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Feeding on the fly: Unravelling feeding strategies in sympatric avian aerial insectivores (Hirundinidae and Apodidae) of West Africa

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(...) in every walk with Nature, one receives far more than he seeks.

John Muir, in *Mormon Lilies* (1877)

Falar duma encosta coberta de neve sem ter a alma branca também,
retratar uma folha sem tremer como ela,
olhar um abismo sem fundura nos olhos,
é para mim o mesmo que gostar sem língua, ou cantar sem voz.

Vivo a natureza integrado nela.

De tal modo, que chego a sentir-me, em certas ocasiões, pedra, orvalho, flor ou nevoeiro.

Nenhum outro espectáculo me dá semelhante plenitude e cria no meu espírito um sentido tão acabado do perfeito e do eterno.

Miguel Torga, in *Diário II* (1942)

Vida, se nos estás a ouvir, sabe que caminhamos na tua direção.

Unknown Author

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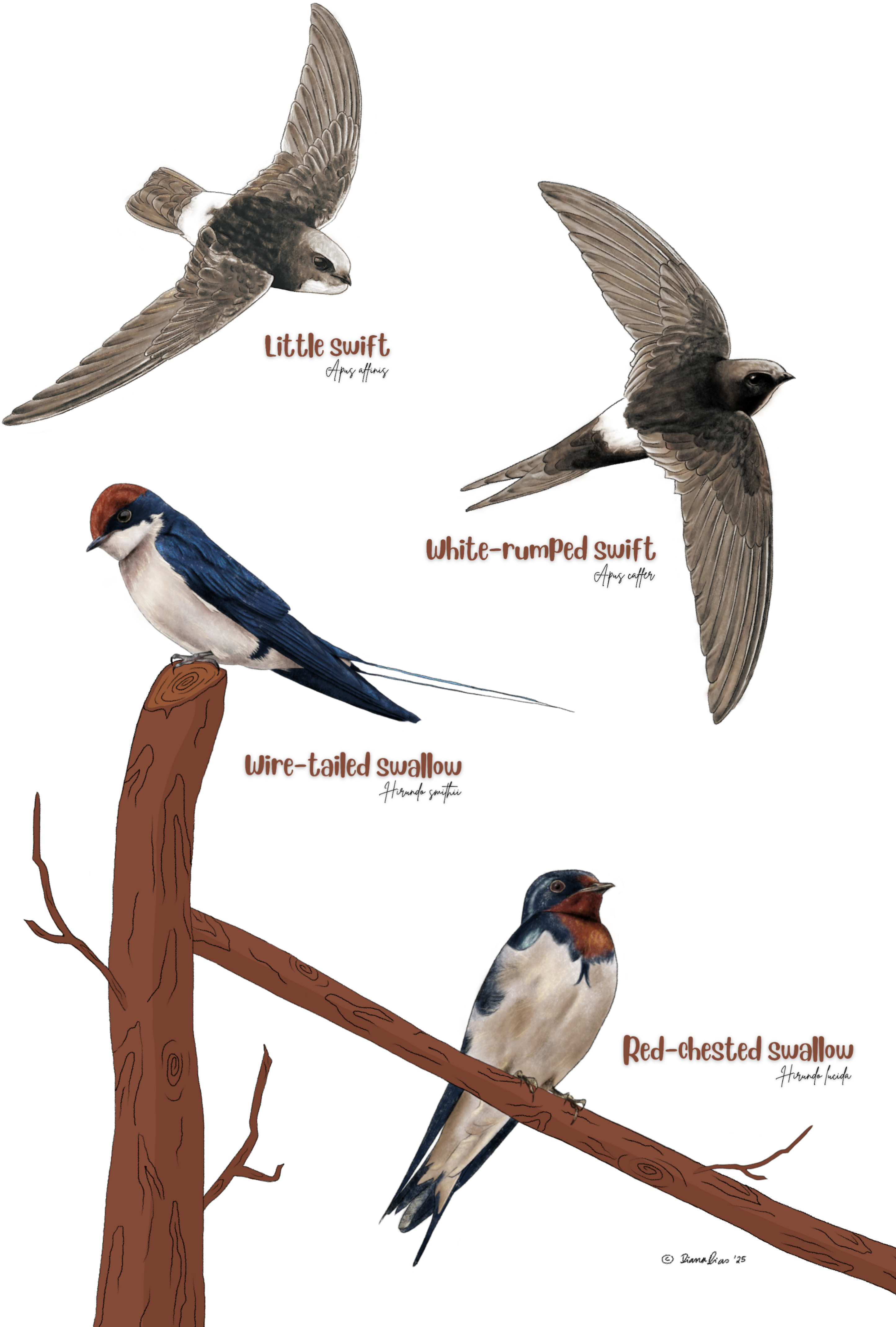
Na capa: Ilustração de andorinha-da-guiné (*Hirundo lucida*), andorinha-rabijunca (*Hirundo smithii*), andorinhão-cafre (*Apus caffer*) e andorinhão-pequeno (*Apus affinis*); Maio de 2025, por Diana Dias.



Little swift
Apus affinis

White-rumped swift
Apus caffer

Wire-tailed swallow
Hirundo smithii

Red-chested swallow
Hirundo lucida

Abstract

Understanding species' dietary ecology is essential to unravelling the mechanisms that enable coexistence and clarifying ecological roles and evolutionary adaptations. Swifts (Apodiformes: Apodidae) and swallows (Passeriformes: Hirundinidae) are highly adapted birds to an aerial insectivorous lifestyle. However, dietary data remain scarce, especially for Afrotropical species. With many of these species breeding and foraging in sympatry, the question arises of how resource partitioning occurs, avoiding competitive exclusion.

In this study, we employed DNA metabarcoding and next-generation sequencing to characterise the diets of four understudied and co-occurring West African aerial insectivores: the red-chested swallow (*Hirundo lucida*), wire-tailed swallow (*Hirundo smithii*), white-rumped swift (*Apus caffer*), and little swift (*Apus affinis*). This study represents the first application of these molecular techniques to dietary analysis for Africa's most highly aerial insectivore bird species. Faecal samples were collected in Guinea-Bissau using mist nets and collection platforms in habitats ranging from smallholder rice fields to urban areas. We aimed to (1) characterise the dietary composition and diversity of the four species, (2) quantify dietary overlap and niche partitioning, and (3) assess temporal shifts in swallow diets.

Our results revealed broad prey diversity and substantial dietary overlap across species, consistent with generalist feeding behaviours and opportunistic prey capture. The pronounced overlap in diet suggests shared exploitation of aerial prey resources and points to convergence in feeding strategies among these aerial insectivores. Still, subtle but consistent dietary differences were detected among species, indicating niche partitioning likely influenced by morphology, habitat use and insect abundance. These small-scale differences may reduce direct competition and facilitate coexistence within shared environments. Combining high overlap and moderate dietary segregation highlights how generalist predators with similar ecological roles can coexist by balancing shared resource use and species-specific environmental filters. Conservation efforts should prioritise protecting diverse foraging habitats to support these species amid ongoing environmental change.

Keywords: Apodidae, Hirundinidae, Dietary metabarcoding, Guinea-Bissau, Sympatric species.

Resumo

O estudo da ecologia alimentar das espécies constitui uma base essencial para entender as funções ecológicas que desempenham e revelar os processos que sustentam a sua coexistência. As aves insetívoras evoluíram no sentido de explorar um recurso diverso e abundante: artrópodes (Phylum Arthropoda). Entre estas, famílias como as andorinhas (Passeriformes: Hirundinidae) e andorinhões (Apodiformes: Apodidae) destacam-se pela sua morfologia adaptada ao voo contínuo e batido, e pela sua capacidade de captura de presas em pleno voo. Ambas as famílias apresentam estratégias alimentares generalistas e oportunistas, sendo capazes de beneficiar de flutuações temporárias na abundância de presas. No entanto, lacunas significativas de conhecimento ainda existem relativamente a membros de ambas as famílias, dado que o seu comportamento altamente aéreo dificulta a amostragem direta da dieta. Para além disso, grandes regiões do continente africano permanecem pouco estudadas, o que contribui para a escassez de dados ecológicos sobre estas aves.

Na região da África Ocidental, a dieta de espécies como o andorinhão-pequeno (*Apus affinis*), o andorinhão-cafre (*Apus caffer*), a andorinha-da-guiné (*Hirundo lucida*) e a andorinha-rabijunca (*Hirundo smithii*) permanece pouco documentada. Os registos disponíveis para estas espécies são escassos, baseados em estudos antigos e metodologicamente limitados, dificultando uma caracterização detalhada e fiável da sua dieta. Além disso, o conhecimento contemporâneo sobre os hábitos alimentares de espécies congenéricas provém maioritariamente de populações em regiões temperadas, como a Europa ou América do Norte, inviabilizando uma extrapolação direta para o contexto Afrotropical, dada a considerável variabilidade geográfica na composição das comunidades de presas. Esta coexistência de espécies morfologicamente e ecologicamente semelhantes implica, frequentemente, a ocorrência de mecanismos de partição de recursos de forma a reduzir a competição. As andorinhas e andorinhões, apesar das suas semelhanças morfológicas e ecológicas, diferem, por exemplo, nos padrões de voo, como a altitude a que se alimentam, sendo expectável que explorem diferentes nichos ecológicos. No entanto, dada a ecologia alimentar oportunista, o aumento efémero de abundância de certos grupos de insetos ou até características semelhantes de habitat em que as espécies se alimentam, podem promover uma sobreposição nas presas ingeridas.

Tradicionalmente, os estudos de dieta em aves insetívoras basearam-se na identificação morfológica de fragmentos de presas em conteúdos estomacais ou bolos alimentares. No entanto, estes métodos apresentam várias limitações, incluindo a sub-representação de presas pequenas ou de corpo mole e a exigência de um elevado conhecimento taxonómico para identificação das presas. Neste estudo, foram utilizadas técnicas de *metabarcoding* e *next-generation sequencing* (NGS) para descrever a dieta destas quatro espécies de aves insetívoras africanas. Para além disso, descrevem-se os seus nichos tróficos e avalia-se a sobreposição alimentar destas espécies simpátricas. Especificamente, procurou-se: (1) caracterizar a composição e diversidade alimentar, (2) quantificar a sobreposição alimentar e a partição de nicho alimentar, e (3) avaliar as flutuações temporais na dieta das andorinhas. Prevemos que a dieta das quatro espécies consista maioritariamente de insetos voadores, com aranhas a aparecerem em proporções menores, e esperam-se hábitos alimentares generalistas e semelhantes, resultantes de estratégias de voo comparáveis, da partilha de habitats e da influência da abundância de presas no ambiente. Ainda assim, são esperadas diferenças na composição da dieta associadas ao consumo de presas maiores e mais ágeis por parte das andorinhas, facilitado pela sua maior manobrabilidade em voo e maior força mandibular. Em contraste, os andorinhões, com um voo menos manobrável e com uma musculatura mandibular menos desenvolvida, poderão estar limitados a insetos de corpo mais mole e com menor capacidade de voo. Adicionalmente, as diferenças na altitude de alimentação entre os grupos poderão influenciar o espectro de presas consumidas. Esperamos também que as diferenças observadas na extensão do nicho alimentar reflitam mecanismos de redução da competição interespecífica. Por fim, prevemos que a composição das suas presas varie sazonalmente possivelmente em resposta a mudanças na abundância e diversidade dos insetos.

As fezes dos predadores foram obtidas através da captura de aves com redes de nevoeiro e da recolha de excrementos em plataformas colocadas imediatamente abaixo de ninhos, de julho a dezembro de 2023, exceto em agosto, na região de Oio, sector de Mansabá, Guiné-Bissau. As fezes recolhidas foram armazenadas em álcool a 96%, sendo posteriormente analisadas com recurso a técnicas moleculares de *metabarcoding* e NGS, através da ampliação do gene *COI*. As unidades taxonómicas operacionais (OTUs) resultantes foram comparadas com as bases de dados NCBI e BOLD, e identificadas até ao menor nível taxonómico possível. Para comparar a diversidade da dieta entre os predadores, curvas de rarefação para cada predador foram geradas para dois níveis de presa, OTU e ordem. Para análise da composição da dieta, foi calculada a percentagem de ocorrência (POO) de cada taxa de presa por amostra. A diversidade alimentar foi quantificada com recurso aos índices de Shannon, Simpson e Pielou's evenness. As diferenças na composição da dieta entre predadores e famílias de predadores (Hirundinidae e Apodidae) foram analisadas através de *Non-metric Multidimensional Scaling* (NMDS) e *Permutational Multivariate Analysis of Variance* (PERMANOVA), e a sobreposição alimentar entre os predadores avaliada pelo índice de Pianka. Utilizando modelos lineares generalizados (GLM), avaliou-se a variação de POO de cada ordem de presa entre espécies de predadores e foi analisada a variação da percentagem de ocorrência de diferentes ordens de presa na dieta das andorinhas ao longo dos meses.

Foram analisadas 203 amostras (excrementos), 29 das quais de andorinhão-pequeno, 56 de andorinhão-cafre, 75 de andorinha-da-guiné e 43 de andorinha-rabijunca. Um total de 459 OTUs distintos foram registados, dos quais 100% foram identificados até ao nível da ordem, 78.76% até ao nível da família, 35.12% até ao nível do género e 18.8% até ao nível da espécie, correspondendo a uma ampla variedade taxonómica, com 10 ordens, 106 famílias e 131 géneros. Desses, 34 (7.4%) OTUs pertenciam à Classe Arachnida, enquanto 425 (92.6%) pertenciam à Classe Insecta. Com base em valores de rarefação ajustados ao número de amostras da espécie menos amostrada (n = 29, andorinhão-pequeno), os andorinhões—andorinhão-pequeno (211 ± 21.70 OTUs) e andorinhão-cafre (198.40 ± 11.88 OTUs)—revelaram uma riqueza de OTUs intermédia, enquanto a andorinha-rabijunca apresentou o valor mais baixo (164.90 ± 13.82 OTUs) e a andorinha-da-guiné o mais elevado (235.07 ± 12.99 OTUs). As curvas de rarefação indicaram que a cobertura da dieta em termos de OTUs foi superior a 85% para todas as espécies de predadores, sugerindo uma boa representação das espécies de presas consumidas. Um número elevado de OTUs foi registado em apenas uma amostra (38.56%, n = 177), o que reflete a natureza oportunista destas espécies. As principais ordens de presas foram escaravelhos (Coleoptera), moscas e mosquitos (Diptera), cigarras, percevejos e pulgões (Hemiptera) e borboletas (Lepidoptera). A dominância de certas ordens partilhadas entre as espécies de predadores foi evidente pelos valores significativamente altos do Índice de Pianka tanto ao nível das ordens das presas como das OTUs. Isto sugere uma exploração semelhante de recursos, que poderá ser acentuada em períodos de condições climatéricas mais adversas, ou uma ingestão de presas baseada na sua disponibilidade. No entanto, apesar da sobreposição, foram observadas diferenças significativas na composição das ordens e OTUs consumidos por cada espécie. Embora tenham surgido diferenças entre as famílias de predadores (Hirundinidae e Apodidae), a variação na composição das presas foi mais claramente explicada ao nível das espécies, possivelmente derivada da agilidade de voo dos predadores e de diferenças no tamanho e mobilidade das presas ingeridas, que podem levar a uma partição parcial de nicho entre estes insetívoros aéreos simpátricos.

Estes predadores, apesar de ecologicamente semelhantes, podem exibir pequenas diferenças na procura por alimento, dado que as andorinhas tendem a capturar presas maiores e mais rápidas do que os andorinhões, geralmente a altitudes mais baixas, enquanto os andorinhões tendem a alimentar-se em camadas de ar mais altas, onde as correntes de vento ascendentes carregam presas com menor capacidade de voo, reduzindo a competição direta. Além disso, pequenas diferenças morfológicas, como na morfologia do bico, podem facilitar a seleção diferencial de presas. A inclusão de presas específicas de cada espécie, apesar de uma estratégia alimentar generalista, pode ser um mecanismo facilitador da coexistência. A variação sazonal observada na composição da dieta das andorinhas, reflete prováveis mudanças na abundância e densidade dos insetos ao longo dos meses de transição entre a época chuvosa e a época seca, potenciado por fatores como a variação na precipitação, temperatura e os ciclos de vida dos artrópodes e da vegetação. Estas dinâmicas sazonais condicionam o comportamento alimentar das aves insetívoras, mesmo em espécies oportunistas, sublinhando a importância de considerar a variação temporal nos estudos ecológicos de dieta.

Estes resultados fornecem uma caracterização detalhada da dieta de quatro espécies simpátricas de insetívoros aéreos na África Ocidental, revelando uma dieta diversa, dominada por insetos voadores, e evidenciando padrões de sobreposição e partição trófica entre as espécies. Estes dados são fundamentais para informar estratégias de conservação, dado que permitem compreender melhor as necessidades alimentares e as interações ecológicas destas aves. Tal conhecimento é crucial para antecipar os impactos de alterações e perda de habitat e a redução da disponibilidade de insetos, e para apoiar ações de gestão eficazes que garantam a preservação destas espécies e dos ecossistemas dos quais dependem.

Palavras-chave: Apodidae, Hirundinidae, Metabarcoding da dieta, Guiné-Bissau, Espécies simpátricas.

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List of Abbreviations

POO – Percentage of Occurrence

OTU – Operational Taxonomic Unit

COI – Mitochondrial Cytochrome c Oxidase I

NMDS - Non-Metric Multidimensional Scaling

CI – Confidence Interval

WGS – World Geodetic System

PCR – Polymerase Chain Reaction

NGS – Next Generation Sequencing

DNA – Deoxyribonucleic acid

BOLD – Barcode of Life Data System

NCBI – National Center for Biotechnology Information

GLM – Generalised Linear Model

1 Introduction

Insectivorous animals have evolved to exploit a diverse and abundant feeding resource: arthropods (Phylum Arthropoda). Some have taken this adaptation one step further. Aerial insectivorous birds developed the ability to chase prey while in flight (Imlay, 2017), with an incredible ability to twist and turn mid-air (Waugh & Hails, 1983), accessing a resource largely unavailable to other predators (Nebel et al., 2010). Swifts (Apodiformes: Apodidae) and swallows (Passeriformes: Hirundinidae) are part of this aerial guild (Spiller & Dettmers, 2019), and both families are highly specialised for life on the wing, sharing streamlined bodies and long wings (Turner & Rose, 1989; Videler, 2005). These adaptations result in an efficient flight with comparatively low energy costs (Hails, 1979; Turner, 1982). Their striking morphological similarities once led naturalists to group them (Forster, 1817), though they are now known to be unrelated lineages shaped by convergent evolution (Hasegawa & Arai, 2018; Videler, 2005). Their generalist, opportunistic diets allow them to exploit diverse aerial prey and respond quickly to fluctuations such as insect swarms (Collins et al., 2010; Kopij, 2000; McClenaghan et al., 2019; Turner & Rose, 1989). Still, many species' diets remain poorly described, primarily due to their restricted distribution in under-studied regions, such as the Afrotropics (Kopij, 2000), and their highly aerial ecology, which presents challenges for sample collection.

Swallows are globally distributed, with Africa hosting the highest diversity (Turner & Rose, 1989). The genus *Hirundo* includes 15 species (Winkler et al., 2020) with metallic blue plumage, long tails, and morphological adaptations for catching flying insects, such as small bills, strong jaw muscles (Gaunt, 1965; Turner & Rose, 1989), and forward-directed loral feathers (Beecher, 1953). The red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*) are two sympatric species in West Africa that remain poorly studied, with the last dietary studies dating back to the mid-20th century. For the red-chested swallow, flying termites (Blattodea) were identified in the diet, highlighting its opportunistic feeding on flying swarms (Chapin, 1953). The wire-tailed swallow's diet was found to consist of bees and wasps (Hymenoptera), beetles (Coleoptera), true bugs (Hemiptera), flies (Diptera), and butterflies (Lepidoptera) (Moreau, 1939). Both species are closely related to the barn swallow (*Hirundo rustica*), a well-studied hirundine (Dor et al., 2010; Schield et al., 2024). In South Africa, *Hirundo* species primarily consumed beetles (Kopij, 2000), while more extensive dietary data for the barn swallow exist from Europe and North America (Harris, 2023; Law et al., 2017; McClenaghan et al., 2019; Orłowski & Karg, 2011, 2013). However, swallows diet varies geographically (Waugh & Hails, 1983), with, for instance, flies (Diptera) dominating in Europe but less so in Africa (Moreau, 1939; Turner & Rose, 1989), cautioning against broad dietary extrapolations.

Swifts are extreme aerial specialists, spending most of their lives in flight (Hedenström et al., 2016). Unlike swallows, swifts have weaker jaw muscles, adapting them to softer-bodied, weaker-flying prey (Rawal, 1971; Waugh, 1978). The white-rumped swift (*Apus caffer*) and little swift (*Apus affinis*) are widely distributed across sub-Saharan Africa, with generalist diets in which small flies (Nematocera, Diptera) are common (Kopij, 2000). In addition, both species consume a broad range of arthropods, including beetles (Coleoptera), termites (Isoptera), true bugs (Hemiptera), mayflies (Ephemeroptera), hymenopterans (Hymenoptera), butterflies (Lepidoptera), grasshoppers (Orthoptera), dragonflies (Odonata), and even spiders (Araneae) (Bradley, 1993; Collins et al., 2010; Keith et al., 1992; Kopij, 2000).

Traditional diet studies have relied on morphological analysis of prey remains in faeces (e.g. Orłowski & Karg, 2011) or gut contents (e.g. Kopij, 2000). These methods require taxonomic expertise

(Pompanon et al., 2012) and often fail to detect soft-bodied prey, like those favoured by swifts, because digestion removes identifiable features (Oehm et al., 2011), potentially biasing prey assessments (Sheppard & Harwood, 2005). Analysing food boluses regurgitated by adults reduces this bias but is invasive, requiring bolus extraction (e.g. Collins et al., 2010) or restricting nestlings from swallowing (e.g. Bryant & Turner, 1982). Molecular techniques, particularly DNA metabarcoding, offer a non-invasive alternative with higher taxonomic resolution (Ando et al., 2020), enabling broad dietary analysis from environmental samples like faeces. Despite limitations, such as reliance on reference databases (Joly et al., 2014) and biases from primer selection and digestion rates (Pompanon et al., 2012), this method improves prey detection even after extensive digestion (Valentini et al., 2009). Success has been documented in Hirundinidae (Deryck, 2022; McClenaghan et al., 2019) and Apodidae (Fernandes et al., 2023), and it has proven valuable for studying dietary overlap and niche partitioning (Kartzinel et al., 2015).

Sympatric species with similar morphology and ecology often rely on resource partitioning to reduce competition (Schoener, 1974; Vieira & Port, 2007), leading to interspecific dietary differences (Bumelis et al., 2022; Cucco et al., 1993; Orłowski & Karg, 2013). Swifts and swallows exhibit distinct foraging strategies and dietary compositions. Swallows tend to capture larger, more mobile prey at lower altitudes, whereas swifts primarily target smaller, weaker-flying insects at higher altitudes (Kopij, 2000; Schoener, 1974; Waugh, 1978). Waugh (1978) observed that swallows perform rapid, agile turns while hunting, whereas swifts approach prey with minimal flight path deviation. Swifts often forage at the higher air layers, where air currents passively lift small insects. In contrast, swallows concentrate on lower levels near the ground, where larger and faster prey are more common (Kopij, 2000; Waugh, 1978), indicating vertical stratification in feeding zones (Orłowski & Karg, 2013). However, prey abundance can be unpredictable, with both predators seeming to exploit these unpredictable fluctuations (Collins et al., 2010; Kopij, 2000; Orłowski & Karg, 2013). Despite these differences, swallows and swifts maintain broad dietary niches with highly generalist diets and overlapping prey species (Bradley, 1993; Collins et al., 2010; Orłowski & Karg, 2013; Waugh, 1978). Additionally, the increasing use of artificial structures by all four species for nesting and roosting may erode spatial segregation and intensify competition (Turner & Rose, 1989).

In this study, we applied DNA metabarcoding and next-generation sequencing to examine the diets of four poorly studied African aerial insectivores. By analysing prey composition, we aim to describe their trophic niches and assess dietary overlap in areas where these species occur in sympatry, providing insight into how closely related species partition food resources and coexist within shared aerial foraging habitats. Specifically, we aimed to (1) characterise the dietary composition and diversity of the four species, expecting all to consume mainly flying insects, with spiders appearing in lower proportions (Kopij, 2000; Orłowski & Karg, 2013); (2) quantify dietary overlap and niche partitioning, anticipating generalist feeding habits with similarities due to shared foraging strategies, but with differences in prey composition. We predict that swallows will consume more agile prey owing to their greater manoeuvrability (Waugh, 1978) and stronger jaw protractor muscles that enable a wider mouth opening (Turner & Rose, 1989; Waugh, 1978), while swifts, with less manoeuvrable flight (Waugh, 1978) and weaker jaw musculature (Rawal, 1971; Waugh, 1978), will be limited to softer-bodied, weaker-flying insects. We also expect differences in dietary niche width to reflect mechanisms to reduce interspecific competition (Kopij, 2000; Orłowski & Karg, 2013) and (3) assess temporal shifts in swallow diets, predicting seasonal variation in prey composition in response to changes in insect abundance and diversity (Ismail et al., 2025; Waugh & Hails, 1983).

This study provides the first molecular characterisation of the diet of the red-chested swallow (*Hirundo lucida*), wire-tailed swallow (*Hirundo smithii*), white-rumped swift (*Apus caffer*), and little swift (*Apus affinis*), offering comparative dietary profiles for these species. By assessing dietary niche breadth and overlap, it aims to shed light on resource partitioning among these aerial insectivores in West Africa. These insights are critical for understanding species' dietary flexibility and reliance on insect prey, particularly in the face of habitat degradation and climate-driven shifts in insect availability.

2 Methods

2.1 Study area

This study was conducted in northern Guinea-Bissau, located in the northern intertropical zone of West Africa. Most of the country lies below 50 meters above sea level and experiences a tropical climate with relatively stable temperatures year-round (Catarino et al., 2008). However, there are marked seasonal changes in relative humidity due to distinct rainfall patterns, with the climate featuring two main seasons: a dry season from late October or early November and a rainy season beginning around late May or early June (Catarino et al., 2008). Annual rainfall ranges between 1,500 and 2,000 mm, with peak precipitation in August (Hayward & Oguntoyinbo, 2019). While most rivers follow a seasonal flow regime, the nearby Farim River, close to the sampling sites, is one of the country's few permanent watercourses (Catarino et al., 2008). The region's landscape is composed mainly of woodland and savannah woodland, interspersed with extensive rice fields (Temudo, 2011; Wymenga, 2011) and increasingly dominated by expanding cashew plantations (Catarino et al., 2015), reducing plant diversity and habitat heterogeneity.

Field sampling took place from July to December 2023 across seven locations: Saliquinhedim, Bereco, Bironqui, Mambonco, Mansaba, and Djalicunda, comprising nine sampling points, all within the Mansaba Administrative Area, Oio Sector (Figure 2.1). Except for Mansaba1 and Djalicunda2, which were sampled within village centres, all fieldwork was conducted in or near rice fields at the forest edge, maintained and cultivated by local communities. These seasonally flooded rice paddies are typical in the region and serve as temporary wetlands during the rainy season (Figure S1). These areas exhibited high swallow and swift activity during the breeding season before the onset of the dry season, leading to the desiccation of cultivated fields and post-wet-season movements (Turner & Rose, 1989).

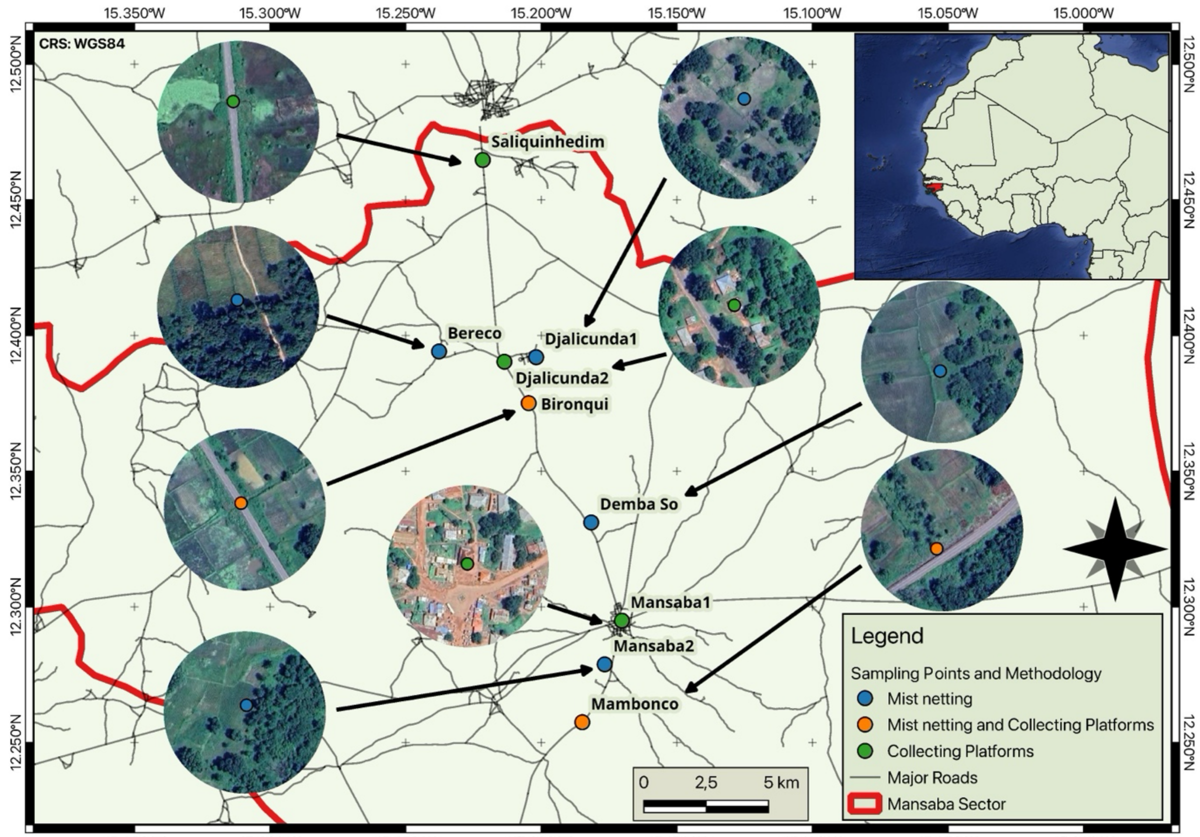

Figure 2.1. Sampling points – Saliquinhedim, Bereco Djalicunda1, Djalicunda2, Bironqui, Demba So, Mansaba1, Mansaba2 and Mambonco - located in the Mansaba Sector, Oio Region, Guinea-Bissau, and the different faeces collecting methods utilised. Map made using QGIS v. 3. The inset at the top right shows the location of Guinea-Bissau within West Africa. Circular satellite images illustrate land cover surrounding each sampling point. Satellite imagery accessed via the Google Satellite plugin in QGIS. Imagery © 2025 CNES / Airbus, Maxar Technologies.

2.2 Sample collection

To capture birds and collect samples, we used mist nets, black nylon nets with 12 × 2.5 metres and five pockets (Ecotone Mist Net 712/2P), deploying them along the edges of smallholder rice fields and at the entryways of nearby bridges. Sampling followed a structured scheme, with two to three mist-netting sessions per site each week, each lasting four to five hours. On average, five 12-metre nets were deployed per session to ensure adequate coverage. We placed captured individuals in sterile paper bags for approximately 30 minutes to collect samples before releasing them on-site. Sampling sessions were timed to coincide with peak avian activity—from 07:00 to 11:00 and from 17:00 until 30 minutes before sunset—allowing birds to return to their roosts or nests before nightfall.

Due to the low capture efficiency of mist nets for aerial foraging birds, we introduced a supplementary method in September 2023, capitalising on the birds' affinity for human infrastructures for breeding and roosting. Faecal collection platforms, adapted from McClenaghan et al. (2019), consisted of plastic tarps placed beneath active nests, 30 cm above the ground (Figure S2). These were deployed at five sites: (1) Saliquinhedim – beneath a bridge where a white-rumped swift breeding pair was nesting (Figure S3); (2) Djalicunda2 – under the ledge of a mosque housing an active wire-tailed swallow breeding pair (Figure S4); (3) Bironqui – beneath a bridge with an active white-rumped swift breeding pair (Figure S5); (4) Mansaba1 – under a house ledge where a little swift breeding colony was located (Figure S6); and (5) Mambonco – beneath a bridge used by a wire-tailed swallow breeding pair and a roosting group of red-chested swallows (Figure S7).

All bridges were along the main paved road connecting Mansaba and Farim, serving as water canal structures within rice field areas. We collected faecal samples from the tarps every two to three days to minimise disturbance and contamination risks (Ando et al., 2018) while accounting for the decreased detectability of dietary DNA with extended environmental exposure (McInnes et al., 2017; Oehm et al., 2011). All faecal samples from both collection methods were stored in sterile 2 ml tubes and preserved in 96% ethanol.

2.3 Sample analysis

Each bird faecal sample was individually processed and underwent DNA extraction. The number of individuals per species and faecal samples included in the analysis was chosen to optimise the accuracy of dietary estimates while balancing financial constraints (Mata et al., 2019). DNA was extracted using the Stool DNA Isolation Kit (Norgen Biotek Corporation, Ontario, Canada), following the manufacturer's protocol. Extractions were conducted in batches of 23 samples, each batch including a negative control containing no faecal material. The extracted DNA was transferred to 96-well plates, which included negative controls, leaving the last well empty for PCR-negative controls.

The FwhF2-R2n COI primers (Vamos et al., 2017) were used to amplify prey DNA and modified to include Illumina adaptors. These primers are well-suited for degraded DNA and amplify a broad range of arthropod taxa (Da Silva et al., 2024; Elbrecht et al., 2019; Mata et al., 2021). The PCR reaction consisted of 5 µL Qiagen Multiplex Master Mix, 0.3 µL of each primer at 10 nmol/L, 3.4 µL water, and 1 µL extracted DNA. Thermal cycling conditions were initial denaturation at 95°C for 15 minutes, 40 cycles of 30 seconds at 95°C, 30 seconds at 50°C, and 30 seconds at 72°C, followed by a final extension step at 72°C for 10 minutes.

Bird identification, particularly in the case of faecal samples collected beneath nests, was confirmed by amplifying a small fragment of the COI gene using Fwhf1-R1 primers (Vamos et al., 2017), as Fwhf2 primers often fail to detect vertebrate taxa. PCR conditions matched those used for prey DNA amplification. PCR products were diluted 1:4 and subjected to a second PCR step to add seven bp-long indexes and Illumina P5 and P7 sequencing adaptors. KAPA HiFi HotStart ReadyMix (Roche, Basel, Switzerland) was used for this reaction, and only eight cycles were performed, with annealing at 55°C. Following amplification, the indexed products were purified with Agencourt AMPure XP beads (Beckman Coulter, Brea, California, USA) at a bead-to-sample ratio of 1:0.8. The DNA was then quantified using an Epoch Microplate Spectrophotometer (Agilent, California, USA), adjusted to a concentration of 15 nM, and pooled by marker. Libraries were further quantified using qPCR (KAPA Library Quant Kit qPCR Mix; Roche), diluted to 4 nM, and sequenced using the MiSeq platform to achieve a target read depth of 30,000 for FwhF2 and 4,000 for FwhF1.

2.4 Bioinformatic analysis

Paired-end reads were merged using Flash software (Magoč & Salzberg, 2011). OBITools commands were utilised to process the data: 'ngsfilter' removed primer sequences, 'obiuniq' dereplicated the reads for each sample, and 'obigrep' eliminated singleton reads within each sample (Boyer et al., 2016). VSEARCH's 'cluster_unoise' command filtered out noise, while the '—uchime3_denovo' option removed chimeric sequences. Reads were clustered into operational taxonomic units (OTUs) at 99% similarity using the '—cluster_size' option, and the '—usearch_global' command mapped reads back to the resulting OTUs (Rognes et al., 2016). Similar OTUs sharing more than 84% sequence similarity and co-occurring in more than 95% of cases were merged using the LULU tool (Frøslev et al., 2017). Any OTUs that did not meet the expected length threshold (205 ± 3 bp; Vamos et al., 2017) were excluded to ensure accuracy based on codon length.

The number of reads for each OTU detected in the extraction and PCR-negative controls was subtracted from the associated sample reads to minimise contamination. The resulting OTUs were identified using comparisons against the BOLD and NCBI reference databases and classified to the most specific taxonomic level possible. In cases where multiple taxonomic ranks (e.g. species or genus) had similar identity scores, the broadest classification was used. Confidence identification thresholds were increased manually from the default BOLD threshold to 90% for Order, 95% for Family, 97% for genus and 99% for species. Based on identity, OTUs were categorised as dietary (e.g. arthropods) or non-dietary items (e.g. birds, fungi, or internal/external parasites). OTUs that could not be identified at least to the Order level were excluded from our analysis, as these unidentified OTUs likely represented taxa that are not typically part of the diet. Non-flying prey item Classes, such as Diplopoda and Chilopoda, were removed from analyses due to the almost strictly aerial foraging habits of these predators. Although spiders (Arachnida) do not fly, they use wind-assisted ballooning to disperse, and swifts and swallows are known to capture them during such events (Collins et al., 2010; Kopij, 2000; Turner & Rose, 1989).

The metabarcoding process does have inherent limitations. One of these is secondary ingestion, where DNA from prey consumed by predatory arthropods may be detected if those predators are later eaten by birds (da Silva et al., 2019; Deagle et al., 2019). However, DNA from gut contents is typically degraded and present in lower quantities, which reduces the likelihood of its detection during PCR amplification (Deagle et al., 2019; Mata et al., 2021). Additional filtering steps were implemented to address this challenge. Samples containing fewer than 100 dietary reads were excluded, and OTUs contributing less than 1% of the total dietary reads in each sample were removed to minimise the effects of secondary ingestion and other artefacts (Deagle et al., 2019).

2.5 Molecular identification of the studied birds

Field identification followed Borrow and Demey (2014) with nomenclature based on Clements (2007) and was validated through molecular analysis (see Section 2.3). FASTA sequences are available in the Supplementary Materials (Table S1). While the field identification of the wire-tailed swallow (Figure S8) was confirmed, identifying the other three species presented some challenges.

Molecular analysis identified red-chested swallow samples as Ethiopian swallow (*Hirundo aethiopica*), matching BOLD and NCBI sequences. However, as red-chested swallow sequences are absent from these databases, distinguishing them from the closely related Ethiopian swallow was challenging (Dor et al., 2010; Schield et al., 2024; Sheldon et al., 2005). The Ethiopian swallow is unknown to occur west of Côte d'Ivoire and has not been recorded in Guinea-Bissau (Turner, 2020). It is morphologically distinguishable from the red-chested swallow by its paler breast and throat (Turner & Rose, 1989). Since all observed individuals matched red-chested swallows morphologically (Figure S9), we classified these samples as red-chested swallows.

Samples from a little swift colony (Figure S10) matched those of house swift (*Apus nipalensis*) (n = 3) and little swift (n = 14) on BOLD (100%), and little swift and house swift on NCBI (>99%). The close match with the house swift likely reflects the low genetic differentiation between both species, which have historically been considered conspecific and are currently placed in the same clade (Päckert et al., 2012). However, the house swift occurs only in parts of Asia, ranging from China to Indonesia and Japan to Nepal, and does not inhabit West Africa (Chantler & Boesman, 2020). Therefore, we assigned all samples from this colony to little swifts.

Samples from Bironqui and Saliquinhedim lacked similarity at the species threshold level (i.e. 99%) in BOLD and NCBI, reaching the highest similarity (98.54%) with the little swift, followed by the house swift and Pacific swift (*Apus pacificus*). Without reference sequences for the white-rumped swift, samples were classified as *Apus* sp. Following our field identification, the white-rumped swift was confirmed based on its size, white rump, deeply forked tail, scythe-like wings, and nest structure—an igloo-shaped nest built by swallows of the Genus *Cecropis*—which distinguishes it from the sympatric little swift and the Pacific swift, the latter of which breeds in natural crevices outside the region (Chantler et al., 2020). Though no adult photos were taken, a juvenile was photographed inside a nest (Figure S11). Given the breeding evidence and elimination of similar species, we attributed these samples to the white-rumped swift.

2.6 Statistical analysis

In our analysis, each faecal sample was treated as an independent event. Given the limited availability of comprehensive molecular reference databases for African arthropods, we utilised OTUs and implemented taxonomy-independent analytical methods (Berry et al., 2017).

To characterise the diets, we adopted a metric based on the occurrence (presence/absence) of prey items, utilising the approach delineated by Deagle et al. (2019). In our context, we focused on the first step of the wPOO calculation, computing the Percent of Occurrence (POO) at the sample level by dividing the number of occurrences of each prey taxon (Order, Family, or OTU) by the total number of prey detections in that sample. While Deagle et al. (2019) used these sample-level POO values only as an intermediate step toward calculating wPOO, we retained both metrics in our analyses: POO for exploring variation at the individual sample level, and average POO, obtained by averaging sample-level POO values across all individuals of a bird species, for representing species-level diet composition. This approach preserves sample-level detail while enabling broader taxonomic or ecological comparisons.

We estimated sample coverage and dietary richness for each predator species using the *iNEXT* function from the INEXT package (Hsieh et al., 2015). Rarefaction and sample coverage curves were constructed based on sample-based incidence data, incorporating the Hill number of species richness ($q = 0$) and 1,000 bootstrap replicates (Chao et al., 2014). These curves were generated for two prey levels, OTU and order, with 95% confidence intervals, capped at 75 samples, corresponding to the sample size of the most sampled species, the red-chested swallow. However, to allow direct comparison among species, prey richness estimates were reported at 29 samples, corresponding to the sample size of the least sampled species, the little swift. Notably, curves for prey families were not produced due to the high percentage of unidentified prey items.

Beyond overall richness, we also assessed prey richness at the sample level to evaluate intra-individual dietary diversity. Prey richness per sample was assessed at three prey levels: order, family, and OTU. As the assumption of normality was not met (Shapiro-Wilk, $W = 0.944$, $p < 0.001$), non-parametric alternatives were employed. We conducted a Kruskal-Wallis test to evaluate significant differences in prey item taxonomic richness among bird species at the sample level. When the Kruskal-Wallis test revealed significant differences, post-hoc pairwise comparisons were performed using Dunn's test through the *dunn_test* function from the RSTATIX package (Kassambara, 2019). *P*-values were adjusted using the Bonferroni correction to account for multiple comparisons, controlling for Type I error (Shaffer, 1995).

To evaluate differences in dietary diversity among the four predator species, three diversity indices were calculated at the sample level: Shannon diversity index (Shannon, H'), Simpson diversity index (Simpson, D), and Pielou's evenness index (J') (Petrén et al., 2023; Tuomisto, 2012), at two prey levels: order and OTU. Diversity metrics were computed for each sample using the *calcDiv* function from the CHEMODIV package (Petrén et al., 2022). The Simpson index was inverted to align with common ecological interpretations and the other diversity metrics, ensuring that higher values consistently indicate greater diversity (Magurran, 2004). A Kruskal-Wallis test was performed using the *kruskal_test* function from the RSTATIX package (Kassambara, 2019) to assess significant differences in diversity indices among bird species. Post-hoc pairwise comparisons were conducted using Dunn's test with the *dunn_test* function from RSTATIX (Kassambara, 2019), with the Bonferroni correction applied to adjust *p*-values for multiple comparisons, controlling for Type I error (Shaffer, 1995).

We used Non-metric Multidimensional Scaling (NMDS) to visualise differences between predator species' diets at the order and OTU prey levels based on Bray-Curtis dissimilarity distance. The Bray-Curtis dissimilarity is appropriate for dietary metabarcoding data, as it minimises the influence of ecologically less meaningful information such as joint absences and rare species (Beals, 1984). We used the *metaMDS* function from the VEGAN package (Oksanen et al., 2024) and the *adonis2* function from the same package to assess dietary differences among predator species by conducting Permutational Multivariate Analysis of Variance (PERMANOVA). Post-hoc pairwise comparisons were conducted using *pairwise.adonis2* from the PAIRWISEADONIS package (Martinez Arbizu, 2017). *P*-values were adjusted using the Bonferroni correction to account for multiple comparisons, controlling for Type I error (Shaffer, 1995).

To analyse how prey order POO varies by predator species, we fitted a Generalised Linear Model (GLM) model using the *glm* function from the STATS package (R Core Team, 2023). Given that the response variable is a proportion and exhibits a high proportion of zeros (37.19%), we used the quasibinomial family, with a “logit” link function. The quasibinomial approach accounts for deviations in variance from the binomial distribution assumptions, providing more reliable estimates when modelling proportion data with many zeros (Gómez–Déniz et al., 2020). The model included the prey order and predator species as predictors and their interaction term. After fitting the GLM, estimated marginal means (EMMs) were computed, representing the average predicted prey order POO values for each predator species. To this end, we used the *emmeans* function from the EMMEANS package (Lenth, 2017), setting the “regrid” parameter to "response" so that the results were interpretable on the original scale. Finally, to assess whether there were significant differences in prey order POO between predator species, pairwise comparisons were conducted using the *pairs* function from the EMMEANS package (Lenth, 2017), with Bonferroni correction, to account for multiple comparisons, controlling for Type I error (Shaffer, 1995).

To evaluate the dietary overlap between predator species, we used the *niche.overlap* function from the SPAA package (Zhang, 2010) to calculate Pianka's niche overlap index between predator species diets. This index emphasises common prey items by placing greater weight on shared presences rather than shared absences (Pianka, 1973). To assess the statistical significance of the observed overlap, we used the *niche_null_model* function from the ECOSIMR package with 5000 replications (Gotelli et al., 2015).

To assess the seasonal variation (using month as a proxy) in prey composition at the order level for the red-chested swallow and the wire-tailed swallow, we performed a separate GLM for each predator-prey order pair using the *glm* function from the STATS package (R Core Team, 2023), with a quasibinomial family. The modelled response was POO of each prey order as a function of month. This analysis tested for significant differences in prey order POO between the two species across months. Estimated marginal means (EMMs) were extracted, setting the "regrid" parameter to "response" so that the results were interpretable on the original scale. For post-hoc comparisons, pairwise contrasts were performed between species within each prey order using the *pairs* function from the EMMEANS package (Lenth, 2017), with Bonferroni correction, to account for multiple comparisons, controlling for Type I error (Shaffer, 1995). Predicted values from the model were calculated using the *predict* function, and confidence intervals (95%) were derived from the standard errors of the predictions. These predictions were then transformed into probabilities using the logistic transformation *plogis* function (R Core Team, 2023) and multiplied by 100 to obtain percentage values. This analysis was restricted to September through November. The other samples were excluded as there was insufficient sample representation for both swallow species. Dragonflies and damselflies (Odonata) were removed from the seasonal analysis, as only two samples from each predator contained the order, not allowing for viable predictions.

All graphs were created using the *ggplot* function from the GGPLOT2 package (Wickham et al., 2007), and all analyses were performed using R Statistical Software (R Core Team, 2023). The statistical significance threshold was considered at $\alpha = 0.05$.

3 Results

Prey items' DNA was successfully extracted from 203 samples, 29 of which were from little swifts (*Apus affinis*), 56 from white-rumped swifts (*Apus caffer*), 75 from red-chested swallows (*Hirundo lucida*) and 43 from wire-tailed swallows (*Hirundo smithii*). A total of 459 distinct prey OTUs were recorded, of which 100% were identified to the order level, 78.76% to the family level, 35.12% to the genus level and 18.8% to the species level. Prey items spanned a broad taxonomic range, comprising 10 orders, 106 families, and 131 genera. 34 (7.4%) OTUs belonged to the Class Arachnida, while 425 (92.6%) belonged to the Class Insecta.

3.1 Dietary composition and diversity

Dietary richness varied among species. When standardising sampling effort through rarefaction to 29 samples—the number of samples available for the least-sampled species—the estimated OTU richness (Hill number, $q = 0$) was 211 ± 21.70 OTUs for the little swift, 198.40 ± 11.88 for the white-rumped swift, 235.07 ± 12.99 for the red-chested swallow, and 164.90 ± 13.82 for the wire-tailed swallow (Figure S12A). Considering all samples, 211 OTUs were detected in the little swift diet ($n = 29$), 246 in the white-rumped swift ($n = 56$), 336 in the red-chested swallow ($n = 75$) and 192 in the wire-tailed swallow ($n = 43$). Coverage for prey OTUs ranged from 85.74% (± 2.58%) in the little swift to 93.90% (± 1.20%) in the white-rumped swift, with intermediate values observed in the swallows: 89.85% (± 1.96%) for the wire-tailed swallow and 92.59% (± 1.12%) for the red-chested swallow (Figure S12B). At the prey order level, coverage was 100% across all species, with extrapolated and observed prey order richness matching, indicating 10 prey orders per predator species.

Average OTU richness per sample differed significantly among predator species. Swifts showed higher per-sample richness values, with the white-rumped swift averaging 20.07 ± 4.31 OTUs and the little swift 20.03 ± 4.42. In contrast, swallows showed lower values, with the red-chested swallow averaging 19.01 ± 6.97 OTUs per sample and the wire-tailed swallow only 15.65 ± 6.80 (Figure 3.1). Statistical tests confirmed these differences: prey OTU richness per sample varied significantly across species (Kruskal-Wallis, $p = 0.001$), as did prey family richness ($p = 0.02$). Post-hoc comparisons showed that the wire-tailed swallow had significantly lower OTU richness per sample than both the little swift (p = 0.016) and the white-rumped swift (p = 0.001). The white-rumped swift also showed significantly higher prey family richness per sample compared to the wire-tailed swallow (p = 0.002).

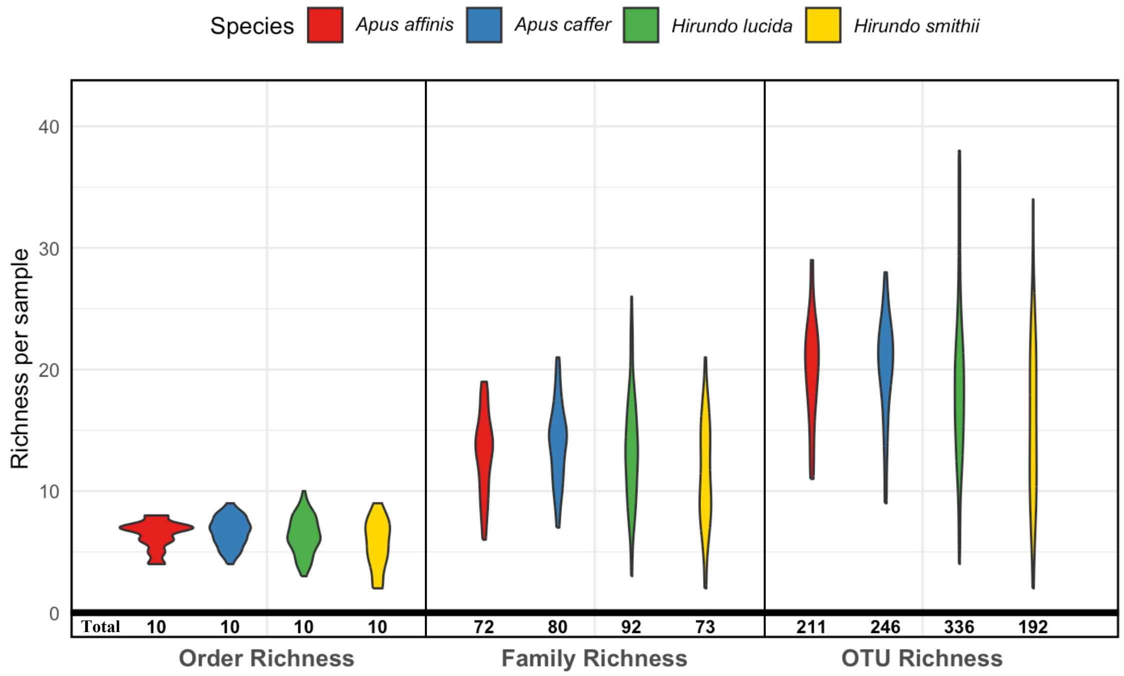

Figure 3.1. Violin plot of average order, family and OTU richness per sample across the four predator species—little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*)—and respective species total.

Rare prey items—those appearing in only one sample—accounted for 38.56% (n = 177) of all recorded prey items. Of these, 6.54% (n = 30) were exclusive to the little swift diet, 5.66% (n = 26) to the white-rumped swift, 17.21% (n = 79) to the red-chested swallow and 9.15% (n = 42) to the wire-tailed swallow. No OTUs were exclusive to either swallows (Hirundinidae) or swifts (Apodidae).

The average prey order POO indicated that beetles (Coleoptera) and flies and mosquitoes (Diptera) were the dominant orders in all predator diets, except in the white-rumped swift, where true bugs (Hemiptera) ranked second (Figure 3.2).

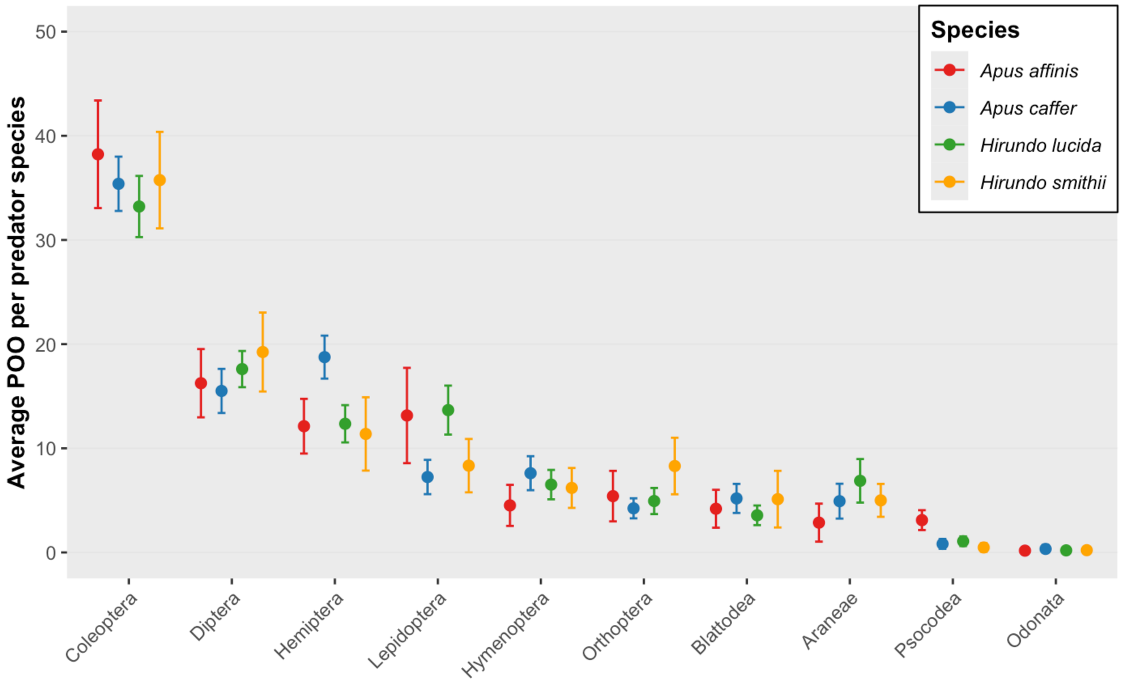

Figure 3.2. Percentage of Occurrence (POO) of arthropod orders in the diet of four highly aerial insectivorous birds— little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*)—in Guinea-Bissau. The points represent the predator species average POO per prey order, and the error bars represent the 95% confidence intervals.

Prey order diversity, assessed at the sample level using Shannon and Simpson indices based on the POO of each prey order within each faecal sample, was similar across the four species (Figure 3.3A). The Kruskal-Wallis test found no significant differences in Shannon diversity (p = 0.313) or Simpson diversity (p = 0.354) among species. However, Pielou's evenness differed significantly ($p < 0.001$), with the little swift showing lower values compared to both swallow species, according to Dunn's test (Table S2).

For prey OTU POO, Pielou's evenness per sample was uniformly one due to the absence of duplicate OTUs, indicating that each OTU was represented only once per sample. As a result, the data lacked ecological variability regarding OTU dominance or rarity and were excluded from further analysis. The Kruskal-Wallis test showed significant differences in both Shannon (p = 0.001) and Simpson diversity (p = 0.001) (Figure 3.3B), with the wire-tailed swallow showing lower diversity values compared to the swift species, as indicated by Dunn's test (Table S2).

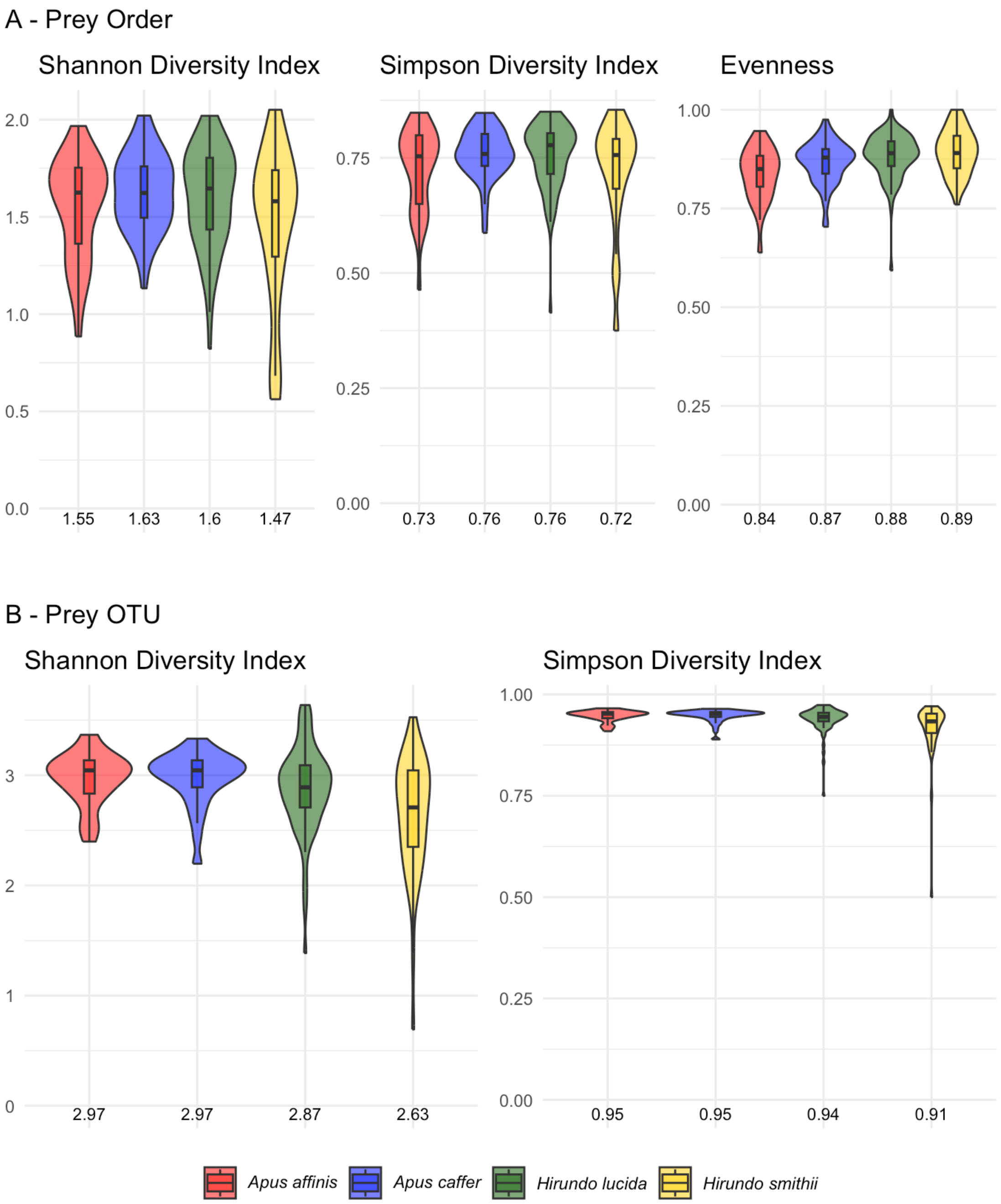

Figure 3.3. Mean from the sample level alpha dietary diversity data for prey items: (A) prey order and (B) prey OTU Percentage of Occurrence (POO) per predator species, across 29 little swift (*Apus affinis*), 56 white-rumped swift (*Apus caffer*), 75 red-chested swallow (*Hirundo lucida*) and 43 wire-tailed swallow (*Hirundo smithii*) samples. The plot presents the Shannon Diversity Index (H'), Simpson's Diversity Index (D), and Pielou's evenness (J') for each predator species, calculated based on the POO of prey items at the order (top) and OTU (bottom) levels. The average value for each diversity metric per predator species is displayed below each plot. For prey OTU POO, Pielou's evenness per sample was uniformly one due to the absence of duplicate OTUs, indicating that each OTU was represented only once per sample. As a result, the data lacked ecological variability regarding OTU dominance or rarity and were excluded from the figure.

At the family level, the most prominent prey in the little swift and the red-chested swallow diet corresponded to beetle families: leaf beetles (Chrysomelidae; 2.09% ± 0.9) and scarab beetles (Scarabaeidae; 2.59% ± 0.82), respectively. In contrast, the white-rumped swift primarily consumed leafhoppers (Hemiptera: Cicadellidae; 2.25% ± 0.64), while the wire-tailed swallow primarily consumed blowflies (Diptera: Calliphoridae; 2.17% ± 0.94).

3.2 Dietary Overlap

Predator species displayed distinct dietary compositions, with prey OTU POO differing significantly across predators ($R^2 = 6.05\%$, $p = 0.001$; Figure 3.4), with pairwise comparisons revealing significant differences between all species pairs (Table S3). Similarly, prey order POO varied significantly among predator species ($R^2 = 5.41\%$, $p = 0.001$; Figure S13), with pairwise comparisons indicating that the white-rumped swift differed significantly from each of the three other species (Table S3).

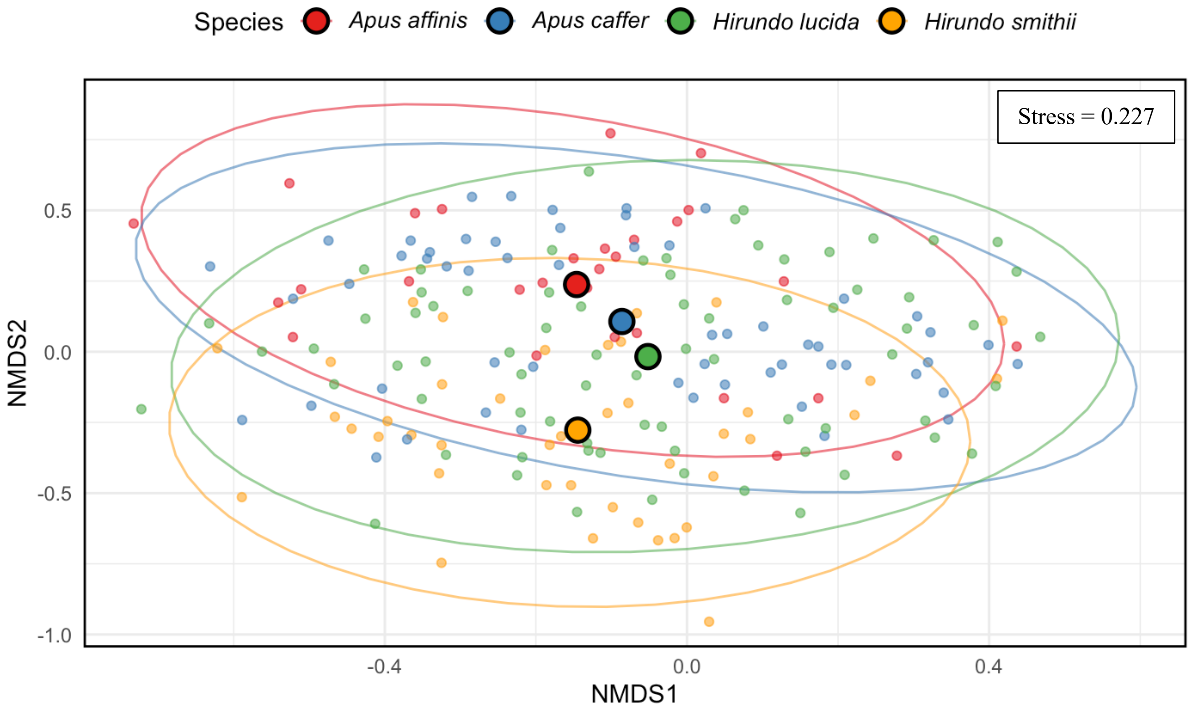

Figure 3.4. Non-metric multidimensional scaling (NMDS) analysis of prey OTU Percentage of Occurrence (POO) based on samples from the four distinct predator species—little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*)—with each point representing a sample. The ellipses represent the 95% Confidence Interval for each predator species.

However, despite the significant differences in prey consumption, the NMDS does not visually reflect strong separation, suggesting that other factors, such as environmental conditions or prey availability, may constrain prey composition and promote dietary overlap. Supporting this, the Pianka's Overlap Index for both prey order and OTU POO revealed a high degree of dietary overlap, with values significantly higher than expected by chance (Table 3.1). This suggests that while predator species consume significantly different prey types, they do so in broadly similar proportions, explaining the NMDS results.

Table 3.1. Pianka's pairwise overlap index of predator species— little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*)—for prey order and prey OTU Percentage of Occurrence (POO). The index values range from 0 (no overlap) to 1 (complete overlap). All comparisons resulted in a significantly higher-than-expected overlap value.

Pianka Overlap Index						
Predator Species	**Order Percentage of Occurrence**			**OTU Percentage of Occurrence**		
	A. affinis	*A. caffer*	*H. lucida*	*A. affinis*	*A. caffer*	*H. lucida*
A. caffer	0.974			0.549		
H. lucida	0.989	0.975		0.611	0.712	
H. smithii	0.985	0.978	0.986	0.360	0.508	0.652

Notably, dietary differences were more strongly associated with individual predator species rather than their taxonomic family. Although grouping predators by family (Apodidae vs. Hirundinidae) yielded statistically significant differences in prey composition—prey order POO (R^2 = 1.70%, F = 3.48, p = 0.005) and prey OTU POO (R^2 = 2.42%, F = 4.97, p = 0.001)— these effects explained considerably less variation than those observed at the species level.

GLM models of prey order POO revealed a significant interaction between predator species and prey order ($F = 3.77$, $p < 0.001$), indicating that predator species differed not only in overall diet composition but also in how frequently they consumed specific prey orders. For instance, the white-rumped swift exhibited significantly higher true bug (Hemiptera) POO values than all three other species. Differences were also observed in butterfly (Lepidoptera) consumption, with the little swift showing significantly higher values than the white-rumped swift, and the red-chested swallow displaying significantly higher values than both the white-rumped swift and the wire-tailed swallow. Other prey orders, such as spiders (Araneae), psocids (Psocodea), and grasshoppers, locusts, and crickets (Orthoptera), also varied significantly among predator species (Figure S14).

3.3 Temporal dietary shifts

Seasonality influenced swallow diets, as GLM models revealed significant temporal shifts in the POO of specific dietary orders (Figure 3.5).

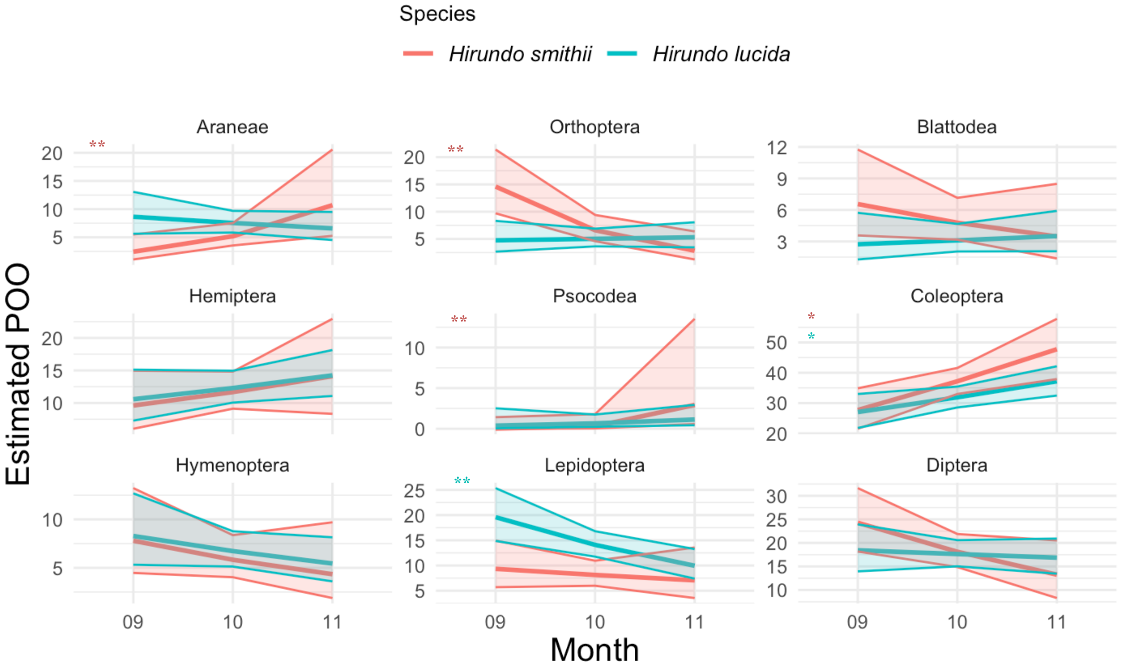

Figure 3.5. Generalized linear model (GLM) of estimated percentage of occurrence (POO) for different arthropod orders consumed by red-chested swallow (*Hirundo lucida*, blue) and wire-tailed swallow (*Hirundo smithii*, red) between September and November. Solid lines represent estimated POO values, and shaded regions indicate 95% confidence intervals. Asterisks denote statistically significant differences: blue asterisks for red-chested swallow and red asterisks for wire-tailed swallow.

However, the temporal trends differed among prey orders. Beetles (Coleoptera) became increasingly prevalent in both swallows' diets from September to November (red-chested swallow: β = 0.23, p = 0.02 and wire-tailed swallow: β = 0.43, p = 0.02, Figure S15). In contrast, grasshoppers, locusts, and crickets (Orthoptera), showed different ingestion trends between both bird species, showing a substantial decline only in the diet of the wire-tailed swallow following the seasonal gradient (β = -0.88, p = 0.01). A similar pattern was observed with butterflies (Lepidoptera), showing a reduction in prevalence in the diet of the red-chested swallow (β = -0.40, p = 0.003), with the decrease not approaching significance in the diet of the wire-tailed swallow. Spiders (Araneae) (β = 0.78, p = 0.01) and psocids (Psocodea) (β = 2.30, p = 0.004) showed significant consumption increases in the diet of the wire-tailed swallow over the same period.

4 Discussion

We applied metabarcoding for the first time to analyse the diet of a community of highly aerial insectivores in West Africa. Our results offer the first metabarcoding dietary description for the little swift (*Apus affinis*), the white-rumped swift (*Apus caffer*), the red-chested swallow (*Hirundo lucida*) and the wire-tailed swallow (*Hirundo smithii*), revealing their prey composition and richness. We found clear differences in prey richness and dietary composition among the four studied aerial insectivores. Still, all species shared some dominant prey orders, especially beetles (Coleoptera), which were a key food item for every studied species. However, all species presented distinct dietary compositions. Only a small fraction of the observed variance in dietary composition was explained by the predator species, highlighting the importance of external drivers such as prey availability and environmental conditions. Seasonality also played a significant role in the diet of the red-chested swallow and the wire-tailed swallow, with dietary shifts occurring over time, notably an increase in beetle (Coleoptera) consumption as the wet season ceased.

Despite species-specific differences, the high overlap in diet suggests they share similar foraging habits. In tropical environments, where insects are often abundant, this overlap likely reduces interspecific competition and facilitates coexistence among ecologically similar species.

Our OTU-based analysis was especially helpful given the incompleteness of tropical arthropod databases. By relying on OTUs rather than only relying on taxonomic names, we captured the true diversity of prey more accurately and avoided problems caused by missing reference data.

4.1 Diet composition and diversity

All four predator species presented broad, generalist diets shaped by local prey availability. This also likely reflects the rich arthropod diversity in the area, which provides numerous feeding opportunities for adaptable predators.

Despite interspecific differences, arthropods from the Orders Coleoptera, Diptera, Hemiptera, Lepidoptera, Hymenoptera, Orthoptera, Araneae, and Blattodea were consistently detected across all predator species, suggesting a shared reliance on abundant flying insect taxa. These results align with previous Afrotropical dietary studies of swifts and swallows (Bradley, 1993; Earl, 1985; Kopij, 2000), despite the high heterogeneity in the relative importance of each prey order (Collins et al., 2010; Kopij, 2000; Law et al., 2017; Orłowski & Karg, 2013). Spiders (Araneae) were the only non-insect group regularly consumed, likely due to their aerial dispersal via "ballooning" (Sheldon et al., 2017). Spiders may be particularly valuable during breeding, as they are rich in taurine, an essential nutrient for the healthy development of chicks in passerine birds (Ramsay & Houston, 2003).

Beetles (Coleoptera) were a major diet component in all four predator species. Weevils (Coleoptera: Curculionidae), some of which are known pests of rice crops (Heinrichs, 2004; Heinrichs et al., 1997), ranked among the top five prey families across all species, and scarab beetles (Coleoptera: Scarabaeidae) were top five prey for three. Similar findings in previous studies on African swifts and swallows (Borrett, 1973; Kopij, 2000) suggest these beetle families are ecologically important and widespread in the Afrotropics. This is supported by insect abundance data from Nigeria, identifying beetles, especially scarabs, as dominant (Okrikata & Yusuf, 2016). The prevalence of beetles also aligns with studies in agricultural areas, where they are particularly abundant (Nyffeler et al., 2018; Orłowski & Karg, 2011). Nutritionally, beetles offer higher crude protein, fat, and essential micronutrients than many other insect orders, such as Diptera (Razeng & Watson, 2015), which may contribute to active selection by aerial insectivores (Law et al., 2017; Cristiano et al., 2018; Orłowski & Karg, 2011). Flies and mosquitoes (Diptera), though more variable seasonally (Denlinger, 1980) and less nutritiously valuable, were also prominent in all diets, aligning with earlier Afrotropical studies (Collins et al., 2010; Kopij, 2000). True bugs (Hemiptera), particularly leafhoppers (Cicadellidae), were prominent in all species diets. Abundant year-round in countries like Kenya (Denlinger, 1980) and with a high number of rice pest species within the family (Dale, 1994), their presence likely reflects the agricultural nature of the study sites (Orłowski & Karg, 2013). Previously identified as dominant prey in swift diets in South Africa, including little swifts (Collins et al., 2010), their prevalence here further supports the influence of agriculture on local insect communities (Evans et al., 2007).

Butterflies (Lepidoptera) were frequently consumed, though such prevalence is uncommon in previous diet studies of swifts and swallows (Collins et al., 2010; Kopij, 2000; McClenaghan et al., 2019; Orłowski & Karg, 2013). An exception can be found in Bradley (1993), who reported butterflies making up ~10% of the diet in a breeding little swift colony in South Africa. Their high representation in our study likely reflects seasonal peaks in butterfly abundance (Okrikata & Yusuf, 2016) within the foraging range of these birds (Collins et al., 2010). Swallows also occasionally consume lepidopteran larvae (Turner, 1981), expanding the prey pool. Beetles and butterflies are rich in crude protein, enhancing their dietary value (Razeng & Watson, 2015). Ants (Formicidae) ranked among the top five prey families for three predator species, yet hymenopterans were less prominent overall. This likely reflects opportunistic feeding during swarming events, which create temporary spikes in availability (Gibbs & Leston, 1970; Lack & Owen, 1955). Flying ants are weak fliers (Hespenheide, 1975), making them an easy, energy-efficient target during these periods (Chung et al., 2021).

The significantly lower OTU richness per sample in the wire-tailed swallow, compared to swifts, likely reflects differences in morphology and ecology. Swallows forage at lower altitudes, where insect communities are more diverse and include larger prey (Waugh, 1978), which may be targeted during periods of prey abundance (McCarty & Winkler, 1999). During breeding, swallows often adopt more selective foraging strategies, remaining near the nest and focusing on locally abundant prey (Bryant & Turner, 1982; McCarty & Winkler, 1999; Waugh & Hails, 1983). As the sampled wire-tailed swallows were breeding pairs, their foraging was likely spatially restricted, contributing to a more specialised diet.

Morphological traits may further explain reduced prey richness: swallows have strong jaws and high agility, enabling them to capture larger or more mobile insects (Turner & Rose, 1989), especially in cultivated habitats where such prey is common (Kopij, 2000; Waugh, 1978). This flight agility may allow targeting of more nutritious prey (Quinney & Ankney, 1985; Razeng & Watson, 2015), reducing the need to consume a broader range of prey types. Similar patterns have been reported in Costa Rica, where sympatric swallows consistently had fewer prey items in their stomachs than swifts, likely due to differences in foraging height and prey size (Hespenheide, 1975). Together, these findings suggest that the narrower dietary breadth of wire-tailed swallows results from localised breeding foraging, morphological adaptations for capturing larger prey, and selective feeding.

A high proportion of rare OTUs (i.e. found in only one sample) was also observed, consistent with previous DNA metabarcoding studies on insectivorous birds (Garfinkel et al., 2022; Shutt et al., 2020). This likely reflects the opportunistic and variable nature of aerial insectivore foraging, where individuals sampled just days or meters apart may show marked dietary differences (Bradley, 1993; Collins et al., 2010), which may in turn reduce competition and support coexistence.

The detection of pest and vector species such as the pinhole borer *Euplatypus hints*, a wood pest, the African rice gall midge *Orseolia oryzivora*, a rice pest, and the mosquito *Aedes simpsoni*, a vector for yellow fever and Zika, among others, suggests a role of these birds in biological pest control (Barnouin et al., 2020; Sang et al., 2022), supporting evidence for the ecological importance of aerial insectivores (Sidhu et al., 2022; Wenny et al., 2011).

Several limitations of our study should be acknowledged. First, our results represent a temporal snapshot and may not reflect broader seasonal or interannual dietary variation. Second, while DNA metabarcoding is powerful, incomplete reference databases for African invertebrates limit taxonomic resolution and ecological interpretation. Third, factors such as digestion rates, DNA degradation, and primer bias may affect prey detectability. We also cannot fully exclude faecal sample contamination during collection from holding bags or plastic sheets under nests, though dominant prey taxa do not suggest contamination. Strict protocols were followed to minimise these risks and ensure robust results.

Despite these limitations, our study provides novel insights into the foraging behaviour of Afrotropical aerial insectivores. All four species exhibited flexible, generalist feeding, demonstrating adaptability to fluctuating prey availability. Non-invasive, non-capture methods proved effective for studying these highly aerial birds. Dietary OTU richness rarefaction exceeded 85% for all species, indicating our sampling captured most dietary diversity and that sample size was sufficient. Comparisons with morphological diet studies should be made cautiously, as methodological differences can affect prey detection and taxonomic resolution.

Importantly, we lack data on insect abundance, which prevents an assessment of active prey selection versus opportunistic consumption. Consequently, conclusions about prey preferences should be cautious. Future research should integrate dietary analyses with prey availability measurements.

4.2 Overlap and niche partitioning

A high dietary overlap across all predator species, shown by Pianka's Overlap Index, indicates these aerial insectivores exploit a shared pool of abundant prey, consistent with findings in sympatric swifts and swallows (Orłowski & Karg, 2013). This high overlap may partly reflect non-random prey selection driven by species-specific traits such as foraging behaviour, morphology, and nutritional needs. However, this overlap may be inflated by the dominance of certain abundant arthropod orders or OTUs in the environment, causing all species to consume these prey items frequently regardless of active selection. Furthermore, adverse weather conditions—such as the heavy rains during the sampled rainy season—can increase dietary overlap by limiting prey availability (Orłowski & Karg, 2013; Waugh, 1978).

Despite this overlap, interspecific differences appeared in prey orders and OTU composition. While all species differed in specific OTUs consumed, significant differences in broader prey orders emerged mainly with the white-rumped swift, supporting Cucco et al. (1993) observation that dietary segregation is clearer at finer prey taxonomic scales. While some divergence between the swallows and swifts as families was expected, species-level differences were more prominent. Factors such as prey size, mobility, and predator flight agility contribute to partial niche partitioning (Hespenheide, 1975; Orłowski & Karg, 2013; Waugh, 1978). The body mass of prey consumed by swifts can be as little as one-third that of the prey eaten by swallows (Orłowski & Karg, 2013), which tend to select against smaller insects (Law et al., 2017; Orłowski & Karg, 2011; Turner, 1982), even when their abundance is higher (McClenaghan et al., 2019). Morphological differences like bill shape also reduce interspecific competition, leading to dietary divergence (Bryant & Turner, 1982; Quinney & Ankney, 1985; Turner & Rose, 1989; Waugh, 1978). Swallows often include unique prey taxa, facilitating coexistence (Bumelis et al., 2022; Orłowski et al., 2015; Orłowski & Karg, 2013). Differences in vertical foraging strata, with swifts feeding at higher altitudes and swallows foraging lower, further promote dietary divergence (Orłowski & Karg, 2013; Waugh & Hails, 1983; Turner & Rose, 1989; Waugh, 1978).

At a finer scale, differences in the consumption of certain insect orders among predator species likely reflect variations in prey abundance across sites (McClenaghan et al., 2019). This is supported by the greater dietary differences observed between species rather than between families. For example, the white-rumped swift's diet contained a significantly higher proportion of true bugs (Hemiptera) compared to the other three species, likely due to habitat-driven prey availability. During sampling, white-rumped swift pairs were breeding near rice paddies, habitats known to be rich in hemipteran insects (Chen et al., 2023; Heinrichs, 2004). Swifts typically forage close to their nests during favorable weather (Lack & Owen, 1955), which may have influenced their diet composition (Orłowski & Karg, 2013). In contrast, little swifts likely foraged in urban areas, wire-tailed swallows were associated with human settlements, and red-chested swallows—none of which were sampled as breeding pairs—probably foraged over more variable landscapes. These habitat differences likely explain the variation in dietary order representation, highlighting the role of fine-scale environmental variation in driving dietary divergence, even among ecologically similar taxa (Lack & Owen, 1955).

We also found substantial dietary variation within species, likely reflecting opportunistic foraging on diverse and dynamic flying insect communities, making it unlikely for any two samples to have identical prey. For instance, little swifts can rapidly shift their diet within a few days (Collins et al., 2010; Bradley, 1993), likely responding to changing weather and insect availability (Lack & Owen, 1955). Such patterns illustrate the flexible and dynamic foraging strategies of aerial insectivores, whose prey choices appear to depend more on immediate factors, like local habitat (Evans et al., 2003, 2007) and insect abundance (Collins et al., 2010; Law et al., 2017; McClenaghan et al., 2019; Orłowski & Karg, 2011), than on fixed preferences. Moreover, temporal and spatial fluctuations in insect density likely introduce short-term variation harder to capture in the models. Future studies should incorporate prey availability data and spatial tracking of foraging movements to disentangle the relative contributions of habitat structure and prey abundance to dietary overlap and segregation.

4.3 Influence of seasonality on the diet

Seasonal variation in prey consumption was evident among the studied swallow species, as found in previous swallow dietary studies (Ismail et al., 2025; Waugh & Hails, 1983). A notable trend was the increased consumption of beetles (Coleoptera) by both species during the transition from the rainy to the dry season. This mirrors findings from Costa Rica, where beetles were the only prey order found to occur at higher densities during the dry season compared to the wet season (Hespenheide, 1975). Therefore, the rise in beetle consumption likely reflects increased beetle availability during the dry season, contrasting with other prey orders (Denlinger, 1980). Although cross-regional comparisons should be made cautiously, these consistent patterns suggest that coleopteran phenology plays an important role in shaping the seasonal diets of swallows.

A clear seasonal trend was also observed in the consumption of psocids (Psocodea) by the wire-tailed swallow, which peaked in November. This aligns with insect phenology data from East Africa (Denlinger, 1980). However, climatic differences between Kenya and Guinea-Bissau, such as Kenya's bimodal rainy seasons versus Guinea-Bissau's single wet season, warrant caution in interpretation. Nevertheless, similar November rainfall levels across both regions may explain coinciding peaks in psocid abundance.

While insect activity and abundance generally increase during the rainy season (Denlinger, 1980), rainfall alone does not fully explain the observed dietary patterns (Wolda, 1989). Insect communities are closely tied to vegetation phenology (Gibbs & Leston, 1970; Mopper & Simberloff, 1995), including many prey items of swifts and swallows. For example, in Borneo, butterfly (Lepidoptera) populations were shown to increase following droughts, coinciding with the emergence of new foliage preferred by their larvae (Itioka & Yamauti, 2004). Young leaves are typically more nutritious and less fibrous than mature leaves, making them ideal food for lepidopteran larvae (Coley, 1983). The observed decline in butterfly consumption by the red-chested swallow at the end of the rainy season may reflect reduced prey availability as new foliage becomes scarce. A similar pattern may explain the decreased consumption of grasshoppers, locusts, and crickets (Orthoptera) by the wire-tailed swallow, since these insects depend heavily on herbaceous vegetation, which is influenced by rainfall patterns (Zografou et al., 2017).

The increase in spider (Araneae) consumption by the wire-tailed swallow towards the end of the rainy season could be linked to the onset of ballooning dispersal—a behaviour inhibited during heavy rain (Vugts & Wingerden, 1976).

Studies have shown that interannual climate variability can have a stronger impact on insect populations than seasonal changes within a single year (Kishimoto-Yamada et al., 2009). This high variability, combined with limited temporal sampling, makes it challenging to detect clear patterns of dietary seasonality. Additionally, different insect families often follow distinct phenological cycles, resulting in asynchronous peaks in prey abundance (Denlinger, 1980). As a result, swallows may opportunistically shift their diets to exploit the most abundant and nutritiously valuable prey available at any given time. Temperature also plays a role in seasonal fluctuations; for example, cooler conditions can induce diapause in some taxa such as sarcophagid flies (Diptera: Sarcophagidae), reducing their availability as prey (Denlinger, 1980).

Swifts and swallows are known to adjust their foraging strategies in response to seasonal prey availability (Cucco et al., 1993; Kopij, 2000; McClenaghan et al., 2019), and we expected to observe similar seasonal shifts in swift diets (Collins et al., 2010). However, due to limited temporal sampling, we were unable to test for this. Nevertheless, this limited timeframe may still explain the patterns observed and raises the possibility that short-term, localised peaks in insect abundance may disproportionately influence dietary composition.

The relatively low explanatory power of our models suggests that important unmeasured factors—such as insect abundance and phenology across different habitats—may significantly shape predator diet composition. The absence of these ecological variables likely limited our ability to fully explain the observed dietary patterns. Including such factors in future analyses could offer deeper insights into the drivers of aerial insectivore foraging. Furthermore, our sampling was restricted to the transitional period between the wet and dry seasons, which was insufficient to capture dietary variation across the full annual cycle. Migratory behaviours, which remain poorly understood for some studied species, further complicate consistent year-round sampling (Turner & Rose, 1989). A longer-term dataset spanning both seasonal peaks is therefore needed to thoroughly understand the dietary ecology of these two swallow species.

5 Conclusion

This study highlights the dietary flexibility of four Afrotropical aerial insectivores, revealing both generalist feeding habits and species-specific dietary patterns that likely facilitate coexistence. Although there is substantial dietary overlap, subtle differences between species and across seasons suggest opportunistic foraging shaped by local prey availability and habitat conditions. These findings demonstrate the power of DNA metabarcoding to uncover fine-scale ecological dynamics in understudied tropical systems and emphasise the importance of preserving heterogeneous landscapes that support diverse insect communities crucial for aerial insectivores. However, rapid environmental changes—such as habitat loss and climate shifts—pose significant threats even to adaptable species like swallows and swifts. Ensuring their long-term survival requires targeted conservation strategies addressing species-specific foraging and habitat needs as well as broader environmental challenges.

A major gap in current knowledge is the migratory behaviour of Afrotropical swifts and swallows. Many undertake seasonal movements, but critical stopover and non-breeding areas remain poorly documented. Understanding these migratory pathways is essential for identifying and protecting key habitats used during pre- and post-breeding periods, vital for their survival and reproductive success. Understanding these dynamics will improve conservation actions that safeguard not just breeding grounds but also the full annual cycle of these birds. Given their close association with open and agricultural landscapes, promoting sustainable farming practices is also crucial. Aerial insectivores can serve as natural pest suppressors (Díaz-Siefer et al., 2022), reducing reliance on chemical pesticides and benefiting both agriculture and biodiversity. Conservation programs should support integrated pest management and maintain insect-rich habitats, such as set-aside lands, which have been shown to enhance insect and bird abundance (Bianchi et al., 2006; Van Buskirk & Willi, 2004).

Understanding how swallows and swifts adjust their foraging strategies in response to fluctuating prey availability is key to effective conservation. Combining behavioral observations with prey population data across habitats and seasons can help identify critical foraging areas. This integrated approach supports habitat management practices that maintain prey diversity and ensure the persistence of aerial insectivore populations.

In summary, conserving Afrotropical swallows and swifts requires a multifaceted strategy that incorporates their dietary plasticity, habitat use, and migratory dynamics. By preserving diverse landscapes and filling knowledge gaps about their life cycles, we can better protect these ecologically important yet understudied birds in a rapidly changing world.

6 References

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7 Supplementary material

Figure S1. Rice paddies maintained and cultivated by local communities. These habitats showed high swallow and swift activity during the breeding season, before the onset of the dry season. Photograph taken in September 2023. © João Albuquerque.

Figure S2. Collection platform adapted from McClenaghan et al. (2019) for gathering faecal samples. Photograph taken in September 2023. © João Albuquerque.

Figure S3. Saliquinhedim sampling point. A collection platform was placed beneath the bridge, where an active pair of white-rumped swifts (*Apus caffer*) was observed. The used nest is visible in the photograph. Photograph taken in November 2023. © João Albuquerque.

Figure S4. Djalicunda2 sampling location. A collection platform was placed beneath a used wire-tailed swallow (*Hirundo smithii*) nest. Photograph taken in September 2023. © João Albuquerque.

Figure S5. Bironqui sampling point. A collection platform was placed under the bridge, where an active white-rumped swift (*Apus caffer*) couple was present. The used nest can be seen on the right ledge. Photograph taken in September 2023. © João Albuquerque.

Figure S6. Mansaba1 sampling point. Left: The ledge that hosts a colony of little swifts (*Apus affinis*). Right: One of the used nests beneath the ledge. Photograph taken in November 2023. © João Albuquerque.

Figure S7. Mambonco sampling point. Left: Wire-tailed swallow (*Hirundo smithii*) chicks in the nest. Right: The bridge structure containing the used nest and overnight roosting spots of the red-chested swallow (*Hirundo lucida*). Photograph taken in September 2023. © João Albuquerque.

Table S1. *COI* sequences from analysed predator species—little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*).

Predator species	***COI* Sequence**
Little swift (*Apus affinis*)	TCTAGCAGGTAACCTAGCCCACGCAGGGGCATCAGTAGACCTCGCCATCTTCTCCCTCCACCTAGCAGGTGTCTCCTCCATCCTAGGTGCAATTAACTTCATCACTACTGCCATCAACATAAAACCCCCTGCCCTCTCACAATATCAAACACCCCTATTCGTATGGTCCGTCCTCATCACCGCCGTCCTACTACTCCTCTCCCTC
White-rumped swift (*Apus caffer*)	TCTAGCAGGTAACCTAGCCCACGCAGGGGCATCAGTAGACCTCGCCATCTTCTCCCTCCACCTAGCAGGTGTCTCCTCCATCCTAGGTGCAATTAACTTCATCACTACTGCTATCAACATAAAACCCCCTGCCCTTTCACAATATCAAACACCCCTATTCGTATGGTCTGTCCTCATCACCGCCGTCCTACTACTCCTCTCCCTC
Red-chested swallow (*Hirundo lucida*)	TAGCCGGAAACCTAGCACACGCGGGGGCCTCTGTAGACCTAGCCATTTTCTCCCTACATCTAGCAGGAATTTCCTCAATCCTAGGTGCAATCAACTTTATCACTACAGCAATCAACATAAAACCCCCAGCCCTATCACAGTACCAAACACCACTATTCGTCTGATCAGTATTAATCACCGCAGTTCTTCTTCTCCTATCACTG
Wire-tailed swallow (Hirundo smithii)	TCTAGCCGGAAACCTAGCACACGCTGGAGCCTCTGTAGACCTAGCCATTTTCTCCCTCCATCTGGCAGGAATCTCCTCTATCCTGGGCGCGATCAACTTTATCACTACAGCAATCAACATAAAACCTCCCGCCCTATCACAATACCAAACACCACTATTCGTCTGATCAGTATTAATCACTGCAGTTCTTCTTCTCCTATCACTA


Figure S8. A wire-tailed swallow (*Hirundo smithii*) captured by mist netting. Photograph taken in September 2023. © João Albuquerque.


Figure S9. Close-up of a captured red-chested swallow's (*Hirundo lucida*) tail feathers (rectrices). The large extent of white on the tail feathers is one distinguishing characteristic that differentiates it from the barn swallow (*Hirundo rustica*). Photograph taken in September 2023. © João Albuquerque.

Figure S10. Little swift (*Apus affinis*) photographed near the nesting colony in Mansaba. Photograph taken in October 2023. © João Albuquerque.

Figure S11. White-rumped swift (*Apus caffer*) chick photographed inside the Bironqui's nest. Photograph taken in November 2023. © João Albuquerque.

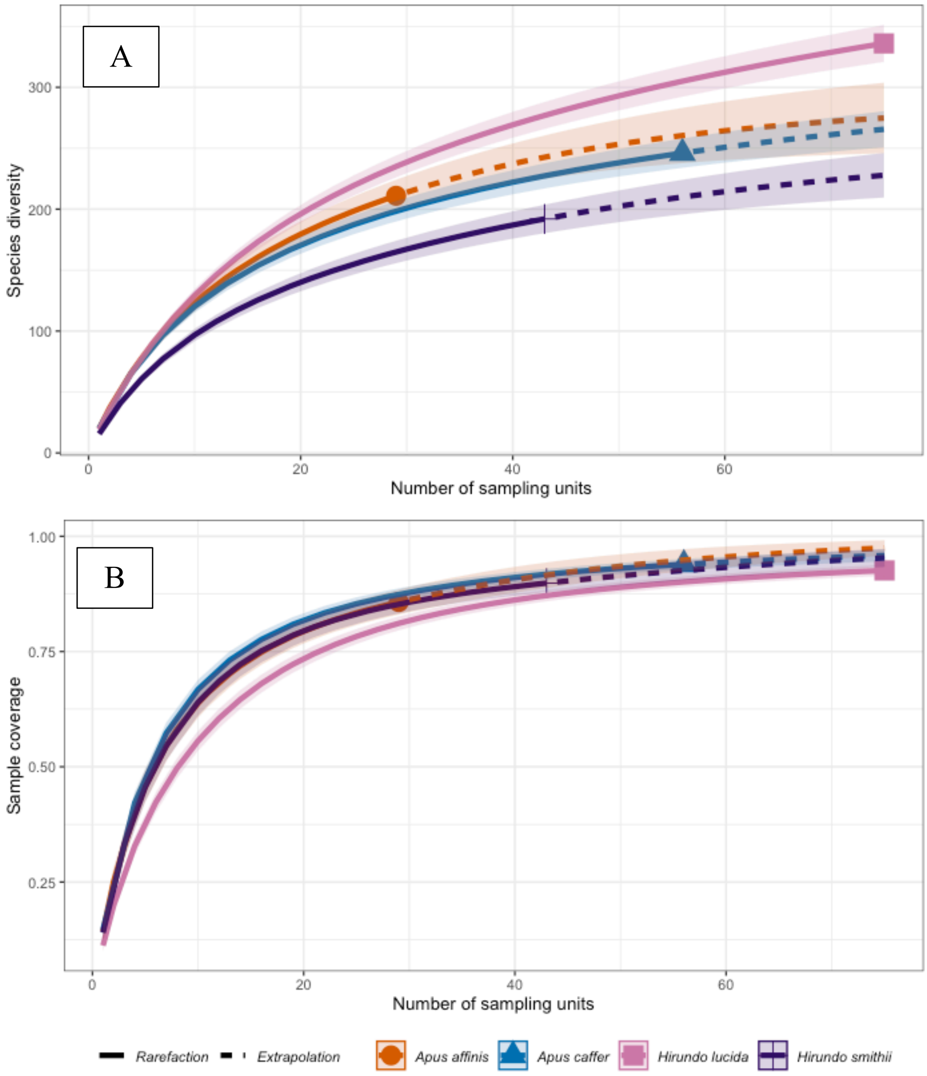

Figure S12. iNext estimates for OTU diversity for four predator species—little swift (*Apus affinis*, orange), white-rumped swift (*Apus caffer*, blue), red-chested swallow (*Hirundo lucida*, pink) and wire-tailed swallow (*Hirundo smithii*, purple). A) observed and estimated species (OTU) richness relative to sampling effort; B) Sample coverage as a function of the number of sampling units. Solid lines represent rarefaction and dashed lines represent extrapolation, with shaded areas indicating 95% confidence intervals. Circle (*Apus affinis*), triangle (*Apus caffer*), square (*Hirundo lucida*), and cross (*Hirundo smithii*) correspond to the observed values of sample coverage, number of samples and OTU richness.

Table S2. Results of pairwise Dunn's tests comparing Proportion of Occurrence (POO) metrics among bird species—little swift (*Apus affinis*, AA), white-rumped swift (*Apus caffer*, AC), red-chested swallow (*Hirundo lucida*, HL) and wire-tailed swallow (*Hirundo smithii*, HS)—, based on prey taxonomical order-level and OTU-level data. The tests were conducted for Shannon diversity, Simpson diversity, and Pielou's evenness indices. For each comparison, the Z statistic and the Bonferroni-adjusted p-value are provided. Significant differences ($p < 0.05$ after Bonferroni correction) are bolded. For OTU-level Pielou's evenness, values are not shown because no duplicate OTUs were found within any given sample, resulting in index values of 1 across all cases, thus rendering comparisons meaningless.

Comparison Order POO	**Shannon Z**	**Shannon Adj. *p*-value**	**Simpson Z**	**Simpson Adj. *p*-value**	**Pielou's Evenness Z**	**Pielou's Evenness Adj. *p*-value**
AA - AC	-0.984	0.976	-1.122	0.786	-1.937	0.158
AA - HL	-0.850	1	-1.366	0.516	-3.507	**0.001**
AC - HL	0.221	1	-0.237	1	-1.839	0.198
AA - HS	0.448	1	-0.132	1	-3.560	**0.001**
AC - HS	1.640	0.301	1.110	0.801	-2.034	0.126
HL - HS	1.534	0.375	1.396	0.489	-0.446	1

Comparison OTU POO	**Shannon Z**	**Shannon Adj. *p*-value**	**Simpson Z**	**Simpson Adj. *p*-value**
AA - AC	-0.170	1	-0.170	1
AA - HL	1.367	0.515	1.367	0.515
AC - HL	1.914	0.167	1.914	0.167
AA - HS	2.997	**0.008**	2.997	**0.008**
AC - HS	3.745	**<0.001**	3.745	**<0.001**
HL - HS	2.202	0.083	2.202	0.083

Table S3. Pairwise comparisons of prey order and prey OTU Proportional Occurrence (POO) among predator species—little swift (*Apus affinis*, AA), white-rumped swift (*Apus caffer*, AC), red-chested swallow (*Hirundo lucida*, HL) and wire-tailed swallow (*Hirundo smithii*, HS)—based on Bray-Curtis dissimilarity using pairwise PERMANOVA. The R^2, F-statistics and corresponding p-values are shown for each comparison. P-values were corrected for multiple comparisons using the Bonferroni correction, with statistically significant differences ($p < 0.05$) bolded.

	Prey Order POO		**Prey OTU POO**	
Species pairs	R^2	*p*-value	R^2	*p*-value
HS - AC	4.40%	**0.012**	5.56%	**0.006**
HS - HL	2.57%	0.084	3.04%	**0.006**
HS - AA	3.29%	0.324	7.24%	**0.006**
AC - HL	4.24%	**0.012**	2.96%	**0.006**
AC - AA	6.05%	**0.006**	4.72%	**0.006**
HS - AA	2.09%	0.324	3.25%	**0.006**

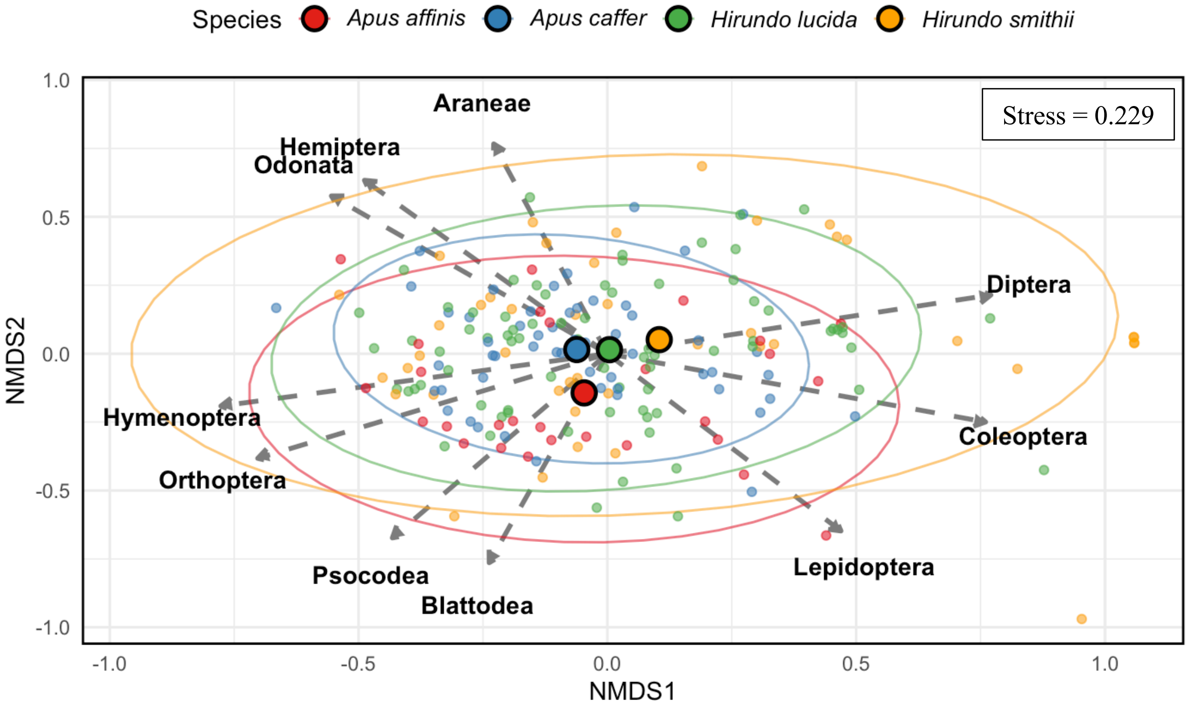

Figure S13. Non-metric multidimensional scaling (NMDS) of prey order Percentage of Occurrence (POO) across samples from the four distinct predator species—little swift (*Apus affinis*), white-rumped swift (*Apus caffer*), red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*). The centroids represent the mean position of each species in the ordination space. Arrows indicate the contribution of each prey order to the positioning of the centroids, with the direction reflecting the direction of the contribution. The ellipses represent the 95% Confidence Interval for each predator species.

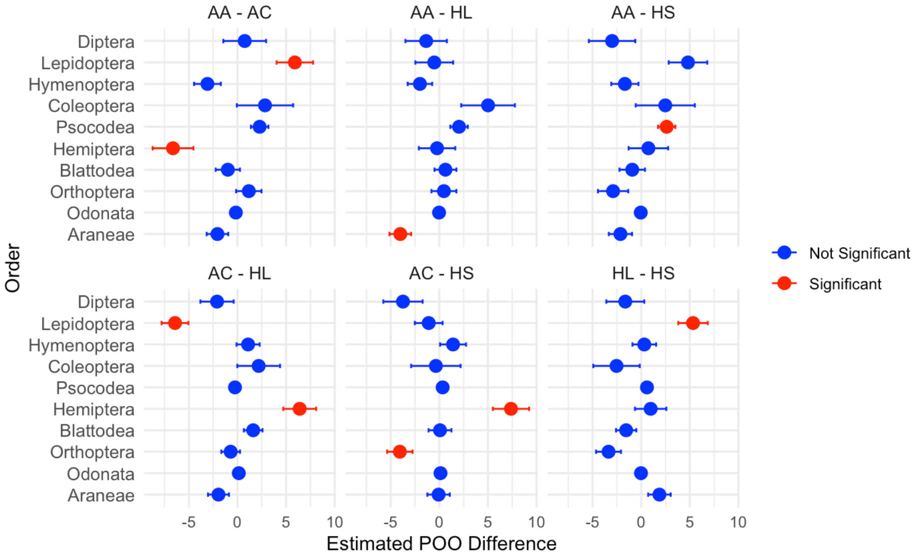

Figure S14. Pairwise comparisons of prey order consumption between predator species. The forest plot illustrates the estimated pairwise differences in prey order Percentage of Occurrence (POO) between predator species— little swift (*Apus affinis*, AA), white-rumped swift (*Apus caffer*, AC), red-chested swallow (*Hirundo lucida*, HL) and wire-tailed swallow (*Hirundo smithii*, HS)—as determined by a generalised linear model (GLM) with a quasibinomial family and logit link function. The dependent variable in the model is the prey order Percentage of Occurrence (POO), and the independent variables are predator species and prey order, along with the interaction between these two factors. Each point in the plot represents the estimated difference in POO between two species for a given prey order, with horizontal error bars denoting the standard error (SE) of the estimate. Colours in the plot indicate statistical significance after Bonferroni correction, with red denoting significant differences ($p < 0.05$) and blue indicating non-significant differences.

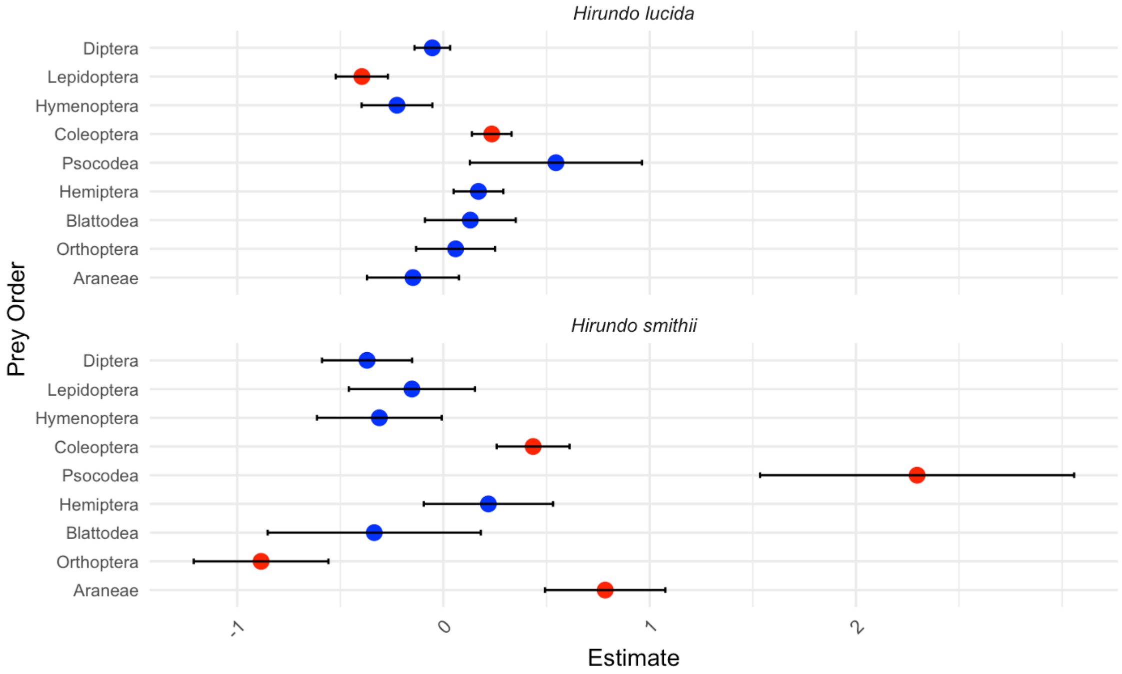

Figure S15. Generalised Linear Model (GLM) results for both swallow species, red-chested swallow (*Hirundo lucida*) and wire-tailed swallow (*Hirundo smithii*), based on the Percentage of Occurrence (POO) of different prey orders across months. Each point on the plot represents the estimated effect (Estimate) of month on the predator species' POO within the respective order. The x-axis shows the Estimate, while the y-axis represents the prey orders. The red points indicate significant results ($p < 0.05$), while the blue points correspond to non-significant results ($p \geq 0.05$). The error bars reflect the standard error around each estimate.