



Influence des facteurs environnementaux sur la répartition et l'abondance de quatre espèces d'oiseaux d'intérêt patrimonial et cynégétique, dans les forêts de Guadeloupe

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Présentée et soutenue par

Aurélie JEAN-PIERRE

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**Influence des facteurs environnementaux sur la répartition et
l'abondance de quatre espèces d'oiseaux, d'intérêt
patrimonial et cynégétique, dans les forêts de Guadeloupe**

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« Si la patience est un chemin d'or, la persévérance est un chemin de diamant. »

Paterne Gnae

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Albert Schweitzer

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RÉSUMÉ

La forêt tropicale abrite aujourd'hui 87% des espèces aviaires connues dans le monde. Or, cet écosystème particulièrement riche de par la diversité de ses biocénoses, est exposée à différentes menaces (déforestation, introduction d'espèces exotiques envahissantes, pollution, surexploitation des espèces, chasse intensive ou encore changement climatique), toutes liées à l'augmentation exponentielle des activités humaines. Ce phénomène touche directement la Caraïbe insulaire, foyer (*hotspot*) de biodiversité mondiale, où l'avifaune forestière compte plusieurs espèces endémiques menacées ou éteintes. Dans ce contexte, les espèces aviaires tropicales insulaires se nourrissant au sol méritent une attention particulière car, bien qu'elles jouent un rôle fondamental dans la dynamique de l'écosystème forestier, très peu de données écologiques fiables sont disponibles pour pouvoir assurer leur conservation, ainsi que leur régulation notamment en lien avec la chasse.

La présente étude visait donc à apporter des éléments scientifiques à la fois fiables et novateurs sur l'écologie de trois espèces de colombidés, la Colombe rouviolette *Geotrygon montana* (statut « préoccupation mineure », avec une population signalée en déclin), la Colombe à croissants *Geotrygon mystacea* (statut « préoccupation mineure », endémique de la Caraïbe, avec une population signalée en déclin) et la Tourterelle à queue carrée *Zenaida aurita* (statut « préoccupation mineure », endémique de la Caraïbe), et d'une espèce de turdidé, la Grive à pieds jaunes *Turdus lherminieri* (statut « quasi menacée », endémique de Dominique, Montserrat, Sainte-Lucie et Guadeloupe).

Dans un premier temps, via le piégeage photographique, nous nous sommes intéressés à l'influence des facteurs biotiques et abiotiques sur la répartition et l'abondance des espèces cibles, dans les forêts de Guadeloupe. Nos résultats ont montré que la Colombe à croissants et la Grive à pieds jaunes affectionnaient la forêt tropicale ombrophile, inversement à la Tourterelle à queue carrée, inféodée aux forêts tropicales sèches et marécageuses. Les effectifs particulièrement faibles observés de la Colombe rouviolette n'ont toutefois pas permis d'étudier de façon concluante l'influence des facteurs sur sa répartition. Alors que l'abondance de la Grive à pieds jaunes était négativement corrélée à l'ouverture de la canopée, celle de la Tourterelle à queue carrée l'était positivement. Nos résultats démontrent aussi que l'abondance de la Colombe à croissants et celle de la Grive à pieds jaunes diminuent avec l'augmentation de la température. Ce résultat est important, compte tenu des prévisions actuelles sur l'évolution du réchauffement climatique. Enfin, nous avons pu observer que la répartition spatiale de différents prédateurs potentiels, en particulier les chats domestiques, *Felis catus*, et la petite mangouste indienne, *Urva auropunctata*, était positivement corrélée à celles de la Colombe à croissants, de la Tourterelle à queue carrée et de la

Grive à pieds jaunes. Sur la base de l'ensemble de ces résultats, et notamment de l'impact potentiel de ces espèces exotiques envahissantes sur les populations aviaires insulaires, nous recommandons un suivi plus régulier de ces espèces aviaires en Guadeloupe.

Dans un second temps, nous avons accordé une attention particulière à l'influence des caractéristiques de la litière sur l'abondance de la Grive à pieds jaunes, de la Colombe à croissants et de la Tourterelle à queue carrée. Nos résultats ont révélé que l'abondance de la Grive à pieds jaunes, principalement insectivore, covariait positivement avec la biomasse d'invertébrés. En revanche, les caractéristiques mesurées de la litière n'ont pas montré d'influence sur l'abondance de la Colombe à croissants ou de la Tourterelle à queue carrée. Dans un contexte mondial de diminution des populations d'invertébrés, il semble opportun de poursuivre ces investigations, afin de mieux comprendre l'étendue de la plasticité alimentaire de la Grive à pieds jaunes, en lien avec les variations saisonnières existantes.

Dans un troisième temps, nous avons comparé l'efficacité de méthodes de recensement classiques et modernes, dans le suivi des populations de Colombe rouviolette et Colombe à croissants. Nos résultats ont confirmé que l'utilisation de la repasse permettait une estimation plus précise de la présence et de l'abondance des espèces cibles. De plus, alors que le recours à des enregistreurs sonores automatisés permettait une meilleure détection de la Colombe rouviolette que le piégeage photographique, aucune différence significative n'a été observée entre ces deux méthodes dans l'estimation de l'abondance de la Colombe à croissants. Il est donc nécessaire de prendre en compte les caractéristiques de l'espèce cible, mais également la variabilité de l'efficacité des méthodes de recensement, dans l'élaboration de tout protocole de suivi aviaire.

Nos résultats soulignent la nette exposition des espèces aviaires insulaires à des facteurs liés à l'activité humaine. Il apparaît nécessaire et primordial de mettre en place un plan de gestion à l'échelle régionale voire caraïbéenne. Ceci permettrait d'améliorer les connaissances sur l'état de conservation des espèces aviaires cibles, dans un contexte insulaire fragilisé par l'anthropisation. Les résultats obtenus au cours de ce travail de recherche constitueraient ainsi un point d'appui pour la mise en place d'un tel plan de gestion.

Mots clés : *Geotrygon montana*, *Geotrygon mystacea*, *Turdus lherminieri*, *Zenaida aurita*, biodiversité, biologie de la conservation, espèces exotiques envahissantes, forêt tropicale, piégeage photographique, région Caraïbe.

ABSTRACT

Tropical forests are home to 87% of the world's known bird species. However, because of the exponential growth of human activities, this particularly biodiversity-rich ecosystem is facing multiple threats (deforestation, introduction of exotic mammals, pollution, overexploitation of species, intensive hunting, and climate change). This phenomenon directly affects the Caribbean islands, the sixth biodiversity hotspot in the world, where the forest avifauna includes several endemic species that are threatened or extinct. In this context, the island's ground-dwelling tropical bird species deserve special attention because, although they play a crucial role in the dynamics of the forest ecosystem, very little reliable ecological data is available to ensure their conservation in relation to hunting.

The aim of the present PhD study was to provide reliable and innovative scientific knowledge on the ecology of three columbid species, the Ruddy Quail-Dove *Geotrygon montana* (Least Concern status, with population reported to be in decline), the Bridled Quail-Dove *Geotrygon mystacea* (Least Concern status, endemic to the Caribbean region, with population reported to be in decline), and the Zenaida Dove *Zenaida aurita* (Least Concern status, endemic to the Caribbean region) and a turdid species, the Forest Thrush *Turdus lherminieri* (Near Threatened status, endemic to Dominica, Montserrat, St Lucia and Guadeloupe).

First, we used camera traps to study the influence of biotic and abiotic factors on the presence and abundance of the target species in Guadeloupe's forests. Our results showed that the Bridled Quail-Dove and the Forest Thrush were more abundant in tropical rainforests, whereas the Zenaida Dove was most often found in dry and swamp tropical forests. However, due to the particularly low numbers of Ruddy Quail-Doves, it was not possible to study the same elements conclusively. Forest Thrush abundance was negatively correlated with canopy openness, whereas the reverse was observed for the Zenaida Dove. Our results also show that the abundance of the Bridled Quail-Dove and the Forest Thrush decreases with increasing temperature. This is an important finding given current predictions on global warming. Finally, we found that the spatial distribution of several potential predators, in particular the domestic cat, *Felis catus*, and the Small Indian Mongoose, *Urva auropunctata*, was positively correlated with that of the Bridled Quail-Dove, the Zenaida Dove, and the Forest Thrush. Based on all these results, and particularly the potential impact of these invasive exotic mammal species on island bird populations, we recommend to improve on the monitoring of these bird species in Guadeloupe.

Secondly, we focused on the influence of litter characteristics on the abundance of the Forest Thrush, the Bridled Quail-Dove, and the Zenaida Dove. Our results show that the abundance of the

Forest Thrush, which is mainly an insectivore, covaried positively with invertebrate biomass. In contrast, measured litter characteristics had no effect on the abundance of the Bridled Quail-Dove or the Zenaida Dove. Given the global decline in invertebrate populations, it seems appropriate to continue these investigations to understand the extent of dietary plasticity of Forest Thrushes in relation to seasonal variation in food availability.

Thirdly, we compared the effectiveness of traditional and modern census methods in monitoring Ruddy Quail-Dove and Bridled Quail-Dove populations. Our results confirmed that the use of playback allows a more accurate estimation of the presence and abundance of the target species. In addition, while the use of automated sound recorders improved the detection of Ruddy Quail-Doves compared to camera traps, no significant difference was found between these two methods for estimating the abundance of Bridled Quail-Doves. It is therefore necessary to consider the characteristics of the target species and the variability in the effectiveness of census methods when designing any bird monitoring protocol.

Our results highlight the clear exposure of island bird species to factors related to human activities. We recommend that local authorities implement a management plan on a regional, if not Caribbean, scale. This would improve knowledge of the conservation status of the target bird species in the context of intense anthropic pressure on tropical island ecosystems.

Keywords: *Geotrygon montana*, *Geotrygon mystacea*, *Turdus lherminieri*, *Zenaida aurita*, biodiversity, camera trap, conservation biology, Caribbean region, invasive exotic mammal species, tropical forest.

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LISTE DES ABRÉVIATIONS

Abréviations en français

CC	:	Colombe à croissants
CR	:	Colombe rouviolette
GPJ	:	Grive à pieds jaunes
PMI	:	Petite mangouste indienne
TQC	:	Tourterelle à queue carrée

Abréviations en anglais

ASR	:	Autonomous Sound Recorder
AV	:	Auditory-Visual method
BQD	:	Bridled Quail-Dove
CB	:	Call-Broadcasting method
CT	:	Camera Trap
FT	:	Forest Thrush
RQD	:	Ruddy Quail-Dove
ZD	:	Zenaida Dove

INTRODUCTION GÉNÉRALE

I. Cadre de la thèse

La perte de biodiversité représente un problème majeur à l'échelle mondiale, et ce, particulièrement en ce siècle présent (Johnson et al. 2017). Cette annihilation de l'ensemble des milieux naturels, de la diversité des formes de vie ainsi que leurs interactions, marque certainement le début de la sixième extinction de masse (Ceballos et al. 2015, 2020). Les activités humaines en sont à l'origine, notamment en raison de la perte d'habitat, la surexploitation des espèces, la chasse intensive et l'introduction d'espèces exotiques envahissantes (Myers 1988; Vijeta et al. 2021). La forêt tropicale est le biome le plus fragilisé par ces facteurs anthropiques. Ces derniers provoquent des dommages souvent irréversibles sur les populations de vertébrés, et en particulier sur les 87% d'espèces aviaires mondiales qui lui sont inféodées (Şekercioğlu et al. 2012). S'interroger sur le devenir des espèces aviaires tropicales insulaires est alors d'une importance cruciale, puisque celles-ci, parfois endémiques, font face à ces facteurs anthropiques tout en étant confinées sur des îles isolées (Milberg & Tyrberg 1993; Steadman 1995; Blumstein & Daniel 2005). Il en découle une probabilité de survie amoindrie, à l'instar de l'extinction de la Dronte de Maurice *Raphus cucullatus*, communément appelée Dodo (Hume 2006). Parmi les îles, la région Caraïbe constitue un point chaud (*hotspot*) de la biodiversité au monde, autrement dit, une région où diversité spécifique et activité humaine se chevauchent largement (Myers et al. 2000). Il n'est donc pas surprenant que bon nombre des espèces aviaires inféodées à la Caraïbe présentent des populations fragilisées (Wunderle 2008; Butchart et al. 2018). Cette situation est particulièrement préoccupante car les espèces aviaires jouent un rôle essentiel dans la dynamique des écosystèmes insulaires, et en particulier, celles qui se nourrissent au sol. Pour exemple, les Columbides majoritairement frugivores et disséminateurs de graines, contribuent largement à la régénération de la forêt (Walker 2007; Ando et al. 2022). Les Turdidés, majoritairement insectivores, se nourrissent d'insectes potentiellement nuisibles et assurent le maintien d'une biodiversité élevée de l'entomofaune (Nyffeler et al. 2018). Bien que la conservation optimale de ces espèces aviaires soit d'une importance capitale dans la Caraïbe insulaire, très peu de données scientifiques fiables sont aujourd'hui disponibles concernant leur dynamique spatiotemporelle, leur abondance ou encore leur écologie.

Fort de ce constat, ce travail de thèse est axé sur l'apport d'éléments scientifiques fiables concernant l'influence des facteurs biotiques et abiotiques sur la présence, l'abondance et la dynamique spatiotemporelle de quatre espèces d'intérêt patrimonial et cynégétique, la Colombe à croissants *Geotrygon mystacea*, la Colombe rouviolette *Geotrygon montana*, la Tourterelle à queue

carrée *Zenaida aurita* et la Grive à pieds jaunes *Turdus lherminieri*, dans les forêts tropicales de Guadeloupe.

Organisation du manuscrit

La thèse par article a été retenue pour le présent manuscrit. L'introduction générale, en français, se décline en 4 parties, incluant le cadre de la thèse, la synthèse bibliographique, l'objectif de la recherche et le site d'étude. Les résultats comprennent 3 chapitres, constitués par des articles scientifiques, en anglais. Enfin, la conclusion générale et les perspectives sont en français.

II. Synthèse bibliographique

II.1. L'érosion de la biodiversité mondiale

La biodiversité, trame vivante de la biosphère, connaît un déclin global sans précédent (Cardinale et al. 2012; Johnson et al. 2017). Cette crise écologique, soulignée par la disparition alarmante d'écosystèmes, de populations, d'espèces végétales et animales, conduit à l'hypothèse d'un processus en cours vers une sixième extinction de masse (Barnosky et al. 2011; Ceballos et al. 2015, 2020; Briggs 2017; Cowie et al. 2022). Lors des cinq précédentes extinctions de masse : la crise de l'Ordovicien-Silurien (-445 Ma), la crise du Dévonien (-370 Ma), la crise du Permien-Trias (-252 Ma), la crise du Trias-Jurassique (-200 Ma) et la crise du Crétacé (-66 Ma), pas moins de 75% des espèces évoluant sur Terre se sont éteintes (Raup & Sepkoski 1982; Harper et al. 2014; Stanley 2016; Isozaki & Servais 2018). Bien que le pourcentage d'extinction spécifique sur les 500 dernières années soit largement inférieur à ce seuil, le rythme de disparition des espèces est exponentiel comparativement à la moyenne d'extinction de ces 10 derniers millions d'années (IPBES 2019).

Plusieurs facteurs, incluant la pollution, la perte d'habitat, la chasse, l'introduction d'espèces exotiques envahissantes, la surexploitation des espèces et le changement climatique sont à l'origine de cette extinction biologique (Myers 1988; Gaikwad & Chavan 2006; Vijeta et al. 2021). En d'autres termes, l'activité humaine, provoquant une destruction du milieu de vie, est le moteur à la fois direct et indirect de l'érosion de la biodiversité, en ce siècle présent. La Terre semble alors être entrée dans une nouvelle époque géologique, l'Anthropocène (Steffen et al. 2011, 2015; Crutzen 2021).

Les vertébrés terrestres sont particulièrement soumis à ce rouleau compresseur, comme en témoignent de nombreux travaux scientifiques (Ceballos & Ehrlich 2002; Ceballos et al. 2015, 2020; World Wildlife Fund 2018; Pinto et al. 2020). Utilisé pour décrire les changements temporels d'état de la biodiversité mondiale, l'Indice Planète Vivante souligne une disparition de 69% des populations de vertébrés suivies entre 1970 et 2018. Ce rythme d'extinction est alarmant, puisque 100 à 1000 fois supérieur au taux naturel d'extinction (Ceballos et al. 2015; Almond et al. 2022). Une récente étude mondiale portant sur les amphibiens, les oiseaux, les mammifères et les reptiles révèle que plus de 500 espèces sont au bord de l'extinction (Ceballos et al. 2020). Ceci concorde avec le récent rapport établi par BirdLife International, soulignant que l'état des oiseaux du monde en 2022 dépeint la situation la plus alarmante pour la nature, à ce jour. Sur 10998 espèces aviaires existantes, 49% (5412) sont en déclin (BirdLife 2022). Parmi les victimes, une majorité d'espèces inféodées aux forêts tropicales.

II.2. Le déclin des espèces d'oiseaux dans les forêts tropicales

II.2.1. La forêt tropicale, un biome fragilisé par les activités humaines

La forêt tropicale est un paysage forestier délimité par le tropique du Cancer et le tropique du Capricorne. Elle est caractérisée par des précipitations annuelles et des températures moyennes élevées ainsi qu'un sol faible en matière organique (Figure 1) (Bashar 2013; Park & Allaby 2013; Butler 2015; Saha 2019).

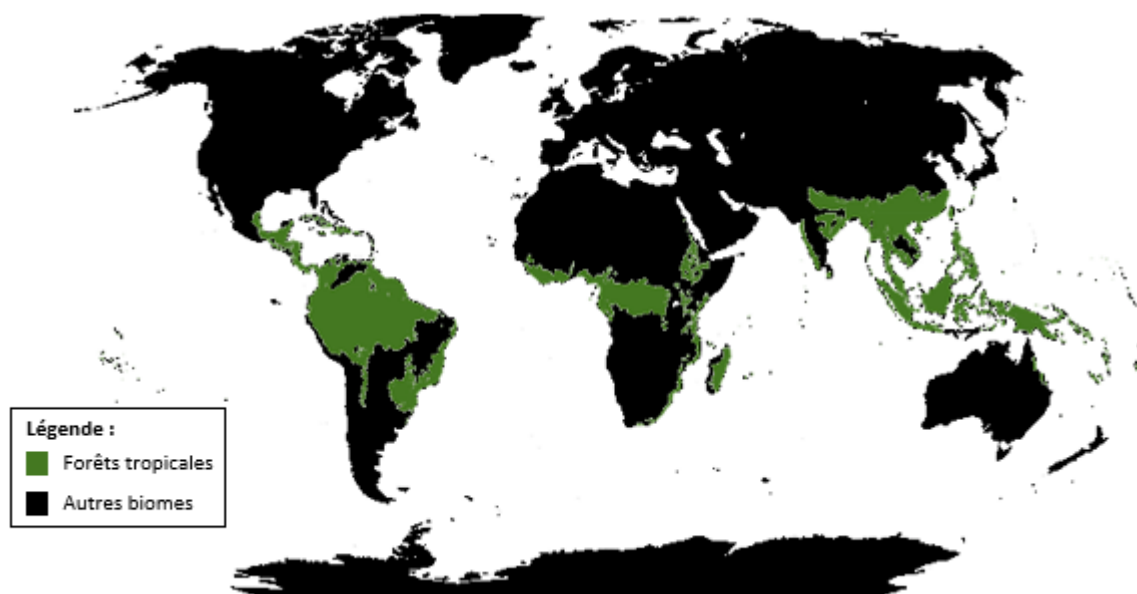


Figure 1. Carte représentant la répartition de la forêt tropicale à l'échelle mondiale (en vert), un puit de carbone hautement vulnérable. Le fond de carte obtenu à partir de Wikipédia (https://fr.wikipedia.org/wiki/For%C3%AAts_d%C3%A9cidues_humides_tropicales_et_subtropicales) a été modifié afin de mettre en évidence la forêt tropicale selon Cole et al. (2014).

Bien que couvrant uniquement 7% de la surface terrestre et 30% de la superficie totale des forêts mondiales, les forêts tropicales abritent environ deux tiers de la biodiversité terrestre mondiale (Myers 1988; Raven 1988; Pimm & Raven 2000; Bradshaw et al. 2009; Nasi 2010). A titre informatif, alors que les forêts d'Europe abritent un maximum de 500 espèces d'arbres, jusqu'à 750 espèces sont retrouvées dans 1 hectare de forêt tropicale (Nasi 2010). Mais, la forêt tropicale est aussi l'un des biomes les plus érodé et fragmenté de la biosphère (Potapov et al. 2008; Sodhi et al. 2011; Malhi et al. 2014), principalement en raison des activités humaines (Geist & Lambin 2002; Wilcove et al. 2013; Laurance et al. 2014; Dávalos et al. 2016). Par exemple, de 2000 à 2012, le taux moyen de défrichement des forêts tropicales était de $91400 \text{ km}^2.\text{an}^{-1}$, ce qui est particulièrement préoccupant. Les zones géographiques les plus touchées étant l'Amérique tropicale, l'Asie tropicale

et l'Afrique (Hansen et al. 2013). Cette dégradation de la forêt tropicale n'est pas sans conséquences sur les populations aviaires, et en particulier sur les espèces insulaires se nourrissant au sol.

II.2.2. La diversité aviaire tropicale menacée

Une grande partie de la diversité aviaire (87%) est inféodée à la forêt tropicale (Sodhi et al. 2011; Sekercioglu 2012). Le déclin des espèces forestières est associé à divers facteurs, tels que la perte et la fragmentation de l'habitat (Feeley & Terborgh 2008; Moore et al. 2008; Korfanta et al. 2012; Newbold et al. 2014a,b; Visco et al. 2015), les espèces envahissantes (Harper & Bunbury 2015; Doherty et al. 2016), la chasse intensive (Sreekar et al. 2015; Benítez-López et al. 2017) ou encore le changement climatique (Şekerciöğlu et al. 2012; Smart et al. 2021). L'action coordonnée de ces différents facteurs concourt à un même phénomène : l'augmentation du taux d'extinction des espèces aviaires tropicales (Brook et al. 2008; Tschardt et al. 2008; Tobias et al. 2013). Ceci est particulièrement alarmant, puisque les oiseaux fournissent de nombreux services écosystémiques tels que la pollinisation, la dispersion des graines ou encore, la lutte antiparasitaire (Sekercioglu 2006, 2012; Wenny et al. 2011).

Le déclin continu des espèces aviaires s'accompagne alors de conséquences écologiques graves (Şekerciöğlu et al. 2004), et ce, particulièrement dans le cadre d'adaptations co-évolutives. Par exemple, les colibris, nectarivores, ont un bec hautement spécialisé, propice à une sélection de plantes à fleurs. Ainsi, la survie de ces deux types d'espèces est dite interdépendante. Cette relation est également retrouvée entre les oiseaux frugivores et les arbres à fruits tropicaux.

II.2.3. La diversité aviaire tropicale insulaire menacée

Les régions tropicales contiennent environ 45000 îles, dont la taille varie de 5 ha à environ 77 millions ha (Arnberger & Arnberger 2001). Le taux d'endémisme des espèces d'oiseaux y est souvent élevé (Myers et al. 2000). Ayant divergé des ancêtres continentaux par isolement, les espèces endémiques se voient généralement confinées sur ces îles, au sein desquels la diversité biologique décroît généralement avec la distance au continent. Il en résulte souvent une perte des comportements de défense face aux prédateurs, la perte ou la réduction des capacités de vol, ou encore une réduction de l'immunocompétence, ce qui rend les oiseaux insulaires particulièrement fragiles (Milberg & Tyrberg 1993; Steadman 1995; Blumstein & Daniel 2005).

L'influence négative de la fragmentation sur les oiseaux insulaires tropicaux est incontestable. Par exemple, sur l'île de Hainan, au sud de la république populaire de Chine, l'abondance des

oiseaux et la richesse des espèces ont connu un déclin phénoménal durant ces 15 dernières années, en raison de la déforestation et du braconnage (Xu et al. 2017). Un constat similaire a été établi sur l'île Sulawesi, en Indonésie (Waltert et al. 2005). Sur l'île de la Guadeloupe, la prévalence des parasites sanguins des genres *Plasmodium* et *Haemoproteus* se voit augmentée chez différentes espèces d'oiseaux en lien avec la fragmentation de l'habitat (Perrin et al. 2023). Des facteurs connexes sont possiblement favorisés par cette fragmentation de l'habitat. Par exemple, sur l'île de Kauai, la plus vieille des îles principales de l'archipel d'Hawaï, la transmission habituellement saisonnière du paludisme s'effectue annuellement en raison de la déforestation (Atkinson & LaPointe 2009; Atkinson et al. 2014). Le tourisme, indispensable à l'économie de certaines îles, peut induire des impacts sanitaires non négligeables sur les espèces aviaires. Par exemple, les bateaux de croisière et les avions seraient à l'origine de la circulation du paludisme aviaire, de l'Équateur continental vers les îles Galapagos (Bataille et al. 2009a,b). Il en est de même dans l'archipel d'Hawaï (Atkinson et al. 2000).

L'introduction d'espèces exotiques envahissantes est également un fléau pour la diversité aviaire insulaire. Les îles sont propices à leur développement, puisque généralement dotées d'une faible superficie, fragmentées et isolées (Doherty et al. 2016). Par exemple, dans les îles Aléoutiennes, les oiseaux de mer constituent une proie pour les renards arctiques introduits (*Alopex lagopus*), ce qui engendre une modification de la structure forestière des îles (Croll et al. 2005). Un autre danger est la dispersion préférentielle de graines d'espèces exotiques végétales par les passereaux envahissants, et ce particulièrement dans les foyers (*hostpots*) de biodiversité mondiale (Mittermeier et al. 2011). Par exemple, en Nouvelle-Calédonie, le Bulbul à ventre rouge *Pycnonotus cafer*, espèce exotique envahissante, disperse des espèces exotiques végétales, ce qui modifie la structure forestière de l'île (Thibault et al. 2018a,b). Le Quinquina rouge *Cinchona pubescens*, est à l'origine de changements drastiques dans la communauté végétale indigène des îles Galápagos, ce qui détruit l'habitat de reproduction du Râle des Galápagos *Laterallus spilonotus* (Shriver et al. 2011).

L'ensemble des facteurs évoqués précédemment peuvent conduire, *in fine*, à l'extinction des espèces aviaires endémiques insulaires. En effet, pas moins de 88% des extinctions d'oiseaux ont été localisées dans les îles tropicales, depuis les années 1600 (Butchart et al. 2006). Parmi eux, la Dronte de Maurice a constitué une proie facile pour les hommes ainsi que pour les espèces exotiques envahissantes (Roberts & Solow 2003; Hume 2006). Le Xénique de Stephens *Traversia*

lyalli, était inféodé aux îles de la Nouvelle-Zélande. La fragmentation de l'habitat et l'introduction des chats sont à l'origine de son extinction (Galbreath & Brown 2004). Le Po-o-uli masqué *Melamprosops phaeosoma*, une espèce de passereau endémique de l'île de Maui à Hawaii, est officiellement éteinte, certainement en raison de l'exploitation forestière, de la récolte du bois et de l'introduction d'espèces exotiques envahissantes (Butchart et al. 2018). L'introduction du Serpent brun arboricole *Boiga irregularis*, sur l'île de Guam, a conduit au déclin puis à la disparition de 17 de ses 18 espèces d'oiseaux endémiques (Wiles et al. 2003).

Parmi les espèces aviaires endémiques des îles, les oiseaux se nourrissant au sol sont particulièrement sensibles aux facteurs anthropiques et ont un taux d'extinction particulièrement élevé (Canaday 1996; Ford et al. 2001; Sigel et al. 2010; Burin et al. 2016). Différents facteurs tels que la faible taille de leur aire de répartition, la perte d'habitat, la grande vulnérabilité face aux mammifères prédateurs introduits, la chasse intensive ainsi que le déclin des populations d'insectes sont à l'origine de leur déclin (Leck 1979; Karr & Freemark 1983; Brash 1987; Greenberg 1987; Kattan et al. 1994; Stouffer & Bierregaard 1995a, b; Canaday 1996; Sekercioglu et al. 2002; Sodhi et al. 2004; Bonnaud et al. 2011; Lewis et al. 2011; Medina et al. 2011; Yong et al. 2011; Morley & Winder 2013; Wilcove et al. 2013; Hervías et al. 2014; Harper & Bunbury 2015; Doherty et al. 2016; Duron et al. 2017a, b; Mansor et al. 2019; Berentsen et al. 2020; Lamarre et al. 2020; Prado et al. 2022a, b).

II.2.4. Le cas de la région Caraïbe, un point chaud (*hotspot*) de la biodiversité mondiale

Le déclin de la biodiversité de la Caraïbe insulaire a commencé avec l'arrivée des premiers Amérindiens (Steadman et al. 1984; Turvey et al. 2007). Il s'est ensuite fortement accentué avec l'arrivée de Christophe Colomb et des européens (Snyder et al. 1987; Brooks et al. 2002). Depuis, la forte croissance démographique humaine et l'activité économique grandissante ont contribué à la réduction de la diversité des espèces, touchant plus particulièrement les espèces aviaires.

La Caraïbe compte 148 espèces aviaires endémiques (Wunderle 2008; Latta 2012). La majorité d'entre elles sont fragiles, en raison de divers facteurs anthropiques (Blockstein 1991; Manne et al. 1999; Wunderle 2008; Arendt et al. 2013; Akresh et al. 2021). La densité de la population humaine est l'un des facteurs les plus néfastes à la diversité aviaire (Cincotta et al. 2000), en raison de la taille limitée des états ou territoires. La dégradation de l'habitat est forte, avec pas moins de 89% des paysages naturels perdus, en raison de l'extension de l'agriculture et de l'urbanisation (Brooks et al.

2002). Ceci est particulièrement observable sur les îles de Cuba, Hispaniola et Jamaïque (Wunderle 2008). A Porto Rico, Vázquez-Miranda et al. (2007) ont montré que l'abondance et la richesse spécifique des oiseaux endémiques diminuaient significativement dans les zones urbanisées comparées à la forêt indigène. Le développement touristique des îles impacte également les oiseaux insulaires. Il est, par exemple, responsable à Sainte-Lucie de la dégradation d'environ 40 % de l'habitat occupé par le moqueur à poitrine blanche *Ramphocinclus brachyurus*, une espèce en voie de disparition (Young et al. 2010).

L'impact négatif des espèces exotiques envahissantes sur les espèces aviaires de la Caraïbe est tout aussi préoccupant. Ainsi, l'Amazone de Porto Rico *Amazona vittata*, est considéré comme en danger critique d'extinction sur la liste rouge de l'UICN, du fait de la concurrence avec les abeilles européenne *Apis mellifera*, pour les cavités naturelles leur servant de nid (Arendt 2000). Le Pétrel de Jamaïque *Pterodroma caribbaea*, est également considéré comme en danger critique d'extinction sur la liste rouge de l'UICN, alors qu'il était très abondant à la fin du XVIII^e siècle. L'introduction de la petite mangouste indienne *Urva auropunctata*, en Jamaïque, dès 1872, serait à l'origine de ce déclin (Collar et al. 1992). Le Moqueur gorge-blanc *Ramphocinclus brachyurus*, retrouvé en Martinique et à Sainte-Lucie, est considéré comme en danger sur la liste rouge de l'UICN. Pour cause, trois ans après l'introduction de la petite mangouste indienne en Martinique (1891), les populations de Moqueur gorge-blanc ont connues un déclin exceptionnel. Malheureusement, cette espèce exotique envahissante, connue mondialement pour son impact non négligeable sur les populations aviaires (Yamada & Sugimura 2004), est bien répartie sur l'ensemble de la Caraïbe (Louppe et al. 2021b). Plus critique, la Tourterelle de Socorro *Zenaida graysoni*, est considérée comme éteinte, possiblement en raison de l'introduction des chats domestiques *Felis catus*, en 1957 (Jehl & Parkes 1983).

L'impact du réchauffement climatique se fait également ressentir dans la Caraïbe (Peterson et al. 2002; Campbell et al. 2011; Karmalkar et al. 2013; Stephenson et al. 2014; Beharry et al. 2015). L'augmentation des températures maximales de janvier à juillet dans les îles bahamiennes (Martin & Weech 2001) et la sévérité de la sécheresse induite, a conduit à une diminution du succès de reproduction de la Paruline de Kirtland *Setophaga kirtlandii*, un oiseau en voie de disparition, hivernant aux Bahamas (Rockwell et al. 2012). De plus, l'augmentation des températures, combinée aux feux incontrôlés, conduit au déclin sans précédent du Bec-croisé d'Hispaniola *Loxia megalaga*, considéré comme en danger sur la liste rouge de l'UICN (Wunderle 2008).

Les catastrophes naturelles sont également susceptibles d'exercer une influence négative sur les oiseaux de la Caraïbe insulaire. À Saint-Kitts, le Père-noir de Saint-Kitts *Melopyrrha grandis*, est considéré en danger critique d'extinction sur la liste rouge de l'UICN en raison de la fragmentation de l'habitat, combinée aux tempêtes et inondations. A Sainte-Croix, 13 ans après l'ouragan destructeur Hugo, la Paruline des ruisseaux *Seiurus noveboracensis*, une espèce de passereau insectivore, spécialiste des zones humides de mangrove, a connu un fort déclin (McNair 2008).

Les espèces de Columbides et de Turdides, se nourrissant au sol et endémiques de la Caraïbe insulaire, sont également menacées par les facteurs précédemment énumérés (Bradley 2000; Walker 2007). Parmi les Columbides, à Porto Rico, le braconnage du Pigeon simple *Patagioenas inornata wetmorei*, et du Pigeon à couronne blanche *Patagioenas leucocephala*, affecte négativement leurs populations respectives (Rivera-Milán et al. 2016). Le Pigeon simple est aussi menacé par les prédateurs exotiques envahissants. En effet, selon Rivera-Milán et al. (2003), la densité des prédateurs diminue significativement le succès de nidification et le nombre de jeunes à l'envol. Enfin, une synergie de menaces anthropiques entraîne le déclin alarmant de la Colombe de la Grenade *Leptotila wellsi*. L'espèce est en danger critique d'extinction, à cause de la déforestation, de la faible couverture de la canopée, ou encore de la prédation par la petite mangouste indienne (Rivera-Milán et al. 2015; Bolton et al. 2016). Parmi les Turdides, le Merle aux yeux blancs *Turdus jamaicensis*, espèce endémique de la Jamaïque, est sensible à la dégradation de l'habitat. Bien que l'espèce ne soit pas considérée comme menacée, sa population est en diminution selon la liste rouge de l'UICN. Sur l'île de Grand Cayman, la disparition du Merle de Grande Caïman *Turdus radivoidus*, est liée aux conséquences d'un ouragan ayant réduit la disponibilité en nourriture dans un contexte de fort isolement géographique (Bradley 2000). Le Merle de la Selle *Turdus swalesi*, espèce endémique de l'île d'Hispaniola, est considéré comme vulnérable sur la liste rouge de l'UICN, avec une population signalée en déclin. Il est particulièrement menacé par la destruction de son habitat (Dávalos & Brooks 2001).

Le déclin des Columbides et des Turdides dans la Caraïbe est particulièrement préoccupant en raison des rôles importants qui leur sont associés. En particulier, les Columbides contribuent à la dispersion des graines et sont, dans certains cas, le seul vecteur par lequel les graines des arbres sont dispersées (McConkey et al. 2004; Meehan et al. 2005; Walker 2007; Wotton & Kelly 2012; Silvina Costán & Sarasola 2017; Ando et al. 2022). Les Turdides, majoritairement insectivores, permettent la régulation des populations d'invertébrés (Van Bael et al. 2003). En particulier,

pendant la période de reproduction, la nécessité de nourrir les oisillons avec des proies riches en protéines entraîne la prédation de milliards d'insectes herbivores, y compris les chenilles et les coléoptères potentiellement nuisibles (Nyffeler et al. 2018). Par conséquent, la gestion et la conservation des populations de Columbides et de Turdides au sein de la Caraïbe insulaire est d'une importance cruciale, notamment en raison de leur rôle majeur dans la dynamique des écosystèmes (Hamann & Curio 1999; Meehan et al. 2002; Van Bael et al. 2003; McConkey et al. 2004; Nyffeler et al. 2018). Néanmoins, très peu de données scientifiques fiables sont aujourd'hui disponibles concernant ces espèces aviaires. Ceci est en partie dû au fait que leur comportement furtif les rend difficilement observables sur le terrain, en plus des difficultés d'accès aux milieux forestiers qu'elles fréquentent.

Afin d'assurer une gestion optimale de ces familles aviaires, l'estimation de leurs paramètres démographiques est un élément essentiel, puisque ceux-ci fournissent de précieuses informations sur l'état de conservation et le risque d'extinction des espèces (Fagan & Holmes 2005). Parmi ces paramètres démographiques, la taille de la population (Fagan & Holmes 2005; Miller et al. 2007). Diverses méthodes ont été développées afin d'estimer efficacement cette dernière.

II.3. Les méthodes de recensement des populations aviaires dans les forêts tropicales

II.3.1. Les méthodes de recensement classiques et leurs limites

Afin d'estimer la taille des populations, des techniques de dénombrement absolues ou relatives peuvent être appliquées (Ferry & Frochot 1958; Fonderflick 1998; Benamammar 2012). Les méthodes absolues consistent à comptabiliser de façon exhaustive les individus à un moment et à un endroit précis (Krebs 1999; Sutherland et al. 2004). Bien que particulièrement précise, cette méthode présente des risques de double comptage et nécessite une certaine immobilité des espèces (Sutherland 2006; Descamps et al. 2011).

Les méthodes relatives consistent à obtenir un aperçu de la taille de la population à l'aide d'indices, de fréquences ou de densités (Krebs 1999; Sutherland 2006). La méthode de Capture-Marquage-Recapture (CMR) consiste à capturer et marquer des individus au sein d'une population, puis à effectuer un nouvel échantillonnage afin de recapter des individus (Krebs 1999). La CMR est largement utilisée pour l'étude d'oiseaux difficilement observables (Sutherland 2006). Bien qu'elle permette une estimation fiable des paramètres démographiques (Chiple 1991; Stouffer & Bierregaard 1993; Seamans & Gutiérrez 2007; Cézilly et al. 2016; Leach & Sedinger 2016), cette méthode nécessite un effort logistique important. De plus, la possibilité de capture est limitée pour

de nombreuses espèces. Qui plus est, l'échantillon obtenu n'est pas forcément représentatif de la population étudiée, si l'efficacité des pièges appâtés utilisés lors de la capture initiale varie avec le degré de néophobie des individus de la population étudiée (Garamszegi et al. 2012; Biro 2013). Des méthodes dérivées de CMR sont parfois préférées, afin de réduire l'effort logistique. La méthode Capture-Mark-Resighting permet d'estimer la taille de la population en évitant de recapter les individus. Pour ce faire, des combinaisons individuelles de bagues colorées doivent être mises lors de la capture. La recapture s'effectue visuellement, ce qui rend la méthode à la fois moins invasive et moins intrusive (Gunnarsson et al. 2005; Henriette & Rocamora 2011; Kentie et al. 2016).

L'échantillonnage par distance de détection consiste à estimer une densité à partir de mesures de distances entre l'observateur et les individus observés, de part et d'autre d'un transect linéaire ou ponctuel (Buckland 2006; Buckland et al. 2008). Le principal biais de cette méthode est lié aux erreurs dans l'estimation des distances (Efford & Dawson 2009). Toutefois, l'emploi de télémètres laser ou de jumelles laser permet de limiter ce biais (Buckland et al. 2004; Buckland et al. 2008; Lee & Marsden 2008; Thomas et al. 2010). De plus, l'échantillonnage par distance peut être assez difficile du fait du caractère discret de certaines espèces aviaires, difficilement observables dans leurs habitats fermés (Chiple 1991; Tayalay 1995; Suwanrat et al. 2015). Enfin, l'efficacité du point d'observation en transect est susceptible de varier au cours d'un cycle annuel, en relation avec les variations saisonnières du comportement des oiseaux (Tayalay 1995; Levesque & Lartigues 2000).

La technique dite de la « repasse » (ou encore du « rappel au magnétophone » Ponce-Boutin et al. 2014) est souvent couplée aux points d'écoute en transect. Elle consiste à diffuser le chant de l'espèce d'intérêt pour induire des réponses comportementales, en particulier lorsque l'espèce d'intérêt est discrète (Sutherland et al. 2004; Sutherland 2006; Kirkpatrick et al. 2007; Fuller et al. 2012). Elle permet notamment d'améliorer sensiblement la détection et l'estimation de l'abondance des oiseaux forestiers (Cambrone et al. 2021).

D'autres techniques, à la fois plus modernes et moins intrusives que les méthodes classiques, ont été développées pour déceler les espèces aviaires rares, furtives et difficilement observables sur le terrain, notamment les pièges photographiques et les enregistreurs sonores (Rowcliffe & Carbone 2008; O'Connell et al. 2011; Rovero et al. 2013; Burton et al. 2015; Jahn et al. 2017; Ducret et al. 2020; Pérez-Granados & Schuchmann 2023).

II.3.2. Les pièges photographiques

Les pièges photographiques sont des appareils photographiques sous forme de boîtier, pourvus d'un objectif grand angle et d'un détecteur, capables de prendre automatiquement des images et/ou des vidéos de sujets passant devant eux (O'Connell et al. 2011; Rovero et al. 2013; Rovero 2016). Ils sont conçus pour rester dans un état de veille électronique quasi-complet. Le détecteur, généralement à infrarouge passif (PIR), reste activé en permanence. Lorsque ce dernier détecte un mouvement, le piège photographique déclenche une suite d'actions afin d'obtenir la capture. Ces actions dépendent des paramètres initialement établis.

Le piège photographique, outil innovant, permet d'obtenir des données écologiques fiables sur une large gamme d'espèces, des plus communes aux plus rares, des plus discrètes aux plus facilement observables (O'Connell et al. 2011; Meek & Pittet 2012). La présence humaine n'est pas nécessaire, puisque la plupart des appareils sont autonomes, fonctionnant possiblement jour et nuit, et sans surveillance pendant plusieurs semaines, voire plusieurs mois (Rovero & Marshall 2009; Rovero 2016).

Le développement de suivis standardisés dans une large gamme d'habitats, parfois difficiles d'accès, devient alors possible et permet d'améliorer la compréhension de la dynamique des populations ainsi que du fonctionnement des écosystèmes (Chancel 2016). Les domaines d'utilisation sont variés, tels que : l'inventaire des espèces en une zone donnée (O'Brien & Kinnaird 2008; O'Brien Kinnaird 2011; Ancrenaz et al. 2012; Ramesh et al. 2012; Silva-Rodríguez & Sieving 2012; Kukiélka et al. 2013; McDonald et al. 2015; Payne et al. 2016; Zapata-Ríos & Branch 2016), l'étude des variations démographique et spatiale des espèces (O'Connell et al. 2011; Sollmann et al. 2013; Spehar et al. 2015; Suwanrat et al. 2015) ou encore l'étude de leur comportement (O'Brien & Kinnaird 2008; Linkie & Ridout 2011; Ramesh et al. 2012; Huang et al. 2014; Suselbeek et al. 2014; Zapata-Ríos & Branch 2016).

Ces dernières années, l'essor de l'utilisation des pièges photographiques dans les domaines de l'écologie et de la biologie de la conservation est sans conteste (Rowcliffe & Carbone 2008). Pour preuve, pas moins de 6009 articles, basés sur cette méthode de recensement, ont été publiés de 2010 à 2023, selon le moteur de recherche Web of Science (date de consultation : 08/10/2023). Elle est particulièrement adéquate pour l'étude de l'avifaune forestière et de ses prédateurs potentiels, en milieu tropical. Plus précisément, le piégeage photographique s'est révélé efficace pour étudier l'organisation de réseaux frugivores (Campos et al. 2012, 2018; Carreira et al. 2020), les rythmes d'activité de certaines espèces (Selvan et al. 2013; Roncal et al. 2019; Fontúrbel et al. 2020; Dahya

et al. 2023), la diversité aviaire (Samejima et al. 2012; Roncal et al. 2019; Santos-Moreno et al. 2019; Antunes et al. 2022), la distribution des communautés aviaires (Samejima et al. 2012; Mugerwa et al. 2013; Roncal et al. 2019), la dynamique spatio-temporelle (de Martins et al. 2006; Ahumada et al. 2011, 2013; Samejima et al. 2012; Suselbeek et al. 2014; Beaudrot et al. 2016, 2019; Rovero & Ahumada 2017), le comportement des espèces aviaires (Delgado-Martínez et al. 2018; Delgado-Martínez et al. 2022) ou la sélection de l'habitat par les espèces aviaires (Selvan et al. 2013; Suwanrat et al. 2015; Murphy et al. 2018; Roncal et al. 2019; Fontúrbel et al. 2020; Malhi et al. 2021; Flatt et al. 2022).

Le piégeage photographique s'est aussi révélé d'un grand intérêt pour surveiller les espèces rares et menacées (Dinata et al. 2008; O'Connell et al. 2011; Mugerwa et al. 2013; Suwanrat et al. 2015; Smith et al. 2017). Par exemple, le Coucou terrestre de Sumatra *Carpococcyx viridis*, une espèce considérée comme en « danger critique » sur la liste rouge de l'UICN, a pu être détecté grâce à cette technique, alors même qu'il avait été vu pour la dernière fois en 1916 (Dinata et al. 2008). Le piégeage photographique permet également de suivre des expériences de compréhension des relations proie-prédateur (Fernandez et al. 2019).

Bien que cette méthode permette l'obtention d'une grande quantité de données en relativement peu de temps, son principal inconvénient est le temps consacré à la reconnaissance visuelle des individus sur chaque capture, ce qui en fait, au final, une méthode assez chronophage (O'Connell et al. 2011). De plus, seule une partie des captures est utilisée, puisque les autres sont des captures vierges, dites « faux-positif ». Il existe également, durant la phase d'acquisition, un risque de dysfonctionnement du piège photographique, entraînant la perte irréversible de données (O'Connell et al. 2011). La faune, interagissant avec son environnement, n'est pas insensible à cette méthode. Ainsi, le choix du flash est primordial, afin de ne pas effrayer ou déranger les sujets (Meek et al. 2014). De plus, l'appareil peut causer des sons qui leur sont audibles (Meek et al. 2016). Certains animaux, capables de préhension peuvent désorienter, dérégler, détériorer, voire détruire le piège (Jordan et al. 2011; Gregory et al. 2014). Inversement, des réactions d'évitement du site peuvent être développées par les animaux, en réponse au dépôt d'odeur lié à la pose de l'appareil (Delmas 2016). Ceci ne semble toutefois pas concerner les reptiles et les oiseaux (Shriver et al. 2011). Les hommes peuvent également désorienter ou dérégler les appareils, par simple curiosité (Wang et al. 2015). Enfin, des actes de vandalisme ou de vol peuvent perturber l'emploi des pièges photographiques (Espartosa et al. 2011; Ancrenaz et al. 2012; Forsyth et al. 2014). Outre les pièges

photographiques, les enregistreurs sonores constituent également une méthode de recensement efficace.

II.3.3. Les enregistreurs sonores

La bioacoustique est une discipline scientifique fondamentale dans le domaine de la conservation, combinant l'éthologie, la physiologie, la neurobiologie, ou encore, la biomécanique (Pijanowski et al. 2011; Towsey et al. 2014; Ozga 2017). Fondamentalement, elle étudie le comportement acoustique, à travers l'émission, la propagation et la réception du son produit par les espèces animales (Frommolt & Tauchert 2014; Sueur et al. 2014). Ces dernières décennies, l'essor important que connaît cette discipline est en lien avec le développement de méthodes et d'outils permettant l'enregistrement, l'analyse et le traitement des signaux acoustiques (Société Française d'Acoustique 2010). Les suivis acoustiques nécessitent ainsi l'emploi de microphones, d'enregistreurs et de logiciels dédiés à la lecture et à l'analyse des sons (Obrist et al. 2010).

L'enregistreur sonore est un outil essentiel dans le suivi des espèces animales caractérisées par leur caractère farouche et les milieux denses et difficiles d'accès qu'elles fréquentent (Mcgregor et al. 1997; Acevedo & Villanueva-Rivera 2006; Obrist et al. 2010; Mennill et al. 2012; Marques et al. 2013; Ulloa et al. 2016; Frommolt 2017; Thomas et al. 2017). Il permet l'étude du comportement, de la richesse spécifique, de la distribution ou encore des cycles temporels de l'activité acoustique des espèces (Harris et al. 2016; Gasc et al. 2017; Jahn et al. 2017; Pérez-Granados & Schuchmann 2023). La surveillance se réalise en toute discrétion, sans déranger les espèces étudiées (Digby et al. 2013; Hedley et al. 2017). Cette méthode permet également la simplification de la réalisation d'études multi-spécifiques (Mcgregor et al. 1997; Bower & Clark 2005; Terry et al. 2005; Heupel et al. 2006; Mennill et al. 2006, 2012; Marques et al. 2013; Griffin et al. 2015; Spillmann et al. 2015). En outre, le suivi des espèces est rendu plus efficace, puisque de nombreuses données fiables peuvent être collectées, sur de courtes ou de longues périodes (Acevedo & Villanueva-Rivera 2006; Obrist et al. 2010; Huetz & Aubin 2012; Digby et al. 2013; Hedley et al. 2017). Celles-ci peuvent être stockées pour des vérifications ou des analyses ultérieures (Borker et al. 2015).

Cependant, différents facteurs, tels que le bruit ambiant, la végétation, la distance séparant la source du microphone et les conditions météorologiques peuvent être à l'origine de la dégradation du son et donc la non-détection des espèces (Richards & Wiley 1980; Mcgregor et al. 1997; Buaka Muanke & Niezrecki 2007; Obrist et al. 2010; Huetz & Aubin 2012; Mennill et al. 2012; Digby et al. 2013; Frommolt & Tauchert 2014; Spillmann et al. 2015; Stepanian et al. 2016). Une autre limite à

l'utilisation de microphone est la perte de sensibilité. Selon une étude de Turgeon et al. (2017), la probabilité de détection de toutes les espèces étudiées serait extrêmement liée à la sensibilité de l'appareil. Une solution serait de visiter régulièrement les microphones afin de les remplacer en cas de perte de sensibilité. La grande quantité d'enregistrements sonores générés nécessite aussi un temps d'écoute et d'analyse assez long. Le caractère initialement chronophage de la méthode tend cependant à diminuer grâce aux progrès accomplis dans la reconnaissance automatisée des espèces animales (Acevedo & Villanueva-Rivera 2006; Shonfield & Bayne 2017; Frommolt 2017). Néanmoins, la quantité d'enregistrements sonores est dépendante de la capacité de stockage et de la longévité des batteries, parfois limitées (Acevedo & Villanueva-Rivera 2006; Obrist et al. 2010; Shonfield & Bayne 2017).

II.3.4. Des méthodes classiques aux méthodes modernes

La surveillance acoustique automatisée et les points d'écoute en transect ont été souvent comparés dans la littérature. Dans le cadre d'études sur les communautés aviaires, tandis que certains chercheurs considèrent que les deux méthodes produisent des données équivalentes et donc redondantes (Sedláček et al. 2015; Alquezar & Machado 2015), d'autres soulignent une complémentarité de ces méthodes et recommandent de les utiliser en tandem. En effet, leur force et leur faiblesse semblent se compenser (Celis-Murillo et al. 2012; Leach et al. 2016).

Plus précisément, les enregistrements sonores sont préférés aux points d'écoute en transect lorsque la richesse spécifique est élevée et les points d'écoute en transect sont préférés aux enregistrements sonores pour la détection des espèces rarement entendues (Haselmayer & Quinn 2000). A contrario Darras et al. (2018) estiment que la surveillance acoustique automatisée est plus efficace que les points d'écoute en transect, car elle se déroule de manière normalisée, vérifiable et exhaustive. Elle permet un échantillonnage continu dans des régions parfois difficiles d'accès, sans biais liés aux observateurs et aux perturbations humaines. Enfin, l'étude approfondie des enregistrements permet la détection d'espèces animales rares.

En conclusion, les points d'écoute en transect, la surveillance acoustique automatisée ou encore les pièges photographiques sont des méthodes essentielles pour la surveillance des espèces aviaires, en milieu tropical. Néanmoins, certains critères doivent être pris en compte afin de choisir la méthode la plus appropriée aux objectifs de l'étude (Zwerts et al. 2021).

III. Objectifs de recherche

Face au besoin de connaissances écologiques fiables sur les espèces aviaires se nourrissant au sol, en particulier en forêt tropicale caraïbéenne, mon travail de thèse avait pour objectif d'étudier l'influence des facteurs biotiques et abiotiques sur la présence, la dynamique spatiotemporelle et l'abondance de la Colombe à croissants *Geotrygon mystacea*, la Colombe rouviolette *Geotrygon montana*, la Tourterelle à queue carrée *Zenaida aurita* et la Grive à pieds jaunes *Turdus lherminieri*, espèces d'intérêt patrimonial et cynégétique, dans les forêts tropicales de la Guadeloupe. Pour répondre à nos objectifs, nous avons successivement utilisé les pièges photographiques, les enregistreurs sonores et les points d'écoute en transect couplés à la « repasse ». Les principaux objectifs de la thèse sont déclinés au sein des différents chapitres.

Dans le **premier chapitre**, sont présentés les facteurs environnementaux affectant l'occupation spatiale et l'abondance locale des espèces précitées.

Dans le **deuxième chapitre**, nous évaluons le compromis entre la recherche en nourriture et le potentiel risque de prédation pour la Grive à pieds jaunes *Turdus lherminieri*, la Colombe à croissants *Geotrygon mystacea* et la Tourterelle à queue carrée *Zenaida aurita*.

Dans le **troisième chapitre**, nous nous focalisons sur l'efficacité des méthodes classiques et des méthodes modernes dans l'estimation de la détection de la Colombe rouviolette et de la Colombe à croissants, en relation avec divers facteurs environnementaux.

IV. Description de la zone d'étude

La Guadeloupe est caractérisée par la grande diversité de ses sols et de ses forêts, ainsi que par celle de ses microclimats. Ces paramètres sont à l'origine de nombreux habitats, notamment occupés par les espèces animales étudiées.

IV.1. Géographie et climat

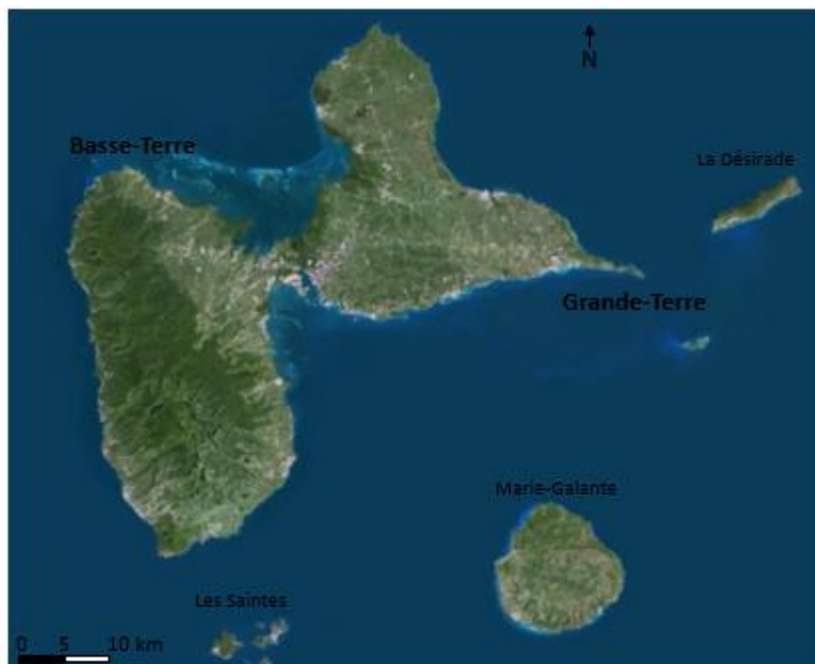


Figure 2. Carte de la Guadeloupe tirée de la plateforme Géoportail.

Archipel des Petites Antilles, la Guadeloupe est composée de deux îles principales accolées, séparées par un étroit chenal, la rivière salée. Tandis que l'île de la Basse-Terre (848 km²) est montagneuse, l'île de la Grande-Terre (586 km²) est à la fois plus basse et plus plane. Les autres îles composant cet archipel sont Marie-Galante (152 km²), La Désirade (22 km²), Petite-Terre (2 km²) et Les Saintes (19 km²). Des petits îlots sont également présents (Figure 2).

L'île de la Grande- Terre, vaste plateau calcaire de la Guadeloupe, présente une géographie, une géologie et un climat particulier, décrit par Lasserre (1961). Elle bénéficie d'un climat plus sec que la Basse-Terre, avec une végétation beaucoup moins dense, dite xérophyte. Des côtes rocheuses constituent son littoral, accompagnées de plages de sable blanc. Des mangroves et forêts marécageuses y sont également observables. La Grande-Terre s'élève à une altitude moyenne d'une centaine de mètres. Elle se résume à des espaces densément urbanisés, entrecoupés par de vastes étendues de terres défrichées pour les cultures maraîchère et vivrière et le pâturage, ainsi qu'une forêt sèche secondaire à forte valeur écologique.

L'île de la Basse-Terre résulte d'une activité volcanique importante engendrée par un phénomène de subduction. Ainsi, elle représente la partie émergée d'une vaste chaîne volcanique située sur le chevauchement des plaques tectoniques. Elle possède le volcan le plus haut des petites Antilles (1467 m), la Soufrière, surnommée aussi *la vieille Dame* (Gadalia et al. 1988).

A travers ce contexte géologique particulier, l'île de la Basse-Terre, vivier écologique, abrite d'immenses forêts extrêmement variées, dont une partie est protégée par le Parc National de la Guadeloupe (créé par décret n°89-144 du 20 février 1989 et couvrant une superficie totale de 21 000 hectares), et demeurant aujourd'hui peu modifiée par les activités humaines. Ces diverses

structures forestières résultent des conditions édapho-climatiques rencontrées le long des gradients d'altitude ou d'aridité du territoire (Rousteau 1996; Laere et al. 2016). Ainsi, la forêt ombrophile est rencontrée sur les pentes de la Soufrière, et est substituée par la forêt d'altitude vers le sommet, toutes deux bercées de pluies abondantes.

Les variations spatiale et temporelle de pluviométrie à l'échelle de la Guadeloupe façonnent trois types de paysages, allant de milieux secs à hyper-humides. Elles confèrent à la Guadeloupe un climat de type tropical insulaire à deux saisons : la saison sèche de décembre à juin et la saison pluvieuse de juillet à novembre (MDDEE 2012).

IV.2. Pédologie

Comme en témoigne sa carte pédologique simplifiée (Cabidoche 1997), la Guadeloupe est dotée de sols diversifiés, dont l'andosol, le ferralsol, le nitisol et le vertisol. L'andosol, développé sur des dépôts volcaniques récents, est principalement retrouvé dans les milieux à forte pluviométrie, à l'instar du sud Basse-Terre. Il se compose majoritairement d'allophanes qui exercent une forte protection de la matière organique (MO), le plaçant parmi les sols les plus riches en MO de la planète (Sierra & Desfontaines 2018). Le ferralsol, développé sur des dépôts volcaniques anciens, est principalement retrouvé au centre et au nord de la Basse-Terre. Il se compose majoritairement d'oxyhydroxydes de fer et d'argiles. Ce sol est particulièrement résistant à l'érosion, en raison d'une infiltrabilité de l'eau et une stabilité structurale élevées (Cabidoche 2011). Le nitisol est semblable au ferralsol, mais est plus jeune et moins évolué que ce dernier. Il est principalement retrouvé au pied des régions volcaniques, au sud de la Basse-Terre. Sa teneur en cations (Ca^{2+} , Mg^{2+} et K^{+}) est plus élevée que le ferralsol (Sierra & Desfontaines 2018). Enfin, le vertisol est lié à un climat subhumide à saison sèche marquée. Il se développe sur des roches sédimentaires ou volcaniques anciennes et est donc retrouvé principalement en Grande-Terre et Côte-sous-le-vent. Il s'agit d'un sol très riche en argile du type 2/1 (argiles « gonflantes »), contenant une couche d'oxyde d'aluminium enserrée par deux couches de tétraèdres de silice. De plus, il est riche en cations et son pH légèrement basique.

IV.3. Végétation

Au total, la couverture forestière de la Guadeloupe est d'environ 74500 hectares, soit près de 40% du territoire (Fournet 2002; MDDEE 2012; Magnin 2018). Les conditions géologiques, altitudinales et pluviométriques de la Guadeloupe génèrent des forêts extrêmement diversifiées.

Les formations inondables (7614 ha), caractérisées par les mangroves et les forêts marécageuses, s'étendent des espaces côtiers jusqu'à quelques mètres à l'intérieur des terres. La mangrove comprend : la mangrove de bord de mer, la mangrove arbustive et la mangrove haute. Le palétuvier rouge *Rhizophora mangle*, est l'espèce emblématique de la mangrove de bord de mer. Il possède des racines aériennes, propices aux sols submergés d'eau. Une faune diversifiée se développe sur ses racines, dont balanes, moules, huîtres, éponges. Les palétuviers noirs, *Avicennia germinans* et *Avicennia schaueriana* sont pratiquement les seules espèces végétales vivant aisément en mangrove arbustive, en raison de la forte salinité de celle-ci. Les racines développent des ramifications, qualifiées de pneumatophores. Les feuilles opposées possèdent des glandes à sels, d'où sa capacité à excréter le sel. Au niveau de la franche interne, les palétuviers rouges se rapetissent en raison de la carence en éléments nutritifs. Enfin, le palétuvier blanc *Laguncularia racemosa* et le palétuvier gris *Conocarpus erectus* sont inféodés à la mangrove haute, opposée à la mangrove de bord de mer. La répartition des palétuviers est proportionnelle à la salinité. En arrière-mangrove, la forêt marécageuse est dominée par le mangle médaille *Pterocarpus officinalis*.

La forêt sèche semi-décidue (55 803 ha) est majoritairement observable sur les littoraux. La pluviométrie y est faible, moins de 2000 mm par an, et la période de sécheresse particulièrement longue. Elle est présente principalement en Grande-Terre, mais aussi sur la côte sous le vent, en Basse-Terre. La végétation y diffère, en fonction de la composition du sol ainsi que de la capacité d'adaptation à la sécheresse. Une strate arborée est retrouvée, notamment avec le Gommier rouge *Bursera simaruba*, le Bois d'inde *Pimenta racemosa*, le Bois de rose *Cordia alliodora*, le Bois-savonnette *Lonchocarpus punctatus*, le Figuier maudit *Ficus citrifolia*, le Poirier *Tabebuia heterophylla*, le Mapou gris *Pisonia subcordata*, le Courbaril *Hymenaea courbaril*, le Mahogany petites feuilles *Swietenia mahagoni*, le Raisinier grandes feuilles *Coccoloba pubescens* ou encore l'Acomat franc *Sideroxylon foetidissimum*. Des arbustes tels que le Campêche *Haematoxylum campechianum*, l'Acacia savane *Vachellia tortuosa*, le Bois chandelle *Amyris balsamifera* ou encore le Goyavier montagne *Myrcia deflexa* sont également présents. Des herbacées, tels que le karata *Bromelia karatas* et *Sansevieria trifasciata* et l'herbe couteau *Scleria secans* y sont aussi observables.

La forêt sempervirente saisonnière (37 610 ha), aussi appelée « forêt mésophile » est toujours verte et moyennement humide (jusqu'à 3000 mm d'eau par an). Elle se concentre uniquement sur la Basse-Terre. Très largement exploitée par l'homme, on y trouve maintenant des plantations agricoles. Parmi la strate arborée, le Mauricif montagne *Byrsonima trinitensis*, l'Acajou rouge

Cedrela mexicana, l'Acajou blanc *Simaruba amara*, le Mahot grandes feuilles *Cordia sulcata*, le Poids doux *Inga laurina*, le Bois d'inde *Pimenta dioica*, le Mahogany grandes feuilles et petites feuilles *Swietenia macrophylla* et *Swietenia mahagoni*. Parmi les arbustes, le Bois lait *Tabernaemontana citrifolia* ou encore le Graines dorées *Picramnia pentandra*.

La forêt dense ombrophile (36 765 ha), aussi appelée « forêt de la pluie » recouvre principalement les hauteurs de la Basse-Terre. Elle s'étend entre 300 et 1000 m de hauteur. Elle est protégée et représente plus de 80 % de la zone du cœur du Parc National de Guadeloupe. Elle regorge d'espèces végétales, en compétition pour atteindre la lumière. La pluviométrie y est très élevée, atteignant jusqu'à 5000 mm d'eau par an. Parmi la strate arborée, atteignant jusqu'à 35 m de hauteur, l'Acomat boucan *Sloanea caribaea*, le Gommier blanc *Dacryodes excelsa*, le Châtaignier *Sloanea massonii*, le Bois rouge carapate *Amanoa caribaea*, le Résolu *Chimarrhis cymosa*, le Marbri *Richeria grandis*, le Laurier rose *Podocarpus coriaceus*, le Mapou baril *Sterculia caribaea*, le Mauricif montagne *Byrsonima trinitensis* ou encore le Magnolias *Talauma dodecapetala*. Parmi les arbustes, le Palmiste *Prestoea acuminata*, le Tamarin des hauts *Phyllanthus mimosoides*, la Grande bleue des hauts *Psychotria urbaniana*, la Côtelette grandes feuilles *Graffenriedia latifolia*. Parmi les herbacées, le Baliser *Heliconia caribaea*, l'Herbe poisson *Lobelia persicifolia*, l'Herbe à Miel *Nautilocalys mellitifolius* ou encore l'Herbe couteau *Scleria secans*. La fougère arborescente *Cyathea arborea* y est également appréciable.

La forêt d'altitude (10 197 ha), aussi appelée « forêt des nuages », apparaît à partir de 1000 m. Elle présente une pluviométrie élevée (jusqu'à 8000 mm d'eau par an) et une persistance de nuages conférant à cet étage une humidité élevée. La végétation n'excède pas 1,50 m de hauteur et prend un aspect rabougri. Parmi les fourrés semi-arborés le Bois siffleur *Weinmannia pinnata* et le Thym montagne *Tibouchina ornata*. Parmi les herbacés et les Broméliacées, largement dominant, l'Ortie montagne, l'Ananas montagne rouge ou jaune *Pitcaimia bifrons* ou *Guzmania plumierii*, ou encore la Siguine blanche *Philodendron giganteum*. Des fougères telles que *Pityrogramma chrysophylla* ou *Cyathea tenera* y sont également observables (Fournet 2002; MDDEE 2012).

V. Présentation des modèles biologiques.

V.1. La Colombe à croissants, *Geotrygon mystacea*

V.1.1. Description morphologique



Figure 3. Photographie de la Colombe à croissants, ©Anthony LEVESQUE.

La Colombe à croissant *Geotrygon mystacea* (Figure 3), est un colombidé terrestre trapu, avec un poids moyen d'environ 220 g et une taille comprise entre 24 et 30 cm. Son corps généralement brun-olive, est ravivé par un cou vert bleuâtre et une face blanc grisâtre (Garrigues 1994). L'iris et la base du bec sont rouges. Les plumes de

couverture sont d'un gris-brun pâle. Les plumes de vol sont d'un brun rougeâtre et à l'extrémité brune (Bond 1990; Gibbs et al. 2001). De plus, une large rayure malaire blanche, reliée à l'arrière du cou, est l'élément morphologique distinctif de cette espèce (Gibbs et al. 2001). Ainsi, cette barre blanche vaut que cette colombe soit aussi appelée "colombe à moustaches" (Bond 1996).

Comme chez la plupart des colombidés (Goodwin 1959; Gibbs et al. 2001; Huallacháin & Dunne 2010), le dimorphisme sexuel semble faible chez la Colombe à croissants. Selon certains auteurs, toutefois, la femelle présenterait des reflets moins vifs que le mâle (Chipley 1991) et sa taille serait légèrement inférieure à celle du mâle (Garrido 1986). Il existerait cependant des différences plus marquées entre les adultes et les jeunes. Alors que la pointe du bec est blanchâtre chez les adultes, les jeunes ont le bec entièrement rose (Pinchon 1976; Puyo 1978). L'abdomen est blanchâtre chez les adultes, tandis que plus foncé et sans reflets verdâtres chez les jeunes (Benito-Espinal 1990; Chipley 1991). Enfin, les pattes sont rosées chez les adultes alors que celles des jeunes sont grisâtres.

V.1.2. Distribution géographique et habitat

La Colombe à croissants est endémique de la Caraïbe, son aire de répartition s'étendant de Porto-Rico à Sainte-Lucie, à l'exception d'Antigua, de Barbuda et d'Anguilla (Figure 4).

Cependant, la structure génétique des populations est inconnue et il n'existe aucune information fiable sur le degré de connectivité entre les populations au sein et entre les îles des Antilles.



Figure 4. Carte tirée du portail de l'UICN, représentant la distribution de la Colombe à croissants.

Elle vit essentiellement dans les milieux naturels, tels que les forêts ombrophiles, les forêts sèches, les forêts marécageuses et les mangroves (Chipley 1991; Levesque & Lartigues 2000; Eraud et al. 2012). Feldman (1998) considère la Colombe à croissants comme plutôt commune en Guadeloupe. Le nombre d'individus estimé en 2012 était compris entre 9420 à 9998 couples (Eraud et al. 2012). Elle semble également commune aux Iles vierges (Boal 2018). En revanche, cette espèce est moins fréquente dans les autres îles des petites Antilles et à Porto Rico (Chipley 1991; Tayalay 1995; Raffaele et al. 1998).

V.1.3. Alimentation, comportement et reproduction

La Colombe à croissants se nourrit principalement de graines et de fruits tombés au sol, en grattant et en fouillant la litière de feuilles (Chipley 1991). Elle complète son menu par des mollusques et des insectes (Seaman 1966; Garrigues 1994). Elle exploite principalement les sols dégagés lors de la recherche de nourriture (Levesque & Lartigues 2000).

On la retrouve seule ou en couple, effectuant de petits vols dans le sous-bois. Ceux-ci sont relativement courts et bas. Les individus se perchent sur les branches des arbres, de 3,5 m à 7 m du sol (Chipley 1991). Ses vocalisations consistent en une série de sons émis en deux parties, sous forme de « waoou waoou ou wooo wooo », pouvant être répétés jusqu'à 12 fois par minute (Chipley 1991; Tayalay 1995). La parade nuptiale est terrestre. Le mâle séduit la femelle avec des hochements de la tête ainsi que des mouvements d'ailes au-dessus du dos, accompagnés de roucoulements (Chipley 1991). La période de reproduction comporterait une période principale de

mai à octobre et une période secondaire d'octobre à décembre. Le pic de reproduction se situerait en juin (Seaman 1966; Raffaele et al. 1998; Levesque & Lartigues 2000). Le nid, principalement construit par le mâle, est une plateforme composée de petites branches et de brindilles (Skutch 1949; Seaman 1966; Chipley 1991). Celui-ci est généralement placé à une hauteur inférieure à 9 m, construit dans les buissons, les épiphytes ou les branches d'arbres (Seaman 1966; Chipley 1991). Les œufs pondus sont au nombre de deux, de couleur saumon-chamois (Skutch 1949; Seaman 1966; Raffaele et al. 1998). L'incubation varie entre 10 à 14 jours, le mâle couvrant aux heures les plus chaudes. En cas de menace, la Colombe à croissants défend son nid par de multiples mouvements et des cris (Skutch 1949; Seaman 1996; Chipley 1991).

V.1.4. Statut et menaces

La Colombe à croissants est considérée de « préoccupation mineure » sur la liste rouge de l'Union Internationale pour la Conservation de la Nature *UICN*, avec toutefois une population signalée en déclin. Néanmoins, elle est considérée en danger en Martinique. L'espèce serait notamment menacée par la prédation (Levesque & Lartigues 2000; Gibbs et al. 2001) et le braconnage. Parmi les prédateurs potentiels, la petite mangouste indienne *Urva auropunctata* (Allen 1911; Hays & Conant 2007).

V.2. La Colombe rouviolette, *Geotrygon montana*

V.2.1. Description morphologique



Figure 5. Photographie de la Colombe rouviolette mâle,
©Anthony LEVESQUE.

La Colombe rouviolette *Geotrygon montana* (Figure 5), est un colombidé terrestre, à la fois charnu et compact. Elle mesure entre 18 et 30 cm et pèse de 80 à 150g (Puyo 1978; Rodriguez et al. 1993; Bond 1996; Raffaele et al. 1998). Bien que les deux sexes aient la cire du bec, l'iris et les pattes rougeâtres, le dimorphisme sexuel est particulièrement marqué chez cette

espèce (Puyo 1978; Bénito-Espinal 1990; Bond 1996; Raffaele et al. 1998). Le mâle présente une coloration brun-rougeâtre uniforme, à l'exception d'une poitrine rosée et d'un ventre beige. Le

front, la calotte et la nuque sont pourpre-rougeâtre. Une bande malaire brun-olive part de la base du bec et souligne l'œil. Les plumes de vol sont brun-rougeâtre terne, avec une terminaison marron (Gibbs et al. 2001). La femelle est semblable au mâle, mais avec une coloration largement plus terne, d'où son appellation « perdrix grise ». Elle présente une coloration marron-vert olive, à l'exception d'une poitrine et d'un ventre plus clairs. La poitrine présente une barre verticale claire. La bande malaire brun-olive est également présente chez la femelle, bien que plus discrète. Enfin, le mâle semble généralement plus grand que la femelle (Puyo 1978; Rodriguez et al. 1993; Bond 1996; del Hoyo et al. 1997; Raffaele et al. 1998).

V.2.2. Distribution géographique et habitat

La Colombe rouviolette est présente de la Caraïbe insulaire (excepté aux Bahamas) jusqu'à la moitié nord de l'Amérique du sud (Puyo 1978; Raffaele et al. 1998). Occasionnellement, elle est retrouvée sur les îles, au large des côtes de Floride (Rodriguez et al. 1993) (Figure 6). Alors que la Colombe rouviolette est considérée peu commune dans les Petites Antilles, elle est plus abondante en Martinique, Porto-Rico, Cuba, Jamaïque, Hispaniola et Amérique du sud (Tayalay 1995; Feldmann 1998; Raffaele et al. 1998). L'espèce est considérée comme partiellement migratrice par certains auteurs (Robertson 1980; Bierregaard 1990; del Hoyo et al. 1997).

La structure génétique, la dynamique et les échanges entre populations sont vaguement documentés. Plus précisément, au Brésil, Stouffer & Bierregaard (1993) ont souligné un pic d'abondance en saison pluviale, similairement à Bierregaard (1989) et Tostain (1989), en Guyane française. Ce pic d'abondance est possiblement lié à la disponibilité alimentaire (i.e., fruits, graines) plus élevée en saison humide qu'en saison sèche (Karr & Freemark 1983; Levey 1988; Paull & Duarte 2011). Néanmoins, aucune variation subsécifique n'a été mise en évidence, ce qui suggère le déplacement des colombes rouviolette, notamment entre les îles de la Caraïbe (Robertson 1980).

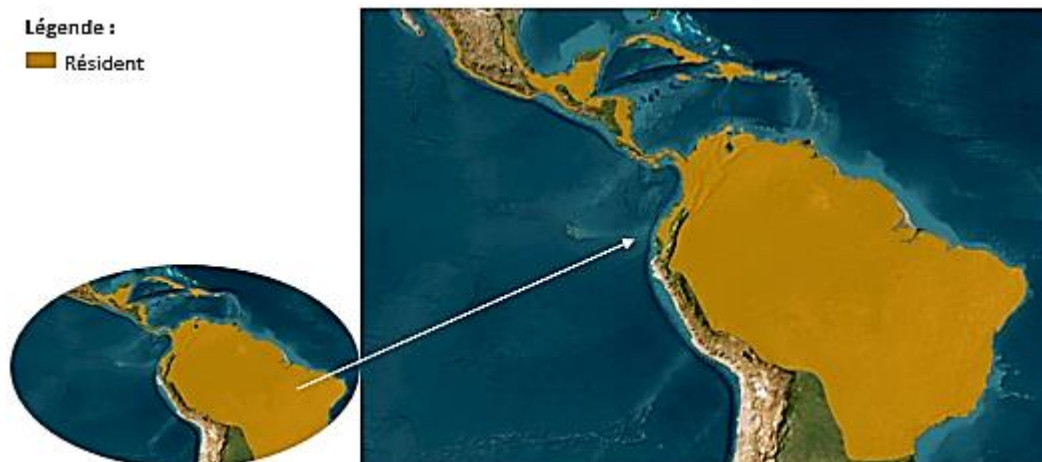


Figure 6. Carte tirée du portail de l’UICN, représentant la distribution de la Colombe rouviolette. Celle-ci est présente de la région Caraïbe (excepté aux Bahamas) à la moitié nord de l’Amérique du Sud.

L'espèce vit essentiellement dans les milieux naturels, affectionnant les forêts denses et humides, les forêts semi-décidues et sempervirentes, et plus rarement, les mangroves (Benito-Espinal 1990; Rodriguez et al. 1993; Garrigues 1994; Imbert et al. 1995; Tayalay 1995). A Porto-Rico, elle est parfois retrouvée dans les plantations de café (Pérez-Rivera 1979; del Hoyo et al. 1997).

V.2.3. Alimentation, comportement et reproduction

La Colombe rouviolette se nourrit principalement de graines et de fruits à même le sol (Rodriguez et al. 1993; Garrigues 1994; del Hoyo 1997). Elle est également capable de consommer des insectes, des vers de terre et des limaces (Pérez-Rivera 1979).

Elle est retrouvée seule, en couple et occasionnellement en groupe (Rivera-Milan 1992). L'espèce est difficilement observable, et vole très bas lors de ses déplacements en forêt (Tayalay 1995). Sa vocalisation correspond à une série de sons très graves et plaintifs, émis sous forme de « waoou ou woou » (Tayalay 1995). Les parades nuptiales sont généralement terrestres, le mâle suivant la femelle de manière brusque, cou tendu, tout en avançant et reculant la tête (Pinchon 1976). Occasionnellement, il écarte les plumes flamboyantes de sa queue et frappe puissamment le sol de ses ailes (Pérez-Rivera 1979). La Colombe rouviolette peut se reproduire quasiment tout au long de l'année, en fonction des latitudes occupées (Gibbs et al. 2001). Ainsi, la période de nidification débiterait en février et durerait jusqu'à octobre, avec un pic s'étalant de mai à juillet (Skutch 1949; Pérez-Rivera 1979; Rivera-Milán 1996). Elle construit des nids peu élaborés, composés d'amas de brindilles sèches et de racines (Pinchon 1976; Pérez-Rivera 1979; Rodriguez et al. 1993; del Hoyo 1997). Ceux-ci sont placés à faible hauteur, allant du sol à 5 m au-dessus du sol (Skutch

1949 ; Pérez-Rivera 1979). Rivera-Milán (1996) indique une corrélation positive entre la densité de nids et l'abondance en fruits.

Les œufs pondus sont au nombre de deux, de couleur blanc-crème (Bond 1976; Pinchon 1976; Rodriguez et al. 1993; Garrigues 1994). L'incubation varie de 10 à 13 jours, avec une implication du mâle aux heures les plus chaudes (Skutch 1949; Pérez-Rivera 1979; Pinchon 1976). Les petits restent au nid moins de 10 jours, ce qui résulte d'une croissance particulièrement rapide, passant de 4 g à une vingtaine de grammes au bout du 3^{ème} jour (Pinchon 1976).

V.2.4. Statut et menaces

La Colombe rouviolette est considérée comme « préoccupation mineure » sur la liste rouge de l'UICN, avec cependant une population globale signalée en déclin. Des spécificités régionales sont applicables, notamment en Guadeloupe, où l'espèce est considérée comme étant quasiment menacée, c'est-à-dire potentiellement menacée si des mesures de conservation ne sont pas prises. Diverses menaces planent sur les populations de Colombe rouviolette, et en particulier, la prédation (Kepler 1977; Tayalay 1995; Vilella 1998; Wunderle & Arendt 2011).

V.3. La Tourterelle à queue carrée, *Zenaida Aurita*

V.3.1. Description morphologique



Figure 7. Photographique de la Tourterelle à queue carrée,
©Anthony LEVESQUE.

La Tourterelle à queue carrée *Zenaida aurita* (Figure 7), est un colombidé terrestre, avec un poids compris entre 120 et 180 grammes et une taille moyenne d'une trentaine de cm (Wiley 1991; Bond 1996; Raffaele et al. 1998; Dechaume-Moncharmont et al. 2011).

Son front est brun, sa calotte gris-brun, ses yeux brun foncé et son bec noir (Quinard et al. 2017). Son corps, généralement brun, est ravivé par une partie inférieure brun-rosé ainsi qu'un éclatant reflet bleu-violet sur le cou. Derrière l'œil et sur les côtés du cou se trouve des fines rayures noires (Bond 1996; Raffaele et al. 1998; Pinchon 1976). Les plumes de

couverture sont brunes, légèrement tachetées de noir et bordées de blanc. Les rémiges primaires et secondaires sont brun-noirâtres. Il est à noter une extrémité blanche sur les rémiges secondaires. La forme carrée de la queue, généralement brune, aux extrémités blanches et avec une bande subterminale noirâtre, est l'élément morphologique phare de cette espèce. Alors que la queue des espèces appartenant au genre *Zenaida* possède généralement 14 rectrices, 12 rectrices sont retrouvées chez la Tourterelle à queue carrée (Wiley 1991; del Hoyo et al. 1997).

Bien que critiqué (Rivera-Milan 1999), un léger dimorphisme sexuel semble être présent chez la Tourterelle à queue carrée. Plus précisément, les mâles seraient plus grands que les femelles, avec une taille moyenne de 2 à 5% supérieure à celle des femelles. Néanmoins, un chevauchement important des distributions de fréquence des tailles des deux sexes a été démontré (Dechaume-Moncharmont et al. 2011). De plus, Wiley (1991) indique que les mâles présenteraient une coloration plus vive du plumage irisé. Il précise que la différenciation entre mâles et femelles est possible à partir de la couleur du plumage à condition d'être à distance faible, d'avoir un éclairage correct et une durée d'observation suffisante. Ces observations ont scientifiquement été infirmées par Quinard et al. (2017). Plus précisément, seules les tourterelles à queue carrée sont capables de percevoir des différences inter et intra sexuelles, à partir de la couleur irisée du plumage.

Il existe des différenciations entre les adultes et les jeunes, permettant alors d'étudier les classes d'âge. Premièrement, les plumes de couverture ont des extrémités brun-clair chez les jeunes (Rivera-Milan 1999), tandis que blanchâtres chez les adultes. En second lieu, les adultes détiennent des pattes rouge-foncé, alors que les pattes sont grises sinon rose-foncé chez les juvéniles (Garrigues et al. 1989).

V.3.2. Distribution géographique et habitat

La Tourterelle à queue carrée est présente dans la Caraïbe insulaire ainsi que sur la côte nord de la Péninsule du Yucatan, au Mexique (Raffaele et al. 1998; Rivera-Milan 1999) (Figure 8).



Figure 8. Carte tirée du portail de l’UICN, représentant la distribution de la Tourterelle à queue carrée. Celle-ci est présente dans la Caraïbe ainsi que sur la côte nord de la Péninsule du Yucatan, au Mexique.

Bien que l’espèce soit principalement sédentaire (Monceau et al. 2013), quelques mouvements erratiques de populations semblent se produire à l’occasion de la reproduction (Nellis et al. 1984; Garrigues et al. 1991). La Tourterelle à queue carrée, terrestre, dort et nidifie dans des arbustes (del Hoyo et al. 1997; Gibbs et al. 2001). Elle vit dans les milieux naturels ou anthropiques, en passant par les mangroves, les forêts secondaires, la forêt xérophile, la forêt sèche côtière, les jardins, les zones périurbaines (Wiley 1991; Rivera-Milán 1997).

V.3.3. Alimentation, comportement et reproduction

La Tourterelle à queue carrée se nourrit principalement de graines trouvées au sol (Pinchon 1976; Levesque & Lartigues 2000), mais peut consommer des fruits et des invertébrés (fourmis, mouches, vers de terre) ainsi que des restes de nourriture humaine, comme du pain ou du riz cuit (Zamore 1981; Wiley 1991; F. Cézilly communication personnelle). Elle localise la nourriture en cherchant elle-même au sol, en exploitant les indices provenant de congénères ou encore, en s’associant pacifiquement à d’autres espèces d’oiseaux (tels que le Sporophile rougegorge *Loxigilla noctis* ou le Vacher luisant *Molothrus bonariensis*) (Webster & Lefebvre 2001; A. Jean-Pierre, observations personnelles; F. Cézilly, observations personnelles).

L’espèce est monogame et est observée seule, en couple ou en groupes familiaux (Wiley 1991; A. Jean-Pierre, observation personnelle). Plus précisément, les mâles et les femelles défendent leur territoire des intrus conspécifiques ou hétérospécifiques, tout au long de l’année (Griffin et al. 2005). Au cours des compétitions agressives (déploiement d’aile en direction de l’adversaire, coups

d'ailes vifs sur l'adversaire) l'implication du mâle est supérieure à celle de la femelle dans la dissuasion des intrus conspécifiques (Sol et al. 2005; Quinard & Cézilly 2012).

La Tourterelle à queue carrée développe des parades typiques des Columbides, alliant des mouvements de la tête, du corps et des ailes. L'oiseau bouge la tête de haut en bas et adopte une posture statique avec le jabot gonflé, tout en roucoulant depuis un perchoir. Des parades aériennes sont également adoptées, avec des battements particulièrement lents et des claquements sonores des ailes suivis d'une phase de glissé. Le mâle rejoint alors un perchoir, tout en oscillant et en déployant ses ailes en V (del Hoyo et al. 1997; Gibbs et al. 2001).

L'espèce peut se reproduire toute l'année (jusqu'à 6 couvées par an), avec un pic réparti entre avril et juin dans les zones sèches. Ce pic de reproduction serait plus précoce, d'environ deux mois, dans les zones plus humides (Nellis et al. 1984; Zamore 1981; Wiley 1991; Rivera-Milán 1996, 1997; Raffaele et al. 1998). La Tourterelle à queue carrée élabore des nids grossiers, constitués de branchettes et de brindilles sèches (Raffaele et al. 1998). Ils sont placés à diverses hauteurs, allant du sol à 5 mètres au-dessus du sol (Burger et al. 1989a; Wiley 1991; Rivera-Milan 1999). Ces derniers peuvent être utilisés une à plusieurs fois (Perez-Rivera 1978; Burger et al. 1991). Les œufs, généralement au nombre de deux, sont blanc-crème, avec un poids irrégulier (allant de 7 à 14 g) suivant la zone biogéographique (Zamore 1981; Wiley 1991; Bond 1996; Raffaele et al. 1998). L'incubation dure 14 jours et est assurée par le mâle et la femelle (Wiley 1991). Le mâle couve aux heures les plus chaudes, de 9 heures à 15 heures. La femelle couve environ deux fois plus que le mâle (Pinchon 1976; Wiley 1991).

Les petits restent au nid de 14 à 20 jours. Au commencement, les parents assurent la surveillance permanente du nid, proportionnellement aux périodes d'incubation. À partir du dixième jour, les parents s'absenteraient de 3 à 5 heures (Pinchon 1976; Nellis et al. 1984). Lorsqu'un prédateur s'approche des œufs au stade éclosion ou des petits au nid, les parents utilisent la "ruse" de l'aile brisée, une parade de distraction pour l'en éloigner (Burger et al. 1989b; Wiley 1991).

V.3.4. Statut et menaces

La Tourterelle à queue carrée est considérée comme de préoccupation mineure sur la liste rouge établie par l'UICN. Plusieurs facteurs pourraient expliquer ce statut. Tout d'abord, le taux de succès des nids et le taux de survie sont généralement supérieurs à 0,50 (Wiley 1991; Rivera-Milan 1999; Rivera-Milan & Vazquez 2000). La productivité est importante, car l'espèce peut se reproduire

tout au long de l'année (Raffaele et al. 1998) et ce, dès l'âge de 10 mois pour le mâle et de 11 mois pour la femelle (Wiley 1991). Il en résulte une production de 2 à 6 jeunes/an (Rivera-Milan 1999). Enfin, dans les Antilles françaises, la bonne régulation de la chasse semble protéger les populations de Tourterelle à queue carrée (Levesque et al. 2020).

V.4. La Grive à pieds jaunes, *Turdus lherminieri*

V.4.1. Description morphologique



Figure 9. Photographie de la Grive à pieds jaunes, ©Anthony LEVESQUE.

La Grive à pieds jaunes *Turdus lherminieri* (Figure 9), est un turdidé terrestre, avec un poids moyen d'environ 100 g et une taille comprise entre 25 et 30 cm. Sa tête, ses rémiges et ses rectrices sont généralement brun-sombre, ravivés de pattes et de contours de l'œil jaune. Alors que son dos est marron-olivâtre, sa poitrine d'apparence écailleuse, oscille entre le blanc, le beige et le brun, avec un

abdomen blanchâtre (Sharpe 1854, Semper 1872, Clement & Hathway 2000, Bénito-Espinal & Hautcastel 2003; Arnoux et al. 2013, 2014).

Bien qu'aucun dimorphisme sexuel n'existe chez cette espèce, une différenciation peut être faite entre les adultes et les juvéniles. Des tâches rousses au niveau de la tête et des plumes de couvertures alaires sont présentes chez les juvéniles. Les rectrices forment un angle prononcé entre le bord de la plume et l'axe du rachis chez les juvéniles (Lawrence 1879; Arnoux et al. 2013, 2014).

V.4.2. Distribution géographique et habitat

La Grive à pieds jaunes est endémique des Petites Antilles. Les critères morphologiques ainsi que la coloration du plumage des populations permettent de mettre en évidence quatre sous-espèces, *Turdus lherminieri dorotheae*, *Turdus lherminieri lherminieri*, *Turdus lherminieri sanctae luciae*, *Turdus lherminieri dominicensis*, résidant respectivement sur quatre îles : Montserrat, Guadeloupe, Sainte-Lucie et la Dominique (Figure 10).

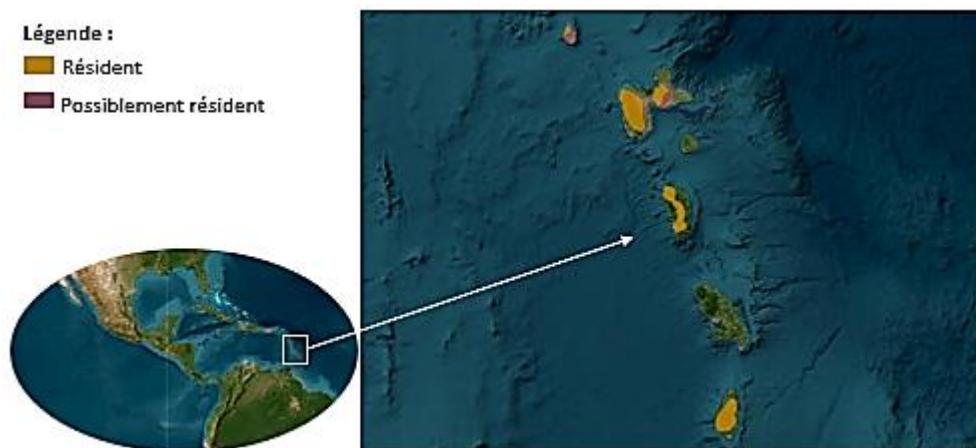


Figure 10. Carte tirée du portail de l’UICN, représentant la distribution de la Grive à pieds jaunes. Celle-ci est présente sur quatre îles des Petites Antilles : Montserrat, Guadeloupe, Sainte-Lucie et la Dominique.

En Guadeloupe, la taille de la population a été évaluée à environ 49 000 individus matures (Eraud et al. 2012), ce qui est largement supérieur à l’estimation pour chacune des îles des Petites Antilles (BirdLife 2023). La Basse-Terre abrite la majeure partie de la population guadeloupéenne, qui semble décliner sur la Grande-Terre (Feldmann 1998; Arnoux et al. 2013, 2014). A Sainte-Lucie, la taille de la population a largement diminué. Considérée comme abondante à la fin des années 1800, elle est aujourd'hui devenue très rare sur l’île, sa dernière détection remonte à 2009 (Keith 1997; Federal Register 2010; Arnoux et al. 2013, 2014). A Montserrat, l’éruption volcanique de la Soufrière en 1995, a décimé deux tiers de la population. Toutefois, en 2008, l’effectif était remonté à 3100 individus, témoignant de la capacité de l’espèce à rapidement compenser un épisode de forte mortalité (Dalsgaard et al. 2007). A la Dominique, l’espèce présente de faibles effectifs (Arnoux et al. 2013, 2014).

La Grive à pieds jaune affectionne les milieux forestiers, avec une faible tolérance aux variations d’habitat (Eraud et al. 2012). Elle est fréquente principalement dans les forêts ombrophiles et sempervirentes, accompagnées d’une dense canopée (Parashuram et al. 2015). Elle est également retrouvée dans les plantations, en forêt mixte, en forêt sèche, ainsi qu’en forêt marécageuse (Benito-Espinal & Hautcastel 2003; Arnoux et al. 2013, 2014).

V.4.3. Alimentation, comportement et reproduction

La Grive à pieds jaunes se nourrit principalement d’invertébrés, dans le sous-bois. Elle complète son menu de baies et de fruits dans les arbres ou tombées au sol (Raffaele et al. 1998; Federal Register 2010). Difficilement observable, ses mœurs sont peu connues (Arnoux et al. 2013, 2014).

L'espèce semble se reproduire entre février et août (Bénito-Espinal & Hautcastel 2003). Elle élabore des nids volumineux en forme de coupe, composés de feuilles sèches, de brindilles et de mousse. Celui-ci peut atteindre 21 cm de diamètre et est placé de 3 à 10 m de hauteur, sur les fougères arborescentes, ou les arbres (Raffaele et al. 1998; del Hoyo et al. 2005). Les œufs pondus sont de 2 ou 3, de couleur vert-bleuté et sans tâches (del Hoyo et al. 2005). Pour les couvées à venir, les nids ne sont pas reconstruits mais réaménagés (Bénito-Espinal & Hautcastel 2003). L'incubation dure environ 14 jours, et serait assurée par le mâle et la femelle. Les poussins restent au nid au moins 16 jours (Renaud 2016).

V.4.4. Statut et menaces

La Grive à pieds jaunes est considérée comme « quasi-menacée » sur la liste rouge établie par l'UICN. Les populations de Sainte-Lucie et de Guadeloupe sont particulièrement surveillées. A Sainte-Lucie, la sous-espèce est considérée « menacée », n'ayant pas été observée depuis 2009. En Guadeloupe, l'espèce est considérée vulnérable. Différentes menaces planent sur la Grive à pieds jaunes, telles que la pression parasitaire (Raffaele et al. 1998; Valkiunas 2005), la fragmentation et la destruction de son habitat naturel, les catastrophes naturelles ou encore, la prédation (Federal Register 2010).

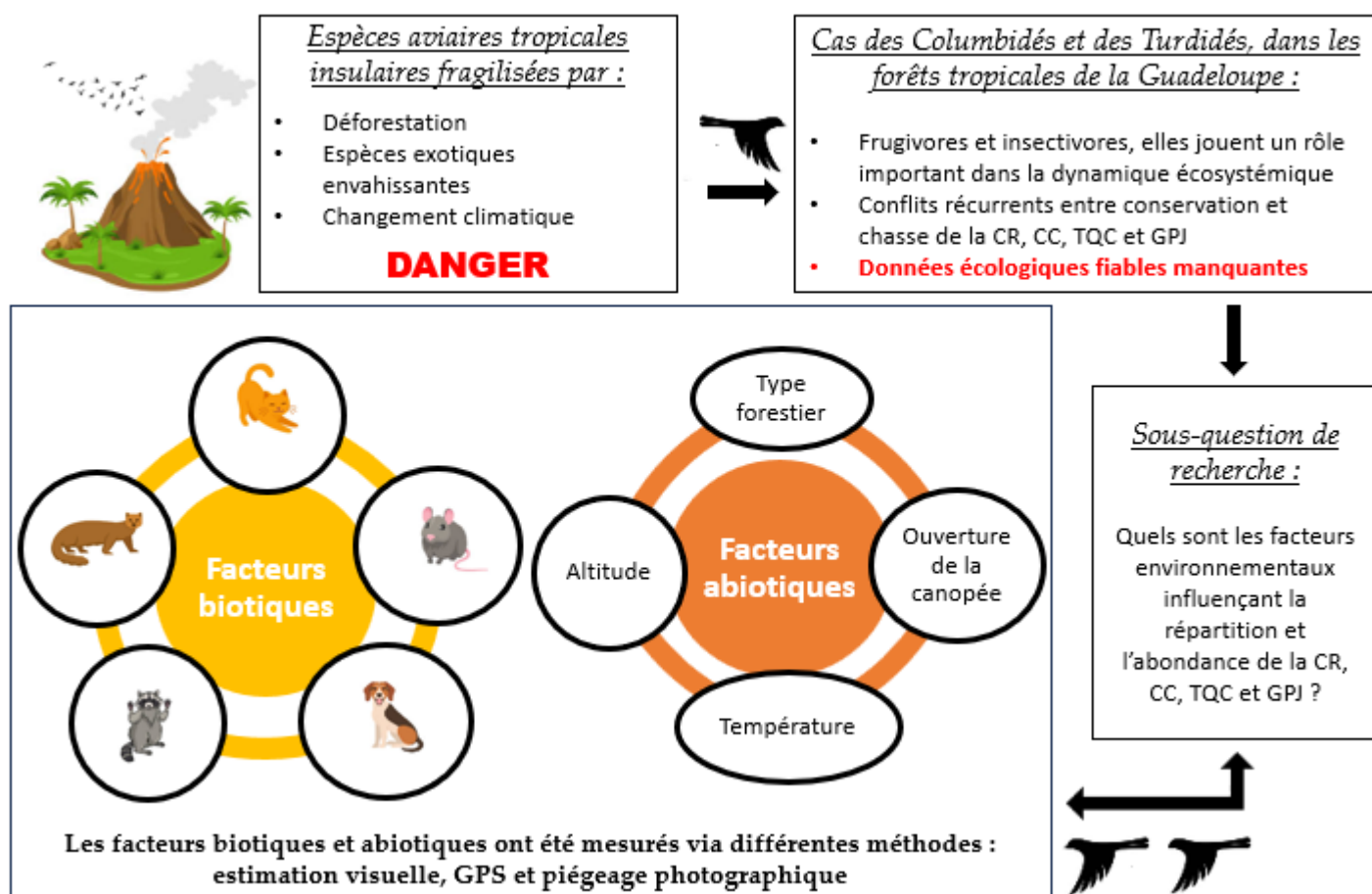
Afin de comprendre l'interaction entre les quatre espèces aviaires étudiées et leur milieu de vie, divers facteurs, à la fois biotique et abiotique ont été mesurés sur chacun des sites étudiés. Tandis que les facteurs biotiques représentent l'ensemble des interactions entre les êtres-vivants dans un biotope donné, les facteurs abiotiques représentent l'ensemble des facteurs physico-chimiques influençant une biocénose donnée.

RÉSULTATS

CHAPITRE 1

Facteurs biotiques et abiotiques affectant l'occupation spatiale et l'abondance locale de la Colombe rouviolette, de la Colombe à croissants, de la Tourterelle à queue carrée et de la Grive à pieds jaunes, dans les forêts de Guadeloupe

1.1. Chapeau introductif du chapitre 1



Ce premier chapitre présente l'influence de différents facteurs biotiques et abiotiques sur la répartition et l'abondance de la Colombe rouviolette *Geotrygon montana*, de la Colombe à croissants *Geotrygon mystacea*, de la Tourterelle à queue carrée *Zenaida aurita*, et de la Grive à pieds jaunes *Turdus lherminieri*, dans les forêts tropicales de la Guadeloupe. La sélection des facteurs biotiques et abiotiques étudiés a été faite selon leurs influences connues sur les espèces aviaires tropicales insulaires ainsi qu'aux moyens financiers et humains disponibles. Les facteurs abiotiques choisis ont été le type d'habitat, la température, l'altitude et l'ouverture de la canopée. Concernant les facteurs biotiques, le choix s'est porté sur la présence et l'abondance de 5 espèces de mammifères, potentiellement prédatrices (le chat domestique *Felis catus*, le chien domestique *Canis lupus familiaris*, la petite mangouste indienne *Urva auropunctata*, le raton laveur *Procyon lotor* et les rats *Rattus spp.*).

Dans un contexte insulaire largement fragilisé par les activités humaines, le piège photographique s'est révélé un outil particulièrement efficace à la mise en lumière de la dynamique spatiotemporelle des colombidés étudiés, en lien avec les facteurs environnementaux considérés.

1.2. Article 1

Article 1

Spatial occupancy, local abundance, and activity rhythm of three ground dwelling columbid species in the forests of Guadeloupe in relation to environmental factors

Jean-Pierre, A.^{1,2}, Loranger-Merciris, G.¹, Cézilly, F.²

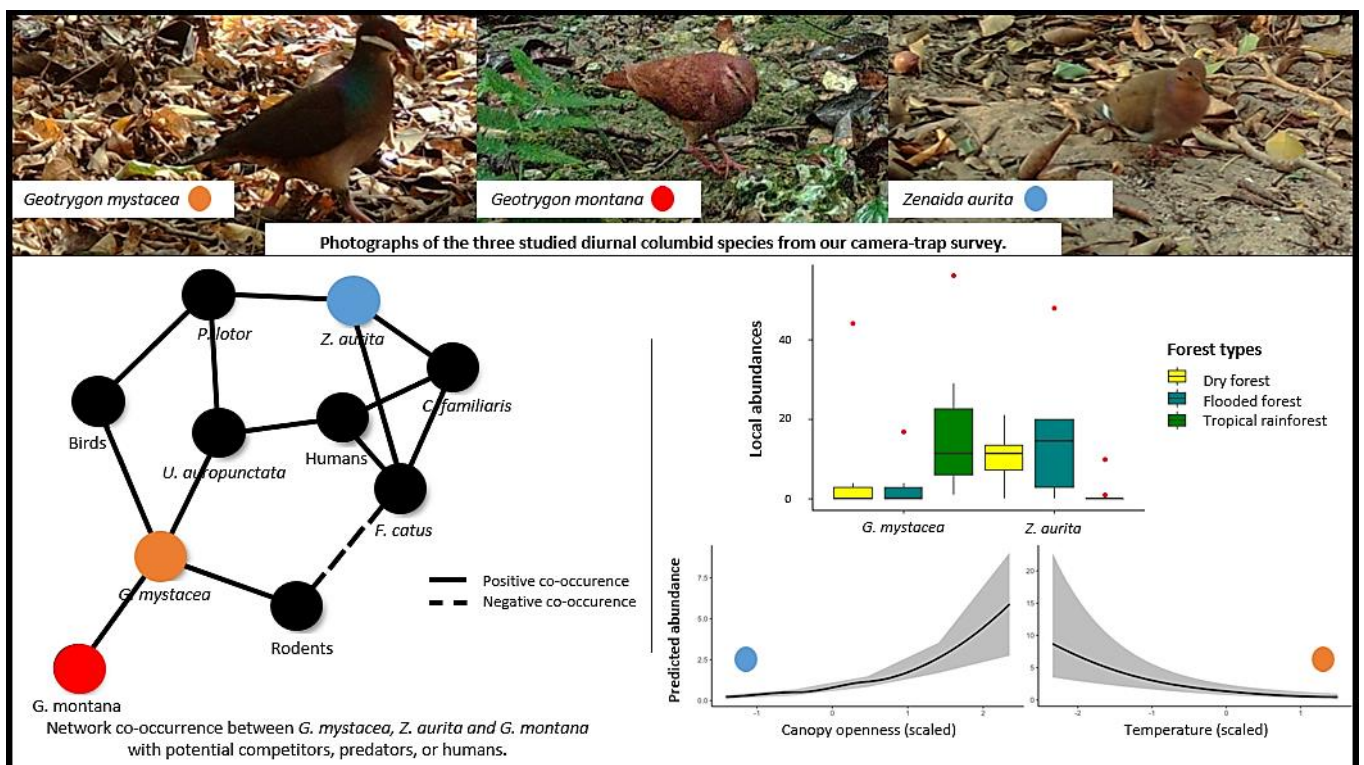
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Graphical abstract



Article

Spatial Occupancy, Local Abundance and Activity Rhythm of Three Ground Dwelling Columbidae Species in the Forests of Guadeloupe in Relation to Environmental Factors

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Abstract: Although forest-dependent, tropical island endemic birds are particularly at risk of extinction, they remain largely understudied. In this context, we assessed the spatial occupancy, local abundance, and diel activity in three forest columbid species of hunting interest, the Ruddy Quail-Dove (RQD), *Geotrygon montana*; the Bridled Quail-Dove (BQD), *Geotrygon mystacea*; and the Zenaida Dove (ZD), *Zenaida aurita*, in Guadeloupe (French West Indies), using 5 camera-traps over 14 days on 24 survey stations, resulting in 1680 trap days. The number of observed RQD was too small to allow for a statistical comparison between habitats. BQD were more frequently observed at camera-trap stations that were dominated by tropical rainforest than those that were dominated by flooded forest. Conversely, ZD were more frequently observed at stations that were dominated by flooded forest and dry forest than at those that were dominated by tropical rainforest. High temperatures negatively affected the abundance of BQD, while the abundance of ZD was significantly lower in tropical rainforests compared to dry and flooded forests and tended to increase with canopy openness. The three species were diurnal. BQD significantly positively co-occurred spatially and temporally with small Indian mongooses, *Urva auropunctata*, whereas the temporal and spatial distribution of ZD overlapped significantly with that of domestic dogs, *Canis familiaris*, and domestic cats, *Felis catus*. Our results provide firm evidence that RQD remains scarce and is largely outnumbered by BQD in Guadeloupe which is in contrast with has been reported for other Caribbean islands.

Keywords: Bridled Quail-Dove; camera-trap; Caribbean; *Geotrygon montana*; *Geotrygon mystacea*; Ruddy Quail-Dove; *Zenaida aurita*; Zenaida Dove



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1. Introduction

The Caribbean islands constitute one of the major hotspots of biodiversity on Earth [1–3] and are particularly characterized by high diversity and high levels of avian endemism [4]. However, several Caribbean endemic bird species [5–9], including species of least concern [10,11], are currently declining as the result of environmental degradation.

In particular, Caribbean forest-dependent columbid species appear to be threatened by habitat fragmentation or destruction, extreme climatic events, introduction of exotic species, and poorly regulated hunting pressure [12–19]. The decline of columbid species is particularly worrying as pigeons and doves often play a crucial role in the dynamics and diversity of tropical or semi-arid forest through seed dispersal [20–24]. However, little information is available on the conservation status, population levels, and habitat use of Caribbean columbid species [25].

In this context, we assessed the spatial occupancy, local abundance, and diel activity patterns of three columbid species of hunting interest in Guadeloupe, French West Indies. The Bridled Quail-Dove (BQD hereafter), *Geotrygon mystacea*, is endemic to the Caribbean region, ranging from Puerto Rico to Saint Lucia [26,27]. The congeneric Ruddy Quail-Dove (RQD hereafter), *G. montana*, has a much wider range, stretching from the Caribbean Basin to the northern half of South America [28]. The Zenaida Dove (ZD hereafter), *Zenaida aurita*, is widely distributed through the Caribbean region, from the tip of the Yucatán Peninsula to the south of the Lesser Antilles, with weak morphological and genetic differentiation between populations [29]. All three species forage on the ground, eating mainly seeds and fallen fruits, but can also feed upon insects, earthworms, and gastropods [30–32].

Although the three species are listed as Least Concern on the IUCN red list, they differ markedly in relation to their conservation status in the Caribbean region and their degree of scientific attention. BQD is uncommon to rare in the Lesser Antilles and is a very rare resident in Puerto Rico [33]. Populations are considered to be declining on most Caribbean islands [14,19,34,35], with the possible exception of Guadeloupe [36,37]. RQD is a common to rare resident in the insular Caribbean [33]. By contrast, ZD is a common and cosmopolite species in the insular Caribbean, being present in large numbers in open woodlands, edges, mangroves, but also in cultivated fields, gardens, and the urban environment [33,38,39]. The behavior and population biology of the species has been well documented (see [40,41] and references therein). In comparison, very little attention has been given to the two quail-dove species in the scientific literature, reflecting a general focus on non-threatened species compared to threatened ones [42].

In Guadeloupe, the ZD and, to a lesser extent, the two Quail-Dove species are highly sought after by local hunters for personal food use [43], although the precise impact of hunting pressure on population dynamics remains undocumented. The three species are likely to be vulnerable to predation by several invasive mammal species [44,45]. However, little is known about the overlap in the distribution and activity rhythms between the three columbid species and their potential predators. Currently, RQD is considered uncommon in Guadeloupe, with a frequency of occurrence being about three to four times lower than that of BQD, based on auditory point counts [37]. However, RQD is especially shy and hard to approach [46]. In addition, the performance of the auditory point count method for the survey of columbid species in tropical forests has been recently shown to be limited [47]. ZD, on the other hand, is very common in Guadeloupe with a marked increase in population size between 2014 and 2019 [37].

We, therefore, relied on camera-traps to document the presence, local abundance, and diel patterns of activity of the three species in various forest habitats in Guadeloupe. The use of camera-traps is a particularly suitable method for the study of both discrete and reclusive bird species such as quail-doves [48–53]. In addition, it is an important tool in modelling species distribution coupled with environmental characteristics [53–57]. Here, we specifically aimed at (1) estimating the local abundance and detection of the three columbid species in Guadeloupe forests, (2) testing for the influence of environmental variables on detection and abundance, and (3) assessing the spatio-temporal co-occurrence between ZD, RQD, and BQD as well as with potential mammal predators, including humans.

2. Materials and Methods

2.1. Study Area and Data Collection

This study took place in Guadeloupe, French West Indies. Covering a surface area of 1628 km², Guadeloupe consists of two main contiguous islands: Basse-Terre and Grande-Terre. The first one is mountainous with the tallest volcano in the Lesser Antilles, culminating at 1467 m [58]. The second is limestone, lower, and flatter [59]. From the coast to the mountains, different forest types can be observed, according to elevation and rainfall. Tropical rainforest is the dominant type, amounting for about 40% of forest cover [60]. Dry forest is characterized by low rainfall, moderate elevation, and limestone or ancient volcanic soils. Flooded forest includes mangroves and swamp forests.

We assessed the presence of the three ground-dwelling columbid species and that of potential mammalian predators using camera-traps. To this aim, 24 stations (each station involving 5 camera-traps operating over two separate 7-day periods) were surveyed between February and May 2019, including 6 dry forest stations, 6 flooded forest stations, and 12 tropical rainforest stations (Figure 1, Supplementary Table S2).

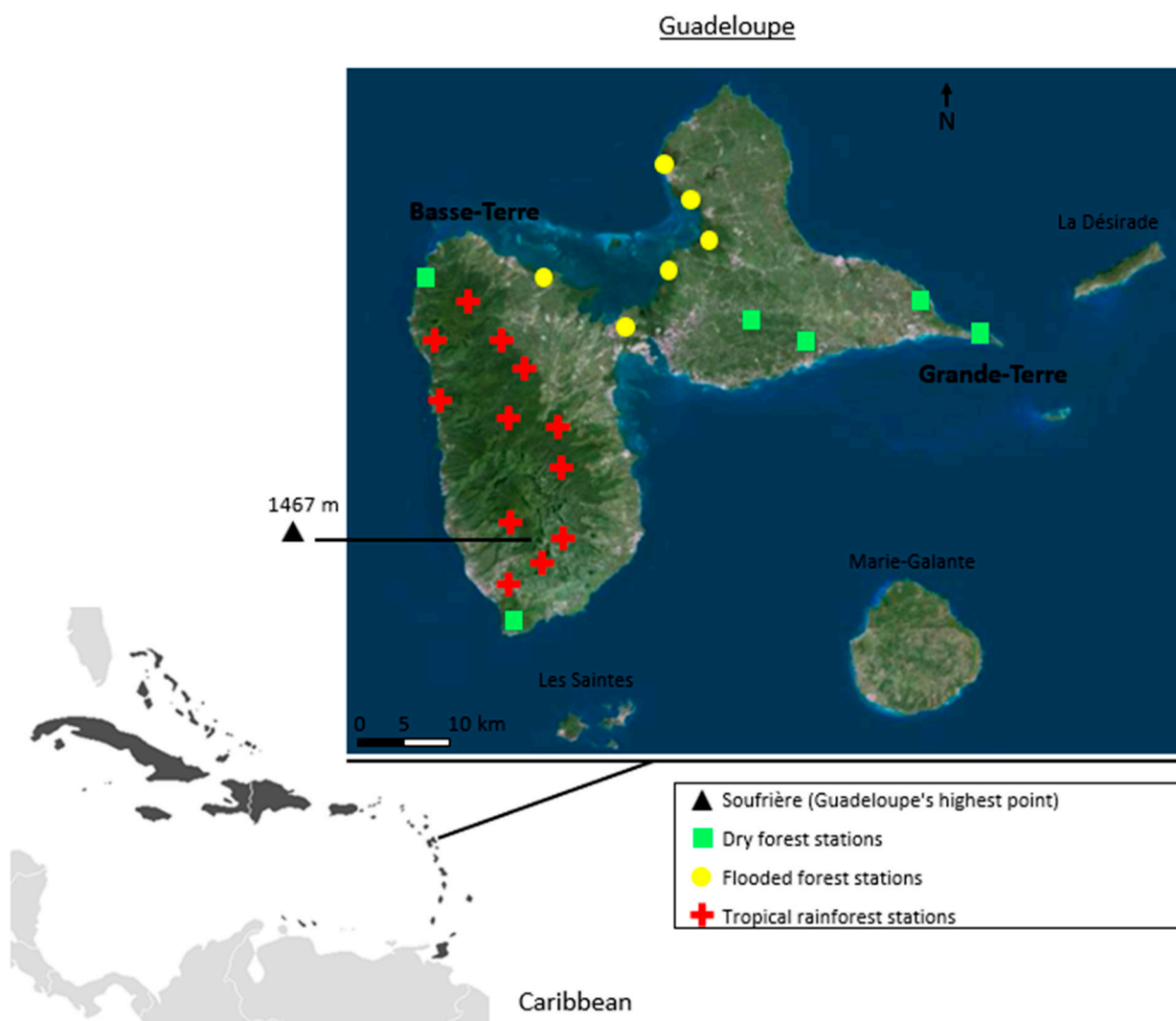


Figure 1. The 24 camera-trap locations that were surveyed between February and May 2019 in Guadeloupe, including 6 dry forest stations, 6 flooded forest stations, and 12 tropical rainforest stations. Each station had 5 cameras that surveyed for two 7-day periods. The distance between these camera-trap locations ranged from 2.82 km to 62 km.

Following Louppe et al. [45], stations were not chosen using an aerial grid due to the very steep landscape and extensive urban areas characterizing Guadeloupe, but rather to best cover the islands high diversity of forest habitats and to obtain a representative sample of elevations [61,62]. At each station (with a distance between stations that ranged from 2.82 km to 62 km), we arranged five passive infrared camera-traps (Moultrie© M-40i, with a detection range of about 24 m over a 125° angle of view) in a straight line, with a 200-m distance between adjacent cameras. The camera-traps were active for seven consecutive days during two separate trapping sessions, one in February–March and the other in April–May, resulting in 1680 days of trapping.

Each single camera was attached to a robust tree at a height of between 20 and 30 cm, in accordance with the small body size of the targeted bird species [48]. However, our traps were also effective in capturing mammal species. The cameras were operational 24 h day⁻¹.

The trigger was set to take three pictures each time a movement was detected, and we set a 30-s delay between the pictures to avoid multiple photographs of the same individual over short time periods [53]. In order to ensure uniformity in the radius of action of each camera, we selected trees at locations where the vegetation was not too dense, thus allowing an optimal range of the camera sensor in closed habitats. The selected parameters (high sensitivity of the shutter trigger, height positioning of the camera-trap, and distance of detection range) maximized the probability that all the columbid species that were present the survey areas would be detected.

To understand patterns of habitat use by columbids and potential mammalian predators, we measured the habitat type, canopy openness, elevation, and temperature at each station. We first assessed the habitat type (dry forest, tropical rainforest, flooded forest) from Rousteau [63] and then obtained confirmation from direct observations in the field. We visually estimated the canopy openness at each camera-trap location. The canopy was considered as open ($\geq 66\%$ open), partially open (33–66 open), or closed (0–33% open), with a corresponding score of 1, 0.5, or 0, respectively. At each station, an average was calculated for the five camera-traps, thus resulting in a continuous canopy openness index ranging from 0 to 1 [64]. We collected the elevation data at each camera-trap location, using a Garmin Dakota 20 GPS. The ambient temperature data was systematically recorded by the camera-traps on each shooting.

2.2. Data Analysis

We estimated the local abundance (the relative representation of a species in a particular ecosystem, measured as the number of individuals found per sample; [65]) from the total number of individuals (captures) of each species at each camera-trap location. Then, we pooled the local abundances for the five camera-traps at each location to assess the total local abundance per station. As the data did not follow a normal distribution (Shapiro–Wilk normality test [66], $p < 0.01$), we relied on a Wilcoxon signed-rank test for the paired data [67] to compare the estimates of local abundance that were obtained at each station between the two sampling periods. We used a Kruskal–Wallis analysis of variance by ranks to compare the median number of more than two groups [68,69], and Dunn's test [70] to make subsequent pairwise comparisons between the groups. We estimated the naïve occupancy for each species by dividing the number of camera-trap locations where at least one individual was photographed by the overall number of camera-trap locations. We calculated the capture per unit effort (camera-trapping sampling occasion) for each species by dividing the number of photographed individuals per 100 trap-days.

We then relied on Royle and Nichols' [71] heterogeneity model, linking abundance and heterogeneous detection probabilities, to assess the influence of environmental variables on detection and abundance. This method is particularly recommended to assess site occupancy at different spatial scales in the case of populations of unmarked individuals that are difficult to detect [72,73]. Detection was considered as a binary variable (1 = detection, 0 = non-detection, correcting for occasional camera dysfunction) at each station for all identifiable species, using data from 7-day trapping sessions. Species detection (1) and non-detection (0), with a 10 min buffer time between detections of the same species, were extracted for each trap day (i.e., 24 h period) at each station. Thus, abundance modelling was not concerned with species abundance history, but only with species binary detection history under specific habitat conditions. According to Royle and Nichols [71], variation in animal abundance, N_i , is the most important source of heterogeneity in site-specific detection probabilities.

The model assumes that all individuals of site i during sample j , have identical detection probabilities, r_{ij} , and that detections are independent. The species is then recorded if at

least one individual is detected within the site. Thus, species detection probability is linked to probability of detection for an individual by:

$$P_{ij} = 1 - (1 - r_{ij})^{N_i}$$

Models were built using the R package « unmarked » v0.13-0 [74]. We analyzed data at the level of stations to maximize observation independence. We modelled abundance (λ) according to temperature, elevation, canopy openness, or forest types, and modelled the probability of detection (p) according to the forest structure and temperature. We ran a first model with both detection probability and abundance being independent of covariate influence, e.g., $p(\cdot), \lambda(\cdot)$. We chose not to include all environmental variables influencing abundance and detection in a global model as several of them were highly correlated between themselves (Spearman rank correlation test; canopy openness and temperature: $r_s = 0.67$; elevation and temperature: $r_s = -0.82$; $p < 0.01$ in both cases). We, therefore, modelled the influence of each environmental variable individually on p while keeping λ constant, and vice versa, e.g., $p(\text{covariate1}), \lambda(\cdot)$ or $p(\cdot), \lambda(\text{covariate1})$. Finally, each environmental variable was tested on p and λ , without additive effects, e.g., $p(\text{covariate1}), \lambda(\text{covariate2})$ and then with additive effects, e.g., $p(\text{covariate1+covariate3}), \lambda(\text{covariate2+covariate4})$, or $p(\text{covariate1+covariate3}), \lambda(\text{covariate2+covariate4+covariate5})$. The covariates that were included in the additive models were not correlated between themselves.

We ranked models using the Akaike information criterion and we considered models with $\Delta\text{AICc} < 2$ to assess the significance of the covariates [75]. We calculated evidence for the best model in comparison to other models from the ratio of AIC weights. We checked for goodness-of-fit and mean dispersion parameter $\hat{c}$ for all valid models, using 10,000 parametric bootstraps [55,76].

In order to assess variation in the diel activity between species, we considered four different periods of unequal length [77–79]: night (from 1 h after sunset to 1 h before sunrise), dawn (from 1 h prior to 1 h after sunrise), day (from 1 h after sunrise to 1 h before sunset), and dusk (from 1 h prior to 1 h after sunset). We accounted for daylength variation between the two trapping sessions by defining the average sunrise and sunset dates for each of the two sampling periods. We first used a Fisher exact test [80–82] to compare the proportions of birds that were captured during the different periods of the diel cycle (night, dawn, day, and dusk) between the two trapping sessions. Then, following Monterroso et al. [79], we used Jacobs Selectivity Index (JSI, [83]), to assess selectivity in diel rhythm activity. JSI ranges from -1 to 1 , with -1 being total avoidance, 0 no preference, and 1 total preference. To determine the average JSI index and 95% confidence intervals for each period and species, we used bootstrap resampling (500 replicates) and recalculated the JSI for each bootstrap sample. The four periods were considered positively (or negatively) selected, whenever the 95% CI of the JSI was positive (or negative) and did not overlap zero (i.e., used as expected by chance). For each species, we compared the JSI index between the two sampling periods using a paired sample Wilcoxon test.

We further assessed the spatial co-occurrence between columbid species as well as with potential competitors and potential predators. To that end, we considered seven different taxonomic groups: birds (pooling all species; Supplementary Table S1), rodents (pooling all species), domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis familiaris* Linnaeus, 1758), small Indian mongooses (*Urva auropunctata*, 1836), northern raccoons (*Procyon lotor*, 1758), and humans. Co-occurrence was assessed using the probabilistic model that was developed by Veech [84], incorporated in the R package “cooccur” v1.0 [85]. This model determines the probability that the frequency of species co-occurrence of two species differ from what would be expected if the two species were distributed independently of each other among a set of sites. This model can then be used to classify associations of species as negative, positive, or random. In addition, we relied on the kernel density estimates of diel activity [86] incorporated in the R “Overlap” v1.1 package [87] to investigate the temporal activity and overlap. Following Ridout and Linkie [88], we favoured $\Delta 4$ over $\Delta 1$ as a nonparametric estimator of the coefficient of overlapping as our sample size was

above 75 [89]. We estimated the precision of overlap coefficients by calculating an average value from 10,000 bootstrap samples for each pair of species.

3. Results

3.1. Camera-Trapping Survey Results and Species Detected

There was no difference in the local abundance of each of the three columbid species at each trapping station between the two trapping sessions (Wilcoxon's test: $P_{\text{BQD}} = 0.55$, $P_{\text{RQD}} = 0.93$, $P_{\text{ZD}} = 0.50$). Therefore, the data were pooled for subsequent analysis.

From a total of 1680 trapping days, we obtained 9450 captures, including 351 captures of BQD on 16 different survey stations, 198 captures of ZD on 12 different survey stations, and 14 captures of RQD on 7 different survey stations. The naïve occupancy rate was equal to 0.67, 0.50, and 0.29, camera-trapping rates (number of individual detections/100 trap-days) were equal to 16, 10, and 1, respectively, for BQD, ZD, and RQD. Overall, columbid species were present on 22 of 24 survey stations, with a 0.92 naïve occupancy rate and an average camera-trapping rate of 9.

Although BQD were found in all forest types that were studied, they were predominant in camera-trap survey stations they were dominated by tropical rainforest ($N_{\text{tropical forest}} = 12/12$, $N_{\text{flooded forest}} = 2/6$, $N_{\text{dry forest}} = 2/6$; Fisher's exact test, $p = 0.001$). Conversely, ZD were detected more frequently in camera-trap survey stations they were dominated by flooded forest and dry forest ($N_{\text{tropical forest}} = 2/12$, $N_{\text{flooded forest}} = 5/6$, $N_{\text{dry forest}} = 5/6$; Fisher's exact test, $p = 0.004$). The proportion of stations where RQD were detected did not differ between the three forest types ($N_{\text{tropical forest}} = 5/12$, $N_{\text{flooded forest}} = 2/6$, $N_{\text{dry forest}} = 1/6$; Fisher's exact test, $p = 1$).

In terms of local abundance, there was a significant difference in the median number of columbids per station between the three habitat types (Kruskal–Wallis analysis of variance, BQD: $X^2 = 8.71$, $p = 0.013$; ZD: $X^2 = 11.32$, $p = 0.003$; Figure 2). BQD were more frequently observed at camera-trap stations they were dominated by tropical rainforest than those they were dominated by flooded forest (Dunn's test adjusted with the Bonferroni method, $p = 0.04$), whereas ZD were more frequently observed at camera-trap stations they were dominated by flooded forest and dry forest than at those they were dominated by tropical rainforest ($p = 0.02$ for each comparison). The number of observed RQD was too small to allow statistical comparison between habitats.

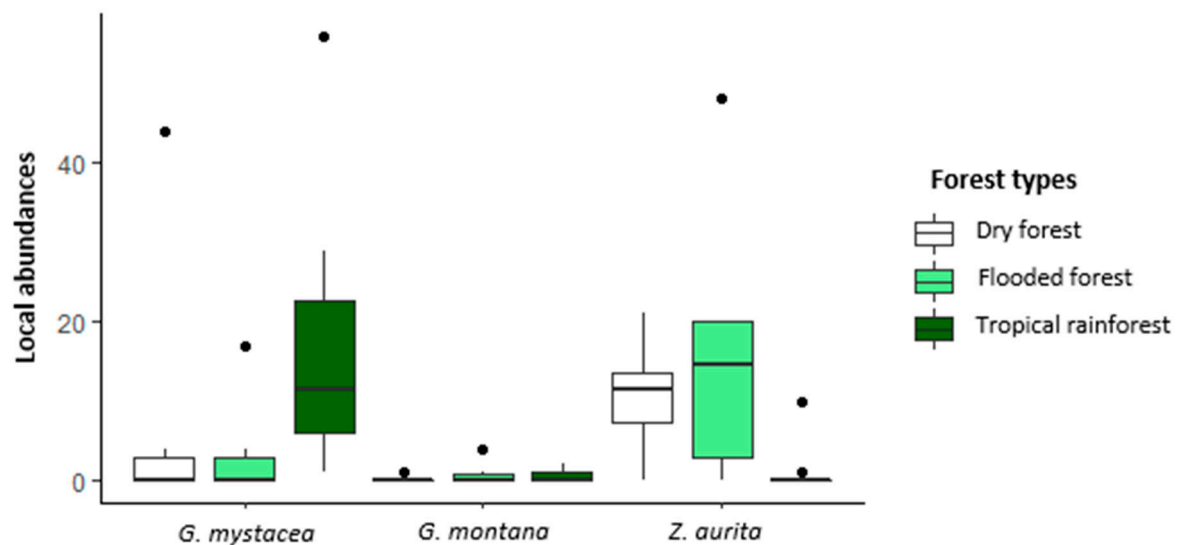


Figure 2. Local abundances of Bridled Quail-Doves, Ruddy Quail-Doves and Zenaida Doves at camera-trap survey locations in Guadeloupe, including three different forest types: dry forest (white), flooded forest (light green), and tropical rainforest (dark green).

3.2. Modelling Abundance and Detection

A subset of our trapping surveys was used for modelling purposes. After considering a 10 min buffer time between detections of the same species, we retained 262, 173, and 13 captures, respectively, for BQD, ZD, and RQD, resulting in 82, 54, and 10 detections in model matrices.

The best model for BQD retained temperature as the only environmental variable that was associated with abundance ($\beta = -0.81$, $SE = 0.19$, $p < 0.01$), with decreasing numbers with increasing temperature (Figure 3).

Table 1. Abundance and detection models for the Bridled Quail-Dove and the Zenaida Dove in Guadeloupe forests. Abundance (λ) was modelled according to the temperature (temp), elevation, canopy openness (co), or forest types (forest), and the probability of detection (p) was modelled according to the forest structure (fs) and temperature (temp). All environmental variables influencing abundance and detection were not included in a global model as they were highly correlated between themselves. We reduced the table to models within delta AIC < 6 (see Table S3 for the full table).

	Models	AICc	Δ AICc	Weight	logLik	d.f.
Bridled Quail-Dove						
M1	$p(\cdot), \lambda(\text{temp})$	146.83	0.00	0.48	−69.82	3.00
M2	$p(\text{temp}), \lambda(\text{temp})$	149.42	2.59	0.13	−69.66	4.00
M3	$p(\text{fs}), \lambda(\text{temp})$	149.44	2.61	0.13	−69.67	4.00
M4	$p(\cdot), \lambda(\text{forest} + \text{temp})$	151.03	4.20	0.06	−68.85	5.00
M5	$p(\text{fs} + \text{temp}), \lambda(\text{temp})$	152.45	5.62	0.03	−69.56	5.00
M6	$p(\cdot), \lambda(\text{forest})$	152.66	5.83	0.03	−71.28	4.00
Zenaida Dove						
M1	$p(\cdot), \lambda(\text{forest})$	129.96	0.00	0.21	−59.93	4
M2	$p(\cdot), \lambda(\text{forest} + \text{co})$	131.06	1.10	0.12	−58.86	5
M3	$p(\cdot), \lambda(\text{co})$	131.17	1.21	0.11	−61.98	3
M4	$p(\cdot), \lambda(\text{elevation})$	132.14	2.18	0.07	−62.47	3
M5	$p(\text{temp}), \lambda(\text{forest})$	132.48	2.53	0.06	−59.58	5
M6	$p(\cdot), \lambda(\text{forest} + \text{elevation})$	133.00	3.05	0.04	−59.84	5
M7	$p(\cdot), \lambda(\text{forest} + \text{temp})$	133.12	3.16	0.04	−59.89	5
M8	$p(\text{fs}), \lambda(\text{forest})$	133.16	3.20	0.04	−59.91	5
M9	$p(\text{temp}), \lambda(\text{co})$	133.42	3.46	0.04	−61.66	4
M10	$p(\text{fs}), \lambda(\text{co})$	133.53	3.57	0.03	−61.71	4
M11	$p(\cdot), \lambda(\text{temp})$	133.94	3.98	0.03	−63.37	3
M12	$p(\text{temp}), \lambda(\text{forest} + \text{co})$	134.11	4.15	0.03	−58.58	6
M13	$p(\cdot), \lambda(\text{forest} + \text{elevation} + \text{co})$	134.23	4.27	0.02	−58.64	6
M14	$p(\text{temp}), \lambda(\text{elevation})$	134.56	4.60	0.02	−62.23	4
M15	$p(\text{fs}), \lambda(\text{forest} + \text{co})$	134.63	4.67	0.02	−58.85	6
M16	$p(\text{fs}), \lambda(\text{elevation})$	135.02	5.06	0.02	−62.46	4
M17	$p(\text{fs} + \text{temp}), \lambda(\text{co})$	135.45	5.50	0.01	−61.06	5
M18	$p(\text{temp}), \lambda(\text{forest} + \text{elevation})$	135.73	5.77	0.01	−59.39	6
M19	$p(\text{fs} + \text{temp}), \lambda(\text{forest})$	135.82	5.86	0.01	−59.44	6

Competitive models are highlighted in bold characters. Mean dispersion parameters ($\hat{c}$) obtained using MacKenzie and Bailey's goodness-of-fit test for best models were: $\hat{c}_{\text{Bridled Quail-Dove M1}} = 0.98$; $\hat{c}_{\text{Zenaida Dove M2}} = 0.66$; $\hat{c}_{\text{Zenaida Dove M6}} = 0.68$; $\hat{c}_{\text{Zenaida Dove M3}} = 0.66$.

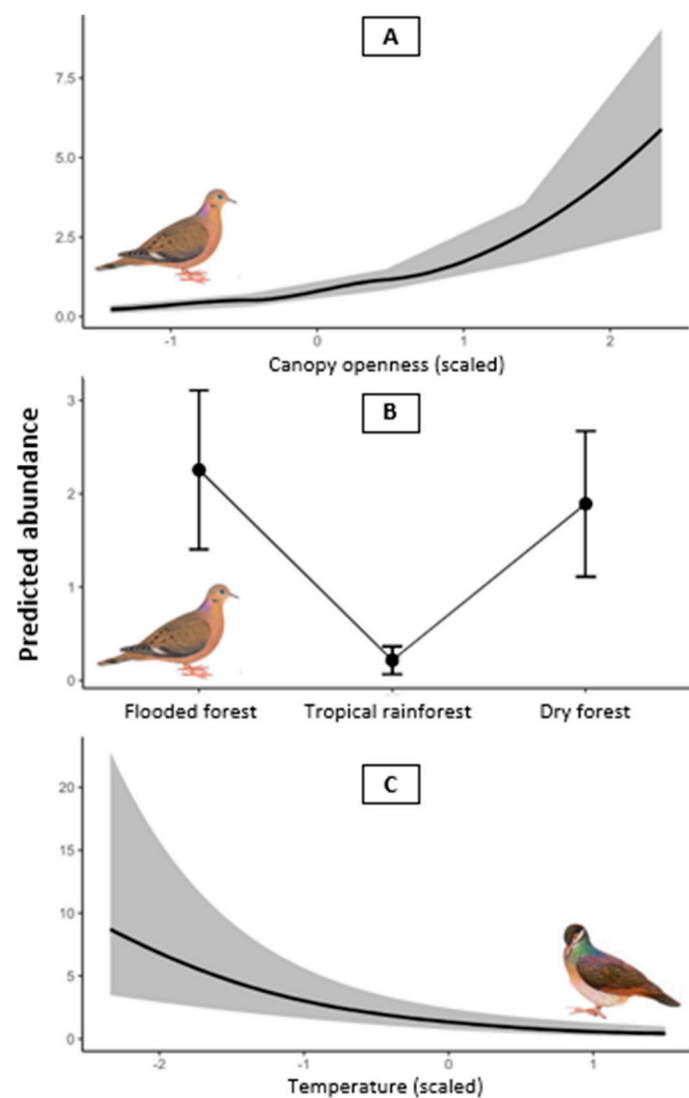


Figure 3. Selected model predictions for Zenaida Dove (A,B) and Bridled Quail-Dove (C), (predicted covariate effects with 95% CI, when all other covariates are held constant at their mean). These model predictions are from the best models for each of these species (see Table 1).

Moreover, this model suggested that none of the environmental variables influenced BQD detection in Guadeloupe (Table 1). Models including an influence of forest structure or temperature on detection were not retained in model selection (Table 1). Abundance-detection was not modelled for the RQD, given the small sample size (10 detections over five different stations).

A total of three models were retained ($\Delta AIC_c < 2$, Table 1) for ZD. The ZD abundance was significantly lower in the tropical rainforest compared to the two other habitats in both the first ($\beta = -2.34$, $SE = 0.76$, $p < 0.01$) and the second best ($\beta = -1.93$, $SE = 0.83$, $p = 0.02$) models. On the other hand, a positive effect of canopy openness on ZD abundance was retained in both the second best model ($\beta = 0.5$, $SE = 0.34$, $p = 0.15$), and the third one ($\beta = 0.86$, $SE = 0.26$, $p < 0.01$; Figure 3). Forest structure and temperature had no influence on detection.

3.3. Circadian Activity, Temporal Segregation and Spatial Cooccurrence

The proportions of birds that were captured during the different periods of the diel cycle (night, dawn, day, and dusk) did not differ between the two sampling periods (Fisher exact test, PBQD = 0.13, PRQD = 1, PZD = 0.24). Therefore, the data were pooled for further

analysis. Table 2 shows Jacobs Selectivity Index (JSI) for each of the defined periods of the diel cycle.

Table 2. Assessing the selectivity in diel rhythm activity of the studied species using the Jacobs Selectivity Index (JSI) for each of the defined periods of the diel cycle (night, dawn, day, and dusk). JSI ranges from −1 to 1, with −1 being total avoidance, 0 no preference, and 1 total preference.

Species	JSInight	JSIdawn	JSIday	JSIdusk
<i>G. mystacea</i>	−1.00 [−1.00; −1.00] *	−0.25 [−0.49; −0.02] *	0.72 [0.58; 0.86] *	−0.61 [−0.85; −0.37] *
<i>G. montana</i>	−1.00 [−1.00; −1.00] *	−0.75 [−1.41; −0.01] *	0.69 [−0.05; 1.33]	−0.81 [−1.31; −0.26] *
<i>Z. aurita</i>	−1.00 [−1.00; −1.00] *	−0.74 [−0.93; −0.56] *	0.93 [0.88; 0.98] *	−0.84 [−1.04; −0.64] *
<i>F. catus</i>	0.52 [0.21; 0.83] *	−0.83 [−1.03; −0.62] *	−0.29 [−0.69; 0.11]	−0.67 [−0.93; −0.40] *
<i>C. familiaris</i>	−0.39 [−0.80; 0.03] *	−0.79 [−1.03; −0.55] *	0.42 [0.01; 0.82] *	−0.73 [−1.06; −0.41] *
<i>U. auropunctata</i>	−0.92 [−1.00; −0.85] *	−0.68 [−0.81; −0.56] *	0.86 [0.79; 0.92] *	−0.61 [−0.77; −0.44] *
Rodents	0.90 [0.86; 0.93] *	−0.75 [−0.85; −0.66] *	−0.94 [−1.00; −0.88] *	−0.64 [−0.74; −0.53] *
<i>P. lotor</i>	0.84 [0.58; 1.11] *	−0.96 [−1.02; −0.91] *	−0.99 [−1.01; −0.96] *	−0.74 [−1.03; −0.44] *
Humans	−0.95 [−0.99; −0.90] *	−0.80 [−1.91; −0.69] *	0.92 [0.89; 0.96] *	−0.76 [−0.89; −0.62] *
Birds	−0.77 [−0.98; −0.56] *	−0.44 [−0.65; −0.24] *	0.70 [0.55; 0.84] *	−0.63 [−0.80; −0.46] *

* $p < 0.05$: Significant selection, whenever the 95 % confidence interval of the JSI did not overlap zero.

The essential diurnal activity of the three columbid species was largely confirmed. However, although they were most active during daytime, the three columbid species showed some activity at dawn and dusk. Domestic dogs and small Indian mongooses were mainly active during daytime, whereas rodents and raccoons were essentially nocturnal. Cats were more active during the night-time, and practically inactive at dawn. Finally, human activity essentially occurred during the daytime, with no recorded activity during the night-time.

BQD positively co-occurred spatially with mongooses, birds, rodents, and RQD (Table 3). However, BQD, mongoose, birds, and RQD presented an explicit diurnal pattern, whereas rodents presented strictly nocturnal activity (Table 2, Appendix A Figure A1).

Table 3. Spatial co-occurrence probabilities of *Geotrygon mystacea*, *Geotrygon montana*, and *Zenaida aurita* with birds (pooling all species; Supplementary Table S1), rodents (pooling all species), *Felis catus*, *Canis familiaris*, *Urva auropunctata*, *Procyon lotor*, as well as humans. Associations of species were classified as positive ($P_{greater}$) or negative (P_{less}). Random associations of species are not reported.

Pair of Species		Obs. Cooccur.	Prob. Cooccur.	Exp. Cooccur.	P_{less}	$P_{greater}$
<i>G. mystacea</i>	<i>U. auropunctata</i>	36	0.24	28.7	0.9998	0.0010
<i>G. mystacea</i>	Birds	33	0.22	26.3	0.9988	0.0049
<i>G. mystacea</i>	Rodents	36	0.24	28.7	0.9998	0.0010
<i>Z. aurita</i>	<i>C. familiaris</i>	14	0.08	9.3	0.9894	0.0311
<i>Z. aurita</i>	<i>F. catus</i>	18	0.08	9.6	1.0000	0.0003
<i>Z. aurita</i>	<i>P. lotor</i>	17	0.07	8.5	1.0000	0.0001
<i>G. montana</i>	<i>G. mystacea</i>	9	0.03	3.3	1.0000	0.0002

As a result, BQD and rodents' activity showed little if any overlap (Table 4).

ZD spatially co-occurred with domestic dogs, domestic cats, and raccoons more than expected by chance (Table 3). As ZD, domestic dogs, and mongooses presented a diurnal activity pattern (Table 2, Appendix A Figure A1), their diel activity overlapped largely, whereas raccoons and domestic cats were more active during night-time period (Table 2, Appendix A Figure A1). This resulted in a very small temporal overlap between ZD and raccoons (Table 4), since raccoons hardly showed any activity during daytime (mean JSIday values ≤ -0.94).

Table 4. Activity patterns of bird species that were detected during the survey using the kernel density estimates of diel activity. We favored $\Delta 4$ over $\Delta 1$ as a nonparametric estimator of the coefficient of overlapping as our sample size was above 75. We estimated the precision of overlap coefficients by calculating an average value from 10,000 bootstrap samples for each pair of species.

Overlap	<i>G. mystacea</i>	<i>G. montana</i>	<i>Z. aurita</i>	<i>F. catus</i>	<i>C. familiaris</i>	<i>U. auropunctata</i>	Rodents	<i>P. lotor</i>	Human
<i>G. montana</i>	0.66								
<i>Z. aurita</i>	0.68	0.45							
<i>F. catus</i>	0.51	0.37	0.45						
<i>C. familiaris</i>	0.71	0.49	0.70	0.66					
<i>U. auropunctata</i>	0.84	0.57	0.84	0.52	0.76				
Rodents	0.11	0.10	0.07	0.60	0.30	0.12			
<i>P. lotor</i>	0.12	0.11	0.08	0.60	0.31	0.13	0.88		
Human	0.68	0.44	0.87	0.44	0.63	0.81	0.06	0.07	
Birds	0.84	0.59	0.75	0.51	0.78	0.82	0.14	0.14	0.68

4. Discussion

Overall, our results confirm the efficiency of unbaited camera-traps in documenting site occupancy, distribution, and local abundance of ground-dwelling bird species in tropical forests [90,91]. The rates of detection and estimates of naïve occupancy were similar or above what has been previously reported in the literature for two other columbids using the same method (*Aplopelia larvata*, 3 detections/100 trap-days, naïve occupancy = 0.29, Ehlers Smith et al. [53]; *Geophaps smithii*, 15 detections/100 trap days naïve occupancy = 0.30, Davies et al. [92]). Camera-traps thus appears to be a reliable tool for the monitoring of columbid species that can be difficult to observe in tropical forests due to their stealthy nature coupled with dense vegetation and limited visibility [93]. Such conditions actually limit the performance of alternative methods such as point-count sampling, distance sampling, or capture-mark-recapture (CMR) [26,50,53,94,95]. In particular, auditory point count method and auditory distance-sampling have maximal efficiency only when conducted during the peak of calling activity [96,97] and/or when broadcasting the call of the target species [47]. The CMR method allows a reliable estimation of demographic parameters of terrestrial columbid species [26,98], but requires a considerable logistical effort [41]. In addition, the sample of captured and banded birds might not be quite representative of the population studied if capture success varies according to the personality of individuals [99,100].

Our models revealed that neither forest structure nor temperature influenced detection probabilities of BQD and ZD in Guadeloupe. We detected ZD more frequently and in higher abundance at camera-trap survey locations that were dominated by flooded forest and dry forest, thus confirming previous observations [32,101,102]. In addition, Model 4 ($\Delta AIC_c = 2.18$) suggested that elevation had a marginal negative influence on the abundance of ZD, confirming recent observations on Hispaniola [103]. Conversely, we observed BQD more often in the tropical rainforest habitat, as previously reported [28]. Indeed, in the Virgin Islands, Boal [19] found that BQD density was 1.13 individuals/ha in dry forests (covering 90% of the island) and 4.63 individuals/ha in rainforests (covering only 5 % of the island).

Importantly, model selection allowed us to separate the effects of temperature, elevation, and canopy openness on the abundance of BQD. Although the three factors did covary to a certain extent, the best model retained only a negative influence of temperature on abundance. The negative influence of temperature on abundance is particularly informative in the context of global warming [104–108] as increased temperatures might affect bird species [109] directly (via their thermal niche) and indirectly (through increased habitat disturbance [110]). However, very little if any information is available on the influence of elevated temperature on the ecophysiology and behavior of tropical columbids. In addition,

the influence of temperature on the distribution and abundance of BQD on other Caribbean islands has not been documented so far.

Therefore, although the species is not currently considered threatened with extinction, more attention should be given to its distribution in relation to elevation and protected areas in the Caribbean islands.

The sample size for the RQD was too small to detect significant differences in the frequency of observations between habitat types. However, significant spatial and temporal co-occurrence between the two quail dove species suggest that they do not differ much in habitat selection. Indeed, a predominance of RQD in rainforest has been reported in various parts of its distribution [30,98,111].

The use of camera-traps allowed us to obtain a large amount of additional data on other species, in particular introduced alien species that potentially prey upon ground-dwelling columbid species, such as mongooses, domestic cats, domestic dogs, rats, or raccoons. Analysis of diel activity confirmed that rodents, cats, and raccoons are essentially nocturnal, whereas mongooses and dogs are mainly active during the day. The small Indian mongoose was the most common invasive alien species at camera-trap survey locations, confirming its ability to thrive in various habitats on Caribbean islands [45,112,113]. Our observed naïve occupancy rate of 0.72 agrees very well with the estimate of 0.66 that was recently reported for Guadeloupe by Louppe et al. [45]. Small Indian mongooses co-occurred spatially and temporally with BQD more than would be expected by chance. On the other hand, the spatial and temporal distributions of domestic dogs and domestic cats significantly overlapped with that of ZD. However, to what extent predation by invasive exotic mammal species affects populations of ground-dwelling columbids in Guadeloupe remains unclear. Predation on terrestrial bird species by the small Indian mongoose is well established [114–117]. At the scale of the Caribbean, the extinction or decline of quail doves in various islands has been attributed to the introduction of the small Indian mongoose [114,118,119]. Although less common than mongooses (naïve occupancy rate of 0.27), feral cats were present in all habitat types, including protected areas.

The role of domestic and feral cats in the decline and extinction of vertebrate species is of major concern in conservation [120,121]. According to Medina et al. [122], domestic cats have contributed to 14% of the 238 global bird, mammal, and reptile extinctions. More specifically, predation by feral cats on several columbid species has been evidenced on Socorro Island, Mexico [123]. In addition, although raccoons and rats are essentially nocturnal, they may prey upon nests and, possibly, incubating quail dove adults that place their nest at no great height [30,124]. The precise impact of exotic invasive mammals, particularly mongooses and feral cats, on columbids and other bird species of conservation interest in Guadeloupe clearly deserves further investigation. This could be achieved through studying diet composition of predators from faecal pellets and/or stomach contents, preferentially relying on modern molecular tools [125–127]. Such information could be particularly useful to contrast the impact of hunting pressure (see Carvalho et al. [128]), which is limited to a restricted hunting season in Guadeloupe, to that of exotic invasive mammals that are supposedly active all year long.

Based on our results, both ZD and BQD appear to be common and relatively abundant in Guadeloupe, unlike RQD. More specifically, the difference in the local abundance between BQD and RQD at the time of the study was particularly strong, with RQD being observed in only one third of all the survey stations and with an average local abundance that was 13 times lower than that of BQD. This result is consistent with the low number of RQD observations that were reported by STOC-EPS monitoring which consisted in detecting birds by sight and/or by hearing, along line transects (RQD naïve occupancy rates of 0.05, in 2019; [37]).

Interestingly, the predominance of BQD over RQD is more an exception than a general rule in the Caribbean region. Indeed, the opposite situation has been observed in Martinique and in the Virgin Islands [94,129,130]. In that respect, further information on RQD and BQD population dynamics and ecology (particularly addressing trophic niche plasticity,

individual feeding specialization, and partitioning of food resources between the two species in sympatry [131–134]) in Guadeloupe and on other Caribbean islands would be particularly valuable to understand the observed patterns of variation in the abundance of the two species. Such information would also be quite useful for the development of hunting regulations.

Based on our results, we suggest that the regular monitoring of forest columbid species of conservation interest in the Caribbean islands using camera-traps and standardized methodology should be encouraged in the future, and possibly coordinated at the regional level. One way to increase information about abundance, demographic parameters, and population trends could involve banding programs using combinations of colour rings allowing for subsequent individual identification in the field from camera-trap recordings [135,136]. Increasing information on the ecology, demographic trends, and current and future distributions of columbids in the insular Caribbean should be a high conservation priority.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d14060480/s1>, Table S1: Names and descriptions of variables used in the models; Table S2: Land cover categories used in this study. Table S3: Full table of abundance and detection models for the Bridled Quail-Dove and the Zenaida Dove in Guadeloupe forests. Abundance (λ) was modelled according to temperature (temp), elevation, canopy openness (co) or forest types (forest), and the probability of detection (p) was modelled according to forest structure (fs) and temperature (temp).

Author Contributions: Conceptualization, A.J.-P., G.L.-M., and F.C.; methodology, A.J.-P. and F.C.; software, A.J.-P.; validation, F.C. and G.L.-M.; formal analysis, A.J.-P.; investigation, A.J.-P.; resources, F.C.; data curation, A.J.-P.; writing—original draft preparation, A.J.-P.; writing—review and editing, A.J.-P., F.C., and G.L.-M.; visualization, A.J.-P.; supervision, F.C. and G.L.-M.; project administration, G.L.-M. and F.C.; funding acquisition, F.C. All authors have read and agreed to the published version of the manuscript.

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Appendix A

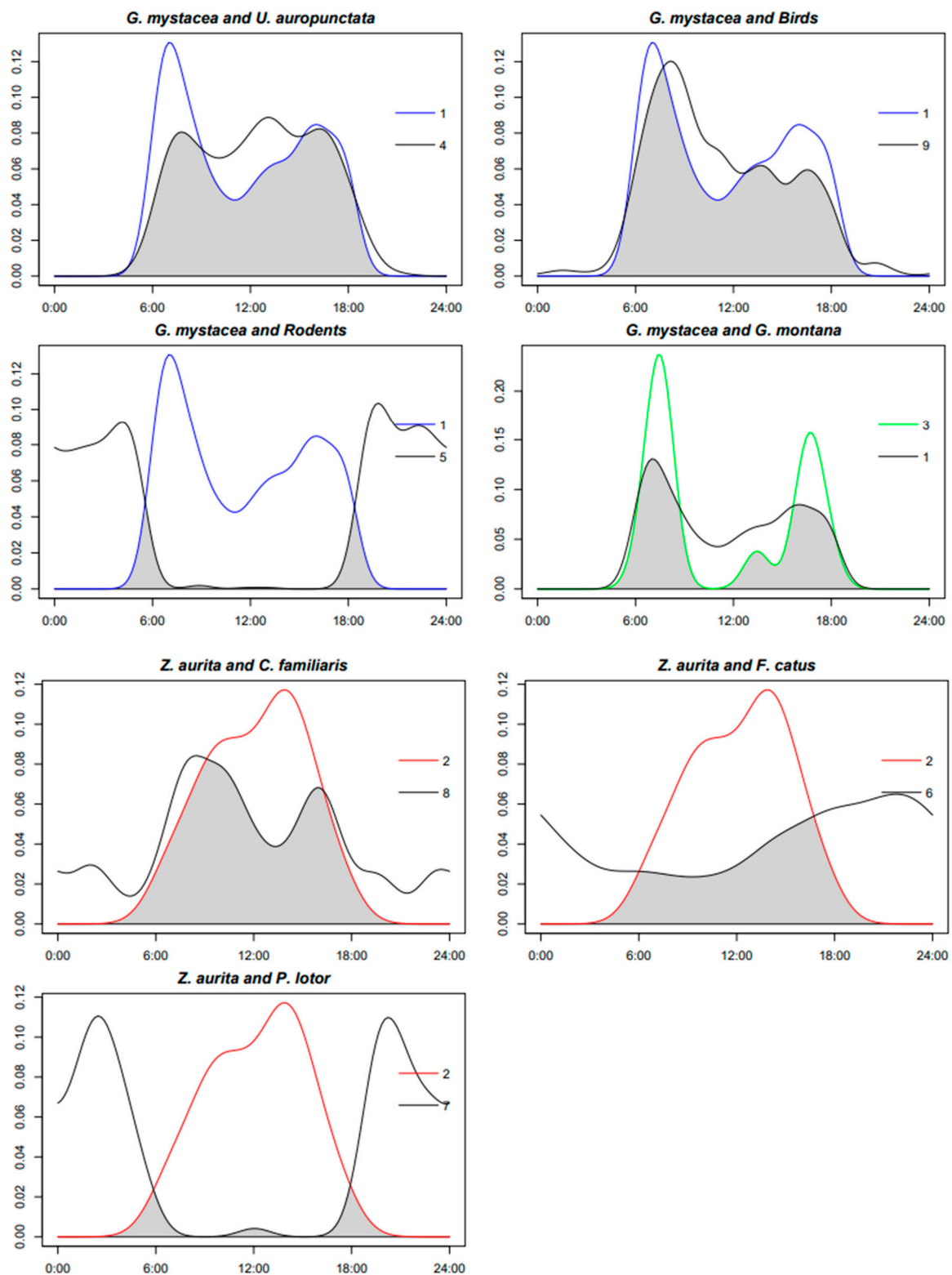


Figure A1. Activity patterns of bird and mammal species detected during this study with 1 = *Geotrygon mystacea*, 2 = *Zenaida aurita*, 3 = *Geotrygon montana*, 4 = *Urva auropunctata*, 5 = Rodents, 6 = *Felis catus*, 7 = *Procyon lotor*, 8 = *Canis familiaris* and 9 = Birds.

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Supplementary Material

Table S1. Names and descriptions of variables used in the models.

Variable	Description	Source
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Co-occurrence analyses.

Zenaida Dove	Detection of Zenaida Dove	This survey camera traps data
Bridled Quail-Dove	Detection of Bridled Quail-Dove	This survey camera traps data
Ruddy Quail-Dove	Detection of Ruddy Quail-Dove	This survey camera traps data
Birds	Among all birds detected: Forest thrush (<i>Turdus lherminieri</i>), Green heron (<i>Butorides virescens</i>), American yellow warbler (<i>Setophaga petechia</i>), Carib grackle (<i>Quiscalus lugubris</i>), Yellow-crowned Night Heron (<i>Nyctanassa violacea</i>), Gray kingbird (<i>Tyrannus dominicensis</i>), Bananaquit (<i>Coereba flaveola</i>), Lesser Antillean bullfinch (<i>Loxigilla noctis</i>), Green-throated carib (<i>Eulampis holosericeus</i>), Chicken (<i>Gallus gallus domesticus</i>), Common ground dove (<i>Columbina passerina</i>).	This survey camera traps data
Raccoon	Detections of northern raccoons	This survey camera traps data
Mongoose	Detections of small Indian mongooses	This survey camera traps data
Cat	Detections of domestic cats	This survey camera traps data
Dog	Detections of domestic dogs	This survey camera traps data
Rodents	Combined detections of all rodent species	This survey camera traps data
Humans	Detections of humans	This survey camera traps data

Occupancy and detection models.

Forest cover	Forest cover categories as described in Table S2	Map of Guadeloupe forests
Forest structure	Visual estimate on each camera-trap survey locations	These camera-trap survey locations
Elevation	Elevation measured at each site	GPS Garmin Dakota 20
Temperature	Daily temperature measured at each site	This survey camera traps data
Canopy openness	Visual estimate on each camera-trap survey locations	These camera-trap survey locations

Table S2. Land cover categories used in this study.

Categories	Description
Tropical rainforest	Montane rainforests, submontane rainforests
Flooded forest	Swamp forest Mangrove
Dry forest	Semi-deciduous forests Semi-deciduous forests on limestone ground Seasonal evergreen forests Formation with predominant edaphic determinism, rocky coastline

Table S3: Full table of abundance and detection models for the Bridled Quail-Dove and the Zenaida Dove in Guadeloupe forests. Abundance (λ) was modelled according to temperature (temp), elevation, canopy openness (co) or forest types (forest), and the probability of detection (p) was modelled according to forest structure (fs) and temperature (temp).

	Models	AICc	Δ AICc	Weight	logLik	d.f.
Bridled Quail-Dove						
M1	p(.),λ(temp)	146.83	0.00	0.48	-69.82	3.00
M2	p(temp), λ (temp)	149.42	2.59	0.13	-69.66	4.00
M3	p(fs), λ (temp)	149.44	2.61	0.13	-69.67	4.00
M4	p(.), λ (forest+temp)	151.03	4.20	0.06	-68.85	5.00
M5	p(fs+temp), λ (temp)	152.45	5.62	0.03	-69.56	5.00
M6	p(.), λ (forest)	152.66	5.83	0.03	-71.28	4.00
M7	p(.), λ (elevation)	152.97	6.14	0.02	-72.88	3.00
M8	p(fs), λ (forest+temp)	153.68	6.85	0.02	-68.37	6.00
M9	p(.), λ (forest+co)	153.89	7.06	0.01	-70.28	5.00
M10	p(.), λ (co)	154.16	7.33	0.01	-73.48	3.00
M11	p(temp), λ (forest+temp)	154.41	7.58	0.01	-68.73	6.00
M12	p(temp), λ (co)	154.63	7.80	0.01	-72.26	4.00
M13	p(temp), λ (forest)	154.96	8.13	0.01	-70.82	5.00
M14	p(temp), λ (elevation)	155.44	8.61	0.01	-72.67	4.00
M15	p(fs), λ (forest)	155.51	8.68	0.01	-71.09	5.00
M16	p(.), λ (forest+elevation)	155.54	8.71	0.01	-71.10	5.00
M17	p(fs), λ (elevation)	155.85	9.02	0.01	-72.87	4.00
M18	p(temp), λ (forest+co)	156.54	9.71	0.00	-69.80	6.00
M19	p(fs), λ (co)	157.06	10.23	0.00	-73.48	4.00
M20	p(fs), λ (forest+co)	157.17	10.34	0.00	-70.11	6.00
M21	p(.), λ (forest+elevation+co)	157.21	10.38	0.00	-70.13	6.00
M22	p(fs+temp), λ (co)	157.34	10.51	0.00	-72.01	5.00
M23	p(fs+temp), λ (forest)	157.62	10.79	0.00	-70.34	6.00
M24	p(fs+temp), λ (forest+temp)	157.66	10.83	0.00	-68.33	7.00
M25	p(temp), λ (.)	158.00	11.17	0.00	-75.40	3.00
M26	p(temp), λ (forest+elevation)	158.53	11.70	0.00	-70.80	6.00
M27	p(fs+temp), λ (elevation)	158.57	11.74	0.00	-72.62	5.00
M28	p(fs), λ (forest+elevation)	158.70	11.87	0.00	-70.88	6.00
M29	p(.), λ (.)	159.50	12.67	0.00	-77.46	2.00
M30	p(fs+temp), λ (forest+co)	159.73	12.89	0.00	-69.36	7.00
M31	p(temp), λ (forest+elevation+co)	160.59	13.76	0.00	-69.79	7.00
M32	p(fs), λ (forest+elevation+co)	160.85	14.02	0.00	-69.93	7.00
M33	p(fs+temp), λ (.)	160.91	14.08	0.00	-75.40	4.00
M34	p(fs+temp), λ (forest+elevation)	161.66	14.83	0.00	-70.33	7.00
M35	p(fs), λ (.)	161.69	14.86	0.00	-77.25	3.00
M36	p(fs+temp), λ (forest+elevation+co)	164.32	17.49	0.00	-69.36	8.00

Zenaida Dove						
M1	p(.),λ(forest)	129.96	0.00	0.21	-59.93	4
M2	p(.),λ(forest+co)	131.06	1.10	0.12	-58.86	5
M3	p(.),λ(co)	131.17	1.21	0.11	-61.98	3
M4	p(.),λ(elevation)	132.14	2.18	0.07	-62.47	3
M5	p(temp),λ(forest)	132.48	2.53	0.06	-59.58	5
M6	p(.),λ(forest+elevation)	133.00	3.05	0.04	-59.84	5
M7	p(.),λ(forest+temp)	133.12	3.16	0.04	-59.89	5
M8	p(fs),λ(forest)	133.16	3.20	0.04	-59.91	5
M9	p(temp),λ(co)	133.42	3.46	0.04	-61.66	4
M10	p(fs),λ(co)	133.53	3.57	0.03	-61.71	4
M11	p(.),λ(temp)	133.94	3.98	0.03	-63.37	3
M12	p(temp),λ(forest+co)	134.11	4.15	0.03	-58.58	6
M13	p(.),λ(forest+elevation+co)	134.23	4.27	0.02	-58.64	6
M14	p(temp),λ(elevation)	134.56	4.60	0.02	-62.23	4
M15	p(fs),λ(forest+co)	134.63	4.67	0.02	-58.85	6
M16	p(fs),λ(elevation)	135.02	5.06	0.02	-62.46	4
M17	p(fs+temp),λ(co)	135.45	5.50	0.01	-61.06	5
M18	p(temp),λ(forest+elevation)	135.73	5.77	0.01	-59.39	6
M19	p(fs+temp),λ(forest)	135.82	5.86	0.01	-59.44	6
M20	p(temp),λ(forest+temp)	136.09	6.13	0.01	-59.58	6
M21	p(temp),λ(temp)	136.42	6.47	0.01	-63.16	4
M22	p(fs),λ(temp)	136.48	6.52	0.01	-63.19	4
M23	p(fs),λ(forest+elevation)	136.61	6.65	0.01	-59.84	6
M24	p(fs),λ(forest+temp)	136.64	6.68	0.01	-59.85	6
M25	p(temp),λ(forest+elevation+co)	137.51	7.55	0.00	-58.25	7
M26	p(fs+temp),λ(elevation)	137.59	7.64	0.00	-62.13	5
M27	p(fs+temp),λ(forest+co)	137.89	7.93	0.00	-58.44	7
M28	p(fs),λ(forest+elevation+co)	138.29	8.33	0.00	-58.64	7
M29	p(fs+temp),λ(temp)	138.99	9.03	0.00	-62.83	5
M30	p(.),λ(.)	139.29	9.34	0.00	-67.36	2
M31	p(fs+temp),λ(forest+elevation)	139.66	9.70	0.00	-59.33	7
M32	p(fs+temp),λ(forest+temp)	139.84	9.88	0.00	-59.42	7
M33	p(temp),λ(.)	140.09	10.13	0.00	-66.44	3
M34	p(fs),λ(.)	141.62	11.66	0.00	-67.21	3
M35	p(fs+temp),λ(forest+elevation+co)	141.98	12.02	0.00	-58.19	8
M36	p(fs+temp),λ(.)	142.99	13.03	0.00	-66.44	4

Competitive models are highlighted in bold characters. Mean dispersion parameters ($\hat{c}$) obtained using MacKenzie and Bailey's goodness-of-fit test for best models were: $\hat{c}_{\text{Bridled Quail-Dove M1}} = 0.98$; $\hat{c}_{\text{Zenaida Dove M2}} = 0.66$; $\hat{c}_{\text{Zenaida Dove M6}} = 0.68$; $\hat{c}_{\text{Zenaida Dove M3}} = 0.66$.

Article 2

Factors affecting spatial occupancy and local abundance of the Forest Thrush, *Turdus lherminieri*, in Guadeloupe forests

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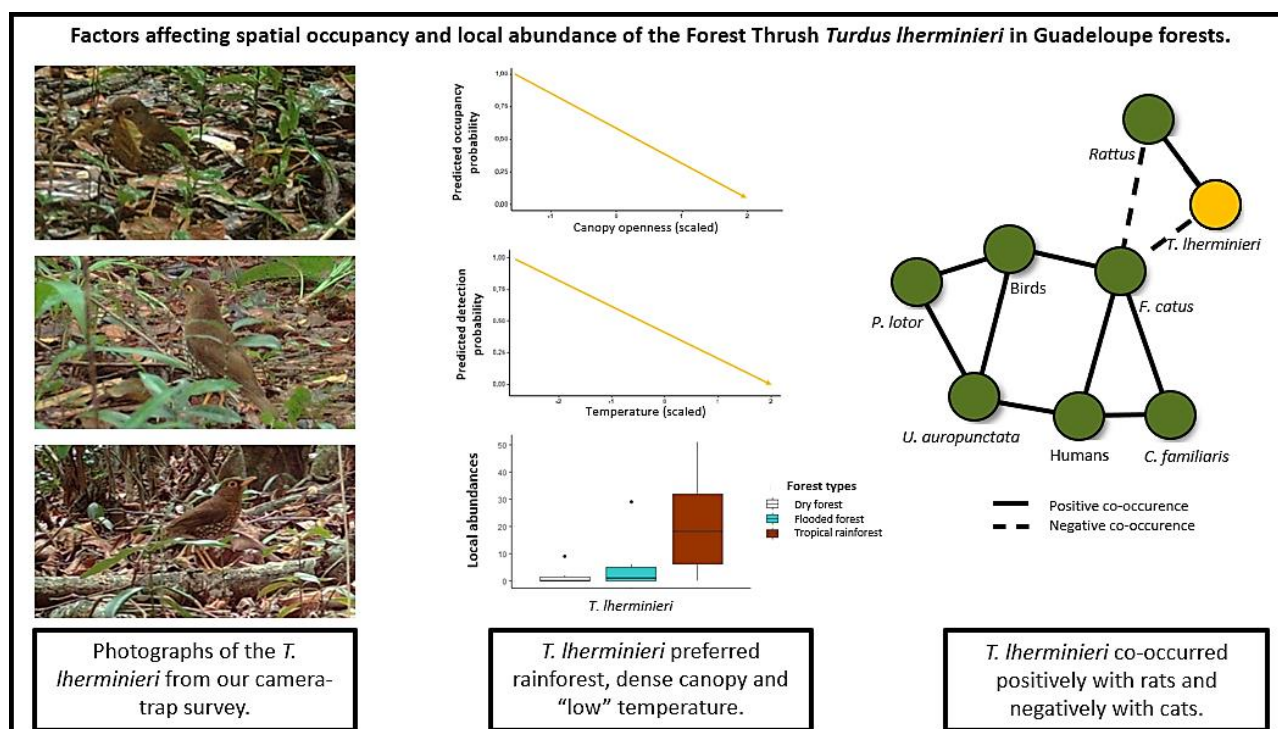
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Graphical abstract





Factors affecting spatial occupancy and local abundance of the Forest Thrush, *Turdus lherminieri*, in Guadeloupe forests

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Abstract

The Forest Thrush (FT), *Turdus lherminieri*, is a secretive, ground-dwelling forest bird species of conservation concern, endemic to only four Caribbean islands. Factors influencing habitat selection and abundance by FT have been seldom documented so far. We assessed variation in the presence and abundance of FT in various forested habitats in Guadeloupe. To that end, we deployed 5-camera-trap arrays over 14 days on 24 different survey stations resulting in 1680 trap days. We observed FT more frequently at camera trap stations where rainforest dominated, with local abundance declining with increasing canopy openness. Furthermore, temperature was the most important factor affecting the presence of FT at our study sites. FT was essentially diurnal, with some activity at dawn and dusk. We document for the first-time spatial co-occurrence between FT and potential mammal predators. FT co-occurred positively with rats and negatively with cats. Although FT is globally listed as near threatened by IUCN, the species appeared to be relatively abundant in Guadeloupe, possibly as a consequence of the suspension of hunting since 2014 and/or the almost total protection of the Guadeloupe tropical rainforest. We recommend the use of camera traps to improve knowledge for the conservation status of the species in other part of its area of distribution and to provide additional information on the potential impact of exotic predatory mammals.

Keywords Bird · Camera-trap · Canopy openness · Exotic mammal predators · Tropical rainforest · Temperature

Introduction

Extensive habitat destruction is a major source of biodiversity loss worldwide (Pimm et al. 2006; Brook et al. 2008). This phenomenon mainly results from human activities such as logging, agricultural expansion, or human settlement (Wilcove et al. 2013; Dávalos et al. 2016). In this respect, the conservation of tropical forests is of prime importance, as they support more than two-thirds of the World's biodiversity despite covering less than 10% of the Earth's land surface. However, they are particularly exposed to unabated deforestation and forest fragmentation (Bradshaw et al. 2009; Hansen et al. 2013; Giam 2017). Consequently, many

tropical forest species are declining, particularly in restricted areas, such as oceanic islands (Alroy 2017). This is particularly true of birds, with more than 600 globally threatened species (Stattersfield et al. 1998; Ricketts et al. 2005) and more than 90% of species extinctions having occurred on islands (Johnson and Stattersfield 1990; Banko et al. 2013).

The Caribbean islands constitute one of the 25 hotspots of biodiversity on Earth (Myers et al. 2000; Pimm et al. 2014), with a high diversity of bird species and high levels of avian endemism (Vázquez-Miranda et al. 2007; Catanach et al. 2021). However, the small extension of this hotspot makes it one of the most vulnerable areas of conservation importance (Brooks et al. 2002). Deforestation is in particular widespread in the insular Caribbean due to human exploitation (Tole 2001; Dolisca et al. 2007; Hedges et al. 2018) and natural disasters (Wiley and Wunderle 1993; Eppinga and Pucko 2018). This phenomenon is particularly affecting the avifauna, with several Caribbean endemic bird species being declining (Wunderle 2008; Arendt et al. 2013; Lloyd et al. 2016; Devenish-Nelson et al. 2019; Akresh et al. 2021). In addition, scientific attention given to Caribbean forest-dependent varies markedly among Caribbean islands and family groups (Devenish-Nelson et al. 2019).

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In this context, we studied the Caribbean-endemic Forest Thrush (hereafter FT), *Turdus lherminieri*, typically found in various forest habitat types (Benito-Espinal and Hautcastel 2003; Arnoux 2012; Parashuram et al. 2015). The species' distribution area is restricted to four islands in the Lesser Antilles, Montserrat, Guadeloupe, Dominica, and St Lucia (Benito-Espinal and Hautcastel 2003; Eraud et al. 2012). Currently, FT is globally listed as near threatened by IUCN, considering the impact of anthropogenic deforestation and introduced predators. The Montserrat population declined abruptly following the 1995–1997 volcanic eruptions but appears to have recovered since then (Dalsgaard et al. 2007). A small, possibly declining, population exists in Dominica (Durand and Baptiste 2008), whereas the St Lucia population might be limited to a few individuals, if not extinct (Toussaint et al. 2009; Arnoux et al. 2014). The larger Guadeloupe FT population appears to be stable, according to data from audio-count surveys and mist netting (Eraud et al. 2013; Guillemot et al. 2020). The four populations have been considered as distinct subspecies according to plumage patterns (Clement and Hathway 2000; Zuccon 2011). Accordingly, Arnoux et al. (2013, 2014) provided some evidence for morphological and genetic differentiation between Montserrat, Guadeloupe, and Dominica, as well as within Guadeloupe, possibly as a result of habitat fragmentation.

At a more local scale, Parashuram et al. (2015) studied the influence of local habitat structure on FT abundance in Montserrat, relying on visual and acoustic detection during point count surveys. They concluded that FT prefers mature mesic and wet forests at mid elevations. However, the performance of methods relying on visual and auditory cues to survey tropical forest birds may vary according to habitat type, in direct relation to habitat characteristics and sound attenuation (Waide and Narins 1988; Anderson et al. 2015), possibly affecting conclusions about habitat selection. In addition, auditory point count method has maximal efficiency only when conducted during the peak of calling activity (Levesque and Lartiges 2000; Rivera-Milán et al. 2022) and/or when broadcasting the call of the target species (Cambrone et al. 2021). A potential alternative survey method consists in relying on camera traps. In comparison with point count surveys, the use of camera traps allows the collection of various and valuable ecological information such as the presence of other species and diel activity. The method is particularly suitable for studying discrete and reclusive bird species such as FT (O'Connell et al. 2011; Suwanrat et al. 2015; Smith et al. 2017; Cook et al. 2020; Jean-Pierre et al. 2022). Finally, species distribution coupled with environmental variables can easily be modelled from camera-trap data (Maseko et al. 2017; Smith et al. 2017).

We therefore relied on camera traps to [1] estimate FT local abundance, detection and occupancy in Guadeloupe

forests, [2] understand the influence of environmental variables on occupancy, detection and abundance, and [3] assess spatiotemporal co-occurrence between FT and potential mammal predators, including humans.

Material and methods

Study area

Field work took place on Basse-Terre and Grande-Terre, the two main islands of the Guadeloupe archipelago, French West Indies, which are separated by a narrow sea channel. The western island of Basse-Terre is mainly mountainous, with a maximum height of 1467 m (Gadalia et al. 1988), whereas the eastern island of Grande-Terre is lower and flatter, with a maximum height of 177 m, and is of coral-limestone formation (Lasserre 1961). The elevation gradient translates into a high diversity of habitats, with tropical forest dominating over tropical dry forest and tropical wet coastal forest (Rousteau 1996a).

Data collection

Data on the presence of FT and that of potential mammalian predators were collected during a study initially aimed at documenting the presence and abundance of two quail-dove species (Jean-Pierre et al. 2022). We relied on passive infrared camera traps (Moultrie© M-40i, with a 125° angle of view) to document the presence and assess the abundance of FT and other species. To that end, we surveyed 24 stations (each station consisting of an array of 5 camera traps) over 2 separate 7-day periods between February and May 2019, including 6 tropical dry forest stations, 6 tropical wet coastal forest stations and 12 tropical rainforest stations (Fig. 1, see Jean-Pierre et al. 2022 for additional information).

Although Guadeloupe has a high diversity of forest habitats, steep landscape and extensive urban areas are particularly present. Consequently, stations were set to be representative of the islands' high diversity of forest habitats, along the altitudinal gradient (Smith 2004; Talvitie et al. 2006; Louppe et al. 2021; Jean-Pierre et al. 2022). Stations were set at elevations ranging from 0.76 m to 768.65 m.

At each station, we set up five camera traps along a straight line, with a 200-m distance between adjacent cameras. Each camera-trap location was surveyed twice for a period of seven consecutive days, between February and March 2019 and again between April and May 2019, resulting in 1680 days of trapping. At each camera-trap location, we attached a single camera to a robust tree at a height of between 20 and 30 cm, according to the small body size of the targeted bird species (O'Connell et al. 2011). We selected trees at locations where the vegetation was not

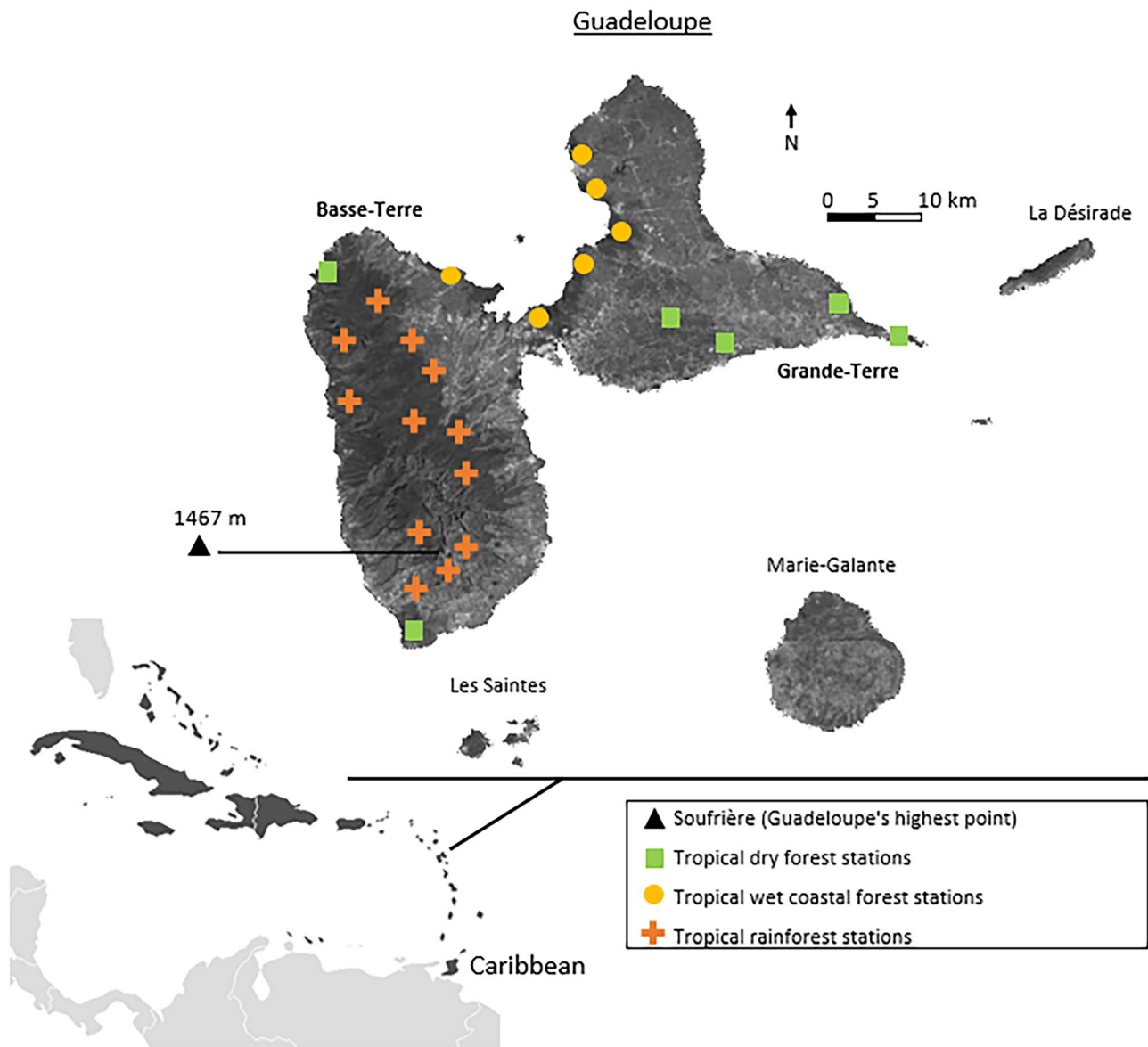


Fig. 1 Locations of the 24 camera trap stations investigated in Guadeloupe between February and May 2019. This includes 6 tropical dry forest stations, 6 tropical wet coastal forest stations and 12 tropical

rainforest stations. Each station had five cameras that were monitored for two 7-day periods. The distance between these stations ranged from 2.82 km to 9.81 km

too dense to allow an optimal range of camera sensor in closed habitats. Cameras were active 24 h d^{-1} . In order to avoid multiple photographs of the same individual over short periods of time, camera-traps were set to take three pictures each time a movement was detected, with a 30-s delay between pictures (Smith et al. 2017). We assessed habitat type, forest structuration, canopy openness and temperature at each camera-trap location. Following (Rousteau 1996b), we considered four forest habitat types (tropical dry forest, tropical rainforest, tropical wet coastal forest) based on direct observations in the field. We visually estimated the forest structuration as dense ($\geq 66\%$ tree cover)

or sparse ($\leq 66\%$ tree cover), with a corresponding score of 1 or -1, respectively. At each station, we calculated an average value for the five camera-traps, thus resulting in a continuous forest structuration index ranging from -1 to 1. We visually estimated canopy openness at each camera-trap location as open ($\geq 66\%$ open), partially open (33–66 open), or closed (0–33% open), with a corresponding score of 1, 0.5 or 0, respectively, (see Jean-Pierre et al. 2022). We then calculated an average for the five camera-traps to obtain a continuous canopy openness index ranging from 0 to 1, for each station (Cook et al. 2020). We collected elevation data and ambient temperature at each camera-trap location

using a Garmin Dakota 20 GPS and camera-trap records, respectively. On each FT detection, ambient temperature was automatically recorded by the camera. Otherwise, we estimated average daily temperature using other diurnal species captured by the camera traps. According to the pattern of diel activity of FT (see [results](#)), we only took into account captures at morning, noon and afternoon.

Statistical analysis

We used the total number of individuals (captures) of each species at each camera trap location to assess local abundance (Preston 1948). Then, we calculated the total abundance per station by combining the local abundances of the five camera traps at each location. We used a Wilcoxon signed-rank test for paired data (Rosner et al. 2006) to compare estimates of local abundance obtained at each station between the two sampling periods, as the data did not follow a normal distribution (Shapiro–Wilk normality test $p < 0.01$; Mohd Razali and Bee Wah 2011).

To compare the median number of more than two groups, we used a Kruskal–Wallis analysis of variance by ranks, followed by Dunn's tests to perform subsequent pairwise comparisons between groups. We calculated naïve occupancy for each species by dividing the number of camera-trap locations where at least one individual was photographed, by the total number of camera-trap locations. For each species, we also calculated capture per unit effort (camera-trapping sampling occasion) by dividing the number of photographed individuals by 100 trap-days.

The influence of environmental variables on detection and abundance was then assessed using Royle and Nichols' heterogeneity model (Royle and Nichols 2003), which links abundance and heterogeneous detection probabilities. This method is especially recommended for assessing site occupancy at different spatial scales in the case of almost undetectable populations of unmarked individuals (Royle and Nichols 2003; Besnard and Salles 2010). Using data from 7-day trapping sessions, detection was considered as a binary variable (1 = detection, 0 = non-detection, correcting for occasional camera malfunction) at each station considering all identifiable species. Species detection (1) and non-detection (0) were extracted for each camera-trap day (i.e., 24 h period) at each station, with a 10 min buffer time between detections of the same species. Thus, abundance modelling was only concerned with species binary detection history under specific habitat conditions, not with species abundance history. According to Royle and Nichols (2003), the most important source of heterogeneity in site-specific detection probabilities is variation in animal abundance, N_i . The model assumes that all individuals of site i during sample j , have the same detection probabilities, r_{ij} , and that

detections are independent. If at least one individual is found within the site, the species is recorded. Thus, the probability of detecting a species is linked to the probability of detecting an individual by:

$$P_{ij} = 1 - (1 - r_{ij})^{N_i}$$

To maximize observation independence, we analysed data at the station level. In addition, we relied on occupancy-detection models to evaluate the influence of environmental variables on FT distribution. We used the R package « unmarked » v0.13–0 (Fiske and Chandler 2011) to build abundance-detection models and occupancy-detection models.

We modelled abundance (λ) and occupancy (ψ) based on temperature, elevation, canopy openness, and forest type, and probability of detection (p) based on forest structure and temperature. We first ran a model in which both detection probability and abundance (or occupancy) were independent of covariate influence, e.g. $p(\cdot), \lambda(\cdot)$ or $p(\cdot), \psi(\cdot)$. We did not include all environmental variables influencing abundance (or occupancy) and detection in a global model because several of them were highly correlated (Spearman rank correlation test; canopy openness and temperature: $r_s = 0.67$; elevation and temperature: $r_s = -0.82$; $p < 0.01$ in both cases). However, we chose to keep all the environmental variables for modelling occupancy and abundance, as model selection allowed us to separately consider highly correlated variables. Accordingly, we modelled the influence of each environmental variable on p while holding λ (or ψ) constant, and vice versa, e.g., $[p(\text{covariate1}), \lambda(\cdot)]$ and $[p(\text{covariate1}), \psi(\cdot)]$ or $[p(\cdot), \lambda(\text{covariate1})]$ and $[p(\cdot), \psi(\text{covariate1})]$. Finally, each environmental variable was tested on p , without or with additive effects, e.g., $[p(\text{covariate1} + \text{covariate2}), \psi(\text{covariate1})]$ or $[p(\text{covariate1} + \text{covariate2}), \lambda(\text{covariate1})]$ or $[p(\text{covariate1}), \psi(\text{covariate1} + \text{covariate2})]$ and $[p(\text{covariate1}), \lambda(\text{covariate1} + \text{covariate2})]$. Only covariates that were not correlated between themselves were included in additive effects.

We used Akaike's information criterion to rank models, and models with $AIC_c < 2$ were considered to assess the significance of covariates (Burnham et al. 2011). The ratio of AIC weights was used to calculate evidence for the best model in comparison to other models. Using 10,000 parametric bootstraps, we checked for goodness-of-fit and mean dispersion parameter $\hat{c}$ for all valid models (Burnham and Anderson 1998; MacKenzie and Bailey 2004).

Following Jean-Pierre et al. (2022), we examined spatial and temporal overlap between FT and potential predators, including: domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis familiaris* Linnaeus, 1758), rodents (pooling all species), northern raccoons (*Procyon lotor*, 1758), small Indian mongooses (*Urva auropunctata*, 1836),

and humans. We then considered four different time periods of unequal length to assess diel activity (Lucherini et al. 2009; Gerber et al. 2012; Monterroso et al. 2014): night (from 1 h after sunset to 1 h before sunrise), dawn (from 1 h prior to 1 h after sunrise), day (from 1 h after sunrise to 1 h before sunset), and dusk (from 1 h prior to 1 h after sunset). We considered variation in daylength between the two trapping periods by defining average sunrise and sunset dates for each of them. We first used Fisher's exact test (Fisher 1922, 1992; Agresti 1992) to compare the proportion of birds caught during different periods of the diel cycle (night, dawn, day and dusk) between the two trapping periods. We then used Jacobs Selectivity Index (JSI, Jacobs 1974) to assess selectivity in diel rhythm activity, as described by Monterroso et al. (2014). The JSI scale runs from -1 to 1, with -1 representing total avoidance, 0 representing no preference, and 1 representing total preference. We employed bootstrap resampling (500 replicates) and recalculated the JSI for each bootstrap sample to determine the average JSI index and 95 percent confidence intervals for each period and species. When the 95 percent CI of the JSI was positive (or negative) and did not overlap zero, the four periods were considered positively (or negatively) selected (i.e., used as expected by chance). A paired-sample Wilcoxon test was used to compare the JSI index between the two sampling periods for each species.

We examined spatial co-occurrence of FT with predators using the probabilistic model proposed by Veech (2013), included in the R package "cooccur" v1.0 (Griffith et al. 2016). This model determines to what extent the frequency of co-occurrence of two species differs from what would

be expected under the null hypothesis of independent distributions.

In addition, to explore temporal activity and overlap, we calculated kernel density estimates of diel activity (Meredith and Ridout 2016), using the R "Overlap" v1.1 package (Niedballa et al. 2016). We favoured $\Delta 4$ over $\Delta 1$ as a non-parametric estimator of the coefficient of overlapping as our sample size was larger than 75 (Schmid and Schmidt 2006), as recommended by Ridout and Linkie (2009). We calculated an average value from 10,000 bootstrap samples for each pair of species to estimate the precision of overlap coefficients.

Results

Out of a total of 9450 detection-events, 330 corresponded to FT, 1056 to rodents, 483 to small Indian mongooses, 107 to dogs, 72 to domestic cats, and 101 to racoons, (see Jean-Pierre et al. 2022).

Forest Thrush naïve occupancy and local abundance

As FT local abundance at each trapping station did not differ between the two sessions (Wilcoxon's test, $P=0.26$), we pooled the two data sets for further analysis. Overall, FT was detected on 16 of the 24 camera trapping stations, corresponding to a naïve occupancy rate of 0.67, and a camera trapping rate (number of individual detections/100 trap-days) of 18. Moreover, FT was found in all forest types, although more frequently in survey stations located in the tropical rainforest [$N_{\text{tropical forest}} = 11/12$, $N_{\text{tropical wet coastal forest}} = 3/6$, $N_{\text{tropical dry forest}} = 2/6$; Fisher's exact test, $p=0.02$; Fig. 2].

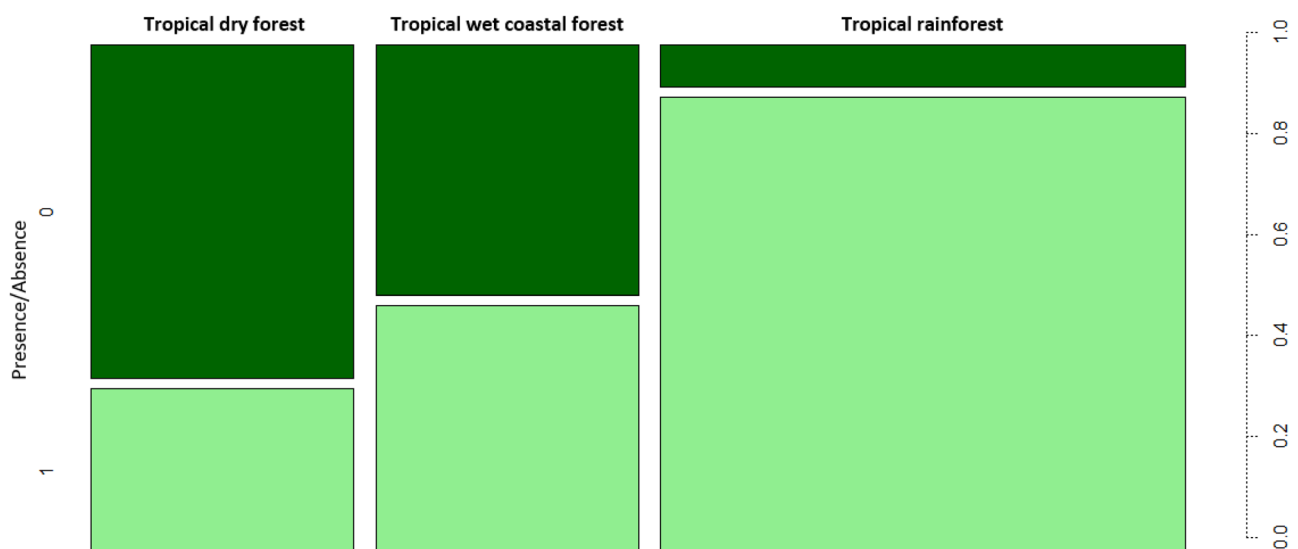


Fig. 2 Presence/absence of the Forest Thrush in all forest types studied, including 12 tropical rainforest stations, 6 tropical wet coastal forest stations, and 6 tropical dry forest stations

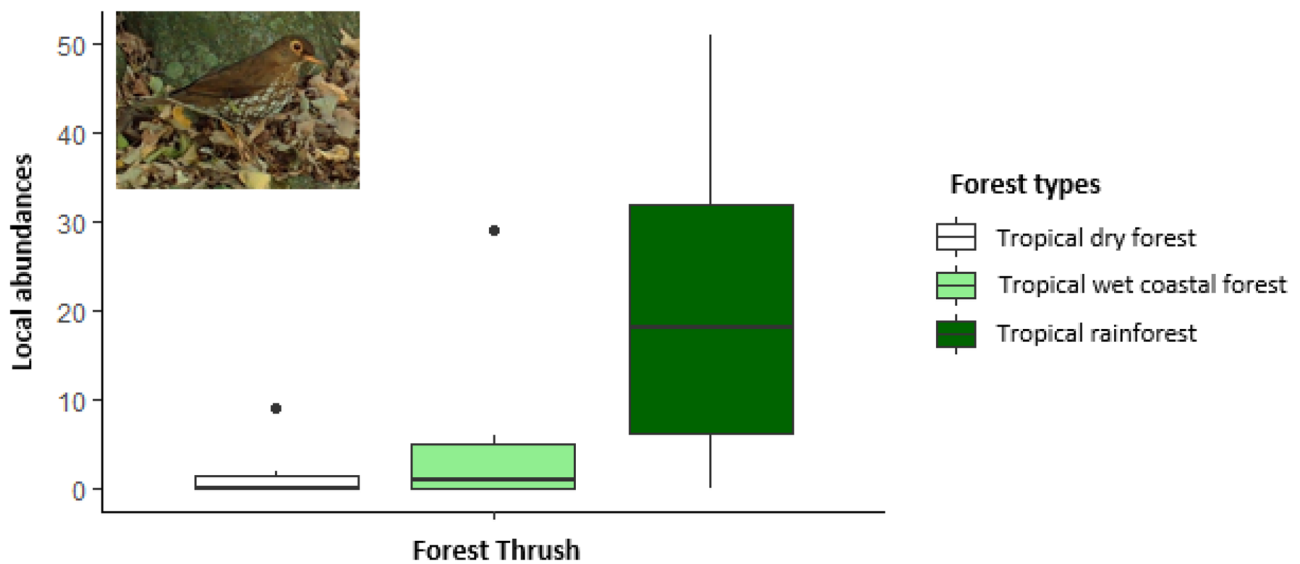


Fig. 3 Local abundance at camera-trap survey locations (including 6 tropical dry forest stations: white; 6 tropical wet coastal forest stations: light-green; 12 tropical rainforest stations: green) where the Forest Thrush was observed in Guadeloupe

Similarly, FT local abundance differed significantly between the three forest habitats, (Kruskal Wallis analysis of variance, $X^2=9.50$, $p=0.009$). However, this was mainly due to FT abundance being significantly higher at tropical rainforest stations than at tropical wet coastal or tropical dry forest stations (post-hoc Dunn's test, $p=0.031$ and $p=0.005$, respectively; Fig. 3), whereas FT abundance does not differ

between stations located in tropical dry forests and tropical wet coastal forests ($p=0.574$).

Modelling occupancy and detection

We used a subset of our camera-trap records for modelling purposes (see [methods](#)). After considering a buffer time of

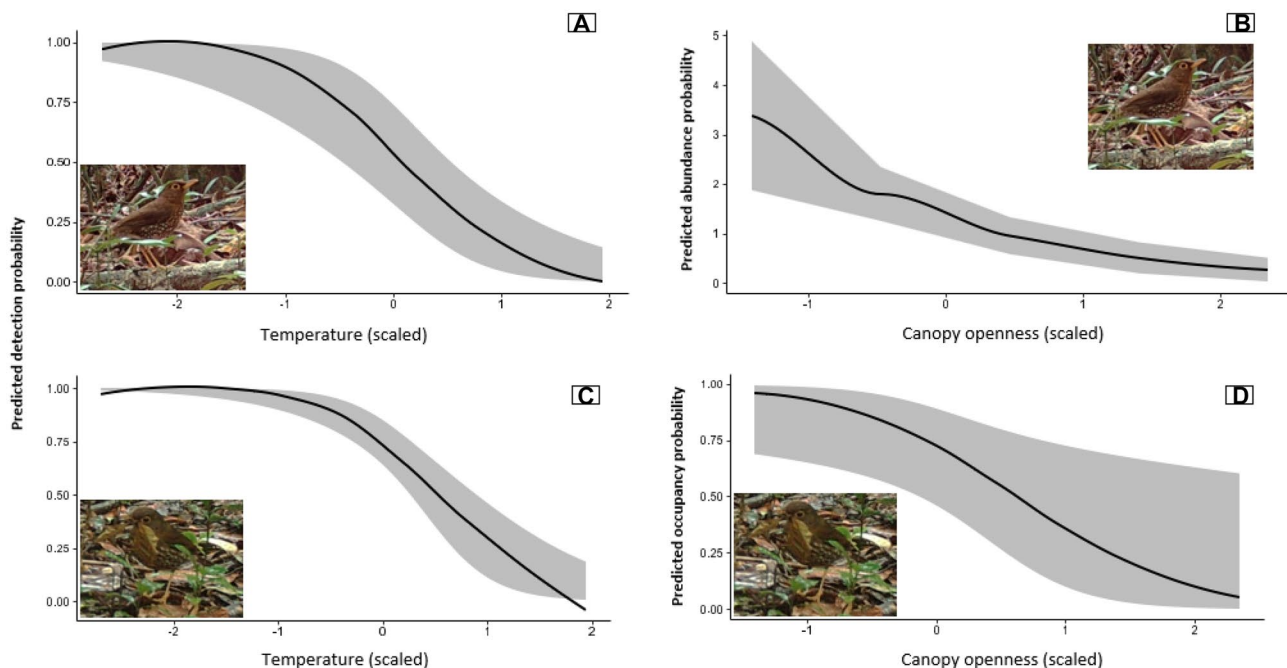


Fig. 4 Predicted detection – abundance probability (A, B) and predicted detection – occupancy probability (C, D) for the Forest Thrush (predicted covariate effects with 95% CI, when all other covariates are held constant at their mean)

10 min between detections of the same species, we retained 297 captures of FT, resulting in 83 detections in model matrices. According to the best model (M1), temperature was the only environmental variable affecting detection ($\beta = -2.27$, $SE = 0.49$, $p < 0.01$), with decreasing detection with increasing temperature (Fig. 4).

In addition, the best model suggested that canopy openness influenced FT occupancy, with decreasing FT occupancy with increasing canopy openness ($\beta = -1.58$, $SE = 0.69$, $p < 0.03$; Table 1).

Mean dispersion parameters $\hat{c}$ obtained using MacKenzie and Bailey's goodness-of-fit test for the four abundance-detection best models were: $\hat{c}_{M1} = 0.70$, $\hat{c}_{M2} = 0.69$, $\hat{c}_{M3} = 0.60$, $\hat{c}_{M4} = 0.66$ and for the occupancy-detection best model was: $\hat{c}_{M1} = 0.78$.

The four best models ($\Delta AICc < 2$) retained temperature as the only informative environmental variable affecting detection ($\beta = -2.17$, $SE = 0.59$, $CI: -3.33, -1$, Table 1), with decreasing level of detection with increasing temperature (Fig. 4). Indeed, although forest structure was retained in model M4, it did not significantly affect FT detection ($\psi = 0.60$, $SE = 0.46$, $p > 0.05$). We therefore retained canopy openness as the only informative environmental variable affecting abundance ($\beta = -0.58$, $SE = 0.31$; Fig. 4). Indeed, although temperature was retained in the M2 model, it did not significantly affect FT abundance ($\lambda = -0.53$, $SE = 0.31$, $p > 0.05$).

Pattern of diel activity and spatial and temporal co-occurrence with potential predators

As the proportions of FT captured during night, dawn, day, and dusk did not differ between the two sampling periods analysis (Fisher exact test, $p = 1$), data were pooled for subsequent analyses. FT was essentially diurnal, with however some activity at dawn and dusk (Table 2).

Domestic dogs, mongooses, humans, were essentially diurnal, whereas rodents, raccoons and domestic cats were essentially nocturnal (see Jean-Pierre et al. 2022). FT positively co-occurred spatially with rodents and negatively with domestic cats (Table 3).

However, rodents were essentially nocturnal (see Jean-Pierre et al. 2022), such that FT activity (Table 2) and rodent activity showed little overlap (Table 4).

Discussion

Forest Thrush local abundance, detection and occupancy in Guadeloupe forests

From previous studies conducted in Guadeloupe (Eraud et al. 2012; Arnoux et al. 2013; Levesque et al. 2020), FT was known to occur mainly in areas of continuous tropical rainforest, from 100 to 1,400 m above sea level and tropical wet coastal forests. On Monserrat, Parashuram et al. (2015) concluded from

auditory and visual point counts that FT prefers mature mesic forest, with birds being more abundant at mid-elevations under closed canopies. We therefore expected to obtain similar results, since tropical rainforests and tropical wet coastal forests have not been much altered by fragmentation, thanks to effective protection by local authorities. Our results confirm the global pattern. We detected FT predominantly in the tropical rainforest habitat and, to a lesser extent, in the tropical wet coastal forest habitat. In addition, their abundance decreased with canopy openness. Comparing to previous studies, however, we also detected the FT in the tropical dry forest habitat, albeit at lower apparent abundance. This is particularly noticeable, as in Guadeloupe this forest ecosystem has been severely degraded by human pressure (Magnin 2018). For example, we detected the presence of FT at Deshaies, a touristic town in Northwestern Basse-Terre. This area, bordering the beaches of Guadeloupe, is particularly subject to human pressure, with high forest fragmentation and intense human frequentation. We therefore suggest monitoring this FT population over the long term in order to estimate demographic trends and connectivity with populations in other habitats, possibly through a capture-mark-recapture study and molecular tools.

In addition, our results provide new information about FT ecology and conservation status in Guadeloupe. First, our data indicate that forest thrushes are relatively abundant in Guadeloupe. Indeed, detection rates and estimates of naïve occupancy obtained in the present study are among the highest values reported so far for ground-dwelling bird species using the same methodology (Supplementary materials Table S1). This might be explained by a combination of factors. First, hunting has been suspended since 2014 in Guadeloupe. More precisely, before the hunting ban, the Guadeloupe FT population was estimated at 46,900–49,500 pairs (93,800–99,000 mature individuals; Eraud et al. 2012). However, the estimation has not been updated since then. On the other hand, from 2015 to 2017, the FT population trend was estimated from 10 sites in Guadeloupe (Guillemot et al. 2020). Although the number of recaptured birds was relatively stable, FT frequency of occurrence increased from 2015 to 2017, possibly as a consequence of the hunting ban. Second, a large proportion of the tropical rainforest habitat is under protection in Guadeloupe (Magnin 2018). Unfortunately, there are no studies comparing FT population trends before and after the protection of its main natural habitat. We then suggest comparing FT population trends between protected and unprotected tropical rainforests to better assess the importance of habitat protection for conservation.

However, a multiyear survey of the Guadeloupe FT population is necessary to ascertain population trends. In particular, comparison of adult survival and breeding success between habitat types would be quite valuable for future management plans. This could be achieved through combining the use of camera-traps with capture that of

Table 1 Occupancy, abundance and detection models for the Forest Thrush in Guadeloupe forests. Occupancy (ψ) and abundance (λ) were modelled according to the temperature (temp), elevation, canopy openness (co), or forest types (forest), and the probability of detection (p) was modelled according to the forest structure (fs) and temperature (temp). All environmental variables influencing abundance and detection were not included in a global model as they were highly correlated between themselves

	Models	AICc	Δ AICc	Weight	logLik	d.f
Occupancy-detection models for the Forest Thrush						
M1	p(temp),ψ(co)	116.70	0.00	0.48	-53.30	4
M2	p(fs + temp), ψ (co)	118.98	2.28	0.15	-52.82	5
M3	p(temp), ψ (temp)	120.51	3.81	0.07	-55.20	4
M4	p(temp), ψ (elevation)	120.93	4.23	0.06	-55.41	4
M5	p(temp), ψ (1)	121.08	4.38	0.05	-56.94	3
M6	p(temp), ψ (forest)	121.22	4.52	0.05	-53.94	5
M7	p(temp), ψ (forest + co)	122.54	5.84	0.03	-52.80	6
M8	p(fs + temp), ψ (temp)	122.91	6.21	0.02	-54.79	5
M9	p(fs + temp), ψ (1)	123.18	6.48	0.02	-56.54	4
M10	p(fs + temp), ψ (elevation)	123.45	6.75	0.02	-55.06	5
M11	p(fs + temp), ψ (forest)	123.92	7.22	0.01	-53.49	6
M12	p(temp), ψ (forest + elevation)	124.56	7.86	0.01	-53.81	6
M13	p(temp), ψ (forest + temp)	124.78	8.08	0.01	-53.92	6
M14	p(fs + temp), ψ (forest + co)	125.83	9.13	0.01	-52.41	7
M15	p(temp), ψ (forest + elevation + co)	126.23	9.53	0.00	-52.62	7
M16	p(fs + temp), ψ (forest + elevation)	127.73	11.03	0.00	-53.37	7
M17	p(fs + temp), ψ (forest + temp)	127.96	11.26	0.00	-53.48	7
M18	p(fs + temp), ψ (forest + elevation + co)	130.08	13.38	0.00	-52.24	8
M19	p(fs), ψ (co)	148.63	31.93	0.00	-69.26	4
M20	p(fs), ψ (temp)	152.25	35.55	0.00	-71.07	4
M21	p(fs), ψ (elevation)	153.00	36.30	0.00	-71.45	4
M22	p(fs), ψ (forest)	153.39	36.69	0.00	-70.03	5
M23	p(fs), ψ (1)	153.89	37.19	0.00	-73.34	3
M24	p(fs), ψ (forest + co)	154.35	37.65	0.00	-68.71	6
M25	p(1), ψ (co)	156.60	39.90	0.00	-74.70	3
M26	p(fs), ψ (forest + elevation)	156.79	40.09	0.00	-69.93	6
M27	p(fs), ψ (forest + temp)	156.84	40.14	0.00	-69.95	6
M28	p(fs), ψ (forest + elevation + co)	158.11	41.41	0.00	-68.56	7
M29	p(1), ψ (temp)	160.51	43.81	0.00	-76.66	3
M30	p(1), ψ (forest)	161.06	44.35	0.00	-75.48	4
M31	p(1), ψ (elevation)	161.45	44.75	0.00	-77.12	3
M32	p(1), ψ (forest + co)	161.64	44.94	0.00	-74.15	5
M33	p(.), ψ (.)	163.23	46.53	0.00	-79.33	2
M34	p(1), ψ (forest + elevation)	164.07	47.36	0.00	-75.37	5
M35	p(1), ψ (forest + temp)	164.14	47.43	0.00	-75.40	5
M36	p(1), ψ (forest + elevation + co)	164.91	48.21	0.00	-73.99	6
Abundance-detection models for the Forest Thrush						
M1	p(temp),λ(co)	115.21	0.00	0.23	-52.55	4
M2	p(temp),λ(temp)	115.91	0.70	0.17	-52.90	4
M3	p(temp),λ(.)	116.08	0.87	0.15	-54.44	3
M4	p(fs + temp),λ(co)	116.80	1.59	0.11	-51.73	5
M5	p(temp), λ (forest)	117.62	2.40	0.07	-52.14	5
M6	p(temp), λ (elevation)	117.63	2.42	0.07	-53.76	4
M7	p(fs + temp), λ (temp)	118.40	3.18	0.05	-52.53	5
M8	p(fs + temp), λ (.)	118.70	3.49	0.04	-54.30	4
M9	p(fs + temp), λ (forest)	119.53	4.31	0.03	-51.29	6
M10	p(temp), λ (forest + co)	120.21	5.00	0.02	-51.63	6
M11	p(fs + temp), λ (elevation)	120.43	5.22	0.02	-53.55	5
M12	p(temp), λ (forest + elevation)	120.56	5.35	0.02	-51.81	6
M13	p(temp), λ (forest + temp)	120.91	5.69	0.01	-51.98	6

Table 1 (continued)

	Models	AICc	Δ AICc	Weight	logLik	d.f
M14	p(fs + temp), λ (forest + elevation)	122.47	7.26	0.01	-50.74	7
M15	p(fs + temp), λ (forest + co)	122.51	7.30	0.01	-50.76	7
M16	p(fs + temp), λ (forest + temp)	123.42	8.20	0.00	-51.21	7
M17	P(temp), λ (forest + elevation + co)	123.75	8.54	0.00	-51.37	7
M18	p(fs + temp), λ (forest + elevation + co)	126.21	10.99	0.00	-50.30	8
M19	p(fs), λ (temp)	132.89	17.68	0.00	-61.39	4
M20	p(.), λ (temp)	133.08	17.87	0.00	-62.94	3
M21	p(.), λ (forest + temp)	136.42	21.21	0.00	-61.54	5
M22	p(.), λ (forest)	137.89	22.68	0.00	-63.89	4
M23	p(fs), λ (elevation)	137.98	22.76	0.00	-63.94	4
M24	p(fs), λ (forest + temp)	138.18	22.97	0.00	-60.62	6
M25	p(fs), λ (co)	138.36	23.15	0.00	-64.13	4
M26	p(.), λ (co)	138.63	23.42	0.00	-65.72	3
M27	p(fs), λ (forest)	138.66	23.45	0.00	-62.66	5
M28	p(.), λ (forest + co)	139.25	24.03	0.00	-62.96	5
M29	p(fs), λ (.)	140.53	25.32	0.00	-66.67	3
M30	p(.), λ (elevation)	140.58	25.37	0.00	-66.69	3
M31	p(fs), λ (forest + co)	140.86	25.65	0.00	-61.96	6
M32	p(.), λ (forest + elevation)	140.95	25.74	0.00	-63.81	5
M33	p(fs), λ (forest + elevation)	142.07	26.86	0.00	-62.57	6
M34	p(.), λ (forest + elevation + co)	142.54	27.33	0.00	-62.80	6
M35	p(fs), λ (forest + elevation + co)	144.61	29.39	0.00	-61.80	7
M36	p(.), λ (.)	148.28	33.06	0.00	-71.85	2

combinations of colour rings allowing subsequent individual identification of marked individuals in the field from photographic records (Toy et al. 2017; Brides et al. 2018; Santangeli et al. 2020).

Second, an important outcome from model selection is that temperature, rather than elevation per se, was the most important factor influencing the presence of forest thrushes at our study sites. Obviously, the two variables are highly correlated between themselves as the species is predominantly found in the tropical rainforest, characterized by its rainy and cold climate due to the higher elevation in the southern half of Basse-Terre (Grubb 1971; Laere et al. 2016). Interestingly, forest type was not retained in the best model, indicating that difference in suitability between habitats might be related to a large extent to difference in ambient temperature. Indeed, due to marked difference in elevations, Basse-Terre, which is

home to the tropical rainforest, has generally higher temperatures than Grande-Terre, which is home to a large part of the tropical dry forest and the tropical wet coastal forest (Rousteau 1996a, b; MDDEE 2012; Laere et al. 2016).

The importance of temperature is particularly relevant in the context of current global warming (Crick 2004; Descamps et al. 2017). Our findings are consistent with other studies, showing that rising temperatures may directly affect bird species, positively or negatively, via their limited thermal niche (Şekercioglu et al. 2012), particularly in rainforest montane birds (de la Fuente et al. 2023). However, the effect of increased mean temperature and variability

Table 2 Jacobs Selectivity Index [JSI] for each of the defined periods of the Forest Thrush diel cycle: night, dawn, day, and dusk

	Night	Dawn	Day	Dusk
JSI	-1.00	-0.45	0.72	-0.46
	[-1.00;-1.00]*	[-0.74;-0.15]*	[0.56;0.88]*	[-0.68;-0.23]*

* $p < 0.05$: Significant selection, whenever the 95% confidence interval of the JSI does not overlap zero

Table 3 Co-occurrence probabilities of Forest Thrush with potential predators, including humans, in Guadeloupe

Co-occurring species	Co-occurrences				
	Observed	Probability	Expected	P_{less}	$P_{greater}$
Domestic cats	8	0.12	13.8	0.0135	0.9960
Rodents	45	0.30	35.8	1.0000	0.0001
Domestic dogs	14	0.11	13.30	0.6887	0.4700
Mongoose	40	0.30	35.80	0.9738	0.0648
Raccoons	10	0.10	12.10	0.2480	0.8685
Humans	22	0.18	21.70	0.6226	0.5243

Table 4 Overlap in diel activity between species detected during the survey

Overlap	Cat	Dog	Mongoose	Rodents	Raccoon	Human
Cat						
Dog	0.66					
Mongoose	0.52	0.76				
Rodents	0.60	0.30	0.12			
Raccoon	0.60	0.32	0.13	0.89		
Human	0.44	0.63	0.81	0.06	0.07	
Forest Thrush	0.53	0.75	0.82	0.16	0.17	0.65

may vary between species depending on their ecology, with forest specialists and insectivores being less able to benefit from increased temperature along an elevational gradient (Dulle et al. 2016). More precisely, comparative evidence suggests that ground-dwelling tropical species with limited dispersal ability, as is the case for FT (Arnoux et al. 2014), might be more affected by climatic instability than arboreal ones (Scheffers et al. 2017). The use of data loggers placed on FT and in their different forested habitats (see Jirinec et al. 2022) in the future may provide a better understanding microhabitat selection in FT in relation to light and thermal niches.

Finally, temperature is likely to co-vary with other variables such as, for instance, soil moisture that was not measured in the present study. Spatiotemporal variation in moisture can have direct influence on arthropods diversity and abundance and, in turn, influence bird distribution in forest habitats (Petit et al. 1985; Smith et al. 2010). Parashuram et al. (2015) suggested that variations of local abundance of FT in different areas may reflect foraging habitat quality. In addition, Stanley et al. (2021) provided strong evidence for an effect of moisture on food abundance and space-use strategies of wood thrushes, *Hylocichla mustelina*, wintering in Belize. In particular, individuals in drier habitats experienced lower food abundance and were in lower body condition.

As other woodland-dwelling thrush species, FT is adapted to forage terrestrially in leaf-litter. Both moisture and a dense canopy could then provide optimal foraging conditions for FT in Guadeloupe, and, possibly, other islands. Future studies should then benefit from assessing to what extent FT spatial distribution and local abundance reflects spatial variation in food availability in leaf-litter, and how this could be affected by climate change.

The use of camera-traps allowed us to document for the first-time spatial co-occurrence between FT and potential mammal predators. FT co-occurred with rats and negatively with cats. Analysis of diel activity indicated that rodents were essentially nocturnal (see Jean-Pierre et al. 2022) whereas FT were essentially diurnal. Rodents may however, prey upon FT eggs since nests are placed at relatively low height from the ground (Benito-Espinal and Hautcastel

2003). The observed spatial segregation between FT and cats may result from active avoidance by FT of areas where cats are particularly abundant or may reflect the local impact of predation by cats on FT. Although, overall, cats were mostly active at night, some individuals were recorded during the day, and it is possible that different individuals have different diel patterns of activity (Hertel et al. 2017), particularly if they specialize on different preys (Dickman and Newsome 2015). Although predation by domestic and feral cats is a major cause of bird mortality in many areas (Loss et al. 2015; Marra and Santella 2016), including islands (Blackburn and Duncan 2007; Medina et al. 2011; Nogales et al. 2013; Doherty et al. 2016), its importance in Caribbean islands has not been documented so far. In the absence of any data on the diet of domestic and feral cats in forested habitats in Guadeloupe, their potential impact on FT populations is difficult to assess. More to the point, the interactions between cats, rats and FT might be particularly complex, particularly through what is known as the "mesopredator release effect" (Courchamp et al. 1999; Ballari et al. 2016; Takimoto and Nishijima 2022). Indeed, superpredators such as feral domestic cats may contribute to control mesopredators such as rats, such that their overall impact on FT is difficult to assess.

The use of camera traps allowed us to obtain valuable ecological information on FT spatial occupancy, abundance, diel activity, spatial co-occurrence with potential mammal predators, and their underlying factors. Similarly, several studies successfully used camera traps to study elusive ground-dwelling avian species (O'Brien and Kinnaird 2008; Ramesh and Downs 2014; Suwanrat et al. 2015; Smith et al. 2017). However, the use of camera-traps comes with some limitations (reviewed in Meek et al. 2015; Cordier et al. 2022). In particular, performance is likely to vary between camera trap models and settings (reviewed in Palencia et al. 2022), such that comparisons between studies should be done with caution. More importantly, camera traps may influence the behaviour of animals through associated mechanical noise, odor, and emitted light, although evidence is mainly limited to mammals (Caravaggi et al. 2020). We therefore used infrared-flash cameras, thus providing back and white pictures, to document the presence

of nocturnal potential predators, to avoid potential biases associated with the use of white flash cameras (Schipper 2007; but see Taggart et al. 2019 for counter evidence in domestic cats). A wise use of camera traps should therefore be based on a balance between the benefit of obtaining high quality data (i.e., color photographs for improved species and/or individual identification) and the risk of interference with the behaviour of targeted species. Faced with all these pitfalls, we suggest that researchers plan a processing time for the captures obtained. In addition, visiting camera trap locations is necessary to verify that the camera traps are working properly.

Conclusions and recommendations

Overall, our study shows that the use of unbaited camera-traps can be a reliable tool to assess spatial occupancy and local abundance of FT, as previously reported in the literature for other ground-dwelling and secretive forest bird species (Suwanrat et al. 2015; Smith et al. 2017; Murphy et al. 2018; Pérez-Irriego and Santos-Moreno 2021; Jean-Pierre et al. 2022). Contrary to auditory point count and auditory distance sampling, the method can be used with the same efficiency independently of seasonal variation in FT vocal activity or meteorological conditions. However, future survey of FT in Montserrat, Guadeloupe, Dominica, and St Lucia, as well as other forest ground-dwelling birds in the insular Caribbean (see Jean-Pierre et al. 2022), may benefit from combining the use of camera-traps with that of acoustic recorders (Buxton et al. 2018). We also suggest to further investigate the potential impact of exotic mammal predators on FT and other ground-dwelling forest birds, possibly through collecting faeces in the wild (Carrión and Valle 2018) or from direct analysis of stomach content (Balestrieri et al. 2011) following control operations.

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Author contributions AJP: Investigation, Methodology, Data collection, Statistical analysis, Writing – original draft, Writing – review and editing. GL: Project administration, Conceptualization, Methodology, Review and editing. LJS: Data collection, Statistical analysis, Writing – original draft. FC: Project administration, Funding acquisition, Conceptualization, Methodology, Statistical analysis, Writing – review and editing.

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Data availability The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Declaration of Competing Interest The authors declare no competing interests.

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Supplementary Information

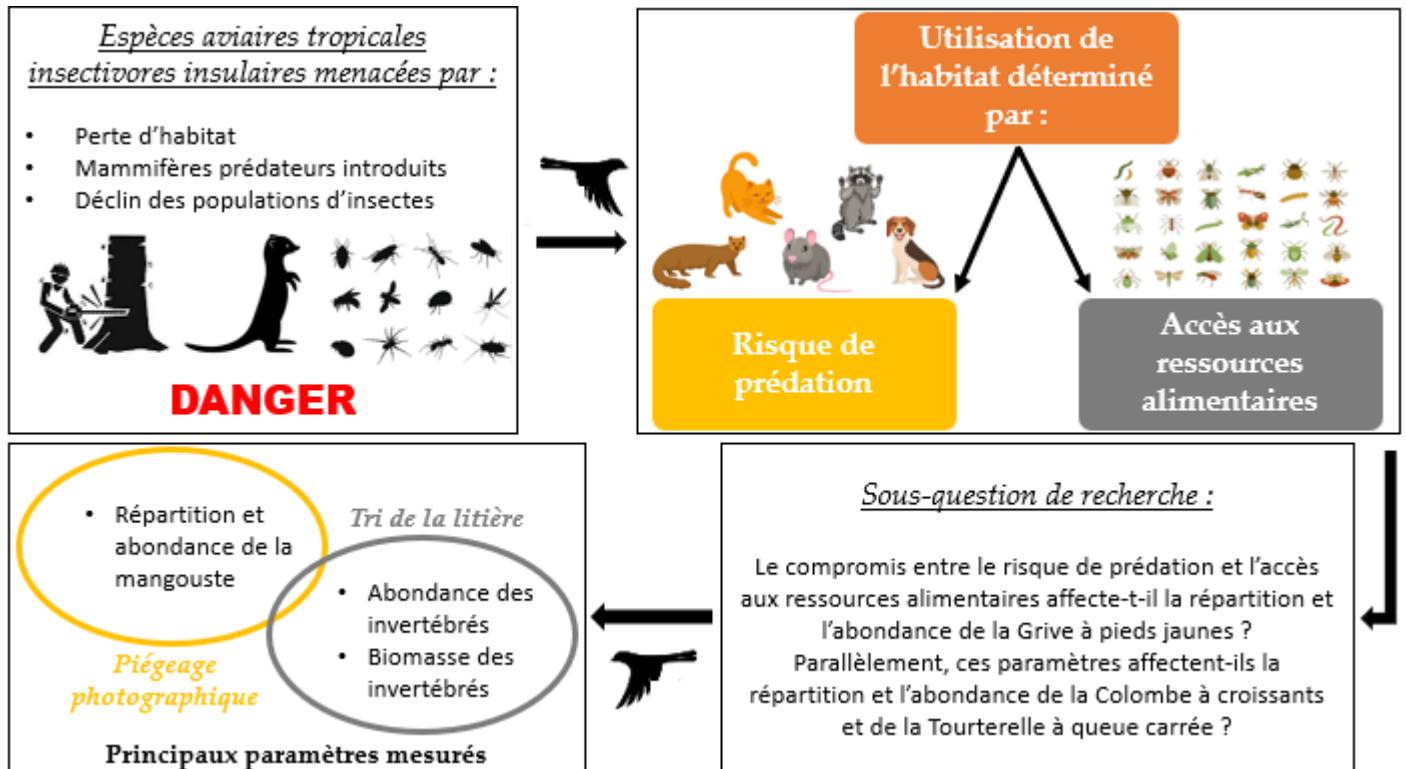
Table S1 Estimates of detection rate and naïve occupancy obtained from camera-traps surveys of ground-dwelling forest bird species of various conservation status (LC = Least Concern; NT = Near Threatened; VU = Vulnerable).

Species		UICN red list status	Detections/100 trap-days	Naïve occupancy	Reference
Lemon Dove	<i>Aplopelia larvata</i>	LC	3	0.29	Smith et al. 2017
Partridge Pigeon	<i>Geophaps smithii</i>	LC	15	0.30	Davies et al. 2019
Bridled Quail-Dove	<i>Geotrygon mystacea</i>	LC	16	0.67	Jean-Pierre et al. 2022
Ruddy quail-dove	<i>Geotrygon montana</i>	LC	0.10	0.03	Hallett et al. 2021
Grey-fronted dove	<i>Leptotila rufaxilla</i>	LC	5.93	0.67	Hallett et al. 2021
Pale-vented pigeon	<i>Patagioenas cayennensis</i>	LC	0.03	0.03	Hallett et al. 2021
Cocoa Thrush	<i>Turdus fumigatus</i>	LC	0.03	0.03	Hallett et al. 2021
Pale-breasted thrush	<i>Turdus leucomelas</i>	LC	0.07	0.03	Hallett et al. 2021
Forest Thrush	<i>Turdus lherminieri</i>	NT	18	0.67	This study
Eyebrowed Thrush	<i>Turdus obscurus</i>	LC	0.14	-	Si et al. 2014
Pale Thrush	<i>Turdus pallidus</i>	LC	0.55	-	Si et al. 2014
Scaly Thrush	<i>Zoothera dauma</i>	LC	2.20	-	Si et al. 2014
Spotted Ground Thrush	<i>Zoothera guttata</i>	VU	1.31	0.28	Ehlers Smith et al. 2017

CHAPITRE 2

Influence de la litière et de la macrofaune sur la répartition et l'abondance de la Grive à pieds jaunes, de la Colombe à croissants et de la Tourterelle à queue carrée, dans les forêts tropicales de Guadeloupe

2.1. Chapeau introductif du chapitre 2



Bien que la Grive à pieds jaune soit inféodée à la forêt ombrophile tropicale, il n'existe aucune donnée scientifique fiable à notre connaissance, sur le compromis entre le risque de prédation et l'accès aux ressources alimentaires, dans ce contexte mondial de déclin des populations d'invertébrés.

Ce deuxième chapitre présente les résultats de l'influence de la litière, de la macrofaune et de l'abondance de la petite mangouste indienne sur la répartition et l'abondance de la Grive à pieds jaunes, dans les forêts tropicales de Guadeloupe. La Colombe à croissants et la Tourterelle à queue carrée se nourrissant occasionnellement d'invertébrés et étant potentiellement soumises à la prédation par les espèces exotiques envahissantes, l'influence de ces facteurs sur la répartition et l'abondance de ces deux colombidés, a également été étudiée. Plus précisément, pour la première fois, un lien a été recherché entre le poids sec de la litière, la biomasse et l'abondance des invertébrés, ou encore la répartition et la dynamique spatiale des espèces cibles, en Guadeloupe.

L'utilisation du piégeage photographique couplé à l'analyse de la biomasse et l'abondance des macroinvertébrés de litière a ainsi permis l'apport d'éléments scientifiques à la fois novateurs et fiables, relatif au compromis entre le risque de prédation et l'accès aux ressources alimentaires de la Grive à pieds jaunes, de la Colombe à croissants, mais également de la Tourterelle à queue carrée.

2.2. Article 3

Article 3

Diurnal Forest Thrush abundance
positively covaries with both prey
availability and small Indian mongoose
abundance

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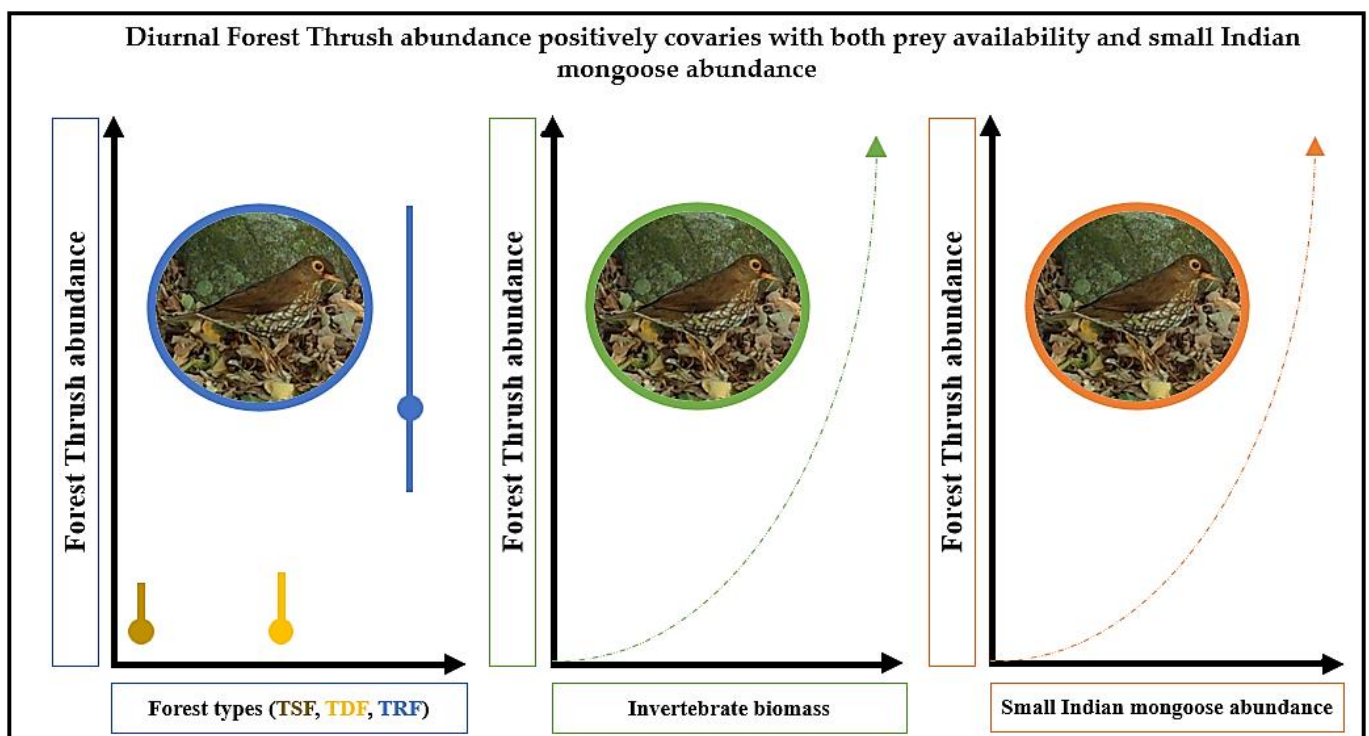
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Graphical abstract



Abstract

Ground-dwelling omnivorous bird species living on tropical islands are particularly vulnerable to deforestation, introduced mammal predators, and declining insect populations. However, little is known about the relative influences of predation risk and invertebrate prey availability on the spatial distribution and abundance of such species in forested habitats. We investigated spatial variation in the diurnal abundance of the near-threatened Forest Thrush (FT), *Turdus lherminieri*, a Caribbean-endemic and secretive ground-dwelling species, in March 2021, corresponding to the dry season, in Guadeloupe, French West Indies. We used camera traps to assess spatial variation in the abundance of FT and that of potential diurnal mammalian predators among three forest types: tropical rainforest (TRF), tropical swamp forest (TSF), and tropical dry forest (TDF). We characterized sampling sites according to temperature, canopy openness, leaf-litter biomass, and estimated local invertebrate abundance and biomass. FT were relatively common, being observed at 21 (35%) of 60 camera-trap locations during the study. FT abundance was significantly higher in TRF compared to the other two habitats, and covaried positively with both invertebrate biomass and the abundance of the small Indian mongoose, *Urva auropunctata*. We discuss our results in relation to previous studies on habitat selection by tropical insectivore, ground-dwelling bird species, and address their overall relevance for FT conservation in the insular Caribbean.

Keywords: avian conservation, camera-trap, invertebrate biomass, tropical forests, *Turdus lherminieri*

1. Introduction

Understanding the causes of avian population decline in tropical forests is of crucial importance for conservation (Robinson and Sherry 2012; Tobias et al. 2013). Indeed, a large part of avian diversity, including the most threatened bird species, occurs in this highly vulnerable ecosystem (Sodhi et al. 2011). The decline of tropical forest bird species has been associated with various drivers, such as habitat loss and fragmentation (Feeley and Terborgh 2008; Korfanta et al. 2012), invasive species (Harper and Bunbury 2015; Doherty et al. 2016; Thibault et al. 2018b), hunting pressure (Sreekar et al. 2015; Benítez-López et al. 2017), and climate change (Şekercioğlu et al. 2012). However, the relative importance of such drivers and of their interactions may differ

between mainland and island species (Doherty et al. 2016), and in relation to diet composition (Curtis et al. 2021).

One avian group of particular concern are tropical, omnivorous ground-dwelling species living on islands, mainly because of their restricted range, habitat loss, high vulnerability to introduced mammal predators, and declining insect populations (Şekercioğlu et al. 2002; Lamarre et al. 2020; Sherry 2021). Many tropical ground-dwelling bird species tend to have omnivorous and generalist food habits, with seasonal variation in their use of fruits, seeds, invertebrates (Herrera et al. 2006; Riehl and Adelson 2008) and, occasionally for some species, small vertebrates (Sandoval et al. 2008). However, avian omnivory is associated with higher extinction rates compared to other specialist diets, possibly constituting a macroevolutionary sink (Burin et al. 2016). In addition, unlike tropical ground-dwelling species living on mainland (González-Castro et al. 2012), insular ones have limited possibilities to expand their home range in response to reduced food availability, particularly during the dry season (Williams and Middleton 2008). Ground-dwelling bird species living on tropical islands are also particularly vulnerable to predation on nests and adults by various introduced exotic mammals, such as rats, *Rattus sp.* (Duron et al. 2017b, a), the small Indian mongoose, *Urva auropunctata* (Lewis et al. 2011; Morley and Winder 2013; Berentsen et al. 2020), and domestic cats, *Felis catus* (Hervías et al. 2014; Medina et al. 2014; Sreekar et al. 2015; Loss et al. 2022). However, although trade-offs between predation risk and access to food resources can shape habitat use by landbirds (McCabe and Olsen 2015; Johnston-González and Abril 2019), little is known about their joint influence on the spatial distribution and abundance of ground-dwelling tropical bird species.

Here, we investigated the extent to which spatial variation in the abundance of the Caribbean-endemic Forest Thrush (FT), *Turdus lherminieri* (Collar 2020) in Guadeloupe, French West Indies, can be explained by habitat type and variation in both food availability and risk of encounter with mammalian predators. The species is listed as Near Threatened (BirdLife International 2023) as its distribution is restricted to the forested habitats of only four islands in the Lesser Antilles, where it is threatened by habitat destruction and fragmentation, exotic invasive species, and hunting pressure (Arnoux et al. 2014; Collar 2020). The species is supposed to feed mainly on the ground, from invertebrates and fallen berries collected in the leaf-litter (Raffaele et al. 1998; Hoyo et al. 2005).

A recent study (Jean-Pierre et al. 2023) found that FT was relatively abundant in Guadeloupe, with however some spatial variation according to forest type, canopy openness and temperature.

Here, we went further by assessing the relative influence of forest type, invertebrate prey availability, and abundance of potential diurnal mammalian predators on spatial variation in FT abundance. We relied on camera traps to assess the abundance of both FT and mammal predators at different stations located in three different forested habitats in Guadeloupe, French West Indies. As known variation in biotic conditions and vegetation structure within forest types in Guadeloupe (Imbert et al. 1996, 2000; Loranger et al. 2002) may affect habitat selection by FT (Parashuram et al. 2015), we characterized each sampling site based on temperature, canopy openness and leaf-litter biomass. In addition, we assessed prey availability (biomass and number of preys) by sampling the leaf litter invertebrate community at each sampling site. We conducted our study during the dry season, at which time reduced resource availability (Tanaka and Tanaka 1982) may have a larger influence on foraging decisions and spatial distribution of ground-dwelling birds (Williams and Middleton 2008; Gumedé et al. 2022).

2. Material and methods

2.1. Study area

Our study was conducted in Guadeloupe, an archipelago composed of several islands in the central Lesser Antilles arc. We focused on Basse-Terre and Grande-Terre, the two main islands of the Guadeloupe archipelago, which are separated by a narrow strait that is crossed with bridges.

While the western island of Basse-Terre is mainly mountainous, with a maximum height of 1467 m (Gadalia et al. 1988), the eastern island of Grande-Terre consists of limestone formation, with a maximum height of 177m (Lasserre 1961).

Variation in elevation, rainfall, and temperature result in distinct vegetal formations linked to the bioclimatic sectors (Murphy and Lugo 1986; Myers et al. 2000; Cavalcanti et al. 2009; Pennington et al. 2018), mainly including tropical rain forest (TRF), tropical dry forest (TDF), and tropical swamp forest (TSF; Rousteau 1996).

TRF is characterised by a rainy and cold climate due to the higher elevation of the southern half of Basse-Terre (Grubb 1971; Laere et al. 2016). More precisely, TRF experiences high annual rainfall coupled with low temperatures (NASA Earth Observatory 2023), whereas TDF is subject to a 5-month period of pronounced drought with high temperature (Holdridge 1967; Bullock et al. 1995). TSF is intermediate in rainfall regime and temperature, and is characterised by the accumulation of partially decayed organic matter at low altitudes (Posa et al. 2011). Canopy openness tends to be

higher in TDF than in TRF or TSF on the island of Guadeloupe. Indeed, TDF mainly consists of small trees with poorly developed foliage and little overlap, resulting in open canopy. In contrast, in TRF and, to a lesser extent, in TSF, trees generally have larger leaves and reach higher heights, due to competition for light (Carvalho et al. 2021).

2.2. Data collection

Based on prior information (Jean-Pierre et al. 2023), we collected data on FT abundance and that of potential predators (diurnal exotic mammals) at 12 different stations (i.e., 6 TRF stations, 3 TDF stations, and 3 TSF stations; Figure 1).

Stations were set along an altitudinal gradient, in order to cover the diversity of forest habitats in relation to local topography (Smith 2004; Talvitie et al. 2006; Louppe et al. 2021a; Jean-Pierre et al. 2022). At each station, we set an array of five passive infrared camera traps (Moultrie® M-40i, with a 125 ° angle of view), arranged along a straight line, with a 200-m distance between adjacent cameras.

We attached each single camera to a robust tree about 20-30 cm above the ground, to maximize the probability of detection of the relatively small-sized FT (O'Connell et al. 2011). We selected trees with little surrounding vegetation, to allow for an optimal range of camera sensor in the closed habitat. We applied a 30-s delay between pictures to avoid multiple photographs of the same individual over short periods of time (Smith et al. 2017).

As we only had 20 camera traps available, our sampling was spread over 3 weeks in March 2020. The different stations were sampled on a random rotation basis.

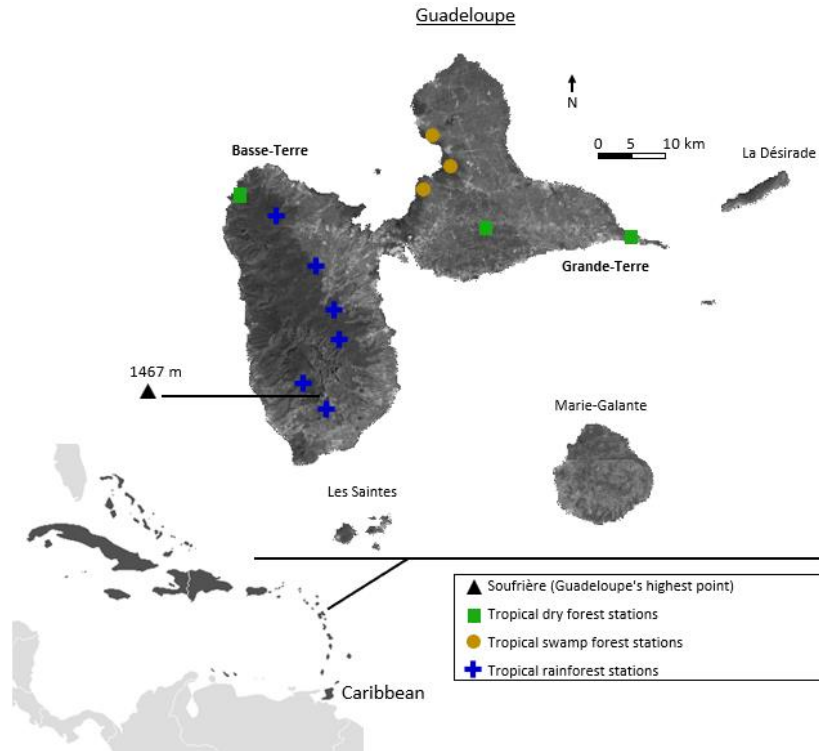


Figure 1. Locations of the 12 surveyed stations investigated in Guadeloupe in March 2020, including 3 tropical dry forest stations (■), 3 tropical swamp forest stations (●) and 6 tropical rainforest stations (+). The distance between stations ranged from 3.6 km to 23.71 km

For each station, each camera trap remained active 24 h d^{-1} to document FT presence of and that of other species over seven consecutive days, resulting in 420 days of trapping.

At each camera-trap location, we assessed surrounding biotic and abiotic factors as putative drivers of FT abundance. Following Cook et al. (2020) and Jean-Pierre et al. (2023), we used an ordinal categorical scale with three categories, to characterise the canopy as closed (0-1/3), partially open (1/3-2/3) or open (2/3-3/3). We obtained data on ambient temperature *TEMP* directly from camera-trap recordings. As the leaf-litter is considered as a prey reservoir (Sánchez et al. 2014; Smith et al. 2017; Mansor et al. 2018, 2019; Martay and Pearce-Higgins 2020; Gumede et al. 2022), we estimated leaf-litter biomass (*LLB*) at each camera-trap location.

To that end, we used 1-m² quadrat frames to sample the ground leaf-litter on the four cardinal points around each camera trap, at a distance of 5 m. After collection of invertebrates (see below), we dried the collected leaf litter in an oven for one week at 60°C, and then weighed it with a balance (with a 0.1 g accuracy, BH 3000 A).

We estimated prey availability from both the abundance and total biomass of invertebrates. Although exhaustive sample sorting is a reliable method for fully describing the structure and

composition of a macroinvertebrate community (Courtemanch 1996; Cao et al. 1998), it requires considerable time and effort (Ciborowski 1991; Vlek et al. 2006). Among the less time-consuming techniques developed, we chose the sieving method to study the ground leaf-litter arthropod communities (Belshaw and Bolton 1993; Agosti et al. 2000; Dietl et al. 2009; Vasconcelos et al. 2009; Barba et al. 2010; Cole et al. 2016; Araújo and Souza 2022; Aponte Rolón and Perfecto 2023). As we were only interested in macroinvertebrates (>2 mm), we manually collected all arthropods from each sieve during a standardised time of 30 minutes, using fine tweezers (Kattan et al. 2006; Niedbala and Ermilov 2022). More precisely, after pooling the four litter samples from each camera-trap locations, we used a succession of sieves stacked in decreasing order (4 mm, 3 mm and 2 mm mesh). After sorting, the animals were placed in bottles of alcohol at 70°, in the laboratory. We considered invertebrate abundance (*IA*) per camera-trap location as the number of individuals recorded per camera-trap location.

We estimated invertebrate biomass (*IB*) per camera-trap location by weighing the individuals collected using a precision balance (with a 0.001 g accuracy, PIONEER™ PRÉCISION PX323M).

2.3. Data analysis

2.3.1. Comparison of biotic and abiotic factors between forest types

We first investigated to what extent our sampling stations located in the three recognized forest types differed according biotic and abiotic factors. A Shapiro–Wilk test (Mohd Razali and Bee Wah 2011) indicated that only *TEMP* followed a normal distribution ($W_{TEMP} = 0.98$, $p = 0.52$). Therefore, we relied on generalized linear model (GLM; Nelder and Wedderburn 1972; Lindsey 2000), to assess variation in *TEMP* between forest types. GLM were fitted with a Gaussian distribution using the R package *Stats* v3.6.2. As *IB*, *IA* and *LLB* did not follow a normal distribution ($W_{IB} = 0.69$, $p < 0.001$; $W_{IA} = 0.85$, $p < 0.001$; $W_{LLB} = 0.92$, $p < 0.001$), we transformed these variables into ordinal variables based on quantile distributions and relied on ordinal logistic regression to assess variation in *CO*, *IB*, *IA* and *LLB* between forest types, using the R package *Ordinal* v.2022.11-16 (sensu Gorczynski and Beaudrot 2021). For all models, we included station as a random effect nested in forest type, since each camera-trap location belonged to one of the 12 different stations, themselves distributed in three different forest types.

We used the R software 3.6.2 (R Core Team 2019) to perform all analyses and figures. Results were considered significant at the 5% level.

2.3.2. Modelling FT abundance

We relied on random effect models, i.e., generalized linear mixed models (GLMMs; Bolker et al. 2009; Stroup 2012), to assess the influence of forest type (i.e., TRF, TDF, TSF), prey availability (i.e., *IB* and *IA*) and potential predator (i.e., mongoose abundance *MONA* and mongoose presence *MONP*, see results) on FT abundance.

Variables that were highly correlated with each other were not included in the same model (Spearman rank-correlation coefficient, *MONA* and *MONP*: $r_s = 0.93$; *IB* and *IA*: $r_s = 0.66$; $p < 0.01$).

For all models, we included nested random effect parameters (i.e., zones nested within forest type). Following Lapin et al. (2013), we considered Poisson, zero-inflated Poisson, negative binomial and zero-inflated negative binomial distributions to model FT abundance data. The zero-inflated binomial distribution (log link) provided the best fit to the data (White and Bennetts 1996). Models were built using the R package *glmmTMB 1.0.0* (Brooks et al. 2017). All possible combinations of covariates were investigated using the R package *MuMIn 1.43.6*, resulting in 18 models without interactions (Bartoń 2019).

We ranked models using the Akaike information criterion corrected for small sample size, AICc, using the R package *AICcmodavg 2.3-1* (Mazerolle and Mazerolle 2017) and considered models with $\Delta AICc < 2$ as equivalent for explaining variation in the local abundance of FT (Burnham et al. 2011). We checked for goodness-of-fit for all valid models using the R package DHARMA 0.2.7 (Hartig 2020). We relied on the R package *glmmTMB 1.0.0* (Brooks et al. 2017) to obtain coefficient (β_i) of model parameters and their associated p values.

3. Results

3.1. Comparison of biotic and abiotic factors between forest types

Temperature was significantly lower at camera-trap locations dominated by TRF than at those dominated by TDF or TSF ($\beta = -3.23$, $p < 0.001$; Figure 2). On the other hand, canopy openness was higher at camera trap locations dominated by TDF than those dominated by TSF or TRF ($\beta = 4.00$, $p < 0.01$; Figure 2). Conversely, leaf-litter biomass was lower at camera-trap locations dominated by TDF than those dominated by TSF or TRF ($\beta = -7.81$, $p < 0.01$; Figure 2).

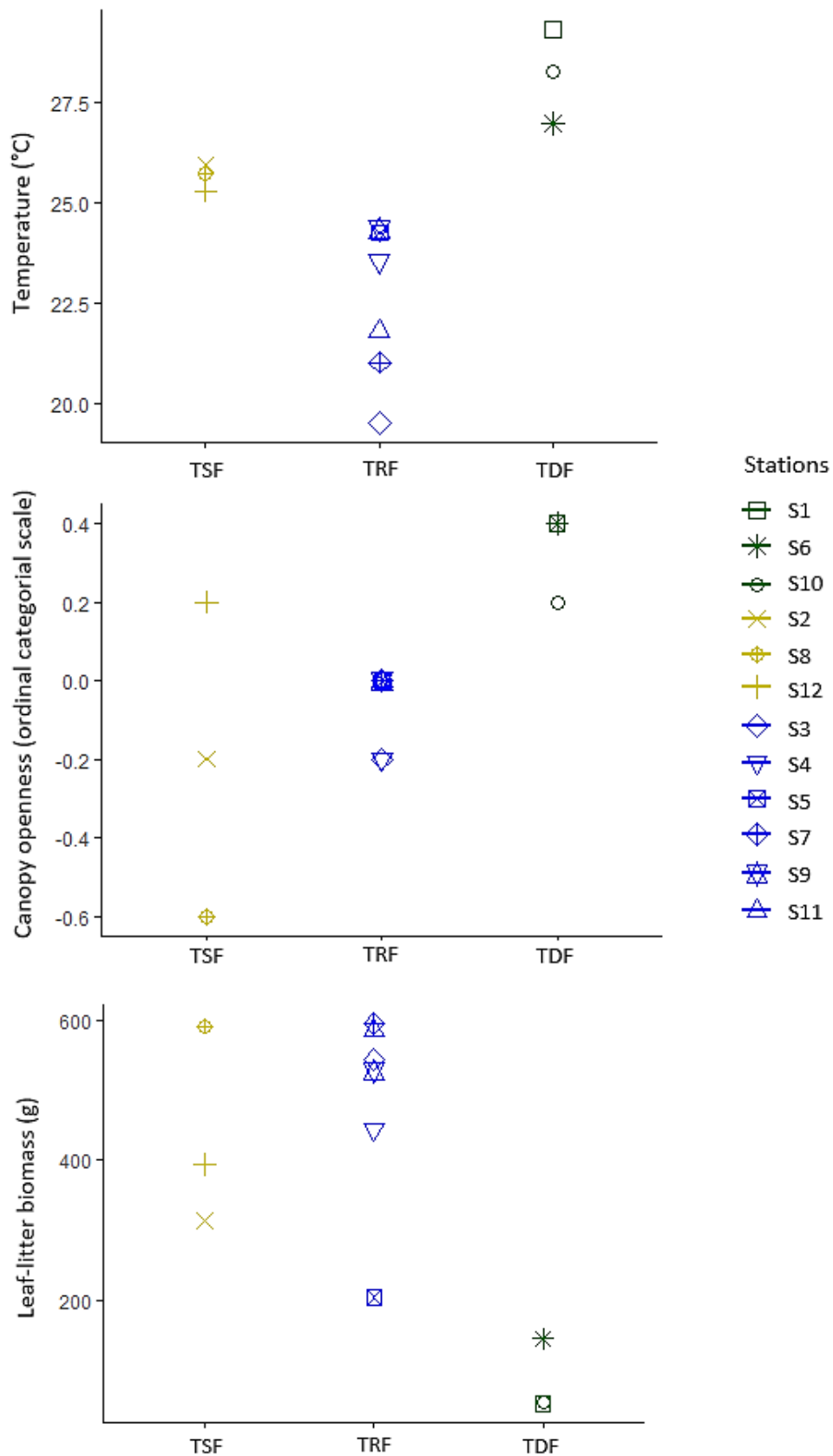


Figure 2. Average values ($n = 5$) of temperature ($^{\circ}\text{C}$), canopy openness and leaf-litter (ordinal categorical scale) biomass (g) per station, measured in Guadeloupe in March 2020, according to the tropical swamp forest (TSF, yellow stations), the tropical rainforest (TRF, blue stations), and the tropical dry forest (TDF, green stations)

3.2. Factors affecting FT abundance

We obtained 158 captures of FTs at 21 different camera-trap locations (35% of all camera-trap locations), 103 captures of mongooses at 28 different camera-trap locations (46.7%), compared to only 16 captures of domestic cats at 4 different camera-trap locations (6.7%). Given their rare occurrence, the abundance of domestic cats was not included in the analyses.

When comparing models based on abundance at all camera-trap locations, the best model (Table 1) included *IB*, *MONA* and *Forest* as meaningful parameters. More precisely, *IB* and *MONA* were positively associated with FT abundance ($\beta_{IB} = 0.98$, $p < 0.001$, Figure 3A; $\beta_{MONA} = 0.91$, $p < 0.001$, Figure 3B). Moreover, FT abundance was higher at camera-trap locations dominated by TRF than at those dominated by TSF or TDF ($\beta = 3.71$, $p < 0.001$; Figure 3C). Analysis of residuals detected no deviation from the expected distributions (Figure S1, available in Supporting Information).

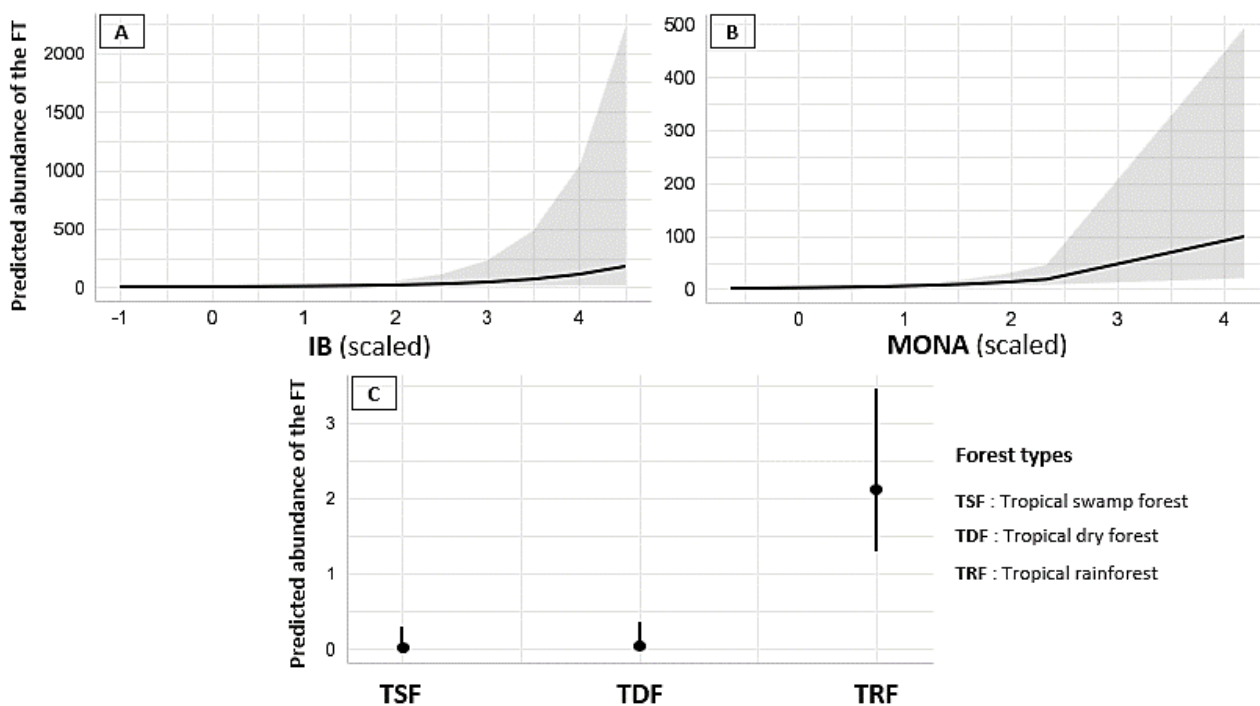


Figure 3. Model covariate effect plots showing change in predicted abundance of the Forest Thrush in March 2020, in relation to invertebrate biomass IB (A, with 95% confidence interval shaded), mongoose abundance MONA (B, with 95% confidence interval shaded) and Guadeloupe forest types i.e., tropical swamp forest TSF; tropical dry forest TDF and tropical rainforest TRF (C, black dots and error bars)

Table 1. Models assessing the influence of invertebrate biomass (Ib), invertebrate abundance (Ia), mongoose abundance (Mona), mongoose presence (Monp) and Forest types (Forest) on FT abundance, with station as a random effect (nested within forest type). Only model with $\Delta AICc < 2$ was considered for explaining variation in the local abundance of FT.

Model	Df	AICc	$\Delta AICc$	Wi	LogLik
Ib + Mona + Forest	7	162,57	0,00	0,98	-73,21
Mona + Ia + Forest	7	171,22	8,65	0,01	-77,54
Ib + Monp + Forest	7	174,42	11,84	0,00	-79,13
Ib + Forest	6	175,80	13,23	0,00	-81,11
Mona + Forest	6	175,84	13,27	0,00	-81,13
Monp + Ia + Forest	7	176,67	14,10	0,00	-80,26
Mona + Ia	5	179,50	16,93	0,00	-84,20
Monp + Ia	5	181,10	18,53	0,00	-85,00
Ia + Forest	6	181,74	19,17	0,00	-84,08
Ia	4	183,11	20,54	0,00	-87,19
Ib + Mona	5	183,69	21,12	0,00	-86,29
Monp + Forest	6	185,23	22,66	0,00	-85,82
Ib	4	186,42	23,85	0,00	-88,85
Mona	4	186,50	23,93	0,00	-88,89
Ib + Monp	5	186,72	24,15	0,00	-87,81
Monp	4	191,70	29,13	0,00	-91,49
Forest	5	195,49	32,92	0,00	-92,19
Null	2	201,60	39,03	0,00	-98,69

Df = Degrees of freedom

AICc = corrected Akaike Information Criterion

$\Delta AICc$ = The difference in AICc score between the best model and the model being compared

Wi = Akaike weight

LogLik = the 2log-likelihood

4. Discussion

Our results confirm the relatively high abundance of FT in Guadeloupe, particularly in TRF (Jean-Pierre et al. 2023). More importantly, our results revealed a positive influence of spatial variation in leaf-litter invertebrate biomass on spatial variation in FT abundance, as well as a positive association between FT abundance and that of one of its potential exotic predators, the small Indian mongoose. Such findings have direct relevance for the conservation and management of this near-threatened species.

4.1. Influence of invertebrate biomass and forest type on the abundance of the Forest Thrush

Spatial variation in invertebrate biomass was the most influential factor explaining spatial variation in FT abundance across forest types. Although FT can feed on both invertebrates and fruits, its diet has not been documented though quantitative data. Future research, possibly based on faecal content and stable isotope analysis (Bosenbecker and Bugoni 2020), would therefore be helpful to assess the extent of FT dietary plasticity and seasonal variation, particularly in the global context of invertebrate loss (Şekercioğlu et al. 2002; Lamarre et al. 2020). However, McKinnon et al. (2017) found that the ecologically similar and omnivorous Wood Thrush, *Hylocichla mustelina*, mainly consumed arthropods, particularly during the driest times of the non-breeding season. In addition, our results are consistent with previous studies of both temperate and tropical forest passerine bird species. For instance, Brown et al. (2011) found that both the taxonomic richness and abundance of large arthropods were significantly greater at sites occupied by Swainson's Warblers, *Limnothlypis swainsonii*, than at unoccupied sites in the southeastern U.S.

Similarly, arthropod abundance was the best predictor of the abundance of the White-breasted Wood-Wren, *Henicorhina leucosticta*, in Caribbean lowland forests of Costa Rica (Sánchez et al. 2014). However, the overall evidence for species of the genus *Turdus* is less conclusive. On the one hand, Martay and Pearce-Higgins (2020) found a positive association between counts of several thrush species and earthworm abundance in the U.K. On the other hand, Newmark and Stanley (2016) found that invertebrate abundance did not differ between territories of the Usambara Thrush, *Turdus roehli*, whereas habitat structure, in terms of tree density and ground cover, did. Similarly, Jirinec et al. (2016) found that habitat structure was more important than prey availability to explain the relative space use of 37 radiotracked male Wood Thrushes on their breeding grounds in coastal Virginia.

Although we did not include measures of habitat structure in our models, forest type significantly influenced FT abundance, with higher abundance in TRF compared to both TDF and TSF, in accordance with previous studies (Eraud et al. 2012; Arnoux et al. 2013; Parashuram et al. 2015; Levesque et al. 2020). However, invertebrate abundance as well as invertebrate biomass did not differ between forest types, such that the influence of forest type and prey availability were not confounded in our analyses.

At a broad scale, the three forest types differ markedly in terms of vegetation structure in the Caribbean islands (Areces-Mallea et al. 1999, Banda-Rodríguez et al. 2016), and, more specifically, in Guadeloupe (Imbert et al. 1996, 2000; Imbert and Portecop 2008). In the present study, stations differed significantly according to forest type in terms of temperature, canopy openness and leaf-litter biomass. Temperature was significantly lower in rainforest stations, as a direct consequence of their higher elevation compared to both dry forest and swamp forest stations. On the other hand, canopy was significantly more open in dry forest stations compared to stations located in the two other forest types. Our results thus suggest that FT may prefer specific light and thermal niches, and favour dim and cool microclimates when foraging for food on the ground as reported for other tropical forest insectivorous bird species (Jirinec et al. 2022). However, as studies on turdids and other ground-dwelling forest birds differ in several respects, including methodology, geographical area and time of the year, a meta-analysis would be of interest to provide an overall assessment of the relative influence of food availability and habitat structure on spatial variation in occupancy and abundance.

4.2. Spatial covariation in abundance with the small Indian mongoose

We found a positive spatial covariation between the abundance of FT and that of the small Indian mongoose in Guadeloupe. Our results thus confirm previous reports of spatial co-occurrence between the two species in Guadeloupe based on camera-trap data (Louppe et al. 2021a). Still, the causes and consequences of this association deserve particular attention. Direct evidence, based on diet or remains analysis, indicates that the small Indian mongoose can prey upon various bird species (Engeman et al. 2006; Lewis et al. 2011; Akrim et al. 2019). The importance of bird predation by mongoose is confirmed by indirect evidence, based on avian extinctions and population trends (Hays and Conant 2007; Berentsen et al. 2020; Yagihashi et al. 2021) or morphological changes

(Heathcote et al. 2021) following mongoose introduction. However, expectations about spatial covariation between prey and predators are not straightforward.

On the one hand, positive spatial co-occurrence can be expected if predators concentrate where their preys are mostly abundant in order to increase encounter rate (Kittle et al. 2017). On the other hand, active avoidance of predators by preys (Gaynor et al. 2019) or strong prey depletion by predators (Holt et al. 2008; Amar et al. 2008) may result in negative spatial co-variation in abundance (Murphy et al. 2019). Accordingly, the few results documenting the influence of mongoose presence on the presence or abundance of avian species have provided mixed evidence. Morley and Winder (2013) concluded that three ground bird species were negatively influenced by the presence of mongoose, as they were observed only on mongoose-free islands among 16 small islands within Fiji. On the other hand, Louppe et al. (2021) recorded the presence of the small Indian mongoose in Martinique in sites known to be restricted territories of two threatened endemic bird species, the Martinique Oriole, *Icterus bonana*, and the ground-dwelling, White-breasted Thrasher, *Ramphocinclus brachyurus*. Therefore, the positive association between FT and mongoose abundance is in itself poorly informative about their possible interaction as prey and predator.

An alternative explanation for the observed correlation between FT and the small Indian mongoose is that their co-occurrence is simply due to similar habitat preferences associated to a third variable. Although mongoose may prey on birds, they are largely omnivorous and the largest part of their diet on Caribbean islands generally consists of invertebrates, reptiles, small mammals and fruits (Pimentel 1955; Seaman 1962; Nellis and Everard 1983).

According to a more recent study (Lewis et al. 2011), invertebrates and lizards accounted for 93% of identified prey items in the stomach content of 217 mongooses in Jamaica. Mongooses in the forests of Guadeloupe may therefore concentrate in areas that provide favourable conditions for invertebrates and reptiles. For instance, leaf-litter moisture is crucial for microhabitat choice in both invertebrates and lizards, which tend to seek out shaded areas during dry periods in order to minimize water loss and thermal stress (Vonesh 2001; Harris et al. 2004; McGee et al. 2020). Obviously, whatever its causes, spatial co-occurrence may expose FT to casual predation by mongoose. Therefore, only a detailed analysis of the diet of the small Indian mongoose, through faecal or stomach content analysis (Mahmood and Adil 2017; Dabholkar and Devkar 2020; Subrata et al. 2021) in various habitats in Guadeloupe, would allow a precise estimation of its impact on FT and the local avifauna.

5. Management implications

Our results show that FT was a relatively common bird species at our study sites. Indeed, FT accounted for 158 (45%) of the overall 351 visual captures of 10 different avian species obtained through camera traps during the present study. Although the species is exposed to several threats in its distribution range, the Guadeloupe population may benefit from more favourable conditions associated with the protection of large forested areas, particularly on Basse-Terre within the boundaries of the Parc National de la Guadeloupe, and hunting regulation. However, its long-term persistence might be affected by several factors.

First, results on the apparent habitat preference of FT suggest that climate change may affect its population dynamics through its effects on tree canopy cover, soil moisture (Scholl et al. 2021) and biogeochemistry (O'Connell et al. 2018), and, in turn, on the availability of leaf litter arthropods (Kaspari et al. 2017). The predicted increase in heat stress in the Lesser Antilles (Di Napoli et al. 2023) may also negatively affect the physiology, and hence fitness, of tropical passerine species such as FT (Pollock et al. 2021). Second, interspecific interactions may increasingly affect FT population growth in the coming years. On the one hand, in the absence of large-scale control measures, introduced exotic mammals such as mongooses, feral cats, raccoons, *Procyon lotor* and rats, *Rattus spp.*, may continue to flourish in forested habitats, with the risk of increased predation on FT nests and adults.

On the other hand, the Guadeloupe FT population is now threatened by a potential competitor, the Spectacled Thrush, *Turdus nudigenis* (Levesque 1997; Benito-Espinal and Hautcastel 2003). Originally native to northern South America and the southern Lesser Antilles, the species has progressively colonized the northern Lesser Antilles over the last century, up to Guadeloupe. The Spectacled Thrush is known to be particularly aggressive towards other turdid species and is suspected to be responsible for the marked decline of the FT population in Saint Lucia (Raffaele et al. 1998; Levesque et al. 2005).

We therefore strongly recommend the establishment of a long-term monitoring programme to document temporal and spatial variation in the presence and abundance of FT in Guadeloupe and to better inform managers, conservationists and hunters of population trends and risks associated with predatory and competitive interspecific interactions. In this regard, the use of remote-sensing techniques, such as camera-traps (Jean-Pierre et al. 2023, this study) and passive acoustic recorders (Shonfield and Bayne 2017) could be particularly effective.

Supporting Information

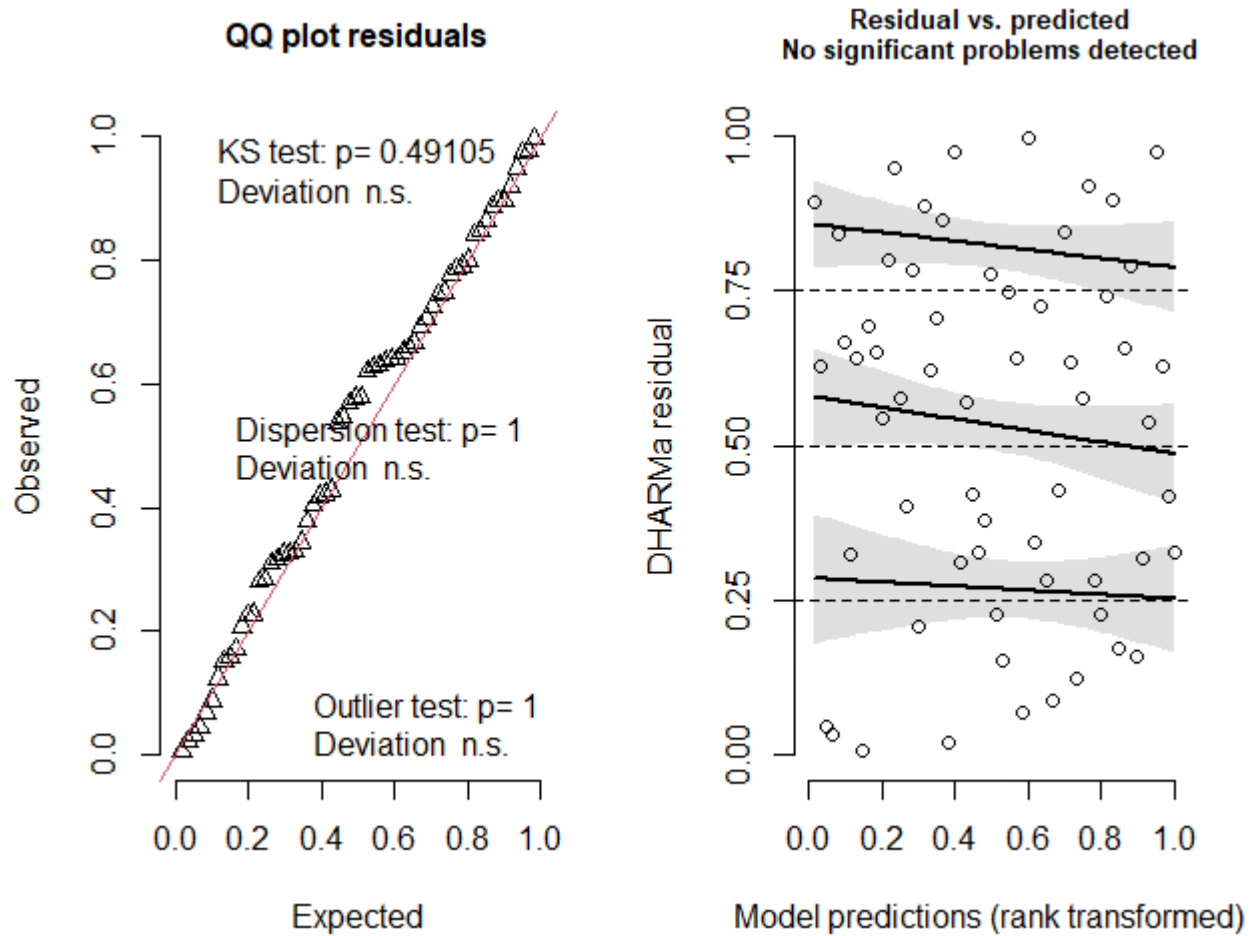


Figure S1: Residual diagnostics plots for the best regression model including the influence of forest type, invertebrate biomass and mongoose abundance on FT abundance. A: qq-plot residuals of deviations from the expected distribution (goodness of fit tests, Kolmogorov-Smirnov test: $p = 0.49$; dispersion test: $p = 1$; outlier test: $p = 1$) B: plot the simulated residuals against predicted values.

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2.3. Influence de la litière, de la macrofaune et de l'abondance de la petite mangouste indienne sur la répartition et l'abondance de la Colombe à croissants *Geotrygon mystacea* et de la Tourterelle à queue carrée *Zenaida aurita*, dans les forêts tropicales de la Guadeloupe

L'étude décrite dans la partie précédente (article 3), nous a également permis d'obtenir des données relatives à deux espèces forestières cibles, la Colombe à croissants *Geotrygon mystacea*, et la Tourterelle à queue carrée *Zenaida aurita*. Si l'analyse du contenu du jabot et du tractus digestif indiquent que ces deux espèces s'alimentent principalement de graines et de fruits tombés au sol (Seaman 1966; Chipley 1991), la nourriture animale n'est cependant pas exclue de leur régime alimentaire (Seaman 1966; Zamore 1981; Wiley 1991; Tayalay 1995). Par ailleurs, la Colombe à croissants et la Tourterelle à queue carrée sont aussi potentiellement exposées à la prédation par certaines espèces de mammifères exotiques lorsqu'elles se nourrissent au sol (Jean-Pierre et al. 2022). Etudier l'influence des variations de l'abondance et la biomasse de la macrofaune, ainsi que le risque de rencontrer un mammifère prédateur, sur l'abondance de ces deux espèces aviaires, peut permettre de mieux comprendre leur écologie.

2.3.1. Matériels et Méthodes

La région étudiée et la collecte des données sont présentées de façon exhaustive dans **l'article 3**. Pour rappel, le piégeage photographique a été utilisé pour déterminer l'abondance des espèces aviaires cibles ainsi que leurs potentiels prédateurs (Figure 11). Le tri de litière, à l'aide de tamis, puis la pesée des invertébrés, a permis d'estimer l'abondance et la biomasse des individus récoltés (Figure 12). L'analyse des données est également présentée de façon exhaustive dans l'article 3.



Figure 11. Piège photographique *Moultre M-40i* posé dans la forêt tropicale sèche de Saint-François en mars 2020, ©Aurélié JEAN-PIERRE.



Figure 12. Schéma représentant la collecte puis le tamisage de la litière. Dans un premier temps (1), la litière est prélevée à l'aide d'un quadrat de 1x1 m². Ensuite (2), elle est tamisée au laboratoire, à l'aide de trois tamis rangés dans l'ordre décroissant de leurs mailles. Pour finir (3), les individus appartenant à la macrofaune ont été récoltés à l'aide de pincettes et pesés au laboratoire avec une balance de précision (0.001 g de précision, PIONEER™ PRÉCISION PX323M).

2.3.2. Résultats

Nous avons obtenu 85 captures de la Colombe à croissants dans 16 stations différentes de piégeage photographique (27%) et 46 captures de la Tourterelle à queue carrée dans 10 stations différentes de piégeage photographique (17%).

2.3.2.1. Colombe à croissants

En comparant les modèles basés sur l'abondance dans toutes les stations de piégeage photographique (Tableau 1), les meilleurs modèles incluait deux paramètres, l'abondance de la petite mangouste indienne *AMAN* et la biomasse des invertébrés *BI*. Néanmoins, après le processus de « moyenne des modèles », seule la variable *AMAN* était significative ($\beta_{AMAN} = 0.34 [0.08; 0.59]$; $\beta_{BI} = 0.20 [-0.19; 0.59]$). Nos résultats montrent donc que l'abondance de la Colombe à croissants est positivement associée à celle de la petite mangouste indienne (Figure 13). L'analyse des résidus n'a révélé aucun écart par rapport aux distributions attendues (Annexe 1, Figure A1).

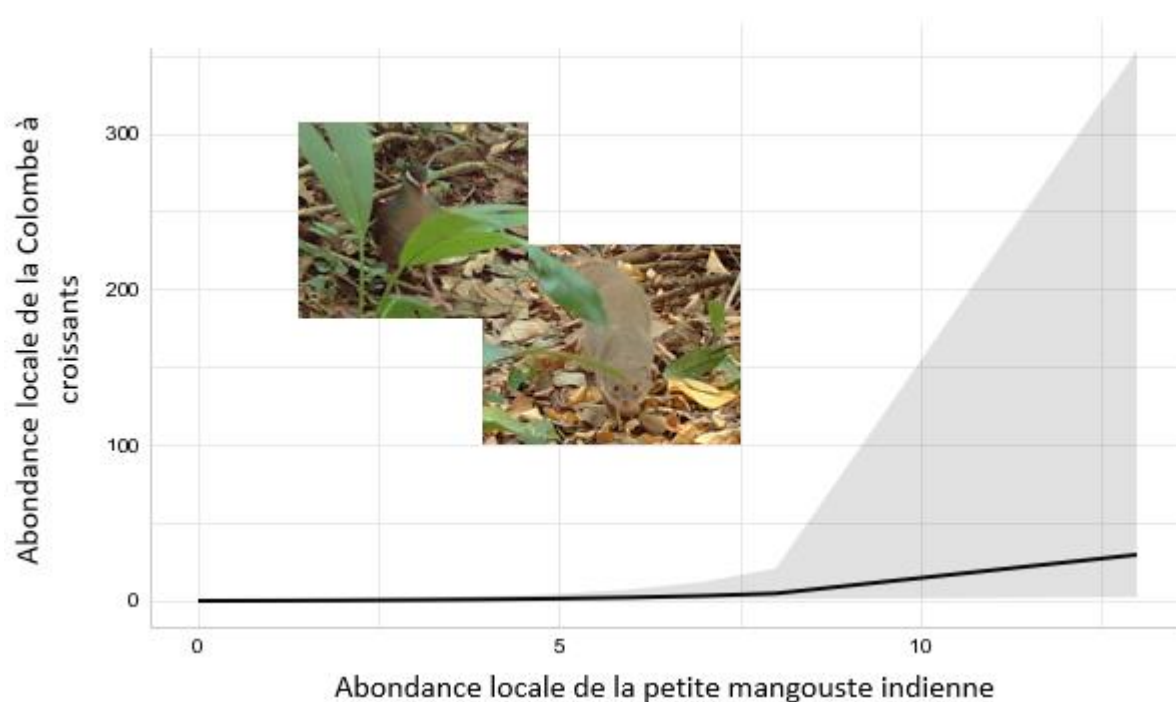


Figure 13. Prédiction de l'évolution de l'abondance locale de la Colombe à croissants en fonction de l'évolution de l'abondance locale de la petite mangouste indienne, selon le meilleur modèle retenu (Tableau 1). L'intervalle de confiance à 95% est représenté en gris.

Tableau 1. Modèles évaluant l'influence de la biomasse des invertébrés (BI), de l'abondance des invertébrés (AI), de l'abondance des mangoustes (AMAN), de la présence des mangoustes (PMAN) et des types de forêts (FORÊT) sur l'abondance de la Colombe à croissants *Geotrygon mystacea* et de la Tourterelle à queue carrée *Zenaida aurita*, avec la station comme effet aléatoire (imbriquée dans le type de forêt).

Modèle	DDL	AICc	$\Delta AICc$	Poids	LL
<i>Geotrygon mystacea</i>					
AMAN	4	139,26	0,00	0,33	-65,27
BI+AMAN	5	140,55	1,30	0,17	-64,72
BI+PMAN	5	141,30	2,04	0,12	-65,10
AMAN+FORÊT	6	142,57	3,31	0,06	-64,49
PMAN+AI	5	142,73	3,47	0,06	-65,81
BI	4	143,02	3,76	0,05	-67,15
AMAN+AI+FORÊT	7	143,19	3,93	0,05	-63,52
PMAN	4	143,24	3,98	0,05	-67,26
BI+AMAN+FORÊT	7	143,64	4,38	0,04	-63,74
BI+FORÊT	6	144,75	5,49	0,02	-65,58
BI+PMAN+FORÊT	7	144,96	5,70	0,02	-64,40
AI	4	146,23	6,97	0,01	-68,75
NULL	2	146,36	7,10	0,01	-71,07
PMAN+AI+FORÊT	7	146,70	7,44	0,01	-65,27
AI+FORÊT	6	147,95	8,69	0,00	-67,18
PMAN+FORÊT	6	148,03	8,77	0,00	-67,22
FORÊT	5	151,60	12,35	0,00	-70,25
<i>Zenaida aurita</i>					
AMAN+FORÊT	6	98,21	0,00	0,27	-42,31
PMAN+FORÊT	6	99,05	0,84	0,18	-42,73
BI+AMAN+FORÊT	7	100,03	1,82	0,11	-41,94
AMAN+AI+FORÊT	7	100,59	2,38	0,08	-42,22
AMAN	4	100,64	2,43	0,08	-45,96
BI+PMAN+FORÊT	7	100,82	2,61	0,07	-42,33
FORÊT	5	101,54	3,34	0,05	-45,22
PMAN+AI+FORÊT	7	101,62	3,41	0,05	-42,73
BI+FORÊT	6	101,99	3,78	0,04	-44,20
BI+AMAN	5	102,04	3,83	0,04	-45,47
AI+FORÊT	6	103,66	5,45	0,02	-45,04
BI+PMAN	5	106,12	7,91	0,01	-47,51
BI	4	107,01	8,80	0,00	-49,14
NULL	2	107,94	9,73	0,00	-51,86
PMAN	4	108,16	9,95	0,00	-49,71
PMAN+AI	5	110,08	11,87	0,00	-49,48
AI	4	111,75	13,54	0,00	-51,51

2.3.2.2. Tourterelle à queue carrée

Parallèlement, les trois meilleurs modèles basés sur l'abondance dans toutes les stations de pièges photographiques incluaient quatre paramètres, l'abondance de la petite mangouste indienne *AMAN*, le type forestier *FORÊT*, la présence de la petite mangouste indienne *PMAN* et la biomasse des invertébrés *BI* (Tableau 1). Néanmoins, selon le processus de « moyenne des modèles », seule la variable *AMAN* était significative ($\beta_{\text{AMAN}} = 0.48 [0.07; 0.89]$; $\beta_{\text{FORÊT}} = -3.31 [-6.95; 0.34]$; $\beta_{\text{PMAN}} = 2.98 [-0.10; 0.06]$; $\beta_{\text{BI}} = 0.19 [-0.17; 0.44]$). Tout comme pour l'abondance de la Colombe à croissants, l'abondance de la Tourterelle à queue carrée est positivement associée à celle de la petite mangouste indienne (Figure 14). L'analyse des résidus n'a révélé aucun écart par rapport aux distributions attendues (Annexe 1, Figure A2).

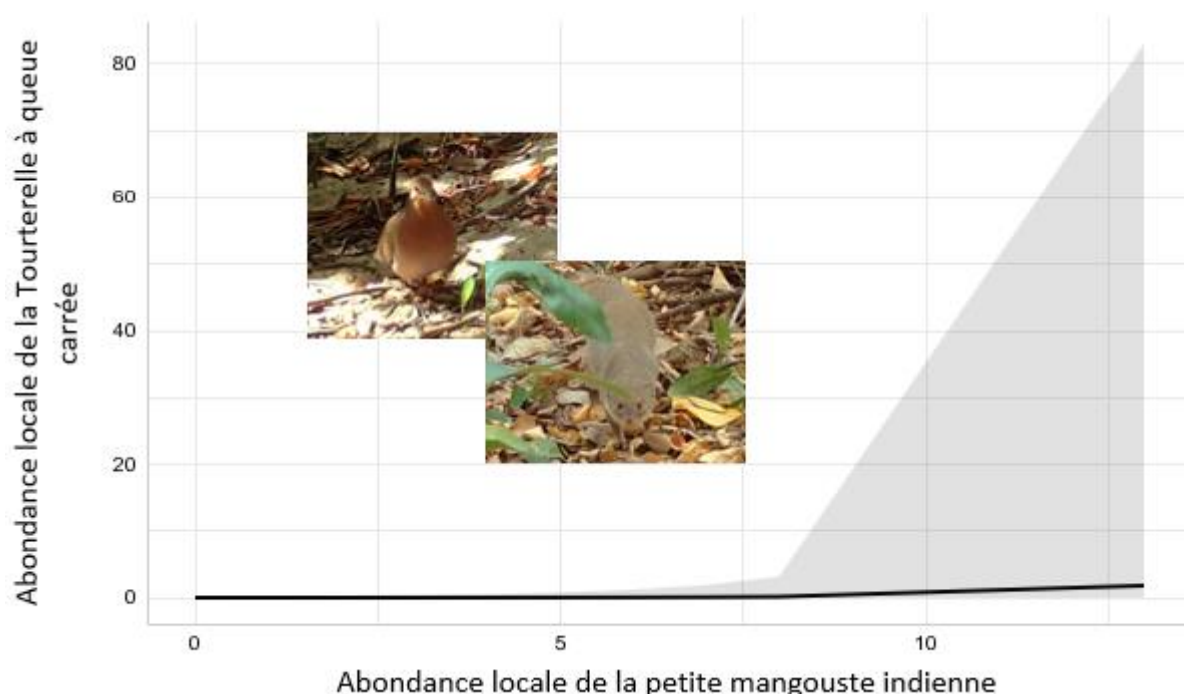


Figure 14. Prédiction de l'évolution de l'abondance locale de la Tourterelle à queue carrée en fonction de l'évolution de l'abondance locale de la petite mangouste indienne, selon le meilleur modèle retenu (Tableau 1). L'intervalle de confiance à 95% est représenté en gris.

2.3.3. Discussion

Nos résultats ont souligné une association positive entre l'abondance à la fois de la Colombe à croissants et de la Tourterelle à queue carrée et celle de la petite mangouste indienne. En revanche, les paramètres mesurés de la litière n'exercent aucune influence significative sur l'abondance des deux espèces aviaires étudiées. Ces constatations sont d'un intérêt pour la conservation et la gestion de ces deux espèces de columbides.

2.3.3.1. Covariation spatiale de l'abondance de la petite mangouste indienne

Au cours de cette étude, nous avons observé une large distribution spatiale de la petite mangouste indienne, avec pas moins de 46.7% des stations de piège photographique visitées. D'autres analyses de suivi ont également mis en évidence cette grande capacité de dispersion de la petite mangouste indienne au sein des îles, sur de grandes distances (Hays 1999; Berentsen et al. 2020). Les analyses génétiques confirment ce constat. Ainsi Louppe et al. (2021b) indiquent une absence de structuration génétique des populations à l'intérieur des îles antillaises étudiées, ce qui traduit la grande dispersion de la petite mangouste indienne au sein de ces dernières. Toutefois, au-delà de la simple cooccurrence spatiale déjà constatée (Louppe et al. 2021a; Jean-Pierre et al. 2022), nos résultats ont permis de mettre en évidence une corrélation positive entre l'abondance de chacune des deux espèces de colombidés et celle de la petite mangouste indienne, parmi les différentes stations étudiées. L'impact de la prédation sur les oiseaux par la petite mangouste indienne repose sur des preuves directes (Engeman et al. 2006; Lewis et al. 2011; Akrim et al. 2019) et indirectes (Hays and Conant 2007; Berentsen et al. 2020; Heathcote et al. 2021; Yagihashi et al. 2021). Plus généralement, l'espèce est considérée comme l'un des mammifères sauvages introduits ayant le plus grand impact sur la biodiversité mondiale (Courchamp et al. 2003; Doherty et al. 2016). Récemment, Cambrone et al. (2023) ont souligné que le risque d'extinction des columbidés est significativement influencé par les espèces exotiques envahissantes. Enfin, outre le fait que la petite mangouste indienne soit une redoutable prédatrice, elle représente également un risque sanitaire pour les espèces aviaires, puisqu'étant un réservoir potentiel de parasites (Cheng et al. 2018), et un vecteur de la salmonellose (Jaffe et al. 2018). L'impact potentiel de cette espèce sur la biodiversité guadeloupéenne mériterait donc une attention particulière.

Nous recommandons donc, d'avoir recours à l'analyse de fèces ou de contenus stomacaux de la petite mangouste indienne (Mahmood and Adil 2017; Dabholkar and Devkar 2020; Subrata et al. 2021) à l'échelle de la Guadeloupe, voire de la Caraïbe.

2.3.3.2. Le régime alimentaire de la Colombe à croissants et de la Tourterelle à queue carrée

L'abondance et la biomasse des invertébrés n'exercent aucune influence significative sur l'abondance de la Colombe à croissants et de la Tourterelle à queue carrée. Ces résultats sont en accord avec les analyses des jabots, qui démontrent que, la matière animale ne constitue qu'une faible partie du régime alimentaire de ces deux columbidés (Seaman 1966; Zamore 1981; Tayalay

1995). Par exemple, Wiley (1961) a estimé que chez la Tourterelle à queue carrée, seul 4% du contenu du jabot était animal. D'autres études ont estimé que la matière animale était complètement absente du régime alimentaire de certains columbidés (Gutiérrez-Galán et al. 2017; Kaouachi et al. 2021).

La consommation marginale de matière animale par les columbidés est notamment liée au besoin de calcium pendant la période de ponte (Murton et al. 2008; Ó hUallachain and Dunne 2013). Etudier la variabilité saisonnière de ce paramètre sur le long terme apporterait plausiblement des informations complémentaires sur les périodes de ponte de la Colombe à croissants et de la Tourterelle à queue carrée, dont la reproduction est estimée à plusieurs fois par an (Wiley 1991; Rivera-Milán 1996, 1997).

Globalement, la dispersion des graines est d'une importance capitale, à la fois pour le maintien de la diversité végétale dans les forêts primaires (Terborgh et al. 2002) et pour la régénération des forêts anthropisées (Wheelwright 1985; Jones et Crome 1990; Gorchov et al. 1993; da Silva and Tabarelli 2000; Corlett 2002). Il serait alors intéressant d'évaluer la variation de la disponibilité des graines et des fruits dans les différentes forêts tropicales de la Guadeloupe, en lien avec la répartition et l'abondance de ces deux espèces, et ce, sur le long terme. Ceci permettrait, par exemple, de mieux comprendre la capacité des frugivores à occuper les stations abondantes en fruits (Rey 1995).

2.3.4. Conclusion

La présente étude souligne, d'une part, la forte présence au sein des forêts de Guadeloupe de la petite mangouste indienne, ce qui concorde avec les études antérieures (Louppe et al. 2021a; Jean-Pierre et al. 2022). A ceci s'ajoute l'existence d'une association positive entre l'abondance de la petite mangouste indienne et celle des espèces aviaires étudiées. Nous encourageons donc les futures investigations à évaluer le succès de prédation de cette espèce exotique envahissante sur les espèces aviaires de la Guadeloupe. Celui-ci est d'ores et déjà démontré dans d'autres régions insulaires (Engeman et al. 2006; Lewis et al. 2011; Akrim et al. 2019). D'autre part, la matière animale n'était nullement liée à l'abondance de la Tourterelle à queue carrée et de la Colombe à croissants au sein des différentes stations forestières échantillonnées. Néanmoins, celle-ci fait partie, dans une moindre mesure, de leur régime alimentaire (Seaman 1966; Zamore 1981; Wiley 1991; Tayalay 1995). De plus, les données sur les variations saisonnières des graines, des fruits et

des invertébrés en lien avec la répartition et l'abondance des columbidés sont inexistantes en Guadeloupe. Face à ces deux constats, nous suggérons que de futures études mettent en lumière ces paramètres, pour une meilleure compréhension des niches écologiques de ces espèces. A cette fin, l'étude des niches isotopiques indiquant, par exemple, la plasticité des niches trophiques ou la répartition des ressources alimentaires (Hobson 1999; Layman et al. 2012), pourrait s'avérer particulièrement efficace.

Annexes

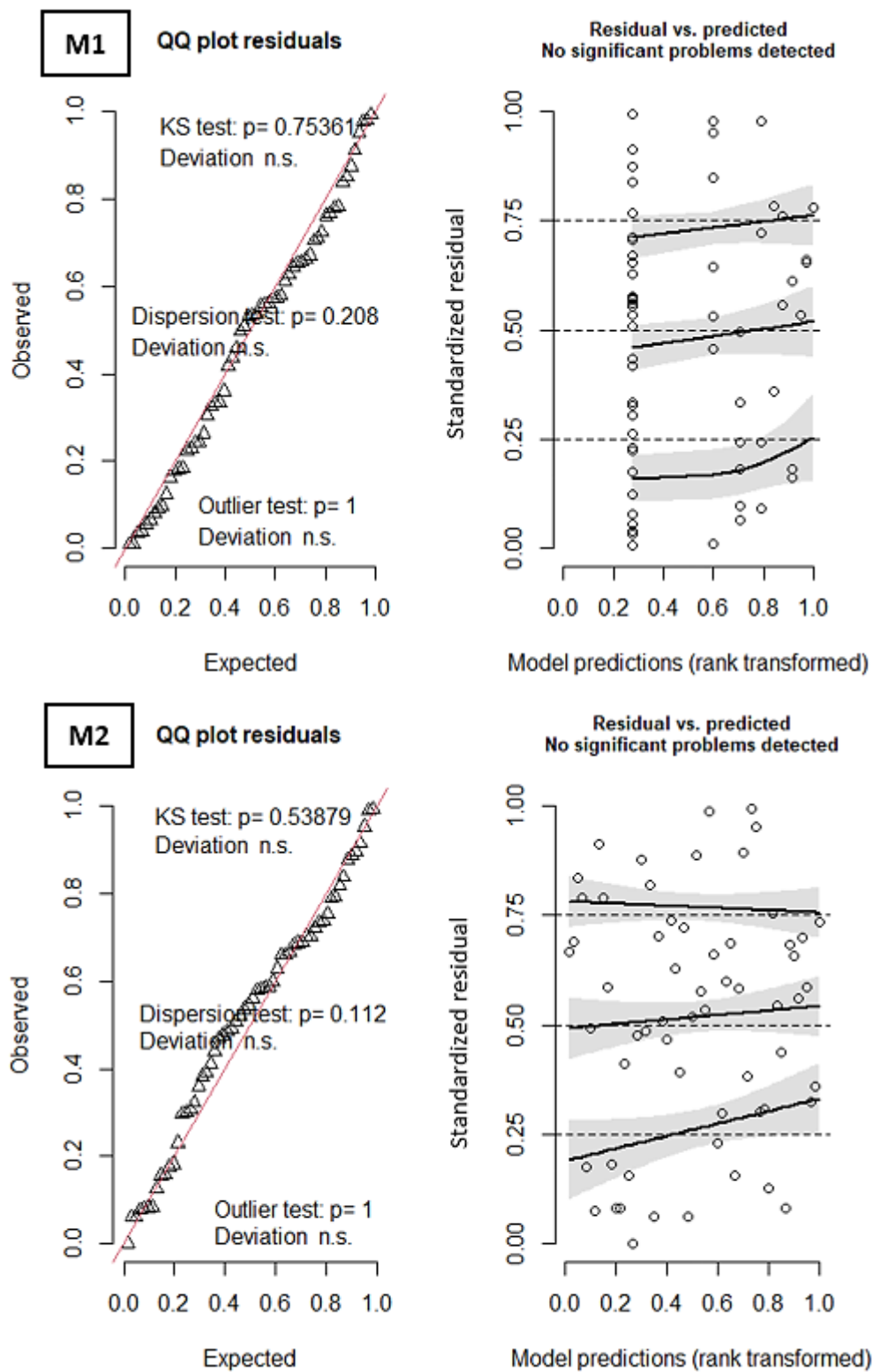


Figure A1. Diagrammes de diagnostic pour les deux meilleurs modèles (M1 et M2, respectivement) visant à estimer l'influence de facteurs biotiques sur l'abondance de la Colombe à croissants.

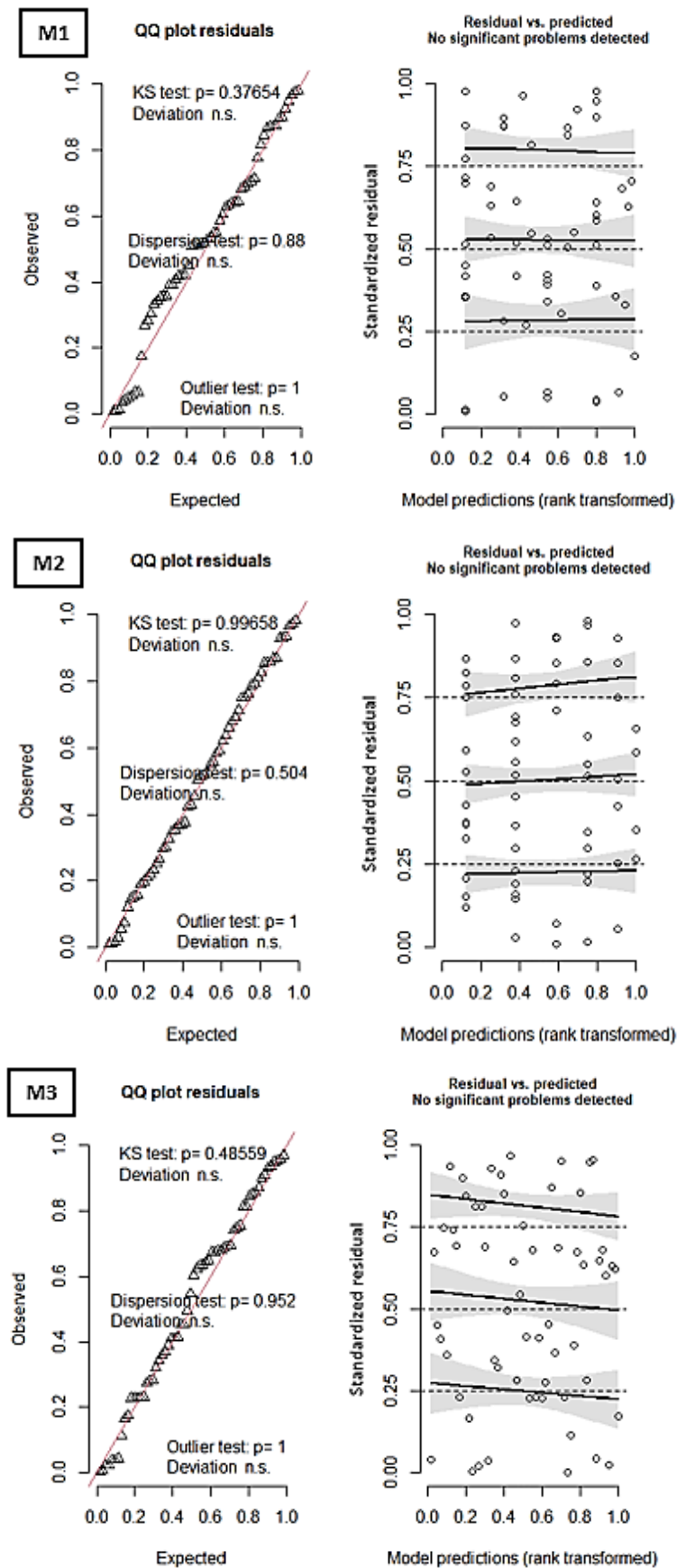


Figure A2. Diagrammes de diagnostic pour les trois meilleurs modèles (M1, M2, M3, respectivement) visant à estimer l'influence de facteurs biotiques sur l'abondance de la Tourterelle à queue carrée.

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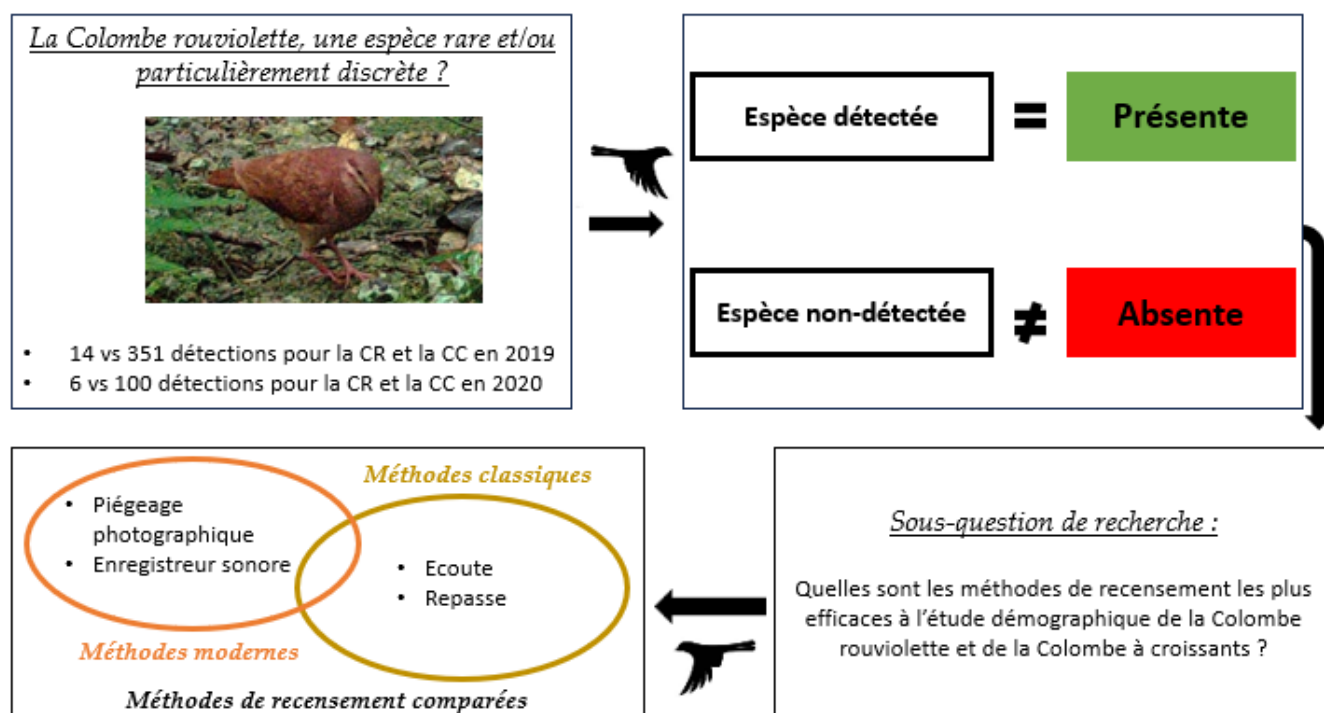
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CHAPITRE 3

Efficacité des méthodes classiques et modernes pour estimer l'occupation spatiale et l'abondance locale de la Colombe rouviolette et de la Colombe à croissants, en relation avec divers facteurs environnementaux

3.1. Chapeau introductif du chapitre 3



Article 4

Efficiency of the observational and remote sensing census method for the detection of two secretive columbid species of cynegetic interest

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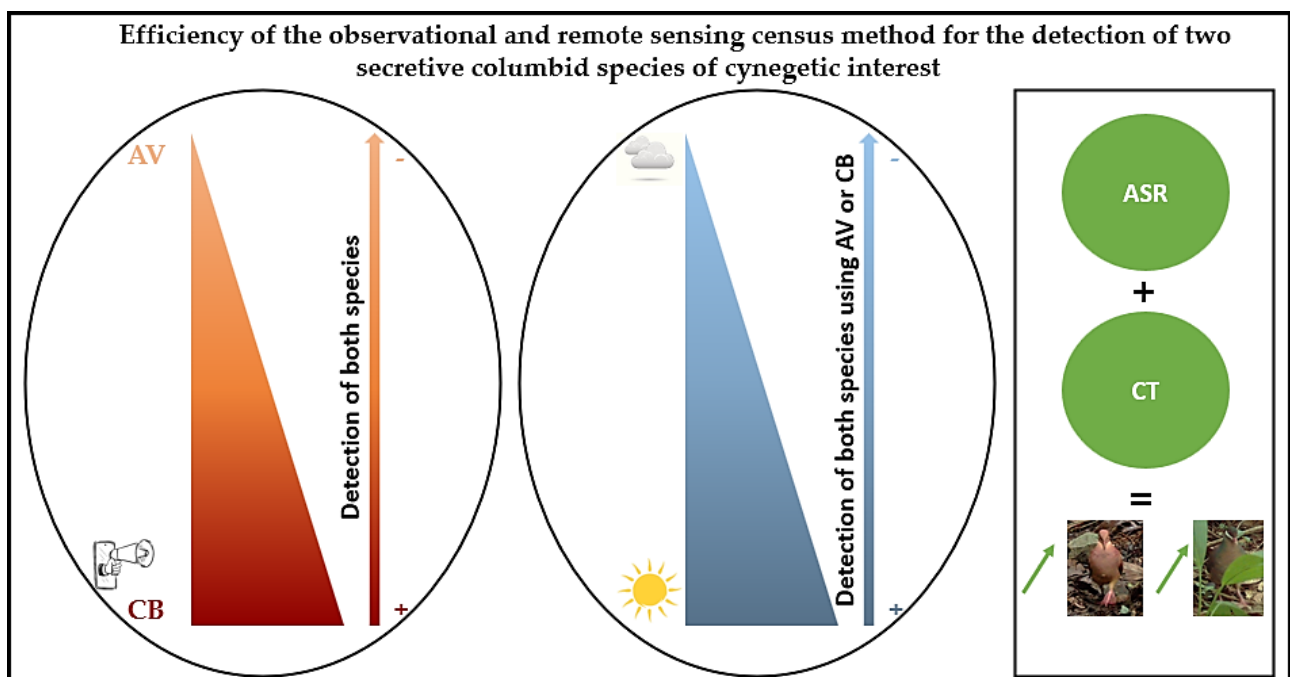
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Graphical abstract



Abstract

Surveys of secretive, ground-dwelling forest bird species can be particularly difficult and time-consuming. However, little effort has been made to compare the efficiency of different methods used to that end. In this context, we assessed the effectiveness of two observational methods (Auditory-Visual method vs Call-Broadcasting method) and two remote sensing methods (Autonomous Sound Recorder method vs. Camera-Trap method), in estimating the presence and abundance of the Bridled Quail-Dove (BQD) and the Ruddy Quail-Dove (RQD) at various stations located in Guadeloupe forests (French West Indies). These two secretive columbid species are of conservation and hunting interest, but have been reported to be declining in Guadeloupe. Overall, our results confirmed that RQD is much less abundant than BQD in Guadeloupe, in contrast to other Caribbean islands. The Call-Broadcasting method proved to be more effective for both species, as it increased the probability of detection by reducing 'false absences'. On the other hand, the Autonomous Sound Recorder and Camera Trap methods proved to be complementary, as at some stations the presence of a species was detected by only one of the two methods. We discuss the relative merits of the different methods in terms of reliability, ease of use, and amount of information obtained.

Keywords: Ruddy Quail-Dove, Bridled Quail-Dove, Secretive columbid species, Auditory-Visual method, Call-Broadcasting method, Autonomous Sound Recorder, Camera-Trap method, French West Indies

1. Introduction

Reliable and accurate surveys are crucial for the effective management of both harvested and threatened bird species (Bibby et al., 2000; Sutherland, 2006). However, some bird species are difficult to detect because of their rarity, low density, secretive behaviour, or occurrence in remote areas (Colyn et al., 2017; Smith et al., 2017; Robinson et al., 2018; Holiman et al., 2022). Estimating their spatial occupancy and abundance often requires large sampling efforts, that can be time-consuming and logistically prohibitive. Designing optimal survey methods is therefore of particular importance to distinguish between "true" rarity (due to low abundance) and "apparent" rarity (due to low detectability; Cerqueira et al., 2013).

Several indirect sampling methods that do not rely on the physical capture of individuals have been used to survey inconspicuous, elusive, or secretive species, such as marsh birds or ground-dwelling forest birds. Among them, conventional distance sampling based on the passive auditory and visual method simply consists of recording birds seen and/or heard along a linear or point transect (Gottschalk et al., 2010; Steidl et al., 2013). The call-broadcast or playback method consists, in addition, in broadcasting the call of the species of interest to elicit a behavioural response, and thus increase detection rate during a linear or point transect (DesRochers et al., 2008; Frieze et al., 2012; Fuller et al., 2012; Okahisa et al., 2016; Yip et al., 2017). However, more recently, remote techniques such as camera-traps and passive sound recorders have become increasingly popular to survey elusive avian species (Sugai et al., 2019; Suwanrat et al., 2015; Jean-Pierre et al., 2023; Pérez-Granados et al., 2023).

Among the secretive forest ground-dwelling avian species, columbids (pigeons and doves) are of particular conservation concern, due to their ecological and patrimonial importance (Walker, 2007; Cambrone et al., 2023). In particular, frugivorous and granivorous columbid species contribute significantly to the regeneration of tropical forests through seed dispersal (Bucher and Bocco 2009; Silvina Costán and Sarasola 2017), especially on islands (McConkey et al., 2004; Tassin et al., 2010; Marrero and Nogales, 2021; Ando et al., 2022). However, tropical islands columbid species are particularly prone to extinction, because of their small distribution area and exposure to invasive predatory mammal species (reviewed in Cambrone et al., 2023). In addition, the level of scientific attention given to columbid species is inversely related to their conservation status and is lower for species living in the southern hemisphere (Cambrone et al. 2023).

Although distance sampling (Rivera-Milán et al. 2015), call-broadcast (Kirkpatrick et al. 2007), camera traps (Ehlers Smith et al. 2017; Jean-Pierre et al. 2022), and passive acoustic monitoring (Pérez-Granados and Schuchmann 2020) have all been used to study elusive columbid species, their relative efficiency remains to be assessed (see however Cambrone et al., 2021). We therefore assessed the performance of different methods for surveying two secretive ground-dwelling columbid species, the Ruddy Quail-Dove, *Geotrygon montana*, and the Bridled Quail-Dove, *G. mystacea*, in Guadeloupe, French West Indies. First, following Cambrone et al., (2021), we compared the performance of the Call-Broadcasting method (CB) to that of the Auditory-Visual method (AV) in detecting the presence and estimating the relative abundance of the two species along line transects. Second, we compared the results obtained on the presence and relative abundance of

the two species at fixed points between camera traps (CT) and autonomous sound recorders (ASR). We discuss our results in relation to the development of coordinated monitoring programs for columbid species of conservation interest in the insular Caribbean.

2. Material and Methods

2.1. Studied species

The distribution of the Ruddy Quail-Dove extends from the Caribbean Basin to the northern half of South America (Gibbs et al., 2001), while the Bridled Quail-Dove is endemic to the insular Caribbean, with a distribution extending from Puerto Rico to St Lucia (Chiple, 1991; Raffaele, 1998). Both species feed on seeds and fruits fallen on the ground and, exceptionally, on insects, earthworms, and snails (Skutch, 1949; Cruz, 1974). Although they are similar in body size and general morphology, they differ markedly in plumage coloration and vocalizations (Kirwan et al., 2019), making them easy to distinguish by visual or auditory observation. However, their secretive behaviour make them difficult to observe in the dense tropical forest environments they inhabit. Although both species are listed as Least Concern on the IUCN Red List, their populations are reported to be declining. In particular, they tend to be rare in the Lesser Antilles (McNair et al., 2005; Platenberg et al., 2005; Boal, 2018; Kirwan et al., 2019; Rivera-Milán et al., 2021). However, contrary to the general pattern at the regional level (McNair et al., 2005; Kirwan et al., 2019; Rivera-Milán et al., 2021), the Ruddy Quail-Dove is considered to be much less abundant than the Bridled Quail-Dove in Guadeloupe (Levesque et al., 2020; Jean-Pierre et al., 2022).

2.2. Study area

This study was carried out in Guadeloupe, French West Indies (Fig. 1). This archipelago consists of two main contiguous islands, Basse-Terre and Grande-Terre, separated by a narrow channel (Rivière Salée, or Salt River) which is dominated by mangroves and swamp forests. While the limestone and flatter island of Grande-Terre is dominated by fragmented semi-deciduous forests, the mountainous volcanic island of Basse-Terre is mainly dominated by tropical rainforest (Guilcher et al., 1978; Rousteau, 1996).

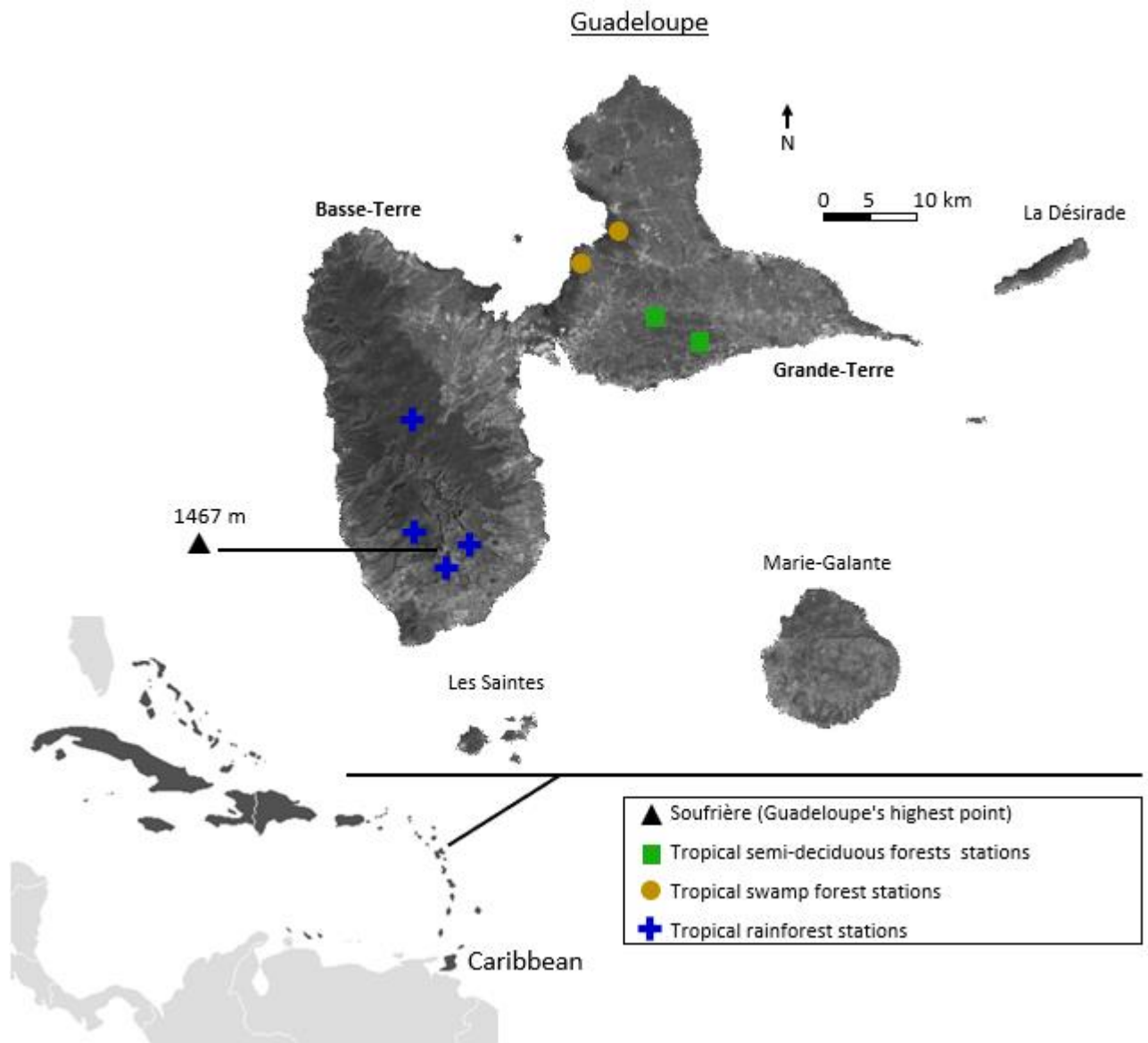


Fig.1. The 8 camera-trap locations that were surveyed between 1st January and 1st February 2023 in Guadeloupe, including two semi-deciduous forests stations (green), two swamp forest stations (yellow), and four tropical rainforest stations (blue). The distance between adjacent stations ranged from 2.82 km to 12.46 km

2.3. Data collection

Eight stations were surveyed in Guadeloupe between October 2022 and January 2023, including two tropical semi-deciduous forest stations, two tropical swamp forest stations and four tropical rainforest stations (Fig. 1). As the main objective of the present study was to compare different detection and counting methods, we selected stations where the presence of both species had previously been confirmed (Jean-Pierre et al. 2022) in order to optimise our sampling effort.

However, the selected stations remain representative of the diversity of forest habitats along the elevation gradient in Guadeloupe.

2.3.1. Auditory-Visual method vs. Call-Broadcasting method

We obtained recordings of calls of each species from the Xeno-canto bird sound collection (Xeno-canto Foundation), from which we removed background noise using the free Audacity® software 3.3.3. We then used a nomadic loudspeaker (4.2 W, JLB Go 4, connected via Bluetooth to a smartphone, to broadcast the recordings in the field. All recordings were standardised at an amplitude of 60 decibels (measured 1 m from the loudspeaker, using the Decibel X application from Skypaw Co), which allowed the experimenter (AJP) to clearly distinguish the recordings at 45 ± 5 m, depending on environmental conditions.

To assess the relative efficiency of the AV and CB methods, we conducted surveys along transects at each selected station. Each transect consisted of five counting points regularly spaced 200 m apart. At each counting point, we first used the AV method, which consist in recording every individual of each species seen or heard during a 5-min period. We then successively broadcast the call of each species during a 5-min period, with a 30-s recording at the beginning of the period and again after 150 s. Following Cambrone et al., (2021), the broadcasted calls of the two species were systematically reversed between each counting station and replicate. We thus spent 15 min at each counting point, during which the observer (AJP) recorded all individuals seen or heard.

Counts along transects at each station were replicated three times (R1: 14 October to 29 October; R2: 14 November to 29 November; R3: 14 December to 29 December) in the morning and in the afternoon, when columbid species are usually most active (Jean-Pierre et al. 2022). Following Cambrone et al., (2021), the order of transect visits during the morning and afternoon surveys was randomised independently for each replicate to avoid systematically sampling a given transect in the morning and afternoon of the same day.

2.3.2. Camera-Traps vs. Autonomous Sound Recorders

We placed a single passive infrared camera-trap (Browning© Spec Ops EDGE, with a detection range of approximatively 18 m over a 42° angle of view) at each station. The eight camera-traps remained active for 31 consecutive days (1 January to 1 February), resulting in 248 trapping days. Following Jean-Pierre et al., (2022), each camera-trap was attached to a sturdy tree, at a height of

between 20 and 30 cm, and remained active 24 h⁻¹. To optimise the range of the camera-trap sensor, we placed camera traps in low vegetation covered areas. Camera traps were set to take three photographs each time a movement was detected, with a 30-s delay between consecutive photographs. However, during data analysis, a 10-min buffer time was applied between detections of the same species to avoid multiple captures of the same individual within a short period of time (Smith et al., 2017; Jean-Pierre et al., 2022).

We conducted playback experiments to determine how efficiently we could record the calls of each species using a full-spectrum acoustic logger (AudioMoth). To that end, we broadcasted the cleaned recordings prepared for the two species (see above) at an amplitude of 60 decibels, using a nomadic loudspeaker (4.2 W, JLB Go 4) connected via Bluetooth to a smartphone, at 10, 25 and 40 m from the automatic recorder. Such playback experiments were conducted at all stations where camera traps were set, during periods of low activity for both species (Jean-Pierre et al. 2022). Using Audacity® software 3.3.3., recordings broadcasted up to 25 m from the acoustic loggers were clearly distinguishable. In parallel, we used a series of different calls, corresponding for each species to 25 recordings of 20-second duration (obtained from Xeno-canto Foundation and eBird), to assess AJP's ability to identify them correctly. The recordings were played in a random order on a MacBook Air (Retina, 13-inch, 2019) in the laboratory, with a 30-second interval between two consecutive songs. Listening was done very carefully as the two species have similar sonograms. However, while the low song of the Bridled Quail-Dove consists of two syllables, the low song of the Ruddy Quail-Dove consists in one single syllable (Fig. 2).

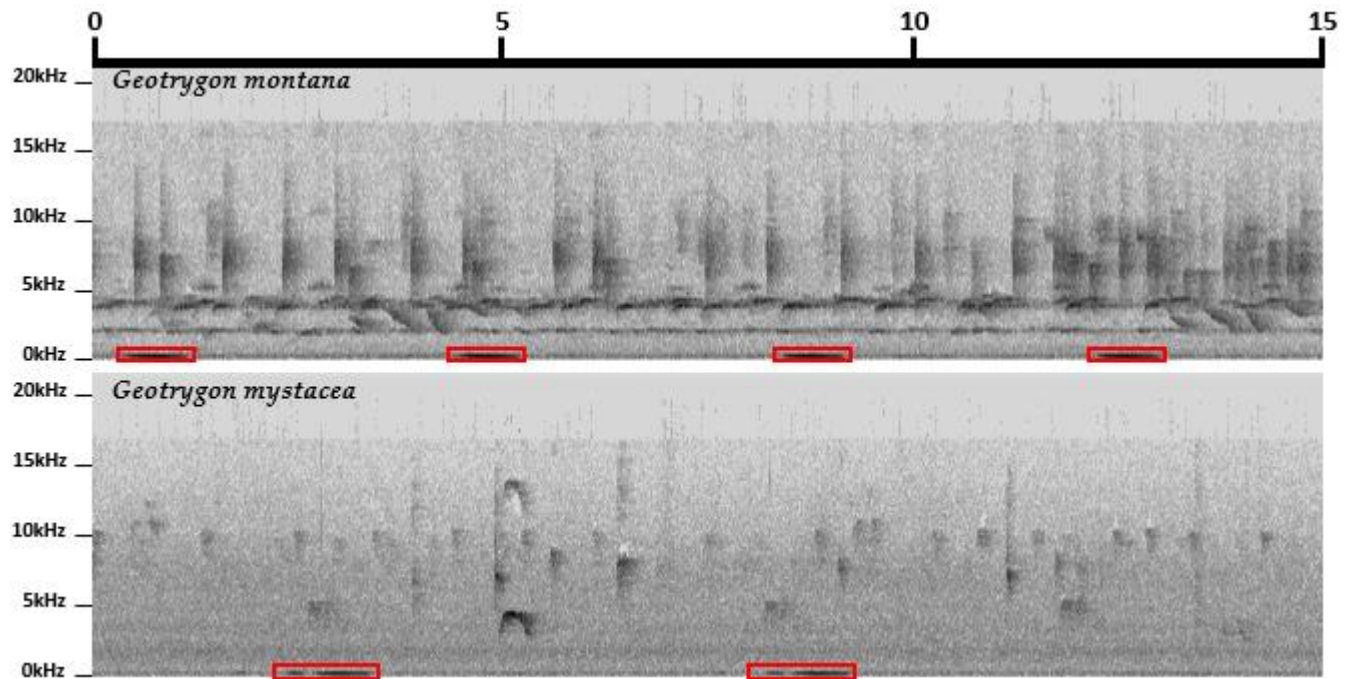


Fig.2. Spectrograms of a sequence of exemplar calls of the Ruddy Quail-Dove (top, red) and the Bridled Quail-Dove (bottom, red), over a period of 15s. On the x-axis, the time (s), and on the y-axis, the frequency (kHz)

Our relative error rate was 0% for both the Ruddy Quail-Dove and the Bridled Quail-Dove. We therefore concluded that the use of acoustic loggers was an appropriate method to survey the two quail dove species.

During the phase of data acquisition, we placed a single acoustic logger on the same selected tree trunks to which a camera trap was attached, at a height between 1 m and 1.5 m above the ground. Acoustic loggers were programmed to record sounds during three distinct periods of the day (i.e., from 05:30 to 8:30, from 11:30 to 14:30 and from 15:30 to 18:30). Following Pérez-Granados et al., (2020) and following preliminary trials, a frequency of 48KHz and 16 bits per sample were used to optimize recording of bird species. Throughout data collection, we considered morning (AM) and afternoon (PM) as two separate sampling periods of the day, and visually assessed meteorological conditions (i.e., 'sunny' or 'overcast') during auditory and visual counts. We saved files obtained from acoustic loggers in the uncompressed waveform audio file (.wav) format, using a 32 GB microSD card. All recordings were subsequently analysed manually by AJP using Audacity® software 3.3.3. We applied a 30-min buffer time between detections of the same species to reduce double counting of the same individual. Thus, only one individual was counted per species,

regardless of the number of vocalisations of the same species during a 30-minute period of recording (Vold et al. 2017).

2.4. Data analysis

We used the R software 3.6.2 (R Core Team 2019) to perform all analyses and draw figures.

As the data did not follow a normal distribution (Shapiro–Wilk normality test, $p < 0.001$), we relied on non-parametric tests to compare average estimates of local abundance obtained at each station between the auditory-visual method and the call-broadcast method, and between camera traps and autonomous sound recorders.

2.4.1. Auditory-Visual method and Call-Broadcast method

We performed a McNemar change test in order to assess to what extent the AV and CB methods agree with each other, using the R package *stats 4.4.0* (R Core Team, 2019). We used Spearman's rank correlation tests to compare the local abundance estimates obtained at each station between the three sampling periods, for each species and each detection method. We used Wilcoxon signed-rank tests for paired samples to compare the number of individuals of each species detected at each station between the two methods.

We then used generalized linear mixed models (GLMMs; Bolker et al., 2009) to assess the influence of detection method (DM), time of the day (TIME, a.m vs. p.m.), weather conditions (i.e., 'sunny' or 'overcast'; WEA), and interactions between DM and TIME and between DM and WEA, on the presence and abundance of each of the two species at each station. More precisely, we fitted GLMMs using a Binomial distribution (logit link) for occupancy (presence/absence) and a Poisson distribution (log link) for abundance, as they provided the best fit to the data. Models were built using the R package *glmmTMB 1.0.0* (Brooks et al., 2017). All possible combinations of covariates were investigated using the R package *MuMIn 1.43.6*, resulting in 13 models (Barton et al., 2019). For all the models, nested random effects were included (i.e., replicate nested within station and station nested within forest type), as we had three temporal replications per station, and counting points were distributed in eight different stations, themselves distributed in three different forest types. We ranked models using the Akaike information criterion in the R package *AICcmodavg 2.3-1* (Mazerolle et al., 2017). Models with $\Delta AICc < 2$ were considered as equivalent for explaining variation in the local abundance of the species studied (Burnham et al. 2011). Goodness-of-fit for

all valid models were checked using the R package DHARMA 0.2.7 (Hartig, 2020). Finally, coefficients (β_i) of model parameters and their 95% confidence interval were estimated from the R package *AICcmodavg* 2.3-1 and were considered significant when they did not overlap zero.

2.4.2. Camera-Trapping vs. Autonomous Sound Recorders

We again performed a McNemar change test to assess the degree of agreement between CT and ASR, using R package *stats* 4.4.0 (R Core Team, 2019). To assess the influence of remote sensing method, time of the day (AM or PM), and interactions between detection methods and time of the day on the abundance of the two species, we retained the zero-inflated binomial distribution (log link) as it provided the best fit to the data (White and Bennetts 1996; Lapin et al. 2013). All possible combinations of covariates were also investigated using the R package *MuMIn* 1.43.6, resulting in five models (Barton et al., 2019). We then relied on model selection as described above.

3. Results

As the proportions of sites with and without detection did not vary between replicates for both species, we pooled the data for further analysis (Table 1; Fisher's exact test, RQD: $P_{AV} = 1$; $P_{CB} = 0.75$; BQD: $P_{AV} = 0.75$; $P_{CB} = 1$).

Table 1. Detection of the Ruddy Quail-Dove and the Bridled Quail-Dove according to the different replicas, using the Auditory-Visual or Call-Broadcast method

	Auditory-visual method			Call-broadcast method		
Replica	R1	R2	R3	R1	R2	R3
Ruddy Quail-Dove						
	6	5	6	8	6	7
	2	3	2	0	2	1
Bridled Quail-Dove						
	8	7	6	8	8	8
	0	1	2	0	0	0

3.1. Auditory-visual method vs. call-broadcast method

For each species and each detection method, we found positive and significant correlations between replications, indicating that variation in presence and abundance between stations was consistent in time (Table 2A and Table 2B).

Table 2A. Values of Spearman's correlation test based on the relative abundance of Ruddy Quail-Doves detected using the Auditory-Visual method and the Call-Broadcast method, over the three replications

	S1	S2	S3
S1		0.38 ($p = 0.01$)	0.54 ($p < 0.001$)
S2	0.54 ($p < 0.001$)		0.48 ($p = 0.002$)
S3	0.71 ($p < 0.001$)	0.48 ($p = 0.001$)	

AV method

CB method

Table 2B. Values of Spearman's correlation test based on the relative abundance of Bridled Quail-Doves detected using the Auditory-Visual method and the Call-Broadcast method, over the three replications

	S1	S2	S3
S1		0.46 ($p = 0.003$)	0.46 ($p = 0.003$)
S2	0.72 ($p < 0.001$)		0.41 ($p = 0.008$)
S3	0.58 ($p < 0.001$)	0.49 ($p = 0.001$)	

AV method

CB method

Overall, the CB method significantly improved the detection of Ruddy Quail-Dove and Bridled Quail-Dove compared to the AV method (McNemar change test, $X^2 = 8.26$, d.f.=1, $P = 0.004$ and $X^2 = 29.47$,

df = 1, $P < 0.001$, respectively). Moreover, local abundance, with data from the three replicates pooled for each station, differed between the two detection methods for both species (Wilcoxon's test: $V_{\text{RQD}} = 0$ and $V_{\text{BQD}} = 0$; $n = 8$, $P = 0.01$). Overall, we detected more individuals using the CB method than using the AV method (RQD: 41 vs. 23; BQDs and 95 vs. 43, respectively).

3.1.1. Modelling variation in the detection of the two species

When comparing the 13 models based on presence, TIME, DM, WEA and the interaction between DM and WEA were retained three models, for both species (Table 3). Quantile-quantile plots and goodness-of-fit tests showed no evidence of lack of fit for any competing model (Supplementary Materials Fig. S1). After model averaging, only DM and WEA were meaningful (RQD: β_{DMCB} [95% CI] = 0.65 [0.10, 1.20]; β_{WEAS} [95% CI] = 0.88 [0.33, 1.42]; BQD: β_{DMCB} [95% CI] = 0.96 [0.51, 1.41]; β_{WEAS} [95% CI] = 1.22 [0.78, 1.66]). More specifically, the estimated probability of detection was significantly higher when using the CB method and in sunny weather conditions, for both species (Fig. 3). Although TIME and the interaction between DM and WEA were retained in the top ranked models for both the Ruddy Quail-Dove and the Bridled Quail-Dove, respectively (Table 3), their overall effect was not significant (RQD: β_{TIMEPM} [95% CI] = 0.19 [-0.35, 0.73]; $\beta_{\text{DMCB:WEAS}}$ [95% CI] = -0.64 [-1.76, 0.52] and BQD : β_{TIMEPM} [95% CI] = -0.08 [-0.52, 0.35]; $\beta_{\text{DMCB:WEAS}}$ [95% CI] = -0.55 [-1.48, 0.38]).

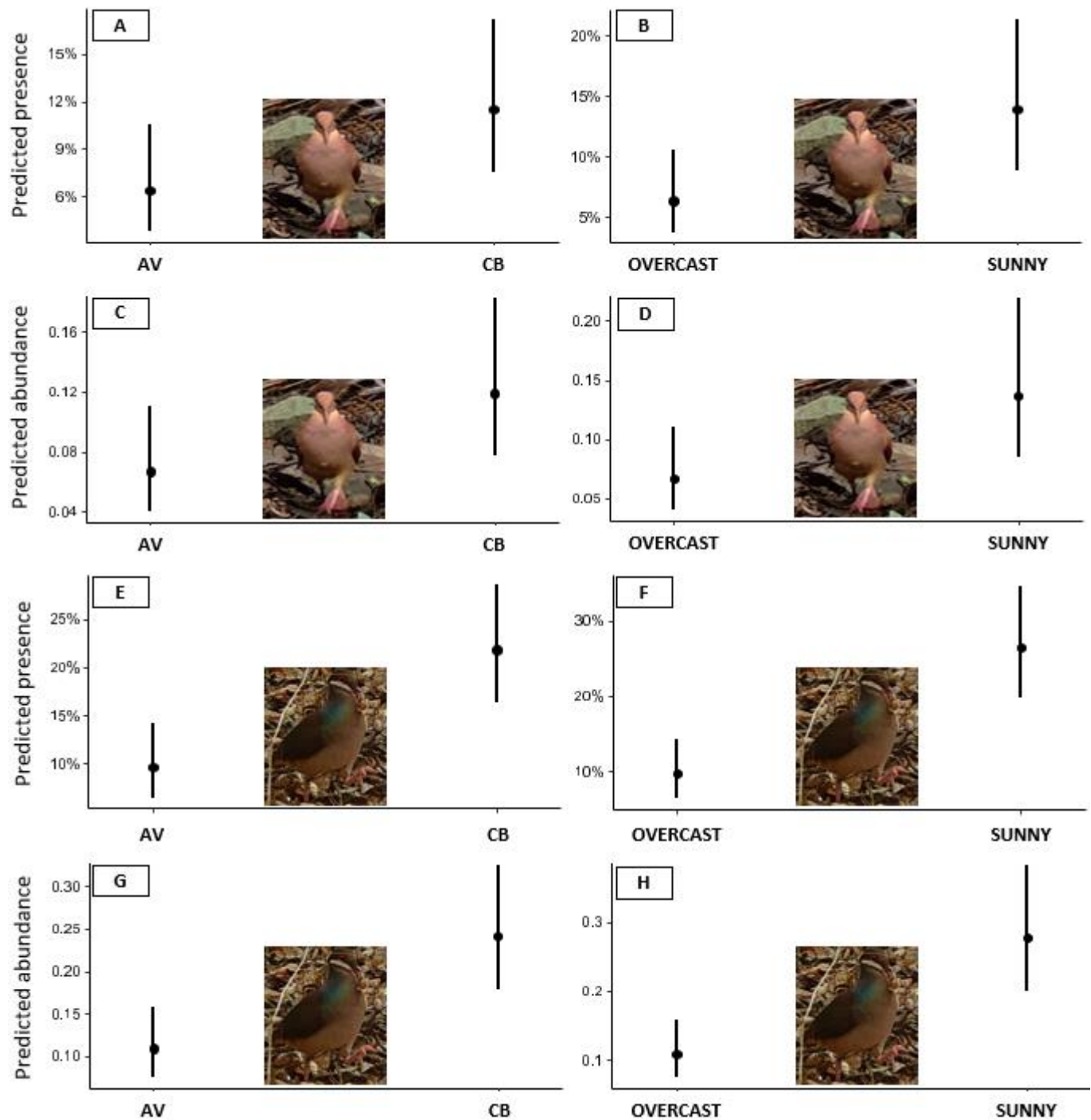


Fig.3. Predictions from selected model for the Ruddy Quail-Dove (A, B, C, D) and the Bridled Quail-Dove (E, F, G, H), according to best models for each species (see Table 3)

Table 3. Detection and abundance models for the Ruddy Quail-Dove and the Bridled Quail-Dove, in Guadeloupe forests. Detection and abundance were modelled according to detection methods (DM), time of the day (TIME), weather conditions (WEA), interaction between DM and TIME as well as interaction between DM et WEA. We reduced the table to models within delta AIC < 4 (see Table S1 for the full table)

	Models	Df	LogLik	AICc	ΔAICc	Weight
	Ruddy Quail-Dove presence					
M1	DM+WEA	4	-178,76	365,61	0,00	0,33
M2	DM+WEA+DM:WEA	5	-178,16	366,45	0,84	0,22
M3	DM+TIME+WEA	5	-178,53	367,18	1,57	0,15
M4	DM+TIME+WEA+DM:WEA	6	-177,93	368,03	2,42	0,10
M5	DM+TIME+WEA+DM:TIME	6	-178,31	368,80	3,19	0,07
M6	WEA	3	-181,49	369,03	3,42	0,06
	Ruddy Quail-Dove abundance					
M1	DM+WEA	4	-187,03	382,14	0,00	0,29
M2	DM+WEA+DM:WEA	5	-186,24	382,61	0,47	0,23
M3	DM+TIME+WEA	5	-186,74	383,61	1,46	0,14
M4	DM+TIME+WEA+DM:WEA	6	-185,95	384,08	1,94	0,11
M5	WEA	3	-189,59	385,24	3,10	0,06
M6	DM+TIME+WEA+DM:TIME	6	-186,58	385,34	3,20	0,06
M7	FULL	7	-185,85	385,93	3,79	0,04
	Bridled Quail-Dove presence					
M1	DM+WEA	4	-244,88	497,85	0,00	0,38
M2	DM+WEA+DM:WEA	5	-244,20	498,53	0,68	0,27
M3	DM+TIME+WEA	5	-244,81	499,75	1,90	0,15
M4	DM+TIME+WEA+DM:WEA	6	-244,13	500,44	2,59	0,10
M5	DM+TIME+WEA+DM:TIME	6	-244,66	501,51	3,66	0,06
	Bridled Quail-Dove abundance					
M1	DM+WEA	4	-298,59	605,27	0,00	0,32
M2	DM+WEA+DM:WEA	5	-297,79	605,70	0,43	0,26
M3	DM+TIME+WEA	5	-298,27	606,67	1,40	0,16
M4	DM+TIME+WEA+DM:WEA	6	-297,47	607,11	1,84	0,13
M5	DM+TIME+WEA+DM:TIME	6	-298,03	608,24	2,97	0,07

3.1.2. Modelling variation in the abundance of the two species

When comparing the 13 models based on abundance (Table 3), only DM and WEA were considered to be meaningful, for both species (RQD: β_{DMCB} [95% CI] = 0.58 [0.07, 1.09]; β_{WEAS} [95% CI] = 0.71 [0.21, 1.21] and BQD: β_{DMCB} [95% CI] = 0.79 [0.43, 1.15]; β_{WEAS} [95% CI] = 0.94 [0.59, 1.29]). Quantile-quantile plots and goodness-of-fit tests showed no evidence of lack of fit associated to the top ranked models (Supplementary Materials Fig. S1). As with the estimated probability of detection, the estimated probability of abundance was significantly higher when using the CB method and in sunny weather conditions, for both species (Fig. 3). Although time of the day TIME and the interaction between DM and WEA was retained in the top ranked models for both species (Table 3), their overall effect was not significant (RQD: β_{TIMEPM} [95% CI] = 0.19 [-0.30, 0.69]; $\beta_{\text{DMCB:WEAS}}$ [95% CI] = -0.68 [-1.76, 0.40] and BQD : β_{TIMEPM} [95% CI] = -0.14 [-0.47, 0.20]; $\beta_{\text{DMCB:WEAS}}$ [95% CI] = -0.50 [-1.28, 0.28]).

3.2. Camera-traps vs. sound recorders

Although the ASR method significantly improved the detection of Ruddy Quail-Dove compared to the CT method, the two methods had similar performance for the detection of Bridled Quail-Dove (McNemar change test, $\chi^2=6.86$, $df=1$, $P = 0.009$ and $\chi^2=0.28$, $df=1$, $P = 0.59$, respectively).

BQD was significantly more abundant than RQD (Wilcoxon's test: $V = 0$; $n = 8$, $P = 0.02$). Local abundance estimated at each station was correlated between the two detection methods for RQD (Spearman rank correlation test, $r_s = 0.75$, $n = 8$, $P = 0.03$), but not for BQD ($r_s = -0.01$, $n = 8$, $P = 0.98$). In addition, the effectiveness of the ASR and CT methods was reversed between the two species (Chi-square test, $\chi^2 = 9.03$, $d.f. = 1$, $P = 0.003$; Table 4).

Table 4. Local abundances of the Ruddy Quail-Dove and the Bridled Quail-Dove according to method used (ASR: Autonomous Sound Recorders; CT: Camera-Trapping)

	ASR	CT
Ruddy Quail-Dove	20	7
Bridled Quail-Dove	74	98

3.2.1. Modelling spatial variation in the abundance of the two species

According to the top ranked models (Table 5), DM and TIME were the only significant environmental variables associated with spatial variation in the abundance of RQD, with higher abundance estimated in the morning and by the ASR method (β_{DMCT} [95% CI] = -1.05 [-1.98, -0.10]; β_{TIMEPM} [95% CI] = -1.29 [-2.26, -0.30]). Although retained in the top-ranked models, the interaction between DM and TIME had no effect on RQD abundance ($\beta_{DMCT:TIMEPM}$ [95% CI] = -0.72 [-3.15, 1.71]). Similarly, according to the top ranked models, DM and TIME were retained to explain spatial variation in the abundance of the BQD (Table 5). However, after model averaging, none of these environmental variables was significantly associated with spatial variation in the abundance of the BQD (β_{DMCT} [95% CI] = 0.15 [-0.37, 0.67]; β_{TIMEPM} [95% CI] = -0.28 [-0.74, 0.19]). Quantile-quantile plots and goodness-of-fit tests showed no evidence of fit problems for the top-ranked models for both species studied (Supplementary Material Fig. S2).

Table 5. Abundance models for the Ruddy Quail-Dove and the Bridled Quail-Dove, in Guadeloupe forests. Abundance was modelled according to detection methods (DM), time of the day (TIME), and interaction between DM and TIME

	Models	Df	LogLik	AICc	$\Delta AICc$	Weight
Ruddy Quail-Dove abundance						
M1	DM+TIME	5	-98,78	207,61	0,00	0,59
M2	FULL	6	-98,59	209,27	1,66	0,26
M3	TIME	4	-101,39	210,83	3,22	0,12
M4	DM	4	-102,61	213,26	5,65	0,03
M5	NULL	3	-105,15	216,32	8,70	0,01
Bridled Quail-Dove abundance						
M1	TIME	4	-404,53	817,11	0,00	0,42
M2	DM	4	-405,03	818,11	1,00	0,25
M3	DM+TIME	5	-404,40	818,87	1,76	0,17
M4	FULL	6	-403,60	819,29	2,18	0,14
M5	NULL	2	-410,20	824,40	7,29	0,01

4. Discussion

This study presents the first assessment of the effectiveness of observational and remote-sensing methods for the census of two secretive ground-dwelling columbid species. Overall, our results confirmed that the RQD is less common than the BQD in Guadeloupe region, conversely to most of the Caribbean region. Therefore, further information on these two sympatric species, particularly on their trophic niche plasticity and food resource partitioning, would be interesting to understand the observed variation in the abundance of the two species (Hobson, 1999; Chesson, 2000; Jackson et al., 2011). Although our sample size is limited, the design of the study and the robustness of the statistical analysis allows for some general considerations on both the design of future survey studies and the relative abundance of the two species of quail doves in Guadeloupe. Concerning the observational census methods, the CB method was more effective than the AV method for a similar sampling effort, and improved counting accuracy during the survey. More specifically, our results showed that detection and abundance were higher using the CB method than the AV method for both species, regardless of the time of day. This confirms earlier findings showing that the CB method increases the number of birds detected by reducing false absences using the broadcast of recorded calls to elicit behavioural responses, particularly for secretive birds with small populations (Johnson et al., 1981; Marion et al., 1981; Sutherland, 2006; Fuller et al., 2012). Our findings are thus congruent with previous studies showing the effectiveness of the CB method for columbid species (Kirkpatrick et al., 2007; Cambrone et al., 2021) and, more generally, for birds (Broughton et al., 2018; Lewis et al., 2018; Warren et al., 2018; Chiatante et al., 2020; Brewer et al., 2023; Darvill et al., 2023). However, our results highlighted the effect of weather conditions on the detectability of individuals, for both species, regardless of the census method used. More precisely, adverse weather conditions can reduce both propagation of calls and bird activity, as other studies have shown (Schieck, 1997; Buckland et al., 2005; Overton et al., 2005; Cambrone et al., 2021). Finally, given that response rates to broadcast calls are highest at the beginning of the breeding season (Kirkpatrick et al., 2007; Rehm and Baldassarre, 2007; Cambrone et al., 2021) and that there is a lack of valuable scientific data on the breeding season of the two target species, we suggest that future studies should focus on providing reliable information on the breeding season of the Ruddy Quail-Dove and the Bridled Quail-Dove.

Regarding the remote-sensing methods, we consider the CT method and the ASR method complementary for estimating the detection of the two species studied, since at some stations one method confirmed the presence of BQD or RQD when the other did not.

However, our abundance estimates are not directly comparable between the two methods, as the camera traps were active 24 hours a day, while the autonomous sound recorders were active for only 9 hours a day. Our results also revealed that RQD activity was higher in the morning, regardless of whether ASR or CT was used. This may be explained by other environmental factors such as weather conditions or temperature. Although we found a significant influence of weather conditions on the effectiveness of observational census methods, we did not measure this factor for the ASR and CT methods. Therefore, further investigation of these environmental factors is important to improve ecological knowledge of RQD.

In addition to providing reliable information on the density of bird species (Frommolt, 2017; Suwanrat et al., 2015; Smith et al., 2017), these two methods allow the study of their behaviour and spatio-temporal distribution in areas that are difficult to access (Mugerwa et al., 2013; Thomas et al., 2017; Roncal et al., 2019; Malhi et al., 2021; Antunes et al., 2022; Flatt et al., 2022), with full autonomy (Rovero and Marshall, 2009; Digby et al., 2013) and discretion (Digby et al. 2013), over short or long periods (Rovero and Marshall, 2009; Digby et al., 2013), and verification of data even years later (Rovero et al., 2013; Borker et al., 2015). In addition, the use of camera traps may be particularly suitable for assessing risk of predation on terrestrial bird species in tropical areas (Jean-Pierre et al. 2022). Obtaining this data is of paramount importance, as the negative impact of invasive exotic species (such as small Indian mongoose *Urva auropunctata* or domestic cat *Felis catus*) on avian species has been well documented (Medina et al., 2011; Morley et al., 2013; Akrim et al., 2019; Yagihashi et al., 2021). However, given the importance of the signal-to-noise ratio of microphones for sampling birds (Darras et al. 2020) and the time saved by automatic song recognition, we recommend improving the cost-effectiveness of automatic sound recorders through better equipment (Darras et al. 2020) and the use of automatic song recognition (Matsubayashi et al. 2022; Marchal et al. 2022; Manzano-Rubio et al. 2022; Lauha et al. 2022).

5. Conclusion

Although call-broadcasting method and autonomous sound recorders coupled with camera-traps are effective tools for monitoring the Ruddy Quail-Dove and the Bridled Quail-Dove, both secretive tropical forest species of hunting interest, it is important to consider the duration of the survey, time of year and available resources to choose the most appropriate method for the study (Zwerts et al. 2021). Finally, relying on e-DNA in places where observations and remote survey techniques have failed to detect the presence of species (Neice and McRae 2021; Macher et al. 2021; Saenz-Agudelo et al. 2022) could be of interest to fully evaluate the performance of the different survey methods.

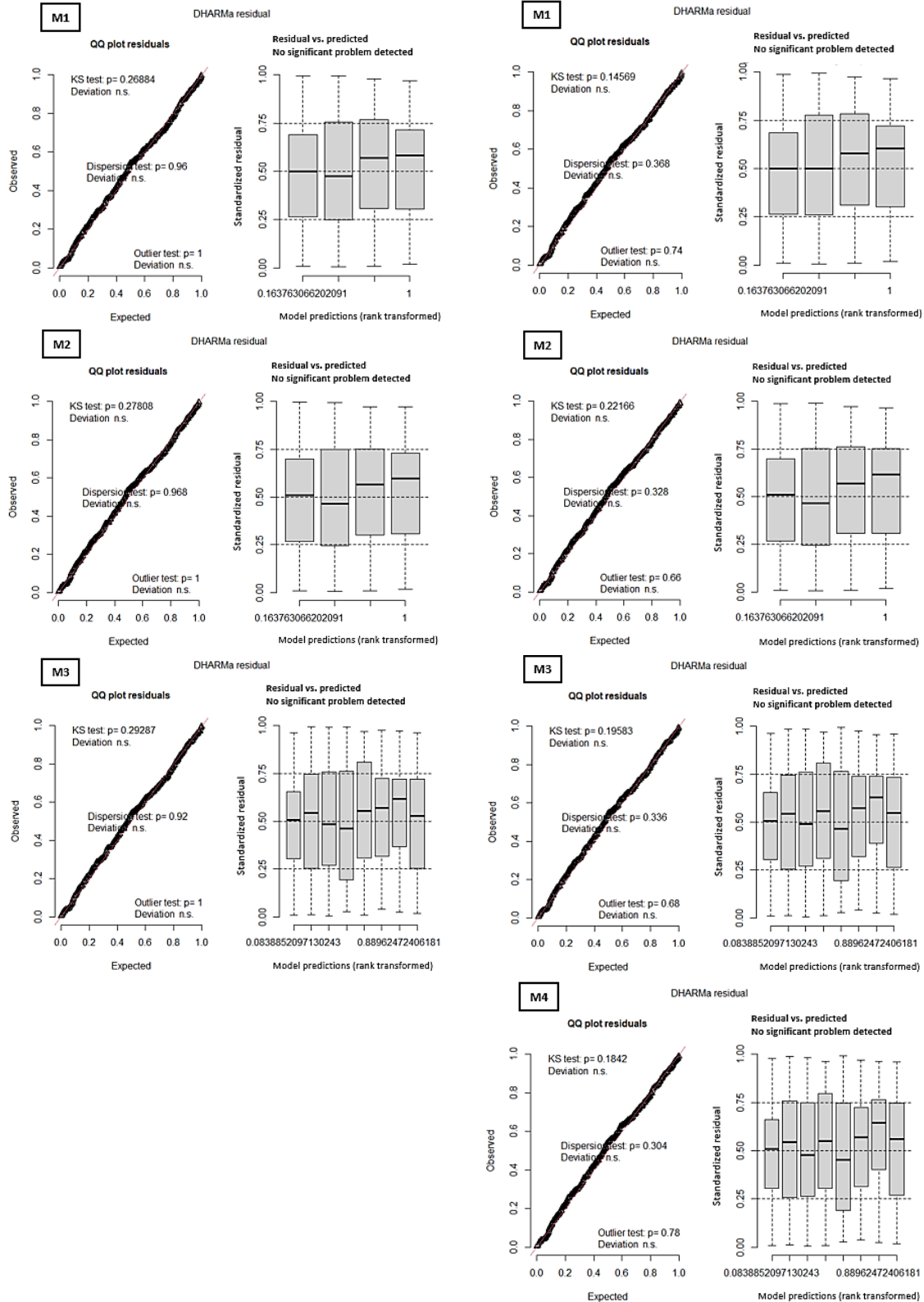
Supplementary materials

Table S1. Detection and abundance models for the Ruddy Quail-Dove and the Bridled Quail-Dove, in Guadeloupe forests. Detection and abundance were modelled according to detection methods (DM), time of the day (TIME), weather conditions (WEA), interaction between DM and TIME as well as interaction between DM et WEA

	Models	Df	LogLik	AICc	ΔAICc	Weight
Ruddy Quail-Dove presence						
M1	DM+WEA	4	-178,76	365,61	0,00	0,33
M2	DM+WEA+DM:WEA	5	-178,16	366,45	0,84	0,22
M3	DM+TIME+WEA	5	-178,53	367,18	1,57	0,15
M4	DM+TIME+WEA+DM:WEA	6	-177,93	368,03	2,42	0,10
M5	DM+TIME+WEA+DM:TIME	6	-178,31	368,80	3,19	0,07
M6	WEA	3	-181,49	369,03	3,42	0,06
M7	FULL	7	-177,76	369,76	4,15	0,04
M8	TIME+WEA	4	-181,26	370,60	4,99	0,03
M9	DM	3	-183,82	373,68	8,07	0,01
M10	DM+TIME	4	-183,36	374,80	9,19	0,00
M11	DM+TIME+DM:TIME	5	-183,15	376,42	10,81	0,00
M12	NULL	2	-186,50	377,03	11,42	0,00
M13	TIME	3	-186,05	378,16	12,54	0,00
Ruddy Quail-Dove abundance						
M1	DM+WEA	4	-187,03	382,14	0,00	0,29
M2	DM+WEA+DM:WEA	5	-186,24	382,61	0,47	0,23
M3	DM+TIME+WEA	5	-186,74	383,61	1,46	0,14
M4	DM+TIME+WEA+DM:WEA	6	-185,95	384,08	1,94	0,11
M5	WEA	3	-189,59	385,24	3,10	0,06
M6	DM+TIME+WEA+DM:TIME	6	-186,58	385,34	3,20	0,06
M7	FULL	7	-185,85	385,93	3,79	0,04
M8	TIME+WEA	4	-189,31	386,69	4,55	0,03
M9	DM	3	-191,08	388,21	6,07	0,01
M10	DM+TIME	4	-190,58	389,24	7,10	0,01
M11	DM+TIME+DM:TIME	5	-190,42	390,97	8,83	0,00
M12	NULL	2	-193,65	391,32	9,18	0,00
M13	TIME	3	-193,15	392,34	10,20	0,00

Bridled Quail-Dove presence						
M1	DM+WEA	4	-244,88	497,85	0,00	0,38
M2	DM+WEA+DM:WEA	5	-244,20	498,53	0,68	0,27
M3	DM+TIME+WEA	5	-244,81	499,75	1,90	0,15
M4	DM+TIME+WEA+DM:WEA	6	-244,13	500,44	2,59	0,10
M5	DM+TIME+WEA+DM:TIME	6	-244,66	501,51	3,66	0,06
M6	FULL	7	-243,92	502,07	4,22	0,05
M7	WEA	3	-254,09	514,22	16,38	0,00
M8	TIME+WEA	4	-254,02	516,12	18,27	0,00
M9	DM	3	-260,16	526,37	28,53	0,00
M10	DM+TIME	4	-260,16	528,39	30,55	0,00
M11	DM+TIME+DM:TIME	5	-260,02	530,16	32,31	0,00
M12	NULL	2	-268,81	541,64	43,80	0,00
M13	TIME	3	-268,80	543,65	45,81	0,00
Bridled Quail-Dove abundance						
M1	DM+WEA	4	-298,59	605,27	0,00	0,32
M2	DM+WEA+DM:WEA	5	-297,79	605,70	0,43	0,26
M3	DM+TIME+WEA	5	-298,27	606,67	1,40	0,16
M4	DM+TIME+WEA+DM:WEA	6	-297,47	607,11	1,84	0,13
M5	DM+TIME+WEA+DM:TIME	6	-298,03	608,24	2,97	0,07
M6	FULL	7	-297,15	608,54	3,26	0,06
M7	WEA	3	-308,64	623,32	18,05	0,00
M8	TIME+WEA	4	-308,31	624,71	19,44	0,00
M9	DM	3	-312,85	631,76	26,49	0,00
M10	DM+TIME	4	-312,80	633,67	28,40	0,00
M11	DM+TIME+DM:TIME	5	-312,56	635,24	29,97	0,00
M12	NULL	2	-322,90	649,82	44,55	0,00
M13	TIME	3	-322,84	651,73	46,46	0,00

A



B

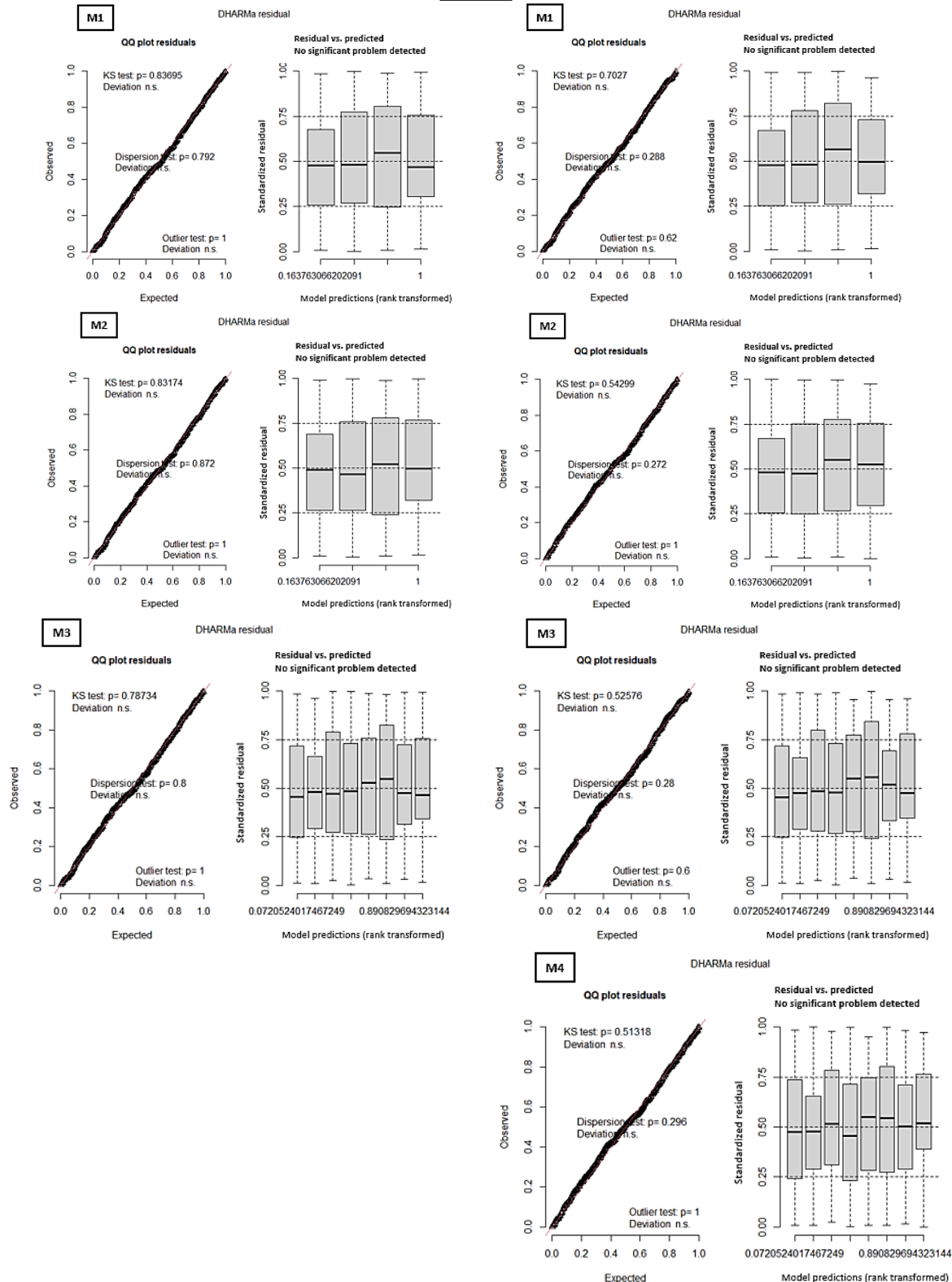


Figure S1. A: Residual diagnostics for the three best models (M1, M2, M3) and the four best models (M1, M2, M3, M4) based on the presence and the abundance of the Ruddy Quail-Dove, respectively. **B:** Residual diagnostics for the three best models (M1, M2, M3) and the four best models (M1, M2, M3, M4) based on the presence and the abundance of the Bridled Quail-Dove, respectively

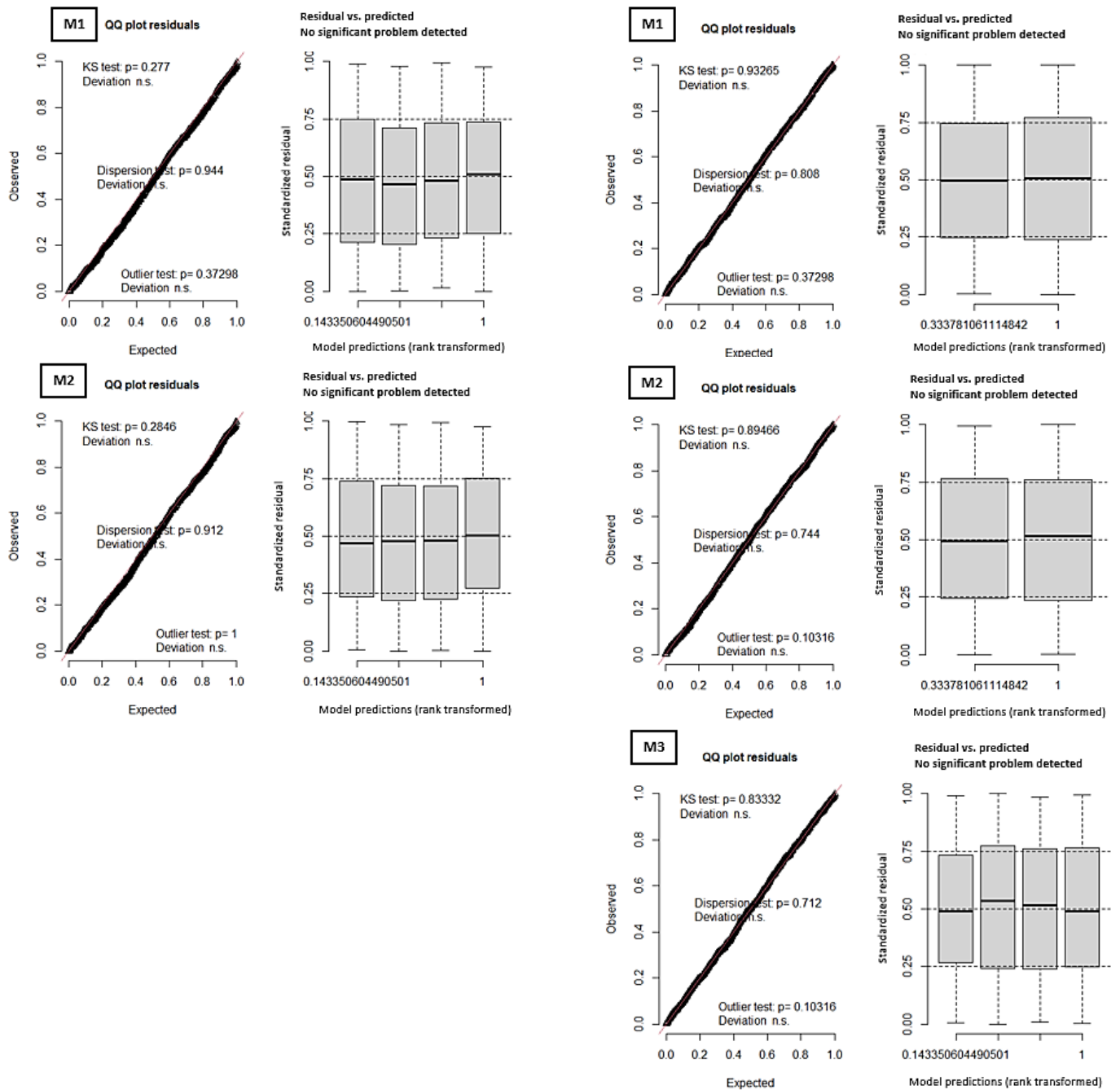


Figure S2. Residual diagnostics for the two best models (M1, M2) and the three best models (M1, M2, M3) based on the abundance of the Ruddy Quail-Dove and the Bridled Quail-Dove, respectively.

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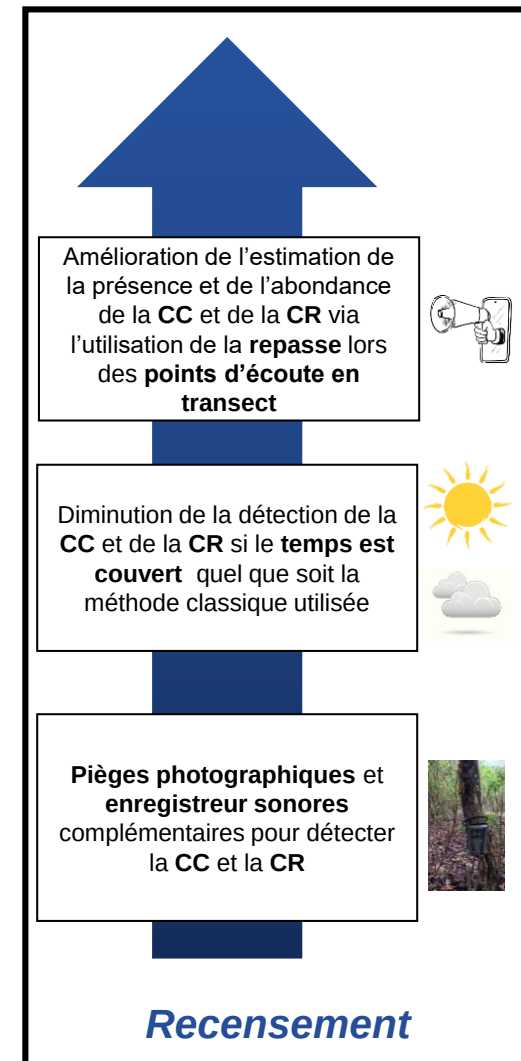
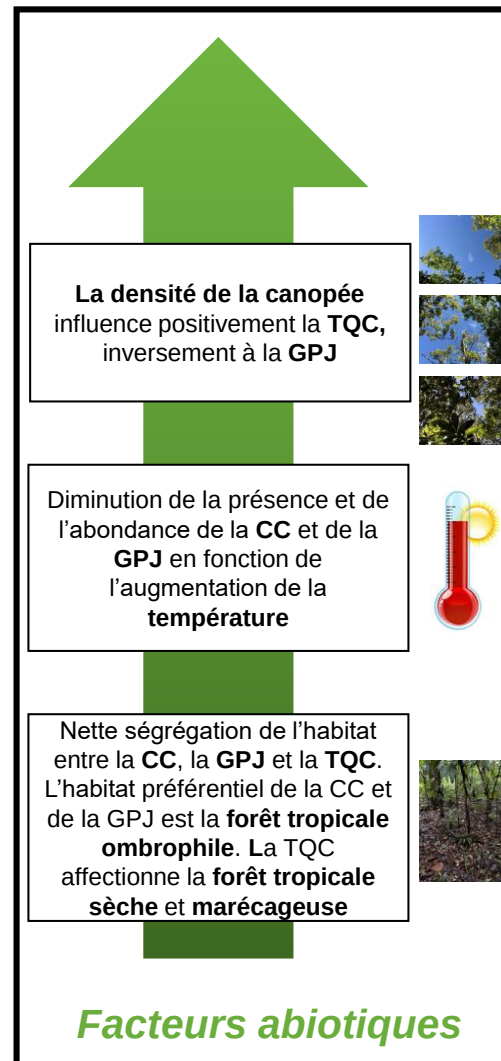
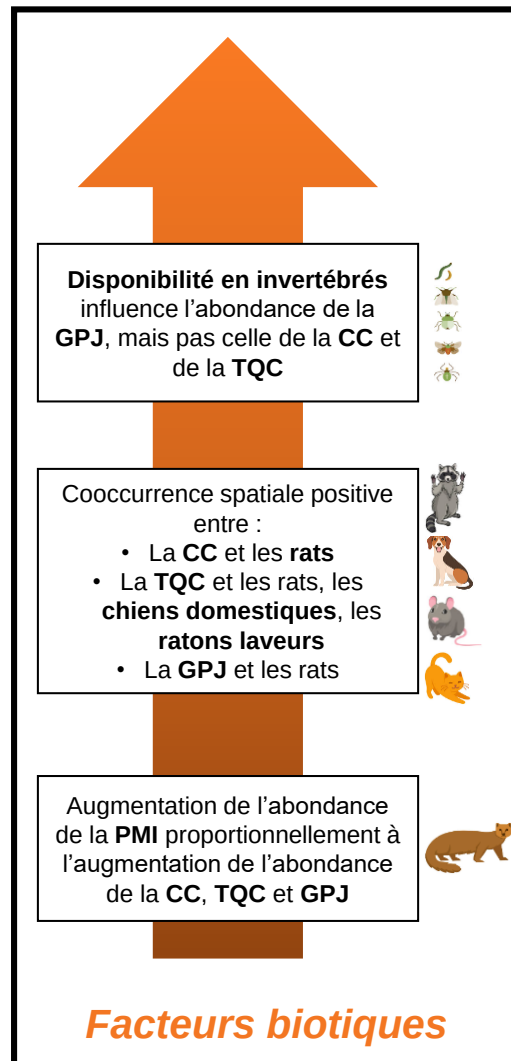
CONCLUSION ET PERSPECTIVES

Dans un contexte où peu de connaissances fiables sont disponibles, l'objectif de ce travail de thèse était de mettre en évidence divers aspects de l'écologie de quatre espèces aviaires d'intérêt patrimonial et cynégétique, à travers : l'étude de l'influence de facteurs biotiques et abiotiques sur leur répartition et leur abondance ainsi que l'étude de l'efficacité des méthodes de recensement, à la fois classiques et modernes, qui peuvent leur être appliquées.

Nos travaux de recherche ont permis l'apport d'éléments scientifiques nouveaux, susceptibles d'aider à la conservation de ces espèces à l'échelle des îles de la Caraïbe, fortement soumises aux pressions d'origine anthropique et au changement climatique. Plus largement, cet ensemble d'informations permet d'améliorer les connaissances sur les espèces aviaires tropicales, dans un contexte mondial de perte de biodiversité.

En conclusion de cette thèse, nous présentons une synthèse graphique des principaux résultats obtenus, puis, nous discutons des apports de la présente étude à la gestion des espèces aviaires d'intérêt patrimonial et cynégétique, en Guadeloupe. Ensuite, nous commentons les limites méthodologiques rencontrées durant cette présente thèse. Enfin, nous présentons quelques perspectives de développement, susceptibles d'accroître les connaissances sur l'écologie de ces quatre espèces.

1. Synthèse graphique des résultats



2. Apport de l'étude sur la gestion des espèces aviaires d'intérêt patrimonial et cynégétique en Guadeloupe

Les îles de la région Caraïbe constituent un point chaud de biodiversité. De plus, ces territoires renferment un grand nombre d'espèces aviaires endémiques (**voir Introduction, section II.2.4**). Du fait de cette biodiversité exceptionnelle, il est primordial de mener des études scientifiques afin de mieux caractériser l'écologie de ces espèces et évaluer les impacts des facteurs biotiques et abiotiques sur leurs populations. Les données scientifiques ainsi obtenues permettraient un meilleur suivi et une meilleure conservation des espèces en anticipant tout risque potentiel sur leurs populations.

De plus, certaines de ces espèces présentent un intérêt cynégétique et font l'objet depuis quelques années en Guadeloupe et en Martinique, de discordes entre certaines associations de protection de l'environnement et les fédérations de chasseurs. A titre d'exemple, le 11 décembre 2014, la Grive à pieds jaunes a été retirée de la liste des espèces chassables sous décision de justice, du fait que cette espèce soit classée comme « Vulnérable » sur la liste rouge de l'UICN et au motif que le recul de l'habitat forestier et la pression exercée par la chasse seraient à l'origine du déclin de la population de cet oiseau. Cette procédure a été initiée par l'Association pour la Sauvegarde et la réhabilitation de la Faune des Antilles (ASFA) et l'Association pour la Protection des Animaux Sauvages (ASPAS). Le 10 septembre 2021, la chasse de la Colombe rouviolette a été suspendue par la justice, à la suite d'une procédure de référé initiée par l'ASPAS, l'ASFA et l'Association pour l'Etude et la protection de la Vie sauvage dans les petites Antilles (AEVA). L'argument avancé était que la période de chasse autorisée chevaucherait la période de nidification, de reproduction et de dépendance de l'espèce. L'article L.424-2 du code de l'environnement stipulant que « *les oiseaux ne peuvent être chassés ni pendant la période nidicole ni pendant les différents stades de reproduction et de dépendance* », ces associations naturalistes ont alors obtenu gain de cause. Le 16 février 2023, à la suite d'un recours juridique initié par plusieurs associations, le tribunal administratif de la Guadeloupe a annulé l'arrêté préfectoral qui avait autorisé la chasse de la Colombe à croissants pour la saison 2022-2023, sur la base des arguments cités précédemment.

Notre étude apporte quelques éléments novateurs concernant la dynamique des populations des espèces aviaires cibles. Tout d'abord, contrairement aux études précédentes menées au sein du territoire, nous avons observé une forte abondance de la Grive à pieds jaunes, similaire à celle de la Colombe à croissants, tout au long de la présente étude. Une explication plausible à ce

contraste entre données est l'amélioration de la méthode de comptage, à travers l'utilisation pour la première fois du piégeage photographique, outil particulièrement efficace dans le recensement des espèces aviaires furtives vivant au sol (Si et al. 2014; Ehlers Smith et al. 2017; Smith et al. 2017; Davies et al. 2019; Hallett et al. 2021). En revanche, nous confirmons une faible abondance de la Colombe rouviolette, à l'inverse des observations faites dans la majorité des îles caraïbéennes occupées par cette espèce (Pinchon 1976; Tayalay 1995; Raffaele et al. 2021).

D'autre part, notre étude apporte également quelques éléments novateurs concernant l'écologie des espèces aviaires cibles. L'étude menée par Cambrone et al. (2023) atteste que la pression de chasse n'exercerait qu'une influence secondaire sur le risque d'extinction et les tendances démographiques chez les columbidés. A l'inverse, la taille de l'aire de répartition géographique, l'étendue de l'habitat et l'introduction d'espèces exotiques envahissantes exerceraient une influence primaire sur le risque d'extinction des columbidés. Ceci est particulièrement alarmant, puisque, mis à part la Colombe rouviolette, les espèces étudiées sont principalement insulaires, ce qui implique une aire de répartition géographique et une étendue de l'habitat restreintes. De plus, nos résultats ont montré une forte corrélation spatiale avec les espèces exotiques envahissantes, connues comme prédateurs potentiels des espèces aviaires (**Chapitres 1 et 2**) (Rodriguez-Estrella et al. 1991; Hays and Conant 2007; Morley and Winder 2013; Akrim et al. 2019; Yagihashi et al. 2021).

Il apparaît donc primordial de mettre en place des plans de gestion de ces espèces impliquant la protection de leur biotope ainsi que la protection envers les espèces exotiques envahissantes. Il serait également judicieux que les autorités locales prennent en considération l'ensemble des données générées au cours de la thèse lors de l'établissement des prochains arrêtés préfectoraux de chasse. En effet, une gestion efficace des espèces aviaires ne peut l'être qu'avec la concertation de l'ensemble des acteurs.

3. Limites de l'étude

Bien que nos résultats soient globalement satisfaisants, quelques limites méritent d'être soulignées.

Premièrement, le traitement des données des pièges photographiques a été extrêmement fastidieux, avec pas moins de 67785 photographies et 2160 heures d'enregistrements analysées manuellement, à trois reprises. Dans le cadre de futures études, le recours aux techniques de

reconnaissance automatisée, résultat d'une étroite collaboration interdisciplinaire, devrait pallier cet inconvénient (Falzon et al. 2019; Miao et al. 2021; Tuia et al. 2022).

Deuxièmement, en raison de la modeste quantité de pièges photographiques et d'enregistreurs sonores disponibles, l'effort d'échantillonnage n'a pas été optimal lors de la dernière campagne de terrain.

Néanmoins, sur la base de nos résultats novateurs, des projets de conservation aviaire similaires ont vu le jour en Guadeloupe et en Martinique. Ceux-ci consisteront à utiliser les méthodes présentées tout au long du manuscrit afin d'optimiser le suivi des populations aviaires chassables, mais également des espèces exotiques envahissantes, avec pas moins de 300 sites de piégeage photographique échantillonnés durant plus d'une année.

4. Perspectives

Au-delà du piégeage photographique, de l'enregistrement sonore automatisé ou des points d'écoute en transect couplés à la repasse, d'autres méthodes d'étude sont disponibles pour améliorer les connaissances sur les quatre espèces aviaires étudiées. Par exemple, l'analyse du contenu stomacal ou des fèces de mammifères potentiellement prédateurs, des niches isotopiques des quatre espèces aviaires étudiées, ainsi que la possible mise en évidence de différenciations génétiques et phénotypiques entre les populations de géotrygons de Grande-Terre et de Basse-Terre sont autant de pistes à explorer à l'avenir.

Le faible effectif de Colombe rouviolette est notamment inquiétant car les espèces insulaires sont particulièrement soumises à l'interaction des différentes forces évolutives (Rohde 1992; Ritchie et al. 1999; Colwell et al. 2000; Ricklefs et al. 2004), à l'origine d'une perte de diversité génétique, et *in fine*, à une possible extinction (Manne et al. 1999; Frankham 2005; Evans et al. 2008). Ce risque d'extinction est d'autant plus élevé lorsque la taille de la population est petite, en raison d'une exposition plus élevée à la dépression de consanguinité (Brooks et al. 2002; Frankham 2005), en lien avec la stochasticité démographique et environnementale (Isik 2011). De plus, la croissance des petites populations aviaires insulaires est fortement contrainte par les perturbations d'origine anthropique. Apporter des informations scientifiques fiables sur la structure génétique, la dynamique et les échanges entre les populations insulaires de la Colombe rouviolette semble alors primordiale. Dans ce cadre, différentes méthodes sont envisageables.

L'utilisation de méthodes génétiques (e.g. ADN mitochondrial ou ADN microsatellite) a permis de mettre en évidence des structures génétiques aviaires divergentes entre certaines îles de la région Caraïbe, pour les populations de Pigeon à cou rouge *Patagionas squamosa* (Cambrone et al. 2022), de Tourterelle à queue carrée *Zenaida aurita* (Monceau et al. 2011), de Pigeon simple *Patagioenas inornata* (Young & Allard 1997) ou encore, de Grive à pieds jaunes *Turdus lherminieri* (Arnoux et al. 2014). Remarquable, la Grive à pieds jaunes présente des divergences génétiques et phénotypiques entre l'île de la Basse-Terre et l'île de la Grande-Terre (Arnoux et al. 2014), ce qui indique une conséquence significative de l'isolement géographique, à une échelle spatiale restreinte.

Nous recommandons donc de développer les études génétiques, afin de mieux comprendre l'écologie de la Colombe à croissants. Néanmoins, l'utilisation unique de méthodes génétiques afin d'évaluer la capacité de dispersion des espèces étant critiquée (Paetkau 1999), elle pourrait être couplée à la télémétrie satellite (Munster et al. 2007; Gaidet et al. 2008, 2010; Crandall et al. 2019; Smetzer et al. 2021; Shizuka et al. 2022; Iverson et al. 2023).

Le réchauffement climatique se faisant particulièrement ressentir dans la Caraïbe (Peterson et al. 2002; Campbell et al. 2011; Karmalkar et al. 2013; Stephenson et al. 2014; Beharry et al. 2015), la surveillance démographique des populations aviaires étudiées au sein des différents types forestiers tropicaux présentant un gradient de température est nécessaire. De fait, nos prédictions suggèrent que l'augmentation de la température pourrait entraîner une diminution de l'abondance de la Colombe à croissants et une augmentation de l'abondance de la Tourterelle à queue carrée, dans les forêts tropicales de la Guadeloupe (**Chapitre 1**). Ceci est alarmant, d'autant plus que la Tourterelle à queue carrée a été recensée à deux reprises, à l'entrée de la forêt ombrophile de Gourbeyre, en Guadeloupe. Ainsi, il n'est pas à exclure que l'augmentation de la température en forêt tropicale ombrophile pourrait favoriser la colonisation de cet habitat par la Tourterelle à queue carrée. Ceci pourrait entraîner l'entrée en compétition de cette espèce, fortement territoriale (Griffin et al. 2005, Quinard & Cézilly 2011), avec la Colombe à croissants.

Malgré le contexte insulaire marqué par la forte présence des espèces exotiques envahissantes et la fragmentation forestière, la part relative de la prédation par les espèces exotiques envahissantes et de la perte d'habitat sur les dynamiques démographiques des espèces aviaires demeure indéterminée. Notre étude démontre toutefois une forte cooccurrence spatiale entre les espèces exotiques envahissantes et les espèces aviaires cibles, même si nous n'avons pas pu

documenter l'étendue de la prédation. A cette fin, il serait intéressant que les futures études s'emploient à analyser le contenu stomacal et/ou les fèces des potentiels mammifères prédateurs (Marcolin et al. 2020; Liu et al. 2021; Subrata et al. 2021). Ceci permettrait de déterminer l'impact de ces derniers sur la dynamique des populations aviaires, et ce, sur le long terme.

Il existe par ailleurs un manque de données fiables sur le régime alimentaire des quatre espèces étudiées, notamment en lien avec les variations saisonnières. Pour pallier ce déficit, l'utilisation de l'approche isotopique serait une bonne alternative (Chesson 2000; Losos 2008). Elle contribuerait à l'appréhension de la discrimination des niches isotopiques de ces espèces, ce qui fournirait de précieuses informations telles que, le partage de ressources similaires, l'identification de régimes spécialiste ou généraliste, ou encore l'étendue de la plasticité alimentaire intraspécifique et interspécifique des espèces aviaires cibles (Minagawa et al. 1984; Hobson 1999; Bolnick et al. 2003; Bearhop et al. 2004; Cherel et al. 2007; Newsome et al. 2007; Jackson et al. 2011; Layman et al. 2012). La récente mise en place d'une collaboration entre les chasseurs et les scientifiques de l'association Caribaea Initiative devrait permettre la collecte des données.

Enfin, compte tenu des nombreux avantages liés à la surveillance automatisée, et de l'inexistence d'un programme de surveillance scientifique sur l'étude des espèces aviaires chassables, nous recommandons la création d'un réseau de suivi de ces dernières dans l'archipel guadeloupéen, et plus largement, dans la région Caraïbe. Ce suivi se ferait via l'utilisation en tandem de pièges photographiques et d'enregistreurs sonores. En outre, ces méthodes de recensement automatisées étant complémentaires (**Chapitre 3**), il est souhaitable de les utiliser simultanément (Figure 15).



Figure 15. Exemple de piège photographique (Browning© Spec Ops EDGE) et enregistreur sonore (AudioMoth), ©Aurélie JEAN-PIERRE.

Par exemple, bien que le réseau d'évaluation et de surveillance de l'écologie tropicale *TEAM* (Figure 16) permette d'estimer les changements d'abondance au fil du temps ainsi que l'évaluation de la qualité de l'habitat (de Martins et al. 2006; Ahumada et al. 2011, 2013; Beaudrot et al. 2016 2019; Rovero et al. 2017), l'unique utilisation du piégeage photographique n'est pas entièrement appropriée à la surveillance démographique optimale de certaines espèces aviaires, à l'instar de la Colombe rouviolette (**Chapitre 1**).

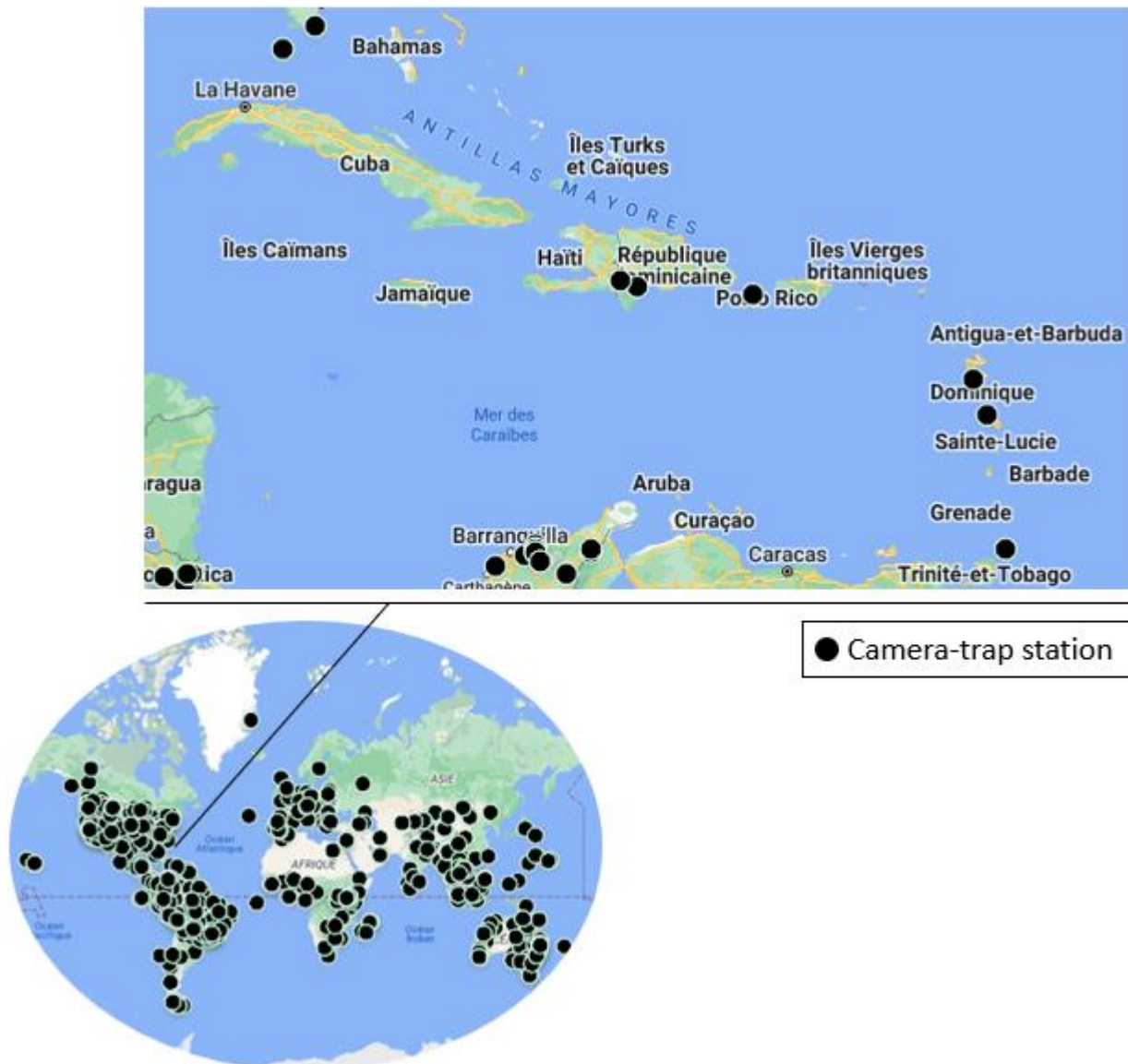


Figure 16. Cartographie du réseau TEAM, montrant la répartition de 35279 pièges photographiques (camera-trap stations) dans 93 pays. Le fond de carte obtenu à partir du site officiel du réseau TEAM (<https://app.wildlifeinsights.org/explore>), a été modifié afin de mettre en évidence le positionnement des pièges photographiques.

Pour conclure, l'ensemble des résultats de ce travail de thèse et l'ensemble des perspectives encore explorables, soulignent la faisabilité d'études scientifiques aviaire fiables en forêt tropicale, vivier de la biodiversité. En effet, malgré la valeur patrimoniale, la grande importance de l'écologie et de la conservation des oiseaux des régions tropicales, le biais en faveur des études sur les oiseaux des régions tempérées demeure important (Amano et al. 2013; Wilson et al. 2016; Reboledo Segovia et al. 2020; Cambrone et al. 2023). Le réseau caraïbéen de surveillance automatisée contribuerait notamment à la réduction de ce biais, mais également à considérablement améliorer la politique environnementale insulaire.

Malheureusement, le produit intérieur brut par habitant, fiable indicateur du niveau d'activité économique, est inégalement réparti au sein de la région Caraïbe (Banque mondiale 2023). Ceci met en lumière l'hétérogénéité dans la capacité des différents pays caraïbéens à s'approprier ces équipements et à pouvoir exploiter les données recueillies en toute autonomie. La démarche fondatrice de l'association Caribaea Initiative prend ici, tout son sens. Elle vise, en effet, à former de jeunes chercheurs caraïbéens dans le domaine de la biologie de la conservation, dans le but qu'ils atteignent une véritable autonomie scientifique et une expertise reconnue.

L'ensemble des perspectives encore explorables souligne également la complexité de la biodiversité aviaire insulaire. Afin d'appréhender celle-ci, il serait opportun qu'un réseau d'observateurs volontaires soit créé à l'échelle de la Caraïbe. En effet, sur la base de protocoles standardisés de recueil des données, cette collaboration entre les chercheurs et un public volontaire, communément appelée sciences participatives, permettrait de maximiser la récolte des données, indispensables à l'optimisation de la conservation des espèces (Couvét et al. 2008; Silvertown 2009; Julliard 2017).

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ANNEXES

Annexe 1. Quelques photographies de la Colombe rouviolette, *Geotrygon montana*,
obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale marécageuse de Babin, Grande-Terre.



Forêt tropicale ombrophile de Capesterre-Belle-Eau, Basse-Terre.

Annexe 2. Quelques photographies de la Colombe à croissants, *Geotrygon mystacea*,
obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale ombrophile de Saint-Claude, Basse-Terre.



Forêt tropicale sèche de Deshaies, Basse-Terre.

**Annexe 3. Quelques photographies de la Tourterelle à queue carrée, *Zenaida aurita*,
obtenues à l'aide des pièges photographiques utilisés**



Forêt tropicale sèche de Deshaies, Basse-Terre.



Forêt tropicale sèche de Port-Louis, Grande-Terre.

**Annexe 4. Quelques photographies de la Grive à pieds jaunes, *Turdus lherminieri*,
obtenues à l'aide des pièges photographiques utilisés**



Forêt tropicale sèche de Deshaies, Basse-Terre.



Forêt tropicale ombrophile de Saint-Claude, Basse-Terre.

Annexe 5. Quelques photographies de chats domestiques, *Felis catus*, obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale sèche de Sainte-Anne, Grande-Terre.



Forêt tropicale sèche de Grands-Fonds Abymes, Grande-Terre.

Annexe 6. Quelques photographies de chiens domestiques, *Canis lupus familiaris*,
obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale sèche de Sainte-Anne, Grande-Terre.



Forêt tropicale marécageuse de Babin, Grande-Terre.

Annexe 7. Quelques photographies de la petite mangouste indienne, *Urva auropunctata*, obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale sèche de Deshaies, Basse-Terre.



Forêt tropicale sèche de Port-Louis, Grande-Terre.

Annexe 8. Quelques photographies du raton laveur, *Procyon lotor*, obtenues à l'aide des
pièges photographiques utilisées



Forêt tropicale sèche de Grands-Fonds Abymes, Grande-Terre.



Forêt tropicale sèche de Grands-Fonds Abymes, Grande-Terre.

Annexe 9. Quelques photographies de rats, *Rattus spp.*, obtenues à l'aide des pièges photographiques utilisés



Forêt tropicale sèche de Deshaies, Basse-Terre.



Forêt tropicale sèche de Deshaies, Basse-Terre.

Annexe 10. Portefolio

I. Formations suivies à l'Université des Antilles

Année	Formations effectuées
2019-2020	B26.1 Gestion de projets de recherche (12 heures) B23.2 Ingénierie de montage pour le financement de projets de recherche (12 heures)
2020-2021	B5.6 Préparation TOIEC (20 heures) B23.1 SIG (15 heures) Gouvernance territoriale et développement insulaire (15 heures) Sensibilité à l'intégrité scientifique (2 heures) Ecriture d'articles en Anglais (4 heures)
2021-2022	LATEX (8 heures) Inscrire son doctorat dans un projet professionnel avant et après la soutenance (11 heures) Connaître les enjeux actuels de la valorisation scientifique (3 heures) Faire de la veille scientifique (2 heures) Exploiter les sources d'informations en Sciences, Techniques, Santé (3 heures) Définition, aspects juridiques de la thèse (2 heures) Rédaction : la feuille de style (4 heures) L'intégrité scientifique aujourd'hui (3 heures) Régression Anova- Ancova avec R (12 heures) Initiation à l'environnement de calculs statistiques et graphiques R (8 heures) Plan national de lutte contre les violences sexistes et sexuelles (2 heures)

II. Missions d'enseignement réalisées (162 heures équivalent TD)

Année	Niveau	Diplôme	Intitulé	Nature	Volume horaire
2019-20 ; 2020-21	L1	Licence	Biologie végétale	CM	24 heures
2019-20 ; 2020-21 ; 2021-22	L1	Licence	Introduction à la Biologie, Evolution, Ecologie	TD	90 heures
2021-22	L1	Licence	SVT, Ecologie	CM	10 heures
2021-22	L1	Licence	SVT, Ecologie	TD	10 heures
2021-22	L2	Licence	Biologie animale	TP	18 heures
2021-22	L3	Licence	Biologie animale	CM	20 heures
2020-21 ; 2021-22	L3	Licence	Terrain disciplinaire (entomologie)	TP	16 heures
2020-21 ; 2021-22	L3	Licence	Terrain disciplinaire (entomologie)	CM	4 heures
2020-21 ; 2021-22	L3	Licence	Biologie évolutive	CM	4 heures
2020-21 ; 2021-22	L3	Licence	Biologie de la conservation	TD	8 heures

III. Collaborations

2022 : Participation au projet PROSPOVERG, dans le cadre du suivi des populations aviaires et des populations d'espèces exotiques envahissantes, en Guadeloupe.

2022 : Participation à l'animation scientifique d'une sortie pédagogique initiée par l'association Caribaea Campus Gwadeloup visant à éclairer les étudiants quant à la biodiversité exceptionnelle de la Guadeloupe.

2021 : Participation au projet PROSPOVERG, dans le cadre du suivi des populations aviaires et des populations d'espèces exotiques envahissantes, en Guadeloupe.

2021 : Encadrement partiel (15%) de Sandy SEBASTIEN et Leïla PALMYRE, étudiantes en Master 2.

2020 : Co-encadrement de Lens SAINT-LOUIS (50%), étudiant en Master 2.

IV. Articles publiés dans des revues internationales avec comité de lecture

1. Jean-Pierre, A., Loranger-Merciris, G., & Cézilly, F. (2022). Spatial occupancy, local abundance and activity rhythm of three ground dwelling columbid species in the forests of Guadeloupe in relation to environmental factors. *Diversity*, 14(6), 480. <https://doi.org/10.3390/d14060480>
2. Jean-Pierre, A., Loranger-Merciris, G., Saint-Louis, L. J., & Cézilly, F. (2023). Factors affecting spatial occupancy and local abundance of the Forest Thrush, *Turdus lherminieri*, in Guadeloupe forests. *European Journal of Wildlife Research*, 69(4), 76. <https://doi.org/10.1007/s10344-023-01698-8>
3. Cambrone, C., Jean-Pierre, A., Bezault, E., & Cézilly, F. (2023). Identifying global research and conservation priorities for Columbidae: a quantitative approach using random forest models. *Frontiers in Ecology and Evolution*, 11, 1141072. <https://doi.org/10.3389/fevo.2023.1141072>

V. Articles soumis dans des revues internationales avec comité de lecture

4. Jean-Pierre, A., Cézilly, F., Saint-Louis, L. J., & Loranger-Merciris, G. (2023). Diurnal Forest Thrush abundance positively covaries with both prey availability and small Indian mongoose abundance in Guadeloupe forests. Soumis à *European Journal of Wildlife Research*.
5. Jean-Pierre, A., Loranger-Merciris, G., & Cézilly, F. (2022). Efficiency of the observational and remote sensing census method for the detection of two secretive columbid species of cynegetic interest. Soumis à *Avian Research*.

VI. Articles en préparation

6. Jean-Pierre, A., Cézilly, F., Saint-Louis, L. J., & Loranger-Merciris, G. The abundance of the small Indian mongoose, unlike the availability of invertebrates, influences the abundance of the Bridled Quail-Dove and the Zenaida Dove in the forests of Guadeloupe.
7. Jean-Pierre, A., Cézilly, F., & Loranger-Merciris, G. Forest type and seasonal effects on soil macroinvertebrate communities in tropical forests.
8. Loranger-Merciris, G., Jean-Pierre, A., Moulin-Rouyard, C. & Angeon, V. Crop type and agroecological practices affect soil fauna and soil physico-chemical properties.

VII. Communication dans des congrès scientifiques internationaux

1. Jean-Pierre, A. Photographic trapping, an effective method for monitoring secretive avian species. 4^{ème} conférence internationale initiée par **Caribaea Initiative**, République dominicaine, juin 2019, *Communication orale*.

2. Jean-Pierre, A. Photographic trapping, an effective method for monitoring secretive avian species. 22^{ème} conférence internationale initiée par **Birds Caribbean**, Guadeloupe, juillet 2019, *Communication orale*.

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