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Amédée Roy

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# Thèse pour obtenir le grade de Docteur de L'Université de Montpellier

En Sciences de la Mer  
École doctorale GAIA  
Unité de Recherche MARBEC

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## Caractérisation et simulation multi-échelle des mouvements d'oiseaux marins tropicaux: une approche par apprentissage profond

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Présentée par Amédée Roy  
Le 30/11/2022

Sous la direction de Sophie LANCO BERTRAND et de Ronan FABLET

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UNIVERSITÉ  
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# RÉSUMÉ

L'étude du mouvement des oiseaux marins est fondamentale pour comprendre la manière dont ils interagissent avec leur environnement, et pour élaborer des politiques de conservation des écosystèmes marins. En réponse à l'accumulation récente des données décrivant leurs déplacements et leurs habitats, cette thèse propose de caractériser et de simuler les mouvements d'oiseaux marins tropicaux en utilisant des approches d'intelligence artificielle, et plus précisément d'apprentissage profond. Dans un premier temps, on utilise des réseaux de neurones convolutifs pour l'identification d'habitats d'oiseaux marins à partir de données satellites, et pour la description de leurs comportements à partir de trajectoires GPS. Ces outils sont en mesure d'exploiter des données hétérogènes en prenant en compte plusieurs échelles spatio-temporelles. Ils définissent des métriques de fouille de données pertinentes de manière automatique et généralisable à l'analyse du mouvement d'autres espèces d'oiseaux. Dans un second temps, on utilise des réseaux génératifs afin de simuler les trajectoires de recherche alimentaires d'oiseaux marins. La plupart des outils existants de simulation du mouvement, tels que les marches aléatoires, se concentrent principalement sur les statistiques à petite échelle des données des trajectoires et ne parviennent pas à reproduire un modèle de mouvement réaliste à grande échelle. On montre ici que les réseaux antagonistes profonds sont capables de reproduire les caractéristiques géométriques aussi bien aux petites qu'aux grandes échelles. Ces résultats suggèrent que les modèles génératifs peuvent devenir une solution pragmatique pour simuler et prédire des processus stochastiques complexes, tels que les trajectoires d'oiseaux marins, dont les règles mécanistes qui les sous-tendent ne sont pas claires ou trop difficiles à formuler de manière analytique.

**Mots clefs :** Oiseaux marins ; Écologie du mouvement ; Bio-logging ; Zone de reproduction ; Zone d'alimentation ; Simulation de trajectoires ; Apprentissage profond ; Réseaux de neurones ; Réseaux antagonistes profonds



# ABSTRACT

The study of seabird movement is fundamental to understanding how seabirds interact with their environment, and to developing conservation policies for marine ecosystems. In response to the recent accumulation of data describing their movements and habitats, this thesis proposes to characterise and simulate the movements of tropical seabirds using artificial intelligence approaches, more specifically deep learning. On one hand, convolutional neural networks are used to identify seabird habitats from satellite data and to describe their behaviour from GPS trajectories. These tools are able to exploit heterogeneous data by taking into account several spatio-temporal scales. They automatically define relevant data mining metrics that can be generalised to the analysis of the movement of other bird species. On the second hand, generative networks are used to simulate foraging trajectories of seabirds. Most of the existing movement simulation tools, such as random walks, focus mainly on small-scale statistics of trajectory data and fail to reproduce realistic large-scale movement patterns. Here we show that generative adversarial networks are able to reproduce geometric features at both small and large scales. These results suggest that generative models can become a pragmatic solution for simulating and predicting complex stochastic processes, such as seabird trajectories, for which the underlying mechanistic rules are unclear or too difficult to be analytically formulated.

**Keywords :** Seabirds ; Movement ecology ; Bio-logging ; Breeding area ; Foraging area ; Trajectory simulation ; Deep learning ; Neural networks ; Generative adversarial networks



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# Résumé en français

## Introduction

Espèces souvent perçues comme charismatiques, et utilisées comme ‘drapeau ou parapluie’ dans les politiques de conservation, les oiseaux marins sont au premier plan des préoccupations de déclin de biodiversité (Hays et al., 2016; Hazen et al., 2019). Dans ce contexte, il est donc fondamental de définir des outils afin d’évaluer la vulnérabilité des oiseaux marins et leurs réponses aux éventuels changements des habitats. L’étude de ces espèces bénéficie depuis une vingtaine d’années des progrès techniques importants du biologging. Des données de plus en plus massives et variées sont collectées sur leurs déplacements (GPS, géolocalisation basée sur la lumière, réseaux de suivi acoustique, etc.), et sur les conditions d’environnement qu’ils traversent (Yoda, 2019; Nathan et al., 2022). La spécificité de ces enregistrements, intrinsèquement spatio-temporels, a conduit à l’émergence d’un champ de recherche propre, l’écologie du mouvement. Cette discipline se concentre sur la caractérisation et la prédiction des mouvements des organismes, afin de comprendre les mécanismes sous-jacents, d’évaluer la source de variabilité liée à des facteurs externes et de prédire les mouvements pour des conditions inédites (Nathan et al., 2008). Il existe donc plusieurs familles d’outils afin de décrire, d’identifier les sources de variabilité, et de simuler les stratégies de mouvements d’oiseaux marins (Turchin, 1998; Smouse et al., 2010; Seidel et al., 2018). En revanche, la plupart de ces outils sont limités, car ils reposent sur des hypothèses trop simplistes sur les mécanismes du mouvement. Par exemple, la plupart des approches qui visent à identifier les facteurs environnementaux du mouvement à grande échelle, reposent sur des outils statistiques classiques sans composante spatiale ou temporelle explicite, et ignorent généralement la nature spatio-temporelle des données de mouvement (Tremblay et al., 2009; Joo et al., 2022). De plus, les outils populaires de simulation de trajectoires, tels que les marches aléatoires, sont calibrés sur les distributions de déplacements élémentaires, et souvent ne considèrent pas les mécanismes à plus large échelle (Codling et al., 2008; Smouse et al., 2010). Les outils statistiques utilisés en écologie consistent souvent en des modèles paramétriques qui sont ajustés aux données d’observation pour révéler des relations statistiques spécifiques à partir d’ensembles de données brutes. Cette famille d’outils statistiques a récemment été étendue avec l’arrivée de l’apprentissage profond dans les années 2010. L’apprentissage profond repose sur les mêmes principes théoriques que les outils statistiques habituels, mais il a récemment obtenu de meilleures performances sur de nombreuses tâches, notamment grâce à l’augmentation récente des capacités de calcul des ordinateurs et des jeux de données. En particulier, il permet d’extraire des caractéristiques de données complexes et multi-échelles directement à partir de données brutes en transformant les entrées en plusieurs couches d’unités de traitement (LeCun et al., 2015; Goodfellow et al., 2016).

L'objectif de cette thèse est donc d'explorer différents outils d'apprentissage profond pour la caractérisation et la simulation des mouvements des oiseaux marins tropicaux. Dans un premier temps, les modèles discriminatifs sont étudiés pour l'identification des zones de reproduction et d'alimentation des oiseaux marins. Dans un second temps, des réseaux génératifs sont introduits et illustrés afin de simuler des trajectoires de recherche alimentaires d'oiseaux marins.

## Données

Historiquement, les mouvements des oiseaux de mer n'étaient enregistrés que par des observations directes, et s'appuyant le plus souvent sur la méthodologie de marquage-recapture. Dans ce contexte, le mouvement est décrit par la présence ou non d'individus à un endroit et un moment donnés. Récemment, des avancées technologiques dans la miniaturisation des capteurs électroniques ont révolutionné la compréhension de l'écologie des mouvements des oiseaux de mer. En attachant directement des capteurs GPS sur les oiseaux, il est désormais possible de mesurer leurs positions au cours du temps. De plus, des capteurs de pression (TDR) sont également souvent déployés pour renseigner leurs plongées. Dans le cadre de cette thèse, nous avons utilisé à la fois des données de présence/absence ainsi que des données de tracking.

### Présence/Absence de site de nidification

Nous avons compilé les informations disponibles sur les sites de reproduction de laridés à Cuba à partir de publications, livres, et rapports de projets scientifiques. Les laridés constituent le groupe d'oiseaux de mer le mieux représenté dans cette zone tropicale avec 25 espèces dont 36% sont des reproducteurs (Navarro, 2021). En revanche, l'archipel de Cuba ne dispose pas d'un inventaire complet des lieux de reproduction des oiseaux marins, en raison de restrictions économiques et logistiques et de la rareté des ressources humaines spécialisées. Au total, 49 sites ont été répertoriés comme lieux de nidifications de neuf espèces de laridés. De plus, afin de comprendre ce qui différencie des sites de reproduction de site non sélectionnés par les oiseaux marins, nous avons choisi 52 sites connus pour ne pas accueillir de colonies de laridés en 2020 sur les côtes de l'archipel de Cuba. Cela constitue donc un petit jeu de données de présence/absence d'oiseaux afin d'étudier les mouvements concernant la sélection d'habitat de reproduction des laridés dans cette zone tropicale peu étudiée.

### Trajectoires de recherche alimentaire en période de reproduction

Nous avons utilisé une base de données de déploiement de 421 GPS, et de 202 TDR sur des sulidés (*Sula variegata*, SV ; *Sula dactylatra*, SD ; *Sula sula*, SS) et des phalacrocoracidés (*Leucocarbo bougainvili*, LB) nichant au Brésil et au Pérou. Ces déploiements permettent en particulier de décrire les trajectoires d'oiseaux à des hautes résolutions (0.05 - 1 Hz). Ils sont en revanche limités aux périodes de reproductions pour des raisons pratiques de probabilités de capture des oiseaux, puisque pendant ces périodes, ils reviennent très régulièrement sur leur nid. La table suivante détaille notamment les données disponibles par site, et par espèce. Une Shiny App a été développée au cours de cette

thèse pour l’exploration et la visualisation de ce jeu de données<sup>1</sup>.

Pays	Colonie	Espèces	GPS	TDR
Brésil	Fernando de Noronha	SS	44	19
		SD	56	35
Pérou	Isla Guanape	SV	46	23
	Isla Pescadores	SV	179	57
		LB	96	68

Table 1: **Résumé des données GPS et TDR utilisées dans cette thèse** - SS = *Sula sula*, fous à pieds rouges ; SD = *Sula dactylatra*, fous masqués ; SV = *Sula variegata*, fous variés ; LB = Leucocarbo bougainvilli, cormorans des Bougainville

Les fous variés et les cormorans de Guanay suivis au Pérou se reproduisent dans un système d’upwelling très productif, le système du courant de Humboldt (HCS), et se nourrissent des mêmes proies, à savoir les anchois du Pérou. Cependant, on sait qu’ils ont des stratégies de recherche de nourriture distinctes : les fous sont des plongeurs qui atteignent en moyenne environ 2 m de profondeur et passent la plupart du temps en vol, tandis que les cormorans plongent plus profondément et plus longtemps en moyenne, atteignant jusqu’à 30 m de profondeur, et passent jusqu’à 40 % du temps à se reposer à la surface de l’eau (Weimerskirch et al., 2012). De plus, leurs comportements sociaux diffèrent puisque cormorans de Guanay quittent leur colonie en se dirigeant vers des groupes d’autres oiseaux au repos, alors que les fous du Pérou se fient principalement à des informations personnelles basées sur la mémoire pour se diriger au départ Weimerskirch et al. (2010). Les fous masqués et à pied rouges qui se reproduisent à Fernando de Noronha ont des techniques de plongées similaires aux fous variés du Pérou. En revanche, ils s’alimentent principalement dans des eaux oligotrophes (de Santana Campelo et al., 2019) et se nourrissent surtout de poissons et d’encornets volants (Mancini et al., 2014). Leurs stratégies de recherche de nourriture diffèrent alors de celles des fous variés, car ils effectuent des trajets plus longs et passent plus de temps à se reposer à la surface de la mer (cf. Chapitre 3).

## Méthodes

Le mouvement est défini par le changement de localisation d’un ou plusieurs individus au fil du temps. Il existe deux approches pour décrire le mouvement, l’approche Lagrangienne qui observe le mouvement d’un organisme individuel, et l’approche Eulérienne qui s’intéresse à la dynamique de la distribution spatiale d’une population (Turchin, 1998). Avant l’utilisation de capteurs électroniques, les analyses de mouvement étaient essentiellement réalisées dans une perspective eulérienne et à l’échelle d’une population. Les données GPS ont permis de décrire les processus sous-jacents au mouvement d’individus précis et donc avec une approche Lagrangienne. Ici, on propose de classer les approches usuelles pour l’analyse de données en trois groupes, en fonction de l’échelle

<sup>1</sup><https://amdroy.shinyapps.io/seabirdmap/>

spatio-temporelle associée : le déplacement élémentaire, la trajectoire ou la population. Les deux premières ont un point de vue Lagrangien du mouvement tandis que la dernière concerne des approches eulériennes.

### Approches classiques

- L'analyse au niveau du **déplacement élémentaire** se concentre principalement sur les distributions des pas successifs qui constituent la trajectoire d'un individu. Ces approches basées sur des marches aléatoires servent la plupart du temps à classer ces déplacements en les associant à un mode comportemental tel que le vol, le repos ou la plongée. Elles sont également utilisées pour simuler des trajectoires, et notamment en servant de 'modèle nul' pour tester différentes hypothèses concernant le mouvement. Par exemple, elles permettent de générer des pseudos-absences qui sont utilisés dans les modèles d'habitat (voir analyse au niveau d'une population). Cela concerne les marches aléatoires corrélées, les marches de Lévy, les modèles de Markov à état cachés, et les équations différentielles stochastiques (e.g. Bergman et al., 2000; Viswanathan et al., 2008; McClintock et al., 2012; Michelot et al., 2018).
- L'analyse au niveau d'une **trajectoire** consiste généralement à décrire les propriétés géométriques d'une trajectoire en utilisant des métriques générales, comme la durée, la distance ou la sinuosité (Seidel et al., 2018). Elles sont ensuite souvent utilisées pour des études statistiques classiques (test statistiques, modèles linéaires généralisés, analyse de variance, etc), afin d'explorer les sources de variabilités (e.g. Kappes et al., 2011; Lerma et al., 2020a; Phillips et al., 2021).
- L'analyse au niveau d'une **population** s'intéresse aux distributions et aux flux d'un groupe d'individus au cours du temps. Elle est généralement associée à la modélisation de l'habitat, qui consiste à modéliser la densité animale à partir des caractéristiques de l'habitat (par ex. caractéristiques océanographiques, disponibilité de la nourriture...). Les outils utilisés pour faire ces régressions logistiques incluent les modèles linéaires, les géostatistiques, ainsi que certaines approches d'apprentissage statistique comme les arbres de décisions aléatoires (e.g. Pettex et al., 2017; Hindell et al., 2020; Fauchald et al., 2021).

Dans la plupart des études, la pratique courante consiste donc à effectuer séparément et parfois séquentiellement ces analyses au niveau des déplacements élémentaires, des trajectoires et des populations. Tout d'abord, en identifiant les plongées des oiseaux marins, puis en évaluant les statistiques des voyages et des plongées, et enfin en modélisant des habitats et des zones d'alimentation. Ces trois niveaux d'analyse sont principalement utilisés pour décrire et caractériser les trajectoires des oiseaux marins, tandis que les outils au niveau de la population sont occasionnellement utilisés pour des tâches prédictives.

### Enjeux et tendances

La clé pour comprendre et simuler un processus écologique, tel que le mouvement, réside dans l'identification des mécanismes qui régissent les données de mouvement observées (Nathan et al., 2008). Les analyses au niveau du déplacement élémentaire sont très utiles pour caractériser les statistiques au niveau des pas, mais elles sont cependant rapidement limitées pour la prédiction et la simulation de trajectoires sur des échelles

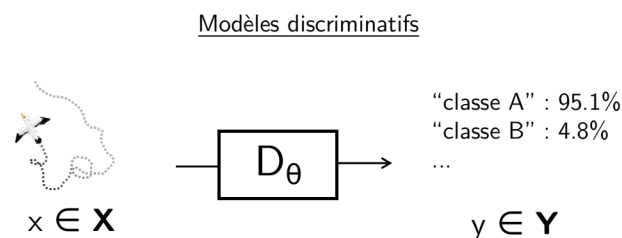
spatio-temporelles plus grandes. En effet, elles reposent sur de nombreuses hypothèses, où l'on suppose souvent que les individus cherchent sans connaissance de leur environnement, et où l'hypothèse markovienne implique que la probabilité de chaque déplacement élémentaire ne dépende que du déplacement précédent. Les oiseaux marins sont pourtant connus pour leurs capacités de navigation, percevant des bateaux de pêche, ou d'autres congénères à des dizaines de kilomètres (e.g. Thiebault et al., 2014; Collet et al., 2017). Ils sont également connus pour leurs capacités cognitives, comme la mémoire, et pour faire appel à des facteurs externes pour naviguer, comme le vent (e.g. Meyer et al., 2020; Ventura et al., 2020). Les trajectoires simulées à partir de marches aléatoires trop simplistes conduisent donc souvent à des trajectoires irréalistes. De plus, la plupart des analyses qui caractérisent le mouvement à l'échelle d'une trajectoire ou d'une population sont basées sur des outils statistiques classiques sans composante spatiale ou temporelle explicite, et qui reposent sur des hypothèses statistiques de normalité, d'homoscédasticité et d'indépendance (Joo et al., 2022). Ainsi, elles ignorent généralement la nature spatio-temporelle des données de mouvement, ou alors, elles traitent l'auto-corrélation de données trajectométriques comme une nuisance pour l'inférence statistique (Tremblay et al., 2009). Ces approches mettent en corrélation les stratégies de mouvement émergentes avec des facteurs externes, mais souvent, elles n'arrivent pas à rendre compte des processus qui les ont engendrés. C'est pourquoi de nombreuses études recommandent le développement de nouvelles méthodes d'analyse des données de mouvement en intégrant plusieurs échelles spatio-temporelles simultanément et en prenant mieux en compte les interactions entre les oiseaux de mer et leurs habitats.

Parmi les méthodes envisagées, une grande partie de la littérature s'applique à développer des modèles de mouvements basés sur des marches aléatoires hiérarchiques et dont les paramètres dépendent de variables environnementales (e.g. Avgar et al., 2016; Leos-Barajas et al., 2017). Ces modèles probabilistes de mouvement sont principalement calibrés par maximisation de la vraisemblance ou par inférence bayésienne approximative. Il est cependant souvent difficile d'en estimer les paramètres, en particulier lorsque la complexité des modèles augmente (Michelot et al., 2017; Adam et al., 2019). Les marches aléatoires sont également parfois intégrées à des modèles individus-centrés qui forment de manière explicite les interactions entre un individu et son environnement (Avgar et al., 2013). S'ils fournissent une solution pragmatique pour simuler des processus écologiques non linéaires, ils manquent cependant de généralité et sont souvent difficiles à calibrer directement à partir de données observées (Grimm et al., 2005; DeAngelis and Grimm, 2014). Pour ces raisons, quelques études ont suggéré d'explorer les méthodes d'apprentissage profond pour la caractérisation et la simulation multi-échelle des mouvements d'humains et d'animaux. Par exemple, des réseaux de neurones artificiels ont été proposés pour faire des modèles d'habitats et pour identifier les modes comportementaux des déplacements élémentaires de trajectoire d'oiseaux (Browning et al., 2018). De plus, d'autres familles de réseaux de neurones ont été utilisées pour prédire la localisation future d'un animal à partir d'une séquence de ses localisations précédentes (Rew et al., 2019; Wijeyakulasuriya et al., 2020), ou pour l'analyse comparative de différents types de trajectoires (Maekawa, 2020). Enfin, des réseaux génératifs ont été appliqués à la simulation de trajectoires de piétons, de taxis ou d'avions, mais à notre connaissance, ils n'ont pas encore été utilisés pour la simulation de trajectoires d'oiseaux marins (e.g. Gao et al., 2020; Wang et al., 2021a; Aksoy et al., 2021).

## Méthodes d'apprentissage profond

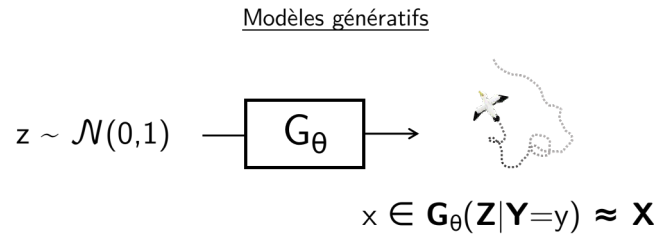
L'apprentissage profond fait référence à un type spécifique d'outil d'apprentissage statistique, basé sur les réseaux de neurones profonds. Un réseau de neurones est une fonction paramétrique composée de multiples unités de traitement élémentaire, appelés neurones. Le terme "neurone" est notamment utilisé pour des raisons historiques, car les premiers réseaux de neurones développés dans les années 1950 étaient directement inspirés du fonctionnement des systèmes nerveux. Dans les réseaux de neurones modernes, il existe désormais une grande variété d'unités de traitement, et leur conception est davantage guidée par des considérations numériques que par des connaissances issues des neurosciences. Les réseaux neuronaux peuvent donc être considérés, de manière plus générale, comme une composition de plusieurs couches d'opérations qui constituent des "blocs" de construction pour des réseaux plus complexes et profonds. En pratique, les réseaux de neurones comportant davantage de couches ont généralement de meilleures performances, et sont appelés réseaux profonds pour cette raison (LeCun et al., 2015).

Pour un réseau de neurones donné, c'est-à-dire avec un nombre et un type de couches définis, l'estimation des différents paramètres qui régissent les unités de traitement élémentaires composant un réseau de neurone, se fait ensuite en utilisant des algorithmes de descente de gradient. Ces approches consistent à estimer des valeurs de paramètres de manière itérative dans le but de minimiser une fonction objectif (ou fonction de coût) définie préalablement. Les outils récents de mise en œuvre des réseaux profonds, tels que la bibliothèque PYTORCH (Paskze et al., 2019), permettent désormais d'optimiser relativement facilement de nouvelles architectures de réseaux profonds, et en définissant des fonctions de coût spécifique à chaque application. Ainsi, il existe une grande variété d'architectures de réseaux et de stratégies d'apprentissage distinctes. En fonction de leurs objectifs et leurs applications, on propose ici de distinguer deux familles de réseaux profonds : les modèles discriminatifs et les modèles génératifs.



**Modèles discriminatifs (ou discriminateur)** Les réseaux discriminatifs cherchent à caractériser des observations en identifiant leurs propriétés spécifiques. La plupart des approches d'apprentissages profonds consistent en des modèles discriminatifs, par exemple pour des tâches de classification, de régression ou de segmentation de données (Goodfellow et al., 2016). Ils sont typiquement entraînés dans un cadre d'un apprentissage dit 'supervisé', où des jeux de données labellisés sont nécessaires pour apprendre aux modèles à prédire un label à partir de l'échantillon associé. Les réseaux de neurones convolutifs (CNN) constituent un exemple d'architecture populaire utilisée dans des modèles discriminatifs. Les réseaux de neurones convolutifs se composent d'une succession de couches dites convolutives, d'activation, de mise en commun et de normalisation. Ils ont été largement

utilisés dans la classification d'images au cours des dernières décennies, puisqu'ils sont capables, grâce à l'alternance de ses couches, d'extraire des métriques abstraites pour décrire et caractériser de la donnée structurée, complexe et multi-échelle telle qu'une image.



**Modèles génératifs (ou générateur)** Les modèles génératifs cherchent à estimer la distribution d'un jeu de données, en particulier en apprenant à générer de nouveaux échantillons statistiquement similaires. Ils prennent donc en entrée un vecteur de bruit et génèrent de la donnée en sortie, et sont notamment utilisés pour des tâches de simulation. Les réseaux antagonistes profonds (GAN) constituent une approche typique pour entraîner un réseau génératif (Goodfellow et al., 2014). Les GAN impliquent l'entraînement de deux réseaux simultanés, qui jouent à un jeu à somme nulle au sens de la théorie des jeux. Le premier est le réseau génératif, et son adversaire est un réseau discriminatif, qui prend en entrée un échantillon et vise à distinguer s'il est réel ou simulé. Le générateur est donc récompensé lorsqu'il génère des échantillons qui trompent le discriminateur, tandis que le discriminant est récompensé lorsqu'il détecte correctement les faux échantillons. Cette approche est particulièrement récente, mais il en existe déjà de nombreuses variantes, notamment pour générer des données conditionnellement à une information supplémentaire, pour interpoler des données manquantes ou pour en faire un outils de prédiction (Isola et al., 2018; Li et al., 2019; Ravuri et al., 2021).

## Résultats

Dans un premier temps, nous avons utilisé des réseaux convolutifs profonds pour différentes tâches de classification. Nous comparons ces approches à l'état de l'art dans le but d'améliorer l'identification des zones de reproduction et d'alimentation des oiseaux marins. Ces informations sont en effet cruciales pour définir des politiques de gestion et de conservation pertinentes des écosystèmes marins. Plus précisément, nous considérons les problèmes (1) de l'évaluation de la qualité des zones d'habitats côtiers à Cuba pour la nidification des laridés à partir d'images satellites et (2) de la segmentation des trajectoires GPS de fous et de cormorans pour identifier des comportements de plongée et en déduire des zones d'alimentation préférentielles. Dans un second temps, nous nous concentrons sur la simulation des trajectoires de recherche alimentaire d'oiseaux marins. La capacité de simuler des trajectoires est en effet fondamentale pour mieux expliquer les mécanismes sous-jacents aux mouvements observés des oiseaux marins et pour tester des hypothèses écologiques.

### Identification des zones de reproduction et d'alimentation d'oiseaux marins

En période de reproduction, les oiseaux marins sont contraints de retourner à terre de manière régulière, pour surveiller leur nid et nourrir leurs poussins. Le choix du site



de nidification a donc un impact fondamental sur le succès de reproduction (Muzaffar et al., 2015). Pour cette raison, les oiseaux marins sont connus pour faire des repérages sur les côtes avant la période de reproduction pour évaluer la qualité des différents sites disponibles (Ponchon et al., 2013). Le mécanisme qui conduit un individu à faire son choix est, en revanche, relativement complexe puisqu'il intègre des informations à différentes échelles spatiales et relatives à deux environnements distincts : la terre et la mer (Clark et al., 2019). À partir de nos données de présence/absence de laridés à Cuba, nous avons défini dans un premier temps différentes métriques descriptives des propriétés géographiques des sites considérés à trois échelles spatiales distinctes (10, 50, et 100 km). Nous avons ensuite utilisé des forêts d'arbres décisionnels (RF) afin d'identifier lesquels de ces facteurs étaient susceptibles d'influencer la sélection des sites de reproduction. Les sites de reproduction des laridés étaient notamment définis par une faible distance aux îles principales de l'archipel de Cuba, une faible couverture végétale et une forte concentration de chlorophylle dans un rayon de 100 km. Dans un second temps, nous avons utilisé des réseaux de neurones convolutifs (CNN) pour identifier les sites de reproduction directement à partir d'images satellites LandSat. Les CNN ont évalué les habitats dans un rayon de 10 km autour des sites de reproduction avec une meilleure précision que les RF (CNN  $\sim$  78% ; RF  $\sim$  70 %). La comparaison de ces approches discriminatives suggère que les réseaux de neurones sont en mesure d'extraire des métriques pertinentes pour caractériser les habitats côtiers, et ce, de manière automatique et directement à partir d'images satellites. L'apprentissage profond est donc particulièrement prometteur, notamment pour évaluer de manière pragmatique les zones d'habitats essentielles à la nidification d'oiseaux marins, et notamment dans des régions tropicales pour lesquelles l'inventaire des sites de reproduction est mal connu et incomplet. De plus, en approfondissant notre compréhension des différentes couches qui composent un CNN, on peut s'attendre à ce que ces outils aident à interpréter et déduire de nouvelles variables d'intérêt pour comprendre les mécanismes de sélection d'habitat (Montavon et al., 2019).

En plus de l'identification des sites de reproductions, l'estimation des distributions des plongées des oiseaux marins est souvent utile pour désigner des zones écologiques d'importance significatives en mer (Hindell et al., 2020). L'approche usuelle est typiquement de segmenter les trajectoires GPS afin d'y détecter les comportements de plongée (Carter et al., 2016). À partir des déploiements joints GPS/TDR de notre base de données, nous avons donc entraîné différentes architectures de réseaux de neurones convolutifs afin de détecter les comportements de plongées définis par les données TDR à partir des trajectoires GPS uniquement. En considérant des séquences de déplacements élémentaires pour identifier simultanément une séquence de comportements de plongée, les réseaux convolutifs ont permis d'obtenir de meilleures inférences que les méthodes de l'état de l'art, tel que les modèles de Markov à états cachés. En particulier, ils arrivent mieux à distinguer les comportements de repos en surface des comportements de plongée, qui dans les deux cas correspondent à des modes de déplacement à faible vitesse. Ainsi, l'utilisation de méthodes d'inférences plus précises permet d'améliorer significativement les estimations des distributions de plongées en mer. De plus, on démontre que ces réseaux sont facilement généralisables pour estimer les plongées à partir de trajectoires GPS d'individus d'autres espèces et d'autres colonies. Plus précisément, les modèles entraînés sur des trajectoires des fous variés du Pérou (SV) ont obtenu de meilleures performances que les modèles de Markov à états cachés lorsqu'ils ont été utilisés sur des trajectoires des fous masqués nichant au Brésil (SD). Les approches d'ajustement fin des paramètres d'un réseau permettent également de généraliser ces modèles à des espèces qui ont des

stratégies de plongées très distinctes comme les fous et les cormorans. Ces résultats motivent le développement de réseaux "prêts à l'emploi" qui pourraient directement être utilisés par les biologistes marins pour prédire les plongées d'oiseaux marins sur leurs nouvelles données, sans nécessiter un ré-ajustement des paramètres du réseau.

### Simulation de trajectoires d'oiseaux avec des réseaux génératifs

Comme les processus de mouvement de nombreux animaux sont relativement mal connus, la simulation de trajectoires est fondamentale pour en comprendre les mécanismes sous-jacents. Les simulations de trajectoires ont notamment servi de 'modèle nul' pour tester diverses hypothèses écologiques concernant le mouvement d'oiseaux marins, comme l'influence de la distribution des proies (Boyd et al., 2016a) ou des interactions sociales sur les mouvements de recherche de nourriture (Bastos et al., 2020). Nous avons donc utilisé des réseaux antagonistes profonds (GAN), afin de simuler les trajectoires GPS des voyages de recherche alimentaires de fous et de cormorans en période de reproduction. En particulier, nous comparons des architectures de GAN convolutifs utilisés classiquement pour la génération d'image, aux méthodes de simulations du mouvement de l'état de l'art comme les chaînes de Markov à état cachés (HMM). Les GAN ont montré une capacité exceptionnelle à reproduire les statistiques à large échelle des trajectoires, comme la distance, la durée et la sinuosité. Les trajectoires synthétiques dérivées des GAN reproduisent en effet mieux la densité spectrale de Fourier des trajectoires observées que celles simulées à l'aide des HMM. Les HMM consistent en des modèles markoviens de premier ordre calibrés à l'échelle locale, ce qui conduit à des simulations trop simplistes des trajectoires animales qui ne parviennent pas à reproduire les propriétés statistiques des trajectoires à large échelle. En simulant correctement ces statistiques, on s'attend donc à ce que les GAN, utilisés comme outils de ré-échantillonnage de trajectoires, puissent être une alternative aux méthodes usuelles de 'modèle nul'. En revanche, les GAN convolutifs standards sont limités par deux aspects pour la génération de trajectoires. Contrairement aux HMM, ils ne capturent pas correctement les statistiques descriptives à l'échelle locale, telles que les distributions déplacement élémentaires (vitesse, direction, etc). De plus, comme ils ne sont pas formulés selon une approche Lagrangienne du mouvement comme pour la plupart des modèles du mouvement, et il peut être relativement difficile d'en interpréter les espaces latents, ce qui peut réduire leur exploitation pour répondre à des questions scientifiques explicatives.

Plus généralement, la plupart des modèles de mouvements existants sont basés sur des représentations Lagrangiennes, ce qui conduit naturellement à des architectures neuronales récurrentes et à des modèles markoviens. Cependant, ces modèles séquentiels se concentrent généralement sur les dynamiques à court terme. Ils accumulent donc des erreurs conséquentes et sont sujets à d'importantes difficultés numériques lorsqu'ils sont utilisés et optimisés sur de nombreuses itérations. Cela motive un changement de paradigme dans la représentation du mouvement pour pouvoir simuler des trajectoires d'oiseaux composées de longues séquences de positions ( $> 100$  positions). Pour cette raison, nous nous sommes inspirés de la représentation duale de la dynamique lagrangienne stochastique par l'équation de Fokker-Planck (Turchin, 1998). Du point de vue de l'apprentissage, cette correspondance entre les représentations lagrangiennes et eulériennes pour les modèles de mouvement permet notamment de bénéficier de la performance des architectures convolutives pour modéliser l'évolution d'un champ de probabilité au cours du temps. Nous proposons donc une architecture de GAN spécifique à la simulation de trajec-

toires. Il est constitué d'un générateur convolutif 3D pour simuler l'évolution temporelle d'une densité de probabilité 2D, à partir de laquelle nous échantillons une trajectoire. En outre, nous utilisons deux discriminateurs pour capturer les caractéristiques à grande et à petite échelle des trajectoires. Nous démontrons la pertinence de cette approche par rapport à l'état de l'art pour simuler des trajectoires diverses et réalistes qui reproduisent les distributions de vitesses des trajectoires réelles, et d'autre part pour apprendre des représentations latentes, spatialisées et interprétables. Plus précisément, l'utilisation de convolutions 3D et d'une spatialisation explicite des espaces latents garantit de bonnes propriétés de stabilité numériques tandis que les multiples discriminateurs permettent d'obtenir un bon compromis entre la diversité et la qualité des trajectoires simulées. Cette architecture est ainsi capable de relier la propagation temporelle de champs probabilité de présence dans une perspective eulérienne à la génération de trajectoires lagrangiennes. Les données de trajectoires consistent en effet en un processus où le temps et l'espace sont intrinsèquement interdépendants, et la plupart des outils existants ont des difficultés à rendre compte de ces interactions complexes et multi-échelles. Ce travail est donc un premier pas vers un modèle qui pourrait générer des trajectoires individuelles à partir des champs externes avec lesquels elles interagissent à plusieurs échelles spatio-temporelles. En utilisant des GAN dits conditionnels, nous pourrions en effet apprendre à simuler des trajectoires au regard d'une description spatio-temporelle de leurs environnements (Isola et al., 2018).

## Conclusion

Cette étude montre que les outils d'apprentissage profond sont pertinents dans plusieurs cas pour l'analyse multi-échelle des mouvements d'oiseaux marins. Dans le cadre de modèles discriminatifs, nous avons illustré comment les réseaux convolutifs sont capables d'extraire automatiquement des connaissances des données brutes pour classer les entrées dans des catégories distinctes. Que ce soit à partir de données d'observation satellites ou à partir de trajectoires GPS, ils ont obtenu de meilleures performances prédictives que les outils de l'état de l'art. Ainsi, ils ont permis d'améliorer significativement l'estimation des zones de reproduction et d'alimentation d'oiseaux marins. Cela constitue un apport essentiel à la gestion et la conservation des écosystèmes marins. Par ailleurs, nous avons introduit de nouveaux outils pour la simulation de processus stochastiques, tels que les trajectoires. Les réseaux antagonistes profonds ont en effet une remarquable capacité à reproduire les propriétés statistiques des trajectoires d'oiseaux marins aussi bien aux petites qu'aux larges échelles spatio-temporelles. Ces outils pourraient être utilisés comme modèle nul pour tester diverses hypothèses écologiques sur le mouvement des oiseaux marins. De plus, il peut s'agir d'une alternative pertinente au suivi des oiseaux marins dans les régions où le suivi d'un grand nombre d'individus n'est pas souvent possible, pour des considérations pratiques ou éthiques. Mais plus important encore, cette technique fournit également une nouvelle solution pour capturer la variabilité de tout ensemble de données. Nous pensons qu'elle ouvre une nouvelle voie de recherche en écologie marine, pour la modélisation, la caractérisation et la prédiction de processus écologiques complexes et multi-échelles.

# General Introduction

♪ *Conference of the Birds*, DAVE HOLLAND

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The sea is a vast and blue desert, where food resources are scarce and dynamic in space and time (Bertrand et al., 2014). Relatively few bird species are adapted to survive in this habitat, as only 3% of them are known to get food from the oceans (Hackett et al., 2008). Birds living in a marine environment have thus very specific motion, navigation and cognitive abilities; they can fly over long distances, dive in water, read marine landscapes, and gather information on the localization of prey aggregations (through memory, social behavior, etc.). Furthermore, in those dynamic ecosystems, they are able to adapt their movement strategies to the environmental conditions in order to obtain their food efficiently and maximize their breeding success (Schreiber and Burger, 2001).

For this reason, the observation of seabird movements was historically crucial to fishermen because they provided visual cues on the location of fish aggregations. Nowadays, the study of their movements keep providing information on the abundance and distribution of preys and more generally on marine ecosystem variability. This is due to advances in remote-sensing technology as well as the miniaturization of electronic devices. Miniaturized electronic devices, such as GPS, are directly attached to seabirds to measure their locations through time, thus providing accurate and high-resolution movement data (Tremblay and Bertrand, 2016; Yoda, 2019). In addition, remote-sensing technology, such as optical and radar sensors, enable to better characterize their vast habitat, including coastal landscapes, as well as water masses (Goddijn-Murphy et al., 2021). Seabirds are often considered as sentinels for environmental variability, and their monitoring and study is crucial to conservation and management frameworks for most ecosystems around the world (Hazen et al., 2019). The analysis of seabirds' movement have proven useful in many cases to indicate changes in temperate and polar marine ecosystems. It is typically illustrated by changes in breeding or foraging locations presumably due to external factors, such as anomalous oceanographic conditions, shifting trophic-level structure, or increasing anthropogenic pressures (Velarde et al., 2019). This knowledge is however more scarce in the tropics, where conservation research remains relatively understudied (Reboredo Segovia et al., 2020), even though seabirds are paradoxically subject to increasing cumulative human impacts (Halpern et al., 2015). There is therefore a need to deepen the study of tropical seabirds, and to better characterize and predict the variability of tropical seabird behaviors, accounting for the complex spatio-temporal processes related to the dynamics of their ecosystems.

The robust monitoring of marine ecosystems from the perspective of seabird movements yet does not simply require seabirds to be sensitive to changes in their environment. It also requires the understanding and predictability of processes underlying movement strategies. Existing animal movement data analyses focus thus on the characterization and prediction of seabird movements to describe movement patterns, to evaluate the source of variability related to external factors and to predict movement for previously unseen conditions. Yet, movements are the result of complex and multiscale processes, driven by large-scale (e.g. climatic conditions, memory), medium-scale (e.g. social interactions, landscape perception), and small-scale (e.g. soaring in air currents, visual detection of preys) interactions between individuals and their environment (Nathan et al., 2008). Existing tools for animal movement characterization and prediction are thus soon limited, as they often rely on overly simplistic assumptions concerning movement data (Joo et al., 2022). For instance, approaches that focus on the identification of large-scale environmental drivers, such as logistic regression habitat models, typically rely on classical statistical tools without any explicit spatial or temporal component, and often ignore the spatio-temporal nature of the movement data (Tremblay et al., 2009). In addition, popular movement simulation tools, such as random walks, focus on elementary step distributions, and generally do not consider larger-scale patterns (Smouse et al., 2010). The time has now come to explore new tools to better characterize and predict the variability of seabird movements, by considering multiple scale and by assessing the impact of environmental heterogeneity.

Statistical tools used in ecology often consist of parametric models that are fitted to observational data to reveal specific statistical relationships from raw datasets. This family of statistical tools has recently been extended with the arrival of deep learning in years 2010s (Goodfellow et al., 2016). Deep learning is based on the same theoretical principles as usual statistical tools, but it has recently obtained better performance on many tasks, notably due to the recent increase in computer calculation capacity and in data availability. In particular, it allows the extraction of complex and multiscale data features directly from raw data by transforming inputs into multiple layers of processing units (LeCun et al., 2015). More precisely, deep learning models can be divided in two main groups: discriminative networks that are applied to identify specific patterns and features in raw data, and generative models that aim to capture the distribution of a dataset (i.e. its variability) and to re-sample it by generating new but related data samples. Although deep discriminative networks are becoming increasingly popular in the field of marine ecology, and have been used on multiple occasions notably to automatically classify animal pictures, they have rarely been applied to movement data such as animal trajectories (Christin et al., 2019; Borowiec et al., 2022). Moreover, generative networks are just beginning to be introduced, and their potential to capture the distribution of ecological datasets and investigate factors of variability have not been explored yet.

The aim of this thesis is thus to explore and develop different deep learning tools for the characterization and the prediction of tropical seabirds movements. A first chapter develops the **biological and methodological motivations**, and introduces concepts from seabird movement ecology and deep learning. The rest of the manuscript is then divided into two parts concerning discriminative and generative models for seabird movement ecology.

- In the first part, our contribution consists of various discriminative networks to better characterize different seabird movement processes into two distinct classification tasks. Chapter 2 discusses a relatively simple application of deep convolutional networks for the estimation of **breeding habitat selection** in tropical larids directly from satellite-based optical descriptions of coastal landscapes. Chapter 3 compares different neural architecture over state-of-the-art tools for the **identification of dives from GPS trajectories**. In particular, it investigates the transferability of deep models for predicting dives in tropical seabirds from distinct ecosystems.
- In the second part, we introduce deep generative networks, and more specifically generative adversarial networks (GAN) for the **simulation of foraging trips**. Chapter 4 evaluates the benefit of using a state-of-the-art deep convolutional GAN over classical simulation tools from movement ecology. Chapter 5 develops a new neural architecture especially dedicated to the simulation of free-ranging trajectory data in the light of Fokker-Planck equation.

As a conclusion, the last chapter proposes a synthesis of this thesis' achievements, and develops a few perspectives for the future use of deep learning in ecology. We discuss its advantages and drawbacks for ecosystem monitoring and conservation research. Moreover, we motivate its use in deep predictive ecology for numerical models to predict future states of marine ecosystems.



# Chapter 1

## Biological and methodological motivations

♪ *Le bal des oiseaux*, THOMAS FERSEN

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This thesis uses both concepts of seabird ecology and deep learning. For this reason, this chapter aims at introducing various notions from both fields. More precisely, the first section details the biological motivations of this thesis, notably by motivating the need to characterize and predict tropical seabird movement relatively to their ecosystems' dynamics. The second section provides a state-of-the-art of tools used for seabird movement analysis, with an emphasis on the analysis of GPS trajectories. Finally, the third section motivates several deep learning tools, some that have already been used in ecology (i.e. discriminative models), and others that are yet to be introduced to marine biologists (i.e. generative models).

Depending on its background, the reader can therefore skip parts of this chapter without missing crucial information for understanding the key achievements of this work.



## 1.1 Why studying the movement of tropical seabirds?

The sea is a highly variable environment, where distribution of marine resources are heterogeneous both in time and space (Margalef and Margalef, 1979; Legendre and Fortin, 1989). This variability is initiated through a combination of various physical oceanographic processes that structures water masses and the patchy distribution of planktonic organisms at large-scale ( $\approx 100$ - $1000$  km; e.g. El Nino oscillation), mesoscale ( $\approx 1$ - $100$  km; e.g. eddies, fronts), and fine-scale ( $\approx 100$  - $1000$  m; e.g. internal waves, tides) (Lennert-Cody and Franks, 2002; Mahadevan et al., 2012; Lévy et al., 2012). These physical processes structure the distribution of productivity at lower trophic level, which propagates then in food webs from zooplankton to marine top predators (Bertrand et al., 2014). Top predators, such as seabirds, are therefore expected to reflect some properties of marine ecosystems in their distributions, diets, behaviors and more particularly in their movements.

In this section, we will precisely present some key aspects of seabird ecology. More precisely, we will illustrate what we can learn from seabirds in marine ecosystems, and how their study have been embedded in the design and evaluation of ecosystem-based management frameworks and conservation policies. Finally, we will detail some specificity of tropical seabirds over seabirds from temperate and polar ecosystems.

### In a nutshell

- ☞ Seabirds represent an emerged part of marine ecosystems, and studying the variability of their movements can help monitor ecosystem dynamics
- ☞ Seabirds are considered as good ecosystem sentinels and environmental indicators when they are both sensitive to environmental variability and in a predictable manner
- ☞ Tropical ecosystem dynamics are less understood, while there are paradoxically relatively understudied and subject to increasing human cumulative impacts
- ☞ Effort is needed to characterize the variability of tropical seabird movements related to their dynamic environment and to predict seabirds movement at unknown colony or relatively to climate change projections

### 1.1.1 Birds in a marine environment

Seabirds obtain at least part of their food from the sea (Furness and Monaghan, 1987). They represent a relatively small number of total bird species ( $\approx 3\%$ ), yet exhibiting a high taxonomic diversity through sphenisciformes (e.g. penguins), procellariiformes (e.g. albatross, petrels), pelecaniform (e.g. pelicans, boobies, cormorants), and charadriiformes (e.g. skuas, gulls, terns) (Hackett et al., 2008). Despite such taxonomic diversity, most seabird species share common life history traits. They are colonial, and generally are long-lived birds with small clutches, late maturity and low adult mortality rates. Seabirds also tend to be larger than land birds, less colorful in plumage, and sexually monomorphic (Schreiber and Burger, 2001). These similarities which set them apart from most other birds (see Table 1.1) suggest therefore important evolutive convergence related to life at sea (Ashmole, 1963).

#### Box 1.1.1: Evolutive Convergence

In biology, evolutive convergence refers to a mechanism leading to morphological or behavioral similarities between unrelated species that are subject to the same environmental selective pressures.

Life History Traits	Seabird	Passerine
Age of first breeding	2-9 years	1-2 years
Clutch size	1-5	4-8
Incubation period	20-69 days	12-18 days
Nestling/Fledging period	30-280 days	20-35 days
Maximum life span	12-65 years	5-15 years

Table 1.1: **Comparison of life history traits for seabird and passerines** - Credits Schreiber and Burger (2001)

A fundamental characteristic of breeding seabirds is that they must return regularly to land in order to brood and feed chicks. Feeding on marine organisms and breeding on land (i.e. central place foraging) present therefore several challenges to seabirds. In relation to these constraints and according to their needs, seabirds have developed a variety of morphological, and physiological abilities that make them able to eventually navigate far from the colony, and dive deep in the water column (Schreiber and Burger, 2001). For example, albatrosses have long and thin wings, and are able to fly over long distances using dynamic soaring, thus spending little energy (Richardson et al., 2018). Cormorants have relative short and wide wings and are able to dive up to 100 meters deep using their legs to propel themselves through water (Watanabe et al., 2011).

### 1.1.2 Seabirds' behavioral plasticity

Long-lived colonial breeding birds also demonstrated great adaptive behavioral strategies to maximize breeding success. If they typically keep the same nesting territory for an extended period, numerous seabird species can switch to a safer nest site in response to invasive species (Barros et al., 2016), to change in oceanographic environmental conditions (Robert et al., 2014), or to anthropic pressures (Salas et al., 2020). Similarly, some seabirds species have a great plasticity of behavior to localize and capture their preys in vast and highly variable marine environments, including flexibility in diet regimes, in foraging zone and effort (Paiva et al., 2010; Fromant et al., 2021; Bourgeois et al., 2022; Botha and Pistorius, 2018). Foraging behavioral strategies are likely to vary, depending on the species, with the biotic and abiotic conditions of the ocean. Numerous studies have established relationships between behavior of seabirds and various type of oceanographic processes such as subtropical dipole events (Bost et al., 2015), El Nino Southern Oscillation (Sprogis et al., 2018), mesoscale fronts (Scales et al., 2014), estuaries flows (Kowalczyk et al., 2015) and tides (Cox et al., 2013). Variations in the spatial and vertical distribution of preys have also been mentioned to influence seabird movements (Boyd et al., 2016a), as well as the effect of anthropogenic pressures, and competition with fisheries (Bertrand et al., 2012; Corbeau et al., 2019).

#### Box 1.1.2: Ecological niche

The niche concept was introduced by Hutchinson (1978). A niche consists in an n-dimensional hypervolume from a space, where dimensions are environmental conditions and resources descriptors. There are commonly two types of niche described:

- The **fundamental niche** that defines the range of conditions in which an individual or a species is able to live.
- The **realized niche**, which is included in the fundamental niche and that defines the range of conditions in which the individual or the species actually lives, due to competition with other organisms and prey availability.

More specifically, seabirds' foraging strategies may also vary depending on competition with other organisms. Seabirds often aggregate in large numbers at suitable breeding sites. This may lead to collective strategies to forage more efficiently, but also to intensive intra- and/or interspecific competition for resources. In both case, this can significantly reduce the availability of resources in the vicinity of their colony. The "Ashmole's halo" describes precisely the zone of food depletion surrounding some of the largest seabirds' colonies (Lewis et al., 2001; Elliott et al., 2009; Weber et al., 2021). Competition for food can typically be reduced by ecological segregation, meaning that ecologically similar species differentiate their habitat and foraging strategies in order to coexist. This is known as niche segregation, and is illustrated in terms of breeding time (Quillfeldt et al., 2020), foraging areas (Ito et al., 2021), diet (Bourgeois et al., 2022), or diving depth (Weimerskirch et al., 2012). Seabirds have thus an impressive ability to adapt to their environment, notably by finding relevant breeding locations, and foraging areas with specific strategies. We refer to this ability as behavioral plasticity (or flexibility).

### 1.1.3 Seabirds as sentinels of marine ecosystem

Seabirds offer a unique perspective into ocean processes and dynamics for two main reasons. First, because they can amplify information about seascape structure and trophic linkages across multiple spatio-temporal scales due to their relatively high mobility and longevity. Second, because their adaptive behaviors provide a near real-time response to complex ecosystems' dynamics and variability. They are thus often considered as sentinels of the environmental variability and bio-indicators for ecosystem structure and dynamics (Hazen et al., 2019). Figure 1.1 details the trophic linkages in a generic pelagic food web, and highlights examples of relationships between marine sentinels and ecosystem components.

#### Box 1.1.3: Ecosystem sentinel

An ecosystem sentinel is a species that responds to ecosystem variability in a timely and measurable way, and that can indicate an otherwise unobserved change in ecosystem function. Key characteristics of sentinel species include conspicuousness, sensitivity to ecosystem processes, and timeliness in their responses. Multiple measurements and indicators can provide insights about variability in seabirds' behavior, including diet, demography, morphometrics, reproduction and movement analysis.

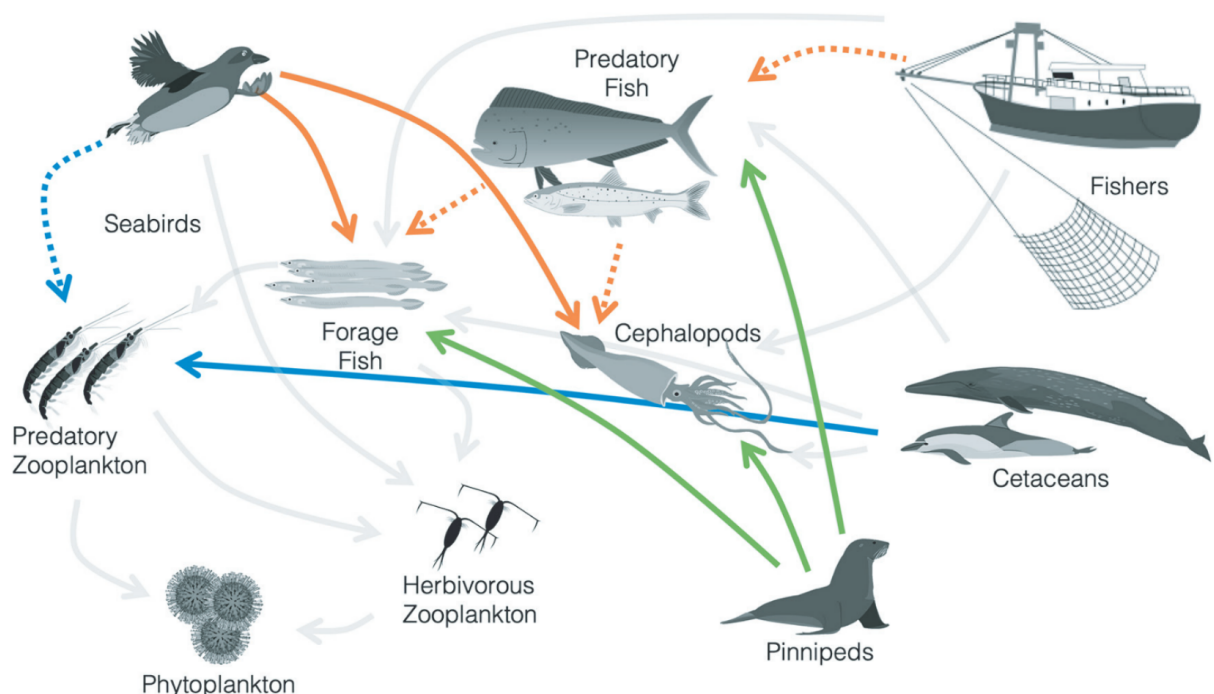


Figure 1.1: **Trophic linkages in a generic food webs** - Solid colored arrows represent examples of studied relationship between sentinels and ecosystem components (i.e. seabirds and marine mammals); dashed colored arrows represent links that can be predicted through the study of a sentinel species. - Credits Hazen et al. (2019)

The majority of global waters are currently experiencing increasing cumulative impact of human activities (Halpern et al., 2015). At the population level, many marine species are declining, threatened, or critically endangered (McCauley et al., 2015; Bronzizio et al., 2019), and the impact of climate warming on species distributions is particularly pronounced in the oceans (Poloczanska et al., 2013; Lenoir et al., 2020). At the ecosystem level, there is mounting evidence of regime shifts around the globe (Möllmann and Diekmann, 2012). For these reasons, many tools and strategies are being studied in order to monitor marine ecosystem and to prevent ecosystems from regime shifting. This is yet challenging due to the intrinsic variability of the ocean structure (Dudley, 2008).

#### Box 1.1.4: Regime shift

Regime shifts consist of ecosystem changes that are abrupt, high-amplitude and low-frequency events that occur over large spatial scales and that are evident in multiple bio-physical attributes over a range of trophic levels. They are often caused by multiple interacting external drivers, they come without warning, and they may be irreversible (Levin and Möllmann, 2015; Darling and Côté, 2018).

Seabirds have thus been used to provide essential information on the state of marine ecosystems, and evidence of ecosystem shifts (Velarde et al., 2019). For example, the diet composition of distinct seabirds, estimated from isotopic analyses of feathers and regurgitates samples, have illustrated the significant long-term shift from higher-trophic level to lower-trophic level prey in the North Pacific over the last 10 decades (Gagne et al., 2018). The colony abandonment of auklets in 2005 have indicated a strong unusually delayed upwelling in the California Current system due to anomalous atmospheric and oceanographic conditions (Sydeman et al., 2006). Similarly, long foraging trips of king penguins from Austral Seas southward to their colony have been related with simultaneous occurrence of subtropical dipole events both in Southern Indian and Atlantic Oceans (Bost et al., 2015). Some species even make it possible to forecast the future state of marine ecosystems. This is the case in the Gulf of California, where seabird diet predicts following-season commercial catch of Sardine and Anchovy (Velarde et al., 2015), and in the Southern Hemisphere where the chick size of sooty shearwaters alone allowed to predict El Niño/La Niña events by up to 12 months in advance (Humphries and Möller, 2017). Over the last decades, seabird studies have also been embedded in the design and evaluation of ecosystem-based management frameworks and conservation policies (Lascelles et al., 2014). Analysis of seabird population and foraging strategies can indeed help to set fishing quotas and restricted areas, for instance by limiting local depletion of fisheries around breeding colonies (Bertrand et al., 2012; Barbraud et al., 2018), and by limiting seabird bycatch (Žydelis et al., 2009; Melvin et al., 2019; Dasnon et al., 2022). Moreover, seabirds distribution have been recently used to assign biodiversity hotspots by identifying areas with a high occurrence of birds, which was particularly enabled by using movement data (Augé et al., 2018; Yurkowski et al., 2019; Hindell et al., 2020; Cleasby et al., 2020; Fauchald et al., 2021). Figure 1.2 illustrates how the use of tracking data has helped the highlighting of areas of ecological significance in the Southern Ocean.

The inclusion of movement data into global conservation strategies to monitor marine ecosystems is indeed a hot research topic in today's ecology of marine top predators

(Hays et al., 2016, 2019), and there is a crucial need to develop tools and framework to collect, manage, harmonize, share, visualize, analyze and archive such data at a global level (Dwyer et al., 2015; Grémillet et al., 2022; Kays et al., 2022). A key challenge in conservation ecology includes the ability to better (1) characterize and (2) predict seabird movement variability, depending on external variables (Authier et al., 2017). Characterization consists on one hand in describing movement patterns through relevant ecological metrics and movement analysis tools (Seidel et al., 2018). On the other hand, it consists in identifying interactions between these highly mobile species and their vast, dynamic and heterogeneous marine environment (Wakefield et al., 2009; Tremblay et al., 2009). Predicting seabird movements supposes then to be able to reproduce and simulate processes underlying animal movement. It is notably crucial to extrapolate potential habitat uses at unknown locations (Augé et al., 2018; Hindell et al., 2020), or to project the effect of climate change on seabirds' movement (Amélineau et al., 2018; Somveille et al., 2020). A good sentinel species need indeed to be not only sensitive to environmental variations but also in a predictable manner, so that we would be able to assess future states of marine ecosystems (Grémillet and Charmantier, 2010; Hazen et al., 2019).

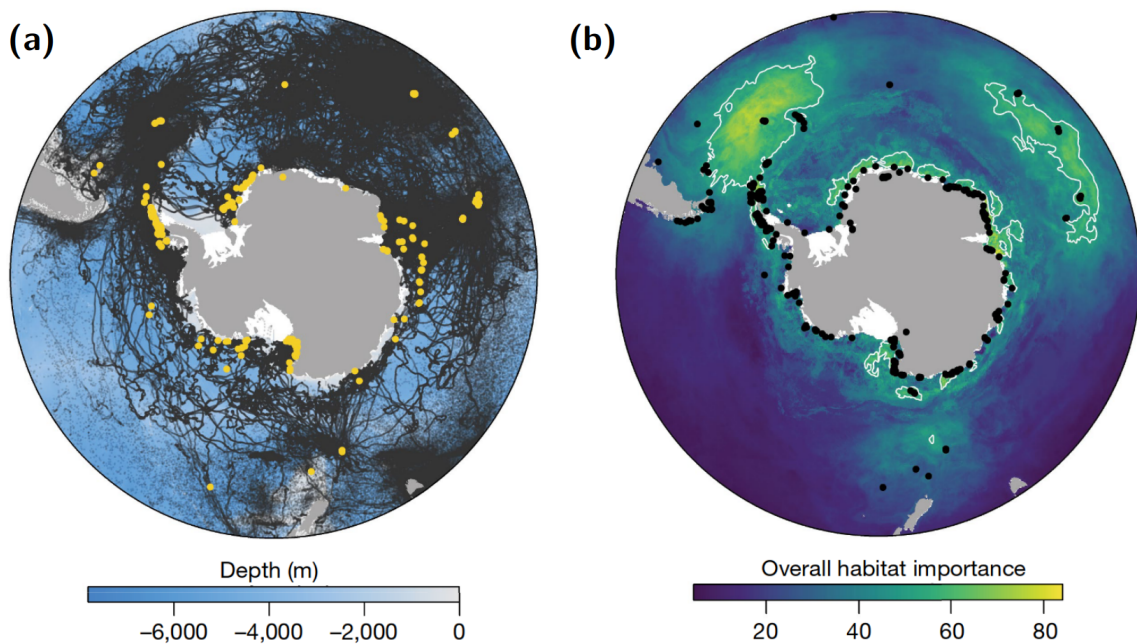


Figure 1.2: **Use of seabird movement data to identify areas of ecological significance in the Southern Ocean** - (a) Black points indicate tracking data from 17 sentinel species and yellow points indicate tagging locations (b) The overall habitat importance is derived from habitat models based on tracking data. The upper decile of overall habitat importance delimits areas of ecological significance (white contours) - Credits Hindell et al. (2020)

#### 1.1.4 Tropical seabirds

In temperate and polar ecosystems, seasonal fluctuations are particularly marked and have a subsequent impact on marine productivity. Therefore, seabirds breed at spe-

cific times of the year, ensuring that the energy demands of reproduction coincides with peak food availability (Frederiksen et al., 2004). At large- and meso-scales, it is generally assumed that seabirds also have a good knowledge of the location and concentrations of prey aggregations (Weimerskirch, 2007). Foraging strategy consist then typically in repeated visits of similar hotspot locations at sea throughout a breeding season (Wakefield et al., 2015; Soanes et al., 2021). In such situation, both breeding period and foraging trajectories are relatively easy to predict, and anomalous change in seabirds' behavior can be straightforward to detect. By contrast, in tropical environments the oceanographic structure and the vertical water column in particular are more stable. As a result, tropical ecosystems are more oligotrophic (i.e. with low levels of nutrients), and marine productivity is less seasonal. Prey distributions are generally thought to be spatially less consistent, thus it may not be profitable for tropical seabirds to systematically frequent the same areas at sea. Tropical seabirds exhibit indeed greater flexibility in their foraging behavior (Weimerskirch, 2007; Jaquemet et al., 2008), and do not display clear patterns in their trophic and spatial segregation (Mancini et al., 2013). Numerous studies thus pointed out the difficulty to predict seabirds' breeding periods and foraging strategies (Soanes et al., 2021), even arguing that tropical seabirds may ignore the distribution of their preys when looking for food (Weimerskirch, 2007). It is however to debate if such difficulty is inherent to their behavioral processes or if it is related to a lack of understanding of small-scale processes driving prey distributions dynamics.

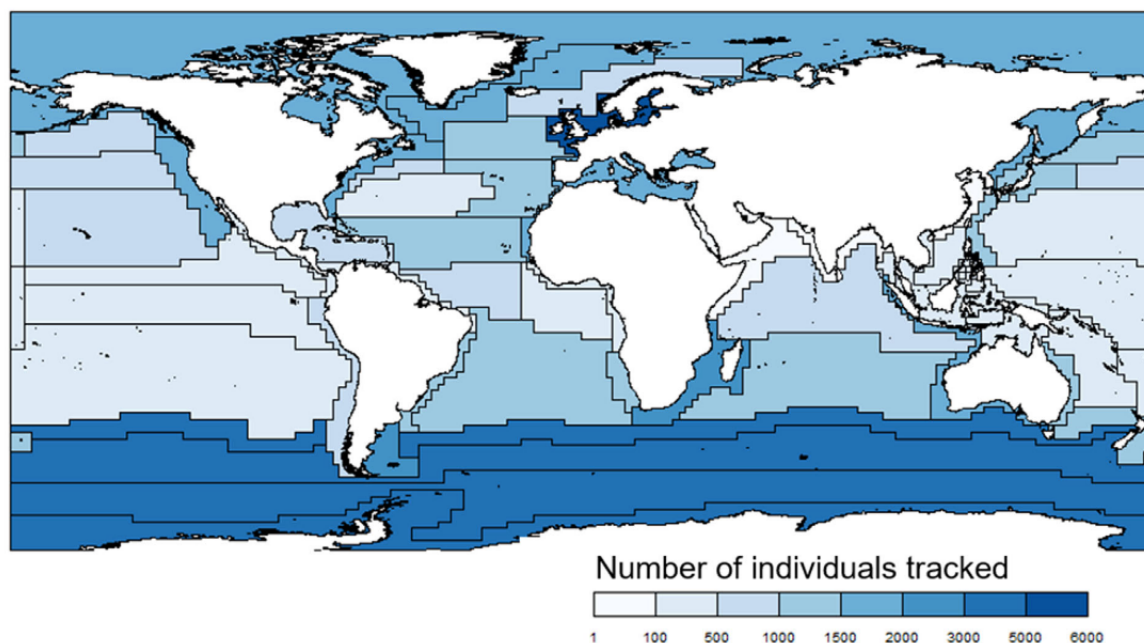


Figure 1.3: **Spatial variation in tracking intensity across Longhurst provinces** - Tracking effort (in number of tracked individuals) - Credits Bernard et al. (2021)

Tropical marine ecosystems are generally less understood, while there are paradoxically understudied (Reboredo Segovia et al., 2020). Figure 1.3 illustrates the spatial variation in number of seabirds tracked along different parts of the world, thus pointing out the effort gap between tropical, temperate, and polar seabird research. In particular,

it is interesting to note that the study of areas of ecological significance in the Southern Ocean illustrated in figure 1.2 was made possible by intensive monitoring of populations in this region. In the same time, tropical ecosystems are facing the most increasing cumulative impact (Halpern et al., 2015). There is therefore a need to deepen the study of tropical seabirds, and to improve conservation research in the tropics and to better characterize and predict the variability of tropical seabird behaviors, accounting for the complex spatio-temporal processes related to the dynamics of their ecosystems.

### **1.1.5 Conclusion**

In this section, we presented key aspects of seabird ecology. Seabirds are an emerged part of marine ecosystems, and we have illustrated how the study of the variability of their behaviors can help monitor ecosystem dynamics. In particular, we have provided evidence of the behavioral plasticity of seabirds, that are able to change breeding site or to adapt their foraging strategies and areas, depending on ecosystems' variability and in order to maximize their breeding success. We have also mentioned that seabirds behavioral strategies are particularly diverse in tropical ecosystems, where preys distributions are less seasonal and consistently distributed. For these reasons, this thesis will focus on the movement of tropical seabirds. The aim is to develop new tools that could be used to better characterize and predict tropical seabird movement relatively to their ecosystems' dynamics.



## 1.2 Seabird Movement Analysis: a state of the art

Movement is a fundamental characteristic of animals. At the individual level, animals move to acquire food, find suitable mates, avoid risk factors such as predation or adverse climatic conditions, or to locate breeding areas with respect to their motion and navigation abilities (Bowler and Benton, 2005). It consists in a decision-making process presumably involving various components, including the internal state accounting for the physiological and psychological states that drive the organism to fulfill certain goals, the motion capacity, accounting for the mechanisms that enable the movement, as well as the navigation capacity, accounting for the ability of an individual to perceive its environment and to localize itself through space and time. Finally, it also involves external factors, and spatio-temporal external fields that can influence an individual in its decisions. Animal movement data is thus the result of a suite of multiscale processes, including habitat selection, and foraging strategies (Nathan et al., 2008; Yoda, 2019).

In this section, we will provide an overview of state-of-the-art methods for analyzing seabird movement data. First, we will detail the different types of data used to study animal movement, then we will provide a description of usual practice for analyzing animal movement at specific spatio-temporal scales. Finally, we will point out some methodological challenges to the multiscale characterization and prediction of seabirds movements, that would depend on heterogeneous landscapes.

### In a nutshell

- ☞ Animal movement data is the result of a suite of multiscale processes, including habitat selection, and foraging strategies
- ☞ Movement data analyses can be categorized into three groups, depending on different spatio-temporal scales and using either Lagrangian or Eulerian perspective: step-, trip- and population-level analysis
- ☞ Most approaches are however limited either because they rely on numerous over-simplistic hypothesis, where individuals are assumed to search with no knowledge of their environment (e.g. basic random walks), either because they ignore the sequential structure of tracking data, and sometimes neglect its inherent spatial dependence (e.g. linear habitat models)
- ☞ Time is now ripe to merge these different analysis levels into a multiscale movement model, that would account for landscape heterogeneity, and navigation abilities, and that would characterize movement processes from step distributions to habitat selection

### 1.2.1 Movement data

Historically, seabird movements were only recorded by direct observations, and most frequently relying on the mark-recapture methodology, as described e.g. by Turchin (1998). In that setting, animals are captured and individually marked at the beginning of the study, so that they can be identified and localized in subsequent capture occasions. Recently, breakthroughs in the miniaturization of electronic tag, have revolutionized the understanding of seabirds' movement ecology and have permitted observations well beyond the reach of mark-recapture techniques. The term 'bio-logging' refers to the use of electronic sensors directly attached to living organisms (Fig. 1.4). Basically, the aim of bio-logging is to record physical parameters using miniaturized electronic tools attached directly to free animals. Various studies have reviewed the measurement of individual locations through time using tracking devices, such as GPS, GLS (light-based geolocation), and Argos transmitters (Ropert-Coudert et al., 2009; Tremblay and Bertrand, 2016; Yoda, 2019). These devices have very different performance characteristics in terms of temporal resolution, accuracy, battery life and device mass, and their use depend directly on the aim of a study and on the tracked species (Wakefield et al., 2009). Movement measurement is crucial to the study of the individuals' spatial distributions, and contains a lot of information on seabirds' habitat use, and foraging behavior in response to anomalous ecosystems conditions (Yoda, 2019). Additionally, other sensors are commonly deployed in order to have a finer description of animal behavior, such as temperature depth recorder (TDR) to detect dives (Browning et al., 2018), video (Tremblay et al., 2014) and accelerometers to detect with accuracy bathing, flapping, gliding or resting behaviors (Leos-Barajas et al., 2017; Patterson et al., 2019; Corbeau et al., 2020). Technological advances provide thus crucial data to address fundamental challenges from seabird movement ecology, and notably to elucidate the processes underlying observed animal movement (Hays et al., 2016).



Figure 1.4: **Example of biologging techniques** - Example of GPS logger fitted to a Peruvian booby (*Sula variegata*) and GLS logger fixed on the tarsus of a breeding albatross - Credits S. Bertrand (left) and C. Barbraud (right)

GPS loggers in particular have been at the forefront of this breakthrough. They have been progressively preferred as tracking devices in movement studies (Joo et al.,

2022), and can now provide precise and accurate data on the movements of numerous seabirds' species (e.g. Wakefield et al., 2009; Yoda, 2019). They are commonly deployed on breeding individuals. As breeders return regularly to their nest for feeding and protecting their chicks, recaptures are considerably eased, what is essential for recovering data from non-emitting loggers . GPS-based seabird trajectories consist thus of central-place trajectories where seabirds perform looping foraging trips from their nest. Figure 1.4 illustrates how a GPS can be attached to a Peruvian booby using tape, and Figure 1.5 provide an illustration of associated information obtained by such sensors; consecutive foraging trips, from which we can get insight on foraging areas.

## 1.2.2 Analysis of movement data

In practice, movement is observed by the change of location of one or many individuals over time. A fundamental distinction to describe movement is whether the focus is on the movement of an individual organism, or it is on the dynamics of the spatial distribution of a population. We refer to both approaches as the Lagrangian and Eulerian perspectives of movement, respectively. Using the Lagrangian perspective, movement is typically described by a trajectory, which is a function that mapped the temporal domain to the spatial domain, providing the sequence of locations of an individual at certain times. Trajectories of moving points are denoted as a sequence of tuples  $\xi = \{(x_1, t_1), (x_2, t_2), \dots, (x_n, t_n)\}$ , where  $(x_i, t_i)$  indicates the location  $x_i$  at time  $t_i$ . In opposition, the Eulerian point of view is centered on a point in the space domain, which is characterized by densities and fluxes of moving organisms. Population density at a fixed location  $x$  is denoted  $d(x, t)$ , and vary over time  $t$ . Before the use of tracking devices, movement analyses were essentially performed using an Eulerian perspective, describing the dynamics of the observations' distribution in space in time (Turchin, 1998). Tracking devices have enabled to shift to the Lagrangian approach in order to describe processes underlying the movement of an individual at finer spatio-temporal scales (Nathan et al., 2008). Based on distinct perspective of movement, here we identified three levels of analysis of movement data related to distinct spatio-temporal scales that are highlighted in Figure 1.5, namely step-, trip-, and population-level analyses.

### Step-level analysis

From a Lagrangian perspective, highly-resolved animal trajectories ( $\approx 1s - 1h$  sampling rate) can be seen as a succession of elementary movement events called steps (Nathan et al., 2008). Each step is simply a vector defined by its norm (i.e. the step length) and its direction (i.e. the heading direction). Step distributions contain crucial information on animal behaviors. Animal movement is indeed composed of different modes related to distinct activities, such as resting, flying, searching and foraging (Morales et al., 2004). Such behavioral heterogeneity is thus typically highlighted in step distributions, as illustrated in figure 1.5. For this reason, the structure of a global movement path is often considered as a reflection of these basic step properties, "in the same way, that the 3D structure of DNA strings is central to the function of a DNA segment" (Nathan et al., 2008).

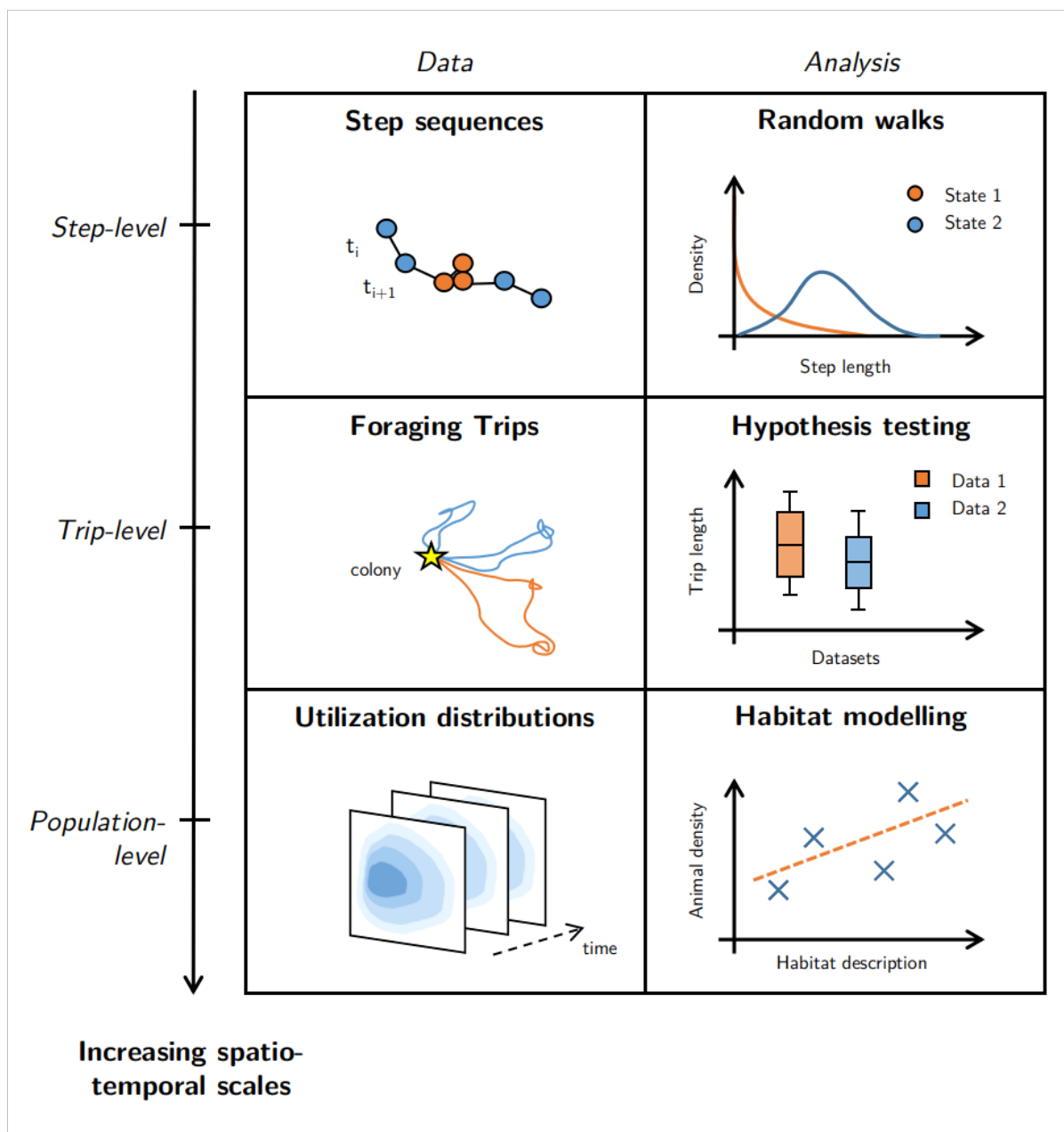


Figure 1.5: **Three main approaches to seabird movement data at distinct spatio-temporal scalings** - Step-level analysis mainly focuses on step distributions and is used to associate behavioral modes to each movement steps. Trip-level analysis consists generally in describing foraging trips using general statistical properties, which are then used for classical hypothesis-testing statistical studies. In population-level analysis, utilization distributions and fluxes at specific locations are estimated through time, in order to describe movement from an Eulerian perspective. It is usually associated with habitat modelling, which consists in modelling animal density from habitat characteristics (e.g. oceanographic features, food availability...).

Many studies have therefore characterized animal movement by modelling their step distributions, and notably through the use of random walk (RW) (Codling et al., 2008). In a random walk, the position of the moving individual at time  $n$  is a random variable  $X_n$ , that consists in a sum of steps described by independent identically distributed random variables  $(Y_i)_{1 < i < n}$ , as expressed in Eq. 1.1:

$$X_n = \sum_{i=1}^n Y_i \quad (1.1)$$

There exists a wide range of RW, offering various ways to model animal movement. The Gaussian random walk is one of the most basic movement model, where each step  $Y_i$  is sampled from a normal distribution. The correlated RW involves a correlation between two successive step directions, which accounts for the tendency of animals to go forward (Bergman et al., 2000). The Lévy flight is also a common type of RW, specially for modelling foraging movement. In this framework, steps are sampled from the Lévy probability distribution, which is heavy-tailed, implying thus the occurrence of rare and very large moves in the trajectory (Viswanathan et al., 2008). Behavioral heterogeneity is also eventually taken into account by considering  $Y_i$  as a mixture distribution, where each mode is referred to a mixture component (Guilford et al., 2008; Garriga et al., 2016). This is also addressed by state-space models, but that additionally consider the sequence of behavioral modes by evaluating the probability to switch from one behavioral modes to another, such as discrete Hidden Markov Models (HMM) (McClintock et al., 2012; Michelot et al., 2017), and continuous-time multi-state correlated RW (Johnson et al., 2008; Michelot and Blackwell, 2018).

They are eventually used to simulate animal behavior, notably to provide a null model for testing various hypotheses concerning movement (Zurell et al., 2010), or to develop methods on synthetic data, without the need to track large numbers of individuals. More generally, they are used to segment GPS trajectory into distinct behavioral modes (Carter et al., 2016), to fill gaps in movement data (Michelot and Blackwell, 2018), and to infer animal movement from noisy and inaccurate geolocation data, such as GLS (Patterson et al., 2008). For what concerns seabirds, these movement models have been particularly useful to detect dives in seabirds GPS-derived trajectories (McClintock et al., 2012; Garriga et al., 2016; Zhang et al., 2019b), but also for characterizing strategies, depending on prey availability (Boyd, 2014; Dunphy et al., 2020) or animal personalities (Cote et al., 2010). Once the GPS-trajectories are segmented, dives are generally used in further trip- and population-level analyses.

### Trip-level analysis

Trip-level analysis aims at characterizing trajectories by global statistics that are not captured by RW. The prevailing approach consists in splitting seabird trajectories in foraging trips, and in deriving metrics, as exposed in Table 1.2. Most metrics are geometrical characteristics of movement path, including trip length, maximal range, straightness index, and fractal dimension (Seidel et al., 2018). Others are derived from step-level description of foraging trips and estimate parameters such as, diving rate (i.e. number of dives per units of time), or energy expenditure. The energy expenditure during a foraging

Scale	Metrics	Description	Suggested references
Step level	step length	The displacement between two consecutive coordinate fixes	Turchin (1998)
	Step direction (or heading)	The direction of heading relative to some standard (e.g. initial direction)	Turchin (1998)
	Turning angle	The change in heading from one step to the next	Turchin (1998)
	Behavioral mode	Association of one of several discrete modes of behavior with step of the trajectory	Carter et al. (2016)
Trip level	Trip length	The sum of all step length of a trajectory	Seidel et al. (2018)
	Maximal range	Maximal distance from the colony	Seidel et al. (2018)
	Trip duration	Total between first and last step of a trajectory	Seidel et al. (2018)
	Straightness index	Maximal range divided by half the trip length	Seidel et al. (2018)
	Fractal dimension	A measure of tortuosity from fractal theory	Benhamou (2004)
	Energy Expenditure	Association of energy rate related to each behavioral mode	Lewis et al. (2004); Louzao et al. (2014)
	Mode rate	Proportion of total time spent in a specific behavioral mode (e.g. dive rate)	Paiva et al. (2010)
	Bearing at departure	Absolute angle of a seabird path when leaving the colony	Weimerskirch et al. (2010)
	Bearing at return	Absolute angle of a seabird path when returning to the colony	Weimerskirch et al. (2010)
	Distance of first foraging patches	Computed for a pair of seabirds	Jones et al. (2018)
Difference in departure times	Computed for a pair of seabirds	Jones et al. (2018)	
Population level	Utilization Distribution	KDE of a set of observed locations	Worton (1989)
	Foraging areas	KDE of a set of locations identified as 'foraging' mode	Worton (1989)

Table 1.2: **Statistics for the description of central-place foraging trips from GPS data**

trip, in particular, is the total energetic cost for a bird to fly, capture preys, and return to its nest. It is usually estimated by associating a metabolic rate to each behavioral mode (e.g. mean resting metabolic rate, mean power required for flight) (Lewis et al., 2004). These metabolic are often provided by specific studies and methodologies, including doubly labelled water trials (Schreiber and Burger, 2001). Statistical metrics have also been extracted from simultaneous foraging trips in order to elucidate social interactions in seabird foraging strategies. It includes mostly metrics such as, difference of trip departure times, overlapping of first foraging areas, and heading direction at departure and return (Table 1.2).

These metrics are then used in classical hypothesis-based statistical frameworks, to compare foraging strategies between groups of individuals. Typically, these approaches rely on parametric tests, to investigate size and mass differences between sexes and seabird species (Kappes et al., 2011; Weimerskirch et al., 2012), or to measure consistency of an individual to forage to the same areas (Weimerskirch et al., 2008). They also explored social interactions by exploring correlations between headings at departure for intra- or inter-individual trips for tropical cormorants Weimerskirch et al. (2010), Gannets (Machovsky-Capuska et al., 2014; Thiebault et al., 2014; Jones et al., 2018), and little penguins (Sutton et al., 2017). However, a large majority of studies have used generalized linear mixed-effects models (GLMM) with an additional analysis of variance (ANOVA) to test for various hypotheses. In these mixed-models, bird identity is often used as a random factor to avoid pseudo-replication, as several trips are recorded for each individual. For instance, it has been used in order to investigate dual foraging strategies (i.e. when seabirds alternate short and long trips) (Ropert-Coudert et al., 2004; Paiva et al., 2010), inter-annual differences in foraging parameters (Lerma et al., 2020b), as well as differences of foraging strategies among species (Delord et al., 2020), by sex (Weimerskirch et al., 2009), by body condition (Botha and Pistorius, 2018), and by breeding stage (Oppel et al., 2017; Phillips et al., 2021).

### Population-level analysis

Population-level analysis mainly relies on an Eulerian description of movement, investigating distributions from multiple individual direct or tag-based observations at different timings. It has been particularly used for the characterization and prediction of large spatio-temporal dispersal processes, such as migration, breeding site selection, and habitat selection. For instance, mark-capture-recapture (MCR) data have been used to evaluate the movement probability among colonies, and fidelity at breeding sites using multi-site models (Cam et al., 2004). They have sometimes tested the impact of various factors on seabirds' settlement to a new colony, such as population size, reproductive performance, and food availability at the destination colony (Fernández-Chacón et al., 2013). This framework has become a core approach to study dispersal processes, which have crucial impact on demographic process as well as on population distributions. It does not focus on paths followed by individuals, but rather evaluate fluxes of individuals between a finite set of sites. As a result, it is often limited to a low number of considered sites for computational reasons (Lagrange et al., 2014; Cayuela et al., 2017).

In addition to the evaluation of migrating seabirds fluxes between known breeding sites, other studies have focused on the habitat selection, including breeding site, as well as foraging areas. Please refer to Box 1.2.1 for a detailed definition of the 'habitat' con-

cept from ecology. The main idea of these approaches is to make use of observations of seabirds during at-sea surveys or through tracking data, and to compare habitats with and without seabird presence. These population-level analyses do not focus on movement process at the individual-level, and do not explicitly model movement dispersal processes. They rather reflect indirectly movement processes by describing seabird habitat based on spatio-temporal external factors. For instance, they have typically described breeding site habitat using descriptors of environmental conditions, such as terrestrial (e.g. vegetation, geography), marine (e.g. surface temperature, chlorophyll, zooplankton), and ecological properties (e.g. competition, territoriality, predation pressure) (Greer et al., 1988; Orians and Wittenberger, 1991; Córdoba-Córdoba et al., 2010; Raynor et al., 2012). Similarly, they have been used to describe population distributions and their associated habitats (Kearney, 2006). For this purpose, utilization distributions or foraging areas are usually estimated using spatial regression tools, such as kriging techniques (Pettex et al., 2017; Bellier et al., 2010), and kernel density estimators (Hindell et al., 2020; Cleasby et al., 2020; Fauchald et al., 2021). These are then associated to habitat data, such as oceanographic features (e.g. surface temperature, chlorophyll, zooplankton), structures (e.g. mesoscale fronts, eddies and filaments) (Scales et al., 2014; Abrahms et al., 2018), tides (Cox et al., 2013), and global climatic indices (e.g. Northern Atlantic Oscillation index) (Cerveira et al., 2020; Reyes-González et al., 2021). Information on other species distributions is also crucial such as others seabird species distributions (Pinaud and Weimerskirch, 2007), prey horizontal and vertical distributions (Kowalczyk et al., 2015; Boyd et al., 2015), and sometimes anthropogenic pressures (e.g. fishing effort) (Bertrand et al., 2012; Corbeau et al., 2019).

### Box 1.2.1: Ecological definitions

**Home Range** : It is an ecological concept understood as "the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range" (Burt, 1943)

**Utilization Distribution** : It is a usual solution to quantify home range, and consists of the "spatial probability density of where an animal might have been found at any randomly chosen time" (Powell and Mitchell, 2012)

**Habitat** : The term 'habitat' is an ecological concept that refers to a set of environmental conditions rather than to geographical locations. It is usually understood as a description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives (Kearney, 2006)

This is known as habitat modelling or species distribution modelling, which consist of logistic regressions, that model the probability of a site being a relevant place for breeding, living or foraging given some descriptive characteristics (Borboroglu and Yorio, 2007; Cox et al., 2013). For what concerns the habitat modelling of foraging areas, we also refer it to as Resource Selection Function (RSF) analysis (Boyce et al., 2002; Boyd et al., 2015). These tools are used to characterize seabird movements but also in predictive



frameworks to estimate potential habitat uses at unknown locations and for future states (Hindell et al., 2020; Somveille et al., 2020). It is usually performed by GLMMs, or by generalized additive mixed models (GAMMs) (Abrahms et al., 2018), or random forest (RF) (Poli et al., 2017). A particularity of these models is that they require both presence and absence data, whereas tracking data provide only presences. This issue is thus addressed by generating 'pseudo-absence' representing where animals could have gone with the same mobility characteristics, but without any knowledge of external factors. RWs used in step-level analysis are typically used for this purpose (Hazen et al., 2021).

### 1.2.3 Challenges and trends

In most studies, common practice is thus to perform sequentially these step-, trip- and population-level analyses. First, by identifying seabird dives, then by evaluating trip and diving statistics, and finally by modelling foraging habitat. These tools focus therefore on distinct scales, and provide separately multiple perspectives of animal movement processes. These three analysis levels are mainly used for characterizing seabird trajectories, while population-level tools are occasionally used for predictive tasks.

#### Limitations of popular tools

Simple RWs are great to characterize step-level statistics, but they are however soon limited for trajectory prediction and simulation as they rely on numerous hypothesis, where individuals are often assumed to search with no knowledge of their environment, and where the Markovian hypothesis implies that the probability of each event depends only on the previous state. Seabirds are however known for their navigation abilities, perceiving fishing boats, or other seabirds at tens of kilometers (Thiebault et al., 2014; Collet et al., 2017), using olfactory cues (Reynolds et al., 2015; Bastos et al., 2020). They are also known for their cognitive abilities, such as memory (Collet and Weimerskirch, 2020; Léandri-Breton et al., 2021), and for making use of external factors to navigate, such as wind (Fritz et al., 2003; Ventura et al., 2020). Simulated trajectories from overly simplistic RWs thus often lead to unrealistic trajectories and their use into further analysis can however be an important issue. For instance, numerous studies have demonstrated the impact of pseudo-absence generation framework on habitat model prediction and relevance (Wiszniewski and Guisan, 2009; Hazen et al., 2021).

In addition, trip- and population-levels analysis also mostly rely on relatively simple descriptive metrics and statistical tools; about 68% of movement studies are based on linear models with no explicit spatial or temporal component in its definition (Joo et al., 2022; Tremblay et al., 2009). This is a major limitation, as such approaches often rely on numerous assumptions concerning normality, homoscedasticity, and independence of residuals. If these assumptions are violated, the estimated confidence intervals of the feature weights, analysis of variance and hypothesis tests are however invalid. However, published applications to data often show little care in checking goodness-of-fit and residual analysis, eventually leading to erroneous conclusions (Breiman, 2001). Moreover, they ignore the sequential structure of tracking data, and often neglect its auto-correlation and inherent spatial dependence bias estimations, such as utilization distribution (Winner et al., 2018). Spatio-temporal autocorrelation is occasionally considered, using autocorrelated

kernel density estimators (Fleming et al., 2015; Winner et al., 2018), or spatio-temporal point processes (Renner et al., 2015; Mercker et al., 2021). These approaches are yet mainly based on simplistic assumptions about the animal's movement, and spatial autocorrelation is often treated as a nuisance for statistical inference (Tremblay et al., 2009).

Habitat models, in particular, make use of spatial data derived from satellite products. These products have great spatio-temporal resolution, such as satellite imagery (e.g. LandSat;  $\approx 30$  m / 1 day), bathymetry (e.g. GEBCO;  $\approx 100$  m), fishing activity (e.g. Global Fishing Watch;  $\approx 1$  km / 1 day), and wind products (e.g. ASCAT;  $\approx 25$  km / 1 h). We invite the reader to refer to Goddijn-Murphy et al. (2021), for an overview of earth observation data used for the study of seabirds and their habitats. Yet, numerous studies have derived temporally- and spatially-averaged statistics from these fields, and thus often ignore small-scale spatial structures and short-term dynamics (Paiva et al., 2010; Fromant et al., 2021). They are, however, known to be sensitive to the resolution of external factors as the use of low spatio-temporal resolutions can be misleading for the identification of movement drivers, and especially in marine ecosystems which are inherently highly dynamics (Scales et al., 2017). Moreover, most studies described water masses only (e.g. sea surface temperature fields) and do not account for the spatial and vertical structures (e.g. thermal fronts, thermocline). In few exceptions, studies have considered geometrical spatial descriptors within habitat models such as distance to breeding colony Fauchald et al. (2021), or distance to mesoscales fronts (Scales et al., 2014). Sea surface temperature and chlorophyll production fields are indeed often not enough to describe accurately food web spatial dynamics (Grémillet et al., 2008; Scales et al., 2014). The choice of external covariates and their representation (i.e. describing water masses or oceanic structure) is not always straightforward, yet crucial for building relevant predictive habitat models (Hodgdon et al., 2021).

Finally, the key to prediction of ecological processes, such as movement, lies in the elucidation of mechanisms underlying observed patterns (Levin, 1992). Trip- and population-level analyses are models that correlate emergent movement patterns to external factors, but that can fail at elucidating the drivers of the processes that gave rise to them. For this reason, numerous studies recommend the development of movement models accounting for the multiscale nature of the interaction between seabirds and their habitats Nathan et al. (2008).

### **Integration of multiscale movement processes**

Over the last decades, technological advances in electronic devices have allowed ecologists to collect animal tracking data (e.g. GPS) at high spatio-temporal resolution. These data contain therefore an amount of information that is not always straightforward to extract and characterize. A seabird foraging trajectory involves indeed oscillations and loop patterns with spatial scales varying from tens of meters to a few kilometers. Figure 1.6 provides a typical illustration of the wide range of nested scales observed along wild animal movement paths sampled every second. Step-level and trip-level metrics detailed in Table 1.2 might therefore be considered insufficient for characterizing movement patterns in all their complexity. For this reason, various studies have investigated multiscale analysis tools, including spectral and wavelet analysis (Fablet et al., 2014; Roy et al., 2021), and changes in fractal dimension within a path (Fritz et al., 2003). These appli-

cations are indeed particularly interesting to extract geometric patterns of interest, and determine characteristic geometrical scales, which is not addressed in most studies (Fablet et al., 2014). Similarly, various step-level movement models based on state-space models have been developed in order to capture large-scale characteristics of animal trajectories. For instance, Michelot et al. (2017) presented a HMM that capture the behavioral cycle of central-place foraging trajectories (i.e. outbound, search, forage, return to colony), and Leos-Barajas et al. (2017) used hierarchical HMMs, incorporating multiple Markov chains at various time scales. It could notably be used to capture foraging trips properties at a daily-scale, by modelling movement as a sequence of foraging trips, or by describing foraging trips as a sequence of distinct foraging bouts.

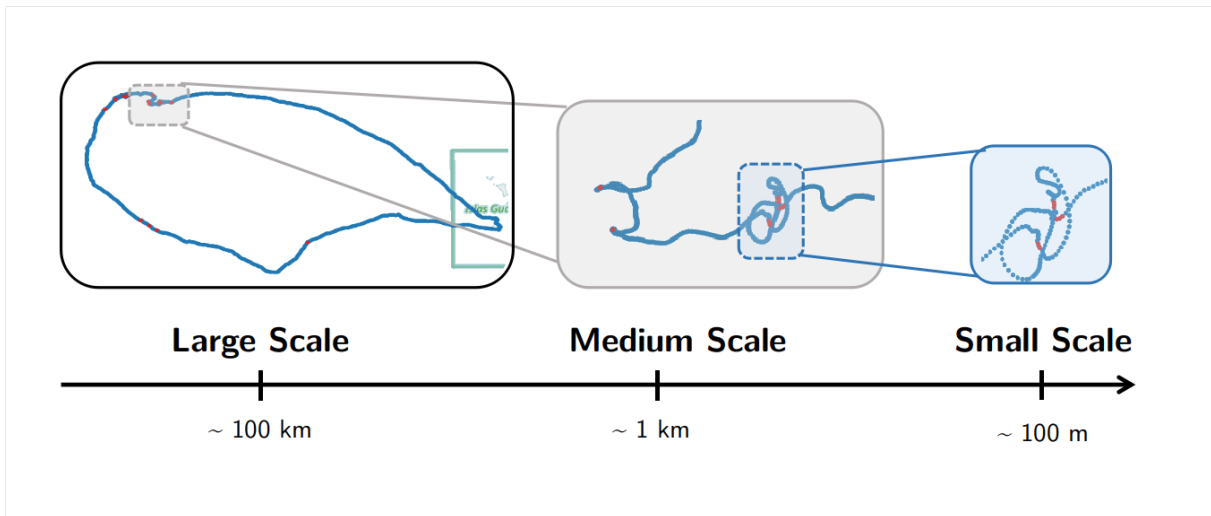


Figure 1.6: **Multiscale properties of seabird foraging trajectories** - Example of the GPS track of a Peruvian booby sampled every second. Large-scale movement patterns might be driven by flight constraints or by landscape perception. Medium-scale movement patterns might be induced by cognitive processes (e.g. memory) or by perception abilities (e.g. fishing boat detection, social interactions). Small-scale patterns are generally interpreted as direct detection of preys, and optimal use of wind

### Assessing the role of heterogeneous landscape

To assess the role of environmental heterogeneity, a solution is therefore to model RW parameters as functions of external variables (Jonsen et al., 2003; McClintock and Michelot, 2018). Animal steps are indeed supposed to depend on landscape, for instance with rapid and directed steps in areas with no resources, and shorter and less directed steps when exploited areas are reached (Togunov et al., 2021). In their study Jonsen et al. (2019) used a correlated RW, whose step length depended on sea ice cover. Fijn et al. (2022) also recently used a HMM, whose state-switching probability depended on external covariates, and thus demonstrated that Sandwich terns tend to forage more often over area with coarser sediments, consistently with the habitat preferendum of their preys. Figure 1.7 provides an example of movement simulation where steps directions depends on a field of sea surface temperature. Continuous time and space Markov process have also

been used to model animal paths, defined as the realization of some stochastic differential equation (SDE). They typically account for heterogeneous landscapes using diffusion models which follows the gradient of a potential surface (Preisler et al., 2013; Gloaguen et al., 2018; Michelot et al., 2018). In these approaches, potential surfaces are estimated from external spatial data and define how much animals are attracted or repelled from specific locations.

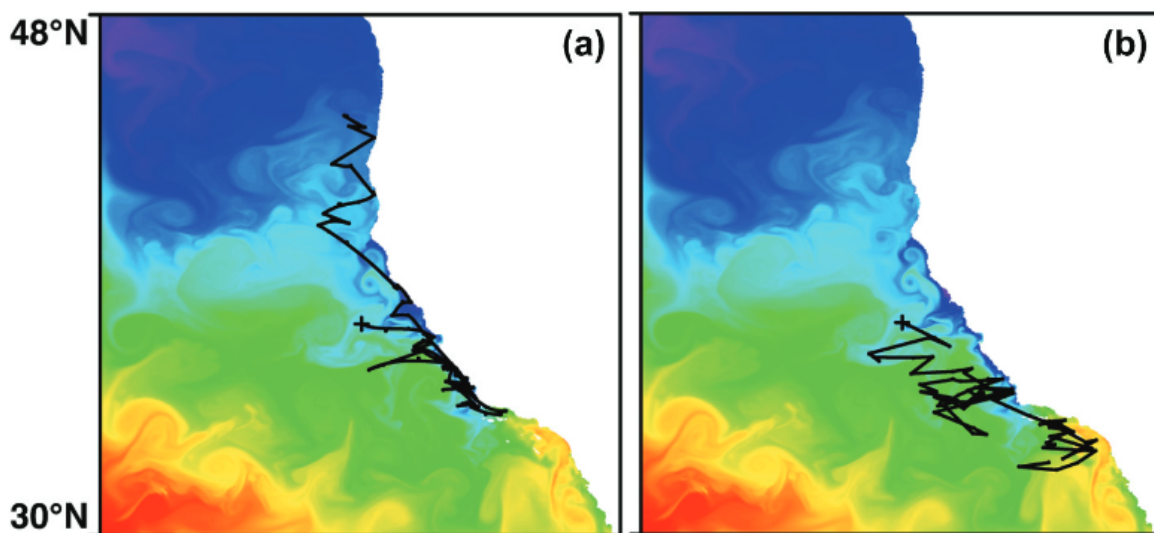


Figure 1.7: **Example of simulated animal trajectories** (a) correlated random walk (CRW) with encoded environmental preference, (b) correlated random walk (CRW) with no environmental preference - Credits Scales et al. (2017)

Another approach to evaluate the impact of external covariates on animal path is the step-selection function framework (SSF), where movement models are defined as the extension of resource selection functions (i.e. habitat modelling) at the step-level (Duchesne et al., 2015). This approach consists indeed in modelling step distributions as a function of external covariates, by comparing how the sites visited by an animal differ from those available locally but not visited (Fortin et al., 2005; Avgar et al., 2016). These approaches accounted for various external covariates such as oceanographic variables, wind and prey distributions, but they also considered distance-to-coast measures (Thurfjell et al., 2014) and memory landscapes (Oliveira-Santos et al., 2016). Empirically-parameterized Individual-Based Models (IBM) are also popular frameworks for a Lagrangian-based description of animal movements (Avgar et al., 2013). IBM aim to explicitly represent the interactions between individuals and their environment based on ad-hoc formulations, and they provide a pragmatic way to simulate non-linear movement processes (DeAngelis and Grimm, 2014). For example, some studies embed HMM (e.g. Boyd et al., 2016a), correlated RW (e.g. Massardier-Galatà et al., 2017) or mixtures of random and deterministic movement (Barraquand et al., 2009) in IBM for the simulation of animal movements.

## **Towards data-driven movement analysis**

Most of the movement models that we presented here are mainly calibrated by likelihood maximization or by approximate Bayesian inference. However, it is often difficult to estimate their parameters, especially when the complexity of the models increases (Michélot et al., 2017; Adam et al., 2019). Some individual-based models even have intractable likelihood and are not always directly calibrated from observed data (Grimm et al., 2005; Hartig et al., 2011). For these reasons, the use of realistic models that manage to both integrate multiple scales and account for heterogeneous landscapes is relatively limited. Given the amount of data now available to describe animal movements, a few studies have suggested that it is time to explore data-driven tools, such as deep learning, for the analysis and simulation of movement data (Wallentin, 2017; Nathan et al., 2022). Deep learning is often considered as a promising tool in ecology as it is able to automatically extract patterns from complex, heterogeneous and multiscale data (Malde et al., 2020; Borowiec et al., 2022). Although its use has so far been limited to image classification (Weinstein, 2018), approaches are beginning to appear for the analysis of animal movement. A more detailed review is proposed in the next section.

### **1.2.4 Conclusion**

In this section, we have presented main data types and tools from movement ecology. In particular, we have highlighted the complexity of high-resoluted animal trajectories that summarize a wide range of nested processes. We have also demonstrated that usual tools are rather limited to specific scales, and that efforts are required to bridge the gap between step-, trip- and population-level analysis. For this reason, in this thesis we aim to explore new tools from deep learning for the characterization and simulation of seabird movements.

## 1.3 Enriching Seabird Movement Ecology with Deep Learning tools

The recent accumulation of movement data have revolutionized our way to observe and understand animal ecology (Yoda, 2019; Nathan et al., 2022). In particular, movement is a complex nonlinear process, where time and space are intrinsically inter-dependent. In order to better extract information from these new datasets, which are large, heterogeneous, complex, and at multiple scales, new dedicated tools must be developed (Joo et al., 2022). In particular, this thesis proposes to explore new tools for data analysis and simulation based on deep learning (Goodfellow et al., 2016).

In this section, we will provide an introduction to deep learning. Deep learning is a specific kind of statistical learning, for this reason we will recall few basic principles using illustrative examples. Then, we will describe popular deep neural network architectures used in deep learning and how they are trained. Finally, we will provide a state-of-the-art of deep learning applications in ecological studies and research frameworks.

### In a nutshell

- ☞ Statistical Learning is a wide family of tools that consists mainly in fitting a parameterized function to data samples, so that it maximizes some metric performance
- ☞ Deep networks are parameterized functions composed of numerous layers combined with each others, which are able to extract complex data characteristics at multiple scales
- ☞ Deep models can be divided in two main groups: discriminative networks that are used for classification and segmentation tasks, and generative models that can be used for simulation and prediction tasks
- ☞ Deep learning in ecology has been mainly limited to discriminative models applied for computer vision applications, few approaches take benefit of these tools for characterization and prediction of trajectory data

### 1.3.1 Statistical Learning

Statistical Learning (or Machine Learning) refers to the very wide concept of 'learning from data'. Formally, as detailed in Mitchell and Mitchell (1997), it consists in a family of algorithms that make use of data to improve a computer program's performance over a specific task. In practice, the computer program is, in most cases, a parameterized function, whose parameters are fitted to data in order to maximize (or minimize) a pre-defined performance metric. There exists therefore a wide range of statistical learning approaches depending on (1) the type of task considered and the available data, (2) the choice of the parameterized function, (3) the choice of the evaluation metrics to be optimized, and (4) the choice of optimization tools. It is therefore to note that most usual statistical tools, notably used in movement ecology, such as random walks, linear models and kernel density estimators are actually included in this wide definition. However, the machine learning community uses a specific terminology and has a specific modeling culture (Breiman, 2001). In this section, we will introduce some important terms through two following classical tools from movement ecology presented from a machine learning point of view, i.e. a linear regression and a mixture of random walks.

#### Box 1.3.1: Learning Frameworks

**Supervised Learning** experiences a dataset containing many features  $x$ , associated with a target  $y$ , and learn how to map these pairs (e.g. generalized linear models, general additive models, random forests)

**Unsupervised Learning** experiences a dataset containing features  $x$ , and learn useful properties to structure the dataset (e.g. principal component analysis, k-means clustering, mixture random walks)

**Reinforcement Learning** is the process by which a computer agent learns to behave in an environment that rewards its actions with positive or negative results.

#### Example 1 - Linear Regression

Regression is a usual **supervised learning** task, where a parameterized function  $f$  is asked to map the relationship between numerical values  $x$  and  $y$ , given a set of  $n$  observations  $(x_i, y_i)_{0 < i < n}$  (see Box 1.3.1). In linear modelling, the core assumption is that the output of such function is linearly related to its input value. The function is thus written as follows:

$$\hat{y} = f_{a,b}(x) = a.x + b \quad (1.2)$$

Here,  $\hat{y}$  is the estimated numerical value for a given  $x$  and  $a$  and  $b$  are the parameters that control the linear behavior of the function. One way to evaluate how this function fits to the observations is to compute a performance metric, such as the Mean Squared Error (MSE). In machine learning, we refer to the parameterized function as the **model**, and to the performance metric as the **loss function**. The evaluation of this loss over the whole available dataset gives the following equation:

$$L_{\text{MSE}}(a, b) = \frac{1}{n} \sum_{i=1}^n [f_{a,b}(x_i) - y_i]^2 \quad (1.3)$$

Thus, the smaller the absolute difference between  $f_{a,b}(x_i)$  and  $y_i$  the smaller is the MSE. Learning from the dataset, consists then to look for the  $\hat{a}$  and  $\hat{b}$  that minimize this loss. With this simple example, the best parameters can be computed analytically, we refer the reader to Goodfellow et al. (2016) for a detailed demonstration. In practice, usual parameterized functions are often more complex, and can involve tens to millions of parameters. Their optimization is thus iteratively estimated using a **gradient descent algorithms**, that are able to converge to  $\hat{a}$  and  $\hat{b}$ . For computational reasons, numerous approaches are also powered by a stochastic variant of gradient descent, the **Stochastic Gradient Descent** (SGD). When dealing with huge datasets, the loss function is indeed not estimated over the whole  $(x_i, y_i)_{0 < i < n}$  combinations, but rather on smaller data subsets referred to as **batch**. The SGD is thus a stochastic optimization algorithm that relies on gradient expectations to guarantee parameters optimization with faster convergence. In this example, we used a simple deterministic gradient descent algorithm that take the following form, with  $l_r$  a pre-defined value refers to as the **learning rate**:

$$\begin{cases} a_{n+1} &= a_n - l_r \cdot \frac{\partial L_{\text{MSE}}}{\partial a}(a_n, b_n) \\ b_{n+1} &= b_n - l_r \cdot \frac{\partial L_{\text{MSE}}}{\partial b}(a_n, b_n) \end{cases} \quad (1.4)$$

We illustrate these equations to model the relationship between features  $x_i$ , defined as the length of seabird foraging trips (in kilometers) and targets  $y_i$ , defined as the total durations of these trips (in minutes). Data has been recovered from Peruvian boobies (*Sula variegata*), breeding in Island Pescadores, Peru and tracked with GPS in 2009. We initially fixed the model parameters  $a, b = 0$ , and we iteratively estimated parameters using equation 1.4 with a learning rate of  $10^{-5}$ . Results are shown in Figure 1.8. In particular, we show that only 50 iterations are enough to converge to the best parameters, thus minimizing the MSE loss function, and providing a relevant relationship in between foraging trip metrics.

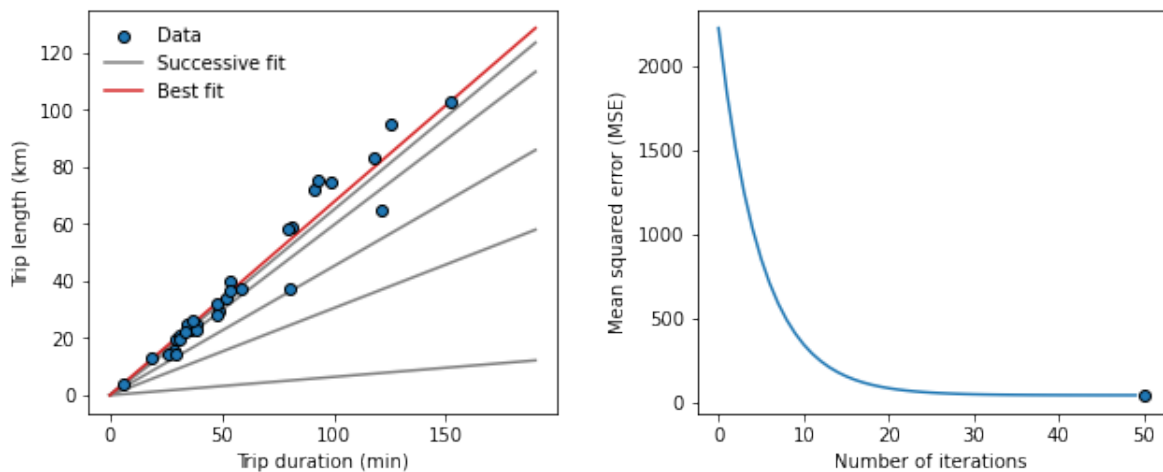


Figure 1.8: **Linear Regression** - Training data and successive fit (left) and Iterative value of MSE for successive fits (right)



Linear models are indeed able to characterize simple data relationships. In classical statistics, we typically add other assumptions about the distribution of the error terms, and about the independence of the observed values of  $y_i$ . It is thus further used to make inferences, such as confidence intervals and tests of hypotheses for model parameters. Thanks to their simplicity, these models are known to be particularly informative and easy to interpret, and that is why there are extensively used in applied statistics, such as in seabird movement ecology. On the counterpart, they are however often limited for modelling more complex relationships, and for forecasting or predicting the value of  $y$  for new values of  $x$  (Breiman, 2001). Existing regression functions, such as linear models, support vector machines, decision trees, random forests, and neural networks are indeed roughly distinguished according to their trade-off between **interpretability** and **generalization** properties. The generalization is the ability of a given model to perform well on previously unseen data points, and its interpretability (or explainability) is the degree to which we can understand the cause of a decision. Linear models have thus low generalization property, but high interpretability. In opposition, neural networks are more difficult to interpret, and they are often considered as 'black boxes'. Not because the mechanisms inside a neural network are unknown, but rather because they have so many parameters, that it can get challenging to extract information directly from their values. Yet, they are by construction very flexible tools, and have recently demonstrated outstanding generalization abilities. For a detailed description of the functioning of neural networks, please refer to the next section on deep neural networks. We often refer to this interpretability/generalization trade-off as the **Occam dilemma**, and depending on their objectives, researchers are expected to choose a regression function with relevant degree of complexity.

The performance of a model for previously unseen inputs (i.e. generalization) is indeed a fundamental challenge in machine learning. To evaluate generalization, a common practice in supervised learning is to split datasets into two subsets, the **training dataset** and the **testing dataset**. These datasets are then used respectively, to estimate model parameters by minimizing some error measure (i.e. training error), and to evaluate its generalization to new inputs (i.e. testing error). Fitting a relevant model with good generalization properties usually involves a double objective (1) making the training error small and (2) making the gap between training and test error small. When the model is not able to make the training error small enough, we say it is **underfitting**. When the model is not able to make the gap between training and test error small enough, we say it is **overfitting**. Hopefully, whether a model is more likely to underfit or to overfit can be regulated, by adjusting its **capacity**. The capacity of a model is its ability to fit a wide variety of functions, we also refer to its **flexibility**. It is determined by the family of regression function it belongs to, and by the number of parameters involved. For instance, the set of functions that a linear model is allowed to select is way smaller than the set of functions considered by a quadratic polynomial. However, the capacity of a parameterized function can also be controlled by a **regularizer**, which consists of a penalty added to the loss function that express preferences of one function over another from the set of considered functions. For instance, the training loss considered in Equation 1.3 is often generalized for any function  $f_{\theta}$  with parameters  $\theta = (\theta_1, \dots, \theta_k)$ , including a L2 norm of the weights involved in the model. The L2 norm is a famous regularization technique that penalizes parameterized functions that have high magnitude weights, and that prevents models to get overly complex:

$$L(\boldsymbol{\theta}) = L_{\text{MSE}}(\boldsymbol{\theta}) + \lambda \cdot \sum_i \theta_i^2 \quad (1.5)$$

For this reason, in machine learning, preferred models for regression are often tools with (very) high capacity such as (deep) neural networks, that are precautionary trained to reduce their generalization errors, and to avoid overfitting using **regularization** techniques. For example, figure 1.9 illustrates the generalization properties of linear models and neural networks fitted to a dataset with trips statistics of Peruvian boobies (*Sula variegata*). The dataset has been split into a training (in blue) and testing (in orange) dataset, considering generally respectively 70% and 30% of the global dataset. In particular, the linear model (left) lacks flexibility to capture the relationship between trip length and duration, and has a high training loss which indicates that the linear model actually underfits the dataset. This linear model is compared to a basic fully-connected neural network composed of 5 consecutive linear layers with sigmoid activations, with a total of about 4300 parameters. This network is particularly flexible, and is able to reduce drastically the train loss after numerous iterations (right). In this situation, the neural network yet overfits data, and tends to memorize training data rather than capturing the general trend. Interestingly, the same network but trained with a L2 norm regularizer (center) gets the lowest test error, and is able to generalize well to unseen data.

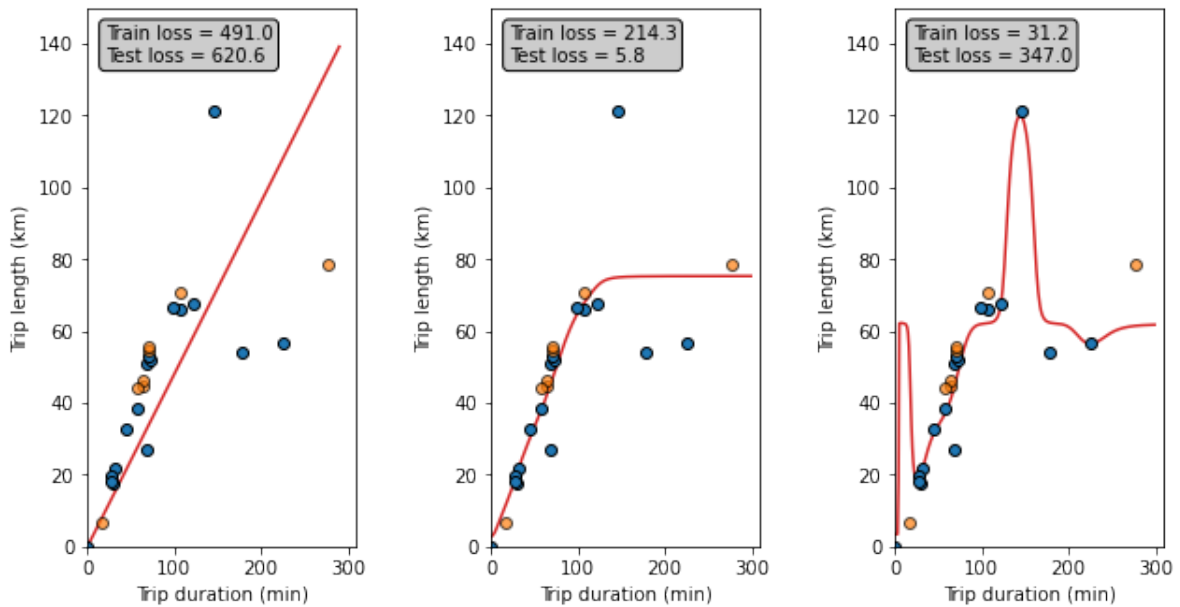


Figure 1.9: **Generalization properties of linear and neural network models** - Train data is shown in blue, test data is shown in orange and red lines are the fitted models. A linear model is fitted to training data (left). The same fully-connected neural network architecture is fitted to training data, with (center) and without regularization penalty (right).

This linear regression example illustrates therefore the main aspects and challenge of supervised learning. Supervised learning is however not restricted to regression tasks, and also includes similar tasks such as **classification** and **segmentation** tasks. In classification, the  $y_i$  values to be estimated are actually categorical values to which inputs  $x_i$  belong to (e.g. identification of animal presence/absence). In segmentation, the  $x_i$  inputs

consist in a group of elementary units, and each unit has to be associated to a categorical value (e.g. detection of behavioral sequences in trajectory data). For such tasks, the most popular loss function is the binary cross-entropy, and performance is also considered in terms of accuracy.

### Example 2 - Mixture Random Walk

Random walks are popular tools for the analysis of animal trajectories, notably for **clustering** elementary steps into distinct behavioral modes. Similarly to classification, clustering is a learning task where a parameterized function is asked to specify which of  $k$  categories some inputs belong. It is however performed in an **unsupervised learning** framework, it is without any feature-target pairs  $(x_i, y_i)$  as in the previous example, but rather by describing and structuring the distribution of available features  $x_i$ . For this reason, the main idea of random walks is to describe trajectory data as a succession of elementary steps, which follow some parameterized probability distribution. For a given sequence of positions  $(lon_t, lat_t)_{0 < t < n}$ , we can indeed express movement in the following correlated model:

$$\begin{cases} lon_{t+1} &= lon_t + d_{t+1} \cos \phi_{t+1} \\ lat_{t+1} &= lat_t + d_{t+1} \sin \phi_{t+1} \\ \phi_{t+1} &= \phi_t + \theta_{t+1} \end{cases} \quad (1.6)$$

Where  $d_t$ ,  $\phi_t$  and  $\theta_t$  are the step length, step direction and step turning angle at time  $t$ . The distinction between step direction and turning angle is described in Table 1.2. It is thus interesting to note, that given initial values of  $lon_0$ ,  $lat_0$ , and  $\phi_0$ , this movement model can be entirely described by step length and turning angle distributions. Modelling movement as a correlated random walk is thus equivalent to fitting probability distributions to empirical step length and turning angle histograms. In movement ecology, step length are generally seen as samples of Gamma, or Log-Normal distributions, and step turning angle as samples of Von Mises or Cauchy distributions. They are also generally considered as mixtures of probabilities, where step distributions are seen as the output of several distributions, so that each distribution describes a specific behavioral mode. More precisely, the density of a mixture distribution is the linear combination of its component densities. For instance, if we consider  $m$  behavioral modes, and that for each of them step length and turning angle are sampled from independent Gamma and centered Von Mises distribution respectively, we can write the joint distribution of steps distance  $d$  and step turning angle  $\theta$  as follows:

$$\begin{aligned} f(d, \theta; \boldsymbol{\kappa}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{w}) &= \sum_i^m w_i \cdot f(d, \theta; \kappa_i, \alpha_i, \beta_i) \\ &= \sum_i^m w_i \cdot f_{\text{Gamma}}(d; \alpha_i, \beta_i) f_{\text{VonMises}}(\theta; \kappa_i) \end{aligned} \quad (1.7)$$

Where each  $\boldsymbol{\kappa} = (\kappa_1, \dots, \kappa_m)$ ,  $\boldsymbol{\alpha} = (\alpha_1, \dots, \alpha_m)$  and  $\boldsymbol{\beta} = (\beta_1, \dots, \beta_m)$  are parameters describing the probability distribution associated to each behavioral mode, and  $\boldsymbol{w} = (w_1, \dots, w_m)$  are the probabilities to be in the considered mode.

Distribution parameters, and mode selection probabilities are generally estimated using **likelihood maximization**. The idea is that we compute the likelihood of all ob-

served steps  $d_t$  and  $\theta_t$ , and intuitively, maximizing likelihood with respect to distribution parameters selects thus the parameter values that make the observed data most probable. Once again, in some case the best parameters can be obtained analytically under some assumptions (e.g. Kalman filter), but it is in most cases iteratively estimated using gradient descent method.

$$L_{\text{LIKELIHOOD}}(\mathbf{k}, \boldsymbol{\theta}, \boldsymbol{\kappa}, \mathbf{w}) = \prod_{t=1}^{n-2} f(d_t, \theta_t; \boldsymbol{\kappa}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \mathbf{w}) \quad (1.8)$$

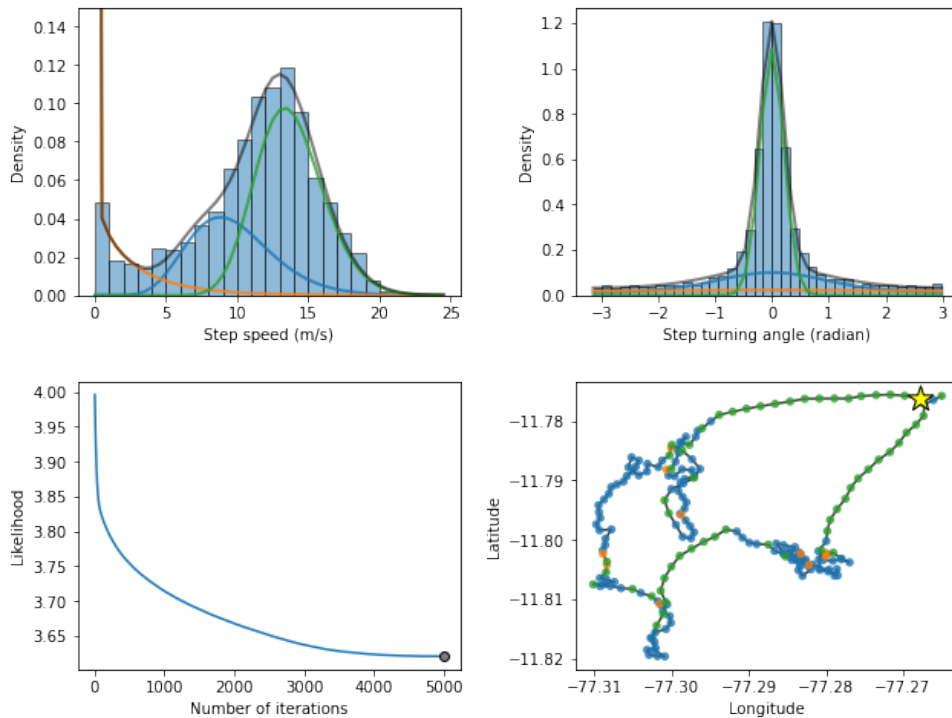


Figure 1.10: **Mixture CRW Regression** - Step speed distribution and associated fit (top left), Step turning angle distribution and associated fit (top right), Iterative value of likelihood through the optimization algorithm (bottom left), and an example of seabird trajectory whose recorded locations have been associated to the most likely behavioral (bottom right)

We illustrate these equations to model the step speed and direction distributions from Peruvian boobies (*Sula variegata*) breeding in Island Pescadores, Peru and tracked with GPS in 2009. We iteratively estimated parameters using a gradient descent on the log likelihood as in equation 1.4 with a learning rate of  $10^{-2}$ . Results are shown in Figure 1.10. In particular, we can observe that this model enables to describe step distributions as a combination of three behavioral modes. One could typically attribute *a posteriori* behaviors to each of these modes, such as foraging, searching and travelling for distributions orange, blue and orange respectively. Once step distributions have been fitted by minimizing likelihood, it is also possible to compute to which mode a step is most likely to belong to. The trajectory can thus be clustered in  $m$  groups of steps and provide important insight on animal behavior. A general issue for clustering task, is however that there exists no single criterion that measures how well an algorithm performs, because of

the absence of true labels. There is indeed no guarantee that behavioral modes estimated by our mixture CRW correspond to real properties of seabird behavior.

For this reason, unsupervised algorithms tend to focus more generally on **density estimation** tasks. It consists in learning the probability distribution of some data, in order to capture its structure and to find relevant **data representation**. The notion of representation is a fundamental aspect of machine learning, it consists typically in finding a way to describe some data feature  $x$  in a simple and relevant manner, yet preserving as much information as possible. In our example, we can think of our mixture CRW as a way to provide a **latent representation** for each step, through the behavioral mode. This is also typically the aim of **dimensionality reduction** methods such as Principal Components Analysis (PCA), that learns a linear transformation of data in order to identify the principal axes of variance. Recently, deep neural networks have shown an interesting capacity for such dimensionality reduction, in particular by integrating complex data, such as images or time series, into latent vectors of descriptive statistics (LeCun et al., 2015).

### 1.3.2 Deep Neural Networks

Deep learning refers to a specific type of statistical learning tool, based on deep neural networks (Goodfellow et al., 2016). A neural network is a parametric function  $f$  composed of multiple elementary processing **units**, i.e. neurons. The term 'neuron' is notably used for historical reasons, as the first neural networks developed in the 1950s, called **multi-layer perceptrons**, were directly inspired by neuroscience and by the functioning of nervous systems. In particular, they were only composed of perceptrons mimicking a neuron's behavior, i.e. a process unit that take a vector of inputs and that produces a single binary output. In modern neural networks, there now exists a wide variety of processing units, and their design is driven more by numerical and mathematical considerations, rather than insights from by biological and neuroscience. Neural networks can thus be thought more generally as a **composition** of multiple building blocks functions with interesting mathematical properties. For example, we might have three functions,  $f_1$ ,  $f_2$  and  $f_3$ , connected in a chain to form the following **feedforward** network  $f$ :

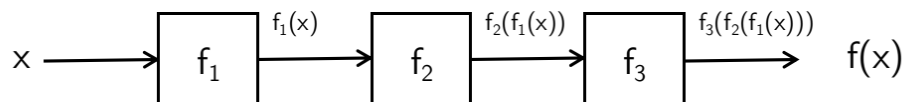


Figure 1.11: **Feedforward neural network**

Here functions  $f_i$  are referred to as **layers**, and ordered depending on their position in the network. In this case,  $f_1$  is called the first (or input) layer,  $f_3$  is the output layer, and intermediate layers such as  $f_2$  are usually refer to as **hidden** layer. A feedforward network is therefore a network where the information moves in only one direction, i.e. from the input layers, through the hidden layers and to the output layers. For example, let assume that the input vector  $x$  has dimension  $n$ . Then if  $f_1$  and  $f_3$  are linear combinations, e.g.  $m \times n$  and  $p \times m$  matrixes respectively, and that  $f_2$  is an activation function, such as a sigmoid, or a hyperbolic tangent, therefore the network  $f$  is a multi-layer perceptron with one hidden layer. The **depth** of the network is given by the total number of

hidden layers, i.e. one only, and the **width** of the network is given by the dimensionality of the hidden layers, i.e.  $m$ .

### Box 1.3.2: Latent representation

In deep learning, inputs are transformed by a composition of layers into one or several internal representations that we also refer to **latent features**, or **data embeddings**. We refer to the multi-dimensional space in which these vectors are encoded as the **latent space**.

The main intuition behind neural networks, is that, in the same way that a nervous system relies on the simultaneous use of multiple simple neurons, a combination of numerous elementary functions organized in a relevant network, can approximate complex and non-linear relationships. This is supported by a fundamental result, the **universal approximation theorem** (Cybenko, 1989; Hornik et al., 1989). In brief, this theorem means that regardless of what function we are trying to learn, we know that it can be represented by a multi-layer perceptron with only one hidden layer. In practice, it however often requires the hidden layer to be highly dimensional, and thus requires a huge amount of parameters. This implies that its estimation is not always guaranteed, and its optimization is not straightforward. In many circumstances, a solution is thus to use networks with more hidden layers (i.e. deep networks). Deep networks can fortunately reduce drastically the number of units required to represent the desired function, and also have better generalization properties. By decomposing the data into multiple layers, deep neural networks allow indeed to learn complex features to represent the data with high level of abstraction (LeCun et al., 2015). For this reason deep networks, remain a preferred option in machine learning and have dramatically improved the state-of-the-art in many disciplines, such as computer vision, speech recognition or genomics, and we refer to this new research field as **deep learning**.

### Popular layers

A key consideration in deep learning is therefore the **architecture** of neural networks, that is the kind of layers taken into account as well as the network's width and depth. The design of hidden layers is an extremely active area of research in deep learning, yet often empirical and therefore lacks guiding theoretical principles. There exists numerous types of layers, that all have their characteristics and specific uses. Here, we will provide a brief overview of all the neural layers used in this thesis.

- A **dense layer** also referred to as a fully-connected layer is basically a linear combination (or a matrix product), as presented in our previous example. This is indeed the historical layer used in multi-layer perceptron, and in the oldest artificial neural networks. This layer is particularly useful as it enables to change the dimensionality of the output from the preceding layer, by a simple linear transformation. Another typical characteristic is that in linear combinations, each value of the output depends on all inputs values. It is thus popular for modelling processes from data inputs with no specific structure (e.g. vector of features), a drawback is yet that

they quickly involve an important number of parameters when used over high dimensional vectors. These layers, may also make use of biases to be added to the output vector and consist thus in affine transformation.

- The other type of historical layers required in a multi-layer perceptron are **activation layers**. Activation layers are basically non-linear operations, that are used to add non-linearity to a neural network. The rectified linear unit (ReLU) function is nowadays an excellent default choice of activation function. It applies basically the function  $\text{ReLU}(x) = \max(0, x)$ . Prior to the use of ReLU, most neural networks used the logistic sigmoid or the hyperbolic tangent functions. The choice of activation function is in most cases driven by numerical reasons, in particular to ensure interesting behavior during the optimization phase.
- **Convolution layers** are a special kind of linear operations, where an operator called **kernel** slides over an input vector (or array), and applies linear combination locally. The output of such operation is called a feature map, and each value of this output vector is thus a linear combination of a small region of the input vector. Moreover, the kernel share the weights of the linear combination whatever the small regions of the input vector considered. In opposition to dense layers, convolution layers focus on local patterns and are particularly relevant for analyzing structured data. By structured data, we refer to data where a value in some vector is highly correlated to neighboring values (e.g. time-series, image).
- Convolutional layers are often associated to **pooling layers**. A pooling operator aims at summarizing some input vector into a vector of lower dimensions, typically by computing summary statistics such as average, or maximum. For many tasks, pooling is essential for handling high-dimensional inputs.
- For numerical reasons, numerous networks make also use of **normalization layers**, that are used to normalize hidden vectors, and to guarantee that these features are on the same scale as each others. It notably helps optimization algorithm to converge to better networks.
- **Recurrent layers** are specific layers, dedicated to the analysis of time-series. They are distinguished by their "memory" as the output of a recurrent neural network depend on the prior elements within the sequence, while traditional deep neural networks assume that inputs and outputs are independent of each other. They are not feedforward layers but rely on backward connections, to account for the data sequence.
- **Attention layers** have also recently been popular in modeling sequences. Attention mechanism consists in a selection process that detects which inputs are particularly more important than others. In opposition to previously seen layers, an attention layer takes three inputs called, key, query, and values vectors. The attention operation can indeed be thought of as a retrieval process, where the aim is to map a query and a set of key-value pairs to an output. It aims thus, (1) at determining similarity between keys and queries generally using a dot product, and (2) to use that similarity measure as weights for a linear combination of the values input vector.

**Box 1.3.3: Keras implementation of a CNN**

```

# import library
from keras.models import Sequential
from keras.layers import Dense, Conv2D, Flatten

# create a model
model = Sequential()

# add sequential layers
model.add(keras.Input(shape=(28,28,1)))
model.add(Conv2D(32, kernel_size=(3, 3), activation="relu"))
model.add(MaxPooling2D(pool_size=(2, 2)))
model.add(Conv2D(64, kernel_size=(3, 3), activation="relu"))
model.add(MaxPooling2D(pool_size=(2, 2)))
model.add(Flatten())
model.add(Dense(2, activation="softmax"))

```

Deep networks are then designed by composing different of the mentioned layers. For instance, multi-layer perceptron (or fully-connected networks) as illustrated in the previous example consist of alternating dense and activation layers. **Convolutional neural network** (CNN) that have been extensively used in data analysis over the last decades consist in a succession of convolutional, activation, and pooling layers. Similarly, **recurrent networks** refer to network with at least one recurrent layers. More generally, it is interestingly to note that by construction any combination of layers can be considered, and research in deep learning proceeds so rapidly that a new best architecture for a given benchmark is published every day. These layers consist in building blocks for more complex neural networks, and any pre-existing networks can also be embedded as a layer of another neural network. Recent tools for implementing deep networks, such as tensorflow, pytorch or keras libraries, make it very straightforward to create new deep network architectures. Box 1.3.3 gives for example the implementation in python using the Keras library of a convolutional neural network, simply by defining the sequence of layers to be considered.

**Stochastic optimization and backpropagation**

While previous paragraphs were dedicated to the description of deep neural networks architecture, we concentrate here on how these networks are trained and fitted to data. As developed in the statistical learning section, the optimization of a parametric function is generally performed using a stochastic optimization algorithm, such as the stochastic gradient descent (SGD). As in equation 1.4, the general equation of the stochastic gradient descent is :

$$\theta := \theta - l_r \cdot \nabla L_i(\theta) \quad (1.9)$$

Where  $\theta$  are the parameters of some neural network,  $L_i(\theta)$  the loss function evaluated over a batch of inputs  $i$ , and  $l_r$  is the learning rate. Popular variants include the Adam optimization algorithm, the most used in practice, as it empirically achieves relative good results fast. Optimization algorithms require nevertheless that we are able to



compute the **gradient** of some loss function ( $\nabla L$ ). For this reason, a specific method is needed to compute the gradients of a neural network, and we refer to this method as the **back-propagation** algorithm. The back-propagation algorithm relies on a fundamental mathematical result, known as the chain rule of calculus. This rule allows to compute the gradient of a composition of two **differentiable** functions. Let assume that we have  $x$  a real number, and two differentiable functions  $f$  and  $g$  defined for real numbers. Then the chain rule states that :

$$\frac{d}{dx}[f(g(x))] = f'(g(x)).g'(x) \quad (1.10)$$

Conceptually, it implies that we are able to compute the derivation of any composition of differentiable functions. Thus, the use of differentiable layers in a neural network guarantee that we are able to compute its gradients. Numerically, **automatic differentiation** is enabled by an efficient technique for quickly calculating derivatives, which is based on **computational graphs**. Recent tools for implementing neural networks offer thus an automatic way to compute gradients for any neural network architecture. These are thus further used in a stochastic optimization procedure, in order to minimize some loss functions. Box 1.3.4 illustrates the training in python using the Keras library of the convolutional neural network presented previously. Here, the `compile` function defines the stochastic optimization procedure to use, and the loss function to minimize. The model is then iteratively fitted to data using the function `fit`. At each step, (1) a batch of data inputs is given to the model, (2) the loss function is computed, (3) gradients are backpropagated, and (4) the weights of the network are adjusted following the Adam optimization framework. These iterations are performed for a given number of **epochs**, i.e. the number of cycles through the training set.

#### Box 1.3.4: Keras optimization of a CNN

```
# download mnist data
from keras.datasets import mnist

# split into train and test sets
(x_train, y_train), (x_test, y_test) = mnist.load_data()

# define optimization properties
model.compile(optimizer='adam', loss='categorical_crossentropy')

# train the model
model.fit(x_train, y_train, validation_data=(x_test, y_test),
          batch_size= 64, epochs=5)
```

## Discriminative and Generative Networks

By construction, a wide variety of network architectures and of learning strategies can be considered. According to their objectives and applications, we propose here to distinguish two families of deep networks: discriminative models and generative models.

Discriminative networks aim to characterize observations by identifying their specific properties. This concerns most of the deep networks trained using a supervised learning framework for classification, regression or segmentation tasks. In opposition, generative networks are unsupervised techniques used to estimate the distribution of a dataset, in particular by learning how to generate new but statistically-related samples. They include variational auto-encoders (VAE) and generative adversarial networks (GAN). GAN have particularly received tremendous attention from the deep learning community these last few years, notably for their outstanding ability to 'fake' images Goodfellow et al. (2014), whose aspect have gained in resolution and quality through recent years (Salehi et al., 2020). Figure 1.12, shows examples of fake images generated by GAN and highlights the remarkable progress made in this field.



Figure 1.12: **5 years of GAN progress on fake face generation** - Credits Salehi et al. (2020)

In GAN, two networks are competing in a zero-sum game, in the sense of the game theory. The first player (or network) is the generator, that takes as input a vector of noise and outputs fake samples. Its opponent is the discriminator, which typically is a classifier that takes as input a sample and aims at distinguishing if it is real or fake. The generator is thus rewarded when it generates samples that fool the discriminative networks, in opposition the discriminator is rewarded when it detects fake samples properly. These generative networks are interesting for many reasons. They can be used for data augmentation, i.e., to increase datasets by generating new but statistically-related samples similarly to usual bootstrap methods. However, deep generative networks are more generally relevant tools to model a stochastic process as a deterministic function that takes as input some stochasticity through a vector of noise and that outputs a realization of the stochastic process. It provides therefore a modelling framework (1) to capture and visualize the variability of a stochastic process in a latent representation, (2) to possibly account for statistically independent and causal factors of variation in data and (3) to simulate the process and predict its response to external factors.

**Box 1.3.5: Discriminative and generative modelling**

A **discriminative** model is a model of the conditional probability of a target  $Y$ , given an observation  $x$ , symbolically,  $P(Y|X = x)$

A **generative** model is a model of the probability of the observable  $X$ , symbolically  $P(X)$ . If the dataset is labelled, it can eventually model the conditional probability of the observable  $X$  given a target  $y$ , symbolically,  $P(X|Y = y)$

**1.3.3 Deep Learning in Ecology**

Neural networks have been developed in the 1950s, but their use exploded only in the 2010s. As described in Cardon et al. (2018), since then deep learning techniques have caused disruption in many scientific communities, by outperforming state-of-the-art tools in fields, such as computer vision, signal processing, speech recognition, or natural language processing, and for many tasks, including classification, segmentation, regression, clustering, anomaly detection, missing data imputation, denoising and density estimation. This is mainly due to the recent increase in computer calculation capacity and the accessibility of gigantic databases. Ecology did not escape this tendency, and deep learning has recently been introduced and illustrated over distinct applications (Weinstein, 2018; Christin et al., 2019; Borowiec et al., 2022; Pichler and Hartig, 2022).

**Image and sound processing**

Most of the applications in ecology have been limited to discriminative models trained in a supervised setting (Christin et al., 2019; Borowiec et al., 2022). Deep learning has been particularly used for classification tasks from pictures recorded by camera traps, smartphones or even drones (Weinstein, 2018). This includes automatic image segmentation and identification of many taxa, from bacteria, through animals, plants and landscapes (Borowiec et al., 2022; Goodwin et al., 2022). Prior to deep learning advances, these analyses were performed manually, and relied on experts annotations. These tasks are however relatively time-consuming, tedious and may be subject to operator-based biases. For these reasons, deep learning methods have proven to be outstanding effective solutions for automating the analysis process, with a relevant predictive accuracy and allowing to work directly from "rawest" datasets (Lumini and Nanni, 2019). Deep networks can free ecologists from the difficult task to identify relevant patterns from data, since using consecutive neural layers, deep networks can learn a latent representation of the data relevant to the task they have been trained for.

A large majority of existing tools and documentations in the deep learning community focus on RGB pictures, which has greatly helped ecologists to get used to these tools. A common practice, referred to as **transfer learning**, consists in taking advantage of pre-existing neural networks that have previously been trained over large public RGB image datasets. Recent studies have shown that features vector from the first layers of deep networks have great generalization properties and are transferable in the sense

that they are applicable to many other datasets and tasks (Yosinski et al., 2014). Despite having relatively small annotated datasets, numerous ecologists are thus able to analyze their RGB image for a specific task, without having to train neural networks from scratch. In addition, ecological applications may make use of other data types for classification tasks, such as passive and active acoustic data for animal vocalization classification (Shiu et al., 2020) or fish school segmentation from multifrequency echosounder (Brautaset et al., 2020), as well as multi-sensor satellite data for the automatic detection of reefs (Ridge et al., 2020), or landscape characterization (Yuan et al., 2020). More generally, the predominant approach focuses thus on the direct interpretation of signal processes (e.g. image, audio, time-series), and in such cases the need of interpretability is often not as important as the ability of a function to classify data input with high accuracy.

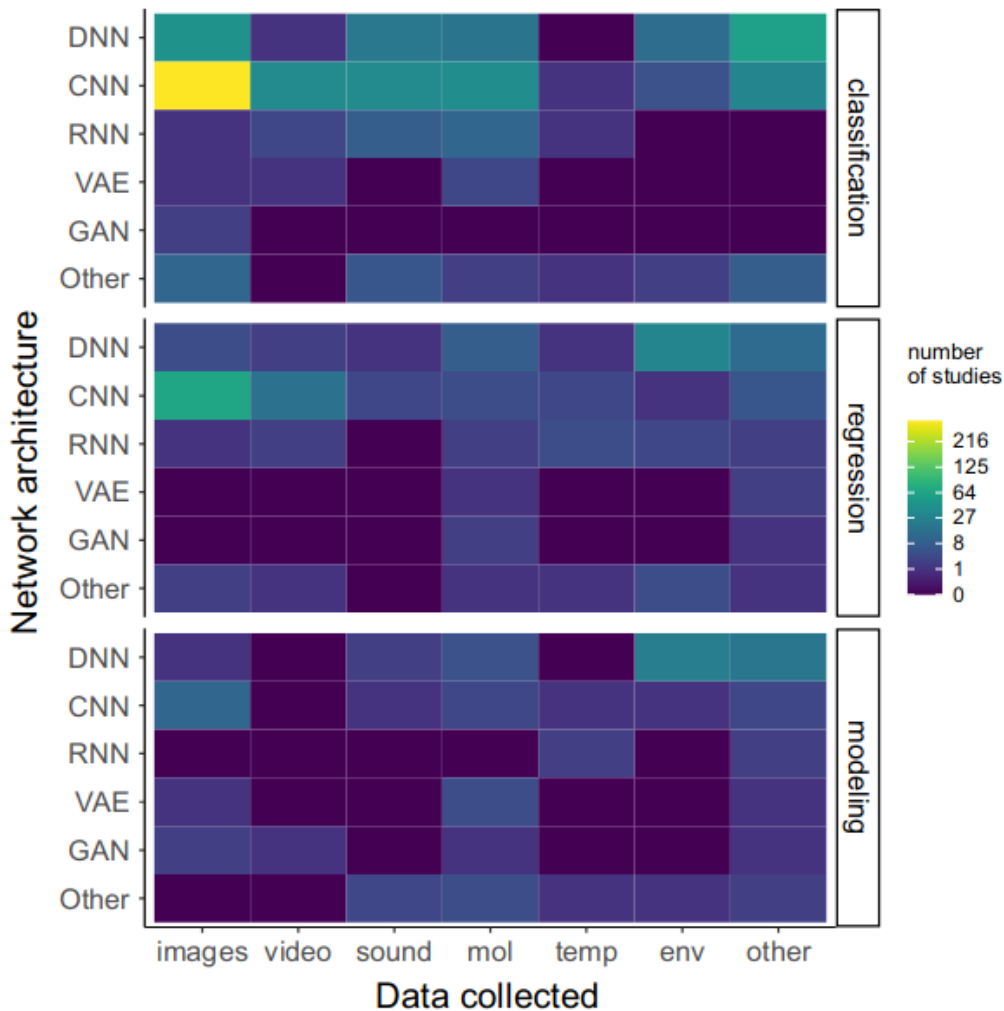


Figure 1.13: **Deep learning approaches in ecology and evolution and their frequency of use by application** - Panels represent three major applications: Classification, regression and modelling. Rows in each panel correspond to different neural network architectures and columns to input data ; Mol=Molecular; temp=Temporal; env=Environmental. Colors and legend numbers reflect the number of studies. - Credits Borowiec et al. (2022)

Fewer studies have explored deep learning tools for modelling ecological processes, and for predicting the response of ecosystems to changes in the input covariates, notably to evaluate the possible impacts of climate change and of anthropogenic pressures. Deep networks have been investigated to model species distribution constrained by environmental variables (Benkendorf and Hawkins, 2020; Rew et al., 2021). Recurrent neural networks have been applied to predict ecological time-series, such as phytoplankton blooms (Cho et al., 2018), or presence/absence time-series of bird populations (Joseph, 2020). However, an important drawback of these supervised approaches is that they require large annotated datasets, both for training and testing deep models. For this reason, future developments in unsupervised learning are expected, and notably through generative modelling. The performance of deep generative networks have not been fully exploited yet in ecology. Few journal reviews currently present these frameworks, and when they do, they often merely discuss their relevance for data augmentation (Christin et al., 2019). VAEs have been applied to inference and visualization of human population structure from genomics (Battey et al., 2021), and deep convolutional GAN have been used for data augmentation in simulating plant or insect images (Lu et al., 2019; Madsen et al., 2019).

## **Movement data analysis**

For what concern animal movement data analysis, most approaches consist in discriminative models. A fully-connected network has also been used for the identification of seabird dives in trajectory (Browning et al., 2018). Recurrent neural networks have been used to predict the future location of an animal from a sequence of its previous locations (Ardakani and Hashimoto, 2017; Rew et al., 2019), and for the identification of characteristic movement patterns (Peng et al., 2019). An attention network has also been proposed for comparative analysis of animal trajectories (Maekawa, 2020). However, these approaches are very few in the field. Generative models have only been applied to human mobility such as pedestrian trajectory prediction (Gao et al., 2020), mobile data (Ouyang et al., 2018), taxi (Wang et al., 2021a) and aircraft (Jarry et al., 2021; Aksoy et al., 2021) trajectories.

Reinforcement learning is also sometimes considered as an appealing paradigm for the study of adaptive problems such as optimal foraging strategies (Frankenhuis et al., 2019). For instance, its variant called Inverse Reinforcement Learning (IRL) has been used for interpolating missing inputs in seabird GPS trajectories (Hirakawa et al., 2018). It relies on a specific problem formalism where an agent is interacting with its environment and learn how to choose actions to maximize some reward. Although considered as a branch of machine learning, it is distinct from supervised and unsupervised learning and does not necessarily rely on deep networks. Moreover, it is mainly used in a context where the environment is perfectly known, and is not able to address problems that involve very large state spaces. For these reasons, it has few applications in ecology and is mostly used in robotics. This thesis will therefore not cover such a topic. However, it is worth to note that recent studies have established a theoretical connection between GAN and IRL, and that GAN has brought important breakthroughs in the performance of reinforcement learning (Finn et al., 2016).

Deep learning already has proven useful in many domains, in order to characterize complex multiscale datasets, such as image, and acoustic data. For this reason, in the following chapters of this thesis we argue in favor of discriminative convolutional networks for the analysis of tropical seabird movement processes. Moreover, we propose to explore the simulation of seabirds trajectories using generative networks. In particular, the different tools used in this manuscript are detailed in Table 1.3.

	Model Abb.*	Model Name	Tasks	Framework	Loss function
Discriminative	RF <sup>2</sup>	Random Forest	Classification	Supervised	Binary cross-entropy
	FPT <sup>3</sup>	First-Passage Time	Clustering	Unsupervised	Variance Maximization
	FCN <sup>3</sup>	Fully-Connected Network	Classification	Supervised	Binary cross-entropy
	CNN <sup>2,3</sup>	Convolutional Neural Network	Classification	Supervised	Binary cross-entropy
	U-Net <sup>3</sup>	U-shape convolutional neural Network	Segmentation	Supervised	Binary cross-entropy
Generative	HMM <sup>3,4</sup>	Hidden Markov Model	Clustering, Density Estimation	Unsupervised	Likelihood Maximization
	GAN <sup>4,5</sup>	Generative Adversarial Network	Density estimation	Unsupervised	Adversarial cross-entropy, Hinge loss

Table 1.3: **Models considered in this thesis and associated learning frameworks and tasks** - Numbers refer to the chapter in which a model is used

### 1.3.4 Conclusion

In this section, we have introduced deep learning tools and their applications in ecology, including movement ecology. In particular, we have illustrated that deep networks are theoretically relatively similar with usual statistical tools, such as linear models. They differ however from usual tools in practice, by their ability to model complex function, and to predict outputs with high accuracy and generalization properties. They already have proven useful in many domains, in order to characterize and predict complex multiscale datasets, such as image, and acoustic data. For this reason, in the following chapters of this thesis we argue in favor of both discriminative and generative deep learning tools for the analysis of tropical seabird movement processes.



**Part I**

**Discriminative models**





## Chapter 2

# Integrated assessment of breeding habitat selection of tropical seabirds using statistical learning

♪ *En qué parte de Cuba nació el son*, IBRAHIM FERRER

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Breeding seabirds are constrained to regularly return to their nest in order to brood and feed chicks. This is an important constraint that determined all their movements during breeding period. The choice of the breeding site is thus fundamental so that reproduction is successful. For this reason, before nesting seabirds realize prospective movements to assess the habitat suitability and select a breeding site. Understanding the mechanisms underlying breeding habitat selection is crucial for the conservation and management of seabird populations. However, many tropical regions lack a full and regular inventory of seabirds' breeding sites due to economic and logistic constraints, as well as the scarcity of qualified human resources. For instance, Laridae breeding in Cuba constitute a large and abundant seabird group from Caribbean seas, ecological information about their colonies is however limited to scarce records of breeding sites. In this chapter, we want to develop statistical learning tools to elucidate environmental drivers of breeding site selection for Laridae breeding in Cuba, and to predict the suitability of Cuban coastlines for them to breed. To this aim, we compiled historical presence/absence data of breeding Laridae from Cuba. Convolutional neural network (CNN) were trained directly on Landsat satellite images in order to provide a prediction map of macrohabitat suitability. Random forests (RF) were used to evaluate the contribution of 18 land- and marine-based physical-geographical pre-defined variables in breeding habitat selection. This work is the subject of an article in preparation.

### Associated publication

- ✍ Garcia-Quintas A., Roy A., Denis D., Demarcq H., Barbraud C. and Lanco Bertrand S. (2022) Integrated assessment of breeding macrohabitat's of tropical seabirds using machine and deep learning approaches. *In Prep.*

## 2.1 Introduction

The quality of environmental conditions in breeding habitat may affect greatly animal fitness. Thus, individuals are under strong selective pressures to select optimal breeding habitats (Orians and Wittenberger, 1991; Piper, 2011). The selection of breeding habitat is a complex process integrating environmental conditions over a large range of spatial scales, and relying on a hierarchical and sequential decision making by animals. In seabirds for example, individuals gather information on habitat quality such as geographical, physical, and biological conditions (Doligez et al., 2002; Cueto, 2006) over a range of spatial scales through prospective movements before breeding (Kristan, 2006; Ponchon et al., 2013).

Several factors have been suggested for explaining how seabirds chose a place to breed: geographical features of the nesting area (area, spatial isolation) (Greer et al., 1988; Orians and Wittenberger, 1991); vegetation characteristics (coverage, height, density) (Muzaffar et al., 2015; Raynor et al., 2012); climate variability (temperature, rainfall, wind) (Córdoba-Córdoba et al., 2010); and socio-ecological factors (competition, territoriality, predation pressure, fidelity to the breeding site, group cohesion, information exchange between individuals, colony recruitment, previous breeding experience) (Greer et al., 1988; Borboroglu and Yorio, 2007; Córdoba-Córdoba et al., 2010). More recently, the development of the use of biologging electronic devices provided information on the type of marine habitats seabirds use to forage during the breeding period (Wakefield et al., 2011). A range of oceanographic conditions surrounding the nesting sites may also be assessed by seabirds when selecting a place to nest: water masses characteristics (temperature, salinity), bathymetry and productivity-related variables (chlorophyll-a concentration, distance to food sources, prey availability and abundance). In particular, water mass properties and zooplankton abundance have been shown as important factors for this selection process in boobies and auklets (Sorensen et al., 2009; Oppel et al., 2015).

Existing studies on breeding habitat selection by seabirds are mostly focusing either on terrestrial habitats, where nests and colonies are installed, or on the surrounding marine areas, that birds use to forage during the breeding (Borboroglu and Yorio, 2007; Raynor et al., 2012). Also, most of these studies focused on a single spatial scale of analysis and were often species or colony specific. More integrative (over land and seascapes), multi-specific and multi-scale approaches should improve our understanding of the breeding habitat selection process by seabirds. In addition to these existing limitations, seabird habitat selection in the tropics is much less understood than that of temperate and polar species. In tropical waters, primary productivity is generally low and seasonally stable compared to the cooler waters of polar and temperate regions (Hockey and Wilson, 2003; Jaquemet et al., 2008). One might therefore expect key factors for habitat selection to differ between tropical, temperate or polar seabirds, and one could hypothesize that tropical seabirds are more influenced by terrestrial than by marine features.

Furthermore, many tropical regions lack a full and regular inventory of seabirds' breeding sites due to economical and logistical constraints, as well as the scarcity of qualified human resources. For instance, Laridae (gulls, terns and skimmers) in Cuba are the most abundant seabird group with 25 species recorded, 36% of them breeding in the archipelago (Navarro, 2021). Information on their colonies is however quite limited: scarce records of sites, species, number of breeding pairs, and basic habitat features and breeding parameters (e.g. Acosta et al., 2022). In particular, the most important variables affecting breeding habitat selection remain poorly known. In order to prioritize the areas

to be monitored, there is therefore an important need to predict potential breeding sites as well as to identify the main drivers of breeding habitat selection at the scale of the entire archipelago. Considering both terrestrial and marine areas should provide a more realistic and eco-functional approach to predict tropical seabirds' breeding sites.

Machine learning is a family of statistical tools that aims to learn statistical relationships from data (Fincham et al., 2020; Olier et al., 2021). Among the most popular models are the neural networks (such as Convolutional Neural Networks (CNN)), and Random Forest (RF). CNNs have become a state-of-the-art approach in the field of computer vision and remote sensing (Mahdianpari et al., 2018; Ma et al., 2019). CNNs are composed of multiple layers of processing units which can learn from complex features and represent data with a high level of abstraction at multiple scales. They are known for their outstanding ability to segment and classify images within end-to-end learning framework, i.e. without requiring any preliminary feature engineering (Fincham et al., 2020; Ma et al., 2019). RF is highlighted for its robustness to heterogeneous predictors, its high accuracy and its ability to provide a contribution level or importance of each covariate (Breiman, 2001). CNNs usually outperform RFs for classification and prediction purposes. Yet, an important advantage of RFs over CNNs is their more explicit understanding of the associations between the response variable and its covariates. In the remote sensing research area, CNNs have been identified as potentially attracting for predicting habitat suitability for animals such as birds (Chilson et al., 2019; Su et al., 2018). "A picture is worth a thousand words" and a satellite image represents an excellent example of that due to its stack of spectral bands with high potential for habitat description. Su et al. (2018) used CNNs (and Support Vector Machine) with satellite images to model the habitat suitability for a migratory geese species. Others, as Chilson et al. (2019) and Wang et al. (2021b), identified birds' habitat elements using radar data and photographic images respectively. Deneu et al. (2021) used CNNs to improve species distribution modeling by capturing complex spatial structures of the environment. CNNs might thus be very relevant to extract multi-scale characteristics of heterogeneous habitats from satellite images.

Considering the main strengths of CNN (high performance to prediction) and RF (assessing of ecological hypotheses a priori through the covariates contribution), the complementary use of both methods could increase our understanding of the patterns and processes involved in habitat selection and be helpful for developing effective management and conservation strategies. Here, we predict the suitability of macrohabitat for the breeding of Laridae in Cuba (using CNN) and investigate the ecological variables driving their habitat selection (using RF) from satellite data. More precisely we (1) predict the breeding macrohabitat suitability of Laridae at the scale of the entire Cuba archipelago using CNN, and (2) assess the selection of the breeding macrohabitat by these seabirds considering the contribution of landscape and seascape covariates, at different spatial scales, using RFs.

## 2.2 Material and Methods

### 2.2.1 Study area

This study focuses on the marine coastal ecosystems of the Cuban archipelago (Figure 2.1). Cuba is the largest Caribbean island (length = 1256.2 km, maximal width = 191 km) and includes four insular groups (Los Colorados, Sabana-Camagüey, Canarreos

and Jardines de la Reina) featuring >1600 cays (small low-elevation sandy islands on the surface of coral reef) and islets with high variation in relief, geology and landscapes. Climate is tropical hot and seasonally wet with marine influence and semi-continental traits<sup>1</sup>. Annual mean temperature varies between 24°C in the plains of the main island and >34°C in the eastern coasts. Mean relative humidity in the island is high (~90%) and mean annual precipitation ~1375 mm (with non-homogeneous spatial distribution). Daily weather variations are more noticeable between November-April while the weather is more stable during May-October due to the influence of a North Atlantic anticyclone. The climatological mean sea surface temperature over the continental shelf varies from 23°C to 28°C in January and from 29°C to 32°C in September, approximately from North to South, with the highest spatial gradients at the vicinity of the shelf break. The mean chlorophyll-a varies from 0.5 to >10 mg.m<sup>-3</sup> with the largest values observed between the coast and the northern islands as well as in the Southwest region, with very low seasonal variations.

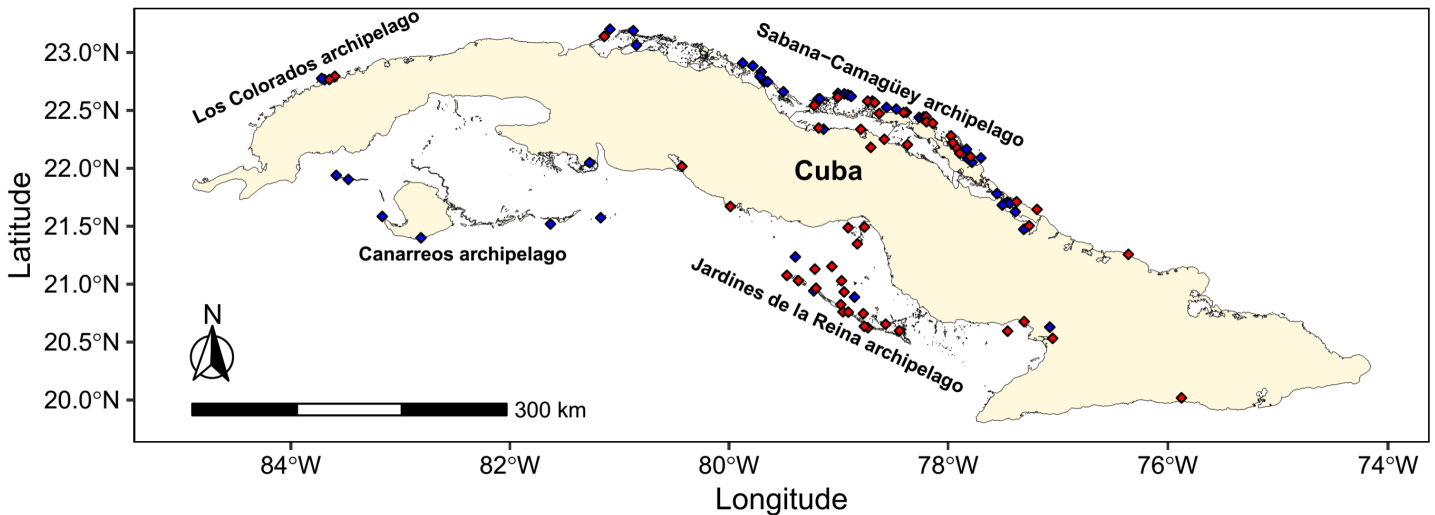


Figure 2.1: Study area of the reproductive macrohabitat selection pattern of nine Laridae species in Cuba - Blue diamonds = observed breeding sites, red diamonds = selected non-breeding sites.

### 2.2.2 Breeding and available localities

We compiled and filtered (deletion of duplicates, erroneous and imprecise data about species identification, location of colonies and date of breeding) all the available information on Laridae observed breeding sites (i.e. cay, islet or coastal site) from scientific publications, books, thesis, project reports and unpublished data. A database was built with the names and coordinates of the 49 observed breeding sites (Figure 2.1), years of observation, breeding species and information sources. Observed breeding species of Laridae were laughing gull *Leucophaeus atricilla* (LAGU), brown noddy *Anous stolidus* (BRNO), sooty tern *Onychoprion fuscatus* (SOTE), bridled tern *Onychoprion anaethetus* (BRTE), least tern *Sternula antillarum* (LETE), gull-billed tern *Gelochelidon nilotica* (GBTE), roseate tern *Sterna dougallii* (ROST), royal tern *Thalasseus maximus* (ROYT)

<sup>1</sup><http://www.insmet.cu>

and sandwich tern *Thalasseus sandvicensis* (SATE). Breeding records of common tern *Sterna hirundo* were treated as ROST due to the misidentification of these colonies (Nisbet, 2000; Navarro, 2021). Additionally, we selected (non-randomly) 52 sites distributed along the coast of Cuba where non-breeding Laridae was known in 2020, according to the criterion of people that know these areas (Figure 2.1). These non-breeding sites represented the potential macrohabitat available, yet not used. Both terrestrial and marine features surrounding the observed breeding sites were considered for predicting suitable breeding macrohabitats.

### 2.2.3 Prediction of breeding macrohabitat suitability

#### Data acquisition and formatting based on satellite images

For each breeding site available we extracted satellite imagery of Landsat 5 and 7 from EOS Data Analytics platform and resized 20 x 20 km square area centered on the site. The date of the image was matched to the year of the breeding colony presence record, and to 2020 for non-breeding sites. Several images were associated to each site (depending on availability) to ensure a good representation of the natural variability during the breeding period (May to August) and to reduce the influence of clouds in some images. In some cases, we incorporated images of both months of April and September (climatology similar to the May-August period) when none was available from May to August of the current year. In total, we selected 136 satellite images describing the conditions of the study sites.

The preprocessing and normalization of Landsat images subscenes included the “Dark Subtraction” (based on the bands minimum digital number) to apply atmospheric scattering corrections to the imagery data and “SLC Gap-Filled” correction for Landsat 7 imagery since 31 May 2003. In the end, standardized GeoTIFF files (299 x 299 pixels, 30 m-spatial resolution) were created for all channels, except panchromatic and thermal because these do not match between Landsat satellites. The definition of subscene size (9.0 x 9.0 km) followed a balanced criterion: sufficiently large image size that included land and sea components, and sufficiently small to minimize the inclusion of other breeding and available sites in the same image subscene (which would affect the prediction quality). We organized the data (images) into two datasets considering the quality of subscene images related with cloud cover to control for cloud-related confounding effects. We randomly mixed the images database of both types of sites (i.e. with and without breeding colonies) and then split them into two groups containing 70% (training) and 30% (validation) of the data for the building and selection of the best CNN model. Additionally, satellite images from 2021 at 12 breeding and 52 non-breeding sites (verified as such that year) were used as test dataset to assess the predictive performance of the CNN model.

For predicting breeding macrohabitat suitability, we applied the same preprocessing to Landsat 7 images of 2021 that covered the entire Cuban archipelago. A mosaic was built with these images, masking mainland to retain only the marine-coastal ecosystems up to the insular shelf. Images with open water only or predominance of land of the main two islands (Cuba and Juventud) were excluded since they were irrelevant to Laridae breeding. Finally, this mosaic image was gridded into 793 subscenes (63805.5 km<sup>2</sup>) with the same format and structure than train and validation datasets. Satellite images were processed using the ENVI 4.7 (ITT VIS Inc) software.

## CNN implementation

A CNN is typically structured by multiple layers of processing units where two main processes occur: convolution and pooling. During convolutions several filters are applied to extract relevant features of data that will be used for calculating the matches at testing phase. Pooling operations capture large images and reduces them, and reduces the parameters to preserve important information. (Kattenborn et al., 2021) offer more details about structure, parameters and functions of CNN models. Here, we use a CNN with three consecutive layers of convolutions and max pooling, followed by a dense network. Finally, the last layer consists of a sigmoid activation so that the output of the network is a value between 0 and 1. This CNN aims therefore to take an image of 299x299 pixels with 6 channels as input and to output the probability of the described habitat to be suitable for breeding seabirds.

Parameters were finally estimated using an Adam optimizer and minimizing a "Sparse categorical cross-entropy" loss. In order to prevent overfitting, we have also added a L2 regularizer, which is a famous technique in Deep Learning to get better generalization and predictive properties (Kussul et al., 2017). Finally, models were trained using the 'training dataset', and selected when minimizing accuracy score over the 'validation dataset'. This work was implemented with the Keras R package (v. 2.6.1) (Allaire and Chollet, 2019).

We performed this training procedure for distinct hyperparameters and the best CNN (better performance and lowest loss in validation datasets) was used to predict the breeding macrohabitat suitability using the satellite images of 2021 along all marine-coastal ecosystems of the archipelago. The most frequently reported metrics, Overall Accuracy, Precision, Recall and F1-score were used to assess CNN performance.

### 2.2.4 Assessing the breeding macrohabitat selection pattern

#### Physical and geographical covariates

Because of the absence of information on the foraging ranges of Cuban seabirds during their breeding period, we did a bibliographic review to compile all information available on the same species observed elsewhere during breeding (from polar to tropical zones). From this review we estimated the potential maximum foraging ranges during breeding for each studied species. Then, we defined three spatial scales (radius of 10, 50 and 100 km from the breeding site) approximately corresponding to the estimated foraging ranges of our study species, and computed several oceanographic characteristics at each spatial scale.

Twelve potentially important features for the establishment of Laridae breeding colonies, described through 18 metrics, were considered at the defined spatial scales (Table 2.1): 11 of them described the conditions of the nesting landscape, and seven of them described the conditions of the surrounding seascape. The variables were measured at the date of the colony observation, and in 2020 for the non-breeding sites.

Factors	Variables	Ecological meaning
Area	Area	Available space for the nests establishment
Perimeter	Perimeter	Indicator of the availability of potential coastal zones for the Laridae breeding
Shape	Shape Index	Related with geographical features (e.g. peninsulas) that could be important for the Laridae breeding
Isolation Degree	Minimum distance from colony to the nearest cay/islet	Indicator of the access level for predators and other disturbance sources
	Minimum distance from colony to the nearest main island of the archipelago	Indicator of the access level for predators and other disturbance sources at high magnitude
	Number of Cays/islets at range = 10, 50 and 100 km from the colony	Indicator of the access potential risk to the colony for predators and other disturbances at different distance ranges
Terrain	Non-flooding zones' cover	Suitability of the breeding locality to the colonies establishment based on the terrain flooding risk
Vegetation	Total vegetal cover	Surfaces occupied by plants (could be suitable to the breeding of some Laridae species or the opposite)
	Moderate-dense vegetal cover	Surfaces occupied by dense vegetation that could influence in the colonies location (in general the Laridae tend to avoid these places types)
Oceanographic characteristics	Sea surface temperature on the range = 10, 50 and 100 km since the colony	Reflects the thermic conditions of the water, that influences on the primary productivity and prey availability at different foraging ranges
Bathymetric characteristics	Minimum distance to the 200-m isobath	Constitutes an approximate measure of the suitable foraging areas for most of the Laridae species. The 200-m isobath marks the limits of the Cuban insular shelf and thus represents the interface zone of the forage strategies inshore/offshore
Prey availability	Chlorophyll a concentration at sea on the range = 10, 50 and 100 km since the colony	Direct indicator of primary productivity and indirect of prey availability associated to the marine flora at different foraging ranges

Table 2.1: **Descriptive variables of macrohabitat in Cuba (breeding site, i.e. cay, islet or coastal site)**



Area, non-flooding zone cover and vegetal covers were calculated using the Landviewer product of the EOS Data Analytics platform<sup>2</sup>. We first calculated the Normalized Difference Water (Gao, 1996) and Vegetation Indexes (NDWI and NDVI respectively) (Rousel et al., 1973) from satellite imagery of the Landsat series. Dates of imagery were between May and August matching the breeding season of Laridae in Cuba. Both spectral indices vary between -1 and 1 with higher numbers correspond to higher humidity (NDWI) or green vegetation (NDVI). Based on the NDWI we then calculated the drought emerged areas (NDWI range = -1 to 0.2) and percent of its non-flooding cover (NDWI range = -1 to 0). The NDVI allowed to quantify the total (NDVI range = 0.2 to 1) and moderate and dense vegetation covers (NDVI range = 0.4 to 1). The perimeter of the nesting sites was calculated after vectorization of the imagery subscenes.

We calculated the index of shape complexity for islands (Hu et al., 2011) on the terrestrial part of the localities:  $SI = P/[2 * (\pi.A)^{1/2}]$  where  $SI$  = shape index,  $P$  = perimeter and  $A$  = area of the site. A SI value of 1 indicates an islet or cay with a perfect circular shape and SI increases as the shape becomes more irregular and complex. Isolation variables (minimum distances to Cuba/IJ and to nearest cay, and cays/islets number at the three spatial scales) were estimated using Google Earth Pro 7.3.3 software. Minimum distances to the 200-m isobath were measured using a bathymetric shapefile of the marine exclusive economic zone of Cuba (using information both from GEBCO and Cuban research agencies databases).

Sea surface temperature (SST) and surface chlorophyll a concentration around the sites were obtained at a spatial resolution of 1 km through the MODIS-Aqua satellite images repository<sup>3</sup>. For both variables we averaged the monthly values between May and August of the last year with a breeding colony recorded at the site and for 2020 for sites with a proven absence of breeding colonies. Nevertheless, due to the absence of logistical support for a systematic monitoring of these variables before 2002, and given the small interannual variability of both variables in Cuba, data for breeding colonies recorded in that period were estimated from the mean of 2002-2021 period for the same months. The eldest colony record, at Rincón del Guanabacoa, was excluded from the study as we could not obtain the same variables from Landsat 4 satellite (fewer bands than Landsat 5 and 7). Breeding macrohabitat was characterized considering both mixed and monospecific colonies.

## RF implementation and contribution of variables

Variables were compared among sites using Mann-Whitney U tests considering significance at  $p < 0.01$ . Breeding macrohabitat selection was analyzed through random classification forests (RFs) models considering the measured variables at three spatial scales. Similar to CNN, we mixed and splitted the data to create the training and validation datasets (70 vs 30% proportions) for the building and selection of the best RF. The same training and validation datasets were used in all RFs to compare their classification performances. We implemented three RFs, one that processed physical-geographical variables registered within a radius of 100 km from the breeding colony (RF\_100), a second within a 50 km radius (RF\_50) and a third one within a 10 km radius (RF\_10). For each RF type we used the 10 best runs in order to get an average and variance of model performance.

<sup>2</sup><https://eos.com>

<sup>3</sup><https://oceancolor.gsfc.nasa.gov>

Same performance metrics than CNN were used to assess the training, validation and test of RFs. Variables contributions were calculated from the mean decreasing Gini index (values are directly proportional to variable importance) derived from the RF with better performance. The randomForest R package (v. 4.6–14) (Breiman, 2018) was used and R 4.1.1 (R Core Team, 2021) for all analysis.

## 2.3 Results

### 2.3.1 Breeding macrohabitats prediction

In general, the performance of CNN exceeded significantly that of RF\_50 and RF\_100, with indicators values  $>80.0\%$  for the validation datasets (Table 2.2). Image quality (according to cloud cover) had no significant consequence on the classification power of CNN models (F1-score = 85.7 and 84.6% for CNNs that used all and best images). We thus worked with the architecture that used all images. Based on the test dataset, the CNN model exhibited good performance indicators with accuracy = 79.7%, precision = 91.5%, recall = 82.7% and F1-score = 86.9%.

When used for predicting over the entire Cuba archipelago, the CNN estimated 32 184.4, 12 069.1, 6 597.8 and 12 954.2 km<sup>2</sup> of suitable habitat for breeding within 0-0.25, 0.26-0.50, 0.51-0.75 and 0.76-1 probability ranges, respectively (Figure 2.2). Probability ranges  $>0.50$  and  $>0.75$  covered 30.6% and 20.3% of the predicted area, respectively. Best areas (high suitability scores) tended to be concentrated in three general types of ecosystems: 1) remote cays/reef islets of all subarchipelagos (Figure 2.1, with Jardines de la Reina archipelago under-represented), 2) coastal zones with sand, rocks or interior lagoons and 3) interior of bays, gulfs and swamps that contained small islets and sand banks (Figure 2.2). The southern region of Cuba had less suitable breeding macrohabitats than the northern region (Figure 2.2).

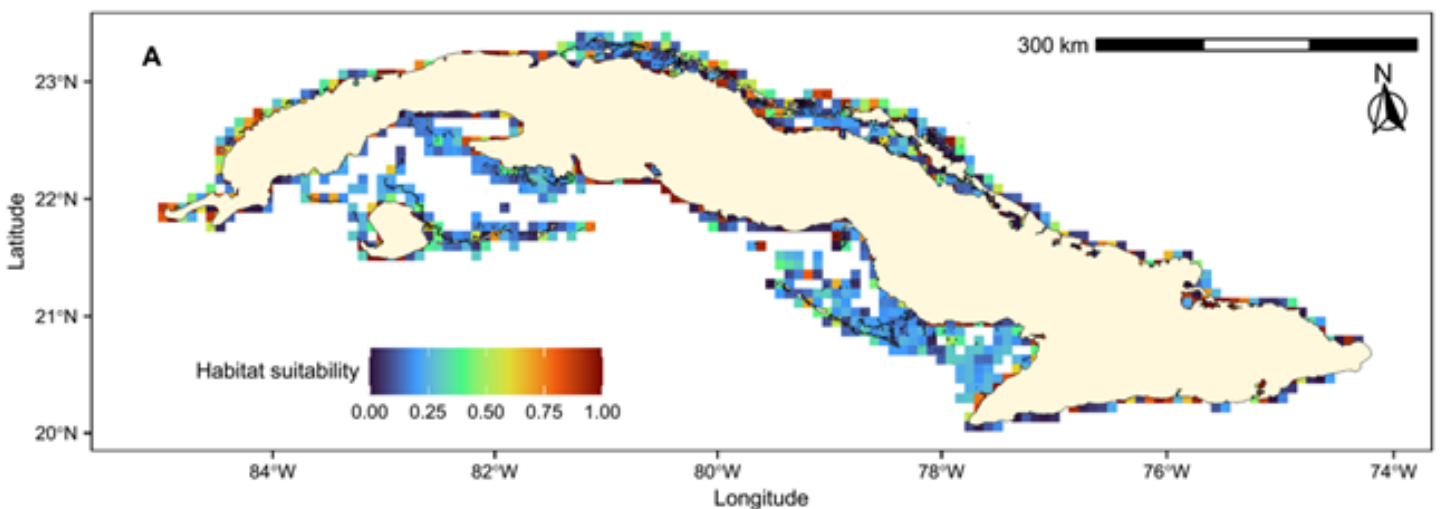


Figure 2.2: CNN prediction of macrohabitat suitability for the breeding of *Laridae* in Cuba, for 2021 breeding season using Landsat images

### 2.3.2 Breeding macrohabitat selection and importance of covariates

The general statistics (median, quartiles) of most covariates were quite similar between breeding and non-breeding sites. Only SST at the three spatial scales and Chl a at 50 and 100 km radii exhibited significant differences: SST was lower and Chl a higher at breeding sites (Figure 2.4). Additionally, breeding sites tended to have a smaller number of cays/islets within 10 km compared to non-breeding sites ( $p = 0.01$ , Figure 2.4). Performance metrics for RF\_50 (200 trees, four variables by split) and RF\_100 (300 trees, four variables by split) were very similar and outperformed RF\_10 (150 trees, three variables by split). For RF\_100, SST had the highest contribution to discriminate breeding from non-breeding sites with Gini index  $>5.0$  (Figure 2.3). A second group of covariates with lower contribution included isolation-related variables (number cays/islets within 10 and 50 km from colonies), Chl a within 100 and 50 km radius (Figure 2.3). Remaining variables exhibited relatively low contributions and non-flooding area cover had the lowest importance (Figure 2.3).

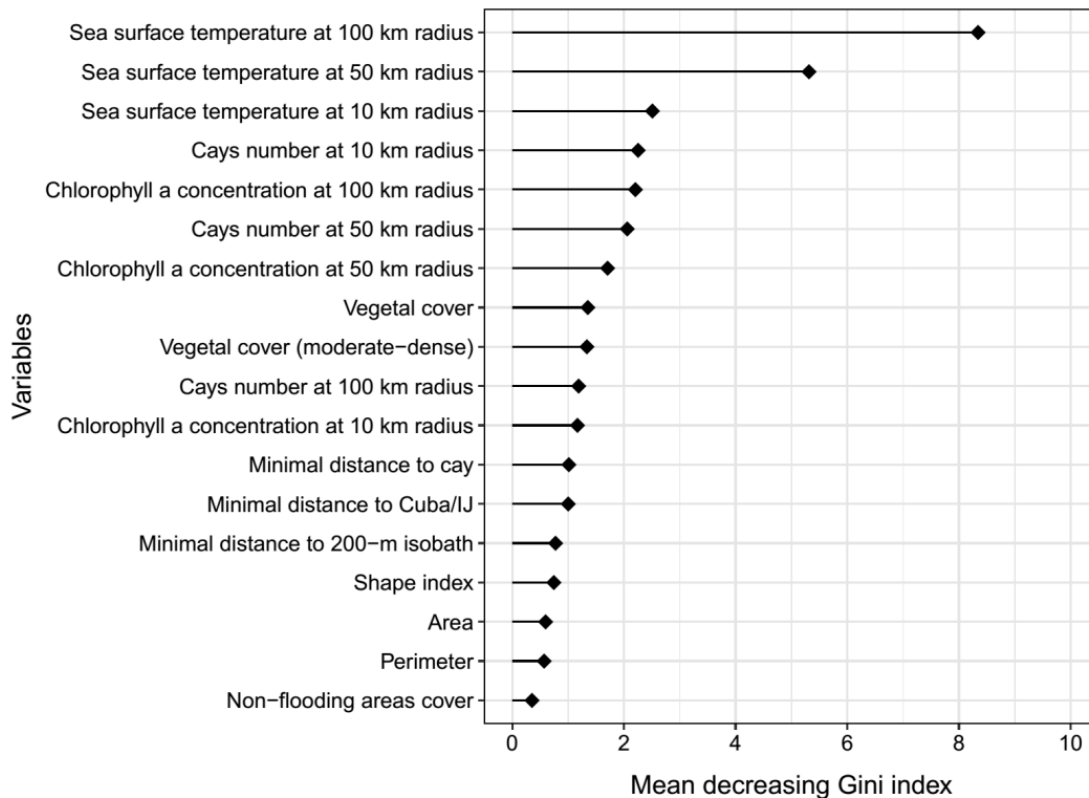


Figure 2.3: Contribution of physical-geographical variables in breeding macrohabitat selection pattern - It is based on random classification forests models.

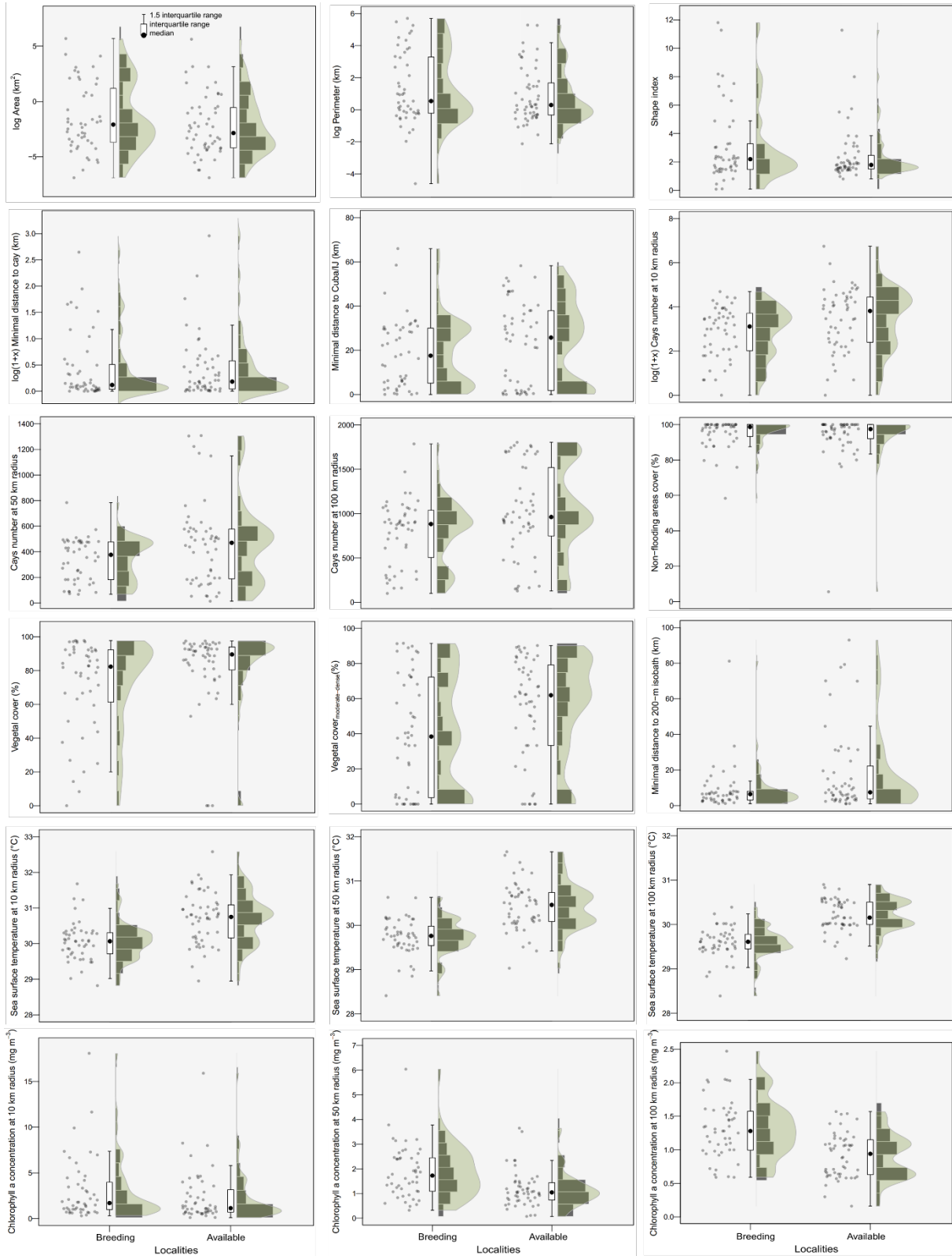


Figure 2.4: Statistical distribution of 18 physical-geographical variables corresponding to 48 breeding and 52 available localities (available macrohabitats) for Laridae in Cuba - Some variables were log-transformed for visualization purpose exclusively.

Model type	Train accuracy	Train F1-score	Val. accuracy	By image			By locality			
				Val. precision	Val. recall	Val. F1-score	Val. precision	Val. recall	Val. F1-score	
CNN	98.4	98.7	75.7	75.5	76.9	76.2	86.7	80.0	92.3	85.7
RF_10	72.0	71.2	-	-	-	-	70.0	67.4	69.3	68.3
RF_50	81.7	80.7	-	-	-	-	77.3	77.8	72.1	74.8
RF_100	85.1	84.5	-	-	-	-	76.7	76.9	71.4	74.1

Table 2.2: **Performance (in %) of a convolutional neural network (CNN) and three random forests (RF) models used to respectively predict breeding site suitability and assess breeding site selection by Laridae in Cuba** - RF\_10, RF\_50 and RF\_100 = models that used physical-geographical variables inside 10, 50 and 100 km radius from localities, respectively; CNN = model that used Landsat images with square areas = 9 x 9 km.

## 2.4 Discussion

### 2.4.1 Prediction of breeding macrohabitat suitability

Based on CNNs we provided a map of macrohabitats suitability over the whole Cuban archipelago. Predictions were based on physical-geographical suitability of marine-coastal ecosystems and it does not imply *per se* the existence of breeding colonies at areas with higher habitat suitability. However, these areas represent the localization of sites with favorable conditions for breeding in 2021 and thus constitute alternatives or additional breeding sites for Laridae around Cuba.

The most suitable breeding sites (probability range  $>0.50$ ) for Laridae exhibited a scattered general distribution along the coasts of Cuba, although a slightly higher concentration of sites occurred in the northern marine-coastal ecosystems. Nevertheless, areas of Los Colorados, Canarreos and Sabana-Camagüey archipelagos showed higher number of favorable breeding sites acting as potential hotspots for Laridae reproduction (Figures 2.1 and 2.2). These predictions are relatively consistent with current field knowledge in these areas, and with the location of historical persistent breeding colonies.

In particular, breeding habitats for Laridae such as beaches, rocky platforms and sand banks in distant or difficult-access cays and islets were often true positive predictions. Two of the most scientifically studied regions, the Sabana-Camagüey and Jardines de la Reina archipelagos, had high and low predicted breeding habitat suitability respectively by CNN what is confirmed by field observations (Figures 2.1 and 2.2). Nevertheless, some predicted areas seemed irrelevant for breeding because of the presence of extensive anthropogenic infrastructures (cities, towns, industries) that cause disturbance.

On the other hand, main false negatives of the predictions were located at Mono Grande, Cinco Leguas, Felipe de Barlovento and Las Salinas breeding sites. Prediction subscenes (grid cells) containing these breeding sites were not highly different (from a visual interpretation) from the training (centered sites at cells). Then, this could suggest the importance of incorporating specific oceanographic (e.g. SST, Chl a) or ecological variables (e.g. prey availability-related) to the CNN model to improve its prediction

quality. It is important to point out that the habitat suitability diversity predicted by the model (that addressed all Cuban Laridae) could result from the different species-specific breeding habitats requirements; especially LETE that has a high dynamic and opportunistic behavior to select its breeding sites (this species may change its nesting sites between consecutive breeding seasons depending on the availability of isolated sand bodies). For this reason, even if CNN obtained relevant predictive performance metrics, the prediction map (Figure 2.2) should be interpreted carefully, and further studies would be required to improve its accuracy. However, the good global quality of the model highlights its potential for application to other species and regions of the world.

### 2.4.2 Breeding macrohabitat selection pattern

Simplistic approaches to the study of breeding habitat selection has been criticized decades ago (Burger and Shisler, 1978) as the environment of many animals, such as seabirds, is the heterogeneous composition of habitat characteristics along several spatial and temporal scales (Danchin et al., 1998). Here, we found that breeding macrohabitat selection by Laridae at Cuba could be partly explained through multiscale seascape and landscape features of the breeding sites.

Overall, breeding site (macrohabitat) selection of Laridae was mainly explained by lower SST values within 100 and 50 km from colonies. Thus, SST at larger scales played a main role despite its relative seasonal stability in tropical waters (Hockey and Wilson, 2003; Jaquemet et al., 2008). The greater contribution of larger spatial scales for SST probably reflects the role of oceanographic conditions (e.g. thermal fronts) at relatively high distances for breeding habitats, coinciding with the foraging range of most species which often exceeds 30 km from colonies. Chlorophyll-a at the same spatial scales was also important, although to a lesser extent, for breeding site selection, highlighting the role of marine productivity for breeding. However, it should be noted that Chl a is an index of productivity that does not match exactly in space with the maximum of forage fish abundance (Zavalaga et al., 2010).

Indeed, SST and chlorophyll-a are considered proxies of sea productivity and food availability, and hence key factors for breeding habitat selection by seabirds (Vilchis et al., 2006). At different world regions these variables have shown important effects on seabirds foraging, demography and population dynamics where mainly cooler SST favored the higher chlorophyll-a, and hence the foraging and breeding success of birds (Barbraud et al., 2012; Carroll et al., 2015; Sydeman et al., 2012). The selective pattern of breeding macrohabitat found for Laridae in Cuba is consistent with this general pattern, although the effect of Chl a appears lesser than SST (Figure 2.3).

Similar to previous studies (e.g. Burger and Gochfeld, 1981, 1986; Greer et al., 1988), areas with moderate to dense vegetation cover were avoided by Laridae for breeding (Figure 2.4). For seabirds, high cover and dense vegetation cover usually constitutes a barrier to breeding as it limits the visibility and social communication between neighbors at colonies, and hence, may increase predation risk (Bukacińska and Bukaciński, 1993; Raynor et al., 2012).

### 2.4.3 Complementarity of CNN and RF approaches

According to our results, prediction of habitat suitability can be obtained by processing satellite images with CNN exclusively. This constitutes a significant advance for

habitat ecology studies and expands the applications and perspectives of image analysis via deep learning approaches. Deep architecture of CNNs conveys a high computation cost but, at same time its versatility provides them a great generalization capacity with a broad applicability in the remote sensing field (Ma et al., 2019; Kattenborn et al., 2021; Yuan et al., 2020). Scene classification with an emphasis on land cover, vegetation and crop types appears as one of the most common applications of CNNs. However, these classifications are based on relatively easily distinguishable element classes (e.g. water, bare soil, marsh, fen, forest, grassland, paddy rice) and animal habitat selection is a more complex phenomenon.

Our CNN had relatively good performance and predicted the breeding habitat suitability using spectral data of terrestrial and oceanographic elements. After visual inspection of the image mosaic of 2021, the more suitable predicted areas included heterogeneous covers such as sands, marshes, bare soils, terrestrial vegetation and mangroves, and waters with contrasting depths and colors. Yet, our ecological understanding here is limited as we have no explicit indication on the metrics CNNs finally used to maximize prediction quality. Some technics exist in order to get insight into the metrics automatically extracted by the CNN, such as layer-wise backpropagation or saliency maps (Montavon et al., 2019; Bae et al., 2020). It is however an active field of research, and using these approaches is beyond the scope of this paper. Based on RFs results and statistical analysis, we could yet hypothesize that important features such as vegetation, number of cays/islets but also ocean color (i.e. Chl a) were captured through Landsat spectral data. Additional analysis could help to identify directly from CNNs' layers the main features used to disentangle breeding from non-breeding localities. Probably, the CNN performance might increase including SST information at radius of 100 km (according to the main results of RF) and being trained over larger datasets.

This study illustrates how benefits can be obtained from a complementary analysis of CNN and RF. Here, RF can be seen as an explicative tool relying on features directly related to our a priori ecological hypotheses, while CNN can act as an evaluative tool in order to assess the relevance of habitat spectral features, as well as an efficient predictive tool producing large scale prediction of habitat suitability in a convenient manner. Moreover, prediction of breeding habitat suitability with CNN should also be systematically updated considering the changing dynamics of marine ecosystems and seabird colonies. Finally, we recommend the exploration of building CNN models that use both spectral and relevant ecological data (identified by RF), to produce finer predictions supported ecologically.

#### 2.4.4 Management and conservation perspectives

The scattered distribution of suitable breeding sites in Cuba offers to Laridae a wide variety of options for colony's establishment, what may allow to dampen the effects of climatic change and anthropogenic pressures. It may also provide flexibility for management agencies as it offers a large number of alternative sites for Laridae conservation in Cuba. Also, possibilities of legal protection of some important breeding colonies (e.g. predicted hotspots) increases because there is a low risk of spatial overlapping of breeding sites with places of social-economic interests.

From a practical point of view, we recommend a field validation of effective presence of colonies in sites predicted to be highly suitable. This could be done through field surveys at these places constituting a proper way to optimize logistical and economical re-

sources for conservation purposes. Then, confirmed breeding sites could be considered to update the Marine Protected Areas coverage in Cuba, improve the governmental strategy of adaptation to climate change, detect negative effects from natural and anthropogenic causes (McGowan et al., 2013; Perrow et al., 2015) and realize a sustainable use of the marine-coastal ecosystems by humans (tourism, fisheries, industry). An effective conservation of seabirds should be based on species' distribution along space including both colonies establishment places and surrounding waters (Oppel et al., 2018). More precisely, according to the complementary approach CNN-RF, the conservation and management actions for Laridae breeding macrohabitats in Cuba should include areas of the predicted breeding hotspots. Also, the characteristics of SST and Chl a (as proxies of food availability) between 50-100 km around cays as well as the coverage degree of dense and moderate vegetation should be considered.





## Chapter 3

# Deep inference of seabird dives from GPS-only records: performance and generalization properties

♪ *O pato*, JOAO GILBERTO & STAN GETZ

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In addition to breeding site selection, the at-sea behavior of seabirds has also been the focus of ecological attention in recent decades. As top predators, seabirds gather information on many trophic levels. For these reasons, their foraging areas are often considered important areas for the overall marine ecosystem, and they have often been used as crucial information for designing Marine Protected Areas. The estimation of these foraging areas rely on the detection of seabird dives. Dives can be directly measured by specific pressure sensors, such as TDRs. However, in many cases TDR data is missing and tools are needed to infer dives directly from GPS trajectories. From a database of about 300 foraging trajectories derived from GPS data and deployed simultaneously with pressure sensors for the identification of dives, in this chapter we benchmark deep neural network architectures trained in a supervised manner for the prediction of dives from trajectory data. Moreover, we further investigate across-species generalization using a transfer learning strategy known as 'fine-tuning'. Is it indeed possible to develop a unique network that can automatically infer the dives of many species? This work has been published as an article in *PLOS Computational Biology*.

### Associated publication

- ✍ Roy A., Lanco Bertrand S., and Fablet R. (2022) Deep Inference of Seabird Dives from GPS-only: Performance and generalization properties. *PLOS Computational Biology* 18(3): e1009890

## 3.1 Introduction

Marine top predators have received significant attention in marine ecology over the last decades Authier et al. (2017). They are known to use vast areas for feeding, thus requiring specific adaptive foraging strategies in order to localize their preys, especially in the pelagic environments which are highly variable Hazen et al. (2019). They offer a unique perspective into ocean processes and dynamics, given that they can amplify information on the structure of the seascape across multiple spatio-temporal scales due to their relatively high mobility and longevity. Often considered as sentinels of the environmental variability and bio-indicators for ecosystem structure and dynamics, their study has been particularly contextualized into ecosystem-based management and conservation issues Lascelles et al. (2014); Hooker and Gerber (2004).

Numerous studies have focused on the variability of seabirds' foraging strategies and in particular of dive distributions. Assessing consistency or shifts in foraging locations Bost et al. (2015); Meier et al. (2015); Oppel et al. (2017), and in the resource spatial partitioning Kappes et al. (2011); Bolton et al. (2019) provide indeed crucial information for understanding marine ecosystems. This has been particularly enabled by great technical advances in the miniaturization and autonomy of biologging devices Ropert-Coudert et al. (2009); Chung et al. (2021). GPS loggers have been at the forefront of this breakthrough, and can now provide precise and accurate data on the foraging trajectories of many free-ranging species, such as seabirds Wakefield et al. (2009); Yoda (2019). Detailed information on the diving behavior has also been gained through the additional use of pressure sensors, such as Time Depth Recorders (TDR) devices Cox et al. (2016); Lewis et al. (2004); Shoji et al. (2015). Yet, for historical, financial and ethical reasons, the deployment of several sensors has not always been possible and a substantial amount of tracking datasets consist in GPS tracks only. The development of tools dedicated to animal trajectories' segmentation (i.e. for dive identification) is therefore needed to extract more out of historical seabird foraging trajectories Browning et al. (2018).

Among existing approaches to dive identification from GPS tracks, many individual-based studies aim to infer behavioral state directly by applying thresholds to various ecological metrics of movement data, such as speed, direction and tortuosity Dean et al. (2015); Seidel et al. (2018). A common example is the so-called First-Passage Time method (hereafter, FPT), which is defined as the time taken for an individual to cross a virtual circle of given radius Carter et al. (2016); Pinaud and Weimerskirch (2007); Sommerfeld et al. (2013). Here foraging behavior is assumed to occur when birds fly at very low speeds Weimerskirch et al. (2008). Statistical methods have also been used to predict diving behavior with clustering schemes such as the Expectation Maximization binary clustering technique Mendez et al. (2017); Garriga et al. (2016) or using hidden Markov models (hereafter, HMM) typically with 2 or 3 distinct behavioral modes to explicitly account for time-related priors Boyd (2014); Dunphy et al. (2020); McClintock and Michelot (2018); Oppel et al. (2015). More occasionally, supervised machine learning approaches such as artificial neural networks, support vector machines and random forests have also been used Guilford et al. (2009); Wang (2019). We may refer the reader to Joo et al. (2020) for a more detailed review of these methods.

Recently, deep learning methods have been suggested to be a potentially useful tool for behavioral pattern segmentation Valletta et al. (2017). Deep learning refers to a neural network with multiple layers of processing units LeCun et al. (2015). By decomposing the data through these multiple layers, deep neural networks may learn complex features for

representing the data with a high level of abstraction at multiple scales. The trajectory of an animal being the result of complex processes at multiple spatio-temporal scales Nathan et al. (2008), deep learning might be able to extract relevant representations of trajectories for performing tasks such as classification, segmentation or simulation. Deep learning has become the state-of-the-art framework for a wide range of problems in text, speech, audio and image processing and applications in ecology have mainly addressed image analysis and computer vision case-studies Weinstein (2018); Christin et al. (2019). Fewer studies have explored deep learning for animal trajectory data. Recurrent neural networks have been used for movement prediction Ardakani and Hashimoto (2017); Rew et al. (2019), and for the identification of representative movement patterns Peng et al. (2019). Very recently, an attention network has also been proposed for comparative analysis of animal trajectories Maekawa (2020). Related to our study, a fully-connected network (hereafter, FCNet) has been used to predict seabirds' diving in European shags, common guillemots and razorbills Browning et al. (2018). With a very simple FCNet with 4 layers comprising hundreds of hidden nodes, this study demonstrated the improved accuracy of this approach over commonly-used behavioural classification methods. These promising results support new investigations to further explore the potential of deep learning schemes for movement ecology studies.

In particular, a central challenge in deep learning is to make algorithms that will not only perform well on the training data, but also on new datasets Goodfellow et al. (2016). Generalization properties are indeed crucial for deep networks to tackle a wide range of problems. For example, it would be relevant to develop a neural network for the segmentation of behavioral patterns of certain species and whose characteristics are transferable to the analysis of the behavior of another species. Transfer learning refers to the fact of using knowledge that was gained from solving one problem and applying it to a new but related problem. For this purpose, a solution known as 'fine-tuning' consists in using a pre-trained model as the initialization of the training scheme rather than training a new model from scratch Yosinski et al. (2014).

As in Browning et al. (2018), this work addresses the inference of seabird diving behavior from GPS data using Deep Learning methods. Besides, their FCNet architecture, we investigated Convolutional Neural Networks and U-Networks Ronneberger et al. (2015), which are state-of-the-art architectures for time series and image data processing and shall better account for the time structure of trajectory data. As case-studies, we considered two tropical seabird genus with distinct diving behavior (Boobies vs Cormorants). The associated datasets comprised 297 foraging trips derived from GPS data deployed simultaneously with pressure sensors for the identification of dives. Our specific objectives were therefore (a) to confirm the performance of deep networks over state-of-the-art tools for dives identification, (b) to demonstrate generalization properties of trained network to predict dives of seabirds from other colonies and (c) to evaluate the benefits of a transfer learning strategy known as 'fine-tuning' for across-species generalization.

## 3.2 Materials and Methods

### 3.2.1 Ethic statement

Tracking data were obtained from electronic devices attached to Peruvian boobies and Guanay cormorants tagged at the Pescadores and Guañape Islands, Peru, from 2007 to 2013, and from masked boobies tagged at the Fernando de Noronha, Brazil, from 2017

to 2019. This work was conducted with the approval of the Peruvian federal agency, Programa de Desarrollo Productivo Agrario Rural, commonly known as “Agrorural”. Headquarters of Agrorural are located at Av. Salaverry 1388, Lima, Peru, and of the Brazilian Ministry of Environment—Instituto Chico Mendes de Conservação da Biodiversidade (Authorization No 52583-5).

### 3.2.2 Dataset

GPS and TDR devices were jointly fitted to breeding tropical seabirds both in Peru (92 Peruvian boobies, 106 Guanay cormorants) and Brazil (37 masked boobies). Peruvian boobies (*Sula Variegata*) and Guanay cormorants (*Leucocarbo Bougainvilli*) were captured at Isla Pescadores (11°46'30.34"S, 77°51.22"W) every year in December from 2008 to 2013 and at Isla Guanupe (8°18.92"S, 78°42.72"W) in December 2007, while masked boobies (*Sula dactylatra*) were captured at Fernando de Noronha archipelago (3°9.71"S, 32°36.11"W) every year in April from 2017 to 2019. The GPS were attached with Tesa tape on the tail feathers for boobies and on the back feathers for cormorants for 1 to 2 days and the TDR were fixed on the bird's leg with a metal band. In total, GPS devices (Gipsy GPS, 25–30 g, Technosmart, Rome, Italy; i-gotU GPS GT 600, 25–30 g, Mobile action Technology, NewTaipei City, Taiwan; MiniGPSlog 30 g, Earth and Ocean GPS, Kiel, Germany; Axy-trek 14g, Technosmart, Rome, Italy) and time-depth recorders (TDRs, 3 g; resolution, 4 cm; G5 CEFAS Technology, Lowesoft, UK) were fitted to 235 seabirds.

After recovery, each GPS track was split into foraging trips by selecting locations further than a given distance to the colony and longer than a given time. Foraging trips were linearly interpolated to the TDR sampling resolution (i.e. 1s) and the coverage ratio was computed as in Browning et al. (2018). It is defined as the ratio between the number of recorded fixes and the number of fixes that should have been recorded with a perfectly regular sampling in a fixed temporal window. The amount of missing data is detailed in Table 3.1. True dives were defined when the depth measured by TDR was higher than 2 meters. Each GPS position was thus associated with a boolean value detailing the 'dive' status. This dataset consists therefore of a total of 297 foraging trips of seabirds with doubled-deployment GPS and TDR (see Table 3.1).

Species	Colony Location	Nb of trips	Trip Duration (min)	Dives* (%)	Dives Duration (s)	Gaps** (%)	Resting*** (%)
SV	Pescadores Island	132	64 ± 37	1.3 %	2.5 ± 1.3	2.2 %	4.4 %
LB	Pescadores Island	79	143 ± 69	9.4 %	12.9 ± 14.1	25.5 %	36.6 %
SV	Guañape Island	22	162 ± 75	0.7 %	3.3 ± 2.5	1.5 %	6.6 %
SD	Fernando de Noronha	64	491 ± 377	0.2 %	2.2 ± 1.4	6.1 %	33 %

\* proportion of positions labeled as 'dive' (TDR-derived depth higher than 2 meters)

\*\* proportion of missing fixes that have been linearly interpolated

\*\*\* proportion of time with speeds inferior to 1 m.s-1 associated to non-diving behaviour

Table 3.1: **Dataset Overview** - General statistics on the four linearly-interpolated datasets used in this study. (m ± s) is for respectively mean and standard deviation. SV, LB and SD stand respectively for *Sula variegata*, *Leucocarbo bougainvilli* and *Sula dactylatra*

### 3.2.3 Deep Neural Network Architectures

In this work, we investigated deep neural networks. As baseline architecture, we considered the fully-connected network (FCNet) proposed in Browning et al. (2018). Besides, as described in Fig 3.1 we considered a fully convolutional neural network (CNNet) and a U-shape network particularly adapted to segmentation problems (UNet) Ronneberger et al. (2015). We describe below these three architectures and the associated supervised training procedure. We refer the reader to Christin et al. (2019) for an introduction to deep neural networks dedicated to ecologists.

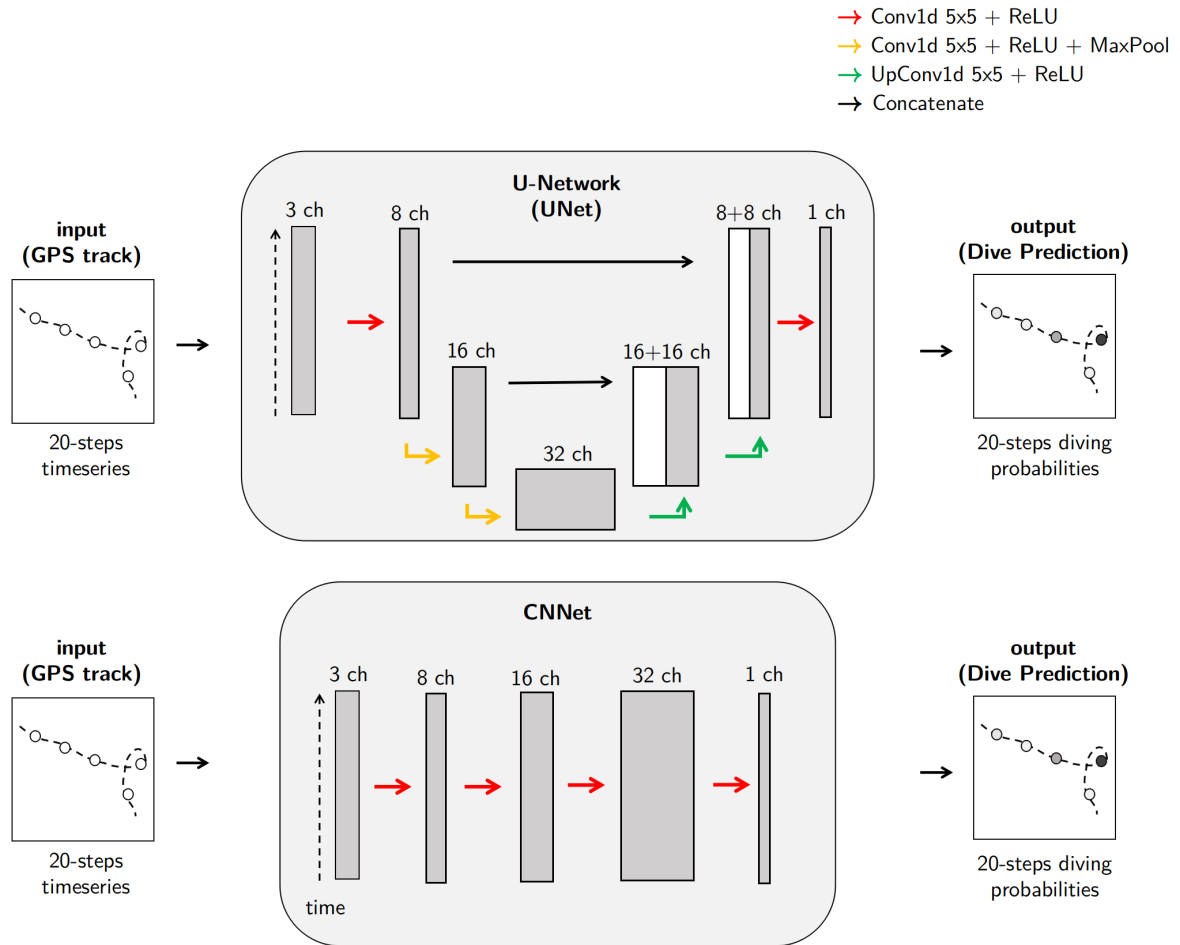


Figure 3.1: **Network Architectures** - CNNet refers to a fully convolutional neural network. UNet refers to a U-shape network. A channel refers to deep learning terminology and describes a representation of the input data as output of some computation layer. Conv1d, MaxPool, and UpConv1d are abbreviations for usual deep learning operations. Details can be found on pytorch's documentation Paskze et al. (2019)

#### Fully-Connected Network (FCNet)

The first architecture implemented was similar to the fully-connected network presented by Browning et al. (2018). As input vector, we used the concatenation of step speed, turning angle and coverage time series for over a 20-second window. This input

vector is fed to a layer of 100 nodes followed by 3 layers of 500 nodes. Each node applies a linear transformation to the incoming data and a non-linear activation chosen as a Rectified Linear Unit (ReLU -  $\text{ReLU}(x) = \max(0, x)$ ). The last layer applied a softmax binary function so that the output of the vector is a time series of values between 0 and 1, which can be interpreted as binary classification probabilities. This architecture is a classical example of a so-called multilayer perceptron, with a rectified linear activation which is the default activation in deep learning architectures. Overall, this architecture involves 500k parameters.

### Fully Convolutional Networks (CNNet)

Convolutional networks exploit convolutional layers and are the state-of-art architectures for a wide range of applications, especially for signal and image processing tasks Alom et al. (2019). Thus, we investigated a basic neural network fully composed of convolutional layers. Similar to FCNet, its input vector is the concatenation of step speed, turning angle and coverage time series over a 20-second window but its output is a vector of diving probability of the same length. Overall, this architecture UNet involves 5k parameters.

### U-Net (UNet)

As the considered problem can be seen as a segmentation task, a UNet architecture naturally arises as a state-of-the-art solution Ronneberger et al. (2015). The key feature of this architecture is to combine the information extracted by convolutional blocks applied at different temporal scales. To achieve this multi-scale analysis, the UNet applies pooling layer to coarsen the time resolution and interpolation layers (UpConv1d layers) to increase the time resolution as sketched in Fig3.1. At each scale, we apply a specific convolution block. We concatenate its output with the interpolated output of the coarser scale to a convolutional block, whose output is interpolated to the finer resolution. Overall, we may notice that the output of the UNet architecture is a time series with the same time resolution as the input time series. Similarly to FCNet and CNNet, the last layer applies a sigmoid activation to transform the output into a time series of diving probabilities. Overall, this architecture UNet involves 20k parameters.

### Network Training and Validation

Given a selected neural network architecture, the training procedure relies on a supervised learning scheme using a weighted binary cross entropy as loss function. This function evaluates the performance of a prediction by comparing the dive prediction (output of the model) with the true dives defined by TDR data. We consider a weighted version of the binary cross entropy because of the unbalanced presence of dive and no-dive behavior in the studied trajectories (see Table 3.1). The objective is to penalize more for mistakes on the smaller class (diving behavior) than for false positive, thus ensuring for convergence. In the reported experiments, the weight was empirically set to 5 for cormorants datasets and 30 for boobies dataset.

The minimization of the training loss exploits the Adam stochastic optimizer Kingma and Ba (2014). A fixed learning rate of 0.001 was used for all training procedures. Networks were evaluated on training and validation datasets every epoch (defined as one pass through the entire train dataset). We consider an early-stopping criterion such that the

training procedure was stopped as soon as the validation loss started increasing. Overall, given a trajectory the diving probability at a given location was assessed by computing the mean probability of all predictions derived from all 20 positions windows. These models were implemented, trained and tested with python using pytorch library Paskze et al. (2019). Our pytorch Code is available on our github repository<sup>1</sup>.

### 3.2.4 Benchmarked methods

Two classical methods for dive prediction First-Passage Time (FPT), and Hidden Markov Models (HMM) were evaluated for intercomparison purposes. FPT was computed following Fauchald and Tveraa (2003), by selecting the radius that maximizes the variance of passage times. Time passage values were converted into a probability of dives with min-max normalization. Regarding HMMs, we applied the momentuHMM R package McClintock and Michelot (2018). We implemented HMMs with 3 (resp. 4) behavioral modes for boobies (resp. cormorants) associated to traveling, searching, diving and resting behaviors. This approach represents trajectories as a sequence of steps and angles. It models steps as random variables following a gamma marginal distribution and angle following a von mises marginal distribution. We may point out that the HMMs directly provide as outputs a likelihood value of the diving behavior.

### 3.2.5 Evaluation scheme

We describe below the evaluation scheme we implemented to assess the performance of the proposed neural network approaches. We first focus on the benchmarking of the performance of the considered approaches in terms of dive prediction accuracy for different data input. For the proposed neural network architectures, we further analyze their generalization properties. The methodological framework is exposed in Fig 3.2.

**(a) Network training** We assessed the dive prediction performance of the 5 benchmarked methods (FPT, HMM, FCNet, CNNet and UNet) considering trajectory data derived from the two dataset from Pescadores Island (see Table 3.1). To test for the effect of temporal resolution, the two datasets have been downsampled every 5, 15 and 30s. When downsampling, temporal windows containing at least one dive were classified as dives. Each dataset were then splitted into training, validation and test datasets with respective size of 50%, 30% and 20%. Deep networks were trained and selected based on the training and validation datasets. All approaches were finally compared on the testing dataset. Overall, this led to the quantitative comparison of the performance of 5 models on 6 datasets all listed in Table 3.2.

As evaluation metrics for dive prediction, we evaluated the receiver operating characteristics curve (ROC) which describes the performance of a binary classifier. It consists in plotting the true positive rate (i.e. true predicted dives) against the false positive rate (i.e. false predicted dives). We obtain this curve by varying the probability threshold defining dive/no dive behaviors. Moreover, we evaluate the area under the curve (AUC) as well as the binary cross entropy (BCE) for the test datasets. Regarding the AUC, it was estimated by integrating the ROC curve along the x axis using the composite trapezoidal rule. For neural network approaches, we also analyzed the value of the training loss for the training and test datasets.

<sup>1</sup><https://github.com/AmedeeRoy/BirdDL>



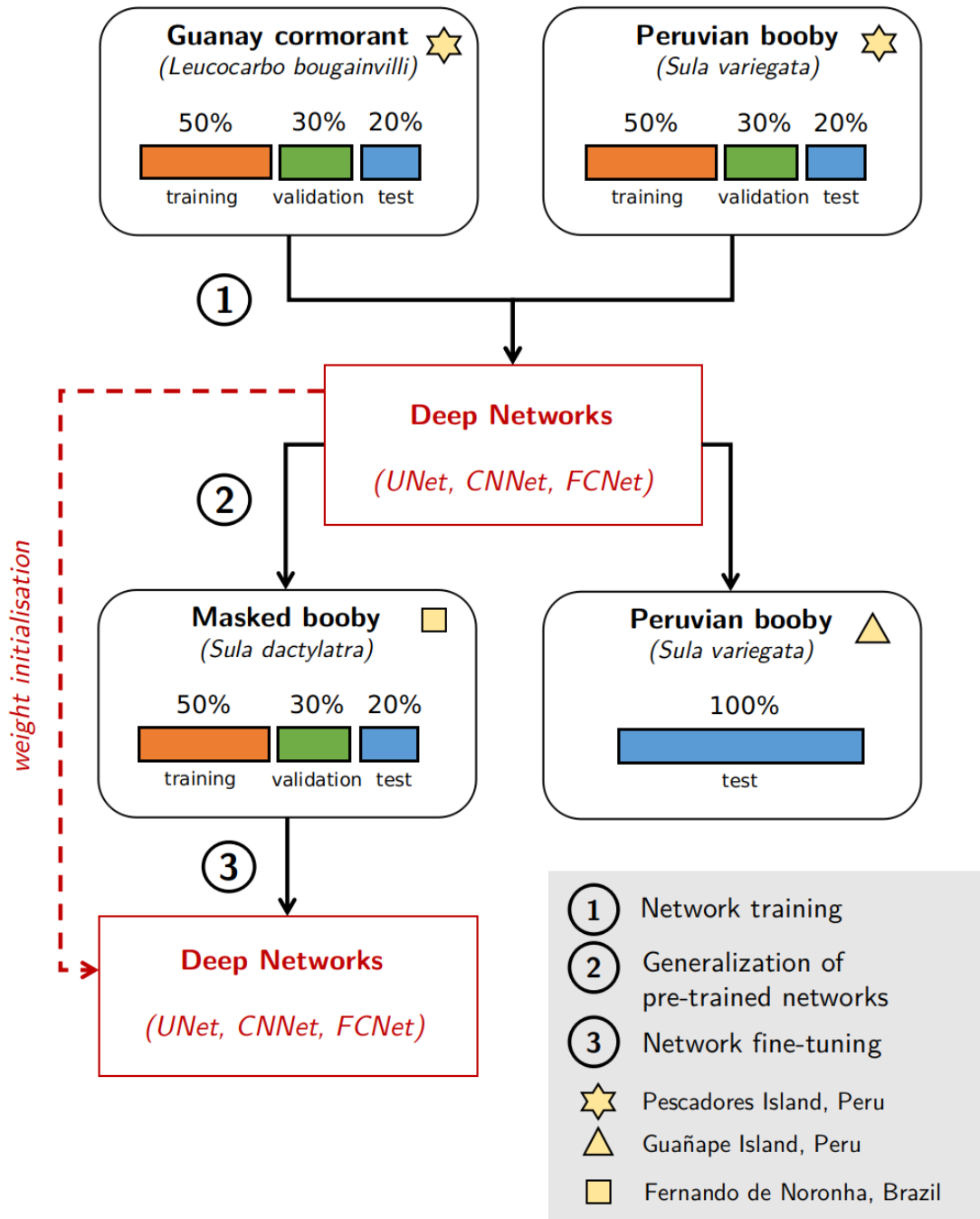


Figure 3.2: **Evaluation scheme** - (1) The datasets from Pescadores Island (see Table 3.1) have been used to train, validate and test deep networks. UNet, CNNet and FCNet refer to the deep network architectures used in this study (see Fig 3.1). (2) The trained networks have been directly used to predict dives on two other datasets without any additional training (Datasets from Guañape Island and Fernando de Noronha). (3) The dataset from Brazil have been used to train, validate and test deep networks. However, the deep networks previously obtained at step (1) have been used for weight initialization. This is known as Fine-tuning.

**(b) Generalization performance of pre-trained networks** In this section, we evaluated the generalization performance through the application of models trained on Pescadores dataset to data that have not been used during the training process. In particular, we evaluate previously fitted deep networks performance on the two datasets from Guañape Island and from Fernando de Noronha Archipelago, composed of Peruvian boobies and masked boobies trajectories, respectively. In this experiment, we compared the dive prediction performance of FPT and HMM methods to the best FCNet, CNNet and UNet models. Beyond AUC and BCE performance metrics, we also evaluated the relevance of the estimated maps of dive distributions. The later were computed using a weighted Kernel Density Estimator (KDE) using dive probabilities as weighing factor. As groundtruth, we considered the map of dive distributions estimated from true dive locations defined by TDR data. Kernel densities were estimated using a  $0.01 \times 0.01^\circ$  grid and a bandwidth of  $0.25^\circ$ . From these maps, we evaluated an means square error (MSE) as an integrated performance metrics for the different approaches Wilson (2011).

**(c) Network Fine-Tuning** We evaluated the benefits of fine-tuning for predicting dives of the 15s-resampled Brazilian dataset (Table 3.1) based on the deep networks fitted on the dataset from Pescadores. The Brazilian dataset was therefore split into training, validation and test datasets with respective size of 50%, 30% and 20%. We then trained models from scratch and using fine-tuning for the three studied network architectures and following the learning procedure presented before. We also evaluate the impact of the training dataset size by randomly selecting respectively 1, 5, 15 and 30 foraging trips for the training step. All models were finally compared to HMM and FPT methods on the testing dataset and using the AUC evaluation metric.

### 3.3 Results

We detail below the numerical experiments performed in this study to assess the relevance of the proposed neural network approaches to predict dive behavior of boobies and cormorants from trajectory data.

**(a) Network Training** On the Pescadores Island dataset used for network training, we reported a contrasted performance of the different methods, with AUC going from 0.61 to 0.96 (see Table 3.2), which corresponds in the best cases to correct prediction rates of diving and non-diving behavior of approximately 95% and of 60% in the worst cases (see Fig 3.3). Overall, all methods performed better at predicting the dives of boobies than those of cormorants. The UNet obtained systematically the best prediction performance with averaged AUC of 0.93 (resp. 0.90) for boobies and cormorants respectively. The CNNet also achieved very good predictions, consistently performing at least as well as state-of-the-art tools with averaged AUC of 0.9 (resp. 0.85). The lowest performance was reported for the FPT approach, which never predicted dives with AUC higher than 0.73. The HMM obtained relatively good performance on the boobies dataset with AUC indices around 0.85, yet it did not get AUC higher than 0.76 on the cormorants dataset. It also obtained the highest BCE, approximately 2 to 10 times higher than the UNet. Regarding the FCNet, the AUC index ranged from 0.65 to 0.89, showing a much greater variability than for CNNet and UNet architectures. The best neural network predictions for Pescadores dataset are illustrated in Fig 3.4. Interestingly, deep networks were rela-

tively sensitive to the sampling resolution, whereas it did not affect much the performance of the FPT and HMM approaches. For both species, the higher the resolution, the better the performance for UNets, CNNs and FCNets. For instance, we reported a mean AUC of 0.92 for a 5s resolution vs. 0.81 for a 30s resolution. This was particularly true for the CNNet and mostly for the FCNet which did not performed better than HMM on the 30s-resoluted datasets, whereas they were able to outperform state-of-the-art approaches on the 5s-resoluted datasets.

Dataset	Resolution	Model	AUC	BCE	F-score	Train Loss	Validation Loss	Reference Name
SV (Pescadores)	5s	FPT	0.62	0.70	0.55	-	-	-
		HMM	0.86	1.07	0.69	-	-	-
		FCNet	0.89	0.38	0.81	0.61	0.61	SV_FCNet_5s
		CNNet	0.94	0.29	0.88	0.48	0.49	SV_CNNet_5s
		<b>UNet</b>	<b>0.96</b>	<b>0.23</b>	<b>0.91</b>	<b>0.48</b>	<b>0.45</b>	<b>SV_UNet_5s</b>
	15s	FPT	0.71	0.79	0.66	-	-	-
		HMM	0.87	2.39	0.84	-	-	-
		FCNet	0.82	0.81	0.80	1.35	1.16	SV_FCNet_15s
		CNNet	0.91	0.58	0.85	0.89	0.86	SV_CNNet_15s
		<b>UNet</b>	<b>0.93</b>	<b>0.57</b>	<b>0.86</b>	<b>0.87</b>	<b>0.79</b>	<b>SV_UNet_15s</b>
	30s	FPT	0.73	0.97	0.70	-	-	-
		HMM	0.84	1.22	0.68	-	-	-
		FCNet	0.82	1.10	0.79	1.69	1.74	SV_FCNet_30s
		CNNet	0.85	0.98	0.80	1.55	1.47	SV_CNNet_30s
		<b>UNet</b>	<b>0.91</b>	<b>0.73</b>	<b>0.86</b>	<b>1.12</b>	<b>1.10</b>	<b>SV_UNet_30s</b>
LB (Pescadores)	5s	FPT	0.61	1.59	0.57	-	-	-
		HMM	0.78	1.42	0.72	-	-	-
		FCNet	0.87	0.40	0.79	0.55	0.67	LB_FCNet_5s
		CNNet	0.92	0.30	0.84	0.48	0.57	LB_CNNet_5s
		<b>UNet</b>	<b>0.93</b>	<b>0.28</b>	<b>0.85</b>	<b>0.46</b>	<b>0.54</b>	<b>LB_UNet_5s</b>
	15s	FPT	0.58	1.73	0.62	-	-	-
		HMM	0.76	3.35	0.72	-	-	-
		FCNet	0.67	0.77	0.75	0.85	0.94	LB_FCNet_15s
		CNNet	0.89	0.43	0.85	0.60	0.73	LB_CNNet_15s
		<b>UNet</b>	<b>0.90</b>	<b>0.37</b>	<b>0.83</b>	<b>0.52</b>	<b>0.76</b>	<b>LB_UNet_15s</b>
	30s	FPT	0.56	1.81	0.62	-	-	-
		HMM	0.75	2.90	0.74	-	-	-
		FCNet	0.65	0.92	0.75	0.96	1.10	LB_FCNet_30s
		CNNet	0.74	0.74	0.76	0.86	1.01	LB_CNNet_30s
		<b>UNet</b>	<b>0.88</b>	<b>0.37</b>	<b>0.83</b>	<b>0.97</b>	<b>1.05</b>	<b>LB_UNet_30s</b>

AUC means the Area Under the ROC curve. BCE is for binary cross entropy computed on the testing trajectories. Train and Validation Loss correspond to the loss computed after model training on respectively training and validation datasets. SV is for Peruvian boobies (*Sula variegata*), LB is for Guanay cormorants (*Leucocarbo bougainvilli*)

Table 3.2: **Performance of deep networks on Train/Validation datasets** - Metrics for all trained deep networks on the trajectories of Pescadores along with benchmarked methods used for comparison.

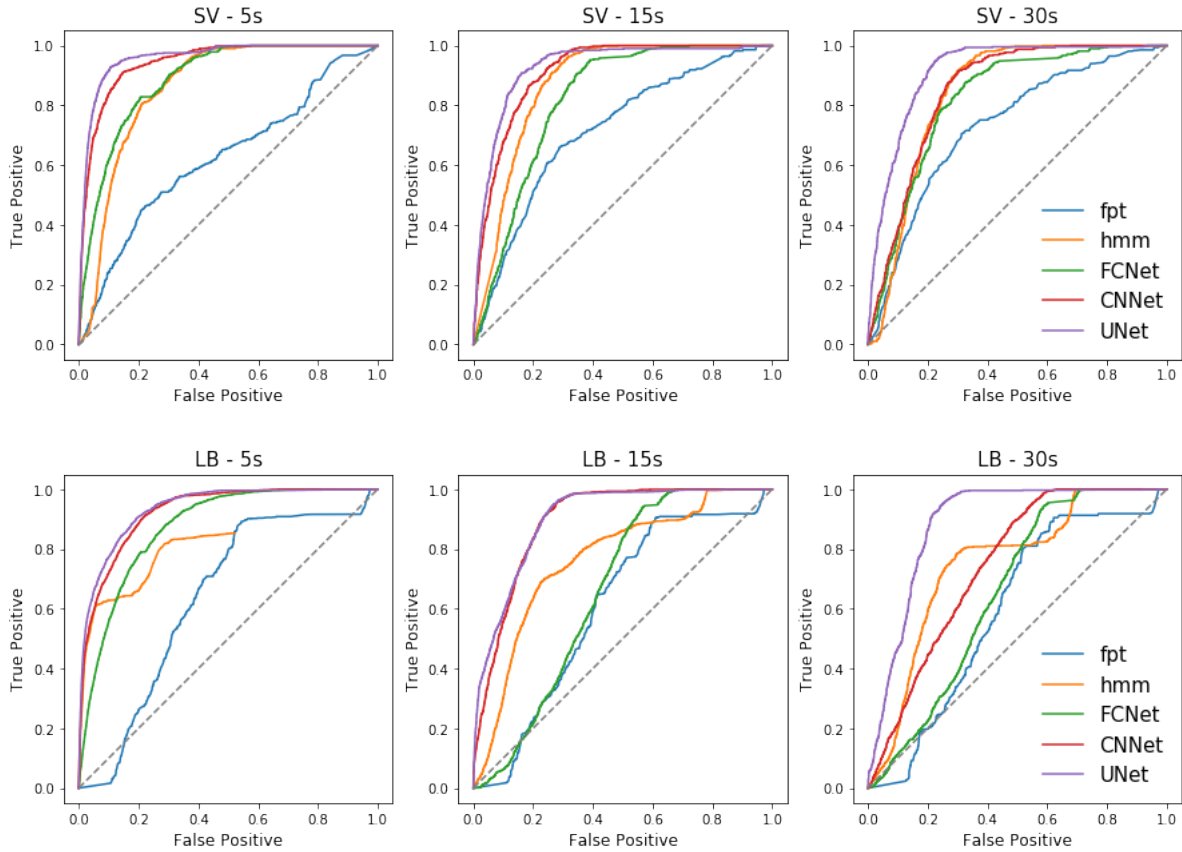


Figure 3.3: **ROC curves of deep networks on the Pescadores dataset** - ROC curves obtained from the prediction of 5 algorithms, First-Time Passage (FPT), Hidden Markov Models (HMM), Fully-Connected Network (FCNet), Fully-Convolutional Network (CNNet) and U-Net) on 2 distinct test datasets resampled at 3 different resolutions (5, 15 and 30s) derived from two seabirds species breeding in Pescadores Island from 2008 to 2013. SV stands for Peruvian boobies (*Sula variegata*), and LB stands for Guanay cormorants (*Leucocarbo bougainvilli*).

**(b) Generalization performance of pre-trained networks** Overall, all networks trained with data from Pescadores reported a AUC performance higher than 0.78 (resp. 0.56) when applied to Guañape (resp. Fernando de Noronha) dataset (Fig 3.5). AUC performance averaged 0.85 when using deep networks trained with the boobies dataset and 0.72 with cormorants data (see Table 3.3). On both datasets, the best models were UNet and CNNet models trained from boobies data with respectively AUC scores of 0.98 and 0.87. In particular, they outperformed the HMM that were specifically fitted to Guañape and Fernando de Noronha data. By contrast, the FCNet used by Browning et al. (2018) that obtained better results than HMM on the Pescadores dataset (AUC of 0.89 vs 0.86 for HMM) did not predict better than HMM when used at Guañape (e.g. AUC of 0.89 vs 0.92 for HMM). The MSE for the estimated dive distribution maps stressed the greater relevance of UNet predictions with a MSE value 1.6 times smaller than the one derived from CNNet estimations and 1.9 times smaller than the one derived from HMM estimations (Table 3.3). As illustrated in Fig 3.6, only the Unet did not overestimate the number of dives in the vicinity of the colony as well as another foraging area southward from the colony.

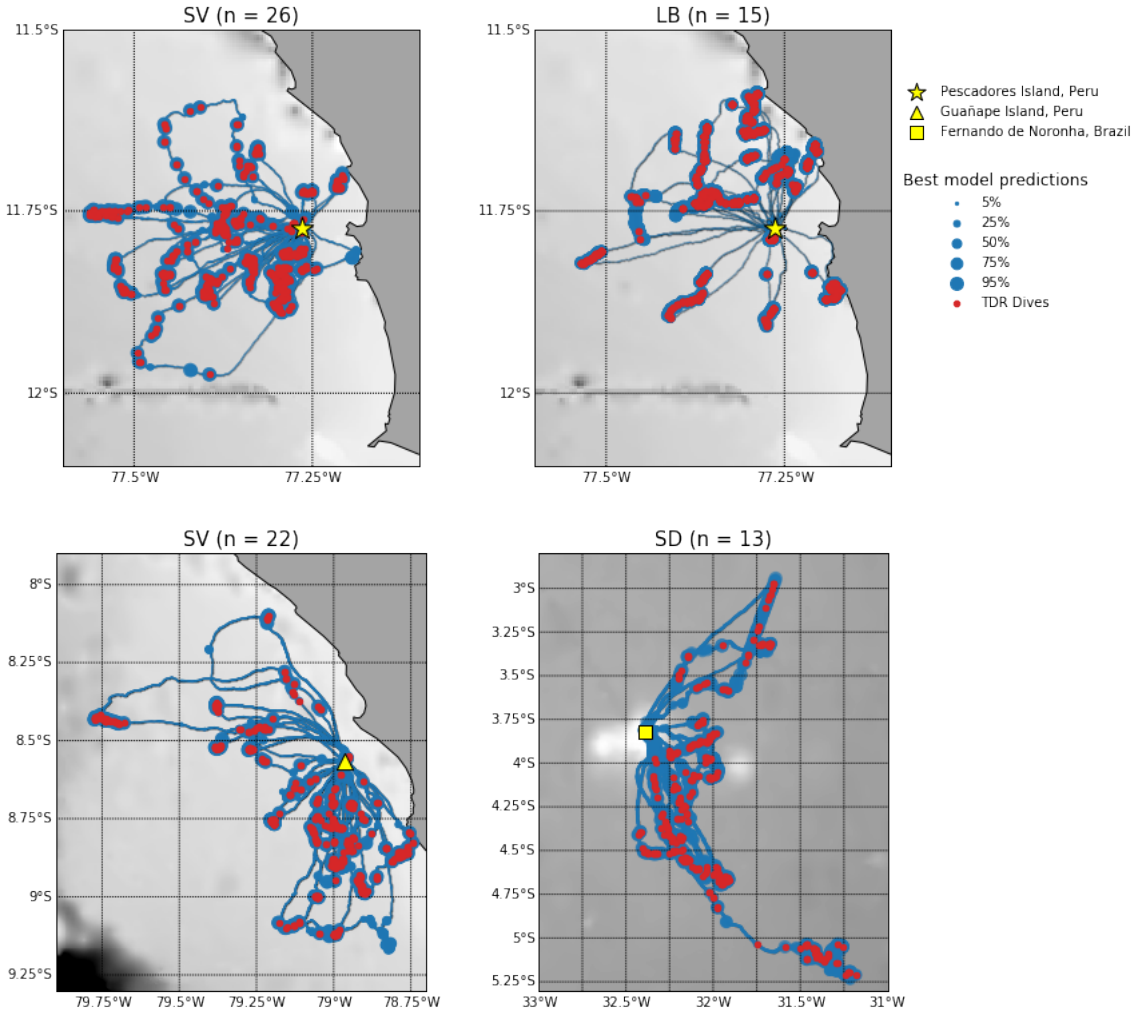


Figure 3.4: **Maps of predicted dives for all 'test' datasets** - Red points represent true dive derived from TDR data. Blue points represent diving probabilities at each location with radius increasing for higher probabilities. These probabilities are the outputs of the best deep networks for each dataset: Peruvian boobies from Pescadores (top left), and from Guañape Island (bottom left), Guanay cormorants from Pescadores Island (top right), and masked boobies from Fernando de Noronha archipelago (bottom right). SV stands for Peruvian boobies (*Sula variegata*), LB for Guanay cormorants (*Leucocarbo bougainvilli*) and SD for masked boobies (*Sula dactylatra*). Bathymetry is shown in grey and is extracted from GEBCO gridded dataset<sup>4</sup>. Land-sea mask is extracted from GSHHG data<sup>5</sup>.

**(c) Network Fine-Tuning** In this section, we evaluated the benefits of a fine-tuning strategy for the prediction of masked boobies dives. As expected, all deep networks initialized using previous models converged more quickly than deep networks trained from scratch. In particular, a dataset of 15 foraging trips (i.e. around 30k GPS positions) was enough for convolutional networks to obtain AUC of 0.9 using fine-tuning, whereas deep networks trained from scratch needed twice as many trips for the same predictive performance (Fig 3.7). The improvement issued from a fine-tuning was notably important for small-to-medium datasets (5-10 foraging trips, i.e. 10k to 20k GPS positions), and for the CNNet. It decreased as the size of the dataset increased. From our experiments,

at least 5 trips were necessary to fine-tune a relevant network compared with the HMM baseline (see for instance bottom-center in Fig 3.7). The best neural network predictions for the Brazilian dataset are illustrated in Fig 3.4.

Dataset	Resolution	Model	AUC	BCE	F-score	MSE
SV (Guañape)	5s	FPT	0.65	0.57	0.43	10.9
		HMM	0.92	2.46	0.88	7.7
		SV_FCNet_5s	0.89	0.31	0.80	7.7
		SV_CNNet_5s	0.97	0.20	0.91	6.5
		<b>SV_UNet_5s</b>	<b>0.98</b>	<b>0.10</b>	<b>0.91</b>	<b>4.0</b>
		LB_FCNet_5s	0.78	0.09	0.05	13.8
		LB_CNNet_5s	0.87	0.07	0.07	7.8
		LB_UNet_5s	0.87	0.08	0.09	14.5
SD (FdN)	15s	FPT	0.50	0.75	0.22	7.5
		HMM	0.84	1.86	0.81	3.4
		SV_FCNet_15s	0.63	1.17	0.71	4.8
		<b>SV_CNNet_15s</b>	<b>0.87</b>	<b>0.59</b>	<b>0.83</b>	<b>3.8</b>
		SV_UNet_15s	0.73	0.58	0.55	5.8
		LB_FCNet_15s	0.56	0.61	0.48	6.5
		LB_CNNet_15s	0.62	0.27	0.08	12.9
		LB_UNet_15s	0.63	0.18	0.08	13.2

AUC is for area under the roc curve. BCE is the binary cross entropy. MSE corresponds to the mean square error of the diving distribution maps estimated with kernel density estimations and plotted in 3.5 to the correct diving distribution. SV is for Peruvian boobies (*Sula variegata*)

Table 3.3: **Performance of deep networks on test dataset** - The deep networks fitted on the dataset from Pescadores have been used for dive prediction in Guañape and in Fernando de Noronha. Deep networks are described by their reference name (see Table 3.2).

## 3.4 Discussion

This study aimed at predicting seabirds dives from GPS data only using deep neural networks trained in a supervised manner based on TDR data to define the groundtruthed dives. In line with Browning et al. (2018), this study further supports the relevance of deep learning approach over classical methods for dive predictions. Using convolutional architectures rather fully-connected ones, we reported even better results with higher stability to the different data inputs, as well as better generalization abilities.

Peruvian boobies and Guanay cormorants tracked in Peru breed in a highly productive upwelling system, the Humboldt Current System (HCS) and feed on the same preys, i.e. Peruvian anchovies Jahncke and Goya (1998). However, they are known to have distinct foraging strategies: boobies are plunge divers reaching in average about 2 m depth and spending most of the time in fly, while cormorants dive deeper and longer on average, reach up to 30 m depth, and spend up to 40% of the time resting on the water surface

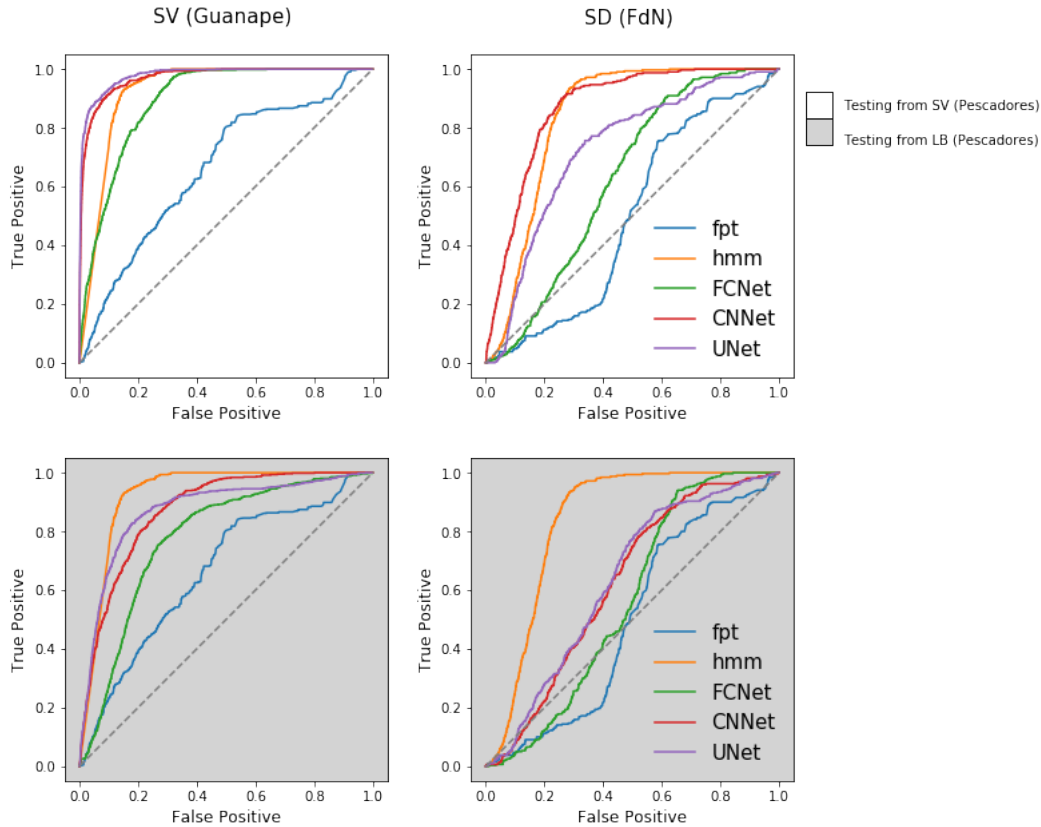


Figure 3.5: **ROC curves of deep networks on test dataset** - ROC curves obtained from the prediction of 5 algorithms, First-Time Passage (FPT), Hidden Markov Models (HMM), Fully-Connected Network (FCNet), Fully-Convolutional Network (CNNet) and U-Net on 2 distinct test datasets. SV stands for Peruvian boobies (*Sula variegata*), and LB stands for Guanay cormorants (*Leucocarbo bougainvilli*). The deep networks used in this figure have been trained on the dataset from Pescadores (see Fig 3.3 and Table 3.2). They have been used for dive prediction of Peruvian boobies in Guañape (left column) and for masked boobies in Fernando de Noronha (right column).

Weimerskirch et al. (2012) (Table 3.1). By contrast masked boobies breeding at Fernando de Noronha are plunge divers similarly to Peruvian boobies, yet they forage mainly in oligotrophic waters de Santana Campelo et al. (2019) and feed mainly on flying fish and flying squids Nelson (2005); Mancini et al. (2014). Their foraging strategies then differ from Peruvian boobies as they perform longest trips and spend more time resting at sea surface (Table 3.1). We demonstrated that for these three species, our best deep network models were able to accurately predict around 95% of dives and outperformed HMM that predicted around 85% of dives. In particular, the proposed U-shape deep network (UNet) demonstrated a greater robustness to different data inputs, as it obtained the best results whatever the sampling resolution (Table 3.3).

Additionally, UNet also resulted in better seabird dive distribution maps (Fig 3.6). Recently numerous studies used seabirds dive as a proxy for prey distribution, and such distribution are usually computed by applying KDE on dive predictions derived from HMMs Delord et al. (2020); Weimerskirch et al. (2020); Zhang et al. (2019b). Here, we show that the error in the estimation of dive distributions maps can be divided by two by using deep learning tools rather than HMM tools. In our specific study, HMMs

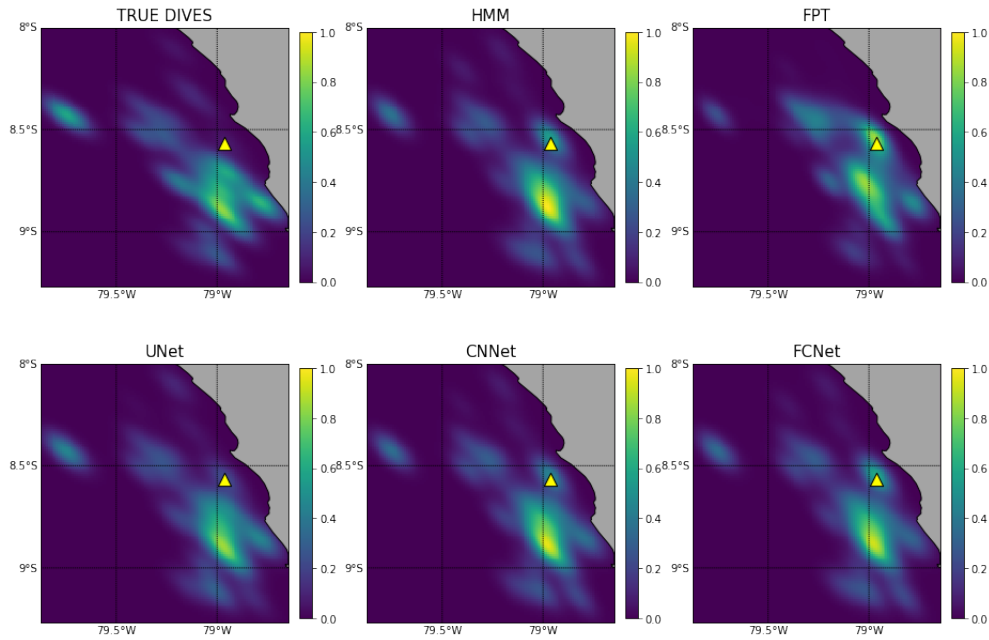


Figure 3.6: **Maps of dive distributions of Peruvian Boobies from Guañape Island** - These density maps were obtained through Kernel Density Estimation. The top left map has been computed from true dives derived from TDR data. The five other maps are estimations of this map, using all points of the trajectories with weights associated to diving probabilities estimated by the studied approaches: First-Passage Time (FPT), Hidden Markov Model (HMM), Fully Connected Network used by Browning et al. (2018) FCNet (top right), fully-Convolutional Network (CNNet), and the U-Net (UNet). Dive map mean square error (MSE) between estimated and reference distribution are in Table 3.3. Land-sea mask is extracted from GSHHG data<sup>7</sup>

over-estimated the frequency of dives at specific locations (including the vicinity of the colony). Sulidae and cormorants spend time bathing near their breeding territories involving vigorous splashing and beating the water with the wings Nelson (2005). Such behaviors associated to low speed might be erroneously classified as diving behavior by state-of-the-art tools which could explain the observed bias. This might also explain why HMM are better at predicting boobies' than cormorants' dives because these birds spend more time resting at the surface, which corresponds to low speed patterns without being dives (see Table 3.1). We may also stress that Cormorants trajectories are characterized by relatively long gaps in the regularly sampled sequence of locations, since these devices do not receive a satellite signal while submerged Boyd (2014); Wilson and Vandenaabeele (2012). This may in turn make more complex the analysis of Cormorants trajectories. In this respect, UNet showed a greater ability to discriminate the resting/bathing behaviors from dives, and a greater robustness to the presence of linearly-interpolated segments. Whereas HMM are mostly driven by fine-scale features (w.r.t. the considered time resolution), UNets exploit a multi-scale analysis of trajectory data and can extract relevant multi-scale information to retrieve dive. Future work could investigate further the key features extracted by UNets. As shown in Fig 3.3, the performance of the deep networks was closely related to the temporal resolution of the sampled dataset. Whereas HMM did not succeed in exploiting higher-resolution data, UNets led to better performance when the resolution increased. This supports a greater ability of UNets both to deal with poten-



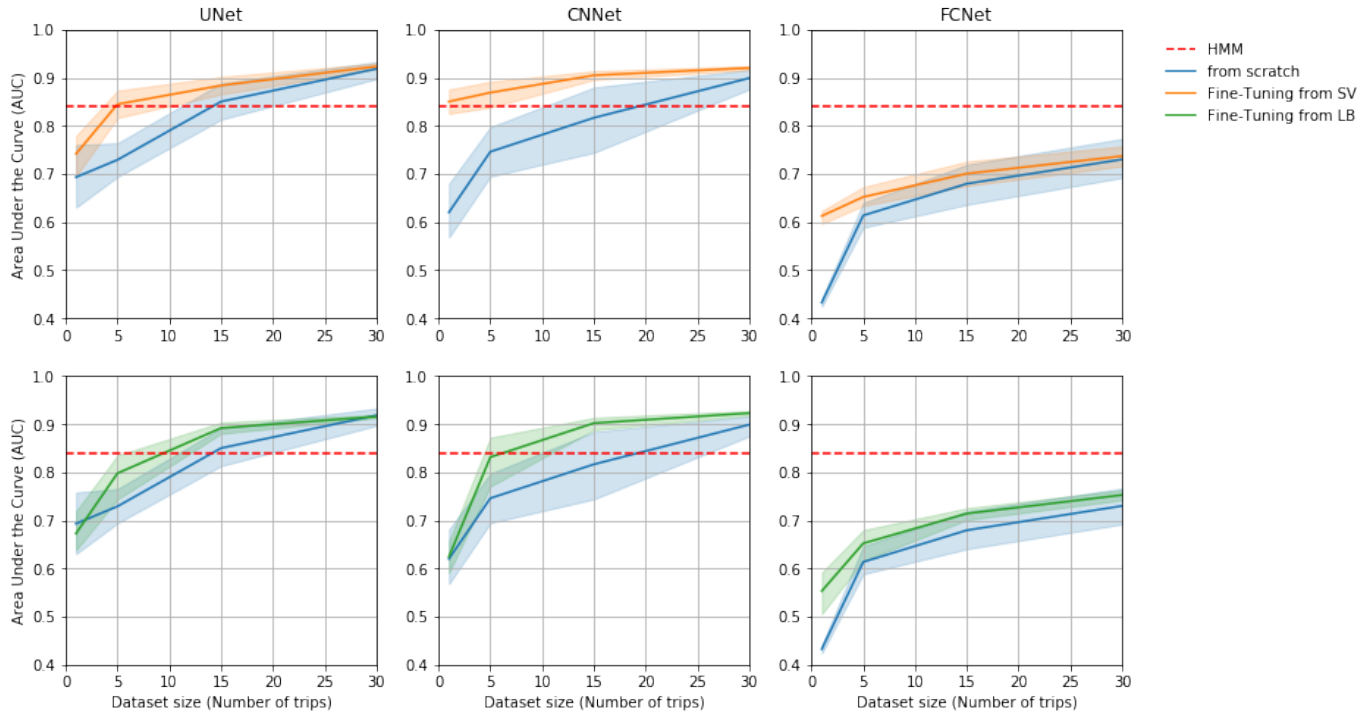


Figure 3.7: **AUC indices of trained deep network function of dataset size** - Performance of deep networks trained using data from masked boobies (SD) from scratch is shown in blue. Deep networks fine-tuned on same data but pre-trained using data from respectively Peruvian boobies (SV) and Guanay cormorants (LB) are shown in orange and green. Performance of HMM fitted using data from masked boobies is shown with the red dotted line.

tial aliasing effects as well as to exploit fine-scale features. With technological advances in sensor technology, ecologists are able to collect larger amount of data than ever before. We might expect GPS with lower consumption and higher resolution in the future. Such an expected trend would make more critical the exploitation of the proposed deep learning approaches to make the most of the collected high-resolution animal trajectories Beyan and Browman (2020); Malde et al. (2020); Yoda (2019).

When considering neural network approaches, training models which may apply beyond the considered training framework is a key feature, generally referred to as the generalization performance of the trained neural networks. Beyond the evaluation of dive prediction performance on a trajectory dataset, which is independent of the training dataset, the question whether a model trained on a given dataset, e.g. for a given species, colony and time period, may apply to other species, colonies and/or time periods, naturally arises as a key question. Numerous studies in the deep learning literature Kawaguchi et al. (2020); Zhang et al. (2017) have highlighted that some neural architectures show relevant generalization properties whereas others may not. Here, we evaluated the generalization performance of the three benchmarked deep networks.

Thus, we demonstrate the ability of deep networks trained at a colony for one species to also apply to an another colony (of the same ecosystem) for the same species. In our example, Peruvian boobies from Guañape Island did have different foraging strategies from their counterparts from Pescadores island, with trips two times longer and dives slightly longer (see Table 3.1). However, the UNet reached similar dive prediction per-

formance when applied to Guañape data. This suggests that dive patterns are highly similar between Peruvian boobies from both colonies. We also show the great ability of the CNNet to generalize dive prediction to a seabird of same genus but from a totally distinct ecosystem. When applied to masked boobies trajectories from a Brazilian colony the CNNet trained from Peruvian boobies data obtained an AUC of 0.87 despite the important difference in foraging strategies (Table 3.3). The same model trained on masked boobies data reached an AUC of 0.93 (Fig 3.7), suggesting that diving characteristics are slightly different. Masked boobies from the Brazilian colony feed indeed on different preys, and spend way more time resting at the surface (Table 3.1). As deep networks trained on cormorants unsurprisingly led to less accurate prediction when used to predict boobies dives, we suggest that the CNNet may capture genus-specific features. These results then support the relevance of deep learning schemes as 'ready-to-use' tools which could be used by ecologists to predict seabirds dives on new (small) datasets, including when these datasets do not include groundtruthed dive data for a supervised training. To make easier such applications, we share online the different models we trained on the considered datasets<sup>8</sup>.

Beyond such a direct application, trained models are also of key interest to explore transfer learning strategies, which refer to the ability of exploiting some previously trained models to address a new task or dataset rather than training a new model from scratch. We illustrated how fine-tuned CNNet and UNet models could outperform HMM with smaller training datasets. For instance, the fine-tuned CNNet for the prediction of masked boobies' dive was able to converge and outperform HMM with a dataset twice as small as the dataset required to reach same performance without fine-tuning (Fig 3.7). Such a result was even possible by initializing neural networks with the model trained with cormorant data. This further supports the ability of deep networks to generalize their prediction from deep diving seabirds (e.g. cormorants) to plunge divers (e.g. boobies). Fine-tuning is thus particularly relevant when the training dataset may not be sufficiently large to train a model from scratch. While the need of large dataset is often presented as a drawback for supersized techniques, we demonstrated that relatively small datasets (5-10 foraging trips, i.e. 10k to 20k GPS data) may be enough to fine-tune deep networks and outperform stat-of-the-art approach to data segmentation. Thus, we expect that our models will be of interest for future work on seabird trajectory segmentation, as they could be used as initialization for fine-tuning procedures.

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<sup>8</sup><https://github.com/AmedeeRoy/BirdDL/models>



# Part II

## Generative models



# Chapter 4

## Using Generative Adversarial Networks (GANs) to simulate central-place foraging trajectories

♪ *Tropic birds*, MASAYOSHI TAKANAKA

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In opposition to the previous chapters, where discriminative networks have been used to better characterize habitat and trajectory data by extracting relevant features, this chapter focuses on the simulation of data. The ability to simulate trajectories is fundamental to better explain the mechanisms underlying observed seabird movements and to test for ecological hypothesis. In this chapter, we introduce a recent deep generative tool known as generative adversarial networks (GAN), in order to simulate animal trajectories. We aim thus at identifying relevant deep network architectures to simulate central-place foraging trajectories, as well as at evaluating their drawbacks and benefits over classical simulation tools, such as state-switching hidden Markov models (HMM). This work has been published as an article in *Methods in Ecology and Evolution*.

### Associated publication

- ✍ Roy A., Fablet R., and Lanco Bertrand S. (2022) Generative Adversarial Networks (GAN) for the simulation of central-place foraging trajectories. *Methods in Ecology and Evolution* 13, 6, 1275-1287

## 4.1 Introduction

Recent advances in telemetry enabled ecologists to track free-ranging animals and to gather large trajectories datasets (Ropert-Coudert et al., 2009; Chung et al., 2021). GPS recorders have been at the forefront of this breakthrough, and can now provide accurate data on the movements of many species, such as mammals (McMahon et al., 2017), seabirds (Yoda, 2019), and many other large-sized vertebrate (Kays et al., 2015). These movement data contain crucial information about animal behaviour, including habitat selection, migration patterns, and foraging strategies but present key challenges for movement ecologists to explain underlying animal movement ecology (Nathan et al., 2008).

Since the movement processes of many animals are relatively poorly known, simulation of trajectories is fundamental to tracking data analysis. Trajectory simulations have notably served as a null model for testing various hypotheses concerning movement (Zurell et al., 2010). For instance, they have been used to generate pseudo-absences in a habitat selection model (Hückstädt et al., 2020), to illustrate the effect of prey distribution on foraging movements (Boyd et al., 2016a), and to demonstrate the effectiveness of social interactions (Bastos et al., 2020). Moreover, for practical and ethical considerations, the tracking of large numbers of individuals is not often possible. Simulated trajectories provide a relevant alternative to develop methods based on synthetic data ; for example, to correct bias in home range estimation (Winner et al., 2018) or for assessing the impact of sample size (Sequeira et al., 2019). Simulation tools may also be of interest in data pre-processing, such as filling gaps and up-scaling the temporal resolution of movement data (Michelot and Blackwell, 2018).

Animal trajectories are generally seen as a succession of elementary movement events called steps (Nathan et al., 2008), and the use of random walk (RW) has received increased attention to describe step sequences (Codling et al., 2008). This includes correlated RW (e.g. Bergman et al., 2000), Lévy RW (e.g. Viswanathan et al., 2008), state-space models (e.g. Patterson et al., 2008) and stochastic differential equations (e.g. Johnson et al., 2008). RW have also been used as 'building blocks' for more complex models to simulate realistic global animal movement patterns. To this end, behavioural heterogeneity is often taken into account by developing state-switching models where animal movements are seen as the outcome of distinct behavioural modes (e.g. travelling, resting and foraging) (Morales et al., 2004). This is notably enabled by discrete multistate RW such as Hidden Markov Models (HMM) (McClintock et al., 2012; Michelot et al., 2017), and by continuous-time multi-state correlated RW (Johnson et al., 2008; Michelot and Blackwell, 2018). The main advantages of continuous-time approaches is that they do not depend on sampling resolution, and that they can deal with irregularly sampled data. Discrete-time models are still an important tool since they are more intuitive and can better handle more than 2 behavioural modes (McClintock et al., 2014). The modelling and simulation of central-place foraging trajectories (CPFT), such as those of seals (Michelot et al., 2017), seabirds (Pirota et al., 2018) and wolves (Ylitalo et al., 2021), are typical applications of discrete-time HMM methods. The fundamental characteristic of central-place foragers is that individuals must return regularly to their central location, and thus perform looping foraging trips. By defining a 'inbound' behavioural mode dedicated to returning home, previously cited studies managed to describe loop-shaped foraging trips.

The above-mentioned statistical movement models are mainly fitted through likelihood maximization or Bayesian statistics (Hartig et al., 2011). They can, however, suffer from challenging parameter estimation, especially as models increase in complexity (e.g.

high number of behavioural modes and covariates) (Michelot et al., 2017; Adam et al., 2019). For these reasons, the simulation of CPFT is also performed using RW embedded within empirically-parametrized Individual-Based Models (IBM). IBM aim to explicitly represent the interactions between individuals and their environment based on ad-hoc formulations, and they provide a pragmatic way to simulate non-linear movement processes (DeAngelis and Grimm, 2014). For example, some studies embed HMM (e.g. Boyd et al., 2016a), correlated RW (e.g. Massardier-Galatà et al., 2017) or mixtures of random and deterministic movement (Barraquand et al., 2009) in IBM for the simulation of CPFT. They, however, often lack generability, have intractable likelihood and are not always directly calibrated from observed data. There has been much work to address these issues, and to parameterize IBM using likelihood-free methods (Grimm et al., 2005; Hartig et al., 2011). In particular, there is a growing interest for data-driven approaches, such as deep learning techniques, in order to calibrate complex ecological systems (Malde et al., 2020).

Deep learning refers to neural networks with multiple layers of processing units (LeCun et al., 2015). By decomposing the data into these multiple layers, deep neural networks allow learning complex features to represent the data with high level of abstraction at multiple scales. Recently, deep learning tools have demonstrated their great ability to simulate complex systems using Generative Adversarial Networks (GAN) (Goodfellow et al., 2014). GAN consist in a pair of deep neural networks that aim to capture the data distribution of some experimental dataset, and that enable to generate new instances of data that share statistical properties. It has become a state-of-the-art approach to generate various types of data, such as image, audio, and spatio-temporal data including human trajectories (Cao et al., 2019; Gao et al., 2020).

This paper investigates generative adversarial networks for the simulation of animal trajectories, and more particularly CPFT. Our key contributions are the design of different GAN architectures and the evaluation of GAN benefits over 'state-of-the-art' tools, i.e. state-switching HMM. We further discuss the pros and cons of GAN with respect to HMM, along with the research avenues opened by GAN to address contemporary ecological challenges.

## 4.2 Material and Methods

### 4.2.1 Generative Adversarial Network

#### Background

The location of an animal is generally represented by a time-continuous or discrete-time stochastic process  $(X_t)_{t \geq 0}$ , where  $t$  denotes the time. A Markovian hypothesis is classically stated for this movement process, assuming that one can fully predict the distribution of the future state of an animal given its current state (Patterson et al., 2008). This hypothesis can only be regarded as an approximation of real movement patterns, which generally also involve long-term dependencies due to factors such as perceptual ranges, memory, social interactions, etc. The calibration of these models generally relies on the maximization of the likelihood of observed trajectories at local scales. It typically comes to estimating the joint distribution of step length and turning angle from GPS tracks.

A wide range of probabilistic models can be restated as the composition of a deterministic function  $G$  and of the sampler of a random latent variable. We may illustrate



this point for correlated RW as presented in Patterson et al. (2008). Let us denote by  $s_t$  and  $\phi_t$  the step length and the turning angle at time  $t$ . The correlated RW can be written as:

$$\begin{pmatrix} (s_1, \phi_1) \\ \vdots \\ (s_n, \phi_n) \end{pmatrix} = \begin{pmatrix} (F^{-1}(z_G^1 | \theta_F), H^{-1}(z_H^1 | \phi_0, \theta_H)) \\ \vdots \\ (F^{-1}(z_G^n | \theta_F), H^{-1}(z_H^n | \phi_{n-1}, \theta_H)) \end{pmatrix} = G(z) \quad (4.1)$$

where  $F$  and  $H$  are cumulative density functions with parameters  $\theta_F$  and  $\theta_H$ , often chosen as Log-Normal and Von Mises distributions, and where  $z_G^i$  and  $z_H^i$  are independent samples from the uniform distribution over  $[0, 1]$ .

The generative model in a GAN also relies on the application of a deterministic function  $G$  to random samples of a latent variable  $z$ , according to a predefined distribution. Function  $G$  is chosen within a parametric family of differentiable functions and implemented as a neural network for flexibility. The other major difference with statistical inference approaches classically exploited in movement ecology lies in the calibration approach from data. Rather than using an explicit likelihood criterion, the calibration of the generator of a GAN involves the simultaneous training of another deep network  $D$  (referred to as the discriminator) that learns how to distinguish simulated data (i.e.  $G(z)$ ) from real data. The typical architecture of a GAN is given in Fig. 4.1. If no discriminator can distinguish the simulated and real data, it means that the generator truly samples the unknown distribution of the training dataset (Goodfellow et al., 2014).

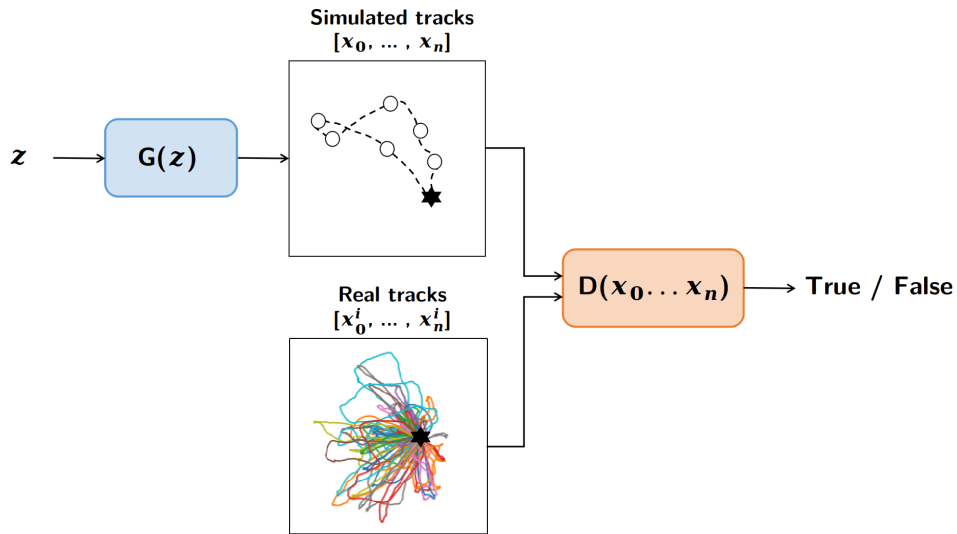


Figure 4.1: **GAN Architecture** - Global architecture of a generative adversarial network.  $G$  refers to the generator network that takes as input a random noise vector  $z$  and outputs a trajectory  $x$ .  $D$  is the discriminator network that aims at distinguishing real trajectories from simulated ones

## Network Architecture

Numerous deep network architectures can be used for both the generator and discriminator networks. Long short-term memory (LSTM) networks and convolutional neu-

ral networks (CNN) are probably the most popular, efficient, and widely used deep learning techniques (Alom et al., 2019). In this study, we used two architectures for the generator and the discriminator, namely CNN-based and LSTM-based architectures (see Fig. 4.2). Here, we briefly present the motivation of these networks and how they function. We refer the reader to Christin et al. (2019) for a detailed introduction to deep networks.

**LSTM** Long Short Term Memory (LSTM) networks are among the state-of-the-art architectures of recurrent neural networks dedicated to the modelling of time series, including trajectories. A key feature of LSTM is its ability to identify and exploit long-term dependencies through gating processes (Alom et al., 2019). LSTM-based architecture have also been used in numerous recurrent GAN for pedestrian trajectory, and medical time-series generation (e.g. Gao et al., 2020; Esteban et al., 2017).

In our study, we used a generator network composed of a LSTM layer that takes a different random seed at each temporal input, and produces a sequence of hidden vectors with 16 features. These hidden vectors encode the state of the trajectory. An additional dense layer maps the 16-dimensional hidden vector at a given time step to the corresponding longitudinal and latitudinal displacements. We derive a time series of positions from the cumulative sum of these elementary displacements (see Fig. 4.2).

We can also exploit a LSTM for the discriminator. Given a sequence of positions (longitude, latitude), the LSTM acts as an encoder of this sequence in some higher-dimensional latent space. A dense layer was then applied to assign a probability to being realistic at each position of the sequence. Overall, the output of the discriminator is the associated mean probability to assess the quality of the whole trajectory (see Fig. 4.2).

**CNN** CNN architectures exploit convolutional layers and are the state-of-art architectures for a wide range of applications, especially for signal and image processing tasks. They are particularly effective in extracting low-level and high-level features from  $n$ -dimensional tensors (Alom et al., 2019).

CNN are also widely exploited in GAN (Radford et al., 2016). Here, we follow the general architecture proposed in Radford et al. (2016) for image generation. The generator takes as input a random noise vector that can be seen as a latent representation of a global time-series. It then applies a series of successive fractional-strided convolutions to map the latent representation into time-series with increasing numbers of points and decreasing numbers of features, until it outputs a 2-dimensional vector of the required length (see Fig. 4.2). In our work, we used a batchnorm and a ReLU activation after each fractional-strided convolution, except for the output that used only a hyperbolic tangent, as suggested by (Radford et al., 2016). We may point out that, in this CNN architecture, there is no explicit sequential modelling of the trajectory and that the latent representation may not be time-related.

Regarding the CNN-based discriminator, we also applied successive strided convolutions in order to transform the initial trajectory into time-series with decreasing lengths and increasing numbers of features, until we obtained a latent vector describing the whole trajectory. We used batchnorm and a LeakyReLU activation after every strided convolution. The last layer is a dense layer with a sigmoid activation that transforms the latent representation into a probability for the trajectory of being realistic (see Fig. 4.2).

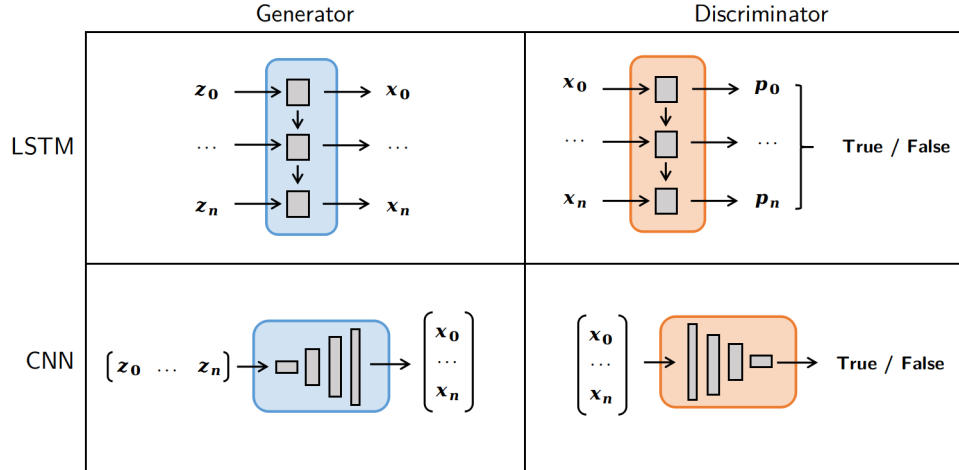


Figure 4.2: **Architecture of LSTM and CNN networks used in this study**

### Adversarial training and spectral regularization

For a given architecture, networks' parameters are estimated using adversarial training, i.e. the two networks compete in a minimax two-player game given by Eq. 4.2. Discriminator  $D$  is trained to maximize the probability of assigning the correct label to both training examples and samples from  $G$ , i.e. to maximize  $\log D(x) + \log(1 - D(G(z)))$ . Generator  $G$  is simultaneously trained to fool the discriminator, i.e. to minimize  $\log(1 - D(G(z)))$ .

$$\min_G \max_D \mathbb{E}_{x \sim p_{data}(x)} [\log D(x)] + \mathbb{E}_{z \sim p_z(z)} [\log(1 - D(G(z)))] \quad (4.2)$$

Numerically, we apply stochastic gradient descents over the discriminator and generator successively where at each iteration, we compute the training losses for a randomly sampled subset of  $m$  trajectories within the training dataset<sup>1</sup>:

$$\begin{aligned} \mathcal{L}_{discriminator} &= \frac{1}{m} \sum_m [\log(D(x)) + \log(1 - D(G(z)))] \\ \mathcal{L}_{generator} &= \frac{1}{m} \sum_m \log(D(G(z))) \end{aligned} \quad (4.3)$$

We may complement the training loss of the generator with additional terms, including both application-specific (Ledig et al., 2017) and regularization (Durall et al., 2020) terms. In particular, recent studies have demonstrated that a spectral regularization may have positive effects, both on the training stability and the output quality of generative networks for image simulation (Durall et al., 2020). We tested here a similar approach with the following spectral loss  $L_{spectral}$  to the generator's gradient descent:

$$\mathcal{L}_{spectral} = \sum [\log(F(x_0, \dots, x_n)) - \log(F(\hat{x}_0, \dots, \hat{x}_n))]^2 \quad (4.4)$$

Where  $F$  is the module of the Fourier transform of a 2-dimensional time-series,  $x$  and  $\hat{x}$  are real and simulated trajectories respectively.

<sup>1</sup>This subset is referred to as a batch in the deep learning literature.

## 4.2.2 Case studies and experiments

### Datasets

GPS recorders were fitted to tropical boobies during their breeding period at the Pescadores Island, Peru in from 2008 to 2013, and at the Fernando de Noronha archipelago, Brazil, from 2017 to 2019 (Table 4.1). This work was conducted with the approval of the Peruvian federal agency, Programa de Desarrollo Productivo Agrario Rural, commonly known as “Agrorural”. Headquarters of Agrorural are located at Av. Salaverry 1388, Lima, Peru, and of the Brazilian Ministry of Environment—Instituto Chico Mendes de Conservação da Biodiversidade (Authorization No 52583-5). Trajectories consist in foraging trips where seabirds look for preys at sea and come back to their colony. Data points have been linearly re-interpolated at regular time steps, and coordinates have been centred on the colony’s location and normalized. In particular, red-footed booby tracks were substantially downsampled in order to provide a simplistic dataset on which to evaluate distinct GAN architectures (see Table 4.1). Finally, trajectories have been padded with zeros so that all longitude/latitude time-series from a dataset would have the same length. Example of real trajectories are given in Fig. 4.6.

Species	Country	Nb of trips	Resolution	Padding
<i>Sula sula</i>	Brazil	30	1 h	20 steps
<i>Sula dactylatra</i>	Brazil	50	5 min	200 steps
<i>Sula variegata</i>	Peru	78	1 min	200 steps

Table 4.1: Datasets Overview with trajectories from red-footed booby (*Sula sula*), masked booby (*Sula dactylatra*) and Peruvian booby (*Sula variegata*).

### Architecture selection experiment

We first designed an experiment to compare different GAN architectures. For this experiment, we considered the simplest dataset with a 1-hour time resolution (see Table 4.1). All trajectories involved 20 time steps. We evaluated four different GAN corresponding to every generator-discriminator pair for the considered CNN and LSTM architectures : e.g., we call ‘LSTM-CNN’ the GAN with a LSTM network as generator and a CNN as discriminator.

For all generators, the input random noise vector consisted in 20 samples from a uniform distribution on  $[0, 1]$ . We trained all networks over 5000 epochs with a learning rate of  $2e-4$  using the loss functions given in Eq. 4.3. The score of each approach was assessed by computing the mean squared error of the logarithmic Fourier decomposition spectrum of simulated and real trajectories,  $\mathcal{L}_{spectral}$  (see Eq. 4.4).

### GAN vs HMM experiment

In this section we compared the best GAN architecture from the previous experiment, namely ‘CNN-CNN’ GAN architecture, to a state-switching HMM. We tested both methods on the two datasets with 200-step time-series consisting in trajectories of tropical boobies from two completely distinct ecosystems and with different foraging strategies (see Table 4.1).

**GAN** The input random noise vector consisted in 256 samples from a uniform distribution on  $[0, 1]$ . We trained the 'CNN-CNN' GAN architecture separately on each dataset over 5000 epochs and with a learning rate of  $2e-4$ . We used a spectral regularization to better reproduce the spectral features of real trajectories, especially for fine time scales, and to increase learning stability.

**HMM** For comparison, we fitted a 'state-of-the-art' state-switching HMM to seabirds CPFT. We followed the methodology presented by Michelot et al. (2017), which relies on a rigorous statistical inference.

Movements were described as a sequence of step lengths and turning angles that we fitted with gamma distribution and von Mises distribution, respectively. Three behavioural modes were used for the Peruvian datasets i.e., 'searching', 'foraging', and 'inbound', while a fourth mode, 'resting', was added with the Brazilian dataset (Fig. 4.6). For the modes of 'searching', 'foraging' and 'resting', we described movement as correlated RW, while for the mode 'inbound' we used a biased RW with attraction toward the colony. In order to force the return to the colony, we fixed some terms of the transition matrix, thus ensuring that the sequence of modes alternates first with 'searching', 'foraging' and 'resting', and is then forced to stay in mode 'inbound'. Additionally, we model the effect of the time since departure on the transition probability from 'searching' to 'inbound'.

These state-switching HMM were fitted to real data according to a maximum likelihood criterion. Fitted models were used to simulate trajectories. The number of modes were defined so that the simulated trajectories would minimize the spectral loss  $\mathcal{L}_{spectral}$  (Eq. 4.4). The initial step was sampled from real data, and we iteratively sampled the next steps, until the trajectory went back to the colony. In practice, we stopped the simulation once a location was simulated within a 1-km radius around the colony.

**Implementation details :** GAN were implemented and trained using Pytorch. HMM were fitted using the momentuHMM R package (McClintock and Michelot, 2018). The code of all the reported experiments is available on our GitHub repository<sup>2</sup>.

## 4.3 Results

### 4.3.1 Architecture selection experiment

Among the four GAN architectures, the fully-convolutional GAN led to the best results with better convergence and lowest computation time (Fig. 4.4 and Table 4.2). GAN with LSTM-based discriminators seemed particularly unstable, with highly variable performance through epochs (4.4). Importantly, only GAN with CNN-based generators managed to simulate looping trajectories. For instance, the 'LSTM-CNN' GAN generated relatively good trajectories with a spectral error  $\mathcal{L}_{spectral}$  lower than 3, yet without being able to loop (Fig. 4.3).

### 4.3.2 GAN vs HMM experiment

On both datasets, GAN and HMM schemes managed to simulate relatively realistic CPFT (see Fig. 4.6). However, the spectral distribution of GAN-derived synthetic trajectories matched the spectral distribution of real trajectories better (Fig. 4.5). In

<sup>2</sup><https://github.com/AmedeeRoy/BirdGAN>

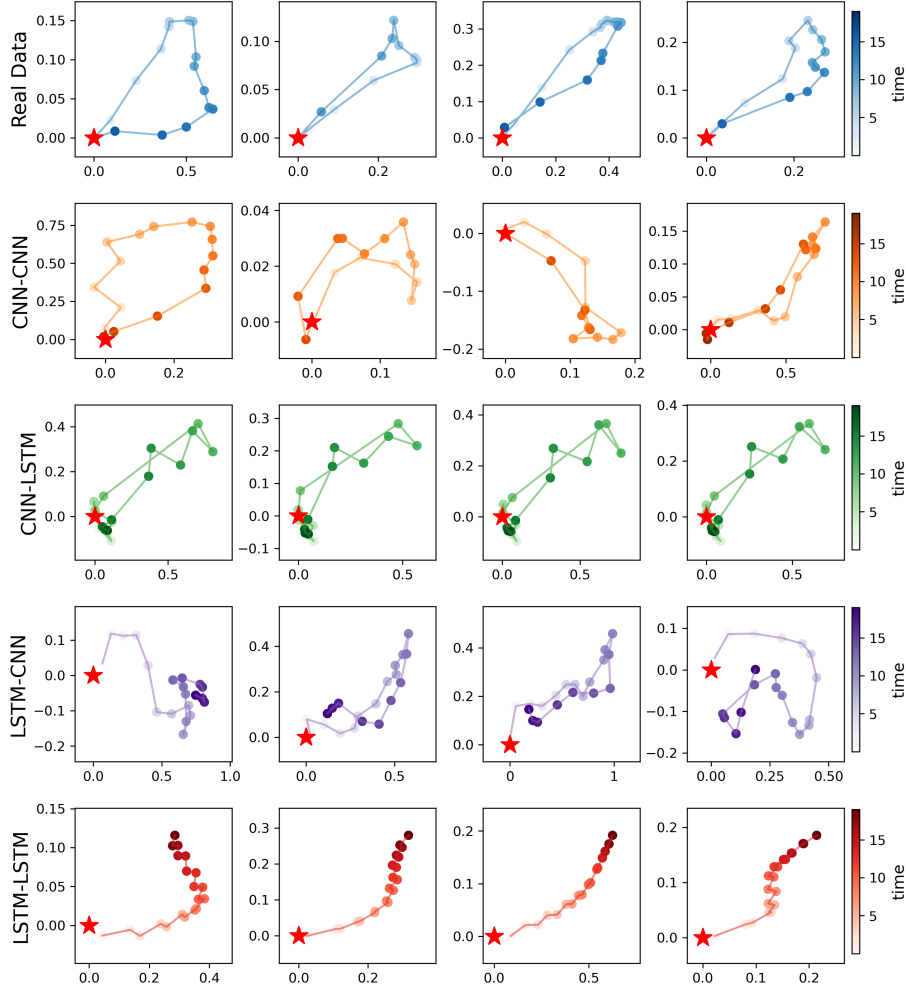


Figure 4.3: **Examples of trajectories generated by different GAN architectures** - The four different GAN correspond to every generator-discriminator pairs tested on the 20-step dataset (see Table 4.1)

Model	Computation Time (min)	$\mathcal{L}_{spectral}$
<b>CNN-CNN</b>	<b>1.95</b>	<b>0.47</b>
LSTM-CNN	2.69	1.93
CNN-LSTM	3.03	3.06
LSTM-LSTM	3.59	4.0

Table 4.2: **Performance of different GAN architectures** - Computations have been run using Google Colaboratory resources and relying on Intel(R) Xeon(R) CPU 2.20GHz

particular, the mean spectral error  $\mathcal{L}_{spectral}$  was about 4 times smaller, using GAN than using HMM (Table 4.3). This was particularly highlighted for the medium frequencies (Fig. 4.5). On the Peruvian dataset, the HMM failed to reproduce spectral features both at lower and higher frequencies (Fig. 4.5A), and on the Brazilian dataset, it failed in the higher frequency range only (Fig. 4.5B). By contrast, HMM outperformed GAN to sample relevant step distributions (Fig. 4.7).

GAN models capture the real data distribution better, as they can simulate a set of trajectories that share global statistics with the reference dataset. For instance, our

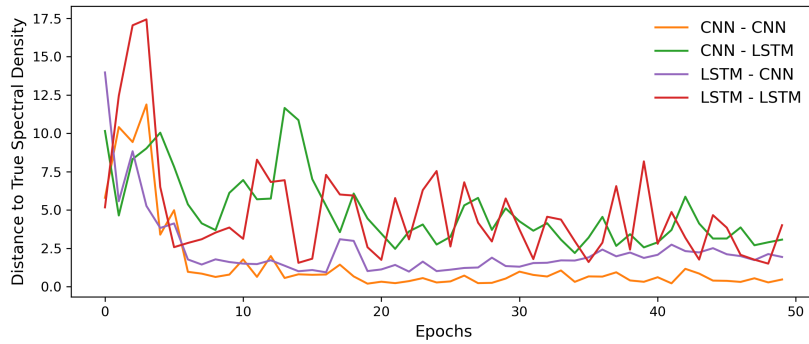


Figure 4.4: **Convergence of GAN architecture over 5000 epochs** - The four different GAN correspond to every generator-discriminator pairs. Distance to true spectral density is computed with Eq. 4.4

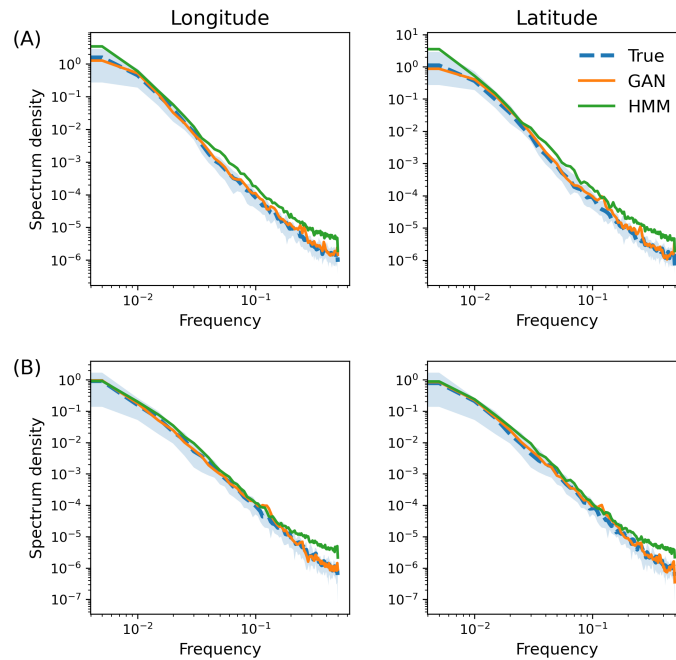


Figure 4.5: **Mean Fourier Spectrum of real trajectories and trajectories generated by GAN and HMM** - derived from real trajectories used for training (blue), 100 synthetic trajectories generated by a 'CNN-CNN' GAN (orange) and by HMM (green). (A) stands for the 200-step Peruvian dataset, and (B) stands for the 200-step Brazilian dataset (see Table 4.1).

synthetic trajectories have consistent trip distance, trip duration and the straightness index distributions (see Fig. 4.7). The straightness index of a trajectory is defined as two times the quotient between the max range to the colony and the trip total distance. The trained GAN also capture spatial information as they reproduce position distributions of observed trajectories (Fig. 4.8 and Table 4.3). GAN-derived synthetic trajectories were indeed mainly heading toward some area of interest (i.e. westward of the colony on the Peruvian dataset, and to the north-east and south-east of the colony on the Brazilian dataset), while HMM-derived trajectories are uniformly spread in all directions around the colony.

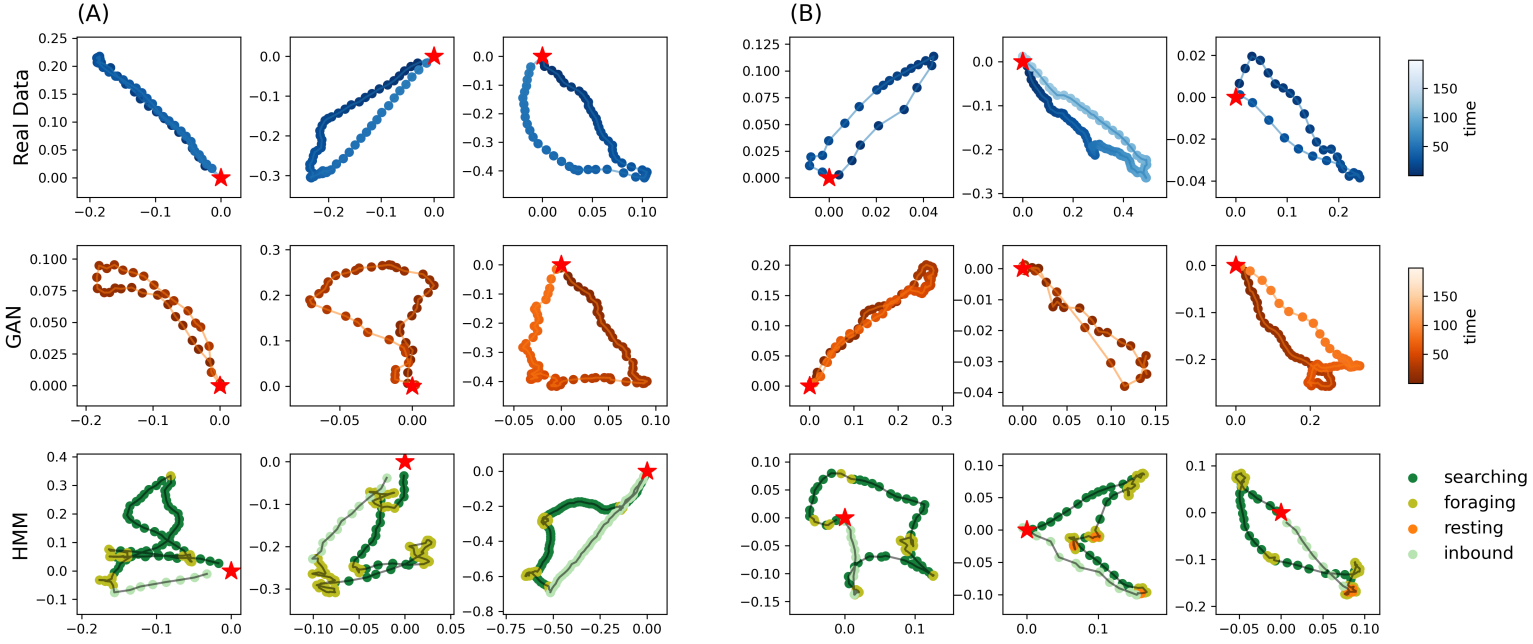


Figure 4.6: **Example of real and generated trajectories** - Real trajectories used for training are in blue, synthetic trajectories generated by a 'CNN-CNN' GAN are in orange, and trajectories generated by HMM are in green. (A) stands for the 200-steps Peruvian dataset, and (B) stands for the 200-steps Brazilian dataset (see Table 4.1). All positions at less than 1 km from the colony were removed.

Dataset	Model	$\mathcal{L}_{spectral}$	$\Sigma$
(A) Peru	<b>CNN-CNN</b>	<b>0.08</b>	<b>1.09</b>
	HMM	0.91	2.63
(A) Brazil	<b>CNN-CNN</b>	<b>0.07</b>	<b>0.03</b>
	HMM	0.88	0.32

Table 4.3: **Statistical properties of GAN and HMM simulations** -  $\mathcal{L}_{spectral}$  stands for the mean squared error of the logarithmic Fourier decomposition spectrum presented in Fig. 4.5 and  $\Sigma$  stands for the mean squared error of the position distributions presented in Fig. 4.8

## 4.4 Discussion

Deep learning has become the state-of-the-art framework for dealing with a wide range of problems in ecology, such as classification and segmentation tasks, mainly for image analysis (Christin et al., 2019). Despite recent advances in deep learning for the simulation of complex systems, few studies have explored generative models, and particularly Generative Adversarial Networks (GAN) to simulate ecological data. To our knowledge, deep convolutional GAN have only been used for data augmentation in simulating plant or insect images so far (Lu et al., 2019; Madsen et al., 2019). This study demonstrates that GAN are also promising tools to generate other ecological data, such as animal trajectories.

CPFT provide an interesting case study in animal movement ecology. Animals performing CPFT are often supposed to maximize their energy intake rate while travelling



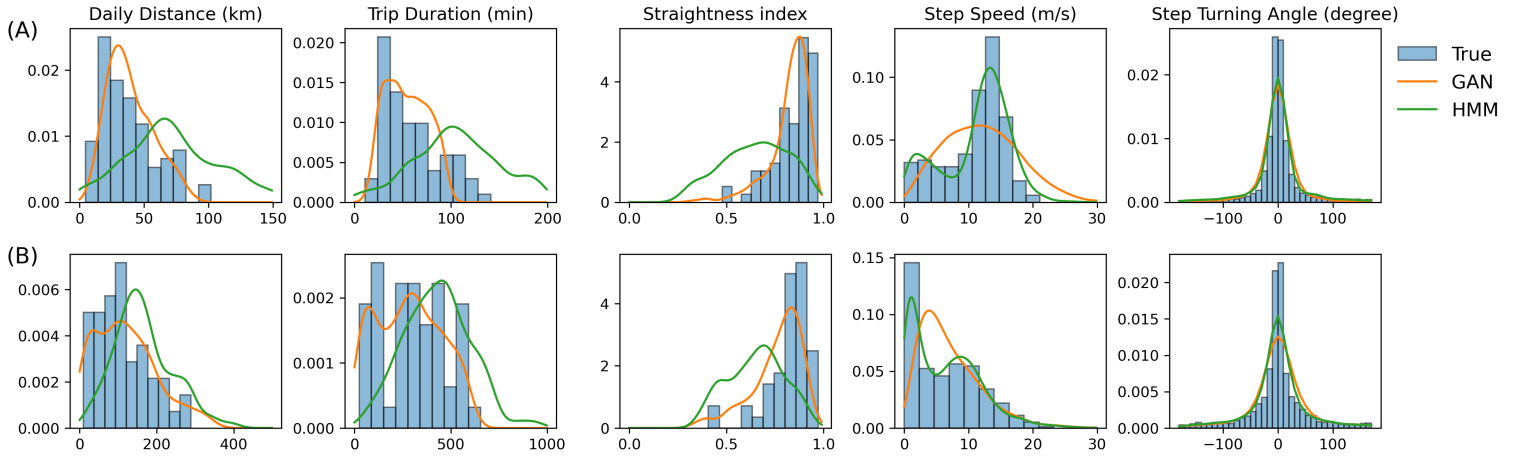


Figure 4.7: **Histogram of descriptive statistics derived from real and generated trajectories** - derived from real trajectories used for training (blue), 100 synthetic trajectories generated by a 'CNN-CNN' GAN (orange) and by HMM (green). (A) stands for the 200-steps Peruvian dataset, and (B) stands for the 200-steps Brazilian dataset (see Table 4.1). The mean squared error of these position distribution estimations are presented in Table 4.3.

away from and back to their central location. Numerous studies have thus investigated how central-place foragers balance their time and energy while foraging (Barraquand et al., 2009; Humphries and Sims, 2014). Capturing the variability of foraging strategies with respect to species, sex, or breeding stage is a key element in understanding what drives the decisions of the animals (Phillips et al., 2021). Peruvian boobies (*Sula variegata*) tracked in this study breed in a highly productive upwelling system, the Humboldt Current System, and feed on relatively abundant Peruvian anchovies (Jahncke and Goya, 1998). For these reasons, they performed mainly short foraging trips of about 25 km, eventually travelling up to 75 km at a mean speed of  $11 \text{ m}\cdot\text{s}^{-1}$  (Fig. 4.7). By contrast, masked boobies breeding at Fernando de Noronha forage mainly in oligotrophic waters (de Santana Campelo et al., 2019). They have to travel way further from their colony during trips of 6-7h in average. They also spend substantial time sitting on water in the vicinity of foraging areas.

We demonstrated the great ability of GAN to capture the global statistical properties of these distinct trajectory datasets derived from seabirds species with distinct foraging strategies. By contrast, the current state-of-the-art approaches such as multi-state HMM are calibrated at a local scale and are unable to bring out global patterns from these local features. In particular, the use of the behavioural mode 'inbound' relies on the assumption that there is a given time when animals decide to return directly to the colony, which is not always the case. Our numerical experiments pointed out that the relationship between local and global features may be complex for real trajectory data. GAN are explicitly trained so that they best reproduce the characteristic multiscale features of real trajectories. Through strided convolutions, it appears that the considered CNN discriminator overlooks the highest frequencies to focus on larger-scale information. Besides, the CNN generator does not explicitly represent a trajectory as a sequential process, which may also impede its ability to reproduce step distribution adequately. This may be a general property of convolution GAN architectures, as they are known not to

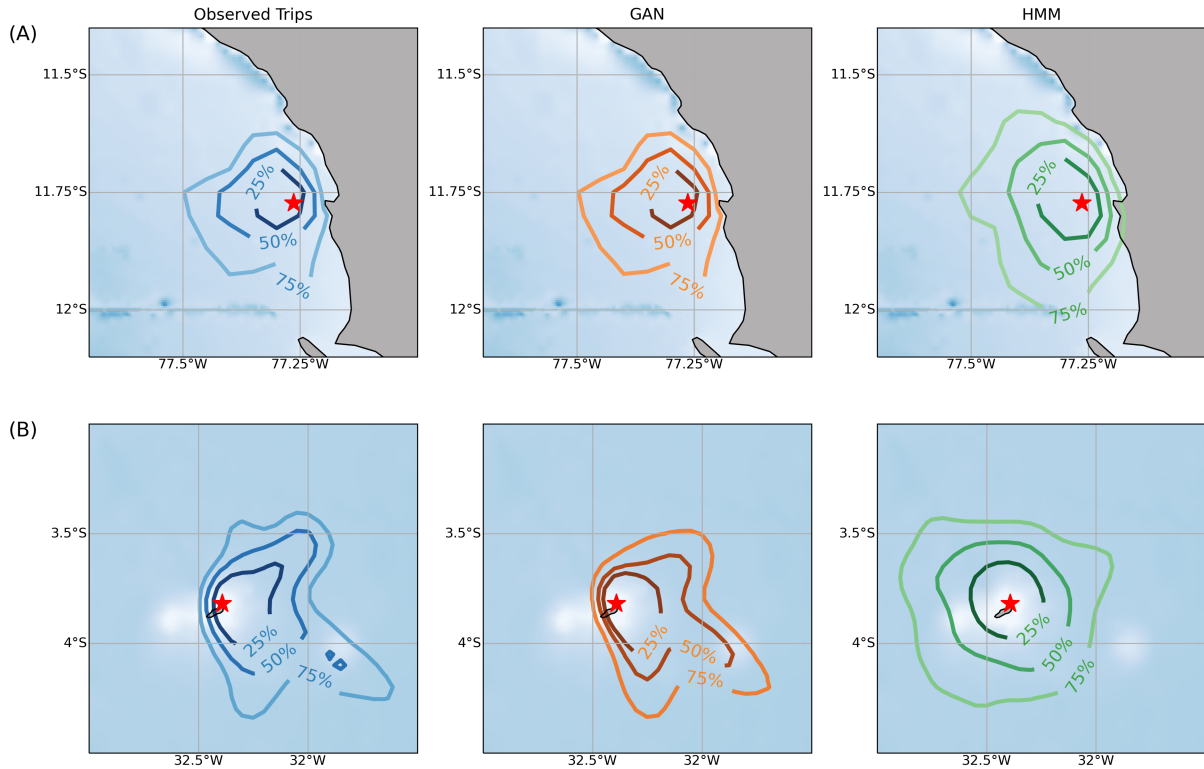


Figure 4.8: **Kernel Density Estimation of position distributions based on real and generated trajectories** - derived from real trajectories used for training (blue), 100 synthetic trajectories generated by a 'CNN-CNN' GAN (orange) and by HMM (green). (A) stands for the 200-steps Peruvian dataset, and (B) stands for the 200-steps Brazilian dataset (see Table 4.1)

simulate realistically fine-scale textures in computer vision (Cao et al., 2019).

The simulation of realistic global trajectory patterns can however be of interest for clarifying numerous ecological challenges, and may benefit from GAN through both generator and discriminator networks. Similarly to usual RW mixture models, the generator network is a sampler of trajectory data. It could be used to provide null distributions within hypothesis testing frameworks, or within a bootstrap procedure to estimate the uncertainties of features of interest (Michelot et al., 2017). The ability of GAN to reproduce large scale also makes it particularly relevant when estimating distributions of usual global statistical estimators, such as home range distribution (e.g. Hazen et al., 2021), prey encounter probabilities (e.g. Sims et al., 2006), or foraging areas distribution (e.g. Ito et al., 2021). For this reason, it could also provide new means to test energy-related hypotheses of foraging trips, and foraging optimality (e.g. Humphries and Sims, 2014). In addition, through the computation of a probability of being a 'realistic' trajectory, the discriminator network provides a metric of data similarity, and could be used within comparative study of foraging strategies to assess sex-specific (Lewis et al., 2005), or breeding stage differences (Lerma et al., 2020a).

Besides, RW capture step speed and turning angle distributions and seem more relevant to understand what drives animal decisions at the step level. They have indeed proven useful to evaluate the effect of a heterogeneous landscape, and various external features on animal movement, notably through step-selection function (Signer et al., 2019),

mixed effect models (Jonsen et al., 2019), or HMM whose transition states depend on external covariates (van Beest et al., 2019). Yet, these approaches often struggle when accounting for processes that impact movement patterns at larger spatio-temporal scales. Various extensions of basic state-space models have been proposed to take these into account, e.g. using hidden semi-Markov models (Langrock et al., 2012), and hierarchical HMM (Leos-Barajas et al., 2017; Adam et al., 2019). In practice, due to their relative complexity to be implemented and to be parametrized, they are rarely used.

Future work should investigate how to combine and take the benefits of both GAN and HMM approaches in order to simulate 'realistic' multiscale animal movement processes. Two research directions naturally come up: modifications to the architectures of generator and discriminator networks, and the exploration of different training frameworks. Regarding the first direction, we may consider the combination of CNN architectures and of HMM-driven or HMM-inspired neural architectures (Lei et al., 2016). Beyond the explicit parameterization of Markovian processes, recurrent architectures such as LSTM seem appealing to embed some latent representation of a behavioural mode sequence, from which one could, for instance, expect to sample the multimodal feature of speed distribution more satisfactorily (Fig. 4.7). Inspired from hierarchical HMM schemes, hierarchical GAN with scale-specific network modules also arise as a relevant direction (Huang et al., 2019). Regarding the training framework, one may first explore different adversarial losses such as the popular Wasserstein GAN (Arjovsky et al., 2017). Though this loss would not lead alone to improvements regarding the simulation of local-scale features, they typically lead to more stable training frameworks, which may be helpful when considering more complex architectures. One could also complement the adversarial loss by a likelihood-based loss derived from a multimodal RW model to explicitly constrain the fine-scale features.

Numerous existing varieties of GAN could also provide great support for movement ecology, especially conditional GAN (Isola et al., 2018). A conditional GAN consists of a GAN with some external variable that conditions its output. One could therefore test for conditions that would explain behavioural variabilities at large scale such as individual characteristics (e.g. sex, mass, breeding stage), or environmental characteristics (e.g. prey distributions, oceanographic features). This typically applies to the assessment of different environmental scenarios and associated animal trajectories, a broad scientific challenge that includes the prediction of the potential impact of climate change on animal behaviour (Hückstädt et al., 2020). Conditional GAN would also provide new means for the interpolation and super-resolution of trajectory data, as performed in computer vision (Ledig et al., 2017).

## Conclusion

GAN provide a powerful framework to simulate complex stochastic processes without requiring any specification of a likelihood function; it also frees ecologists from the assumption of first-order Markovianity. This study notably illustrates their ability to reproduce large to medium scale properties statistics of seabird trajectories when used in their most classical form. It is also an ultra-flexible tool that could further benefit from existing tools, such as HMM that are calibrated on step distributions, but that usually fail to reproduce large scale properties. We believe GAN to be a truly promising tool for movement ecology, opening thus new research avenues to simulate and further our understanding of animal trajectories.

# Chapter 5

## A spatially-explicit convolutional GAN to generate free-ranging trajectories with heterogeneous behavioral modes

♪ *L'oiseau*, FEU! CHATTERTON

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In this chapter we aim at exploring new GAN architectures for the generation of seabirds foraging trajectories, and at better capturing step distributions than deep generative networks presented in chapter 4. Whereas most deep networks rely explicitly or implicitly on a Lagrangian representation of movement patterns, which naturally leads to recurrent neural architectures and Markovian models, we draw from the dual representation of stochastic Lagrangian dynamics through Fokker-Planck equation. The latter provides an Eulerian representation of movement patterns through the dynamics of the space-time distribution of the positions. It advocates for learning multidimensional convolutional latent representations of movement patterns. Within a GAN setting, we combine these representations with multiple discriminators to capture both large-scale and fine-scale features of free-ranging trajectories. Numerical experiments for real seabird trajectory datasets support the relevance of the proposed framework w.r.t. state-of-the-art approaches to better simulate complex free-ranging trajectories while learning visually-structured and interpretable latent representations. This work is the subject of an article in preparation.

### Associated publication

- ✍ Roy A., Lanco Bertrand S. and Fablet R. (2022) A spatially-explicit convolutional GAN to generate free-ranging trajectories with heterogeneous behavioral modes. *In Prep.*

## 5.1 Introduction

Recent technical advances in the miniaturization and autonomy of tracking devices have enabled the collection and documentation of a wide range of trajectory data derived from human movement (e.g. pedestrian Choi et al. (2020), vehicles Nguyen and Fablet (2021)), physical processes (e.g. aerosol particles Gan et al. (2019), oceanic drifters Elipot et al. (2016)), and biological processes (e.g. animal movement Block et al. (2011); Kays et al. (2015)). In this context, trajectory data mining has become an increasingly important research theme, providing tools for numerous tasks such as trajectory clustering, classification, outliers detection, and pattern mining Zheng (2015); Feng and Zhu (2016).

A trajectory represents the sequence of locations of a moving object/individual at certain times, and it is usually defined as a function mapping from the temporal domain to the spatial domain. Trajectories of moving points are denoted as a sequence of tuples  $\xi = \{(x_1, t_1), (x_2, t_2), \dots, (x_n, t_n)\}$ , where  $(x_i, t_i)$  indicates the location  $x_i$  at time  $t_i$ . Trajectories can be defined either on discrete or continuous, regular or irregular spatio-temporal domains, and can be categorized in distinct types, including continuous free-ranging trajectories (e.g. aircraft, and animal trajectories), place-based trajectories (e.g. mobile phone records, social media check-in data), and road-based trajectories (e.g. vehicles, bicycles, and pedestrian in urban environments) Liu et al. (2018).

Numerous studies have focused on modelling the mechanisms underlying movement from various trajectory data types and for mobility-related simulation tasks, such as trajectory prediction and global trajectory generation Michelot et al. (2017); Gao et al. (2020); Luca et al. (2021). Trajectory prediction consists in the simulation of future locations of an object  $\{(x_{k+1}, t_{k+1}), (x_{k+2}, t_{k+2}), \dots\}$ , given some or all of its previous locations  $\{(x_1, t_1), \dots, (x_{k-1}, t_{k-1}), (x_k, t_k)\}$ . Here, we address the problem of the simulation of global movement tracks. This is a key issue for a variety of scientific domains such as, epidemiology for modelling virus spreading Feng and Zhu (2016), urban planning for estimating changes of traffic Kitamura et al. (2000), animal ecology for evaluating the impact of environmental changes on animal movement Boyd et al. (2016b), or for geo-privacy concerns Fiore et al. (2020).

From a learning point of view, the generation of a realistic long sequence of positions is still a real challenge. Trajectories are indeed the result of complex multiscale processes that are characterized by local, medium and global statistical properties to be reproduced Nathan et al. (2008); Fablet et al. (2014). Most previous works rely explicitly or implicitly on a Lagrangian representation of movement patterns, which naturally leads to recurrent neural architectures and Markovian models Smouse et al. (2010); Choi et al. (2020); Luca et al. (2021). These sequential models however typically focus on short-term dynamics and accumulate important errors when used over numerous iterations for long-term simulations Jeha and Mercado (2022); Roy et al. (2022). Overall, this results in a limited success of state-of-the-art generative models to reproduce the exhibited space-time patterns.

In this study, we explore GAN architectures for the generation of free-ranging trajectories. We draw from the dual representation of stochastic Lagrangian dynamics through Fokker-Planck equation. The latter provides an Eulerian representation of movement patterns through the dynamics of the space-time distribution of the positions. It advocates for learning multidimensional convolutional spatially-explicit latent representations of movement patterns. Within a GAN setting, we combine these representations with multiple discriminators to capture both large-scale and fine-scale features of free-ranging trajectories. Numerical experiments for real seabird trajectory datasets support the rel-

evance of the proposed framework w.r.t. state-of-the-art approaches to better simulate complex free-ranging trajectories while learning visually-structured and interpretable latent representations.

This paper is structured as follows. Section 2 briefly reviews the related work. We detail the proposed GAN framework in Section 3 and report numerical experiments for real seabird trajectories in Section 4. We further synthesize the main findings in Section 5.

## 5.2 Problem statement and related work

### 5.2.1 Generative modeling for movement patterns

Free-ranging trajectories are the results of complex spatio-temporal processes depending on internal and external factors influencing movement at multiple scales (e.g. environment, landscapes, cognitive ability, navigation capacity...), and characterized by specific patterns associated to distinct behavioral modes, transportation modes or activities (e.g. resting, travelling...) Nathan et al. (2008); Luca et al. (2021). From a modeling point of view, they are often considered as the realization of stochastic processes including both discrete-time Markovian processes and random walks Langrock et al. (2012); McClintock et al. (2012) as well as time-continuous representation according to some underlying stochastic differential equation (SDE) Smouse et al. (2010); Michelot and Blackwell (2018). Within a time-continuous setting, the SDE commonly involves two main components, a deterministic drift term and a stochastic component as follows.

$$dX_t = V(X_t, t)dt + \sigma(X_t, t)dW_t \quad (5.1)$$

with  $x_t$  the position at time  $t$ ,  $V(X_t, t)$  the drift term at position  $x_t$  and time  $t$ ,  $dW$  a Brownian process and  $\sigma(X_t, t)$  the time-location-dependent spread of the Brownian component.

The deterministic term has typically a crucial role in movement prediction and describes how the acceleration of the animal interacts with some external field such as winds and ocean currents for birds and marine animals van Sebille et al. (2018); Frankish et al. (2020). For movement patterns considered as 'unpredictable', studies have given more emphasis on the parameterization and calibration of the stochastic term Johnson et al. (2008). We may point out that the time discretization of the above SDE formulation leads to classical discrete-time Markovian processes and associated extensions, especially through recurrent neural networks (RNN) in the recent deep learning literature Rew et al. (2019); Peng et al. (2019); Wijeyakulasuriya et al. (2020). The calibration of these time-continuous or discrete-time stochastic representations arises as a critical issue. The underlying Markovian assumptions simplifies the maximum likelihood estimation of model parameters to matching first-order Markovian statistics. This has been widely explored in applied statistics and movement ecology Patterson et al. (2008); Smouse et al. (2010). By construction, such approaches reproduce well fine-scale patterns but may show a limited ability to capture large-scale ones as illustrated in Roy et al. (2022) for seabird trajectories. This is a strong motivation for exploring other training strategies.

GANs have rapidly become state-of-the-art generative tools for data simulation and prediction, especially image and time-series Goodfellow et al. (2016); Esteban et al. (2017). GANs are composed of two deep networks: a generator that aims at simulating

'realistic' data, and a discriminator (or critic) that aims at distinguishing simulated data from real data. These two networks are then jointly trained in a zero-sum game, where each network competes against its adversarial network, and it is therefore considered as a relevant tool for likelihood-free calibration of stochastic processes Goodfellow et al. (2014). Regarding specifically movement patterns, recent studies have explored GANs to calibrate Lagrangian representation of movement patterns. It has been performed using recurrent GANs with RNNs for both the generator and the discriminator for pedestrian and vehicle trajectory prediction Gao et al. (2020); Luca et al. (2021). These applications address rather short-term prediction contexts, typically by predicting less than 10 time steps. Such schemes are unlikely to apply to the generation of long synthetic trajectories Kulkarni et al. (2018); Feng et al. (2020), such as free-ranging movement patterns targeted in this study. RNNs are indeed confronted to important vanishing gradient problem when simulating time-series over 100 time-steps Pascanu et al. (2013). Besides, as shown in Roy et al. (2022), RNN-based GANs seem likely to fail in the generation of large-scale movement patterns. As an alternative, other approaches have used non-sequential generators, where a convolutional neural network (CNN) is used as generator and maps a random vector to a whole trajectory. This framework has been used to simulate mobile data Ouyang et al. (2018), taxi data Wang et al. (2021a) but also free-ranging trajectories such as aircraft Jarry et al. (2021); Aksoy et al. (2021) and animal trajectories Roy et al. (2022). Deep convolutional GANs (DCGAN) are however subject to limitations for reproducing small-scale statistics, and contrary to RNN-based schemes, these GANs also lack some interpretability of the trained latent representations which may lessen their exploitation to address explanatory scientific questions.

## 5.2.2 Lagrangian and Eulerian representations of free-ranging movement

As mentioned in the previous Section, free-ranging trajectories are classically stated as Lagrangian dynamics (5.1). Computationally speaking, a complexity of this Lagrangian formulation lies in the parameterization of the drift  $V()$  and spread operators  $\sigma()$ . Interestingly, this Lagrangian formulation relates to an Eulerian representation through Fokker–Planck (FP) equation or Kolmogorov forward equation:

$$\frac{\partial}{\partial t}p(x, t) = -\frac{\partial}{\partial x}[V(x, t)p(x, t)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[\sigma^2(x, t)p(x, t)] \quad (5.2)$$

where  $p()$  is the probability density function of the position of the moving individuals/objects. Rather than modeling the time evolution of the position of the moving entity, Equation (5.2) states the time evolution of its probability density function Turchin (1998). Thus, we shift the representation from an individual level to a population/group one. The resulting differential equation is a deterministic partial differential equation (PDE) which explicitly involves a drift term and a diffusion term, the latter parameterized by a diffusion tensor depending on the spread operator.

From a learning point of view, we believe this correspondence between Lagrangian and Eulerian representations for movement patterns to be of key interest to design relevant GANs for free-ranging trajectories. Regarding computational issues, Eulerian representations and PDE nicely relate to convolutional architectures as illustrated by studies which explore deep learning architectures for the identification and resolution of PDE Lu et al. (2018); Kim et al. (2019). This appears particularly relevant to improve training performance and address vanishing gradient issues for the simulation of long free-ranging

trajectories. It also supports the identification of spatially-structured latent spaces to represent Lagrangian dynamics. Equation (5.2) suggests a latent representation through the time series of pdf of positions of the object, where the last layer of the generator would map the latent space to a trajectory given by a time series of positions. An extension to multivariate  $2D+t$  latent representations seems appealing to match latent representations classically considered in deep convolutional GANs for image and video generation applications Li et al. (2018); Wang et al. (2020).

### 5.2.3 Reproduction of fine-scale statistical properties

Deep convolutional GANs are yet limited for capturing fine-scale texture as simulated images are often noisy or blurry Goodfellow et al. (2014); Radford et al. (2016), and simulated trajectory failed at reproducing fine-scale statistics, such as step distributions (e.g. speed and turning angle) Roy et al. (2022). Step distributions are yet a key aspect of many trajectory data analyses, notably for the identification of behavioral/transportation mode, for anomalous event detection, and for the specification of area-of-interest Zheng (2015); Feng and Zhu (2016). In animal movement ecology, the structure of a global movement path is even often considered as a reflection of these basic step properties, "in the same way, that the 3D structure of DNA strings is central to the function of a DNA segment" Nathan et al. (2008).

For what concerns image simulation, adding a specific loss to help the generator to identify the texture differences between fake and true images appeared as a promising solution, for instance using perceptual and contextual losses Johnson et al. (2016); Mechrez et al. (2018). A solution is also to use a Markovian discriminator (or PatchGAN) Li and Wand (2016); Isola et al. (2018). The idea is to force the discriminator to focus on high-frequencies, by restricting its attention to local image patches. To classify a global image as real or fake the Markovian discriminator classifies each patch of the image and averages over all responses. Alternatively, other studies used wavelet transformations of the high frequencies of images to be given as input of the discriminator Huang et al. (2020); Zhang et al. (2022). As suggested by Roy et al. (2022), it seems thus relevant to explore such techniques and to adapt them to trajectory data in order to generate multiscale trajectories with heterogeneous behavioral modes.

## 5.3 Proposed GAN framework

This section presents the proposed Fokker-Planck-inspired generator with multi-adversarial framework for the simulation of free-ranging trajectories, the FPGMAN. We first describe the considered neural architectures for the generator and the discriminator (Section 5.3.1) before detailing the training losses (Section 5.3.2) and the evaluation metrics (Section 5.3.3)

### 5.3.1 Model Architecture

**Generator:** Following Fokker-Planck representation (5.2) of Lagrangian dynamics discussed in the previous section, we design a two-stage neural architecture: the first stage aims at generating a time sequence of 2D probability density functions with a 3D-convolutional network, the second stage involves sampling a trajectory from this sequence with a spatially-explicit linear transformation.



The 3D-convolutional network takes as input a random noise vector  $z$  that can be seen as a latent representation of the global trajectory. It is then projected in a reduced spatio-temporal space with low spatial and temporal resolution, which is progressively upsampled and structured through successive 3-dimensional convolutional, normalization and activation layers. When this sequence reaches the required spatial and temporal dimension, a 'softmax' layer is finally applied in order to transform the output of the layer in a sequence of probability densities  $p(x, t|z)$ . It can therefore be seen as a numerical modeling of the evolution of a 2D probability density over time. The generation of a trajectory from this PDF-based representation relies on the spatially-explicit expectation at each time step of the associated pdf according to the predefined grid and space resolution of the considered 2D+T latent space.

Our generator is therefore fully convolutional similarly to the DCGAN previously used for the simulation of free-ranging trajectories Jarry et al. (2021); Aksoy et al. (2021); Roy et al. (2022). It differs however from these approaches on two aspects: (i) the use of a 3D latent embedding and (ii) the use of an explicit linear relationship to sample a trajectory from a sequence of probability densities. In this sense, this architecture brings some additional interpretability of the trained latent representations.

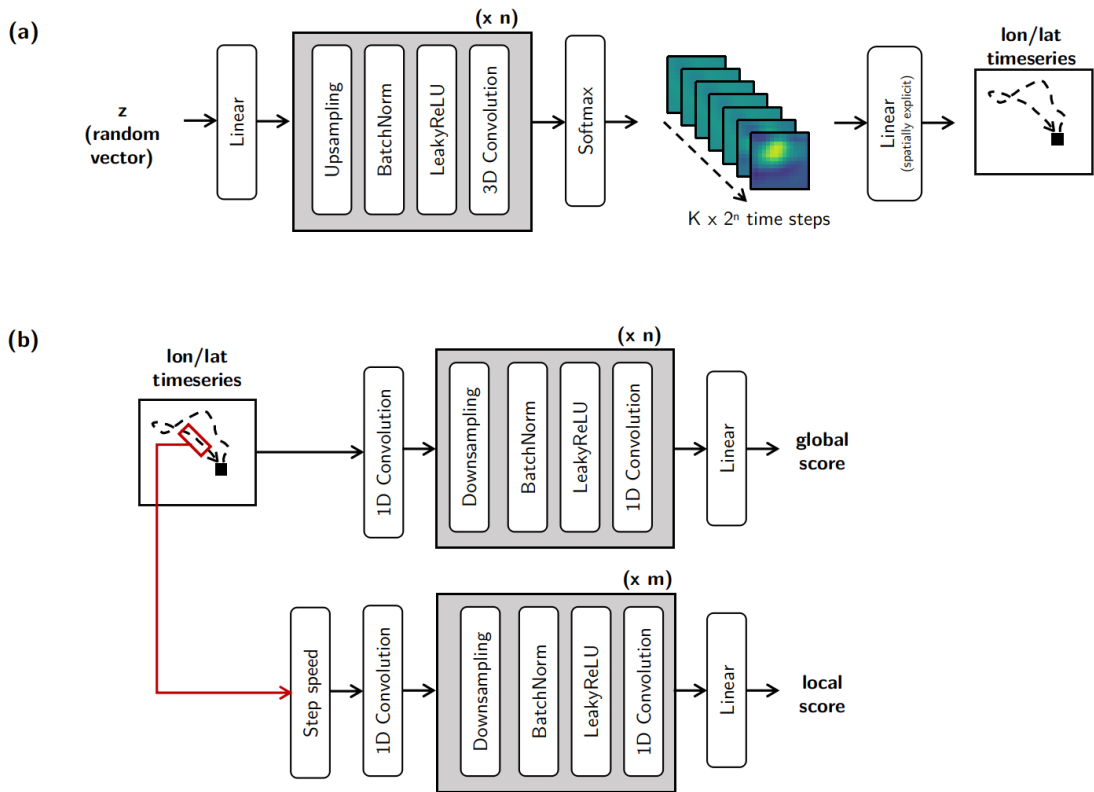


Figure 5.1: **Architecture of the FPGMAN** - (a) Generator ( $G$ ) (b) Multi-Discriminator ( $D_{global}$  and  $D_{local}$ ).  $D_{local}$  is also known as the PatchGAN that only discriminates by sliding a window over the input.

**Multi-Discriminator** To address the limitations of state-of-the-art convolutional GANs to account both for fine-scale patterns, we consider two different discriminators in order

to distinguish fake and real trajectories at different spatio-temporal scales. Training a generative network using feedback aggregated over multiple discriminators is indeed a known solution to achieve faster convergence to a higher quality Durugkar et al. (2017).

Following Demir and Unal (2018), we consider a global discriminator and a local one dedicated to small scale statistics. The global discriminator exploits the architecture used by Roy et al. (2022). It takes as input the whole trajectory  $\xi$  described as a sequence of coordinates, which is progressively downsampled. The local discriminator is similar to a PatchGAN Isola et al. (2018), a convolutional network that takes as input small-time windows of step speed directly computed from each pairs of consecutive two locations, as illustrated in Fig. 5.1.

### 5.3.2 Loss functions

**Adversarial loss** We use a state-of-the-art training procedure in order to handle the mode-collapse problem, namely the hinge-loss-based GAN, with a Lipschitz continuity constraint to the generator and to discriminators through spectral norms (Lim and Ye, 2017; Miyato et al., 2018). It is based on a geometric interpretation of the mean feature matching GAN, that converges to the Nash equilibrium of the minmax game and that minimizes the distance between observed and simulated data defined by the integral probability metric. Analytically, it consists in alternatively optimizing generator and discriminator networks with the following losses :

$$\begin{aligned}\mathcal{L}_{global} &= -\mathbb{E}_{z \sim p_z}[\min(0, -1 - D_{global}(G(z)))] - \mathbb{E}_{x \sim p_{data}}[\min(0, -1 + D_{global}(x))] \\ \mathcal{L}_{local} &= -\mathbb{E}_{z \sim p_z}[\min(0, -1 - D_{local}(G(z)))] - \mathbb{E}_{x \sim p_{data}}[\min(0, -1 + D_{local}(x))] \\ \mathcal{L}_G &= -\lambda_{global}\mathbb{E}_{z \sim p_z}[D_{global}(G(z))] - \lambda_{local}\mathbb{E}_{z \sim p_z}[D_{local}(G(z))]\end{aligned}\quad (5.3)$$

### 5.3.3 Evaluation metrics

The evaluation of GANs' ability to reproduce realistic data is however challenging, and currently is an active area of research Borji (2022). The two most widely used evaluation measures are Inception Score (IS) and Fréchet Inception Distance (FID). In particular, FID is often preferred to IS because it can detect mode collapse, and because it is considered to be relatively consistent with human perception. Mode collapse is a key challenge in GAN training, and it refers to the situation when the generator fails to generate samples as diverse as the distribution of the real-world data. For instance, when it produces very realistic, but identical samples. The FID metric consists in the Fréchet distance between two groups of feature vectors calculated for real and generated images, using the inception v3 model used for image classification. This approach is however specific to the evaluation of generated images. We however lack a similar evaluation scheme for trajectory data. In order to evaluate the performance of GAN we therefore used three metrics: the spectrum metric, the step distribution metric and the context-FID score, which is variant of FID score for time-series.

**Step distribution error** In order to characterize movement trajectory, research in human mobility and animal movement typically focused on the description of elementary steps, possibly considering steps as the DNA of movement data Nathan et al. (2008). Steps descriptors include speed, turning angles and acceleration, which are often associated to specific behavioral and/or transportation modes Seidel et al. (2018); Yang et al. (2018).

In order to evaluate the ability of GAN to reproduce such characteristics, we estimate the L2 distance (i.e. Euclidean) between real and fake joint distribution of step speed and turning angle distributions.

**Spectrum error** Spectral power distributions are usual representations of time-series to assess their frequency properties. In particular, spectral signature of trajectory data has indeed proven useful for statistically detecting and characterizing temporal dependency in movement data Polansky et al. (2010); Zaki and Sayed (2013). Additionally, it has been used as evaluation metric in GAN frameworks dedicated to time-series analysis Hartmann et al. (2018); Roy et al. (2022). Here, we define the spectrum score as the mean squared difference between log power spectral density of real and simulated trajectories, as detailed in Roy et al. (2022). It has been shown to efficiently relate the ability of GAN to reproduce medium- to large-scale characteristics of animal trajectories.

**Context-FID error** The context-FID score has been proposed by Jeha and Mercado (2022), and consists in an adaption of the FID score for time-series. Similarly, it consists in a Fréchet distance between two groups of features vector, but replacing the InceptionV3 with the encoder proposed by Franceschi et al. (2020). This encoder is based on causal dilated convolutions with a novel triplet loss employing time-based negative sampling, and a relevant embedding representation of long time-series Franceschi et al. (2020). It has been trained on both trajectory datasets presented in this study before any other experiments.

## 5.4 Experiments and Results

### 5.4.1 Dataset and Baselines

GPS recorders were fitted to Peruvian boobies (*Sula variegata*, SV) and Guanay cormorants (*Leucocarbo bougainvilli*, LB) during their breeding period at the Pescadores Island, Peru in from 2008 to 2015. This work was conducted with the approval of the Peruvian federal agency, Programa de Desarrollo Productivo Agrario Rural, commonly known as ‘Agrorural’. Headquarters of Agrorural are located at Av. Salaverry 1388, Lima, Peru. Trajectories consist in foraging trips where seabirds look for preys at sea and come back to their colony. Data points have been linearly re-interpolated at regular 1-min time steps, and coordinates have been centered on the colony’s location and normalized. Finally, trajectories have been padded with zeros so that all longitude/latitude time series from a dataset would have the same length of 720 time steps. In this study, trajectories from boobies and cormorants are considered into distinct datasets, hereafter called SV and LB. They are respectively composed of 309 and 71 different trajectories.

**Benchmarked methods** We benchmarked our method w.r.t. to the following state-of-the-art GAN architecture used for trajectory data or other time-series generation:

- **RGAN**, the Recurrent GAN, makes use of RNN both for the generator and the discriminator. It has been widely used to generate temporal data such as medical time-series Esteban et al. (2017), music Mogren (2016), financial time-series Moritz et al. (2021), and trajectory Kulkarni et al. (2018); Feng et al. (2020).

- **DCGAN**, the Deep Convolutional GAN, makes use of CNN both for the generator and the discriminator trajectory. It has been notably illustrated with encephalogram signals Hartmann et al. (2018); Sumiya et al. (2019), smart grids Zhang et al. (2018) and seabird trajectory Roy et al. (2022).
- **TCGAN**, the Temporal Convolutional GAN, makes use of CNN with dilated causal convolutions for the generator and usual convolutions for the discriminator. It has been recently used for generating financial time-series Wiese et al. (2020).
- **SAGAN**, the self-attention GAN was originally designed for image generation Zhang et al. (2019a) and has recently been introduced for time series Jeha and Mercado (2022). It relies on convolutional networks with residual connections and attention mechanisms for both generator and discriminator.

RGAN and DCGAN have already been tested from trajectory data generation. TCGAN and SAGAN are however recent tools from time-series generation that have not been used to generate trajectory data to our knowledge.

## 5.4.2 Training details and implementation

All models have been trained over 1000 epochs using the hinge-based loss presented before, and with a batch size of 32. For all models, we use the Adam optimizer with betas of (0.9, 0.999) and learning rates of  $1e-4$ . While training our networks with the multi-discriminator we set the learning rates for discriminators to  $5e-5$ , and  $\lambda_{global}$  and  $\lambda_{local}$  to 0.1 and 0.9, respectively. Moreover, for numerical stability we alternated the training steps for each discriminator with a training step for the generator. Through the training phase, we selected the 5 best models minimizing the context-FID score. All models in this paper have been implemented using PyTorch Paskze et al. (2019), and code and training data are available on GitHub<sup>1</sup>.

## 5.4.3 Direct Evaluation on performance metrics

Evaluation metrics for all methods are presented in Table 5.1. The recurrent GANs lead to the poorest performance on both datasets, with particularly high context-FID and spectrum errors. This illustrates their inability to reproduce the large-scale properties of long trajectories, and in this case, the looping characteristic of seabird foraging movements. Moreover, despite the fact they are formulated as a sequential process, they also failed at reproducing step distributions, and did not obtain smaller step distribution errors than non-recurrent GANs. Among all networks, our method has produced the trajectories with most 'realistic' trajectories with lowest context-FID score and best step distributions. It has reduced in average by 25.5% step distribution errors and context-FID score of the second-best models. The second-best models after our method in terms of context-FID score are SAGAN and DCGAN on the SV and LB datasets respectively. In particular, it is interesting to note that on the SV dataset the SAGAN is able to substantially improve spectral power distributions of trajectories in comparison to the DCGAN. This is rather consistent with previous studies that pointed out the relevance of attention mechanism to capture long-range dependencies Brock et al. (2019); Zhang et al. (2019a). Finally, the TCGAN obtained systematically worse performance than the

<sup>1</sup><https://github.com/AmedeeRoy/FPGAN>

DCGAN, which suggests that the use of causal convolutions may be ineffective to describe complex movement patterns.

dataset	architecture	step distribution error	spectrum error	context-FID score
SV (n=309)	RGAN	1.45 ± 0.04	8.82 ± 0.15	1.72 ± 0.23
	DCGAN	1.11 ± 0.06	0.24 ± 0.35	0.35 ± 0.19
	SAGAN	1.12 ± 0.03	<b>0.05 ± 0.04</b>	<u>0.31 ± 0.24</u>
	TCGAN	<u>1.11 ± 0.04</u>	0.62 ± 0.50	0.36 ± 0.20
	FPGMAN (Ours)	<b>0.79 ± 0.06</b>	<u>0.07 ± 0.02</u>	<b>0.20 ± 0.02</b>
LB (n=71)	RGAN	1.18 ± 0.08	7.15 ± 0.06	1.9 ± 0.13
	DCGAN	<u>0.87 ± 0.01</u>	<u>0.52 ± 0.16</u>	<u>0.30 ± 0.07</u>
	SAGAN	1.11 ± 0.07	0.87 ± 0.40	0.62 ± 0.20
	TCGAN	1.21 ± 0.02	1.5 ± 0.37	0.91 ± 0.45
	FPGMAN (Ours)	<b>0.65 ± 0.03</b>	<b>0.11 ± 0.04</b>	<b>0.26 ± 0.07</b>

Table 5.1: **Evaluation metrics of benchmark methods on two datasets** - Best (i.e. lowest) values are shown in bold. (SV) stands for *Sula variegata*, Peruvian boobies; (LB) stands for *Leucocarbo bougainvilli*, Guanay cormorants

#### 5.4.4 Ability to reproduce heterogeneous modes

The multimodal nature of animal movement trajectories is directly related to the variety of underlying behavioral modes. To assess the extent to which the proposed GANs capture these modes, we proceeded as follows. We used mixture models of step distributions with four distinct modes supposedly referred to as 'resting', 'diving', 'searching' and 'flying'. Each one consisted in a LogNormal distribution over step speeds and a Von Mises distribution for step turning angle. These models were trained separately on each dataset using a likelihood maximization criterion. They were then further used to segmentate real and fake trajectories generated by our models into distinct behavioral modes. One of the most striking result of our model is its ability to generate 'realistic' trajectories, not only in terms of global morphology, but also in terms of these behavioral modes (see Fig. 5.2). Boobies tend to spend more than half of the time flying during their foraging trips, and perform short and shallow dives. In opposition cormorants spend the majority of their foraging time swimming during long and deep dives. These patterns are well reproduced by our model, because it is able to reproduce the multi-modal step distributions in opposition to benchmark methods, as illustrated in Figure 5.3. The FPGMAN provides thus a significant improvement for free-ranging trajectory generation as it is the only model able to properly identify step speed modes, and to ensure that the motion characteristics of moving individuals are well reproduced.

#### 5.4.5 Interpolation in latent space

By construction GANs map a pre-defined latent distribution from which we sample the  $z$  vector, to the distribution of observed data. Numerous studies have therefore

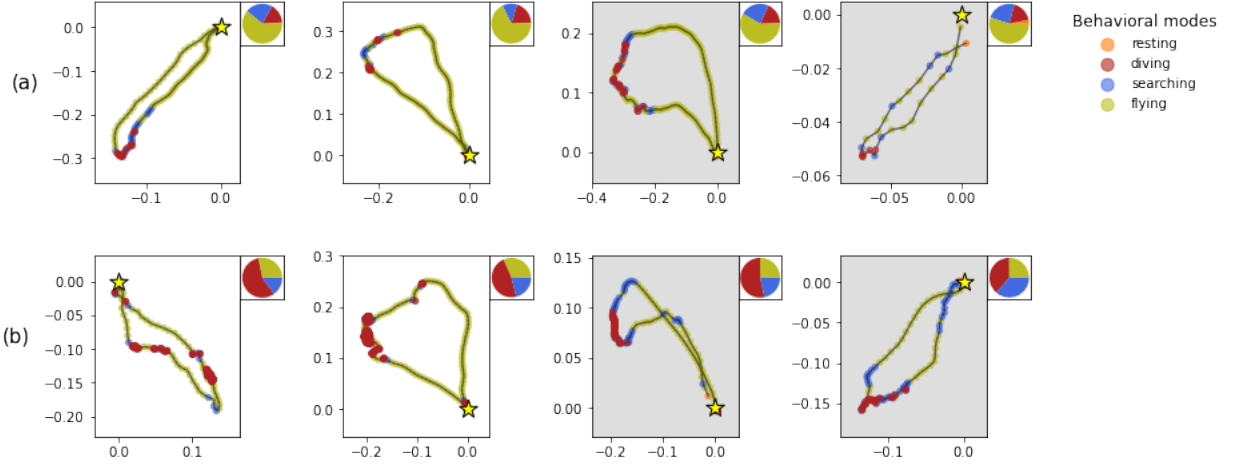


Figure 5.2: **Examples of real and fake seabird trajectories** - Colors correspond to behavioural modes from a model of mixture of speed and turning angle joint distributions fitted on observed trajectories. The star stands for the colony where every seabird trajectories starts and ends. Real trajectories are plotted on a white background, while trajectories generated by our FPGMAN are plotted on a grey background. (a) and (b) stand for the Peruvian boobies (SV) and Guanay cormorants (LB) datasets respectively.

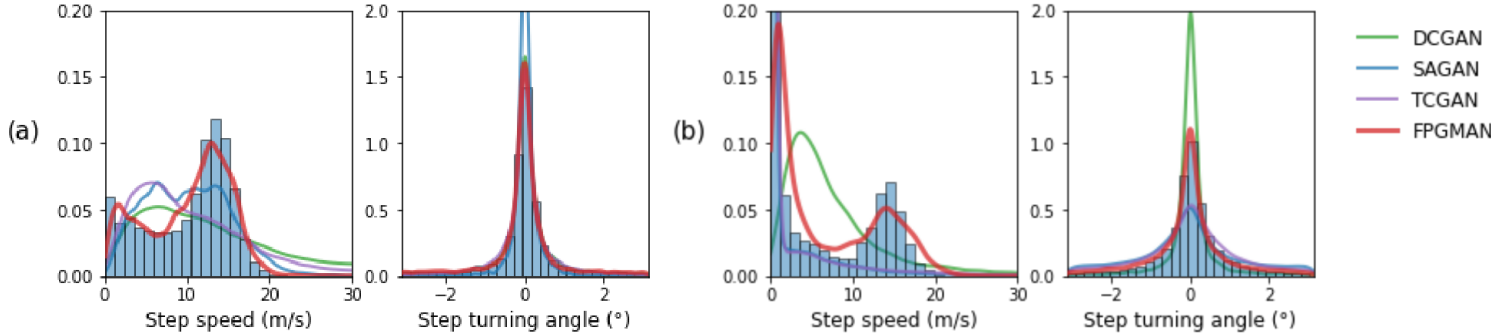


Figure 5.3: **Step distributions derived from real and fake trajectories** - Real step histograms are shown in blue. Simulated distributions estimated using a kernel density estimator. The left panel is for Peruvian boobies trajectories, and the right panel is for Guanay cormorants trajectories. Colors lines show the step distributions of trajectories simulated by the convolutional GAN used in this study.

aimed at exploring this latent distribution, by disentangling factor of variations or by interpolating within the latent space Karras et al. (2019). The measure of how outputs change as we perform interpolation in the latent space, is thus often considered as a proxy for GAN samples quality. Intuitively, perceptual smooth transitions of outputs are indeed supposed to result from a well-structured latent space. The perceptual path length (PPL) is therefore often used to quantify such metric Karras et al. (2019). A usual definition is the following :

$$l_z = \mathbb{E}\left[\frac{1}{\epsilon^2}d(G(\text{slerp}(z_1, z_2, t)), G(\text{slerp}(z_1, z_2, t + \epsilon)))\right] \quad (5.4)$$

Where  $z_1$  and  $z_2$  are sampled from the normal latent distribution, epsilon is fixed

to  $10^{-4}$ , slerp refers to the spherical linear interpolation and  $d(.,.)$  defines some metric distance between generated object. Here we used the Fréchet distance, which is known to be relevant to define similarities between pairs of animal movement trajectories Cleasby (2019). A major drawback of this metric is however that it is unable to identify mode collapse. Figure 5.4 provide an estimation of such metric for the state-of-the-art tools. Surprisingly, the RGAN obtained the smoothest latent space with lower PPL on both datasets. This is probably due to the fact that the training of recurrent GANs experienced a mode collapse characterized by low PPL and high context-FID. However, among convolutional GAN, our FPGMAN obtained best results in terms of both PPL and context-FID. This suggests that our model did not undergo mode collapse and manage to converge to a well-structured latent space. For convolutional GANs we can thus observe a correlation between image quality (context-FID score) and latent space entanglement (PPL metric), which is consistent with previous analyses Borji (2022); Karras et al. (2019). Illustration of trajectories interpolated within the latent space are shown in Fig. 5.4. In particular, it shows not only realistic-looking trajectories, but also smooth transformation from one to another when interpolating into the latent space. Such smooth latent space is then potentially of interest for many further analyses. We could indeed benefit from it for trajectory embedding, reconstruction, and denoising, as it is performed in image in-painting Yeh et al. (2017).

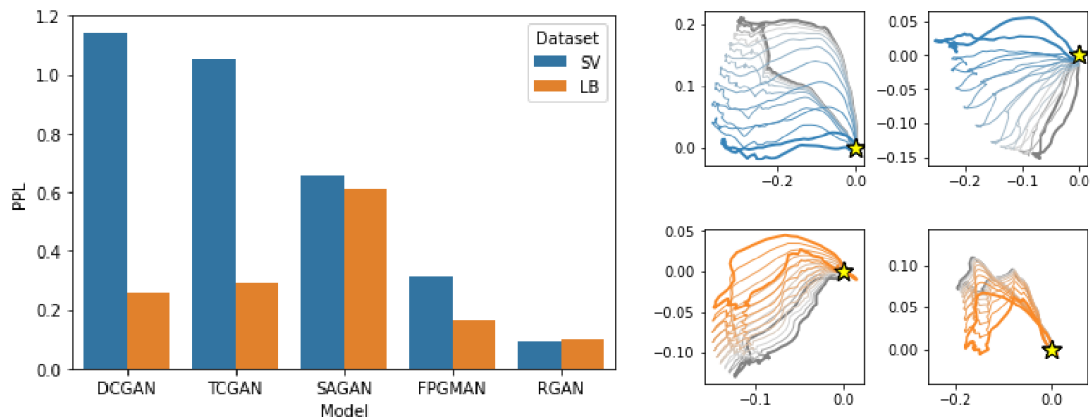


Figure 5.4: **Perceptual length path and interpolation of trajectories in the latent space** The left plot shows Perceptual Path Length metric computed for all state-of-the-art GANs on both datasets. The right plots show examples of latent interpolation between two randomly sampled trajectories for the FPGMAN and for both datasets: SV (blue) and LB (orange).

### 5.4.6 Ablation study

In order to assess the contributions of the different part of our network we performed an ablation study, whose results are presented in Table 5.2. More precisely, we tested the following architectures:

- **w/o 3D** refers to the architecture of FPGMAN but without using a 3D latent space.
- **w/o spatial** refers to the architecture of FPGMAN but without the softmax normalization of the latent space and the associated spatially-explicit linear transformation.

- **w/o local CNN** refers to the architecture of FPGMAN with the step speed time-series directly as input of the global discriminator and without the additional local discriminator.
- **w/ local RNN** refers to the architecture of FPGMAN but with a local discriminator based on RNNs.
- **w/ likelihood loss** refers to the architecture of FPGMAN without the additional local discriminator, but with an additional likelihood-explicit loss. It is defined as the likelihood of the generated step distributions given the mixture model presented in Section 5.4.4

dataset	architecture	step distribution error	spectrum error	context-FID score
SV	FPGMAN (Ours)	<b>0.79 ± 0.06</b>	0.07 ± 0.02	0.22 ± 0.04
	w/o 3D	0.81 ± 0.03	0.34 ± 0.12	1.51 ± 0.21
	w/o spatial	0.88 ± 0.05	<b>0.04 ± 0.01</b>	0.23 ± 0.06
	w/o local CNN	1.41 ± 0.03	0.77 ± 0.16	<b>0.19 ± 0.13</b>
	w/ local RNN	1.46 ± 0.03	0.30 ± 0.15	0.30 ± 0.10
	w/ likelihood loss	1.61 ± 0.03	0.94 ± 0.76	0.39 ± 0.25
LB	FPGMAN (Ours)	<b>0.65 ± 0.03</b>	0.11 ± 0.04	0.26 ± 0.07
	w/o 3D	0.86 ± 0.08	<b>0.09 ± 0.02</b>	0.24 ± 0.13
	w/o spatial	0.73 ± 0.05	0.10 ± 0.07	0.64 ± 0.30
	w/o local CNN	0.82 ± 0.04	0.59 ± 0.23	<b>0.16 ± 0.03</b>
	w/ local RNN	0.88 ± 0.04	0.44 ± 0.18	0.16 ± 0.07
	w/ likelihood loss	0.93 ± 0.03	0.72 ± 0.37	0.68 ± 0.36

Table 5.2: **Performance of the FPGMAN : an ablation study** - (SV) stands for *Sula variegata*, Peruvian boobies; (LB) stands for *Leucocarbo bougainvilli*, Guanay cormorants

The main idea of this work was to construct a GAN inspired from the Fokker-Planck equation. This motivated the use of 3D convolutions and of a spatially-explicit linear transformation from a sequence of pdf to a trajectory. It is interesting to note that these two components were necessary to obtain the best results. The model without 3D latent space obtained a good step distribution metrics, but failed to obtain a low FID score on the SV dataset, while it experienced the opposite on the LB dataset. This suggests that this model encountered numerical instability during training, as it failed to achieve a good trade-off between the distribution and context-FID scores. Furthermore, the model without the spatially explicit linear component observed on average an increase in distribution error of 12% compared to our original FPGMAN. This supports the idea that this component may help the FPGMAN to capture step distributions. However, the key feature of FPGMAN to generate trajectories with relevant statistical properties on a small scale was the use of the local convolutional discriminator. The distribution errors increased by 78% and 26% respectively on the SV and LB datasets when it was removed. It is also worth noting that using FPGMAN with only a global discriminator led to the



lowest context-FID scores. This suggests that when training with multiple discriminators, the FPGMAN has probably experienced a slight collapse mode that caused it to reduce the variability of the simulated trajectories (i.e. implying an increase of context-FID score), in order to ensure the reproduction of the step distribution statistics (i.e. a decrease of the step distribution score). This is supported by the drawing of several examples of trajectories in Figure 5.5. We can observe that trajectories derived from FPGMAN properly reproduce local texture of real trajectories while the ones derived from the 'w/o local CNN' model are too smooth. In opposition, the diversity of large-scale structures of generated trajectories decrease when using multiple adversarial networks and particularly on the LB dataset. This trade-off between quality and diversity is a well known aspect of GAN for image generation Adiga et al. (2018); Brock et al. (2019). GAN training strategies are therefore a hot topic of research in order to improve stability, quality and diversity of generated samples at the same time. It includes notably progressive growing strategies Karras et al. (2018); Jeha and Mercado (2022), and regularization techniques Karras et al. (2020); Saxena and Cao (2021).

In addition, the two tested alternative strategies to capture small-scale texture through the 'w/ local RNN' and 'w/ likelihood' models did not lead to relevant performance. The use of the recurrent local discriminator enable to approximately divide by two the spectrum error, while increasing the step distribution error in comparison to an approach without any local discriminator. Moreover, the model with an additional explicit-likelihood loss based on mixture model, suggested by Roy et al. (2022), led to a decreasing of performance along the three metrics and for both datasets. It is not necessarily because it cannot work, but it is undeniably more difficult and unstable to train. In the end, a local convolutional discriminator that is forced to focus on texture and local-statistics was the best way to capture step distributions. It could therefore be interesting to look for the best size of the time windows used as input of local discriminators, and for best hyperparameter calibration.

### 5.4.7 Illustrations of spatial embeddings

As highlighted in the ablation study, the use of spatially-explicit 3D convolutions helped our model to stabilize during training. This feature is also particularly important to provide visual interpretation of the latent embeddings. In opposition to 1D convolutional GAN, it is indeed possible to visually inspect these latent embedding that consist in maps spatially- and temporally-structured. Before the computation of the sequence of pdf, our generator outputs indeed a sequence of latent maps. Figure 5.6A illustrates example of such maps associated to specific behavioral modes. Although the meaning of these latent maps is abstract, we can identify that distinct behaviors such as 'resting' or 'diving' are associated with high values in specific areas of latent maps, and that the latent structure differ for both datasets. A linear combination of these maps with a softmax normalization enable then the computation of pdf as illustrated in Figure 5.6B. This demonstrates the ability of our architecture to link the propagation of space-time fields using an Eulerian perspective and the generation of associated Lagrangian trajectories. In contrast to most time-series and multivariate signals, trajectory data consists indeed in a process where time and space are intrinsically inter-dependent. This work is therefore a first step towards a model that could generate individual trajectories from the external fields with which they interact. Based on the literature that explored conditional adversarial networks as a general-purpose solution to image-to-image translation problems Isola et al. (2018), we

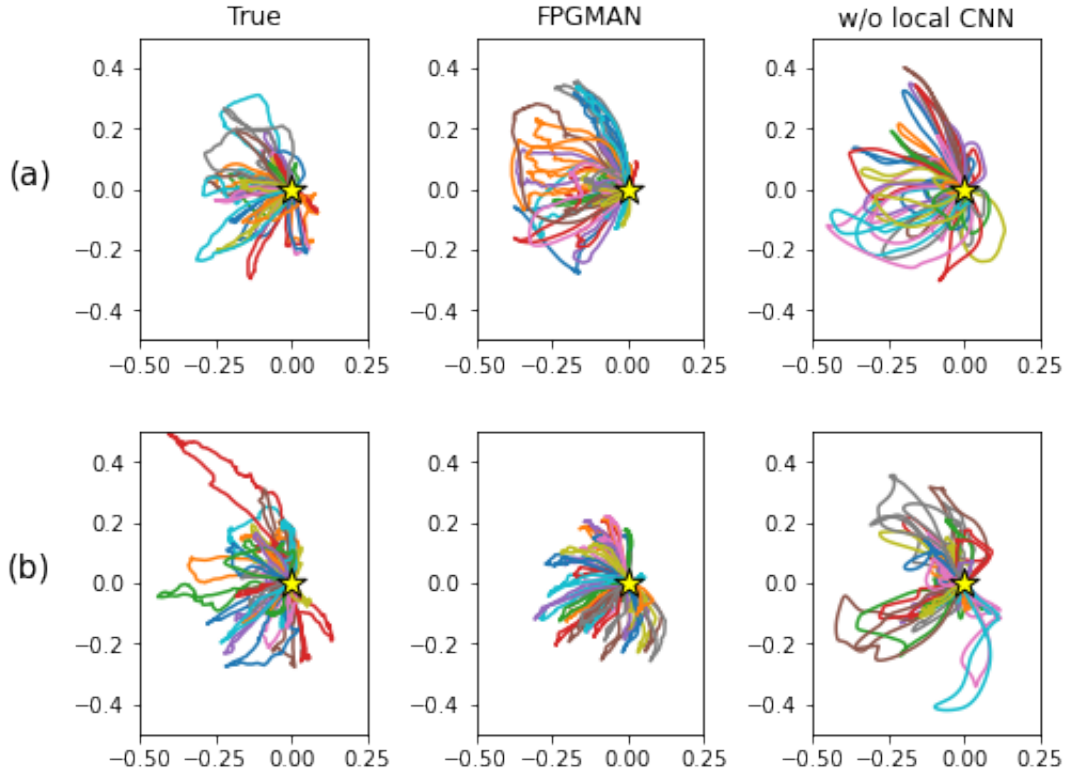


Figure 5.5: **Random selection of seabird foraging real/fake trajectories** - Left, middle and right columns represent a subset of 50 trajectories derived from respectively true observation, FPGMAN and w/o local models. (a) and (b) stands for SV and LB datasets

could explore image-to-trajectory problems and identify the spatio-temporal drivers of distinct movement processes Michelot et al. (2018); Luca et al. (2021).

## Conclusion

We have presented FP-GMAN, a generative multi adversarial networks, that produces long realistic trajectories of free-ranging animal movements using spatially-explicit latent embeddings. Thanks to its convolution layers, it is able to generate long time-series (here, 720 steps) without suffering from exploding or vanishing gradients. Through its multiple discriminators, it enables significant improvement and reproduces key small-scale statistics of trajectories, such as multi-modal distributions of step speed and distributions, which other state-of-the-art GAN do not account for well. It also provides spatially- and temporally-structured embedding maps, which can be crucial for interpretation and for further simulation, such as conditioning trajectories with spatio-temporal dynamic fields. Future work will address these research avenues, for instance for the simulation of seabird trajectories based on the description of oceanographic features.

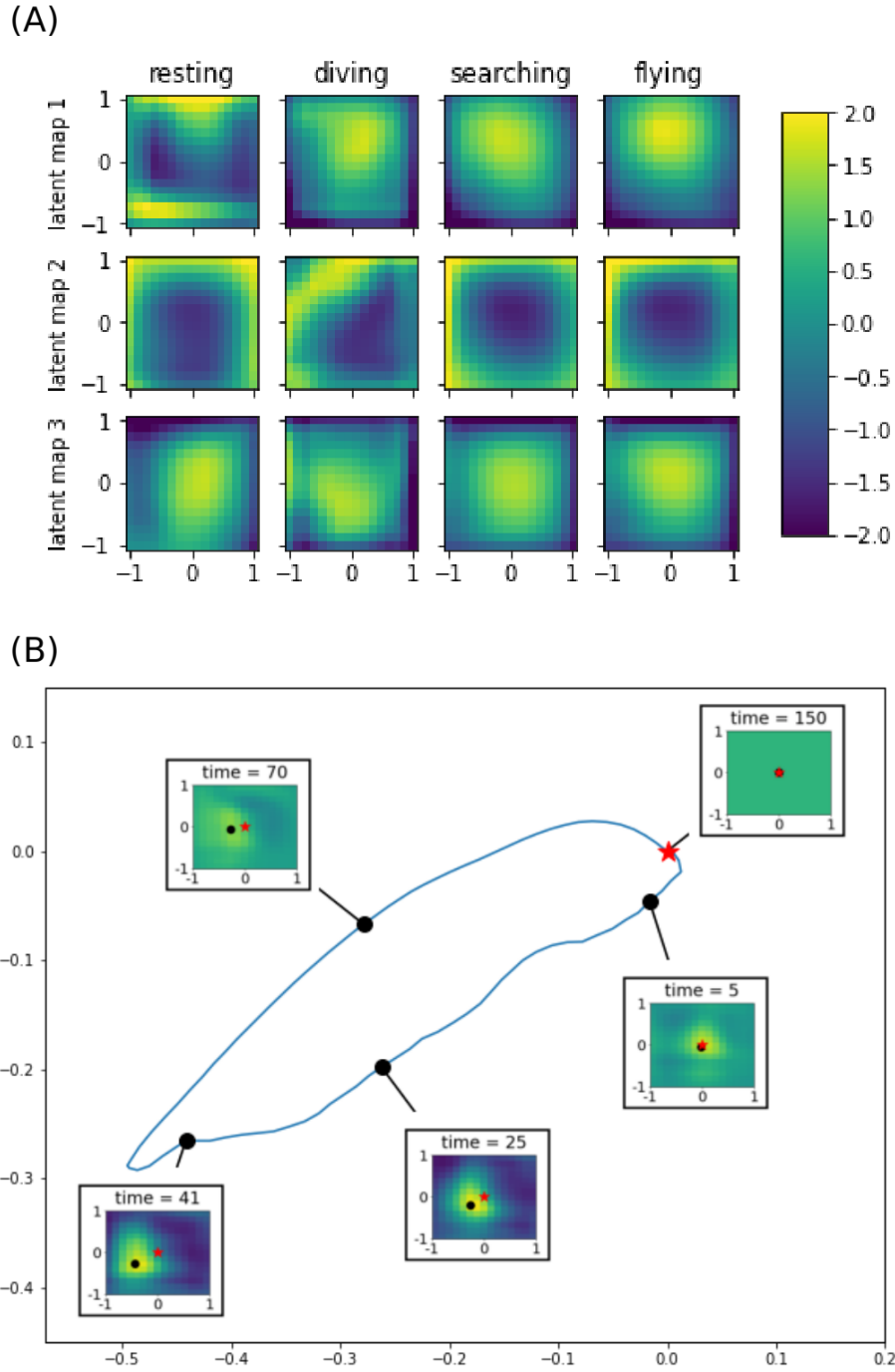


Figure 5.6: **Illustration of spatial embeddings of the FPGMAN** - The FPGMAN generates a sequence of spatially-explicit latent maps. (A) represents such standardized latent maps. These maps have been clustered and averaged according to distinct behavioral modes defined by a mixture model of step distributions. These latent maps are then linearly combined and normalized to output a sequence of probability density functions. (B) illustrates a generated trajectory and some of the associated pdf at distinct time steps

# General Conclusion

♪ *Le roi et l'oiseau*, WOJCIECH KILAR

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This study has introduced deep learning for discriminative and generative tasks to tackle distinct challenges from seabird movement analysis: the identification of breeding and foraging areas, and the simulation of foraging trajectories. We considered different movement processes, including breeding site selection and foraging trajectories for the study of Laridae, Sulidae, and Phalacrocoracidae from three tropical ecosystems. In this general conclusion, we first provide a synthesis, and then we draw perspectives of the deep learning / ecology interface.

## Synthesis

Using discriminative models, we illustrated how convolutional networks are able to automatically extract knowledge from raw data for classifying inputs into distinct categories. It has been applied to image data derived from satellite observation of coastal and marine habitats in Chapter 2, but also to time-series derived from GPS data in Chapter 3. In both cases, trained neural networks enabled to accurately classify new data samples in a systematic manner. For this reason, we have suggested that this makes deep learning tools particularly relevant for ecosystem monitoring and conservation research. Protecting marine ecosystems requires not necessarily to understand the processes underlying movement, which is often a difficult and time-consuming task, but rather to efficiently estimate animal distributions and their habitat uses as accurately as possible, so that it can help managers and policymakers (Evans, 2012; Malde et al., 2020). In Chapter 2, deep learning allowed to improve the automatic identification of potential breeding site of larids from satellite data, which is crucial to evaluate sensitive coastal areas in understudied regions of the world. Moreover, in Chapter 3, the use of relevant deep networks lead to a substantial improvement of the estimation of foraging areas, which are fundamental to the identification of biodiversity hotspots. We have also demonstrated the cross-species and cross-ecosystems generalization properties of deep networks. The transferable deep networks that we trained in Chapter 3 are able to accurately segment trajectories of pantropical Sulidae, and may thus be used throughout the tropical belt. These results motivate the development of 'ready-to-use' networks that could be directly used by marine biologists to predict seabird dives on their new data, without necessarily having to readjust the network parameters.

In addition, we have introduced and illustrated Generative Adversarial Networks (GAN) for the simulation of seabird foraging trajectories. In Chapter 4, we have shown their outstanding ability to reproduce large-scale properties of foraging trips in opposition

to usual tools based on random walks. Several improvements have been proposed in Chapter 5, including the use of multiple discriminative networks in order to improve the step-level statistical properties of simulated paths, as well as the use of spatially-explicit latent representations of trajectories to improve the interpretability of generative networks. We have demonstrated that generative tools are relevant to simulate new data samples, and that they could be used as a null model for testing various ecological hypotheses, such as habitat selection, or social interactions. It can be seen as a bootstrap technique, that would enable to statistically increase the size of existing datasets (Dahl and Sørensen, 2022). This is crucial as the tracking of large numbers of individuals is not often possible for practical or ethical considerations. But more importantly, this unsupervised learning technique provides also a new solution to capture the variability of any dataset. We think that it opens new avenue of research in marine ecology, for modelling, characterizing and predicting complex and multiscale ecological processes, such as animal movement.

## Perspectives

Although deep learning has recently been adopted in ecology and evolution its use has often been limited for studying ecological processes (Borowiec et al., 2022). Deep learning and artificial intelligence concepts have often yields to skepticism about the relevance, opportunities and future of these tools in ecology. The main concern is the difficulty to interpret neural networks, which are typically considered as 'black boxes'. The need for large labelled datasets and high computing power in order to train a neural network is also often used as an argument against deep learning. We however think that it can become a complementary reference tool for ecologists for three main reasons: (1) it relies on the same statistical concepts as usual tools from marine ecology but with higher predictive accuracy, (2) it is flexible to multiscale and heterogeneous raw data inputs and (3) for a given objective function it is able to automatically extract relevant features in an end-to-end framework, which can be valuable for ecologists to identify new interesting metrics. Moreover, recent trends in deep learning focus on the explainability of deep network architectures and on unsupervised approaches to overcome the main limitations cited before. We further discuss three main aspects, namely the explainability of deep networks, the wide variety of existing deep generative models and their potential relevance for developing deep predictive tools.

### On the black box issue

In many deep learning applications, as illustrated in this thesis, the features guiding the network's decisions are poorly understood. For numerous ecological pre-processing tasks such as classification, imputation of missing value, or anomaly detection, using an opaque neural network is often considered acceptable (Breiman, 2001). However, to identify what features play in favor or against the external factors of an ecological process random forests and generalized additive models remain a preferred option, as in Chapter 2 where we used random forests to estimate the contributions of external variables to the suitability of breeding habitats. Yet, there is a growing interest for tools to interpret 'black boxes', using tools such as class activation mapping or layer wise relevance propagation (Montavon et al., 2019; Bae et al., 2020). By taking advantage of the inherent differentiability of deep networks, it is indeed possible to evaluate the influence of small variations in the inputs or outputs on any weight of a neural network, and vice-versa.

Using layer wise relevance propagation on our convolutional neural networks presented in Chapters 2 and 3, we could for instance provide a map of which pixels (resp. location) in the original image (resp. time-series) contribute to the prediction. In addition, self-explainable neural network include deep network architectures that are thought to be interpretable (Alvarez Melis and Jaakkola, 2018). For example, the generative network introduced in Chapter 5 is formulated so that the latent representation of trajectories is spatially explicit and interpretable. This is crucial notably to better identify spatial drivers of animal movement. Similarly, some layers such as attention mechanisms can also deliver useful insights on the contribution of structured data inputs to model predictions (Vaswani et al., 2017).

### Entering the golden age for deep generative models?

Unsupervised learning has often been considered as the future of deep learning (LeCun et al., 2015; Goodfellow et al., 2016). Supervised learning requires labelled datasets which is a core limitation in practice. For instance, many challenges from seabird movement ecology, such as behavioral segmentation of accelerometer data, can not be tackled with supervised learning as true behavioral modes are unknown. For this reason, the deep learning community has experienced a growing interest for generative modelling, and generative adversarial networks in particular. Deep generative models are unsupervised tools, that offer a new framework to capture data distribution and offer new data representation (Goodfellow et al., 2014). In recent years a considerable number of GAN variants have been introduced and illustrated on various applications. We propose here to group together some of them that may be relevant to the study of seabird movements :

- **Conditional GAN** consist of a basic GAN, as exposed in Chapter 4 and 5, but with an additional condition as input to both generative and discriminative networks (Isola et al., 2018). It can be used to disentangle factors of variation of a dataset. For example, we could imagine a habitat model based on a conditional GAN, that would take as input descriptors of the habitat and output 'realistic' tracks with respect to the conditions.
- GANs used in this thesis lack a way to invert the generator in order to map a given observation, to a vector in latent space. It is possible to add such as mechanism, and we refer to it as **GAN with inference models**. This could provide a way to embed data inputs into small latent variables, to be used for further regression or classification tasks. For example, it has also been used to generate data samples from incomplete and noisy data inputs (Demir and Unal, 2018; Li et al., 2019).
- By forcing the discriminator network to output class labels, it is also possible to extend GANs to a semi-supervised context, i.e. when a limited amount of labelled data is available. Such **semi-supervised GANs** have shown interesting properties as they can improve both the performance of a basic classifier, and the quality of samples from a basic GAN (Odena, 2016). This approach is thus eventually relevant to improve the classifiers presented in the part I.

This thesis is therefore a preliminary work to the exploration of the GAN for the analysis of animal movement. We think that many ecological challenges could benefit from all of these GAN variants developed in the deep learning community. Moreover,

current practice in deep learning is to benchmark new network architectures and training algorithms on standard datasets freely available online. Sharing ecological datasets is therefore needed so that both community could benefit from it (Williams et al., 2020).

### Motivating deep predictive ecology

In ecology, predictive approaches consist typically in habitat models that are used to project future animal distributions based on climatic and environmental scenarios. This is a crucial approach to monitor marine ecosystems and their variability. The use of deep networks for such predictive tasks is yet relatively unexplored nowadays, because numerous studies claim that predictive models require more interpretability. Over the last decades, there has been an important debate on the ability of numerical models to predict future states of marine ecosystems. Numerous scientists consider that the explicit understanding of biological mechanisms is fundamental to predict outside the range of conditions for which the process has been directly observed. This opposition between basic but interpretable models and complex but accurate models is interestingly similar to debates that other scientific communities have experienced a few years ago, for instance in computer vision and signal processing.

At the time, numerous scientists were claiming that image processing required some "human knowledge" in the creation of rules, and metrics to describe data. Deep learning has nevertheless caused a disruption in years 2010s by eliminating any explicit modelling of data features, and leading to spectacular results. The sudden success of these approaches is all the more important because it involves a paradigm shift, from hypothetical-deductive to inductive cultures (Breiman, 2001; Cardon et al., 2018). The **hypothetical-deductive** culture rather considers the creation of rules, and the extraction of features from data as a fundamental human input to their analysis, and is the predominant approach in applied ecology. It relies on the assumption that it is possible to identify important features and simple data relationships from data visualization, that reproduce the complex mechanisms observed in the nature (Breiman, 2001). However, the **inductive culture** rather make use of huge parametrized functions such as deep learning tools, based on raw data, and are often considered as data-driven, end-to-end frameworks. In the same way that, by observing nature through thousands of years, humans have tested and theorized numerous physical and biological laws, deep networks converge towards a specific sequence of operations that, without having been explicitly implemented, is the emergent effect of a network being optimized under architectural constraints.

We expect therefore a shift in predictive ecology modelling culture towards deep learning techniques. Deep generative networks have indeed the potential to predict complex natural processes, by fully exploiting the huge amount of available datasets. They consist in a pragmatic solution to provide predictive stochastic models, when mechanistic rules underlying observed processes are unclear and too difficult to be analytically formulated. Moreover, as illustrated by recent advances in physics, they are also flexible enough to combine the advantages of deep networks and theoretical understanding of physical processes in hybrid neural networks (Cai et al., 2021; Ayed et al., 2020). We hope that ecologists will keep following the advances in deep learning and embrace deep networks to address current and future conservation issues.

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# Appendixes

## A. GPS and TDR datasets

The following table regroups tracking data that has been used in this thesis. **Chapter 3** uses joint GPS-TDR deployment on masked boobies, Peruvian boobies and Guanay cormorants. **Chapter 4** uses GPS data deployed on masked boobies, red-footed boobies, and Peruvian boobies (in 2008 only). Finally, **Chapter 5** uses GPS data from Isla Pescadores, Peru.

Table 5.3: GPS and TDR data used in this thesis

Country	Colony	Species	Year	GPS	TDR
Brazil	Fernando de Noronha	SS	2015	12	6
			2016	20	8
			2017	8	2
			2018	4	3
			<b>Total</b>	<b>44</b>	<b>19</b>
		SD	2017	28	13
			2018	16	13
			2019	12	9
			<b>Total</b>	<b>56</b>	<b>35</b>
			Peru	Isla Guanape	SV
<b>Total</b>	<b>46</b>	<b>23</b>			
Isla Pescadores	SV	2008		48	9
		2009		12	1
		2010		45	0
		2011		8	8
		2012		33	27
		2013		16	12
		2015		17	0
		<b>Total</b>		<b>179</b>	<b>57</b>
		LB	2008	16	9
			2009	3	3
2010	11		6		
2011	37		27		
2012	1		1		
2013	28		22		
<b>Total</b>	<b>96</b>		<b>68</b>		



We also develop an R Shiny App in order to explore this dataset<sup>2</sup>. Peruvian boobies and Guanay's cormorants tracked in Peru breed in a highly productive upwelling system, the Humboldt Current System (HCS), and feed on the same prey, namely Peruvian anchovies. However, they are known to have distinct foraging strategies: boobies are divers that average about 2 m in depth and spend most of their time in flight, whereas cormorants dive deeper and longer on average, reaching up to 30 m in depth, and spend up to 40% of the time resting at the water's surface (Weimerskirch et al., 2012). In addition, their social behaviors differ as Guanay's cormorants leave their colony by heading toward groups of other resting birds, whereas Peruvian boobies rely primarily on personal information based on memory to direct their departure (Weimerskirch et al., 2010). Masked and red-footed boobies that breed in Fernando de Noronha have similar diving techniques to the varied boobies of Peru. However, they feed mainly in oligotrophic waters (de Santana Campelo et al., 2019) and feed mainly on fish and flying squid (Mancini et al., 2014). Their foraging strategies then differ from those of the varied boobies, as they make longer trips and spend more time resting at the sea surface (see Chapter 3).



Figure 5.7: **Tracked seabirds** - SS (Top left), SD (Top right), SV (Bottom left) and LB (Bottom right) - Credits H. Weimerskirch and S. Lanco Bertrand

<sup>2</sup><https://amdroy.shinyapps.io/seabirdmap/>