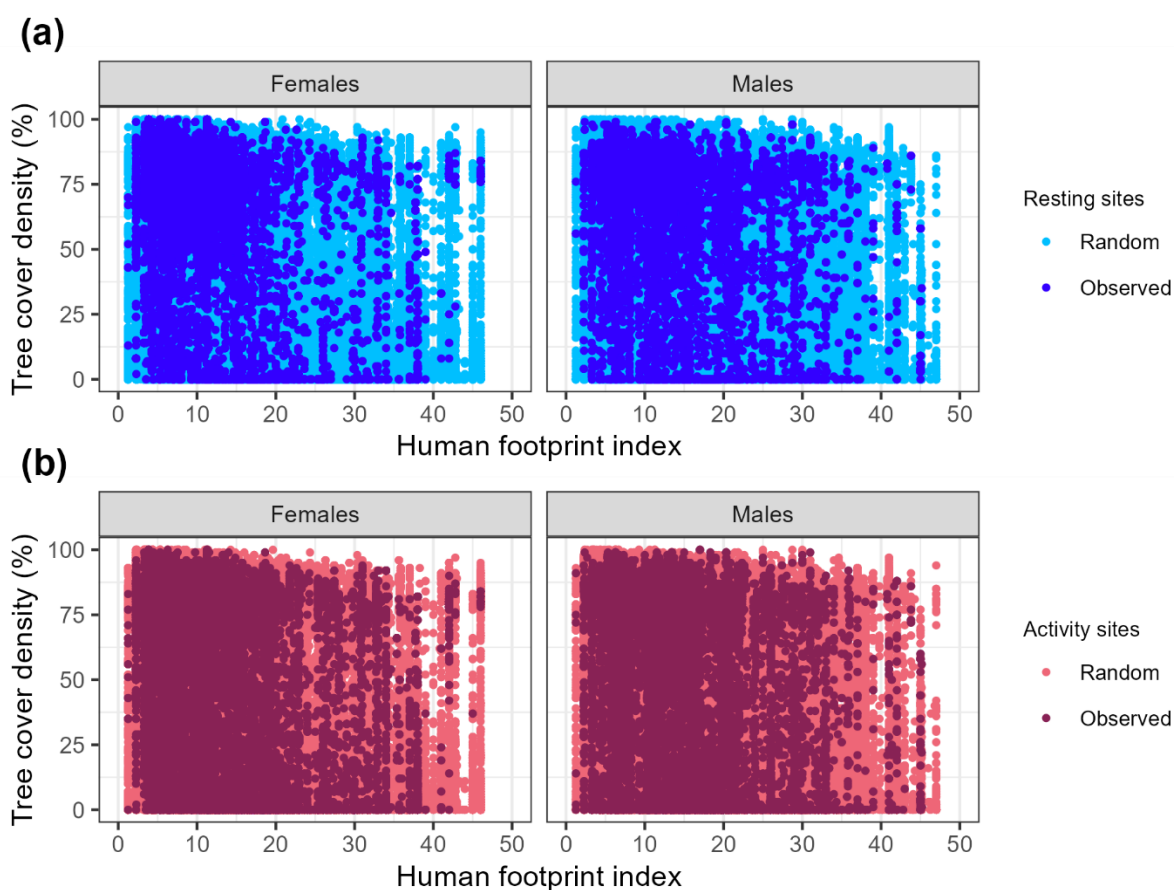
**Table S2 (next page).** Parameters and statistics of the model estimating the contribution of the resting sites' contribution to connectivity for home ranges of varying levels of tree cover density (TCD) and human footprint index (HFI), at four spatial resolutions (50 m, 100 m, 150 m and 250 m). The conditional  $R^2$  are respectively 0.34, 0.3, 0.27 and 0.21. The marginal  $R^2$  are respectively 0.11, 0.11, 0.09 and 0.06.

Variable	$\beta$	SE	z-value	p-value
<b>Grid resolution: 50 m</b>				
Intercept	3.22	0.44	7.30	<0.001
Male	-0.51	0.59	-0.86	0.39
mean HFI	-0.01	0.02	-0.68	0.49
mean TCD	-0.01	0.01	-1.92	0.06
(Home range size)1	-12.72	1.48	-8.59	<0.001
(Home range size)2	8.46	1.28	6.62	<0.001
Male x mean HFI	0.02	0.03	0.54	0.59
Male x mean TCD	0.01	0.01	0.85	0.39
mean HFI x mean TCD	0.00	0.00	1.26	0.21
Male x mean HFI x mean TCD	-0.00	0.00	-0.91	0.37
<b>Grid resolution: 100 m</b>				
Intercept	3.27	0.41	8.03	<0.001
Male	-0.75	0.56	-1.35	0.18
mean HFI	-0.02	0.02	-1.23	0.22
mean TCD	-0.02	0.01	-2.52	0.01
(Home range size)1	-12.38	1.42	-8.70	<0.001
(Home range size)2	7.81	1.23	6.34	<0.001
Male x mean HFI	0.03	0.03	0.97	0.33
Male x mean TCD	0.02	0.01	1.46	0.14
mean HFI x mean TCD	0.00	0.00	1.84	0.07
Male x mean HFI x mean TCD	-0.00	0.00	-1.32	0.19
<b>Grid resolution: 150 m</b>				
Intercept	3.01	0.42	7.24	<0.001
Male	-1.07	0.57	-1.88	0.06
mean HFI	-0.02	0.02	-0.83	0.41
mean TCD	-0.02	0.01	-2.08	0.04
(Home range size)1	-11.14	1.46	-7.61	<0.001
(Home range size)2	6.75	1.28	5.28	<0.001
Male x mean HFI	0.04	0.03	1.25	0.21
Male x mean TCD	0.02	0.01	1.87	0.06
mean HFI x mean TCD	0.00	0.00	1.59	0.11
Male x mean HFI x mean TCD	-0.00	0.00	-1.34	0.18
<b>Grid resolution: 250 m</b>				
Intercept	2.95	0.60	4.92	<0.001
Male	-0.21	0.81	-0.26	0.79
mean HFI	-0.00	0.03	-0.12	0.9
mean TCD	-0.01	0.01	-1.16	0.24
(Home range size)1	-12.73	2.16	-5.88	<0.001
(Home range size)2	8.93	1.93	4.64	<0.001
Male x mean HFI	-0.01	0.04	-0.31	0.76
Male x mean TCD	0.01	0.02	0.59	0.56
mean HFI x mean TCD	0.00	0.00	0.60	0.55
Male x mean HFI x mean TCD	-0.00	0.00	-0.32	0.75

'Female' is the default sex. 'Male' is the alternative.

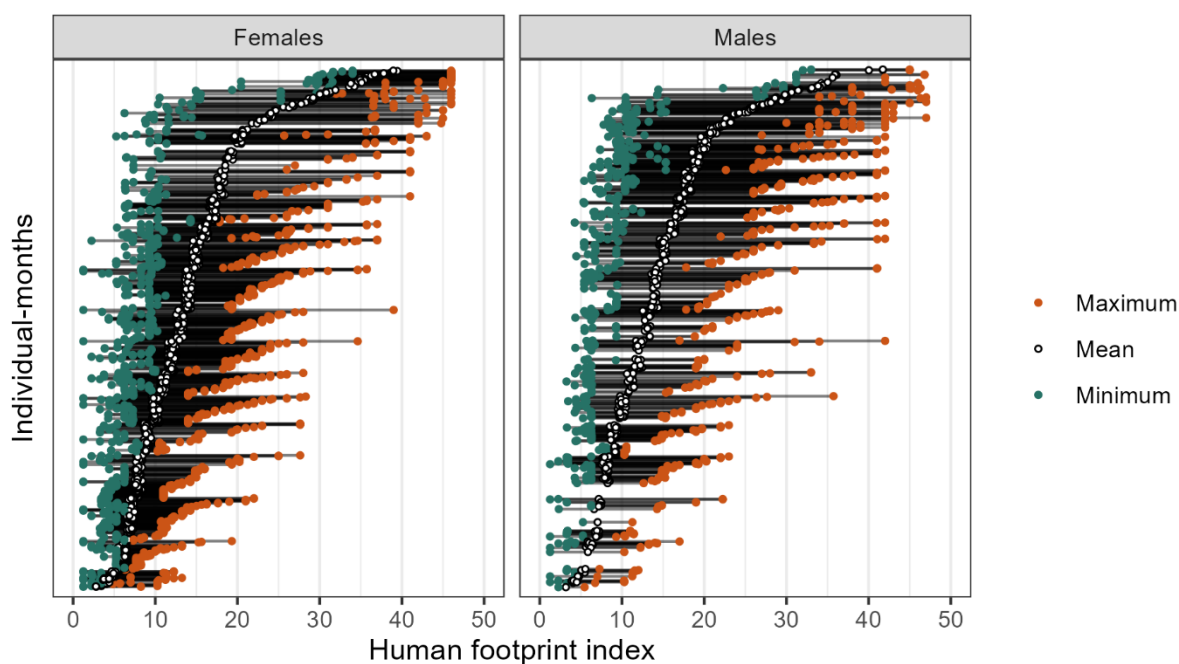
### Appendix 3. Range of HFI and TCD values within data

The wild boars in this study had access to a wide range of human footprint index (HFI) and tree cover density (TCD). All the possible combinations of HFI and TCD were available to them (*Figure S6*). Highly anthropized areas ( $> 35$ ) were less frequent within (and 1 km around) the wild boars home range. Interestingly however, any TCD could be found within the highly anthropized areas that were available to the wild boars.



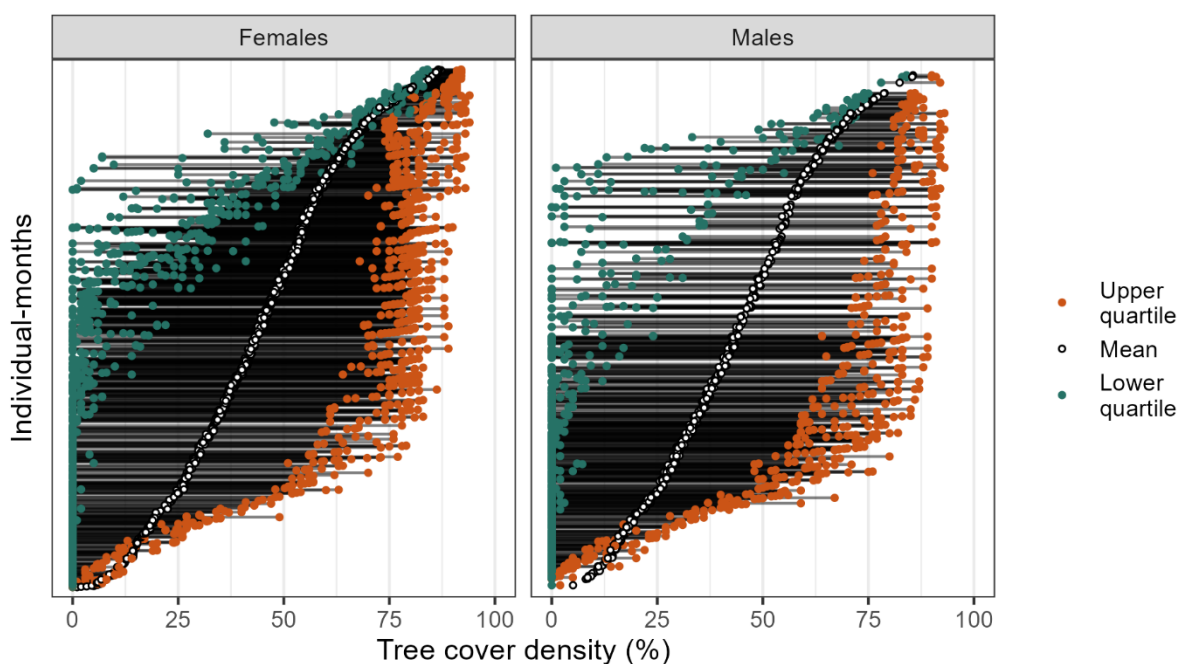
**Figure S6.** Availability and use by the wild boars of the possible range of HFI and TCD. (a) Represents the use of the habitat for resting, and (b) represents the use of the habitat for activity. The random points displayed in (a) and (b) correspond to the 10 random locations extracted per observed location, to represent availability in the resource selection function. These points were extracted within an area corresponding to the animal's home range enlarged with a 1 km buffer.

The values of HFI and TCD available in the environment strongly depended on the individual-month considered. Although the bottom end of the HFI range was well represented in the wild boars' home ranges (*Figure S7*), 75% animal-months did not have access to any area with a HFI higher than 30. The mean HFI within the home range was higher than 20 in 14% individual-months, and only exceeded 30 in 5% of the 1340 individual-months considered.



**Figure S7.** Ranges of human footprint index across the wild boars' home ranges. Each horizontal line represents the home range of one individual-month. Colored dots highlight the minimum, mean and maximum values of human footprint index across monthly home ranges, enlarged with a 1 km buffer.

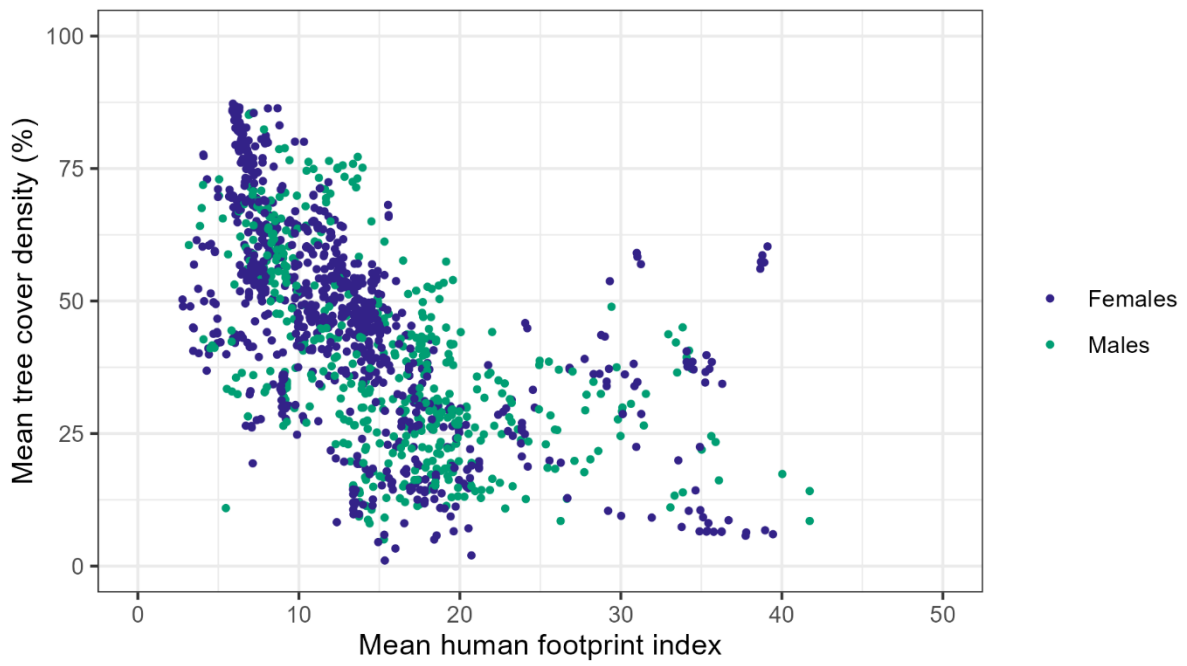
Wide ranges of TCD were much more frequently available within home ranges (*Figure S8*), and most animals had both access to some areas with null TCD and some areas above 95% of TCD. Many animals had access to large extents of both forested cover and unforested patches. For example, 42% individual-months had a low TCD (< 10%) over at least 25% of their home range, and a high TCD (> 50%) over 25% of their home range. Some individuals had mainly forested home ranges: 8% individual-months had more than 90% of their home range covered with forest (TCD > 50). Conversely, some animals had access to a particularly little amount of forest cover: 18% individual-months had more than 75% of their home range below a TCD of 50%. The mean values of available TCD were very well distributed from 1% to 87% (*Figure S8*).



**Figure S8.** Availability in tree cover density across the wild boars' home ranges. Each horizontal line represents the home range of one individual-month. Colored dots highlight the upper quartile, mean and lower quartile of the distribution of tree cover densities across monthly home ranges, enlarged with a 1 km buffer.

The mean HFI and mean TCD in the wild boar's home ranges were negatively correlated (Pearson's product-moment correlation = -0.59). This is not surprising as the amount of landscape modification is one of the factors accounted in the calculation of the HFI. However, the distribution of the combinations of mean HFI and mean TCD suggests that this correlation is only strong for low HFI (<15). For the individuals with a mean HFI higher than 15, the correlation does not seem to persist (Figure S9). Areas with mean HFI above 25 and mean TCD above 50 are not represented in this dataset. Such areas do exist and are visited by wild boars (Figure S6), but they never cover enough land to represent the mean conditions in a wild boars' home range.





*Figure S9. Mean HFI and TCD in each individual-month's home range, enlarged with a 1 km buffer.*





## Références du second axe

Allwin B, Swaminathan R, Mohanraj A, Gokkan N, Vedamanickam S, Sathish G, Kumar M. 2016. The Wild Pig (*Sus scrofa*) Behavior – A Retrospective Study. *Veterinary Science and Technology*. 7:1–10. doi:10.4172/2157-7579.1000333.

Apollonio M, Andersen R, Putman R. 2010. *European Ungulates and Their Management in the 21st Century*. Cambridge University Press, Cambridge.

Ballari SA, Barrios-García MN. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*. 44(2):124–134. doi:10.1111/mam.12015.

Barrios-Garcia MN, Ballari SA. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol Invasions*. 14(11):2283–2300. doi:10.1007/s10530-012-0229-6.

Bastille-Rousseau G, Douglas-Hamilton I, Blake S, Northrup JM, Wittemyer G. 2018. Applying network theory to animal movements to identify properties of landscape space use. *Ecological Applications*. 28(3):854–864. doi:10.1002/eap.1697.

Bastille-Rousseau G. 2023. *\_moveNT: An R package for the analysis of movement data using network theory\_*. R package version 0.0.0.9000. <https://github.com/BastilleRousseau/moveNT>.

Bateman PW, Fleming PA. 2012. Big city life: carnivores in urban environments. *Journal of Zoology*. 287(1):1–23. doi:10.1111/j.1469-7998.2011.00887.x.

Bieber C, Ruf T. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*. 42(6):1203–1213. doi:10.1111/j.1365-2664.2005.01094.x.

Bisi F, Chirichella R, Chianucci F, Von Hardenberg J, Cutini A, Martinoli A, Apollonio M. 2018. Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study. *Annals of Forest Science*. 75(2):46. doi:10.1007/s13595-018-0726-6.

Bobek B, Furtek J, Bobek J, Merta D, Wojciuch-Ploskonka M. 2017. Spatio-temporal characteristics of crop damage caused by wild boar in north-eastern Poland. *Crop Protection*. 93:106–112. doi:10.1016/j.cropro.2016.11.030.

Boitani L, Mattei L, Nonis D, Corsi F. 1994. Spatial and Activity Patterns of Wild Boars in Tuscany, Italy. *Journal of Mammalogy*. 75(3):600–612. doi:10.2307/1382507.

- Bojarska K, Maugeri L, Kuehn R, Król W, Theuerkauf J, Okarma H, Gula R. 2021. Wolves under cover: The importance of human-related factors in resting site selection in a commercial forest. *Forest Ecology and Management*. 497(119511). doi:10.1016/j.foreco.2021.119511.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. *Ecological Modelling*. 157(2):281–300. doi:10.1016/S0304-3800(02)00200-4.
- Brivio F, Grignolio S, Brogi R, Benazzi M, Bertolucci C, Apollonio M. 2017. An analysis of intrinsic and extrinsic factors affecting the activity of a nocturnal species: The wild boar. *Mamm Biol*. 84(1):73–81. doi:10.1016/j.mambio.2017.01.007.
- Brogi R, Brivio F, Bertolucci C, Benazzi M, Luccarini S, Cappai N, Bottero E, Pedrazzoli C, Columbano N, Apollonio M, et al. 2019. Capture effects in wild boar: a multifaceted behavioural investigation. *Wildlife Biology*. 2019(1):wlb.00497. doi:10.2981/wlb.00497.
- Burger AL, Fennessy J, Fennessy S, Dierkes PW. 2020. Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. *Ecol Evol*. 10(6):2917–2927. doi:10.1002/ece3.6106.
- Cahill S, Llimona F. 2004. Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. *Galemys*. 16(1) :37-52.
- Calenge C, Maillard D, Vassant J, Brandt S. 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. *Game and Wildlife Science*. 19(4):281–301.
- Campbell SS, Tobler I. 1984. Animal sleep: A review of sleep duration across phylogeny. *Neuroscience & Biobehavioral Reviews*. 8(3):269–300. doi:10.1016/0149-7634(84)90054-X.
- Candolin U, Fletcher RJ, Stephens AEA. 2023. Animal behaviour in a changing world. *Trends in Ecology & Evolution*. 38(4):313–315. doi:10.1016/j.tree.2023.02.006.
- Cavazza S, Brogi R, Apollonio M. 2023. Sex-specific seasonal variations of wild boar distance traveled and home range size. *Current Zoology*. doi:10.1093/cz/zoad021.
- Červený J, Burda H, Ježek M, Kušta T, Husinec V, Nováková P, Hart V, Hartová V, Begall S, Malkemper EP. 2017. Magnetic alignment in warthogs *Phacochoerus africanus* and wild boars *Sus scrofa*. *Mammal Review*. 47(1):1–5. doi:10.1111/mam.12077.
- Chamaillé-Jammes S. 2020. A reformulation of the selection ratio shed light on resource selection functions and leads to a unified framework for habitat selection studies. *bioRxiv*. doi:10.1101/565838. hal-03029445.

Croney CC, Adams KM, Washington CG, Stricklin WR. 2003. A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. *Applied Animal Behaviour Science*. 83(4):303–308. doi:10.1016/S0168-1591(03)00128-X.

Dardaillon M, Beugnon G. 1987. The Influence of Some Environmental Characteristics on the Movements of Wild Boar (*Sus Scrofa*). *Biology of Behaviour*. 12(2):82–92.

Focardi S, Gaillard J-M, Ronchi F, Rossi S. 2008. Survival of Wild Boars in a Variable Environment: Unexpected Life-History Variation in an Unusual Ungulate. *Journal of Mammalogy*. 89(5):1113–1123. doi:10.1644/07-MAMM-A-164.1.

Fournier-Chambrillon C, Maillard D, Fournier P. 2014. Diet of the wild boar (*Sus scrofa* L.) inhabiting the Montpellier garrigue. *Journal of Mountain Ecology*. 3.

Fradin G, Chamaille-Jammes S. 2023. Hogs sleep like logs: Wild boars reduce the risk of anthropic disturbance by adjusting where they rest. *Ecol Evol*. 13(7):e10336. doi:10.1002/ece3.10336.

Freiberg A. 2020. Why We Sleep: A Hypothesis for an Ultimate or Evolutionary Origin for Sleep and Other Physiological Rhythms. *Journal of Circadian Rhythms*. 18. doi:10.5334/jcr.189.

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. *Science*. 360(6394):1232–1235. doi:10.1126/science.aar7121.

Gehring TM, Swihart RK. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biological Conservation*. 109(2):283–295. doi:10.1016/S0006-3207(02)00156-8.

Génin F. 2010. Who sleeps with whom? Sleeping association and socio-territoriality in *Microcebus griseorufus*. *Journal of Mammalogy*. 91(4):942–951. doi:10.1644/09-MAMM-A-239.1.

Gieling ET, Nordquist RE, van der Staay FJ. 2011. Assessing learning and memory in pigs. *Anim Cogn*. 14(2):151–173. doi:10.1007/s10071-010-0364-3.

Gilbert NA, McGinn KA, Nunes LA, Shipley AA, Bernath-Plaisted J, Clare JDJ, Murphy PW, Keyser SR, Thompson KL, Nelson SBM, et al. 2023. Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution*. 38(4):324–336. doi:10.1016/j.tree.2022.10.008.

Glass TW, Breed GA, Robards MD, Williams CT, Kielland K. 2021. Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*. 175:163–174. doi:10.1016/j.anbehav.2021.02.017.

Gordigiani L, Viviano A, Brivio F, Grignolio S, Lazzeri L, Marcon A, Mori E. 2021. Carried away by a moonlight shadow: activity of wild boar in relation to nocturnal light intensity. *Mamm Res*. doi:10.1007/s13364-021-00610-6.

Herrero J, García-Serrano A, Couto S, Ortuño VM, García-González R. 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *Eur J Wildl Res*. 52(4):245–250. doi:10.1007/s10344-006-0045-3.

Iacolina L, Scandura M, Bonghi P, Apollonio M. 2009. Nonkin Associations in Wild Boar Social Units. *Journal of Mammalogy*. 90(3):666–674. doi:10.1644/08-MAMM-A-074R1.1.

Ikeda T, Kuninaga N, Suzuki T, Ikushima S, Suzuki M. 2019. Tourist-wild boar (*Sus scrofa*) interactions in urban wildlife management. *Global Ecology and Conservation*. 18:e00617. doi:10.1016/j.gecco.2019.e00617.

Jacoby DMP, Brooks EJ, Croft DP, Sims DW. 2012. Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*. 3(3):574–583. doi:10.1111/j.2041-210X.2012.00187.x.

Janmaat KRL, Polansky L, Ban SD, Boesch C. 2014. Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences*. 111(46):16343–16348. doi:10.1073/pnas.1407524111.

Jayadevan A, Nayak R, Karanth KK, Krishnaswamy J, DeFries R, Karanth KU, Vaidyanathan S. 2020. Navigating paved paradise: Evaluating landscape permeability to movement for large mammals in two conservation priority landscapes in India. *Biological Conservation*. 247:108613. doi:10.1016/j.biocon.2020.108613.

Johann F, Handschuh M, Linderoth P, Dormann CF, Arnold J. 2020. Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. *BMC Ecology*. 20(4). doi:10.1186/s12898-019-0271-7.

Johann F, Handschuh M, Linderoth P, Heurich M, Dormann CF, Arnold J. 2020. Variability of daily space use in wild boar *Sus scrofa*. *wbio*. 2020(1). doi:10.2981/wlb.00609.

Kaminski G, Brandt S, Baubet E, Baudoin C. 2005. Life-history patterns in female wild boars (*Sus scrofa*): mother–daughter postweaning associations. *Can J Zool*. 83(3):474–480. doi:10.1139/z05-019.

Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A, Podgórski T, Prevot C, Ronnenberg K, Sodeikat G, et al. 2013. Mortality rates of wild boar *Sus scrofa* L. in central Europe. *Eur J Wildl Res*. 59(6):805–814. doi:10.1007/s10344-013-0733-8.

Keuling O, Stier N, Roth M. 2008a. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *Eur J Wildl Res.* 54(3):403–412. doi:10.1007/s10344-007-0157-4.

Keuling O, Stier N, Roth M. 2008b. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *Eur J Wildl Res.* 54(4):729–737. doi:10.1007/s10344-008-0204-9.

Keuling O, Stier N, Roth M. 2009. Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mamm Biol.* 74(2):145–152. doi:10.1016/j.mambio.2008.05.007.

Keuling O, Strauß E, Siebert U. 2016. Regulating wild boar populations is “somebody else’s problem”! - Human dimension in wild boar management. *Science of The Total Environment.* 554–555:311–319. doi:10.1016/j.scitotenv.2016.02.159.

Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jędrzejewska B, Smit C. 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS One.* 9(1):e84607. doi:10.1371/journal.pone.0084607.

Laguna E, Barasona JA, Vicente J, Keuling O, Acevedo P. 2021. Differences in wild boar spatial behaviour among land uses and management scenarios in Mediterranean ecosystems. *Science of The Total Environment.* 796:148966. doi:10.1016/j.scitotenv.2021.148966.

Latorre L, Miquel J, Chamailé-Jammes S. 2021. MEMS based low-power multi-sensors device for bio-logging applications. In: 2021 Symposium on Design, Test, Integration & Packaging of MEMS and MOEMS (DTIP). p. 1–4. doi:10.1109/DTIP54218.2021.9568669

Lemel J, Truvé J, Söderberg B. 2003. Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. *wbio.* 9(s1):29–36. doi:10.2981/wlb.2003.061.

Lewis JS, Farnsworth ML, Burdett CL, Theobald DM, Gray M, Miller RS. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. *Sci Rep.* 7(1):44152. doi:10.1038/srep44152.

Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ. 2005. Sleeping under the risk of predation. *Animal Behaviour.* 70(4):723–736. doi:10.1016/j.anbehav.2005.01.008.

López-Calderón C, Martín-Vélez V, Blas J, Höfle U, Sánchez MI, Flack A, Fiedler W, Wikelski M, Green AJ. 2023. White stork movements reveal the ecological connectivity between landfills and different habitats. *Movement Ecology.* 11(1):18. doi:10.1186/s40462-023-00380-7.

Lowry H, Lill A, Wong BBM. 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews.* 88(3):537–549. doi:10.1111/brv.12012.



Lutermann H, Verburgt L, Rendigs A. 2010. Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*. 79(6):1211–1219. doi:10.1016/j.anbehav.2010.02.017.

Maillard D, Fournier P. 1995. Effects of shooting with hounds on size of resting range of Wild boar (*Sus scrofa* L.) groups in mediterranean habitat. *IBEX J Mt Ecol*. 3(102):e107.

Maillard D, Fournier P, Lagarrigue V. 1995. Organisation spatiale des sites de repos des sangliers en milieu méditerranéen. *Forêt Méditerranéenne*. XVI(3):313-324. hal-03557280

Malmsten A, Jansson G, Lundeheim N, Dalin A-M. 2017. The reproductive pattern and potential of free ranging female wild boars (*Sus scrofa*) in Sweden. *Acta Veterinaria Scandinavica*. 59(1):52. doi:10.1186/s13028-017-0321-0.

Markham AC, Alberts SC, Altmann J. 2016. Haven for the night: sleeping site selection in a wild primate. *Behavioral Ecology*. 27(1):29–35. doi:10.1093/beheco/arv118.

Markov N, Economov A, Hjeljord O, Rolandsen CM, Bergqvist G, Danilov P, Dolinin V, Kambalin V, Kondratov A, Krasnoshapka N, et al. 2022. The wild boar *Sus scrofa* in northern Eurasia: a review of range expansion history, current distribution, factors affecting the northern distributional limit, and management strategies. *Mammal Review*. 52(4):519–537. doi:10.1111/mam.12301.

Martin C. 1987. Garrigues en pays languedocien. Lacour.

Marzano M, Dandy N. 2012. Recreationist behaviour in forests and the disturbance of wildlife. *Biodivers Conserv*. 21(11):2967–2986. doi:10.1007/s10531-012-0350-y.

Maselli V, Rippa D, Russo G, Ligrone R, Soppelsa O, D’Aniello B, Raia P, Fulgione D. 2014. Wild boars’ social structure in the Mediterranean habitat. *Italian Journal of Zoology*. 81(4):610–617. doi:10.1080/11250003.2014.953220.

Massei G, Kindberg J, Licoppe A, Gačić D, Šprem N, Kamler J, Baubet E, Hohmann U, Monaco A, Ozoliņš J, et al. 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*. 71(4):492–500. doi:10.1002/ps.3965.

Massei G, Roy S, Bunting R. 2011. Too many hogs?: A review of methods to mitigate impact by wild boar and feral hogs. *Human-Wildlife Interactions*. 5(1):79–99. doi:10.26077/aeda-p853

Mathevet R, Bondon R. 2022. Sangliers, géographies d’un animal politique. *Actes Sud Nature*.

McClintock BT, Michelot T. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*. 9(6):1518–1530. doi:10.1111/2041-210X.12995.

Mendl M, Held S, Byrne R. 2010. Pig cognition. *Current Biology*. 20:R796–R798. doi:10.1016/j.cub.2010.07.018.

Michelot T, Langrock R, Patterson TA. 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*. 7(11):1308–1315. doi:10.1111/2041-210X.12578.

Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P. 2015. Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*. 45(1):15–29. doi:10.1111/mam.12028.

Mortlock E, Silovský V, Güldenpfennig J, Faltusová M, Olejarz A, Börger L, Ježek M, Jennings DJ, Capellini I. 2022. Individual identity and environmental conditions explain different aspects of sleep behaviour in wild boar. *bioRxiv*. doi:10.1101/2022.11.23.517569.

Mounet C. 2007. Les territoires de l'imprévisible. Conflits, controverses et "vivre ensemble" autour de la gestion de la faune sauvage. Le cas du loup et du sanglier dans les Alpes françaises. Université Joseph-Fourier, Grenoble. theses.hal.science/tel-00207766.

Mumme S, Middleton AD, Ciucci P, De Groeve J, Corradini A, Aikens EO, Ossi F, Atwood P, Balkenhol N, Cole EK, et al. 2023. Wherever I may roam—Human activity alters movements of red deer (*Cervus elaphus*) and elk (*Cervus canadensis*) across two continents. *Global Change Biology*. doi:10.1111/gcb.16769.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*. 4(2):133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*. 105(49):19052–19059. doi:10.1073/pnas.0800375105.

Ohashi H, Saito M, Horie R, Tsunoda H, Noba H, Ishii H, Kuwabara T, Hiroshige Y, Koike S, Hoshino Y, et al. 2014. Erratum to: Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research*. 60(567). doi:10.1007/s10344-012-0661-z.

Olejarz A, Faltusová M, Börger L, Güldenpfennig J, Jarský V, Ježek M, Mortlock E, Silovský V, Podgórski T. 2023. Worse sleep and increased energy expenditure yet no movement changes in sub-urban wild boar experiencing an influx of human visitors (anthropulse) during the COVID-19 pandemic. *Science of The Total Environment*. 879:163106. doi:10.1016/j.scitotenv.2023.163106.

Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*. 94(1):109–119. doi:10.1644/12-MAMM-A-038.1.

Poteaux C, Baubet E, Kaminski G, Brandt S, Dobson FS, Baudoin C. 2009. Socio-genetic structure and mating system of a wild boar population. *Journal of Zoology*. 278(2):116–125. doi:10.1111/j.1469-7998.2009.00553.x.

Quirós-Fernández F, Marcos J, Acevedo P, Gortázar C. 2017. Hunters serving the ecosystem: the contribution of recreational hunting to wild boar population control. *Eur J Wildl Res*. 63(3):57. doi:10.1007/s10344-017-1107-4.

Raynal J-C. 2020. Pratiques cynégétiques, transformation territoriales et régulations sociales: Vers une gestion concertée des populations de sangliers dans le Sud de la France. Presses universitaires de la Méditerranée.

Riede SJ, van der Vinne V, Hut RA. 2017. The flexible clock: predictive and reactive homeostasis, energy balance and the circadian regulation of sleep-wake timing. *Journal of Experimental Biology*. 220(5):738–749. doi:10.1242/jeb.130757.

Rosalino LM, Teixeira D, Camarinha C, Pereira G, Magalhães A, Castro G, Lima C, Fonseca C. 2022. Even generalist and resilient species are affected by anthropic disturbance: evidence from wild boar activity patterns in a Mediterranean landscape. *Mamm Res*. 67(3):317–325. doi:10.1007/s13364-022-00632-8.

Russo L, Massei G, Genov PV. 1997. Daily home range and activity of wild boar in a Mediterranean area free from hunting. *Ethology Ecology & Evolution*. 9(3):287–294. doi:10.1080/08927014.1997.9522888.

Sáez-Royuela C, Tellería JL. 1986. The increased population of the Wild Boar (*Sus scrofa* L.) in Europe. *Mammal Review*. 16(2):97–101. doi:10.1111/j.1365-2907.1986.tb00027.x.

Saïd S, Tolon V, Brandt S, Baubet E. 2012. Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. *Eur J Wildl Res*. 58(1):107–115. doi:10.1007/s10344-011-0548-4.

Salvatori M, De Groeve J, van Loon E, De Baets B, Morellet N, Focardi S, Bonnot NC, Gehr B, Griggio M, Heurich M, et al. 2022. Day versus night use of forest by red and roe deer as determined by Corine Land Cover and Copernicus Tree Cover Density: assessing use of geographic layers in movement ecology. *Landsc Ecol.* 37(5):1453–1468. doi:10.1007/s10980-022-01416-w.

Schley L, Roper TJ. 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review.* 33(1):43–56. doi:10.1046/j.1365-2907.2003.00010.x.

Schmidt MH. 2014. The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience & Biobehavioral Reviews.* 47:122–153. doi:10.1016/j.neubiorev.2014.08.001.

Scillitani L, Monaco A, Toso S. 2010. Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications. *Eur J Wildl Res.* 56(3):307–318. doi:10.1007/s10344-009-0314-z.

Servanty S, Gaillard J-M, Toïgo C, Brandt S, Baubet E. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology.* 78(6):1278–1290. doi:10.1111/j.1365-2656.2009.01579.x.

Siegel JM. 2009. Sleep viewed as a state of adaptive inactivity. *Nature Reviews Neuroscience.* 10(10):747–753. doi:10.1038/nrn2697.

Sodeikat G, Pohlmeier K. 2007. Impact of drive hunts on daytime resting site areas of wild boar family groups (*Sus scrofa* L.). *Wildlife Biology in Practice.* 3:28–38. doi:10.2461/wbp.2007.3.4.

Spitz F, Janeau G. 1990. Spatial strategies: an attempt to classify daily movements of wild boar. *Acta Theriol.* 35:129–149. doi:10.4098/AT.arch.90-14.

Spitz F, Janeau G. 1995. Daily selection of habitat in wild boar (*Sus scrofa*). *Journal of Zoology.* 237(3):423–434. doi:10.1111/j.1469-7998.1995.tb02772.x.

Stillfried M, Gras P, Börner K, Göritz F, Painer J, Röllig K, Wenzler M, Hofer H, Ortmann S, Kramer-Schadt S. 2017. Secrets of Success in a Landscape of Fear: Urban Wild Boar Adjust Risk Perception and Tolerate Disturbance. *Frontiers in Ecology and Evolution.* 5(157). doi:10.3389/fevo.2017.00157.

Thurfjell H, Ball JP, Åhlén P-A, Kornacher P, Dettki H, Sjöberg K. 2009. Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. *Eur J Wildl Res.* 55(5):517–523. doi:10.1007/s10344-009-0268-1.

Thurffield H, Spong G, Ericsson G. 2013. Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology*. 19(1):87–93. doi:10.2981/12-027.

Tisdale RK, Lesku JA, Beckers GJL, Vyssotski AL, Rattenborg NC. 2018. The low-down on sleeping down low: pigeons shift to lighter forms of sleep when sleeping near the ground. *Journal of Experimental Biology*. 221(19):jeb182634. doi:10.1242/jeb.182634.

Toïgo C, Servanty S, Gaillard J-M, Brandt S, Baubet E. 2008. Disentangling Natural From Hunting Mortality in an Intensively Hunted Wild Boar Population. *Journal of Wildlife Management*. 72:1532–1539. doi:10.2193/2007-378.

Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Can J Zool*. 87(12):1129–1137. doi:10.1139/Z09-101.

Torres-Blas I, Mentaberre G, Castillo-Contreras R, Fernández-Aguilar X, Conejero C, Valdeperes M, González-Crespo C, Colom-Cadena A, Lavín S, López-Olvera JR. 2020. Assessing methods to live-capture wild boars (*Sus scrofa*) in urban and peri-urban environments. *Vet rec*. 187(10). doi:10.1136/vr.105766.

Touzot L, Schermer É, Venner S, Delzon S, Rousset C, Baubet É, Gaillard J-M, Gamelon M. 2020. How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. *Ecological Applications*. 30(6):e02134. doi:10.1002/eap.2134.

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*. 359(6374):466–469. doi:10.1126/science.aam9712.

Ungurean G, van der Meij J, Rattenborg NC, Lesku JA. 2020. Evolution and plasticity of sleep. *Current Opinion in Physiology*. 15:111–119. doi:10.1016/j.cophys.2019.12.013.

Urbano F, Cagnacci F, Euromammals Collaborative Initiative. 2021. Data Management and Sharing for Collaborative Science: Lessons Learnt From the Euromammals Initiative. *Frontiers in Ecology and Evolution*. 9. doi:10.3389/fevo.2021.727023

Vajas P, Von Essen E, Tickle L, Gamelon M. 2023. Meeting the challenges of wild boar hunting in a modern society: The case of France. *Ambio*. 52(8):1359–1372. doi:10.1007/s13280-023-01852-1.

Veeroja R, Männil P. 2013. Population development and reproduction of wild boar (*Sus scrofa*) in Estonia. *Wildlife Biology in Practice*. doi:10.2461/wbp.2014.un.3.

Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, Fekete BM, et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun.* 7(1):12558. doi:10.1038/ncomms12558.

Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Levy MA, Watson JE. 2018. Last of the Wild Project, Version 3 (LWP-3): 1993 Human Footprint, 2018 Release. doi:10.7927/H4H9938Z.

Vetter SG, Puskas Z, Bieber C, Ruf T. 2020. How climate change and wildlife management affect population structure in wild boars. *Sci Rep.* 10(1):7298. doi:10.1038/s41598-020-64216-9.

Wam HK, Eldegard K, Hjeljord O. 2012. From overlooking to concealed: predator avoidance in an apex carnivore. *Eur J Wildl Res.* 58(6):1001–1003. doi:10.1007/s10344-012-0670-y.

Weinberger IC, Muff S, Kranz A, Bontadina F. 2019. Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape. *Mamm Biol.* 98(1):179–187. doi:10.1016/j.mambio.2019.09.001.

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology.* 96(7):1741–1753. doi:10.1890/14-1401.1.

Wilson CJ. 2013. The establishment and distribution of feral wild boar (*Sus scrofa*) in England. *Wildl Biol Pract.* 10(3):249. doi:10.2461/wbp.2014.un.1.

Wilson MW, Ridlon AD, Gaynor KM, Gaines SD, Stier AC, Halpern BS. 2020. Ecological impacts of human-induced animal behaviour change. *Ecology Letters.* 23(10):1522–1536. doi:10.1111/ele.13571.

Wittemyer G, Keating LM, Vollrath F, Douglas-Hamilton I. 2017. Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography.* 40(5):598–605. doi:10.1111/ecog.02379.

Wittemyer G, Northrup JM, Bastille-Rousseau G. 2019. Behavioural valuation of landscapes using movement data. *Philosophical Transactions of the Royal Society B: Biological Sciences.* 374(1781):20180046. doi:10.1098/rstb.2018.0046.



A photograph of a brown bear walking through a field of tall grass. The bear is in profile, facing right, and its fur is a rich brown color. The background is a soft-focus landscape with more grass and a hint of a body of water or a path.

# Discussion générale

## 1 Résumé des chapitres et résultats

### 1.1 Contexte général

Ce travail de thèse a émergé du constat selon lequel malgré leur omniprésence dans la vie des animaux, les comportements inactifs sont généralement peu étudiés en écologie. Ces comportements sont pourtant essentiels mais aussi vulnérables face aux pressions d'origine anthropique. Par ailleurs, leur flexibilité peut constituer un important levier pour l'ajustement aux contraintes qui découlent de l'anthropisation. L'étude des facteurs influençant les stratégies de repos, ainsi que leurs conséquences écologiques semble donc crucial pour comprendre et anticiper les effets des activités humaines sur la biodiversité.

L'essor du bio-logging a permis aux chercheurs de documenter les aspects les plus cryptiques du comportement animal (Wilmers et al. 2015), mais les études au sujet de l'inactivité demeurent rares, et les impacts de l'anthropisation sur ces comportements sont presque systématiquement oubliés (Candolin et al. 2023). Même le sommeil, qui a reçu le plus d'intérêt parmi les comportements inactifs, et dont la télémétrie a permis l'étude en milieu naturel (Rattenborg et al. 2017), demeure relativement peu étudié. En effet, même lorsqu'elles sont menées en milieu naturel et sur des espèces sauvages, les études portant sur le sommeil visent souvent à comprendre sa fonction et son histoire évolutive (Reinhardt 2020; Ungurean et al. 2020; Lesku and Rattenborg 2022). Ses implications écologiques sont, malgré quelques exceptions (Korstjens et al. 2010; Mohanty et al. 2022), le plus souvent éludés, et les impacts de l'anthropisation ne sont



quasiment jamais traités. De manière générale en écologie, les comportements inactifs, ne sont que rarement considérés comme un ensemble, malgré les nombreuses contraintes et conséquences partagées.

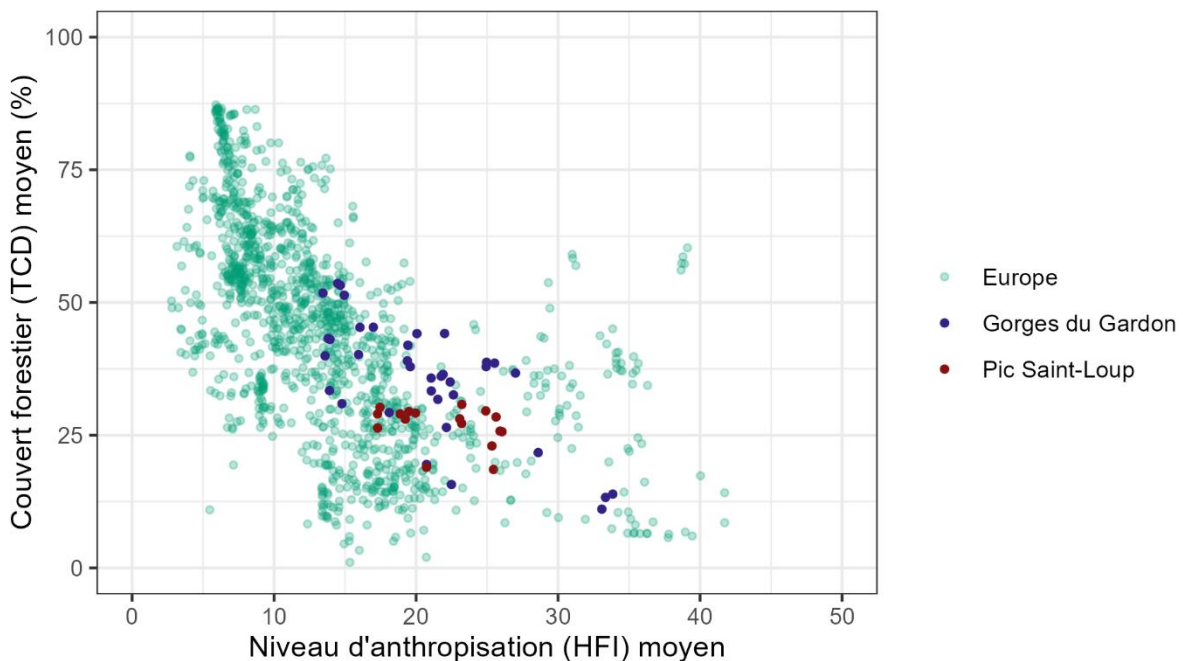
### **1.2 Conclusions du premier axe**

Dans le premier axe de cette thèse, nous avons présenté une revue de littérature (chapitre 1) dans laquelle nous soulignons l'importance du repos du point de vue de l'écologie. Nous y avançons que dans ce domaine, le déficit d'études portant sur le sommeil et autres comportements inactifs découle en partie des difficultés éprouvées pour distinguer ces comportements entre eux. Nous proposons de définir le repos de manière inclusive, en regroupant tous les comportements inactifs qui alternent avec des comportements actifs selon une cyclicité inférieure à 24 heures. Cette définition facilite l'étude de l'inactivité par télémétrie. Bien que les comportements relevant du repos soient hétérogènes à plusieurs égards, ils imposent ensemble une fixation prolongée dans l'espace. La nécessité de trouver des conditions compatibles avec le repos contraint l'utilisation de l'espace et du temps. Par ailleurs, lorsqu'un individu choisit où, quand, et comment se reposer, il définit les conditions qui prévaudront durant toute la phase de repos. Il est pour cela à la fois motivé et contraint par de nombreux facteurs internes et externes, dont le métabolisme, les conditions environnementales, ou encore le risque de prédation. Il est donc sensible aux altérations des conditions environnementales, et notamment celles liés à l'anthropisation. En permettant la description des stratégies de repos, la définition proposée a le potentiel d'aider à comprendre les conséquences écologiques des perturbations des comportements inactifs.

Dans cette revue de littérature, nous avons détaillé les stratégies de repos employées par les vertébrés terrestres, en décrivant les mécanismes par lesquels les contraintes physiologiques (métabolisme, rythmes circadiens, régulation homéostatique du sommeil, etc.) et écologiques (risque de prédation, conditions climatiques, disponibilité alimentaire, etc.) influencent ce comportement. Nous avons résumé l'état actuel des connaissances au sujet des impacts possibles de l'anthropisation sur le comportement de repos, et des ajustements de ce comportement en réponse aux activités humaines. Comme nous l'avons souligné, de nombreuses lacunes existent dans ce domaine, et avons proposé certains mécanismes que nous imaginons potentiellement importants. De cet exercice, il ressort que les dérangements directs liés à la présence humaine dans les espaces naturels et les modifications du paysage (notamment la fragmentation et la destruction des habitats et des structures utilisées pour le repos) sont particulièrement susceptibles de perturber le repos animal, et de provoquer des ajustements comportementaux.

### 1.3 Conclusions du second axe

Dans le second axe de cette thèse, nous avons utilisé la définition proposée dans le premier axe pour étudier l'ajustement du comportement de repos du sanglier (*Sus scrofa*) en réponse à l'anthropisation, avec une attention particulière pour la dynamique spatiale d'utilisation des sites de repos. Le sanglier vit et se multiplie dans des contextes extrêmement variés, et tout le long du gradient d'anthropisation. Grâce à sa grande flexibilité comportementale, il s'accommode de diverses pressions d'origine anthropiques, comme la modification du paysage et les dérangements directs, qui comprennent la chasse et la présence d'êtres humains non-chasseurs dans les milieux naturels. Dans les chapitres 2 et 3, nous avons vu que le sanglier modifie son comportement de repos en fonction du niveau d'anthropisation, notamment en ajustant le type d'habitat sélectionné, ainsi que le nombre de visites à chaque site de repos.



**Figure 1.** Niveau d'anthropisation (human footprint index ; HFI) et couvert forestier (tree cover density ; TCD) moyens pour chaque individu-mois considéré dans le chapitre 3. Les individus-mois dont les données ont aussi servi dans le chapitre 2 sont indiqués en bleu (Gorges du Gardon), et en rouge (Pic Saint-Loup).

#### 1.3.1 Echelles des variables environnementales utilisées

Dans les chapitres 2 et 3, nous avons décrit, à deux échelles différentes, la stratégie de sélection des sites de repos en réponse à l'anthropisation, chez le sanglier. Dans le chapitre 2, nous avons quantifié le risque de dérangement lors du repos en calculant précisément la distance de chaque site de repos aux routes et aux villages, dans un paysage agricole anthropisé du sud de la France. Dans le chapitre 3, nous avons également évalué l'impact de l'anthropisation sur la stratégie

spatiale de repos du sanglier, mais à une échelle différente. Nous nous sommes intéressés à des sangliers répartis sur le plus large gradient d'anthropisation possible, à travers l'Europe entière, et nous avons quantifié le taux d'anthropisation à l'échelle du km<sup>2</sup>, en utilisant le « human footprint index ». La couverture végétale associée à chaque site de repos était renseignée à l'échelle de l'hectare, sous forme pourcentage de couverture forestière, dans le chapitre 3, et de manière plus grossière dans le chapitre 2, où nous avons seulement caractérisé chaque site de repos par son appartenance ou non à un patch de végétation dense. La *Figure 1* présente les caractéristiques environnementales des sites d'études utilisés dans le chapitre 2 selon les critères utilisés dans le chapitre 3.

### *1.3.2 Sélection des sites de repos*

Les deux études du second axe de cette thèse utilisent des variables différentes pour caractériser l'anthropisation et le couvert forestier au niveau de chaque site de repos. Par une description sous deux angles différents, elles donnent une vision d'ensemble sur l'impact de l'anthropisation sur la stratégie d'utilisation des sites de repos par le sanglier. Dans le chapitre 3, nous avons observé que, dans les environnements les moins anthropisés comme les zones de montagnes ou les forêts les plus reculées, le sanglier ne montre pas de forte préférence pour les couverts forestiers denses pour se reposer. Une telle préférence apparaît cependant, et s'intensifie à mesure que l'anthropisation augmente (chapitre 3). Ainsi, en sélectionnant les sites où la végétation est dense, le sanglier est capable se reposer au plus près de l'être humain. Dans le sud de la France, le sanglier est indifférent à la proximité des villages lorsqu'il choisit où se reposer (chapitre 2). Il se repose ainsi régulièrement à quelques mètres des habitations, dans des paysages qui pourtant lui offrent une grande variété de sites plus distants de l'activité humaine. Tous les niveaux d'anthropisation existant à l'échelle de l'Europe sont utilisés par le sanglier pour se reposer (chapitre 3). Le besoin de trouver des sites adéquats ne l'empêche donc pas d'utiliser les zones où le risque de dérangement est grand lors de ses phases de repos.

### *1.3.3 Réutilisation des sites de repos*

Cette capacité à se reposer même au plus près des humains vient de l'utilisation du couvert végétal par le sanglier, mais aussi de sa stratégie de réutilisation des sites de repos. Les laies reviennent plus fréquemment se reposer dans les mêmes sites de repos lorsque ceux-ci sont situés dans des zones fortement anthropisées, ou bien dans des zones peu anthropisées mais peu boisées (chapitre 3). Dans les deux cas, cela suggère que là où les sites adéquats sont rares, lorsqu'un site de bonne qualité est identifié, il est utilisé intensément. Ce comportement n'est pas observé chez les mâles à cette échelle (chapitre 3). En revanche, à une échelle plus fine, nous avons observé que les mâles ajustent leur taux de réutilisation des sites de repos à la proximité avec l'être humain. Dans le sud de la France, plus un site de repos est proche d'un village, plus il

est fréquemment réutilisé, en dehors de la saison de chasse (chapitre 2). Cet ajustement comportemental se produit à une échelle probablement trop fine pour transparaître à l'échelle de l'Europe à travers le « human footprint index ». Les mâles étant plus mobiles que les femelles, leur taux de réutilisation des sites de repos est par ailleurs globalement moindre. Leur mode de vie peut aussi participer à réduire l'intensité de la réutilisation des sites de repos en milieux anthropisés, car les mâles solitaires sont certainement capables de se reposer dans des refuges de petite taille, où une compagnie entière ne pourrait pas se cacher. Enfin, l'effet de la distance au village le plus proche sur le nombre de visite chez les mâles disparaît pendant la saison de chasse, probablement en raison de la mobilité accrue des animaux (chapitre 2). Le même ajustement comportemental pourrait exister à l'échelle de l'Europe, masqué par le fait que nous n'avons pas distingué les saisons de chasse dans cette analyse, car la grande diversité des pratiques cynégétiques dans les sites d'étude considérés rendait sa prise en compte excessivement complexe (chapitre 3). Tous ces arguments concordent pour suggérer que la réutilisation fréquente des sites de repos dans les milieux où ils sont rares permet aux sangliers de se reposer partout, même dans les milieux les plus anthropisés.

#### 1.3.4 *Efficacité de la stratégie*

Dans le premier volet du second axe (chapitre 2), nous avons cherché à évaluer l'efficacité des ajustements du repos par le sanglier pour limiter le risque de dérangement anthropique. Pour cela, nous avons utilisé la probabilité qu'un sanglier change de site de repos au cours de la journée comme une estimation de la probabilité de dérangement. Nous avons constaté que ce risque de dérangement reste toujours relativement faible, et n'est que faiblement influencé par la saison et les jours de chasse. En particulier, nous n'avons pas trouvé d'effet de la distance au village le plus proche sur le risque de relocalisation diurne. Cela suggère que la stratégie d'ajustement à la proximité des villages, qui consiste à réutiliser plus fréquemment quelques sites bien identifiés compense le risque accru de dérangement. Bien sûr, nous sommes conscients des nombreuses limites inhérentes à notre méthode. Le risque de dérangements anthropiques et la fréquence des dérangements effectifs ne peuvent être que grossièrement estimés par la distance aux infrastructures humaines et la fréquence des relocalisations diurnes, respectivement. Néanmoins, cette étude constitue, à notre connaissance, la première tentative d'évaluation de l'efficacité d'un ajustement du comportement de repos pour limiter le risque de dérangement. Elle fournit par ailleurs une estimation de la fréquence des dérangements de la phase de repos du sanglier, jusque-là peu documentée (Olejarz et al. 2023). Il semble que le sanglier parvienne à réduire la probabilité d'être dérangé pendant le repos, en sélectionnant un couvert végétal adapté, et en privilégiant les sites connus dans les zones les plus risquées.

### 1.3.5 *Impact de la stratégie de repos sur les déplacements*

Dans le second volet du second axe (chapitre 3), nous avons cherché à intégrer la stratégie spatiale de repos du sanglier dans le contexte de ses déplacements. La prise en compte des sites importants pour l'activité dans l'étude de la sélection des sites de repos est généralement difficile, car l'utilisation de l'espace est radicalement différente entre le repos et l'activité. Notre approche basée sur les réseaux de déplacement permet d'identifier les lieux importants pour la circulation des sangliers dans leur domaine vital, afin d'évaluer la centralité des sites de repos. Nous avons cherché à tester l'hypothèse selon laquelle l'anthropisation, en contraignant les déplacements des animaux, modifie l'influence de la nécessité de trouver des sites de repos sur l'utilisation du paysage lors de l'activité.

Nous avons montré que lorsque le couvert forestier dans le paysage diminue, l'importance des sites de repos pour la circulation du sanglier dans son domaine vital augmente. Bien que le sanglier soit capable d'ajuster sa sélection de sites de repos au niveau d'anthropisation (en augmentant sa fréquence de réutilisation), il semble donc que sa dépendance envers les sites de repos forestiers pourrait le limiter dans son utilisation du paysage lors des phases d'activité, dans les paysages les moins forestiers. Nous n'avons pas trouvé d'effet direct de l'anthropisation sur la centralité des sites de repos. Néanmoins, il semble que la colinéarité du niveau d'anthropisation et du couvert forestier pourrait cacher une relation bel et bien existante. En effet, la diminution du couvert forestier est une caractéristique habituelle de l'anthropisation (Venter et al. 2016). Elle figure parmi les modifications du paysage pour l'agriculture, qui sont prises en compte dans le calcul du « human footprint index ». Ainsi, il est probable qu'en ajustant son comportement à la densité de couvert arboré, le sanglier réponde en réalité souvent à une modification du paysage liée aux activités humaines.

Par ailleurs, nous avons détecté un probable effet de l'interaction entre la densité du couvert forestier et le niveau d'anthropisation sur la contribution des sites de repos à la circulation des sangliers dans leur domaine vital. Ainsi dans les sites anthropisés mais dont le couvert forestier est important, l'utilisation de l'espace par le sanglier semble tout de même fortement contrainte par la localisation des sites de repos. Cet effet est nécessairement lié à des caractéristiques de l'anthropisation indépendantes de la réduction du couvert forestier. En particulier, le risque de dérangements (lié à la densité de peuplement qui est prise en compte dans le calcul du « human footprint index ») pourrait participer à réduire la disponibilité des sites de repos, et contraindre les déplacements du sanglier. Cependant, cet effet pourrait tout de même être lié à la structure de l'habitat, par exemple à une densité de sous-bois réduite dans les zones forestières anthropisées. Cet exemple illustre la difficulté que représente l'étude des effets des dérangements anthropiques sur l'utilisation de l'espace par les animaux sauvages. Le recours à des dérangements

expérimentaux peut être nécessaire pour mieux comprendre ces effets (Ordiz et al. 2013). L'étude des effets des variations temporaires de la présence humaine dans les milieux naturels (comme celles liées aux week-ends ou aux confinements liées à la pandémie de Covid-19) peut aussi s'avérer utile (Green et al. 2023; Olejarz et al. 2023).

## 2 Perspectives

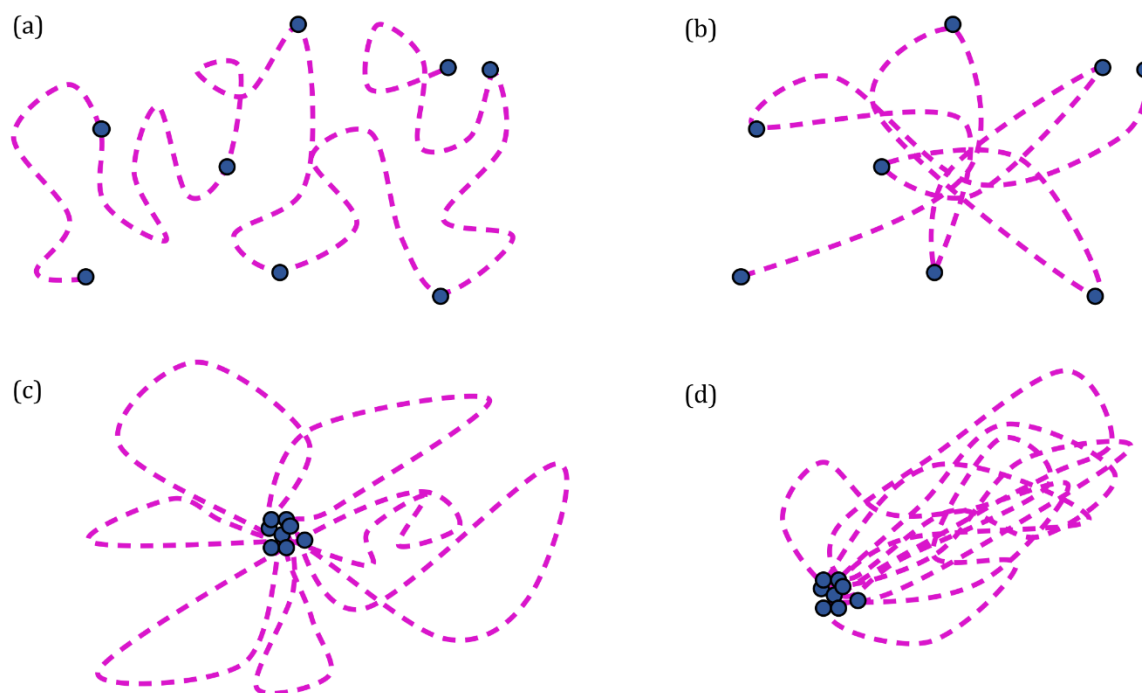
### 2.1 Patrons spatiaux d'utilisation des sites de repos

La disposition spatiale des sites de repos que le sanglier utilise influence sa capacité à circuler dans son domaine vital. Nous avons cherché à quantifier cet effet, en le reliant aux caractéristiques de l'environnement (taux d'anthropisation et couvert forestier). Nous avons montré que la centralité des sites de repos dans les patrons d'utilisation des domaines vitaux dépend des caractéristiques de l'environnement. Cependant les taux de réutilisation des sites de repos et des sites d'activité peuvent produire de nombreux patrons d'utilisation de l'espace (exemples en *Figure 2*), et des patrons contrastés peuvent certainement aboutir à un même rapport entre la centralité moyenne des sites de repos et celle des sites d'activité. Pour mieux comprendre l'influence de l'anthropisation sur les patrons d'utilisation des sites de repos des sangliers, il est donc nécessaire d'aller plus loin qu'un simple rapport entre valeurs moyennes de centralité. Il est probable que des patrons contrastés d'utilisation de l'espace (comme ceux présentés en *Figure 2*) puissent être distingués entre eux à l'aide de la distribution des valeurs de « betweenness centrality » (ou d'autres métriques issues des réseaux de déplacements) calculées pour chaque nœud. Néanmoins, inférer un patron d'utilisation de l'espace à partir de la distribution des valeurs de centralité liées aux différents sites de repos n'est pas intuitif. Il serait donc utile de recourir à un modèle individu-centré afin de simuler des trajectoires types, telles que celles présentées en *Figure 2*. Cela permettrait de définir pour chaque patron théorique d'utilisation de l'espace, les distributions types pour différentes métriques issues d'une analyse par les réseaux de déplacement, et ainsi de mieux interpréter les résultats issus d'animaux réels. Une telle approche pourrait permettre d'identifier des ajustements globaux de la stratégie spatiale d'utilisation des sites de repos et d'activité, en fonction de l'environnement.

### 2.2 Ajustements temporels du repos

Dans les chapitres 2 et 3, nous avons limité notre étude de la stratégie de repos du sanglier à son aspect spatial. Cependant, le sanglier répond également à l'anthropisation en modifiant son patron temporel d'activité. En effet, la nocturnalité, qui est le plus souvent observée chez cette espèce, représente en réalité un ajustement comportemental aux activités humaines omniprésentes, et notamment à la chasse (Podgórski et al. 2013; Johann et al. 2020). Plusieurs auteurs ont rapporté que les sangliers vivant dans des zones naturelles peu anthropisées sont

actifs en journée, tout comme le sont les sangliers élevés dans des parcs, et préservés de tout risque de dérangement anthropique (voir Johann et al. 2020). Une telle inversion du cycle d'activité a bien entendu de nombreuses conséquences sur les comportements actifs. Par exemple, l'efficacité de la recherche alimentaire, ou encore les interactions sociales sont certainement impactées par la différence de luminosité entre le jour et la nuit. Cependant, l'ajustement du patron temporel d'activité du sanglier impacte également les conditions dans lesquelles le repos se produit, et ces effets ne sont quasiment pas documentés.



**Figure 2.** *Patrons de mouvement d'individus présentant un contraste dans leurs taux de réutilisation des sites repos (cercles bleus) et des sites d'activité (lignes pointillées roses). (a & b) Faible et (c & d) fort taux de réutilisation des sites de repos. (a & c) Faible et (b & d) fort taux de réutilisation des sites d'activité.*

En se reposant de jour, le sanglier s'expose à des conditions climatiques différentes de celles qui prévalent la nuit, et en particulier, à des températures plus élevées. Cet animal, qui ne possède pas de glandes sudoripares, est sensible aux hautes températures, dont il se protège en se baignant. Ainsi, on peut imaginer que pour se reposer de jour, le sanglier soit contraint de sélectionner spécifiquement des sites plus frais et humides que ceux dans lesquels il pourrait se permettre de se reposer de nuit. Cette conséquence du repos diurne devrait être d'autant plus contraignante dans les environnements chauds et secs, dans lesquels les sites de repos frais et humides sont aussi les plus rares. Il a été proposé que la nocturnité du sanglier puisse constituer une stratégie de thermorégulation comportementale, par la concentration des comportements

actifs lors des périodes les plus fraîches (Brivio et al. 2017). Dans ce contexte, il se pourrait que la distribution spatiale des sites de repos devienne une contrainte importante à l'utilisation du paysage. Si la sélection d'un site thermiquement tamponné n'est pas suffisante à éviter l'hyperthermie lors des journées chaudes, la qualité du repos pourrait elle aussi être impactée (Harding et al. 2019). Pour aborder ces questions, une approche basée sur des relevés physiologique, au moyen de thermomètres embarqués enregistrant conjointement les température externe et température sous-cutanée serait pertinente (Ruf et al. 2023).

Par ailleurs, le niveau de vigilance requis constitue une autre contrainte liée au repos diurne, qui concerne plus spécifiquement les milieux anthropisés. En se reposant de jour, le sanglier accepte de soumettre sa phase de repos aux perturbations anthropiques, et en particulier, au risque de chasse. Or pour répondre efficacement à ce risque, un sanglier doit être en mesure de le percevoir, et de s'enfuir à temps si nécessaire. Les états comportementaux permettant la meilleure réactivité étant également les moins économes en énergie, on s'attend à ce qu'un compromis entre la qualité du repos et la sécurité émerge, dans les milieux concernés par la présence humaine. Olejarz et al. (2023) ont montré que dans une forêt récréative, un grand nombre de promeneurs pouvaient réduire la qualité du repos chez le sanglier, et augmenter les dépenses énergétiques. Les auteurs n'ont cependant pas détecté de conséquences notables sur les comportements actifs. On peut pourtant imaginer que la réduction de la qualité du repos puisse avoir un impact sur les performances des animaux lors de l'activité. De plus, il est probable que ces effets soient exacerbés chez des populations soumises à des pressions de chasse intenses. On pourrait alors peut être observer des phénomènes de compensation du temps de repos, avec par exemple des périodes de repos plus longues après les battues. Certains auteurs ont d'ailleurs observé une réduction des déplacements journaliers du sanglier à la suite d'évènements de chasse (Morelle et al. 2015), ce qui pourrait suggérer un phénomène de compensation, potentiellement lié à la dégradation du repos. Un tel mécanisme se rapprocherait du « rebond » souvent observé en laboratoire après privation de sommeil chez de nombreuses espèces (Marinesco et al. 1999; Raap et al. 2016), mais rarement documenté dans des conditions naturelles (Reinhardt 2020). La meilleure approche pour documenter l'existence d'un phénomène de compensation du temps de repos faisant suite à un dérangement serait de mener des dérangements expérimentaux sur des animaux suivis par télémétrie. Un protocole similaire aux essais réalisés au cours de cette thèse pourrait être mis en place, mais nécessiterait un suivi télémétrique adapté à la détection de plusieurs niveaux de vigilance, comme par exemple un suivi accélérométrique fin ou un suivi du rythme cardiaque (Libourel 2022; Olejarz et al. 2023).



### 2.3 Influence de la socialité

Dans les chapitres 2 et 3, nous avons ignoré un aspect peut être fondamental du comportement de repos : son contexte social. Malgré le caractère profondément social du sanglier, l'influence des interactions intraspécifiques sur son comportement spatial demeure mal connue (Morelle et al. 2015). Ce déficit de connaissance est fortement lié aux difficultés que représentent les observations des comportements sociaux chez cette espèce. L'étude du comportement souvent cryptique du sanglier passe généralement par une approche télémétrique, qu'il est difficile d'adapter à l'étude de la socialité. Pour être exploré, ce sujet nécessiterait par exemple le déploiement de capteurs de proximité sur tous les individus de plusieurs groupes sociaux, à la suite de captures groupées.

Le sanglier est capable d'apprendre de ses congénères, et garde en mémoire les endroits qu'il visite (Mendl et al. 2010; Gieling et al. 2011). Il est probable qu'il ait recours à des informations acquises auprès d'autres individus pour s'orienter au cours de ses déplacements. On peut imaginer que de la même façon, des informations circulent entre individus à propos de la localisation et de la qualité des sites de repos existant dans le paysage (Kaminski et al. 2005). Ainsi, le caractère social du sanglier joue probablement un rôle important dans la dynamique d'utilisation de l'espace pour le repos. Les sangliers forment des groupes sociaux dont l'organisation matrilineaire est relativement stable (Podgórski and Śmietanka 2018), mais laisse place à des mouvements d'individus entre groupes, en particulier de la part des mâles (Maselli et al. 2014), mais aussi de certaines femelles (Kaminski et al. 2005; Poteaux et al. 2009). Par ailleurs, cette organisation sociale peut être déstabilisée par les prélèvements liés à la chasse (Poteaux et al. 2009; Maselli et al. 2014). En plus d'être transmises aux juvéniles, les informations concernant la localisation et la qualité des sites de repos pourraient donc aussi circuler entre groupes sociaux par les déplacements d'individus, permettant ainsi la découverte de nouveaux sites de repos de manière plus probable qu'à travers une exploration aléatoire du paysage. Dans les paysages anthropisés, où les déplacements sont contraints, et où les sites de repos adéquats sont rares, un tel transfert d'informations pourrait grandement faciliter l'installation et la persistance d'une densité importante d'animaux. Ce mécanisme pourrait être particulièrement efficace dans les paysages soumis à des transformations rapides, dans lesquels la disposition des sites de repos potentiels, ainsi que leur qualité, sont temporellement instables.

Qu'il y ait partage d'informations concernant leur localisation ou non, une disponibilité limitée des sites de repos peut donner lieu à un usage simultané de ces sites par plusieurs groupes sociaux. L'influence des interactions entre groupes sociaux dans le comportement spatial du sanglier est mal comprise (Morelle et al. 2015), et diffère peut-être le long du gradient d'anthropisation. On peut se demander si plusieurs groupes peuvent se tolérer dans le même site

de repos, et si le niveau de tolérance est affecté par la disponibilité en sites potentiels. Si les groupes sociaux ne se tolèrent pas lors de leur phase de repos, la compétition pour les sites de repos est inévitable dans les paysages où ceux-ci sont rares. Dans le cas contraire, le regroupement d'individus au niveau de sites de repos stratégiques pourrait favoriser les échanges de pathogènes, et jouer un rôle dans les dynamiques épidémiologiques de maladies telles que la peste porcine africaine (Podgórski and Śmietanka 2018). Dans tous les cas, les aspects sociaux du comportement du sanglier ont certainement un impact important sur la dynamique d'utilisation des sites de repos, dans les paysages où ceux-ci sont rares.

### 3 Conclusion

De nombreuses espèces animales subissent une réduction de la disponibilité des sites de repos dans les milieux anthropisés, parfois de manière très contraignante. Cela ne concerne pas seulement les milieux urbains, mais aussi de nombreux paysages agricoles et semi-naturels. Dans les milieux pauvres en sites de repos, les espèces peuvent entrer en compétition pour ces sites. Par ailleurs, les milieux anthropisés exposent de nombreuses espèces animales à des dérangements directs du repos, par la présence d'êtres humains dans les milieux où les animaux se reposent. Les animaux qui le peuvent ajustent leur comportement de repos aux conditions nouvelles, pour limiter les effets négatifs de l'anthropisation. Afin de mieux comprendre l'influence actuelle et à venir de l'anthropisation sur le comportement des animaux, ainsi que sur l'abondance et la distribution des espèces, il est essentiel d'étudier plus en détail les stratégies de repos animales, qui recèlent d'une part inexploree des ajustements comportementaux aux activités humaines. Pour survivre dans certains milieux anthropisés, les animaux doivent modifier les conditions dans lesquelles ils se reposent. Bien que ces modifications du comportement de repos permettent la persistance de certaines espèces là où elles auraient disparu sans ajustement, elles sont également à l'origine de contraintes qui dépassent le cadre des phases de repos. Ainsi, l'étude du comportement de repos pose un grand nombre de questions qui relèvent de l'utilisation de l'espace, des patrons temporels d'activité, mais aussi des conditions physiques et physiologiques des individus. L'approfondissement des questions liées aux stratégies de repos semble essentiel à la compréhension des enjeux liés à l'anthropisation, et pourrait apporter de nouvelles perspectives aux champs de la conservation et de la gestion des populations animales.



## Références

Brivio F, Grignolio S, Brogi R, Benazzi M, Bertolucci C, Apollonio M. 2017. An analysis of intrinsic and extrinsic factors affecting the activity of a nocturnal species: The wild boar. *Mamm Biol.* 84(1):73–81. doi:10.1016/j.mambio.2017.01.007.

Candolin U, Fletcher RJ, Stephens AEA. 2023. Animal behaviour in a changing world. *Trends in Ecology & Evolution.* 38(4):313–315. doi:10.1016/j.tree.2023.02.006.

Gieling ET, Nordquist RE, van der Staay FJ. 2011. Assessing learning and memory in pigs. *Anim Cogn.* 14(2):151–173. doi:10.1007/s10071-010-0364-3.

Green AM, Young E, Keller H, Grace T, Pendergast ME, Şekercioğlu ÇH. 2023. Variation in human diel activity patterns mediates periodic increases in recreational activity on mammal behavioural response: investigating the presence of a temporal ‘weekend effect.’ *Animal Behaviour.* 198:117–129. doi:10.1016/j.anbehav.2023.02.002.

Harding EC, Franks NP, Wisden W. 2019. The Temperature Dependence of Sleep. *Frontiers in Neuroscience.* 13. doi:10.3389/fnins.2019.00336.

Johann F, Handschuh M, Linderoth P, Dormann CF, Arnold J. 2020. Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. *BMC Ecology.* 20(4). doi:10.1186/s12898-019-0271-7.

Kaminski G, Brandt S, Baubet E, Baudoin C. 2005. Life-history patterns in female wild boars (*Sus scrofa*): mother–daughter postweaning associations. *Can J Zool.* 83(3):474–480. doi:10.1139/z05-019.

Korstjens AH, Lehmann J, Dunbar RIM. 2010. Resting time as an ecological constraint on primate biogeography. *Animal Behaviour.* 79(2):361–374. doi:10.1016/j.anbehav.2009.11.012.

Lesku JA, Rattenborg NC. 2022. The missing cost of ecological sleep loss. *SLEEP Advances.* 3(1):zpac036. doi:10.1093/sleepadvances/zpac036.

Libourel P-A. 2022. Chapter 9 - Wireless vigilance state monitoring. In: Murillo-Rodriguez E, editor. *Methodological Approaches for Sleep and Vigilance Research.* Academic Press. p. 171–189. doi:10.1016/B978-0-323-85235-7.00009-0

Marinesco S, Bonnet C, Cespuglio R. 1999. Influence of stress duration on the sleep rebound induced by immobilization in the rat: a possible role for corticosterone. *Neuroscience*. 92(3):921–933. doi:10.1016/s0306-4522(99)00045-7.

Maselli V, Rippa D, Russo G, Ligrone R, Soppelsa O, D’Aniello B, Raia P, Fulgione D. 2014. Wild boars’ social structure in the Mediterranean habitat. *Italian Journal of Zoology*. 81(4):610–617. doi:10.1080/11250003.2014.953220.

Mendl M, Held S, Byrne R. 2010. Pig cognition. *Current Biology*. 20:R796–R798. doi:10.1016/j.cub.2010.07.018.

Mohanty NP, Wagener C, Herrel A, Thaker M. 2022. The ecology of sleep in non-avian reptiles. *Biological Reviews*. 97(2):505–526. doi:10.1111/brv.12808.

Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P. 2015. Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*. 45(1):15–29. doi:10.1111/mam.12028.

Olejarz A, Faltusová M, Börger L, Güldenpfennig J, Jarský V, Ježek M, Mortlock E, Silovský V, Podgórski T. 2023. Worse sleep and increased energy expenditure yet no movement changes in sub-urban wild boar experiencing an influx of human visitors (anthropulse) during the COVID-19 pandemic. *Science of The Total Environment*. 879:163106. doi:10.1016/j.scitotenv.2023.163106.

Ordiz A, Støen O-G, Sæbø S, Sahlén V, Pedersen BE, Kindberg J, Swenson JE. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*. 50(2):306–314. doi:10.1111/1365-2664.12047.

Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*. 94(1):109–119. doi:10.1644/12-MAMM-A-038.1.

Podgórski T, Śmietanka K. 2018. Do wild boar movements drive the spread of African Swine Fever? *Transboundary and Emerging Diseases*. 65(6):1588–1596. doi:10.1111/tbed.12910.

Poteaux C, Baubet E, Kaminski G, Brandt S, Dobson FS, Baudoin C. 2009. Socio-genetic structure and mating system of a wild boar population. *Journal of Zoology*. 278(2):116–125. doi:10.1111/j.1469-7998.2009.00553.x.

Raap T, Pinxten R, Eens M. 2016. Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution*. 215:125–134. doi:10.1016/j.envpol.2016.04.100.

Rattenborg NC, de la Iglesia HO, Kempnaers B, Lesku JA, Meerlo P, Scriba MF. 2017. Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 372(1734):20160251. doi:10.1098/rstb.2016.0251.

Reinhardt KD. 2020. Wild primate sleep: understanding sleep in an ecological context. *Current Opinion in Physiology*. 15:238–244. doi:10.1016/j.cophys.2020.04.002.

Ruf T, Vetter SG, Painer-Gigler J, Stalder G, Bieber C. 2023. Thermoregulation in the wild boar (*Sus scrofa*). *J Comp Physiol B*. doi:10.1007/s00360-023-01512-6.

Ungurean G, van der Meij J, Rattenborg NC, Lesku JA. 2020. Evolution and plasticity of sleep. *Current Opinion in Physiology*. 15:111–119. doi:10.1016/j.cophys.2019.12.013.

Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, Fekete BM, et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun*. 7(1):12558. doi:10.1038/ncomms12558.

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*. 96(7):1741–1753. doi:10.1890/14-1401.1.







**Résumé :** Le repos est essentiel dans la vie des animaux et occupe une part prépondérante de leur temps quotidien. Le repos répond à de nombreux stimuli internes et externes et les animaux développent des stratégies de repos pour s'accommoder des contraintes physiologiques et écologiques. Les conditions dans lesquelles le repos a lieu sont ajustés de manière flexible aux conditions environnementales changeantes, mais les conséquences de ces ajustements sont rarement étudiées. L'anthropisation est une cause majeure d'ajustements comportementaux, et peut affecter le repos à travers de nombreux mécanismes. Pourtant, ses effets sur les stratégies de repos restent peu étudiés à ce jour. Dans cette thèse, nous résumons la littérature scientifique existant au sujet des déterminants et des conséquences des stratégies de repos, et nous étudions les mécanismes par lesquels les activités humaines peuvent affecter le repos chez les animaux. Dans un second temps, nous explorons les effets de l'anthropisation sur les stratégies de repos du sanglier (*Sus scrofa*). Nous utilisons des données GPS et actimétriques provenant de suivis télémétriques pour nous concentrer sur la sélection des sites de repos par cette espèce. Nous examinons les effets de deux aspects de l'anthropisation : les dérangements directs et les modifications de l'habitat. Nous décrivons comment les sangliers adaptent leur utilisation du paysage pour se reposer en réponse à l'activité humaine. Nous évaluons ensuite l'efficacité de cette stratégie pour atténuer le risque d'être dérangé. Enfin, nous explorons l'effet de la sélection de sites de repos sur la capacité des sangliers à circuler dans le paysage.

**Abstract:** Resting is an essential aspect of animals' lives and represents substantial portions of time budgets. Animals may rest in response to a variety of internal and external stimuli and they develop resting strategies to cope with both physiological and ecological constraints. When, where, how and how long animals rest is tuned to flexibly deal with changing environmental conditions. Yet the outcomes of these adjustments of resting are rarely investigated. Anthropization is a major driver of behavioral adjustments and resting behaviors are sensitive to human activities through a variety of mechanisms. Yet, the effects of anthropization on resting strategies are understudied to date. In this thesis, we review the literature about the drivers and outcomes of resting strategies, and we investigate the possible mechanisms through which human activity may affect animals' rest. As a case study, we explore the effects of anthropization on wild boars' (*Sus scrofa*) resting strategies. We use GPS and actimetric data from various telemetric surveys of wild boar populations to focus on the selection of resting sites by this species. We examine the effects of two aspects of anthropization: direct disturbances and habitat modifications. We describe how wild boars adjust their use of the landscape for resting in response to human activity. We then evaluate the efficiency of this strategy in mitigating the risk of being disturbed. Finally, we explore how resting site selection may affect wild boars' ability to circulate through the landscape.