The influence of predation danger on the distribution of non-breeding shorebirds in a tropical estuary system

by

Richard Johnston-González

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Name:	**Richard Johnston González**
Degree:	**Doctor of Philosophy (Biological Sciences)**
Title:	**The influence of predation danger on the distribution of non-breeding shorebirds in a tropical estuary system**
Examining Committee:	Chair: Leithen K. M'Gonigle Assistant Professor

Ronald C. Ydenberg
Senior Supervisor
Professor

Dov B. Lank
Supervisor
Adjunct Professor

David Green
Supervisor
Professor

John Reynolds
Internal Examiner
Professor

Juan Navedo
External Examiner
Associate Professor
Instituto de Ciencias Marinas y Limnológicas
Universidad Austral de Chile

Date Defended/Approved: April 5, 2019

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Abstract

I studied non-breeding shorebirds in the extensive mangrove-mudflat system of Northern Nariño, Colombia. I asked how the non-breeding distributions of 18 species are influenced by functional traits, the interplay between food and danger attributes of landscapes, and interactions with other species. I found that almost all the area's ~8000 Whimbrels (*Numenius phaeopus*) roost together on just one of the hundreds of available mangrove islands. Much smaller numbers occasionally roost on a few other islands. The larger roost site is distinguished by its location, having a larger amount of Whimbrel feeding habitat (mudflat) within a 12 km radius than almost any other mangrove island, and being more isolated from the mainland and thus from terrestrial predators, but not more isolated from villages or shipping channels than other islands. Within a subset of nine shorebird species, an increase in body mass predicted an increase in wing load both within and between species. Contrary to expectations, wing load did not correlate strongly with escape performance (take off speed), but as expected, heavier wing loads did correlate with stronger escape responses (flight initiation distances) across species. Species with higher escape performance use habitats that are more productive, but also more dangerous, while species with lower escape performance reacted sooner to predator stimulus. Tactile and gregarious species show stronger responses to safety gradients. An analysis of co-occurrence of species pairs demonstrated that non-random patterns were prevalent within communities of non-breeding shorebirds. Species pairs tracking same or opposing environmental gradients explain some positive and negative associations, but a large proportion of the associations was due to residual variation linked to the species themselves. Positive associations could be explained by heterospecific attraction associated with reducing predation danger and public information about resources. The fewer negative associations could indicate competitive interference. Alternatively, other sources of environmental variation not captured in this study could explain these "species only" associations. Our results contrast with previous studies of avian communities for which shared environmental responses play a larger role and suggest that social interactions are as important in structuring shorebird communities. This thesis demonstrates how using distribution models informed by species' morphology, behavior, and interactions with other species, we will be better equipped to understand the effects of habitat conversion on the conservation of migratory shorebirds.

Keywords: Shorebirds; behavioural ecology; habitat selection; escape performance; species distribution modelling; predation danger

I dedicate this thesis to:

Dad, who wonder how the birds find their ways. I didn’t have the chance to answer it for you, but you would be pleased to know that I have being working on it.

Mom, who inspired me to be a better person.

Vi, who brought colours to my life.

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Chapter 1.

Introduction

Food resources, environmental features affecting water/heat balance, the avoidance of predators and parasites, and interactions with other species are some of the factors affecting habitat selection in shorebirds (Jones, 2001a; Stillman and Goss-Custard, 2010; van den Hout et al., 2009). Managing these four habitat axes (i.e., food, water/heat, danger, and competition/sociality) requires individual shorebirds to make decisions about habitat selection (Piersma, 2012). These individual decisions are in turn reflected in species distribution patterns that could be measured to assess habitat quality for populations and species (Johnson, 2007)

Studies investigating habitat quality frequently focus on food availability (Reiter et al., 2015; Taylor et al., 2016). A less-studied aspect of habitat quality is danger (Lank et al., 2003). Even without being present, predators can affect habitat decisions of their prey (Lima and Dill, 1989). Habitats perceived as too dangerous could be avoided altogether or require additional investment in antipredator behavior (Lank and Ydenberg, 2003). Individuals and species better equipped to escape predators could use more dangerous habitats (Burns and Ydenberg, 2002; Nebel and Ydenberg, 2005). Contrasting the distribution of species with different morphological and physiological properties across danger and other environmental gradients could increase our understanding of species-specific habitat selection. These 'functional traits' related to the features of "an individual or a species that potentially affect performance or fitness" (Cadotte et al., 2015) could inform species distribution modelling. In this thesis I describe 'functional traits' related to the ability to detect and escape a predator (Chapter 3), the distribution of shorebirds across environmental gradients in relation to these functional traits (Chapter 4) and compare the role of the environment in shaping shorebird community assemblages with patterns arising from interactions with other species (Chapter 5). In addition, I include a case study illustrating how we can use danger-food landscapes to account for the distribution of nocturnal roost sites (Chapter 2).

At least since Darwin (1861), ecologists have searched for the signals of the outcomes of interactions between coexisting species. In ecology, there is a strong dichotomy between theory and empirical studies examining deterministic processes that structure ecological communities, and more recent studies that focus on random processes. The former dates back to Diamond's "assembly rules" (Diamond et al., 1976) used to explain the prevalence of some species combinations and the apparent existence of "forbidden" pairs of species, and has been extensively studied (Weiher and Keddy, 1999). The latter refers to the neutral theory (Hubbell, 2001) and has resulted in so-called 'null' models suggesting that some portion of community composition patterns could emerge from entirely random processes.

Both frameworks help us to understand the composition of communities, and the role of random and non-random patterns in their assembly. But once we establish that a pattern is deterministic, we still face the challenge of attributing these non-random patterns to environmental filters (Kraft et al., 2015), biotic interactions (Stillman and Goss-Custard, 2010) or both or in the cases where each applies, and also to dispersal limitations (D'Amen et al., 2018). Disentangling the direct effects of environment and species' interactions continues to be an active area of inquiry in ecology (Warton et al., 2015). Methods such as classic multivariate analysis and novel probabilistic (Veech, 2013a) and joint distribution modelling (Niku et al., 2017; Warton et al., 2015) provide new methods for describing the randomness of community assembly patterns and in isolating the signals of environment or interactions producing those patterns. In this thesis I use a combination of comparative studies of functional traits (chapter 3), classic species distribution modelling (chapter 2 and 4) and joint distribution modelling (chapter 5) to peer into the mechanisms that give rise to assembly patterns in non-breeding shorebird communities.

1.1. Study area

My study area in the north of Nariño Department, on the southern Pacific coast of Colombia (Fig 2.1) (2.3-2.5°N, -78.5 °-78.3 °W), covers nearly 100,000 ha across an extensive delta dominated by the Sanquianga, Tapaje and Iscuandé rivers and their tributaries. An interconnected network of estuarine channels with a high tidal influence extends up to 35km inland (Restrepo and Kettner, 2012). The area has high precipitation and the upstream basins of these tributaries occupy one of the rainiest regions on the planet (Fick and Hijmans, 2017). This coastal landscape is dominated by mangrove forests, shallow estuarine waters, and tidal flats, with sand beaches, coastal shrubs, pastures and human settlements in its lower extent (Anónimo, 2005). The main shorebird habitats are tidal flats, which occur interspersed across estuarine channels and surrounded by a matrix of mangrove vegetation. Tidal flats experience a semidiurnal cycle, with monthly tidal height varying by up to 4.6 m (IDEAM, 2016), restricting availability for shorebirds to a few hours during day and night. The diversion of the Patía river in 1973 extended the incursion of freshwater and sediment in this system, increasing the sedimentation and extension of tidal flats (Restrepo and Cantera, 2011). The effects of this “environmental collapse” (Parra and Ángel, 2014) on biodiversity associated with tidal flats, including shorebirds, is not well understood.

1.2. Non-breeding shorebirds

I studied the community of shorebirds in the Southern Pacific coast of Colombia. Thrity-two shorebird species have been registered in the area (Ruiz-Guerra et al., 2007; Ruiz-Guerra, 2004), of which Whimbrel (*Numenius phaeopus*), Spotted Sandpiper (*Actitis macularia*), Western Sandpiper (*Calidris mauri*) and Semipalmated Sandpiper (*C. pusilla*) are the most abundant (Asociación Calidris y Consejo Comunitario Esfuerzo Pescador Iscuande, 2017). I focused on the period of non-breeding “winter residence” between November and early February. In doing so I prevented effects of spring migratory movements that could influence counts, behaviour or flight performance. Occasional species or those registered only outside “winter” were not considered. As a result, ~16 shorebird species were considered non-breeding residents in the study area and are the focus of this thesis. Two additional species, with breeding populations in the area, Wilson’s plover (*Charadrius wilsonia*) and American Oystercatcher (*Haematopus palliatus*) were also included in the analysis. Their breeding seasons start later in the year (Cifuentes-sarmiento and Ruiz-guerra, 2013; Ruiz-Guerra et al., 2008), so we considered them “non-breeding” during the study period. They could be labelled as “breeding/non-breeding residents” (Table 1.1).

1.3. Thesis Outline

In this thesis, I emphasize whether predation danger effects contribute to the distribution and composition of non-breeding shorebird communities in the tropics.

Table 1.1. Functional traits of shorebird species present in mangrove coast of southern Colombia. Subfamilies and species sorted by phylogenetic order following SACC classification (Remsen et al. 2017). Species were categorized by size using mean mass: Small (S<100g), Medium (M=100-200g), Large (L>200g). Mass and sociality (Gregarious=G, S=solitary) from The Birds of North America (Poole et al. 2016) species accounts: (1) Poole et al. (2016), (2) Nol & Blanken (2014), (3) Zdravkovic et al. (2018), (4) Hayman (1986), (5) American Oystercatcher Working Group, (6) Skeel & Mallory (1996), (7) Gratto-Trevor (2000), (8) Nettelship (2000), (9) Baker et al (2013), (10) Macwhirter et al. 2002, (11) Hickilin et al. (2010), (12) Franks et al. (2014)., (13) Nebel & Cooper (2008), (14) Jehl et al. 2001, (15) Reed et al (2013), (16) Lowther et al. (2001), (17) Tibbits & moskoff (2014), (18) Elphick & Tibbits (1998). Predominant feeding modes (V=visual, T=Tactile) using personal observations and secondary information (Barbosa, 1995).

Taxonomic	Code and Species		Mass (g)	Source	Size	Feeding mode	Sociality
Charadriidae	BBPL - Black-bellied Plover	*Pluvialis squatarola*	180	1	M	V	S
	SEPL - Semipalmated Plover	*Charadrius semipalmatus*	47	2	S	V	S
	WIPL - Wilson's Plover	*Ch. wilsonia*	55-70	3	S	V	S
	COPL - Collared Plover	*Ch. collaris*	35	4	S	V	S
Haematopodidae	AMOY - American Oystercatcher	*Haematopus palliatus*	400-700	5	L	V	G
Numeniinae	WHIM - Whimbrel	*Numenius phaeopus*	310–493	6	L	V	S
Limosinae	MAGO - Marbled Godwit	*Limosa fedoa*	285–454	7	L	V	G
Arenariinae	RUTU - Ruddy Turnstone	*Arenaria interpres*	84-190	8	M	V	G
	REKN - Red Knot	*Calidris canutus*	135	9	M	V	G
	SAND - Sanderling	*C. alba*	40-100	10	S	T	G
	SESA - Semipalmated Sandpiper	*C. pusilla*	17.3-47.3	11	S	T	G
	WESA - Western Sandpiper	*C. mauri*	22-35	12	S	T	G
	LESA - Least Sandpiper	*C. minutilla*	19-30	13	S	V	S
Scolopacinae	SBDO - Short-billed Dowitcher	*Limnodromus griseus*	90-120	14	M	T	G
Tringinae	SPSA - Spotted Sandpiper	*Actitis macularia*	43-50	15	S	V	S
	WILL - Willet	*Tringa semipalmata*	200-330	16	L	V	S
	LEYE - Lesser Yellowlegs	*Tringa flavipes*	67–94	17	M	V	S
	GRYE - Greater Yellowlegs	*Tringa melanoleuca*	111-235	18	L	V	S

In **Chapter 2** I examine the link between danger and food landscapes in the selection of nocturnal roosting sites. I focus on the Whimbrel, a shorebird whose members congregate in only a few sites while roosting at night. From all the hundreds of available mangrove islands, nocturnal roosts occur in some of the most isolated locations. Locations of nocturnal roosts of this species allow easy access to feeding sources and are isolated from the mainland and other sources of terrestrial predators. Food and danger landscapes explained the location of the roosts but could not account for the extreme concentration of individuals in some of them. Additional factors explaining the hyperabundance of Whimbrel in specific roosting locations could involve the presence of conspecifics. This chapter introduces the reader the effect of food-danger landscapes in the distribution of roosting sites. In addition, it highlights the potential role for a social component in habitat selection by shorebirds.

The ability to escape a predator could influence habitat selection decisions by shorebirds. In **Chapter 3**, I study escape performance and antipredator responses of shorebirds during their non-breeding period. Species with lower escape performance could require extra investment in vigilance or longer flight initiation distances during (perceived) predator attacks, or they might avoid dangerous sites altogether. I use morphometric data, wing pictures and video-recorded take-off speeds of released birds to estimate the escape performance of nine shorebird species. As expected, wing load increased linearly with the log transformed body mass, both within and between species. Species with heavier wing loads tend to have slower take-off speeds, but some heavy wing loaded species managed to achieve similar escape performance than lighter ones, so there was not a strong relationship. In addition, heavy wing loaded species have an earlier reaction to an approaching predator. Overall these results indicated that in shorebirds the ability to escape a predator is linked to body size and wing load, and species with higher wing loads compensate by increasing the investment in escape flights and complimentary antipredator responses.

Based on the results of Chapter 3, I predicted that differences in escape ability and antipredator repertoires could influence habitat selection decisions. Thus, in **Chapter 4** I investigate habitat selection by shorebird species that differ in escape ability and feeding modes. I use six years of shorebird monitoring data to build models of occupancy and abundance in relation to habitat data. I compared the support for four non-mutually exclusive hypotheses of shorebird distribution: area-effects, safety in the open, primary productivity and marine influence on occupancy and abundance of shorebirds. As expected, area is one of the most important predictors of shorebird occupancy and abundance. In addition to area-effects, shorebirds tend to have greater occupancies and abundances in areas far from vegetation, which supported the prediction that most shorebirds seek safety in the open areas. However, some species did not follow this pattern and showed a clear affinity for covered areas with higher productivity. Part of this segregation in habitats can be explained by differences in escape ability. I also suggested that some shorebird species could experience cover as a safer habitat and that this could work in combination with a suit of alternative antipredator strategies.

In **Chapter 5** I compare the importance of the environment and species interactions in the assembly of shorebird communities in Southern Colombia. I use two novel modeling frameworks: probabilistic species co-occurrence modelling and joint distribution modelling to assess the proportion of the variation in distribution of communities attributed to environmental variables directly versus species interactions. I showed that shorebird species associated in non-random, mostly positive patterns and that some of these associations occur in species sharing functional traits (e.g., plovers, sandpipers). Co-occurrences and co-abundance of species could be attributed to a combination of shared environmental responses, but also to species interactions. This chapter highlights the potential role of heterospecific attraction in the assembly of shorebird communities and in contrast with other groups where correlated responses to the environment appear to play a stronger role.

Overall, this thesis helps to understand the relative contribution of functional traits, habitat, space, and species interactions in shaping the distribution of species. I propose considering those multiple factors when examining the consequences of habitat change on the assembly of migratory bird communities. The methods outlined here could be used to assess change in habitat suitability and distribution of shorebirds at larger temporal and spatial scales.

Chapter 2.

Predation risk and resource availability explain roost locations of Whimbrel *Numenius phaeopus* in a tropical mangrove delta

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2.1. Abstract

Roosts are important sites for shorebirds in non-breeding areas at night and during high tides. How the spatial configuration of food and risk of predation and disturbance influence roost site use in tropical locations remains poorly known. We analysed the locations of nocturnal roosts of Whimbrel *Numenius phaeopus* in mangroves of Sanquianga National Park, Colombia, with respect to variation in spatial variables related to food resources and risk of predation and disturbance. We contrasted characteristics of all 13 known nocturnal roost locations with those of all other mangrove islands (n = 209) within the limits of the park. We estimated the distance from roosts and other mangrove islands to foraging sites, and sources of predators and human disturbance. Larger areas of feeding habitat surrounded nocturnal roosts than other mangrove islands, and the average distance to individual feeding patches was shorter. Roosts were also more isolated than other islands, but proximity to sources of human disturbance did not differ. We conclude that Whimbrel roost site use in Sanquianga was best explained by a combination of access to feeding territories and isolation from potential sources of mainland predators, but not by avoidance of human disturbance. Beyond identifying factors influencing roost site selection, the large aggregations of individuals in single locations may suggest that presence of conspecifics itself also plays a role in the formation of Whimbrel roosts. We highlight the interaction of food and risk landscapes with intraspecific attraction on the roost site selection by Whimbrels and the importance of mangroves as roosting sites in tropical regions.

Keywords: Colombia; mangroves; habitat selection; predation avoidance.

2.2. Introduction

Communal roosting is a widespread behaviour within birds and social mammals (Beauchamp 1999, Beauchamp 2014). Three general explanations have been proposed for communal bird roosts: thermoregulatory benefits, greater foraging efficiency, and protection from predation (Ydenberg & Prins 1984). Roosting with companions can provide protection against extreme weather and reduce energetic costs associated with thermoregulation (Yom-Tov *et al.* 1977, Du Plessis & Williams1994, Rehfisch *et al.* 2003, Burton & Evans 2008, Williams & Du Plessis 2013). Roosts can also increase foraging efficiency through information transfer (Ward & Zahavi 1972), recruitment of foragers at the roost (Burton et al., 1996) or attraction of conspecifics to food sources (Buckley, 1996). Roosting with companions can improve predator detection and dilute individual predation risk (Eiserer, 1984), and/or it can offer a safety buffer to birds roosting at the centre of the flock (Weatherhead, 1983). These explanations highlight the social value of roosting with conspecifics, but an alternative fourth explanation is that communal roosts are coincidental aggregations of individuals that are searching independently for roost sites with similar characteristics (Beauchamp, 1999).

Comparing the habitat features of roosts and other locations may shed light on the relative importance of competing explanations for roost-site formation in birds. Studies using this approach have demonstrated that birds can aggregate near foraging patches (Caccamise & Morrison 1988), at sites offering safety from predators (Rosa et al., 2006), or lower levels of disturbance (Peters & Otis 2007). On the other hand, roosts are not static. Conklin *et al.* (2008) argued that Pacific Dunlin *Calidris alpina* constantly shifted between a wide suite of readily available roost sites in part to avoid predators. Habitat features of roosts may also provide shelter against cold wind (Colwell and Sundeen 2000, Peters & Otis 2007) or extreme heat conditions (Danny I Rogers et al., 2006).

Most migrant and non-breeding shorebirds typically roost at night, but also may aggregate when foraging areas are covered by high tides during the day. When high tide limits the availability of roosts safe from diurnal predators, small shorebirds can take to extremes, making hours-long overwater flights rather than land (Ydenberg et al., 2010). It has been suggested that the availability of sites offering favourable characteristics can constrain the location of both nocturnal and high-tide roosts of shorebirds (Rogers *et al.* 2006b, but see Conklin *et al*. 2008). The time or energetic costs of travelling between roosts and feeding areas could therefore constrain shorebird distributions (Rehfisch et al., 2003, 1996). On one hand, individuals may prefer to use roost sites closer to their feeding territories. But with respect to safety, shorebirds could choose roosting sites with features that prevent or impede predator attacks. For example, to reduce the risk of surprise attacks from raptors, shorebirds may favour roosting on open mudflats far from vegetation (Piersma *et al*. 2006, Rosa et al., 2006). Shorebirds are more vulnerable to predation by mammals when close to vegetation or at roosts lacking isolation (Hockey, 1985). The availability of roosts safe from terrestrial predators could constrain distribution of non-breeding shorebirds (Rogers et al., 2006).

Human activity can impose high energetic costs to roosting shorebirds (Rogers et al., 2006), impact the choice of roosting habitats (Yasué, 2006), and cause long-term effects on the use and abandonment of roosting sites (Burton et al. 1996, Colwell & Sundeen 2000, Peters & Otis 2006). To fully understand the influence of feeding areas, predator risk and disturbance on roost selection by non-breeding shorebirds, further work is necessary on the spatial distribution of shorebird roosts in relation to sources and types of potential predators in non-breeding areas, particularly in tropical habitats.

Mangroves are widespread habitats in tropical regions across shorebird flyways (Butler *et al.* 2001, Bamford *et al.* 2008). Mangroves are strong predictors of feeding habitat productivity and high shorebird densities at global and regional scales. (Butler et al., 2001, 1997). Beyond feeding, mangroves provide roosting habitat for several species of shorebirds, in particular for the Whimbrel *Numenius phaeopus* (Johnston-González *et al.* 2006, Zharikov & Milton 2009). This study focuses on the use of mangroves as roost sites for the Whimbrel in Sanquianga National Park, along the southern Pacific coast of Colombia (Fig. 2.1). This large tropical river delta covers ~ 480 km^2, including barrier islands and sand spits along 60 km of coastline and ~ 200 mangrove islands, providing many potential locations for feeding and roosting shorebirds.

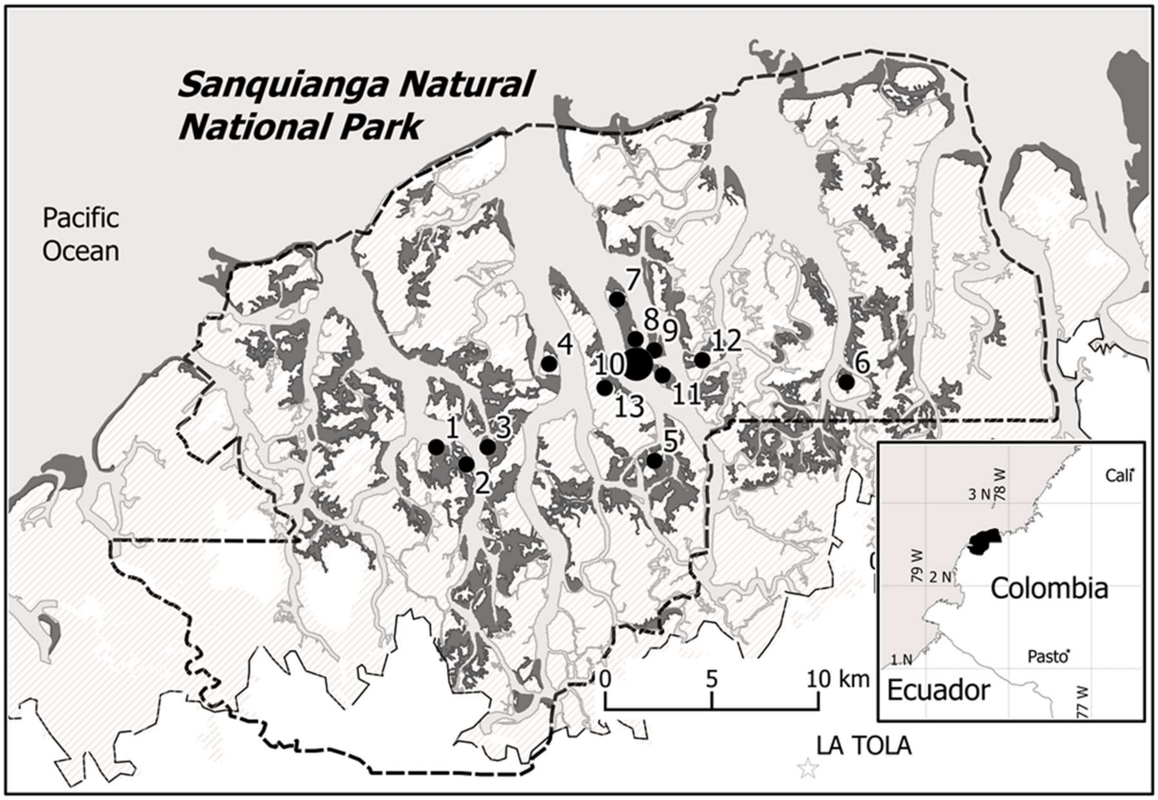


Figure 2.1. Whimbrel roosts (black dots) in Sanquianga National Park (dashed line), Colombia. The main roost is indicated by a large circle. Mudflats are shown in dark grey and mangroves in diagonal grey pattern, while emerged lands are shown in white. The mainland extends below the broken lines at the bottom of the map. (1) Isla Cocal, (2) Campo Alegre, (3) Conguero, (4) Punta Isla Grande, (5) Estero El Carmen, (6) Aguacatal, (7-13) "El Parguero" (see Appendix A for details).

In Sanquianga, as in other non-breeding locations (Skeel & Mallory. 1996), Whimbrels occupy individually-defended diurnal foraging territories (Ruiz-Guerra 2004). Those territories are widely dispersed throughout the entire delta (Anchico et al. 2015). Typically, birds arrive at their foraging territories as tide recedes after dawn and they move into adjacent mangroves, grass and beaches during diurnal high tides (Abril, 2011). On rising evening tides, they leave these territories and congregate at a small number of nocturnal roost sites (Hevia 2011). Roosts are established on mangrove islands, where Whimbrels perch on top of roots and lower branches of Red Mangrove *Rhizophora mangle*, the most common mangrove species within the delta (Abril 2011, Hevia 2011). To date, only 13 Whimbrel roost sites have been identified in the study area and up to 3500-4000 individuals, comprising 55-60% of the local population, may aggregate at a single roost site (Johnston-González et al. 2006, Abril 2011, Hevia 2011).

Many individuals thus make lengthy daily commutes of several kilometers, raising the question of why some Whimbrels in Sanquianga make daily commutes to a distant roost that are more expensive in time and energy than roosting closer to their feeding territories, as many do by day.

In this study, we tested predictions from hypotheses for nocturnal roost site choice in relation to spatial variables that can be related to the distribution of food resources, predation risk and human disturbance. If the distribution of feeding locations affects that of roosting sites, occupied Whimbrel roosts should be more centrally located relative to larger areas of feeding substrate than other potential roost sites, thereby allowing average distances to feeding territories to be shorter. On the other hand, if roost use is a strategy to reduce predation risk, the locations of occupied roosts, relative to other potential roost sites, should reflect avoidance of sources of potential predators. Finally, if human disturbance plays a role, we predict occupied roost sites to be more distant than other potential roost sites from human villages and aquatic transportation routes. In summary we expect that Whimbrels occupy roosting sites close to sources of feeding habitat and far from sources of predation risk and disturbance.

2.3. Methods

2.3.1. Study area

Sanquianga National Park lies on the estuary of the Sanquianga and the diverted Patía rivers (Parra & Ángel 2014), on the southern portion of Colombia's Pacific coast (Fig 2.1; 2.5º N, 78.3º W). The park comprises 80,000 ha of coastal habitats, including mangroves (48%), extensive mudflats (15%), and estuarine waters along four major basins. A semi-diurnal tidal regime immerses much of the area under saline/brackish waters twice daily (IDEAM, 2016). Shorebird habitat is widely distributed, with hundreds of mangrove islands and mudflat patches interspersed across thousands of kilometres of tidal channels. Forests other than mangrove, crops and human settlement are restricted to islands with lands above the tidal influence (non-flooded) and the mainland in the southern end of the Park. Together with sandy beaches, these habitats occupy only 4–6% of the park (UAESPNN, 2010). The delta lacks road access, and the shallow waters and marked tidal regime limits cargo transport by water. As a result of its inaccessibility and the designation as a National Park and Afro-Colombian collective territories

(UAESPNN, 2005), there is no large-scale industrial, urban or tourism development within the park. Human population is very sparse, averaging 8 inhabitants/km², and it is concentrated around major villages. Nevertheless, approximately 10,000 inhabitants live within the park, and a further 20,000 people live in surrounding municipalities (UAESPNN, 2005). People obtain food and materials for fuel and shelter from the park, and there are artisanal fisheries for shrimp, estuarine fishes and mangrove cockles. Medium-sized vessels and small boats for personal transport are common on the major waterways (UAESPNN, 2005).

Sanquianga NP holds one of the largest concentrations of non-breeding Whimbrels in northern South America (Wilke & Johnston-González 2010). Between 6800–8000 birds, comprising 8–10% of the continental population (Andres et al., 2012), are estimated to winter in Sanquianga (Johnston-González and Eusse-González, 2009). As elsewhere in the non-breeding range, Whimbrels establish feeding territories that are maintained throughout the non-breeding season (Skeel and Mallory, 1996). In Sanquianga these feeding territories average 2.2–2.8 ha, predominantly in mudflats (Abril, 2011), but occasionally in pasture or on sandy beaches (Ruiz-Guerra 2004, Hevia 2011).

2.3.2. Identifying roosting locations

Roost locations and the maximum number of Whimbrels recorded at each roost were pooled from Ruiz-Guerra (2004), Abril (2011), Hevia (2011), and during additional visits made by RJG between 2009 and 2014 (Appendix A). “Islerias”, the main roosting location was originally identified by Park rangers and local fishermen in 2006 and described as containing ~1000 individuals (Johnston-González et al., 2006). Later surveys revealed that more than half of Sanquianga's Whimbrels (3500-4000 individuals) often gather at this site (Hevia, 2011). A satellite-tagged individual (L. Tibbits pers. com) revealed the location of a second roost containing about 200 individuals and other small roost sites with fewer than 100 individuals were identified during winters of 2007–2008 (Abril, 2011) and 2009 and 2012-2014 (Johnston-Gonzalez pers. obs.). The largest and second largest roosts have been persistently used to date but we lack the evidence for others. All such observations were completed within two hours prior to sunset when Whimbrels leave their feeding territories and gather in flocks before approaching their roosts. For each site we made efforts to remain as close as possible to sunset and assumed the roost will be used at night. Given safety concerns, we did not attempt to remain at night. We considered a nocturnal roost, when at least 4 individuals were recorded making use of an island within this time. Using these opportunistic observations, we gather information for 13 “occupied roosts” or mangrove islands with evidence of roost use by Whimbrels, covering 70—80% of the local Whimbrel population. There is scope to find other roosts, but a complete survey of potential roost sites seemed impossible, given safety and logistical restrictions to cover >80,000 ha of mangroves within only a 2 h window before sunset. The other 209 available islands were considered “potential roosts” for which we lack evidence of Whimbrel use but were not systematically searched.

We used digital cartography at 1:100,000 (UAESPNN, 2005) and 1:500,000 (IDEAM et al., 2007) and several tools from the QGIS software (QGIS Development Team, 2015) to extract spatial attributes of occupied and potential roost sites and their surrounding habitat covers. We used the “mean coordinates tool” to calculate the centres of each mangrove island (occupied and potential) and “distance matrix tool” and “variable distance buffer” to estimate distances between them and other habitat covers using different radius or “buffers”. Below we describe those attributes in more detail.

2.3.3. Access to feeding sites and centrality

To determine whether roost location correlated with access to foraging sites, for each mangrove island (occupied and potential) we measured the proximity and amount of feeding habitat available. The Whimbrel uses sand beaches and artificial pastures within the study area, but the amount of those habitats in the Park (UAESPNN, 2010) and bird density is marginal. In comparison, mudflats represent the main feeding habitat with respect to both area of the habitat and the density of birds observed in that habitat (Abril, 2011). We used habitat maps of the study area (IDEAM *et al.* 2007, UAESPNN 2010) to identify mudflats. We overlapped and compared areas classified as mudflats with free satellite data from Google Earth and confirmed that the map accurately represented mudflats near low tide. Using these habitat maps we were able to identify all mudflats >0.5 ha at low tide within the Park and in a 35 km radius around its limits. This distance is marginally larger than the maximum daily commute reported for other shorebird species (Rehfisch *et al.* 2003, Rogers *et al.* 2006b), and is thus expected to contain all foraging areas used by Whimbrels roosting within the park. Using this threshold, we included more than 11,000 ha of mudflats within the park (Fig. 2.1) and a further ~3000 ha surrounding it. We computed (a) distance to each mudflat within a 35 km radius distance of each mangrove island and (2) accumulated area of all potential feeding sites at incremental radii from 0 to 35 km from the centre of each mangrove island.

It is likely that many birds will fly shorter distances to roosts than the maximum of 35 km, therefore, to compare feeding habitat available around occupied and potential roosts we use one additional buffer at 12 km. We consider what will be the minimum buffer around an ideal roost, on which all birds will access feeding territories. As a reference we use the population estimated on the main roost (~3000 individuals, Hevia 2011) and 2.5 ha as the average size of feeding territories in the study area (Abril, 2011). For all Whimbrels in the main roost to hold a feeding territory, ~7500 ha of mudflats will be required. This area was reached within a buffer ~12km from the centre of the main roost and was chosen to compare with other occupied and potential roosts.

We also estimated if roosts were centrally located in relation with major river basins or the entire study area. We extracted the geographic centre of each basin and of the entire study area from digital charts of the National Park, which match approximately the geography of the delta (UAESPNN, 2010). We estimated the proximity of each roost to the centre of the nearest basin and to the centre of the study area to determine if roosts were located centrally (close to the nearest basin centre) and in relation to the entire landscape (close to main centre) and compared those distances with all other potential roosts.

2.3.4. Isolation from terrestrial predators

Wintering shorebirds are prey for native and introduced terrestrial predators worldwide (Hays & Conant 2007, Geering *et al.* 2008, Colwell 2010, Aarif *et al.* 2014). Low-land forests in the study area harbour a diverse mammalian community including South American Raccoon *Procyon cancrivorus*, Ocelot *Leopardus pardalis* and Crab-eating Fox *Cerdocyon thous* (Asociación Calidris & Consejo Comunitario Esfuerzo Pescador Iscuande 2017). In addition to these medium-sized carnivores-omnivores, domestic and feral cats and dogs could potentially prey on shorebirds. We have no quantification of depredations by terrestrial predators on wintering shorebirds, but anecdotal evidence suggest that shorebirds avoid proximity of cats and dogs (Ruiz-Guerra 2004, R. Johnston-González pers.obs.). Most mangrove islands are below tidal level and unsuitable for habitation by terrestrial mammals; only the mainland in the southern border of the park and a dozen islands with sections above the tide level are likely to support terrestrial predator populations (Fig. 2.1). Using habitat maps of the study area (IDEAM *et al.* 2007, UAESPNN 2010) we identified all "non-flooded land", namely non-flooded forest, open-vegetated areas, and croplands as potential source of terrestrial predators (Ruiz-Guerra *et al.* 2011, Asociación Calidris & Consejo Comunitario Esfuerzo Pescador Iscuande 2017). We reasoned that locations farther from these sources would be less prone to incursion from terrestrial predators, as would islands with larger proportions of water surrounding them. For each island, we therefore calculated the distance to the nearest non-flooded land and to the mainland, and the proportion of mangrove vegetation versus water in a 1 km buffer around the island's centre.

2.3.5. Avoidance of human disturbance

Human disturbance (hereafter disturbance) can arise from presence and activities of humans and their vehicles or pets (Robinson & Cranswick 2003). Disturbance can affect a range of shorebird behaviours (Frid & Dill 2002), including the use of roosting sites by shorebirds (Peters & Otis 2007). Whimbrels and other large shorebirds react strongly to the presence and proximity of disturbances by initiating escape responses (Weston et al., 2012). Proximity to sources of disturbance such as car or boat traffic have been used to quantify roost habitat selection (Burger *et al.* 2007, Conklin *et al.* 2008). For each island, we measured (a) the distance from occupied and potential roost sites to the nearest village site; (b) the distance from occupied and potential roost sites to the nearest waterway used for transport; and (c) the human population density (km²) within a 1 km radius.

2.3.6. Statistical analysis

We first determined whether values of feeding, isolation and disturbance variables differed between occupied (*n* = 13) and potential roost sites (*n* = 209). In the case of feeding areas, we tested for differences at multiple distances ("buffers") between 1 and 35 km, while we used fixed buffers for other variables. Visual inspection of frequency histograms and Mann-Whitney U tests were used to examine univariate distributions, and variables with overlapping distributions between occupied and potential roost sites were considered non-informative and discarded. We then applied generalized linear models to evaluate how the presence of roost locations could be explained by a combination of remaining habitat variables. We excluded variables that had similar means and distribution in the earlier univariate tests, and as proportion of mangrove and water were highly correlated ($r = -0.60$), models included only one of these terms at a time. We evaluated the impact of linear terms because preliminary analysis found no evidence for non-linear relationships. The candidate set included three univariate models, three bivariate models, and the null model (roost site use is not explained by a location of foraging sites, proximity to predators or disturbance). We evaluated the support for the six candidate models and selected the model with lowest AIC (Akaike's Information Criterion) and a delta value < 2 below other models. All statistical analysis were carried out in R software (R Core Team, 2017a).

2.4. Results

2.4.1. Roost centrality and foraging habitat

Whimbrel nocturnal roosts occupy central locations within Sanquianga river basins, and half of them are clustered around the park's geographic centre (Fig 2.1). Occupied roosts were located on average less than half the distance (5.4 km ± 2.91 sd) from the geographic centre of the park compared with potential roost sites (11.2 km ± 4.5 sd). Distances from occupied roost to the centre of their respective basin (3.51 km ±1.67 sd) were slightly shorter, but not significantly different than for potential roost sites (5.6 ± 3.00 sd) (Table 2.1). Between 7 and 22 km radii, there is up to 30% more area of mudflats surrounding occupied roosts than potential roost sites (Fig. 2.2). In the initial 7 km and after 22 km, average cumulative areas were similar between occupied and potential roost locations (Appendix B). At 20 km, the mean distance from occupied roosts to potential feeding areas was 2.5km shorter than for potential roosting sites (Fig 2.3b). At 12 km radius, roosts have a median of mudflat area around them >10 km^2 than other locations (Fig 2.3a).

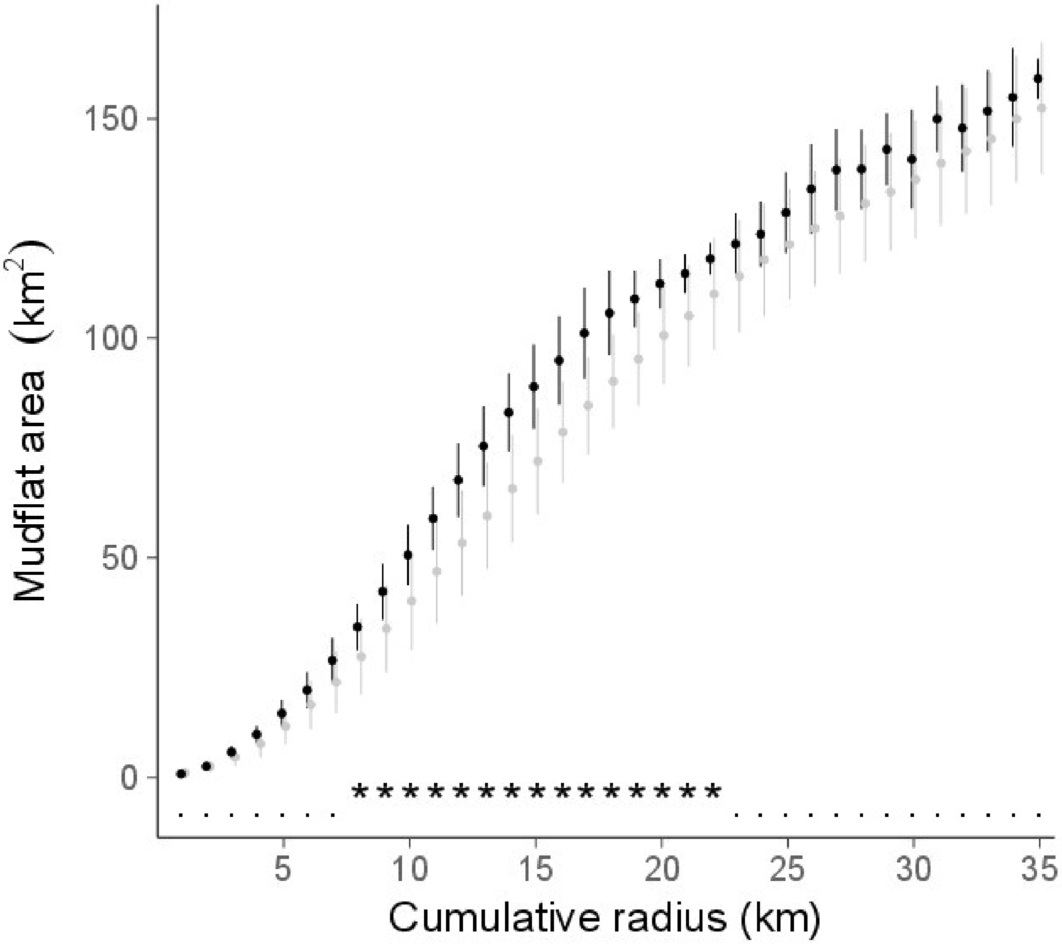


Figure 2.2. **Mudflat area (km2) accumulated on concentric 1 km buffers around occupied (black, n=13) and potential roost sites (light grey, n=209). Dots represent median values and lines the minimum and maximum values for each bin. Significant results of Wilcoxon tests at P <0.01 are indicated with asterisks (see Appendix B for detailed results).**

2.4.2. Avoiding human disturbance

The occupied Whimbrel roosts in Sanquianga did not differ from potential roost sites in terms of their average proximity to villages or human population (Table 2.1 and Fig. 2.3 d—f, Table 2.1). Distance from the main roost to the nearest village was 2.52 km, only slightly farther than smaller occupied roosts (2.12 km ± 1.26 sd) and potential roost sites (2.26 km, ± 1.15 sd). As a result, most occupied roosts and potential roost sites have no permanent inhabitants within their immediate vicinity (1 km radius from its centre). Occupied roosts were at least 1 km away from major waterways used for transportation (range 1—5.62 km), and the two largest roosts were even further away

(2.85 km), but not statistically different. These results do not support our prediction of larger distance to sources of disturbance in occupied roosts.

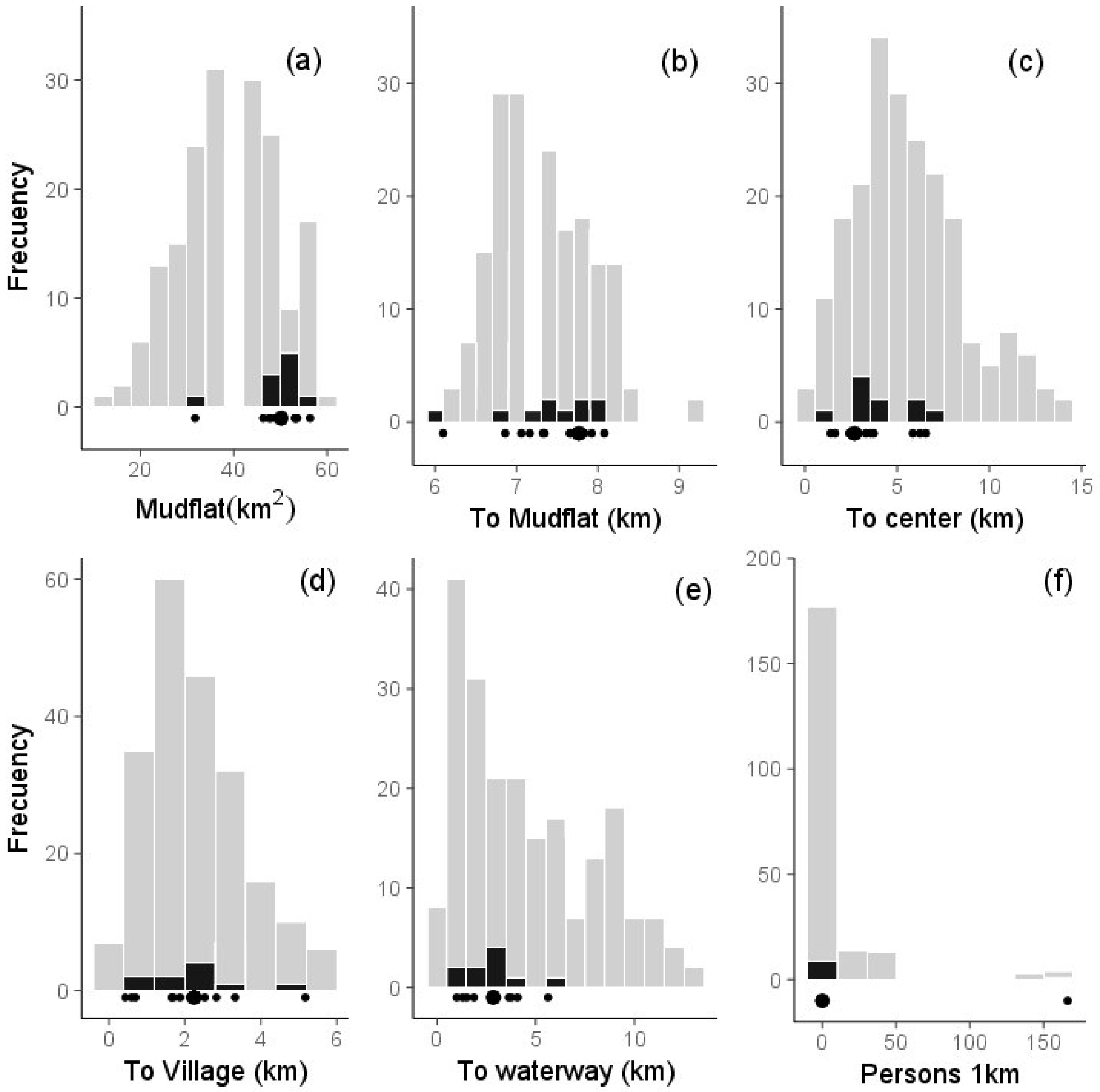


Figure 2.3. **Frequency distribution of spatial attributes associated with access to feeding areas and human disturbance on occupied (black, n = 13) and potential roost sites (grey, n = 209) for Whimbrel in Sanquianga National Park. Black dots denote occupied roosts and the larger dot indicates the main roost. The height of the bar shows the number of islands within each bin. (a) Mudflat area (km²) in 12 km buffer, (b) Average distance to mudflat (km²) in 12 km buffer, (c) distance to centre of basin (km), (d) distance to nearest village (km), (e) distance to nearest shipping route (km), (f) human population in 1km buffer (number of persons).**

Table 2.1. Habitat features of occupied Whimbrel roosts and other potential roosting sites in mangrove islands of Sanquianga National Park, Colombia

	Occupied (*n* = 13)		Potential (*n* = 209)		Mann-Whitney Test	
	Median	Min-Max	Median	Min-Max	U	*P*
GENERAL						
Island Size (ha)	57.46	4.7 – 1012.8	15.2	1.9 – 6131.4	774	0.150
Distance to centre of study area (km)	4.4	1.6 – 10.8	11.2	2.5 – 21.3	1821	< 0.001
Distance to centre of basin (km)	3.4	1.4 – 6.6	5.1	0.1 – 14.5	1434	0.060
FEEDING						
Mudflat area, 12 km buffer (km^2)	50.3	31.7 – 56.3	39.6	12.6 – 58.5	411	< 0.001
Average distance to mudflat, 12 km buffer(km)	7.5	6.1 – 8.1	7.2	6.1 – 9.2	847	0.284
DISTURBANCE						
Distance to nearest Village (km)	2.2	0.6 – 5.2	2.1	0.2 – 5.9	1074	0.946
Distance to nearest Ship Route (km)	2.9	1.0 – 5.6	3.7	0.3 – 13.1	1316.5	0.197
Human population 1km buffer (No. persons)	0.0	0 – 166	0.0	0 – 523	1122.5	0.634
ISOLATION						
% Water in 1km buffer	48.3	17.4 – 71.4	25.1	0 – 74.9	420	< 0.001
% Mangrove in 1km buffer	27.4	7.0 – 60.2	44	7.1 – 96.7	1534.5	0.017
Distance to mainland (km)	10.4	5.6 – 13.9	8.3	0.4 – 20.1	736	0.103
Distance to nearest land (km)	5.2	1.6 – 6.6	3.3	0.0 – 11.5	773	0.149

2.4.3. Isolation from terrestrial predators

Occupied roosts were at least 1.6 km from the nearest point of land, and 5 km from the mainland, located on small islands that lack emerged lands and are expected to be completely immersed by water at high tide, but those conditions were similar to those of potential roosts (Table 2.1. and Fig 2.4a—c, f). Occupied Whimbrel roosts were surrounded by more water and less mangrove forests than potential roost sites (Table 2.1, Fig. 2.4d—e). Mangrove and shallow waters are the main habitats covering the park and are negatively correlated with each other ($r = -0.60$). The main roost was at the extreme of this continuum. Amongst all mangrove islands, it had the lowest proportion of mangrove (7%) and the third highest proportion of water (71%) in a 1 km radius from its centre (Appendix C). Other occupied roosts were also among the most isolated locations (upper 10% of the distribution) and are surrounded by at least 50% of water. Size of islands of occupied roosts did not differ from the size of potential roost sites.

2.4.4. Relative importance of predictors

The generalized linear model that included potential foraging area (within 12 km radius) and the proportion of water (within a 1 km radius) was the most informative of the six models evaluated, accounting for 84% of cumulative weight of evidence, better than the next-best model by more than 4 AIC units (Table 2.2). Under this model, the odds of a mangrove island being used as a roost by Whimbrels increased 1.14 times (1.04—1.28; odds-ratio of roost vs. non-roost) for every 1 km^2 increase in the area of mudflats; and by 2.5 times (1.86—5.85) for each 1% increase in the proportion of water surrounding the islands (Table 2.3, Fig. 2.5 and 2.6). Models based on only a single variable were uninformative, and all models performed better than the null model. Model selection including models with quadratic terms, produced the same best model (analyses not shown). As explained in the methods, 12 km was selected as reference buffer, given it will contain tidal flat area for 3000 individuals, the estimated population of the main roost. Although not evaluated it is plausible that the area of tidal flats in other buffers within 7—22 km range will render similar results if used as an explanatory variable.

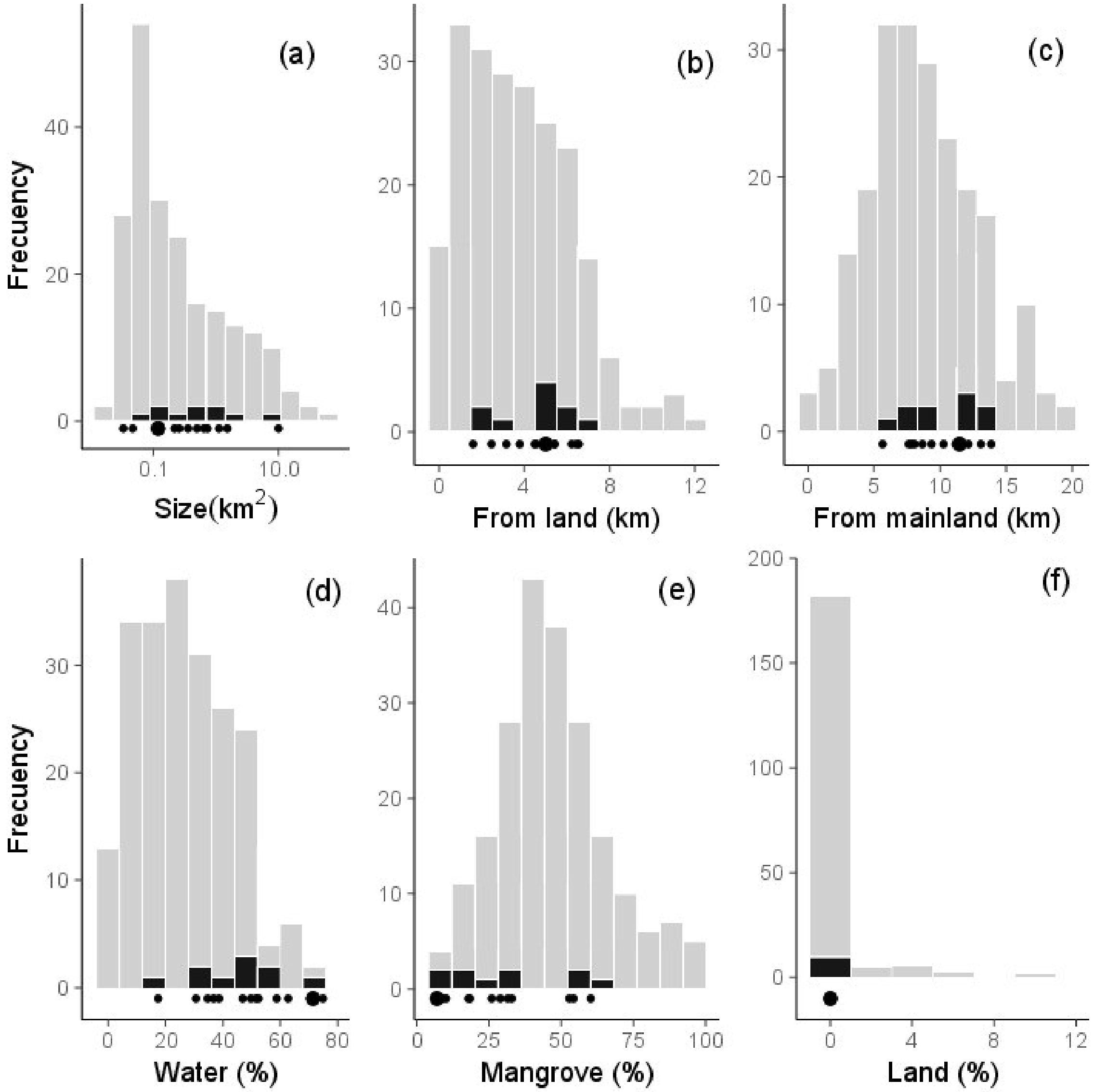


Figure 2.4. **Frequency distribution of spatial attributes associated with isolation from predators on occupied (black, n = 13) and potential roost sites (grey, n = 209) for Whimbrel in Sanquianga National Park. Black dots denote occupied roosts and the larger dot indicates the main roost. The height of the bar shows the number of islands within each bin. (a) Island size (km²), (b) distance to nearest land (km), (c) distance to mainland (km), (d) % water (e) % mangrove and (f) % land in 1 km buffer.**

Table 2.2. **Generalized linear models with binomial error distribution and logit-link function explaining the location of Whimbrel roosts in Sanquianga National Park. The model including feeding area (in 12 km radius) and % water (1 km radius) was the most parsimonious explaining the presence of Whimbrel roosts in mangrove islands.**

Model	K	AICc	Δ AICc	AIC Weight	Cumulative Weight	Log Likelihood
FeedArea12km + %water1km	3	68.13	0	0.84	0.84	-31.01
FeedArea12km + %mang1km	3	72.75	4.62	0.08	0.92	-33.32
FeedingArea12k	2	74.51	6.38	0.03	0.96	-35.23
%water1km	2	74.63	6.5	0.03	0.99	-35.29
%mang1km	2	77.57	9.44	0.01	1	-36.76
Null	1	83.56	15.44	0	1	-40.77

Table 2.3. **Parameter estimates and upper and lower limits for 95% confidence intervals for coefficients in the best model of roost site selection by Whimbrel in Sanquianga National Park**

Variable	Estimate	Lower limit	Upper limit	Z statistic	*p*
Intercept	-12.631	-18.186	-7.076	-4.456	<0.0001
Feeding Area 12 km	0.156	0.054	0.259	2.983	0.0028
% water 1 km	7.430	3.407	11.453	3.620	0.0003

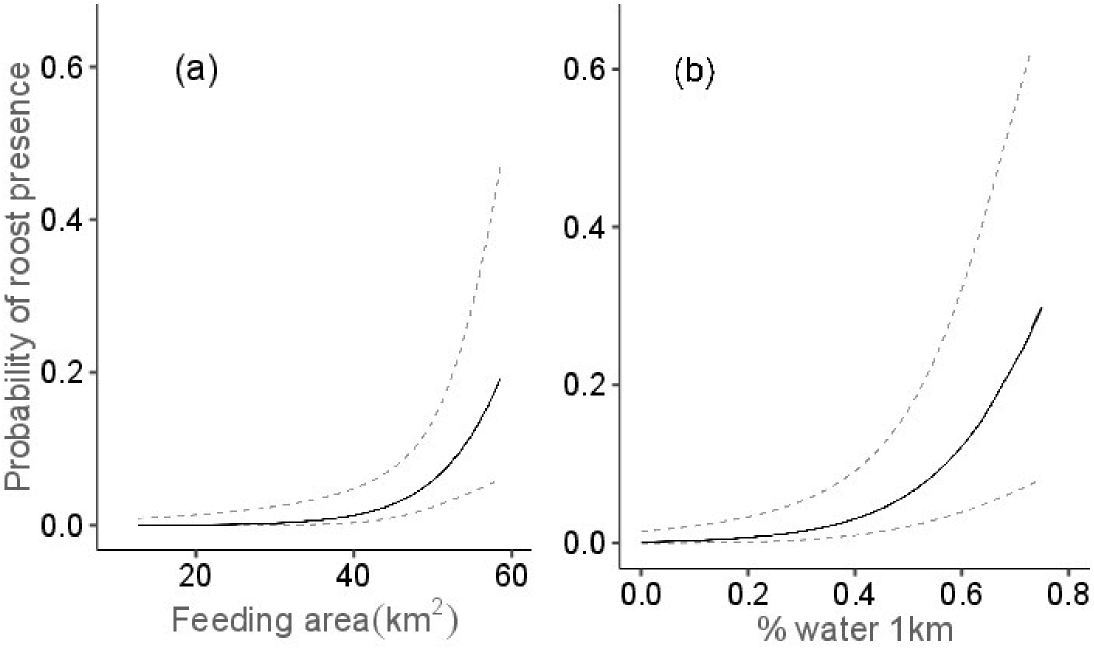


Figure 2.5. **Predicted relationships between probability of presence of a Whimbrel roost and (a) feeding area in 12 km buffer and (b) proportion of water in 1 km buffer. Dashed lines indicate the 95% confidence interval on predicted probabilities. Raw data and combined probabilities are shown in fig 2.6.**

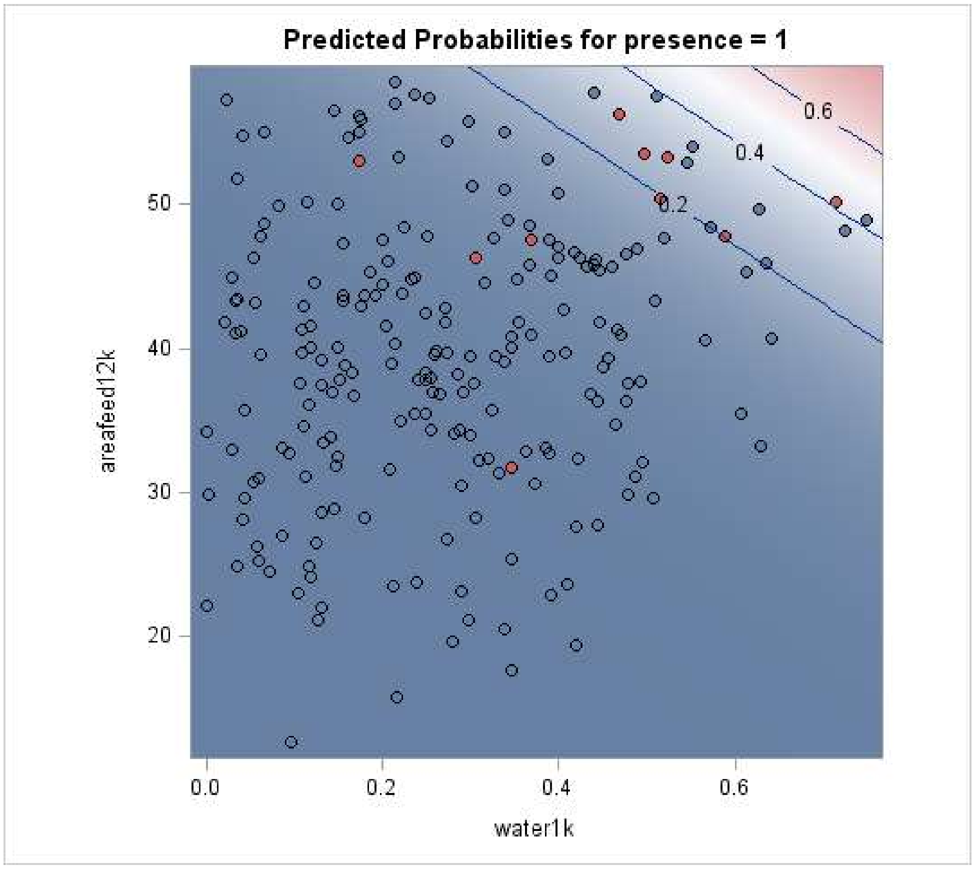


Figure 2.6. **Predicted relationships between probability of presence of a Whimbrel roost feeding area in 12 km buffer (in the Y axis) and proportion of water in 1 km buffer in the x axis. Red dots show the locations of roosts and empty dots indicate other locations. The gradient of colour shows the change in probability from low values (blue) to higher values (red). The lines show 0.2 increase in probability.**

2.5. Discussion

Despite hundreds of mangrove islands available in the study area, Whimbrel roosts were found in only a small number of them. Such roosts can gather a few dozen individuals or in a unique case, hundreds to several thousands of birds (Johnston-González *et al.* 2006, Abril 2011, Hevia 2011). Our opportunistic survey covered only a fraction of the Whimbrel population (70—80%), so there is scope for other roosts to be found. We found two strong independent predictors of Whimbrel roost location compared with other mangrove islands within the Sanquianga Delta. Roost sites were closer to potential foraging sites and more distant from potential sources of terrestrial predators. The largest roost and adjacent smaller roosts indeed occupy the most isolated island cluster in the delta. We found no evidence that roosting islands were different from other mangrove islands with respect to their distance to sources of human disturbance.

2.5.1. Foraging opportunities and patch-sitting hypothesis

We found support for our prediction that Whimbrel roost sites provide easier access to feeding areas than other islands. At intermediate distances (7—22 km), the area of mudflats available around roosts was up to 30% larger than for other mangrove islands thought to be unused (Fig. 2.2). At 12 km buffer, roosts averaged shorter distances to individual patches of mudflats (Fig 2.3a—b). Both features (larger foraging area and shorter distance to potential foraging sites) could explain why a large proportion of the local Whimbrel population aggregates in centrally located roosts. The mudflat area required for all 6800—8000 Whimbrels in the park to hold a feeding territory of ~2.5 ha is 18,500 ha. Mudflat area required for all Whimbrels estimated in the main roost (~3000 individuals, Hevia 2011) to hold a feeding territory is ~7500 ha. This area is reached at a radius of ~12km from the main roost. At a similar radius, the accumulated area of mudflats around non-roosting locations is on average 1000 ha less, which could hold about 400 fewer feeding territories. Up to 60% of the local Whimbrel population could find feeding territories within 12.5 km radii of the main roost.

Roosting in the centre of the basins with access to more and closer feeding areas could offer a common solution for a larger number of Whimbrels. Our results partially align with the proximity to foraging-patch hypothesis (Caccamise & Morrison 1988), such that roosts can be understood as the result of birds aggregating near rich sources of food, rather than or in addition to social aggregations per se. Raptors (Laura *et al.* 2013, Watts & Turrin 2017), colonial waterbirds (Sparling & Krapu 1994), corvids (Gorenzel & Salmon 1995, Sonerud *et al.* 2001) and other birds and mammals (Beauchamp, 2014) form aggregations around food-rich patches. In such cases, roosts are thought to work as “information centres” and individuals participating could alter their daily behaviour to follow successful foragers. However, Whimbrel territoriality alters the application of this hypothesis; they may occur at higher densities at richer sites, but not necessarily alter their foraging behaviour or roosting locations in response to temporal and spatial changes in resource abundance. Rather than aggregate close to richer food sources, roosting aggregations can result from multiple territorial Whimbrels choosing to roost in the vicinity of their territories (Beauchamp, 1999).

Alternative feeding habitats and differences in Whimbrel density across the delta could affect estimates of availability of feeding sites around roosts. In the first case, sand beaches and artificial pastures offer foraging opportunities for Whimbrels in Sanquianga (Ruiz-Guerra, 2004), but these habitats are scarce and harbour lower bird densities compared to mudflats (Abril 2011). Sand beaches and pastures also occupy a marginal proportion of the habitat (<2%) in relation to almost 15% of the area occupied by mudflats (UAESPNN, 2005). On the other hand, our current estimates of the availability of feeding sites assume an even distribution of Whimbrels across the study area. But broad scale surveys (Anchico *et al.* 2015) revealed that Whimbrel densities are higher towards the central-West portion of the delta. Whimbrel densities could be associated with differences in profitability of feeding territories. Thus, in addition to a larger availability of mudflats, individual patches near current roosts can harbour more birds. We do not have historic survey data, but we suspect that conditions for Whimbrels and shorebirds in general have been changed since 40 years ago when the Patía river was partially diverted into Sanquianga estuary, increasing its volume and sediment load, and doubling the size of mudflats (Restrepo & Kettner 2012, Parra & Ángel 2014). It is likely that the increase in mudflats provided conditions for redistribution of Whimbrels and could have an impact in the roost use but lacking historic survey data we cannot test this.

Roosting near feeding areas could explain Whimbrel roosting congregations in central sections of Sanquianga, but not necessarily the precise islands on which roosts are located. Other mangrove islands close to the roosts are equally or slightly more central than the ones currently used. Furthermore, if access to food were the exclusive driver, Whimbrels would roost adjacent to their territories rather than commute several kilometres to reach the central roosts. Thus, other factors besides feeding site proximity must be involved.

2.5.2. Avoidance of predators

Most of Sanquianga is under tidal influence and the surface permanently above the tide line is very restricted, offering a largely unsuitable habitat for terrestrial predators. Although roosts and other mangrove islands had similar average distances to land, no roosts were located on islands with emerged lands and all were at least 5km from the mainland. Islands used as roosts by Whimbrels lie on the tail of the distribution of proportion of water versus the proportion of mangrove within 1 km of the island. Protection from predators that could reach roost sites by traveling overland could explain this result. In our study area one extreme example is the cluster of roosts in the middle of the Sanquianga basin, placed in the most isolated locations of the delta, hosting an estimated nearly 95% of observed roosting Whimbrels. By roosting in isolated islands, Whimbrels can potentially reduce their vulnerability to terrestrial predators. This conclusion is consistent with most other studies on roosting shorebirds where they select isolated locations, and when barriers to predator movement are weak, those can result in higher shorebird predation (Hockey, 1985).

By roosting on islands surrounded by large stretches of water, Whimbrels may gain isolation from predators that could use nearby mangroves to move between islands. Whimbrels arrived at the roost, predominantly from SW and SE of the park (Hevia 2011), where both a high proportion of feeding habitat is available and individual mudflats are closer to potential sources of predators in the mainland. It is possible then that territories near mainland contribute more Whimbrels to the main roost.

The Peregrine Falcon *Falco peregrinus* and domestic cats *Felis silvestris catus* are the only confirmed predators on shorebirds in our study area (Ruiz-Guerra, 2004). For Whimbrel we have not recorded any predation events. However many shorebird predators able to take a Whimbrel are likely to occur in the vicinity of southern Colombian mangroves, including several species of diurnal raptors (Ruiz-Guerra *et al.* 2007, Calderón-leytón *et al.* 2011), owls (Chaparro-Herrera *et al.* 2015) and a diverse small- to medium-sized mammal community (Ruiz *et al.* 2011). Elsewhere, terrestrial mammals are among the main predators of shorebirds at night. For example mongooses, foxes and other mammals are the main predators of African Oystercatcher *Haematopus moquini* (Hockey, 1985). Whimbrel preference for mangroves as observed in the study area and elsewhere (Zharikov & Milton 2009) contrasts with a predominance use of open roosts found in other shorebirds (Conklin *et al.* 2008, Rehfisch *et al.* 2003, Rogers *et al.* 2006a, Piersma *et al.* 2006). Whimbrel roosting in isolated locations, including mangrove islands (Andres et al., 2007) could decrease exposure to terrestrial mammals at night.

2.5.3. Human disturbance

We expected that Whimbrel roosts be located at greater distances from sources of human disturbance, but we found no evidence of this. Whimbrel roosts were closer than other mangrove islands to waterways used for aquatic transportation and distances to villages and human density around roosts were similar to other mangroves islands. A first interpretation would be that human settlements and shipping activities are not perceived as threats by Whimbrel, but this seems unlikely, given that in other localities this species shows strong responses to both immediate and continued disturbance by humans. For example, Whimbrel show greater flight initiation distances to approaching humans than smaller shorebirds (Weston et al., 2012) and their selection of roosting sites can be negatively influenced by boat activity (Peters & Otis 2007). Therefore, we interpret our results in two parts: low levels of disturbance in our study area and a non-linear response to avoidance of disturbance. In the first case, although more populated than the average National Park, human settlements are sparse and evenly distributed in Sanquianga (UAESPNN, 2005). Nearly 90% of the mangrove islands have no human presence in their immediate proximity (1 km radius) and cargo ships use waterway routes only a few times per day. Compared with shorebird sites close to cities, touristic developments, or industrial facilities, where disturbance could limit roost availability (Danny I Rogers et al., 2006), human influence in roosts in Sanquianga is probably of low intensity.

Additionally, Whimbrels could select roosting sites not at the maximum distance from human intervention, but rather above a threshold distance. None of the roosts were located on islands containing villages on them. Similarly, most roosts were at least 1 km away from waterways, but the largest roosts were up to three times more distant. Thus, current roosts could be just far enough to avoid major sources of disturbances. We were not able to identify potential thresholds due to the linear, untransformed nature of the variables used to predict the roost location. We did not measure the direct influence of specific disturbance events, but rather the proximity to sources of such disturbances. We do not discard disturbance as an explanation for the location of Whimbrel roosts, but our analysis does not support its importance. Disturbance is regarded as one of the most important threats to populations of Numeniini (Upland sandpipers *Bartramia longicauda*, Whimbrels, curlews, godwits), however the evidence of its impacts at population level remain uncertain (Pearce-Higgins et al., 2017). While this does not appear to influence current Whimbrel roost locations in our study area, human population growth and increase of fishing activities in the park (UAESPNN, 2005) should be monitored to ensure disturbances are not impacting critical sites for roosting Whimbrels.

2.5.4. Do Whimbrels prefer more complex habitats for roosting?

Across their non-breeding range, Whimbrels use a variety of natural and artificial substrates for roosting (Andres *et al.* 2007, Colwell 2010), but in Sanquianga the use of sand spits and beaches occurs mostly diurnally at high tide (Abril 2011, Hevia 2011) or during the pre-migratory periods (RJG pers. obs.). In our study area nocturnal roosting of Whimbrel appears to be limited to mangroves. At other locations with mangroves, Whimbrels also exhibit preference for this habitat for roosting (Zharikov and Milton, 2009). If available, structurally complex habitats as mangroves could provide additional protection in comparison to open habitats, during night when visual detection of predators could be impaired.

2.5.5. On the advantage of congregating

We have assessed Whimbrel roost locations in relation to habitat features, but social aspects could play a role in the large concentration of Whimbrels at certain sites in our study area. If individuals were making completely independent decisions, we would expect some greater occupancy of other central and isolated islands than we observe. The advantage of the dilution effect (Beauchamp and Ruxton, 2008) tapers off with such large numbers. Our surveys are not sufficient to prove that additional roosts do not exist, but our known roosts account for a high proportion of local feeding population (70—80%) choosing to roost in single or a few islands. To the extent that true social factors contribute to roost formation, they would likely result in the magnification of other effects determining roost location.

2.6. Conclusion

We contrasted the spatial features of known Whimbrel roosts with all other potential locations available in mangrove islands of Sanquianga National Park. The location of current roosts was best explained by a combination of access to feeding resources and isolation from potential terrestrial predators. Explanations based on the avoidance of disturbances were not supported by our data. Roosts are situated in central locations, with access to larger areas of mudflats and within shorter distances to individual feeding patches. Those roosts were also located on some of the most inaccessible islands in the delta, surrounded by large extensions of water and isolated from other mangroves and non-flooded lands. Whimbrels may perceive these islands as less vulnerable to incursion from terrestrial predators than mangroves closer to their feeding territories. Whimbrels may use a simple rule of thumb to reduce predation risk at night: stay away from land that might be used by terrestrial or aerial predators. Current locations provide safe sites while maintaining feeding opportunities within short commuting distances for a larger number of territorial birds that otherwise would use other more peripheral locations.

Chapter 3.

Escape performance and antipredator behaviour of shorebirds during the non-breeding period in southern Colombia

3.1. Abstract

Body mass and wing load affect take-off performance and hence the ability of shorebirds to escape potential predators. During migratory periods, when they carry fat stores, shorebirds should invest heavily in vigilance, escape performance, or avoid dangerous sites entirely. Such anti-predator behaviour might be less important during non-migratory periods, but this has not been tested broadly, and in general we know little about the escape performance of shorebirds. I estimated the investment in antipredator behaviour in shorebird species with differences in escape ability. I captured and obtained morphometrics of 1059 birds, measured their wing loading (N = 450) and video recorded (N = 300). In addition, I obtained observations of vigilance time (N = 200, 12 species) and flight distance in response to an approaching human (N = 153, 13 species). I expected that shorebird species with lower escape abilities (higher wing load, lower take-off speed) should invest more time in vigilance and be more prone to early escape responses. As expected, take-off speed decreased with an increase in wing loading. Small species were faster than medium-sized shorebirds. Larger birds invested more time in vigilance and fled earlier.For the species measured (small and medium but not large), early response and vigilance are more strongly related to wing loading than with size *per se*. Species with slower take-offs compensated by investing more time in antipredator responses. The results from this study could be used to test if differences in escape performance produce different patterns of habitat selection in shorebirds, for example to avoid dangerous sites in proximity to vegetation.

3.2. Introduction

Escaping from a predator has costs in the form of energy expenditure and lost foraging opportunity (van den Hout et al., 2009). Therefore, it is expected that animals do not necessarily flee from an approaching predator at first detection; rather, they should assess the risk of each situation and delay escape until the fitness benefits (probability of successful escape) exceed the costs (Ydenberg and Dill, 1986). Animal morphology influences the ability and decision to escape predators (Cooper and Frederick, 2007). The risk of predation therefore has two components, namely the intrinsic 'danger' of the habitat, and the animal's intrinsic 'vulnerability' (Lank and Ydenberg, 2003). Animals seeking to maximize survival should combine relevant environmental information (e.g. complexity of predators) with information about their own state and ability to escape (Lima and Dill, 1989). Deciding where and when to forage or deciding how much time to spend in vigilance are the first lines of defense of animals looking to manage "danger". Once a predator is detected, animals must then decide if and how to escape (Lima and Dill, 1989).

Migration exerts strong selection in many bird taxa, and not surprisingly much study of the determinants of wing morphology and its effects on flight performance have focused on this context (Alerstam et al., 2003). For example, migration distance is a driver of wing shape (Burns, 2013; Minias et al., 2015; O'Hara et al., 2005). But escaping predators involves contrasting selection pressures on the evolution of wings and morphology to those posed by migration (Lockwood et al., 1998). These opposing pressures can result in divergent morphology within single species (Minias et al., 2013) and entire clades (Minias et al., 2015). Wing morphology, e.g. wing area (wing mass/wing area) and aspect ratio (wing length/ wing area) could be used to predict the differential abilities of bird species and sexes to escape predators (Burns and Ydenberg, 2002).

A more direct measure of escape ability, take-off flight, has been used to investigate escape in birds, particularly the critical initial moments of the response to simulated predator attacks (Nebel and Ydenberg, 2005; Tobalske et al., 2004; Tobalske and Dial, 2000). For example, in the Phasianidae, which use flight to escape predators, body mass influenced the speed of take-off (Tobalske and Dial, 2000): larger species are slower and use different take-off maneuvers. In hummingbirds, take-off flights motivated by escape are faster and involve different roles of leg thrust and wingbeat (Tobalske et al., 2004). Burns and Ydenberg (2002) related wing morphology with escape ability in two sandpiper species by using wing load, correlating wing area and body mass with escape performance in a sample of wild-caught migrants. Least sandpipers are faster than western sandpipers, and within species, sexes show different take-off angles. In another study differential distribution patterns of Western Sandpiper were explained by segregation of heavier birds (mostly females) towards safer sites, demonstrating a link between wing shape, the ability to escape predators and ultimately the use of stopover sites (Nebel and Ydenberg, 2005). This pattern of segregation linked to escape performance was found consistently both within and across latitudes, explaining the cline in sexual segregation of Western Sandpipers (Nebel et al., 2002) and potentially other migratory birds.

In addition to direct measurement of escape performance, a complementary tool to assess anti-predator tactics of animals is the flight initiation distance - FID (Cooper and Frederick, 2007). In FID experiments, an animal is approached in a standardized way by a simulated predator, usually a human or a model, until a reaction is shown, either the detection of the “approaching predator” or actually fleeing (Blumstein et al., 2015). Both of those experimental approaches (take off flights, FID) assume that a startling stimuli or disturbance caused by human proximity causes responses similar to those of a real predator (Frid and Dill, 2002). Although the response on these experimental approaches could be weaker than that of real attacks (Hope et al., 2014), they provide a standardized and quantified index of escape responses.

Here I investigate the allometry of escape performance and flight response in a community of non-breeding shorebirds. Specifically, I use take-off flights and flight initiation distances to assess shorebirds’ response to predator attacks in relation to intrinsic differences in body size and morphology. My objectives were three-fold. First, I determined the intra and interspecific allometry of wing load (g/cm^2) and wing-aspect ratio (cm^2/cm) in relation to their components: body mass (g), wing-area (cm^2) and wing length (cm). Second, I explored the effect of wing loading and wing aspect (rounded/pointed) on escape performance, measured as take-off speed (m/s) from video-recorded take-off flights, within and between species of shorebirds. Finally, I set up experiments of flight initiation distance to compare flight responses of species with differences in escape performance. I made three predictions: (1) shorebirds with higher mass would have heavier wing loading, both within and between species; (2) the ability to escape a predator would decrease with wing loading, and with a change in wing aspect ratio from rounded to pointed, both within and between species; (3) species with slower escape responses, and those with higher vulnerability (tactile as opposed to visual foragers) would show greater antipredator investment.

3.3. Methods

3.3.1. Capture and measurements

I captured 1059 individuals from 13 shorebird species on the delta of the Iscuande River, in south-west Colombia. Captures were made November–February of 2013—2014 and 2014—2015, with the aim of limiting observations to birds in the non-breeding period. Birds were held in mesh cages while they were processed. Standard morphological measurements were taken, including wing chord (cm), tarsus length (cm), bill size (cm) and mass (g). In addition I used a wing board to obtain wing areas from photographs of the extended wing within a natural range of movement, similar to the wing during flight (Burns and Ydenberg, 2002). The board fit small to medium sized birds (*Calidris, Charadrius, Arenaria* Spp.) but not larger birds. For the latter, I used the back of the board with the wing extended at a similar angle as that for small shorebirds. I analyzed the pictures using ImageJ software (Ferreira and Rasband, 2012) to obtain wing area (cm^2). Wing length was divided by wing area to obtain a modified version of wing aspect ratio (Vanhooydonck et al., 2009) and mass was divided by wing area to obtain a modified version of wing load (Burns and Ydenberg, 2002).

3.3.2. Take-off flights

Following the methods of Burns & Ydenberg (2002) I released each bird in front of a fabric screen 1.5 m in height by 3 m long, with a 10 cm grid drawn on it. The bird was allowed to take-off from a plastic platform ~20cm above ground, where it was previously keep covered for 20 seconds with a mesh cage. I recorded the take-off flight of the birds using a video camera (30 fps). The screen was aligned perpendicular to the wind to minimize wind effects. Measures of birds that ran, did not fly, or had erratic flight paths were discarded. I used Kinovea video-analysis software to track the movement of a focal point (the eye) and extracted the vertical and horizontal distances travelled at each time-frame (= 0.033 s) during the flight. From these data I calculated the take-off angle, and the vertical and horizontal speeds (cm/s), as well as the mean speed during the early (0–0.1s), middle (0.1–0.2 s) and late (0.2–0.3 s) portions of the take-off flight.

3.3.3. Flight initiation distance

Flight initiation distance experiments were carried out January 25–February 6, 2015, on the estuary of the Iscuande River in southern Colombia. The area experiences a semidiurnal tidal cycle, with tidal heights varying by up to 4.6 m (IDEAM, 2016). To maximize encounters with actively foraging birds, the observation period was restricted to ebbing tides (1–3h after high tide) and all observations were completed between 0700–1100h, local time. A trial proceeded as follows: one observer (the ‘predator’) was positioned ~ 80m distance from a focal bird (the ‘prey’), and allowed ~30s for the prey to detect the predator before commencing to approach the prey at a constant walking speed of 1 m/s, using a direct angle of approach (Blumstein et al., 2015). The observer approached until the bird fled, either by walking/running or flying. The observer marked their position with a GPS and continued the approach until the prey’s initial position was reached and marked with GPS. A second observer recorded the time and distance at which the bird fled (the ‘flight initiation distance’, or FID), flock size (single, 2—10 individuals, and more than 10 individuals) and distance to the nearest shorebird of any species (<1m, 1—10m, >10m). The locations were geo-referenced and a map used to measure distance to nearest vegetation cover (unless less than 50m, in which case we estimated this distance directly in the field). I expected FID to be greater (i.e. birds more apprehensive) for smaller groups and with closer proximity to cover.

3.3.4. Analysis

I modelled the allometric relationship of body mass with morphology (length, area and aspect ratio) and wing load (g/cm^2). I log$_{10}$-transformed body mass to provide a more appropriate scale to represent the range of variation from less than 20g to up to 250g. Log$_{10}$ is a common transformation aiding in comparing coefficients across species and usually providing a better fit than non-linear relationships (Bigman et al., 2018). To allow a meaningful comparison of body-mass across species, I choose the value of 50g to represent the mid-point of body mass of the shorebirds in the study area and centered all mass data by subtracting log$_{10}$ of 50g. This value is close to the median body mass of species in the dataset (49.1g, for the Wilson’s Plover) and provides a standardized intercept for comparison across species.

To explore the effect of wing load and wing aspect on escape performance, I fitted a generalized linear mixed model with wing load and wing aspect as predictors and take-off speed as response, allowing variation of the intercept and slope within species. I repeated the analysis with a log-transformed version of both predictors and response and compared the results. Finally, to assess the strength between escape response and performance across species, I fit a linear regression between the mean FID and the mean take-off speed per species.

3.4. Results

I measured the morphometry and mass of 1051 (of 1059 captured) shorebirds of 12 species (Table 1). The wing area was measured from pictures of 720 individuals, from all 12 species. I video-recorded and estimated take-off flight characteristics of 384 individuals of nine species. The body mass of shorebird species ranged from less than 20 g in Least Sandpipers, to 160 g in Black-Bellied Plovers and Greater Yellowlegs. Wing loading ranged from less than 0.5 g/cm^2 in Least Sandpipers up to nearly 2.5 g/cm^2 in Red Knots.

3.4.1. Allometry of wing morphology: length and area

Wing area of 13 shorebird species ranged from 40.91 cm^2 on Least Sandpipers up to 229.5 cm^2 on Willets, over a mean wing length ranging from 88.73–209 cm and body mass range of 17.4–254 g for the same species, respectively (Table 3.1). Across species, body mass was positively correlated and explained a large percentage of the variation of wing length (R^2_{adj} =98%, p<.001001) and wing area (R^2_{adj} =0.94%, p=<.001,001Table 3.2). Several shorebird species have wing lengths larger than expected by interspecific linear relationship with their body mass (Fig 3.1a), including Black-Bellied Plover, Greater Yellowlegs, Red Knot, Sanderling and Semipalmated Plover. Species with lower residual wing length include four sandpipers (Least, Western, Semipalmated and Spotted), and the Willet. This is inverse to the pattern obtained for wing area (Fig. 3.1b). These same sandpipers and the Willet (with shorter wings for their size) have larger wing areas than expected from a linear relationship with the mean mass. In contrast, some, but not all shorebirds with longer wings have lower mean wing areas than expected from a linear relationship against mean body size (Ruddy

Turnstone, Black- Bellied Plover and Greater Yellowlegs). Within species, there was large variability in the intercepts and slopes of the linear relationships of wing length (Fig 3.2a) and wing area (Fig 3.2b) with body mass. Larger species have steeper allometric relationships between wing length and mass (Fig 3.3a), and between wing area and mass (Fig 3.3b). Overall, I found: (1) strong positive relationships between changes in body mass and wing length and wing area across shorebird species, (2) species mean response deviated in both directions, with shorter and longer wings and larger and smaller wing areas than expected by size, and (3) larger shorebirds had steeper relationships, with the increases in mass correlating with larger increases in wing length and wing area.

Table 3.1. Wing lengths, wing areas and masses of thirteen shorebird species in southern Colombia, arranged by mean mass (species codes in Table 1.1)

	Mass (g)			**Wing length (cm)**			**Wing area (cm²)**		
Species	N	Mean	sd	N	mean	sd	N	mean	sd
LESA	15	17.4	1.53	15	88.73	4.45	11	40.91	2.82
SESA	280	20.76	1.73	280	94.82	2.72	159	40.77	3.46
WESA	404	23.26	1.78	404	98.3	2.5	340	42.05	4.32
SPSA	57	32.02	2.47	57	100.4	4.15	55	48.09	5.48
SEPL	90	35.35	2.57	90	120.6	3.26	7	55.17	1.82
SAND	5	44.54	4.36	5	124.8	2.28	3	54.29	1.55
WIPL	32	49.91	3.3	32	117.25	4.2	18	56.17	3.12
RUTU	6	88.55	7.46	6	147.83	6.31	4	77.39	5.81
SBDO	54	99.21	5.95	54	148.44	4.26	48	88.5	5.84
REKN	3	103.47	7.71	3	167.67	2.89	3	95.94	7.71
BBPL	1	160		1	191		1	109.01	
GRYE	3	163.33	5.77	3	196	3.61	3	122.35	25.58
WILL	3	254	19.29	3	209	7.81	2	229.5	17.68

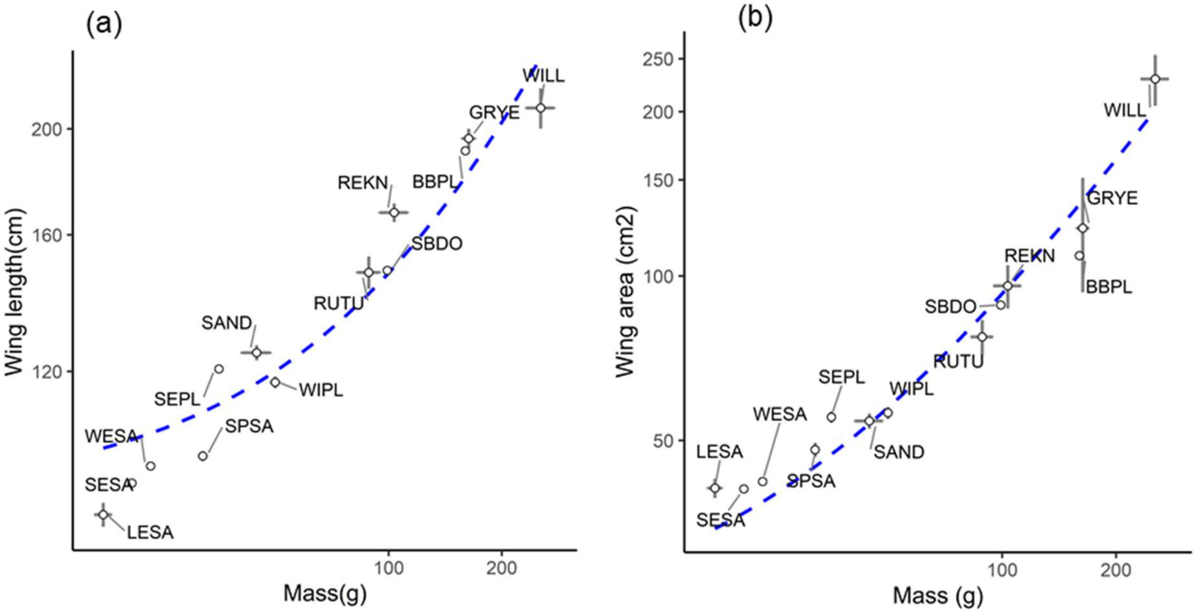


Figure 3.1. **Allometric relationship of mean wing length (a) and mean wing area (b) against $\log_{10}$ mean mass of thirteen shorebird species. Both axes are displayed in a $\log_{10}$ scale to emphasize the slightly different slope of wing length and wing area for small sandpipers (<100 g) comparedp to medium (100—200 g) and large (>200 g).**

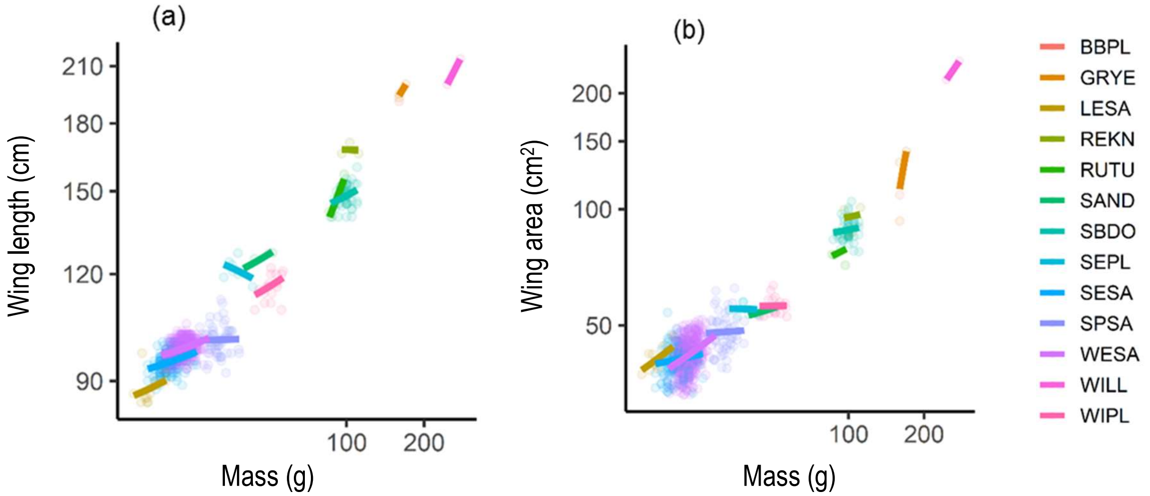


Figure 3.2. **Model predictions from linear models of wing length (cm) and wing area (cm^2), with body mass (g) of thirteen species of shorebirds. Each colour line and dots represent the estimated relationship and data for thirteen species. Axes are displyed in $\log_{10}$ scale.**

Table 3.2. **Overall fit, intercept and slope of allometric relationships of wing length (cm), wing area (cm^2), wing aspect (cm^{-1}), and wing load with log of body mass (g), fromf linear models including interaction terms with species. Significant terms (*p*<0.5 are in bold).**

Parameter	Length	Area	Aspect	Load
Fits				
*R*2	0.98	0.94	0.51	0.92
*R*2 *adj*	0.98	0.94	0.49	0.92
p-value	**<.0001**	**<.0001**	**<.0001**	**<.0001**
F-statistic	1067.68	442.97	26.94	304.06
Intercept				
estimate	122.26	108.29	0.57	-1.42
se	31.77	48.97	2.46	0.65
CI-Upper	184.65	204.45	5.39	-0.15
CI-Low	59.86	12.14	-4.26	-2.69
p-value	**<.0001**	**0.027**	**0.818**	**0.028**
F-statistic	3.85	2.21	0.23	-2.2
Slope				
estimate	0.43	0	0.01	0.02
se	0.2	0.3	0.02	0
CI-Upper	0.82	0.6	0.04	0.03
CI-Low	0.04	-0.59	-0.02	0.01
p-value	**0.030**	0.988	0.628	**<0.0001**
F-statistic	2.17	0.01	0.48	4.49

3.4.2. Escape speed. wing loading and aspect ratio

Wing load ranged from 0.42 g/cm^2 in the Least Sandpiper up to 1.47 g/cm^2 in the Black-Bellied Plover (Table 3.3). Across species, the increase in mass explained a large proportion of the increase in wing load (R^2_{adj} = 92%, p < 0.00010001). Several species have either lower or higher wing loads that will be expected for their mass (Fig. 3.3) Small shorebird species have longer wings (Table 3.3, fig. 3.2) ranging from a mean aspect ratio of 2.6 (sd = 0.17 cm/cm^2) in the Least Sandpiper to 0.9 (sd = 0.03) in the Willet. Across species body mass explained approximately half of the proportion of the variance in aspect ratio (R^2_{adj} = 49%, p < 0.00010001).

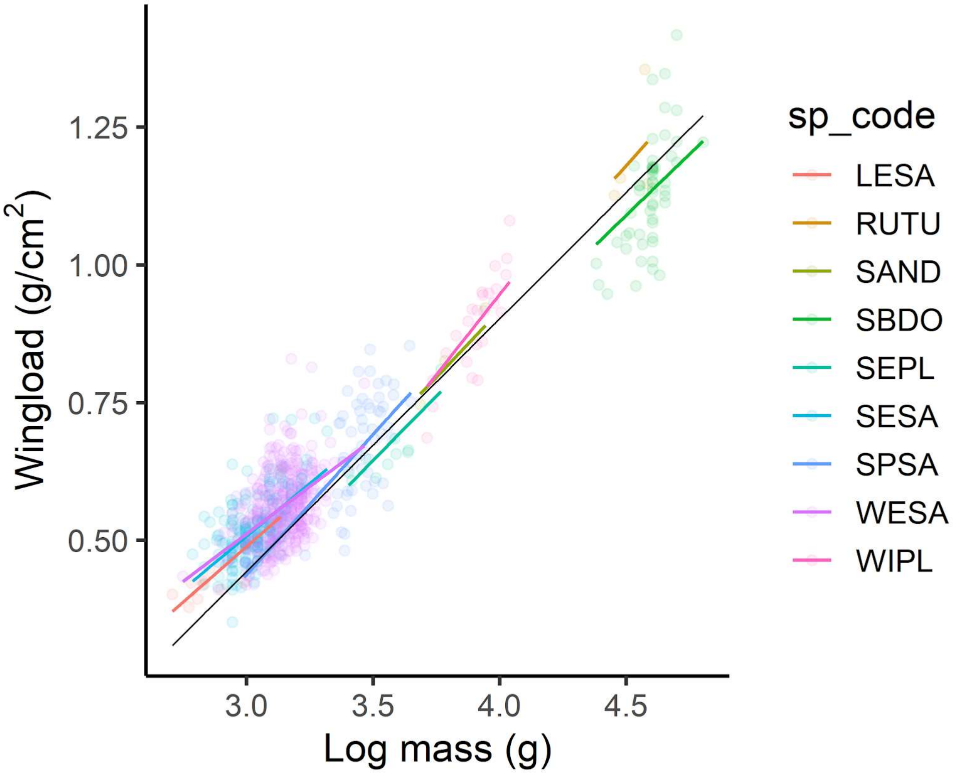


Figure 3.3. **Model predictions from linear models of wing load (g/cm^2) vs. Log of the mass (g) in nine species of shorebirds. Each colour line and dots represent one estimated relationship and data, for each species. Black line show the overall ("mean") relationship.**

Average take off speed of shorebirds in the study area ranged from 1.49 m/sec in Short-Billed Dowitcher up to 3.26 m/sec in Wilson's Plover (table 3.2.). Overall medium size shorebirds tend to have lower take off speeds, but several species have faster (Wilson's Plover, Ruddy Turnstone) or slower (Sanderling, Short-Billed Dowitcher) than expected by their wing load (Fig.3.3). Within species wing load was a better predictor of take-off speed than aspect ratio, but overall these relationships were weak. There was no support for a linear relationship between average wing load (R^2_{adj} =0.127%, p<.167) and take off speed or average wing aspect (R^2_{adj} =0.102%, p<.192) and take off speed across species (table 3.4). Is important to notice than three species lack information on take-off speed (Black-bellied Plover, Greater yellowlegs and Willet and therefore were not included on this analysis. Four species have samples of 2 or 1 individuals for take-off speed were retained (Sanderling, Wilson's Plover, Ruddy Turnstone, Red Knot).

Table 3.3. Wing load, wing aspect ratio and take-off speed of thirteen shorebird species in southern Colombia, arranged by mean mass.

Species	Wing load (g/cm^2)			Wing aspect (cm^2/cm)			Take Off Speed (cm/sec)		
	N	mean	sd	N	mean	sd	N	mean	sd
LESA	11	0.42	0.03	11	2.16	0.17	8	3.15	1.03
SESA	159	0.51	0.06	159	2.34	0.19	144	2.75	0.7
WESA	340	0.56	0.06	340	2.36	0.25	135	2.6	0.69
SPSA	55	0.67	0.09	55	2.11	0.22	13	2.92	0.76
SEPL	7	0.67	0.06	7	2.2	0.08	33	2.63	0.86
SAND	3	0.83	0.09	3	2.29	0.05	1	1.9	
WIPL	18	0.91	0.08	18	2.08	0.13	2	3.26	1
RUTU	4	1.2	0.11	4	1.91	0.14	2	2.88	0.35
SBDO	48	1.13	0.09	48	1.68	0.11	14	1.49	0.85
REKN	3	1.08	0.11	3	1.76	0.18	1	1.95	
BBPL	1	1.47		1	1.75				
GRYE	3	1.38	0.29	3	1.65	0.36			
WILL	2	1.14	0	2	0.9	0.03			

Table 3.4. Overall fit, Intercept and slope for relationship of take-off speed against wing load and wing aspect (cm^{-1}) across species. Residual degrees of freedom (df.res), negative log-likelihood (-LL), deviance (Dev), adjusted R^2 (Adj R^2) and t-statistic (*t*). Significant terms (p<0.001) are in bold.

TOS~	**df.res**	**-LL**	**AIC**	**Dev**	**R^2_{adj}**	**t**
Wing Load	8	-7.007	20.014	2.377	0.127	2.311
Wing Aspect	8	-7.147	20.294	2.445	0.102	2.026
Intercept	estimate	se	t	p		
Wing Load	3.355	0.554	6.045	**<0.001**		
Wing Aspect	0.233	1.638	0.142	0.890		
Slope	estimate	se	*t*	*p*		
Wing Load	-1.005	0.661	-1.520	0.166		
Wing Aspect	1.110	0.780	1.423	0.192		

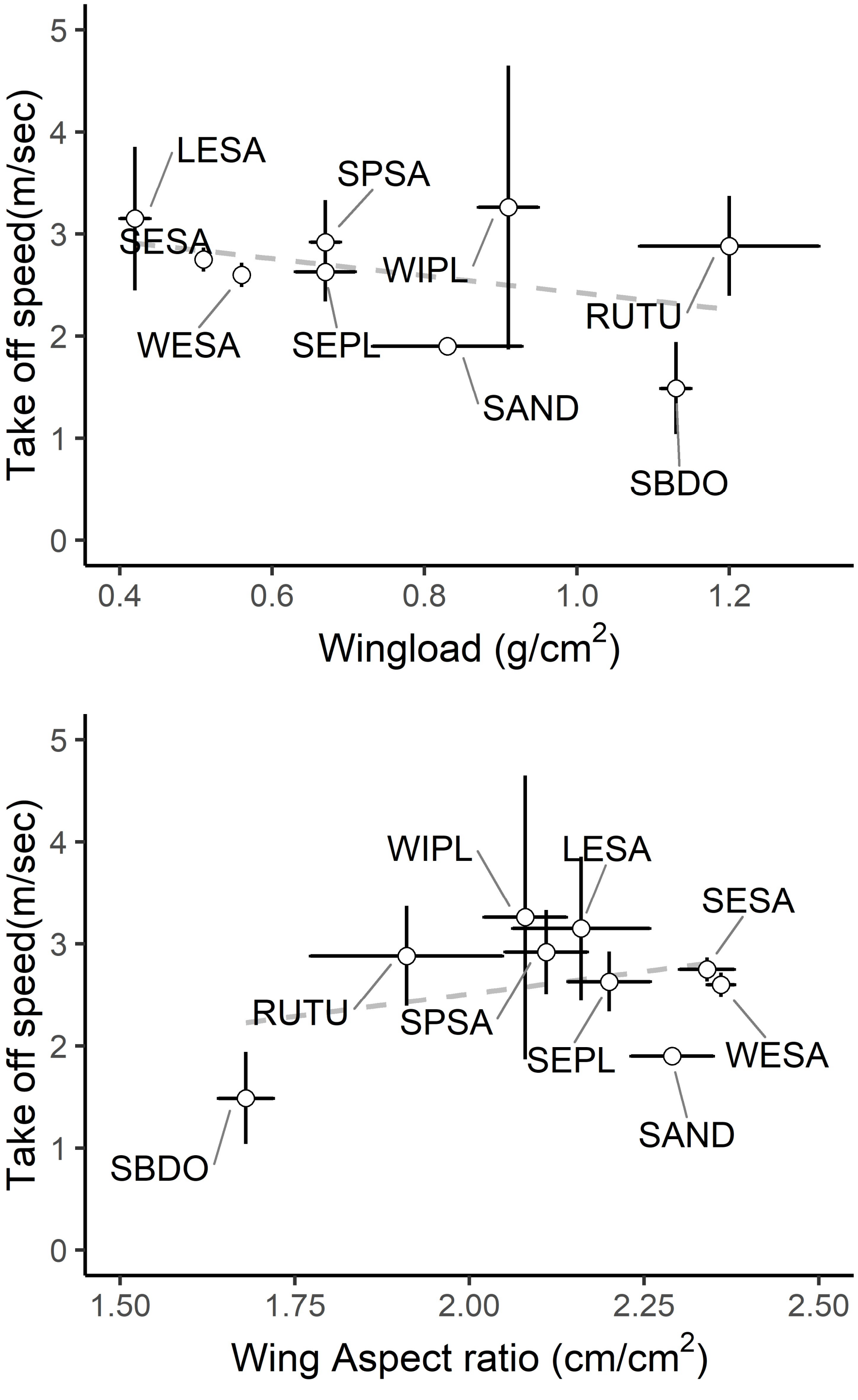


Figure 3.4. **Mean take-off speed (m/sec) and wing load (g/cm2) and aspect ratio of nine shorebird species. Dots are mean values and bars are 95% confidence intervals. Dashed lines show the mean relationship (in both cases nmon-significative).**

3.4.3. Escape speed and FID

I recorded 148 FID experiments involving 15 shorebird species (Table 1). Average flight initiation distance ranges from less than 10 m in the Least Sandpiper (*Calidris minutilla*) to 50m in American Oystercatcher (Fig 3.5). The intraspecific variation in FID within species was large (Table 3.6, Fig 3.5) and hugely overlapped between species. Take off speed had a poor explanatory power of FID ($R^2_{adj} = 0.185$), although the slope of this relationship had the expected direction, it wasn't significant (-7.487 ± 4.289, $p = 0.119$). But the relationship between wing load and FID occurred in the predicted direction, with mean FID increasing with increase in mean wing load (slope= 14.378 ± 2.712, $p < 0.0001$) and strong explanatory power ($R^2_{adj} = 0.731$). Shorebird species with higher wing loads reacted stronger to simulated predator attacks, the mean on FID increased 14 m ± 2.7 for each g/cm^2 of increase in mean wing load.

Table 3.5. Flight initiation distance (Mean and standard error in m) of 15 species of shorebirds in southern Colombia organized from small to larger body mass (g).

SPECIES	N	FID (m)	
		mean	se
Least Sandpiper	14	8.6	0.9
Semipalmated Sandpiper	8	14.4	2.6
Western Sandpiper	33	14.7	1.4
Spotted Sandpiper	4	20.3	5.5
Semipalmated Plover	20	18.4	1.7
Wilson's Plover	13	17.7	1.1
Sanderling	10	23.3	3.2
Short Billed Dowitcher	9	19.3	5.4
Ruddy Turnstone	14	18.1	2
Red Knot	1	40	
Black Bellied Plover	1	38	
Willet	9	18.6	5
Marbled Godwit	1	30	
Whimbrel	10	26.4	4.8
American Oystercatcher	1	50	

Table 3.6. Overall fit, Intercept and slope of relationships of mean FID against mean take-off speed and mean wingwing load. Residual degrees of freedom (df.res), negative log-likelihood (-LL), deviance (Dev), adjusted R2 (Adj R2) and t-statistic (t). Significant terms ($p < 0.0505$) are in bold.

FID ~	**df.res**	**-LL**	**AIC**	**Dev**	**R^2_{adj}**	**t**
Take-Off Speed	8	-33.221	72.441	449.822	0.185	3.046
Wing load	9	-32.266	70.532	227.375	0.731	28.107

Intercept	estimate	se	t	p
Take-Off Speed	38.466	11.209	3.43	**0.008**
Wing load	6.860	3.074	2.23	0.053

Slope	estimate	se	t	p
Take-Off Speed	-7.487	4.289	-1.745	0.119
Wing load	14.378	2.712	5.302	**<0.001**

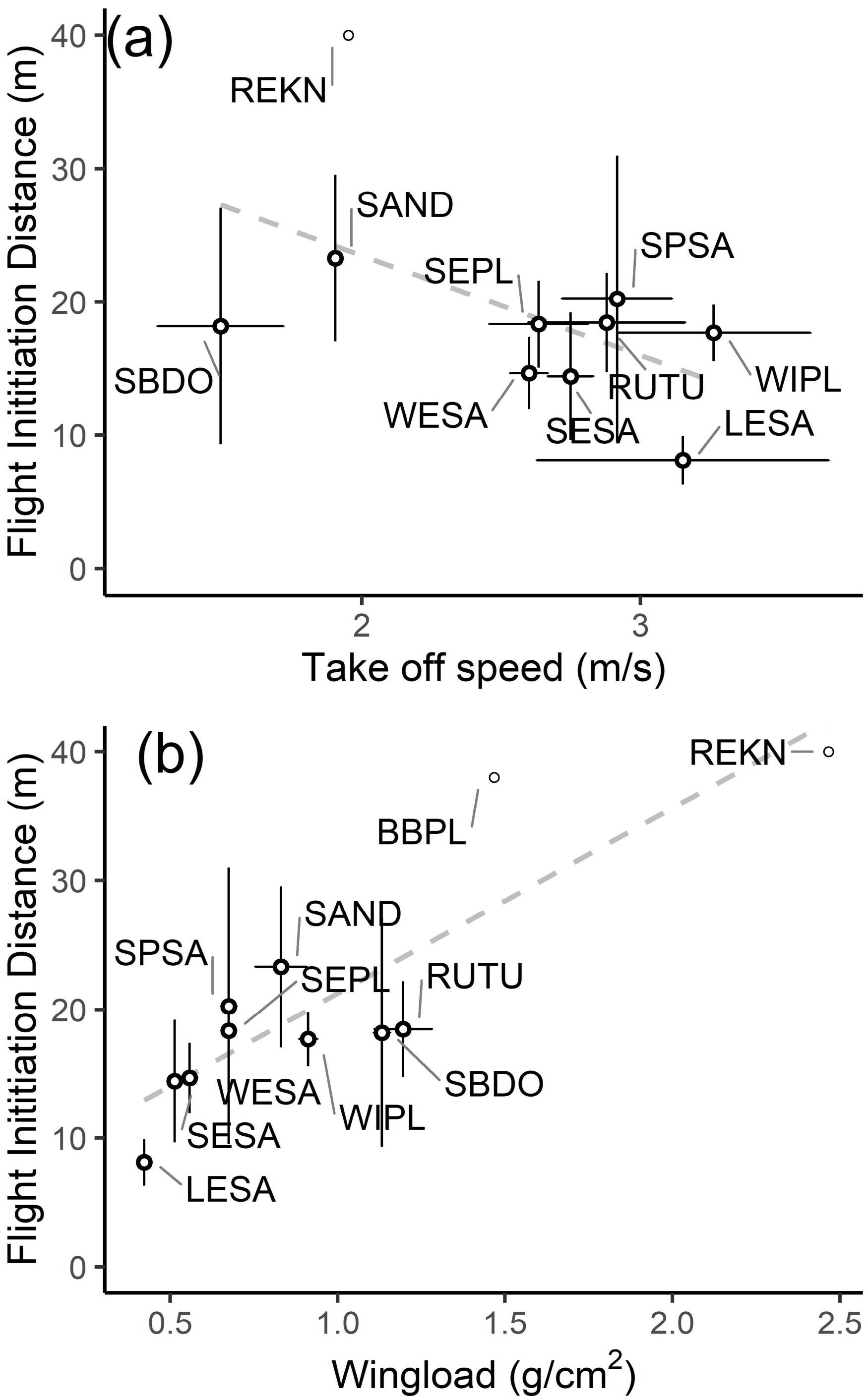


Figure 3.5. **Antipredator response and escape performance. Relationship between flight initiation distance-FID with Take-off Speed ((TOS) (a) and Wing load -WL (b). Circles indicate means and each error bar indicates 95% CI for FID, TOS and WL. Grey line shows the fitted linear relationship. Black-bellied Plover lack take-off speed measurements, and so is included only in (b).in (b)**

3.5. Discussion

Animals can control certain components of their “predation risk”. An animal’s assessment of risk should influence the decision to escape, and this assessment should include the danger, a property of the environment and the vulnerability, inherent to the animal, that is affected by its morphology and body condition (Lank and Ydenberg, 2003). I found strong support for an allometric relationship in the escape performance of non-breeding shorebird species. As expected, wing load increased with body mass, resulting in larger birds carrying heavier wing loads, both within and between species, although the magnitude of this relationship was highly variable within species. Overall, species with heavier wing load (e.g. Short-billed Dowitcher) have slower take-off speeds than lighter shorebirds, as predicted. However, there was no evidence for a relationship across species; increased wing loads do not strongly result in decreased take-off speeds. Wing loads and wing aspect ratio interacted, such as species with rounder wings could reach similar take-off speeds that those with 30—40% lighter wing loads but longer wings. Finally, I found partial support for a relationship between lower escape performance and strong antipredator response. Mean FID decreased with mean TOS across species, but contrary to expectation, this relationship was weak. Wing load has a stronger linear relationship with FID than TOS. Overall, I have shown a link between body size, escape performance and antipredator investment, with a large range of variability within species, but a consistent allometric relationship across shorebird species.

Variation in body mass, morphology and escape performance was high within-species, and not always in the expected direction. Within species, heavier birds could reach similar escape responses than lighter ones, suggesting that other unaccounted mechanisms contributed to fine-tune escape performance. For species where data allowed intraspecific comparison, the range of FID responses also suggested that the decisions available to individual shorebirds are dependent on social and habitat contexts. In a sample of nine non-breeding shorebird species, those with higher wing load have lower take-off speed, with medium size shorebirds, in general, being slower than their lighter counterparts. In the Banc d’Arguin, Mauritania, large species that forage close to the shore show higher mortality to falcons than smaller species foraging further away from the shore (Van Den Hout et al., 2008). Unfortunately, my sample of take-off speeds did not include large shorebirds (>150 g). While no definitive measure of the allometric relationships between body size, wing load and take-off speed suggest that birds with larger size would have slower take-off speeds and could therefore face higher vulnerability to predator attacks.

Wing morphology in shorebirds has been extensively studied in connection with long-distance migration, but less so with respect to escape performance. Wing morphology has been shown to influence migration strategies within species (O'Hara et al., 2005), particularly the distance flown between stopover sites (Minias et al., 2015, 2013). In Phasianidae, which uses flight only to escape predators, wing mass influenced the speed of take-off (Tobalske and Dial, 2000). In hummingbirds, wingbeat frequency decreases and the amount of mass lifted (a measure similar to wing load) increased with log of body mass (Altshuler et al., 2010). One of the few studies that used wing morphology to study escape performance suggested that while on migration, two species of sandpipers had different escape abilities (Burns and Ydenberg, 2002), the smaller species being faster. In the current study of 11 shorebird species during the lean non-breeding season, I found that both wing load and wing morphology (wing aspect) were strong predictors of escape performance across species of shorebirds. Escape performance decreased with higher wing loading, but only in the extreme case of Short-billed Dowitcher; across other species there was no evidence of decreased take-off speed with increases in wing loading. Some shorebirds showed higher escape performance than other species of similar size with more pointed wings. Plovers (Charadriidae) had rounder wings than *Calidris*. spp. and other Scolopacidae in general. In addition, Wilson's Plover is the species with the shortest migratory distance, and at least part of their population is resident in the study area. Ruddy Turnstone were also faster than expected by their wing loading. With a similar body shape to Plovers, Ruddy Turnstone have more rounded wings, and yet it has some of the longest migratory distances (Nettleship, 2000).

Escaping a predator is a hierarchical process that starts with decisions that reduce chances of encountering it in the first place (Lima and Dill, 1989) or that increase the probability of detecting and escaping a predator encounter (Lima, 1993). Based on this assessment of the habitat, animals can control where and when to perform their daily activities to manage "danger". But once a predator is encountered, shorebirds must decide if and how to react, for example deciding what is a safe distance and when to initiate an escape (Cooper and Frederick, 2007). In this study I have shown that body size and wing shape influenced the ability to escape predators, as directly measured through take-off speed. I expected that lower escape performance would impose higher costs, and thus perhaps longer FIDs. The direction of the relationships between FID and TOS or wing load were in the expected directions, but the strength of those relationships was weak

The large intraspecific variation of flight initiation distance within species suggests that other factors like group size, habitat and other unaccounted variables also play roles in FIDs. Non-breeding shorebirds with more companions and those far from vegetation could react less strongly (allowing shorter FID) to simulated predator attacks (Blumstein et al., 2016). There are multiple non-exclusive explanations for these patterns. Tactile foragers with lower escape performance have similar flight initiation distances that birds with higher escape performance. However other species with high escape performance have similar fleeing responses than slower shorebirds. Solitary species or species that form small flocks (Semipalmated Plover, Wilson's Plover, Spotted Sandpiper) have residual variations above the average, suggesting a stronger response to predators than species forming larger groups (Semipalmated and Western Sandpiper).

In this chapter, I have shown that the ability of non-breeding shorebirds to escape predators is related to body size and morphology, specifically the wing load and aspect-ratio of the wings. Those flight parameters scaled both within and between species. I found support for an allometric effect of those parameters acting as constraints on escape performance; in general, heavier birds were slower, however species with rounded wings reached similar speeds. My dataset of experimental flight initiation distances was small and only provided partial support for the hypothesis of decreased antipredator investment with higher escape performance. The large variation within species in escape performance and antipredator response suggest that other factors also play a role in ability and decisions to escape in non-breeding shorebirds. To my knowledge this is the first attempt to characterize escape performance and antipredator responses of an entire non-breeding shorebird community.

Chapter 4.

Danger, food, body size and sociality predict shorebird species' distributions in a tropical delta

4.1. Abstract

Shorebirds must consider predation danger when selecting foraging locations. During migration, small shorebirds such as the Western Sandpiper lower the risk of predation from raptors by avoiding sites close to vegetation, even when doing so diminishes food availability. As a result, their spatial distributions are biased towards safer stopover sites. However, the applicability of this pattern outside migratory periods and across other shorebird species with different ecological traits is less clear. In an extensive tropical delta complex, I investigated foraging habitat usage by 12 shorebird species with different body sizes, foraging modes, and escape performances. I modelled the presence and density of each species using counts made at 136 tidal flats that varied in area, indices of safety and productivity, and distance from the outer coast, which was used as an index of salinity. I predicted that shorebirds generally would favor safer and more productive habitats. Primarily due to presumed trade-offs with time spent on individual vigilance, I expected these relationships to be stronger for species with tactile versus more visual foraging modes, for solitary versus flocking species, and for those with slower escape performance. I expected that larger shorebirds might be less sensitive to danger because they were less vulnerable to some avian predators. As expected, most species had their highest presence in large open sites. However, the opposed was found for abundance, with many species having lower densities in larger sites. After area itself, safety (openness) was the strongest general predictor of variation in shorebird distribution. Area and safety effects were stronger in tactile than in visual foragers, matching the expectation based on foraging mode vulnerability. In contrast, productivity effects were opposite to those expected, with shorebirds more likely to use tidal flats with lower productivity, controlling for other factors. However, Spotted Sandpiper and Whimbrel (territorial species) responded positively to the gradient of productivity. Territorial species did not have higher usage of open sites; their distributions appear to be more strongly driven by body size and escape performance,

both of which may alter the prioritization of open habitat safety characteristics. Future work on migratory bird distribution across food-danger landscapes could explore patterns of shorebird habitat segregation across other wintering regions and within species variation in safety distributions.

4.2. Introduction

The presence of deterrents and crypsis are classical examples of traits that might influence habitat usage decisions. Fishes with armor or camouflage could use riskier habitat and/or delay their escape from potential predators (Benevides et al., 2018). In shorebirds, visual foragers that stalk and hunt prey could more easily be simultaneously scanning the surroundings (Barbosa and Moreno, 1999), whereas species that spend more time with their heads toward the ground (e.g. probing, or any other more tactile foraging) should experience a stronger trade-off against time spent being vigilant (Barbosa, 1995). This could lead to them experiencing greater interference from conspecifics (Fuller et al., 2013), or suffer the consequences of being less aware of attacks. Similarly, a species' body size will affect its vulnerability to a given potential predator; some may find safety simply by being either too large for a predator to take or too small to be profitable. How ecological and behavioural traits influence the habitat use across danger and other environmental gradients is of great relevance for understanding species distribution and for potential applications in conservation of multi-species communities.

Danger management drives habitat usage decisions of many animals because of the large potential negative fitness consequences of failing to do so (Brown and Kotler 2004). At a habitat or site choice level, small sandpipers often favor using large open sites (Hope, 2018; Piersma et al., 2006; Pomeroy et al., 2008), apparently because the proximity of vegetation or physical barriers reduces the probability of detecting approaching raptors (Pomeroy et al., 2006; Verkuil and de Goeij, 2003). In the estuary of the Thagus, Portugal, migratory shorebirds make less use of narrow coastal bands, which could be interpreted as having a lower tolerance to danger, than birds more familiar with the site that are spending the winter there (Martins et al., 2015). Habitat usage decisions prioritizing safety can occur despite an apparent cost in terms of local site food availability or potential foraging rates (Ydenberg et al. 2002). In other systems, however, indices of food resources alone, either as macroinvertebrates (Lourenço et al.,

2016) or biofilm (Jiménez et al., 2015) can be strong predictors of site usage. The interplay between these two main drivers of distribution, danger and food landscapes, has been well documented in the Fraser River estuary of British Columbia with respect to habitat usage by Western Sandpipers and Dunlin (Rourke et al., 2018; Zharikov et al., 2008) and for larger communities of shorebird species wintering in the Thagus, Portugal (Martins et al., 2015) and Banc d'Arguin, Mauritania, (Van Den Hout, 2010), but seldom in other places

In addition to safety and food, habitat conditions known to influence distributions for shorebirds include other environmental variables related to heat or water balance (Piersma et al. 2012). For example, different species segregate spatially following marine-estuarine gradients, with some species preferring locations close to the ocean (Dias et al., 2017; Martínez-curci et al., 2015). As in many other animal groups (Michalski and Peres, 2017), area effects per se can influence the usage of habitats, and area is usually taken into account when assessing the distribution of shorebirds (Albanese and Davis, 2015). Social aspects, including population density (Gill et al., 2001) and the presence and abundance of heterospecifics can affect habitat use by shorebirds. Habitat selection by shorebirds thus occurs along axes of safety, food, environment and sociality (Piersma, 2012).

Many studies have shown that shorebird species exhibit different patterns of distribution across these multiple habitat dimensions (Kober and Bairlein, 2006), but few approach the subject from a comparative view that integrates multiple life-history traits that may produce different approaches to ensuring safety and sustenance through differences in tactics beyond habitat choice (Fernández and Lank, 2010; Lind and Cresswell, 2006; Sansom et al., 2008). Animals with different physical and ecological traits should exhibit different trade-offs. Most comparative studies of shorebird segregation and life history traits have been focused on food acquisition alone. For example, at wintering sites in California (Colwell and Landrum, 1993) and northern Brazil (Kober and Bairlein, 2009), plover-like shorebirds forage in drier substrates, while sandpipers and larger shorebirds show stronger preference for substrates near water. But few studies have examined how the interplay of food availability and vulnerability to predation (Lima and Dill, 1989), measured through either the ability to detect, avoid or escape from predators (Cooper and Frederick, 2007), affect habitat usage across a suite of related species.

The interpretation of species habitat distribution analyses must also consider differences in social structures (Paracuellos, 2006). Safety-food trade-offs made by highly social flocking species will differ from those of territorial species. The former gain safety simply by flocking, at a potential theoretical cost of conspecific foraging interference, while the latter avoid such interference but must rely more on their own vigilance. These differences translate into differences in the interpretation of density as a measure of habitat quality or preferences. Theoretically, species could show density distributions that match the quality of available feeding habitat (Fretwell and Lucas, 1970). However patchiness or dominance dynamics (Ens et al., 1995) can invalidate the common interpretation that higher density indicates better habitat quality (Van Horne, 1983).

Here I investigate habitat selection by shorebirds in an important non-breeding area of the Americas' Pacific migratory Flyway (Senner et al., 2016a). Specifically, I use non-breeding surveys to model factors responsible for spatial distributions in relation to safety and other environmental predictors among a community of shorebird species that differ in sociality, feeding mode, body size and escape performance. My specific objective was to determine whether foraging patch area, indices of danger and food availability, and marine gradients influence the presence and density of species, and of groups of species defined by behavioural and ecological traits. Although the trade-offs made by small sandpipers are well documented across their migratory stopover ranges, they have been less investigated at tropical sites. Further, the general applicability of prioritizing the usage of safer habitat patches has not been well documented across a community of shorebird species that may differ in their anti-predator tactics. We will improve the interpretation of species distribution models and advance our understanding of non-breeding shorebird distribution and of species distribution modelling in general by including ecological traits linked to life history and using a comparative approach to summarize modelling results.

I expected that controlling for other factors, shorebird species in general would favor larger, presumably safer tidal flats, and those with higher productivity. I predicted that the magnitude of the relationship with safer sites would be stronger for more vulnerable species, e.g., those that spend more time in tactile foraging, are smaller, and/or have slower escape performance (Chapter 3). I expected that having a small or large body size might provide intrinsic protection from some avian predators, due to lower profitability per hunt or difficulty with killing or handling, respectively, and therefore that these species would be weakly associated with gradients of safety. While I have included foraging patch area and the marine gradient in these models, since shorebird species are known to segregate with respect to them, I made no *a priori* predictions about their relationships to shorebird distributions.

4.3. Methods

4.3.1. Study area

Sanquianga-Iscuandé (2.3–2.5°N, -78.5 °– -78.3 °W) is a deltaic-estuarine complex on the northern coast of Nariño Department, Colombian Pacific Coast. It has tropical weather with mean temperatures of 26ºC and precipitation of 3000–3500 mm (Fick and Hijmans, 2017), and a predominant biome of tropical rain forest (Van Wyngaarden and Fandiño-Lozano, 2005). The delta encompasses more than 1000 km^2 of tidal flats, interspersed with mangroves, beaches, shallow waters and other coastal habitats (Unidad Administrativa Especial del Sistema de Parques Nacionales Naturales de Colombia., 2005). The area experiences a semidiurnal tidal cycle, with monthly tidal variation up to 4.6 m (IDEAM, 2016). Sanquianga-Iscuandé harbors the largest concentration of non-breeding shorebirds in Colombia (Johnston-González and Eusse-González, 2009), and is a site of international importance on the Pacific flyway (Senner et al., 2016b). The area is partially protected under the Sanquianga National Park (800 Km^2), is recognized as an Important Bird Area, and in the case of the Iscuandé River mouth, as an International Reserve for Shorebirds (Asociación Calidris y Consejo Comunitario Esfuerzo Pescador Iscuande, 2017). The thousands of tidal flats patches spread across a band of 35 km from coast to mainland (Fig. 4.1) provide a rich opportunity to assess the distribution of a community of non-breeding shorebirds selecting from a range of environmental conditions.

4.3.2. Shorebird surveys

My coworkers and I carried out six annual surveys (2012–2017) in the Sanquianga-Iscuandé delta complex (Fig. 4.1). Initially, eighty of nearly 900 mudflat sites identified in the five river mouths of Sanquianga National Park were selected at random (Anchico et al., 2015). Additional sites were added to replace selected areas that proved difficult to survey due to the flats being submerged, navigation or personal security being compromised, or to include specific areas that were more relevant for management purposes or located in extreme geographical locations (e.g. upper river mouth of Sanquianga river and outer Iscuandé river mouth). Overall, between 54–116 sites were sampled each year (Appendix D), and across the six-year period, a total of 152 sites were sampled, representing ca. 15% of the tidal flats in the area**.** To focus on wintering populations, we restricted the timing of our surveys to between the last week of January through the first week of February, thereby avoiding counting shorebirds during active migratory periods (Ruiz-Guerra, 2004). Using boats and canoes, two teams of surveyors covered routes of 10–15 sites/day during 4–5 successive days. Each team had at least one observer with extensive training in shorebird identification and censusing techniques. Surveys were concentrated during periods of the greatest tidal flat availability, three hours before and after low tide, and surveys were repeated on similar dates and tidal heights each year. If a site could not be completely surveyed due to visual obstructions, the proportion of the mudflat sampled was recorded and numbers of shorebirds attributed to the entire site was extrapolated, assuming no spatial bias between sampled and unsampled areas.

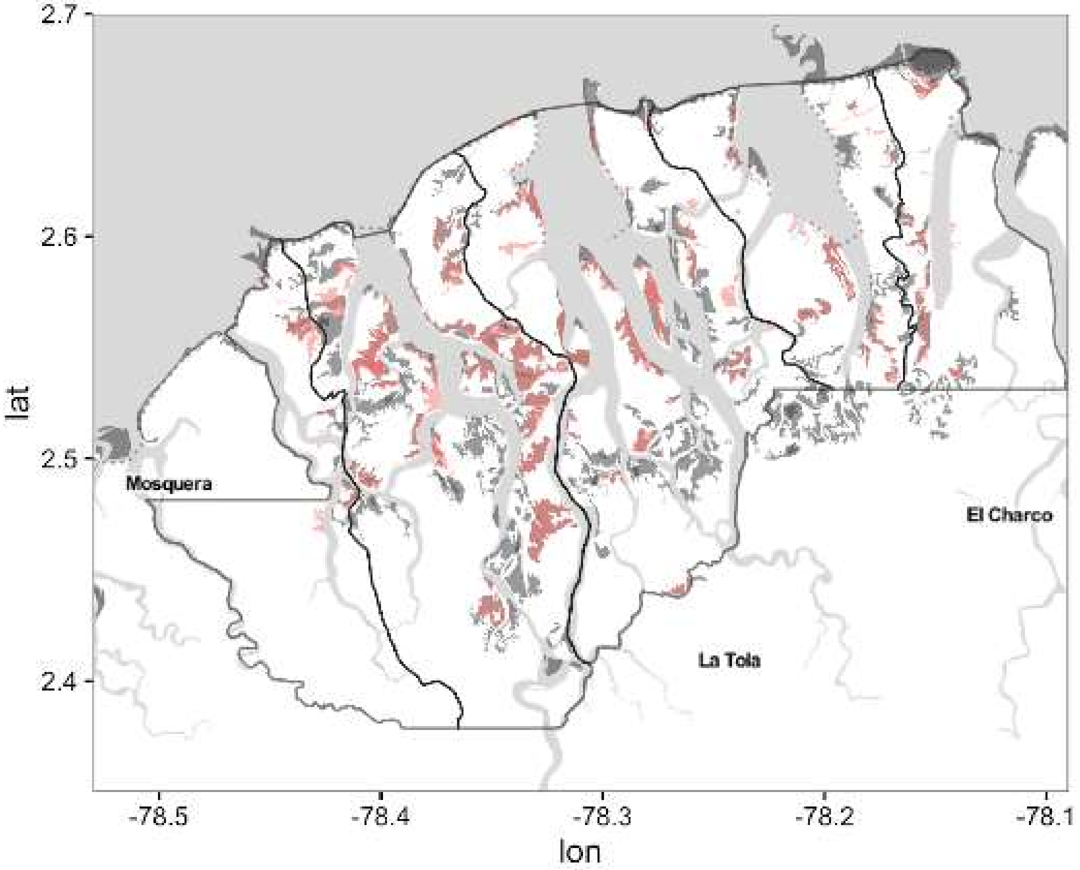


Figure 4.1. **Location of survey units (2012–2017) across Sanquianga-Iscuandé, Nariño, Colombia. Tidal flats in grey and sampled tidal flats in red.**

4.3.3. Environmental variables

I obtained variables representing area, safety, primary productivity, and marine gradients, all of which are known to affect habitat suitability for shorebirds. Using Landsat 8 images, I obtained a 5-Year composite of Normalized Water Difference Index (NDWI), used to aid in differentiating water and non-water habitats (McFeeters, 1996). Using Random forest, a machine learning approach and reference points on the ground, I ran a supervised classification and obtained a highly accurate map (accuracy = 0.9) of the current extent of tidal habitat. I used the map to calculate spatial features of tidal patches.

I estimated the area of each tidal patch by adding the area of all tidal cells that were contiguous and multiplying by the cell resolution of 30 x 30 m, resulting in mudflats ranging from 1.5–905 ha. To quantify openness, a presumed danger-safety gradient, I used the distance to vegetation (0–6km) averaged across all the cells of each tidal patch (Hope, 2018; Pomeroy, 2006). To represent the freshwater-marine gradient, I used the distance to the coastline taken from the geometrical center of each tidal patch (0–35 km, Dias et al., 2017).

To quantify potential feeding resources, I used the Normalized Difference Vegetation Index (NDVI) to assess relative primary productivity, which could be available either as feeding resources for the benthic invertebrate communities used by shorebirds (Kober and Bairlein, 2009) or as a direct food resource (e.g. biofilm) (Kromkamp et al., 2006, Kuwae et al., 2012). Measuring shorebird food offers two big challenges: (1) the diversity of potential feeding sources ranging from macro and meiofauna (Kober and Bairlein, 2009; Lourenço et al., 2016), and biofilm (Kuwae et al., 2012), and (2) the patchiness of those resources, which makes ground measures difficult and time consuming. As a result, large-scale studies of distribution have used proxy measures of food availability. For example, Butler et al. (1998) working in Panama Coast and later in selected areas around the world (Butler Et al. 2001) found that large concentrations of shorebirds were associated with areas with oceanic upwelling systems, near mangroves and in general, where coastal waters were more productive. They use satellite images to estimate chlorophyll density and used it as a measure of near-shore productivity. Similarly, the Normalized Difference Vegetation Index (NDVI) is a widely used measure of productivity and health of terrestrial (Leisher et al., 2013) and coastal vegetation (Alatorre et al., 2016a) and has been proposed as a measure of primary productivity in tidal flats (Kromkamp et al., 2006). In temperate estuaries NDVI could be a robust proxy for sediment productivity [chl a + phaeo] and allow quantification of microphytobenthic biomass in muddy sediments. In this chapter I use NDVI as a proxy for productivity of tidal flats. I calculated separate 5-Year average NDVI values for each tidal cell and averaged these across the tidal patch to quantify productivity.

I obtained additional measures of spatial pattern to quantify landscape structure of the tidal flats (McGarigal and Marks, 1995), including core area, perimeter-area ratio and connectivity. All these metrics correlated strongly and positively with size of the tidal flat (*R* > 0.7), so I retained only size in my models. Similarly, “tidal exposure”, or how likely tidal flat would remain submerged, was obtained from a 5-year composite of NDWI, but this correlated strongly and negatively with NDVI (Spearman Rank = -0.96), therefore only NDVI was utilized as a predictor. The supervised classification and accuracy analysis were conducted in Google Earth Engine (Gorelick et al., 2017). Area, distances and spatial patterns were calculated with raster (Hijmans, 2014) and SDMTools (Van der Wal et al., 2014) packages in R.

4.3.4. Species-specific ecological and behavioural traits

I examined the relationships between the signs and magnitudes of environmental coefficients produced by the species-specific distribution models versus four specific behavioural and ecological traits: sociality, feeding mode, body size and take off speed (Table 1.1, 3.1, 3.2). Species' sociality was categorized as territorial, if their predominant foraging pattern involved solitary feeding and territoriality, as with e.g. Willet and Whimbrel (McNeil and Rompre, 1990; Skeel and Mallory., 1996), or flocking if they tend to forage in groups, as with e.g. Short-billed Dowitcher and Western Sandpiper (Fernández and Lank, 2010). Feeding mode was categorized as predominantly tactile or visual based on personal observations and secondary information (Barbosa, 1995; Barbosa and Moreno, 1999). I used the log of body mass as a measure of body size and take off speeds were measured directly in 8 species (Chapter 3).

4.3.5. Analysis

I modeled variation in shorebird usage of tidal flats in southern Colombia with respect to the four environmental gradients, and then evaluated how usage patterns were related to differences in species' ecological and behavioural traits. Sixteen sites were dropped because they were sampled in only 1 or 2 years, leaving 136 sites retained for analysis**.** The habitat variables represented *a priori* hypothesis of factors expected to influence shorebird distributions: area, safety, food and marine conditions (fixed factors). Given the differences in scale and range of variation across them, I centered and scaled those predictors to allow a meaningful comparison of the modeled effect sizes. Area and distance to cover have a correlation higher than 0.5, but this was reduced after log transformation (Appendix E), therefore I retained both predictors. To incorporate temporal and spatial structure, each year's count was used as a data point, with year and site treated as random factors, thus allowing intercepts of models to vary by year and site.

I modelled each of the 12 species with permanent presence in the area (>4 years) and moderate to large presence (>10% sites). Three other species had less data and models of abundance did not converge or were considered unreliable. Each species' usage of tidal sites was modeled separately for both presence/absence ('presence', or occupancy) and density. I defined presence as whether a species was counted at a site, and density as the number of individuals present per unit area, defined only for occupied sites. For both conceptual and statistical reasons, I modeled the two response variables separately. Presence could be considered as defining 'habitat suitability' for a species, in that sites that were never used in any year were considered as 'unsuitable', or 'non-habitat'. Statistically, presence models were run as General Linear Mixed Models (GLMMs) that included all four predictor variables and a binomial expected distribution. To compare the relative importance of all environmental variables for all species, I present the log-odds for effect size of the parameter values for predictor variables from the full models. The density of birds, calculated for each species' occupied sites only, was used as a positive measure of "habitat quality", recognizing that for territorial species, this interpretation might be inappropriate (Van Horne, 1983). Species-specific sample sizes (number of sites and site-years) for both presence and density analyses are given in Table 4.1. The log of densities was modeled with Linear Mixed Models (LMMs). To help with interpretation, I examined the relationship between species' presence rates and densities (Fig. 4.2).

To determine the best model or models for predicting the distributions of each species, I built candidate models to represent all possible combinations of habitat variables. I fit a full model including all habitat variables in their linear form. I considered possible interactions between pairs of variables, but collinearity increased when adding interactions, with variance inflation factors >2, so only additive effects were included in the final models. To allow for the possibility that none of these factors could substantially explain the presence or density of nonbreeding shorebirds in the study area, a null model with constant intercept (1) and no additional predictors was included in the model set. The complete candidate set for each species included 16 models.

I used information theory to assess the support for each hypothesis. I compared alternative models for each species using the difference in the AICc (AIC corrected for small sample sizes) in relation to the top-ranked model, with values of ΔAICc ≤2 indicating plausibly comparable models (Burnham and Anderson, 2002). I used Akaike weights (Δi) to estimate the relative likelihood of each model, ranging between 0.0 (least important) to 1.0 (most important). I used multi-model inference (Grueber et al., 2011) to assess the possibility that individual models were not the single most parsimonious explanation for distribution of some species.

To estimate and describe the effect size of each predictor on presence by a shorebird species, I averaged coefficients of predictor variables within the top-ranked model set for each species. I considered habitat variables to be informative of shorebird presence if they occurred within the top-ranked models and their averaged 95% confidence intervals did not overlap zero. All analysis were carried out in R (R Core Team, 2017b), with models built in lme4 (Bates et al., 2018), model selection conducted in Mumin (Bartón, 2018), model performance and cross-validation with caret (Kuhn, 2008) and pROC (Robin et al., 2011), and graphical outputs with broom (Robinson, 2017) and SjPlot (Lüdecke, 2017).

I estimated the effect of ecological and behavioural traits on the presence of shorebirds with respect to multiple environmental variables. I focused this part of the analysis on presence. To test the relationships between behavioural and ecological traits and habitat usage, for categorical traits, I averaged the relevant parameter coefficients (intercepts and slopes) from the set of best fitting species-specific presence models and used these values in comparisons between categories of sociality and feeding mode. For the continuous traits, I correlated changes in intercept and slope in relation to variation in body size and escape performance. I tested for the significance of categorical trait differences with Wilcoxon tests, and used correlations (*F* tests) for continuous traits.

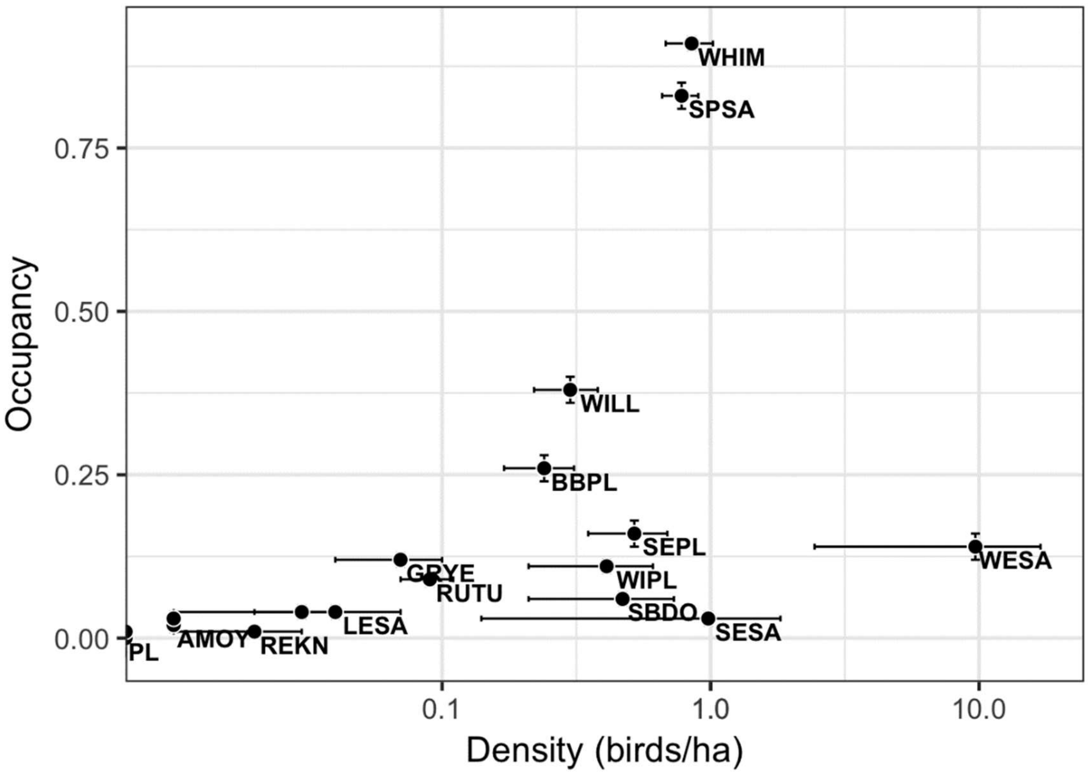


Figure 4.2. **Occupancy (proportion of mudflats occupied) and density (on occupied mudflats) of shorebirds in in tidal flats of Sanquianga-Iscuandé, southwestern Colombia, 2012 - 2017. Mean –and 95% CI shown.**

4.4. Results

We counted 75,261 shorebirds of 18 species between 2012–2017 (Table 4.1). 18,021 individuals were from unidentified shorebird categories ("peeps", "plovers", “yellowlegs”, etc.); these were partitioned and assigned to each potential species (Western/Semipalmated/Least Sandpiper, Semipalmated/ Wilson’s Plover, Greater/Lesser yellowlegs) based on their documented proportional representation of identified birds during each survey. The most widespread shorebirds in the study area were Whimbrel and Spotted Sandpiper occupying 84% and 83% of sampled sites, followed by Willet and Black Bellied Plover present at 53% and 39% (Appendix F). Four shorebird species (Semipalmated and Wilson’s Plover, Western Sandpiper, Greater Yellowlegs) occupied between 20–30% of potential sites and the remaining 10 species occupied 20% or fewer sites. Eleven species were recorded during all years surveyed, an additional four species in at least five years, and three species in four or fewer years and at fewer than 5 sites (Red Knot, Marbled Godwit and Collared Plover). Larger shorebirds tended to occupy a larger proportion of the tidal flats in the Sanquianga-Iscuandé landscape than smaller shorebirds (Fig. 4.2).

There was a generally positive relationship between presence and density, but four species were much more widely distributed than would be expected based on the relationship among the other species. Whimbrel, Willet and Black-Bellied Plover and Spotted Sandpipers were the four most territorial (McNeil and Rompre, 1990; Reed et al., 2013; Skeel and Mallory., 1996), and three of the largest species present in the delta. In contrast, the most gregarious species were all small or medium sized. Semipalmated and Western Sandpipers, Semipalmated and Wilson's Plover and Short-Billed Dowitchers all fall below a regression the upward trend shown by the most territorial species

Table 4.1. Number of surveys and sites where 18 shorebird species were present in Sanquianga-Iscuande, Colombia (2012-2017). Species sorted descending by the proportion of sites occupied

Species	Species Code	Surveys (N=7)	Proportion	Sites (N=152)	Proportion
Whimbrel	WHIM	7	1	128	0.84
Spotted Sandpiper	SPSA	7	1	126	0.83
Willet	WILL	7	1	80	0.53
Black-Bellied Plover	BBPL	7	1	60	0.39
Semipalmated Plover	SEPL	7	1	46	0.3
Western Sandpiper	WESA	7	1	41	0.27
Greater Yellowlegs	GRYE	7	1	40	0.26
Wilson's Plover	WIPL	7	1	31	0.2
Ruddy Turnstone	RUTU	7	1	24	0.16
Short-billed Dowitcher	SBDO	7	1	18	0.12
Least Sandpiper	LESA	6	0.86	17	0.11
Lesser Yellowlegs	LEYE	6	0.86	16	0.11
Semipalmated Sandpiper	SESA	6	0.86	12	0.08
Sanderling	SAND	7	1	10	0.07
Marbled Godwit	MAGO	3	0.43	5	0.03
American Oystercatcher	AMOY	6	0.86	4	0.03
Red Knot	REKN	4	0.57	3	0.02
Collared Plover	COPL	1	0.14	1	0.01

Shorebird distributions in the study area were not random with respect to the habitat variables used to predict their presence of a site. For eleven of twelve species, the top model of presence ranked well above the null model (ΔAIC_c ranged from 6 to 21; Table 4.2;); only Short-Billed Dowitcher had the null model within the top <2 ΔAIC_c. As might be expected, the most generally informative variable was Area of the tidal patch (Fig. 4.3). The odds of finding a shorebird increased with area, ranging from 1.2 times for the Spotted Sandpiper to 6.7 times for the Semipalmated Sandpiper. Only Sanderling showed a potential negative relationship between presence and area, but confidence intervals overlapped zero. The safety index was the second-most generally predictive environmental variable, being included in the top models of presence for 10 of 12 species. It was an informative variable (non-overlapping zero after model averaging top models) for Spotted Sandpiper, negatively rather than positively; Spotted Sandpiper presence was also strongly negatively related to distance to cover (Fig 4.4). Productivity was the most important predictor for Least Sandpiper and was also informative for Ruddy Turnstone and Spotted Sandpiper, being negative for Least Sandpiper and positive for Spotted Sandpiper and Ruddy Turnstone. The marine gradient was informative and negative for the presence of Whimbrel and Ruddy Turnstones, indicating a bias towards more marine-ward sites.

Table 4.2. Model selection results for the presence of shorebirds as a function of area (AR), safety (SA), marine (MA) and productivity (PR) gradients in tidal flats of the Sanquianga- Iscuandé delta, Southern Colombia. Only models ΔAICc <2 and the Null model are shown. All models include random effects of year and sampling unit. Variables in bold have 95% confidence intervals of parameter estimates that do not overlap zero. For all species N = 136 sites.

Model	K	AIC_c	ΔAIC_c	W_i
Black-Bellied Plover				
AR + MA	5	496.79	0	0.28
AR	4	497.35	0.56	0.21
AR + MA + PR	6	498.61	1.82	0.11
AR + PR	5	498.68	1.9	0.11
Null	3	510.71	13.92	0
Greater Yellowlegs				
AR + PR	5	353.99	0	0.37
AR	4	355.82	1.83	0.15
AR + SA + PR	6	355.93	1.94	0.14
Null	3	361.25	7.26	0.01
Least Sandpiper				
PR	4	153.99	0	0.22

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	***W$_i$***
AR + **PR**	5	154.7	0.71	0.15
SA + **PR**	5	155.09	1.1	0.13
AR + MA + **PR**	6	155.15	1.16	0.12
SA + **PR**	5	155.43	1.44	0.11
MA + SA + **PR**	6	155.77	1.79	0.09
Null	3	160.81	6.83	0.01
Ruddy Turnstone				
MA + SA + **PR**	6	222.48	0	0.3
SA + **PR**	5	223.44	0.96	0.18
AR + SA + **PR** + **MA**	7	224.45	1.97	0.11
Null	3	234.86	12.38	0
Sanderling				
SA + PR	5	104.13	0	0.31
AR + **SA** + PR	6	106.12	1.99	0.11
MA + **SA** + PR	6	106.12	2	0.11
Null	3	109.89	5.76	0.02
Short-Billed Dowitcher				
AR + SA	5	163.53	0	0.14
AR	4	164.03	0.5	0.11
SA	4	163.99	0.46	0.11
Null	3	164.09	0.56	0.11
AR + MA	5	164.28	0.76	0.1
SA + PR	5	165.08	1.55	0.06
AR + PR	5	165.38	1.85	0.06
AR + SA + MA	6	165.38	1.85	0.06
MA	4	165.45	1.92	0.05
Semipalmated Plover				
AR + MA + PR	6	395.15	0	0.14
AR + SA + MA	6	395.17	0.03	0.14
AR + MA	5	395.45	0.3	0.12
AR + SA + PR + MA	7	395.65	0.5	0.11
MA + SA + PR	6	395.78	0.63	0.1
SA + PR	5	396.38	1.23	0.08
AR + SA + PR	6	396.66	1.51	0.07
SA + PR	5	396.89	1.74	0.06
AR + SA	5	396.98	1.83	0.06
Null	3	408.86	13.72	0
Semipalmated Sandpiper				
AR + SA	5	116.12	0	0.23
AR + MA	5	116.46	0.35	0.19
AR + SA + MA	6	116.89	0.78	0.15
AR + SA + PR	6	117.92	1.81	0.09
AR	4	117.99	1.87	0.09
Null	3	122.78	6.66	0.01

Model	**K**	**AIC_c**	**ΔAIC_c**	**W_i**
Spotted Sandpiper				
AR + **SA** + **PR**	6	410.69	0	0.4
AR + **SA** + **PR** + MA	7	412.03	1.34	0.21
Null	3	429.6	18.91	0
Western Sandpiper				
AR + **SA** + PR	6	342.1	0	0.21
AR + **SA**	5	342.75	0.65	0.15
SA + PR	5	342.81	0.71	0.15
AR + PR	5	343	0.89	0.13
AR + **SA** + PR + MA	7	344.03	1.93	0.08
Null	3	355.06	12.96	0
Whimbrel				
AR + PR	5	280.99	0	0.37
AR + SA + PR	6	281.51	0.52	0.28
AR + **MA** + PR	6	282.61	1.62	0.16
Null	3	292.05	11.06	0
Willet				
AR + MA	5	542.66	0	0.36
AR + SA + MA	6	543.66	1	0.22
AR + MA + PR	6	544.42	1.76	0.15
Null	3	564	21.34	0

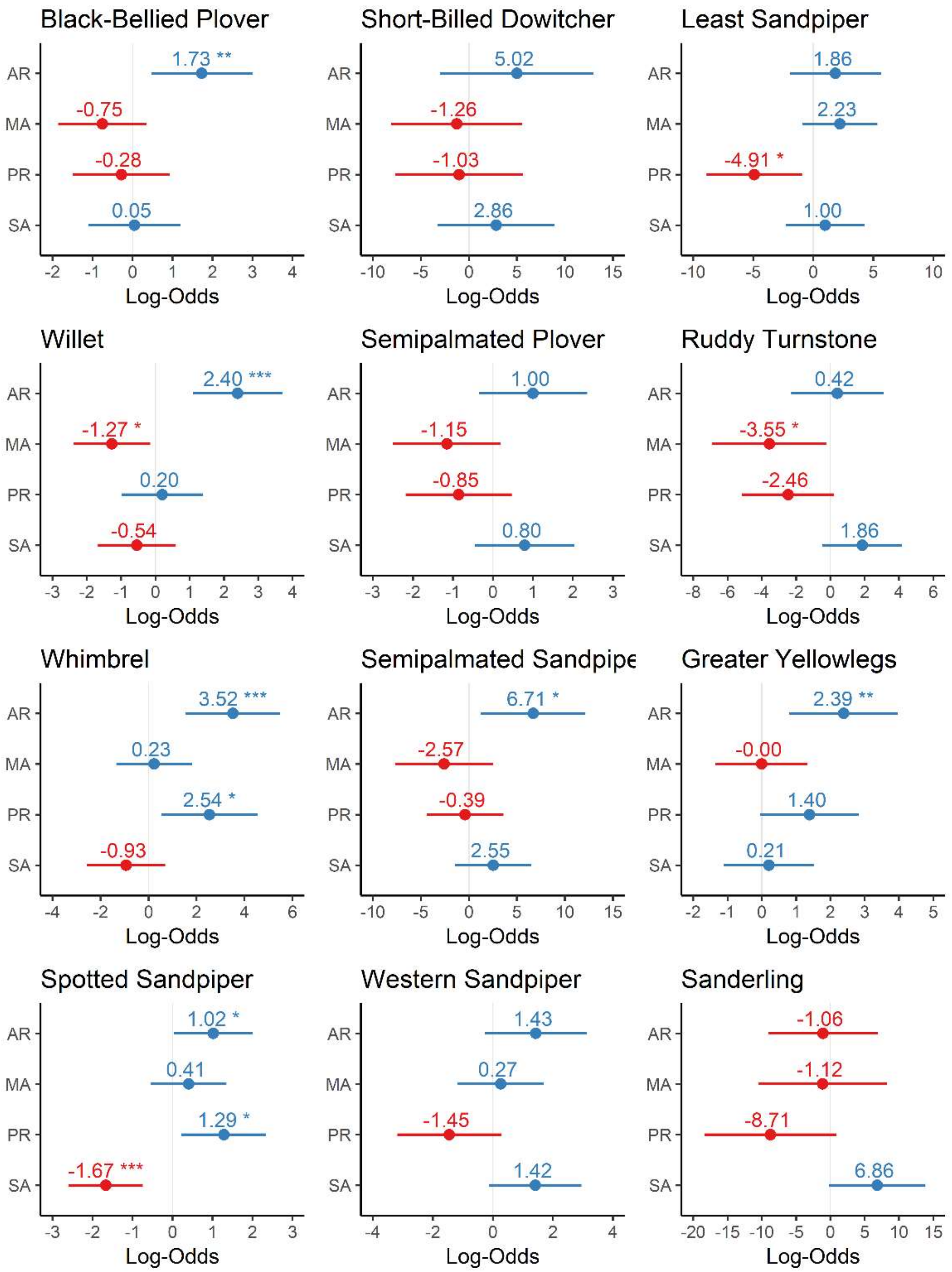


Figure 4.3. **Standardized effect sizes of environmental variables on the log-odds of presence for twelve shorebird species on tidal flats of southern Colombia. The dots and bars represent average parameter coefficients and 95% CI from Full Generalized Linear Mixed Models. AR = Area, MA = Marine, PR = Productivity and SA = Safety gradients. Positive effects for presence are in blue, and negative in red. Significance * = 0.05, ** = 0.01 and *** < 0.001**

The single most important predictor of shorebird density was also the area of the tidal patch, appearing in all plausible LMM models (< 2 ΔΔAIC) for nine out of twelve species (Table 4.3). For all those species, density increased with area of tidal patch, with the largest effect size for Western and Semipalmated sandpipers (Fig. 4.4). However, area of the tidal patch had no explanatory power for Willet, Whimbrel and Spotted Sandpiper, the three most territorial species. The second most important predictor of shorebird density was productivity, appearing in plausible models for six species. Contrary to expectations, the effects were negative; density decreased with increased productivity, with the strongest effect in Semipalmated Sandpiper. Safety was part of the most plausible model explaining density of five species (Semipalmated Plover, Short-billed Dowitcher, Semipalmated and Western Sandpiper and Willet). For other three species, it was an informative variable included within the subset of plausible models (Greater Yellowlegs, Sanderling and Western Sandpiper). The estuarine gradient was only present in models for four species, including the Whimbrel, for which it was the sole predictor. In all except the Western Sandpiper, the marine gradient had a negative effect; density decreased away from the coast. For one species, the Spotted Sandpiper, no single model accounted for density.

Standardized slopes of presence in relation to safety differed strongly for two ecological traits: feeding mode and sociality. They were weakly related to escape performance, but not at all with body mass (Fig. 4.7). Tactile foragers and gregarious species had steeper slopes for presence in relation to safety than solitary species. Species with lower take off speed also tend to have higher slopes for presence ($R^2 = 0.45$, $p = 0.06$, Fig.4.7, bottom right panel). Slopes of presence and other habitat variables did not differ with respect to other ecological traits.

Table 4.3 Model selection results for candidate models comparing $\log_{10}$ (shorebird density) as a function of area (AR), safety (SA), marine (MA) and productivity (PR) gradients for twelve shorebird species in tidal the Sanquianga-Iscuandé delta, southern Colombia. Only models within 2 delta AICc units are shown.

Species	*df*	AR	SA	MA	PR	logLik	AIC$_c$	delta	wi
BBPL	5	0.51				-920.52	1851.16	0	0.6
BBPL	6	0.47			-0.19	-919.9	1851.96	0.8	0.4
GRYE	5	0.13				-121.36	252.84	0	1
LESA	5	0.23				-502.2	1014.52	0	1
RUTU	6	0.24			-0.07	-278.99	570.16	0	1
SAND	5	0.12				-159.56	329.24	0	1
SBDO	5	2.62				-1567.5	3145.12	0	0.47
SBDO	6	2.4	0.4			-1566.91	3145.99	0.88	0.31
SBDO	6	2.56			-0.3	-1567.23	3146.64	1.52	0.22
SEPL	5	2.1				-1267.73	2545.59	0	0.69
SEPL	6	1.95	0.28			-1267.53	2547.23	1.64	0.31
SESA	7	1.8	0.83		-1.33	-2189.58	4393.39	0	0.23
SESA	8	1.84	0.69	-0.45	-1.25	-2188.62	4393.52	0.14	0.21
SESA	7	2.2		-0.6	-1.33	-2189.84	4393.9	0.51	0.18
SESA	6	2.24			-1.48	-2190.87	4393.91	0.52	0.18
SESA	7	1.94	0.91	-0.69		-2190.37	4394.97	1.58	0.1
SESA	6	1.88	1.16			-2191.49	4395.14	1.76	0.1
SPSA	4					-819.1	1646.29	0	1
WESA	8	63.29	6.38	0.56	-0.94	-3221.9	6460.1	0	1
WHIM	5			-0.21		-847.39	1704.9	0	1
WILL	5				-0.18	-686.65	1383.42	0	0.26
WILL	5		0.17			-686.9	1383.93	0.51	0.21
WILL	5			-0.15		-687.05	1384.22	0.8	0.18
WILL	6		0.13		-0.14	-686.38	1384.92	1.5	0.12
WILL	4					-688.46	1385.01	1.58	0.12
WILL	6			-0.12	-0.15	-686.52	1385.21	1.79	0.11

Table 4.4. Average effect of habitat variables (AR = Area, MA = Marine, SA = Safety, PR = Productivity) on the presence of shorebird species in relation to four ecological traits: sociality, feeding mode, log of body mass and take off speed. Average slope is shown for categorical traits and adjusted r-squared is shown for the linear relationship between slopes and continuous traits

	Feeding			**Sociality**		
Habitat	Tactile	Visual	*P*	Gregarious	Solitary	*p*
Area	0.692	0.620	0.570	0.578	0.692	1.000
Marine	-0.227	-0.218	1.000	-0.385	-0.104	0.106
Productivity	-0.623	-0.038	0.283	-0.639	0.057	0.432
Safety	0.744	-0.007	**0.016**	0.702	-0.084	**0.003**

	Log body mass		**Take off Speed**	
Habitat	R^2adj	*p*	R^2adj	*p*
Area	0.020	0.674	0.020	0.717
Marine	0.170	0.242	0.030	0.682
Productivity	0.060	0.492	0.090	0.470
Safety	0.000	0.951	0.450	0.068

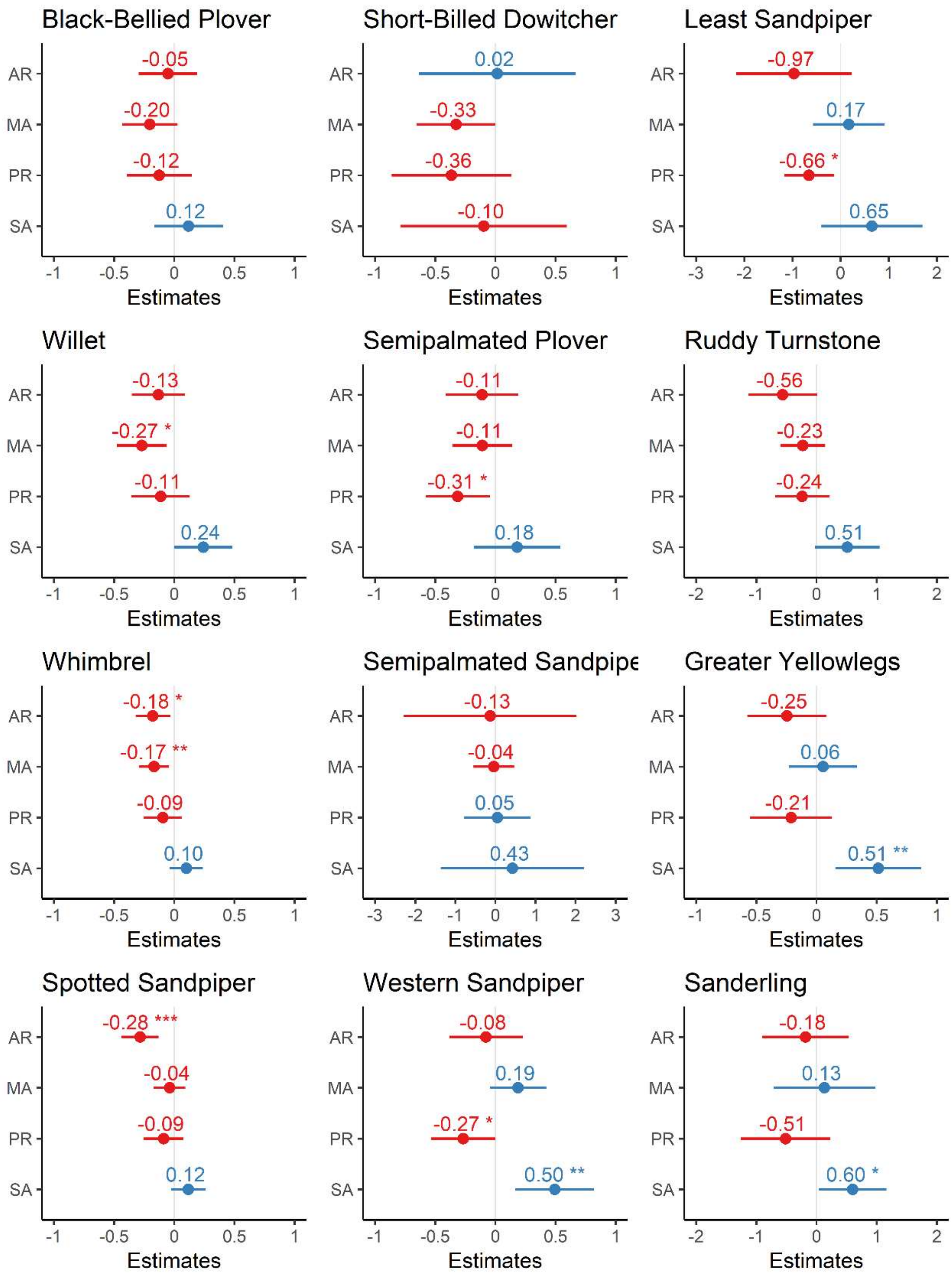


Figure 4.4. Effect of environmental variables (AR = Area, MA = Marine, SA = Safety, PR = Productivity) on the density of twelve shorebird species in southern Colombia. The dots and bars represent model averaged parameter coefficients and 95% CI from Full Linear Mixed Models. Significance * = 0.05, * *= 0.01 and * < 0.001.**

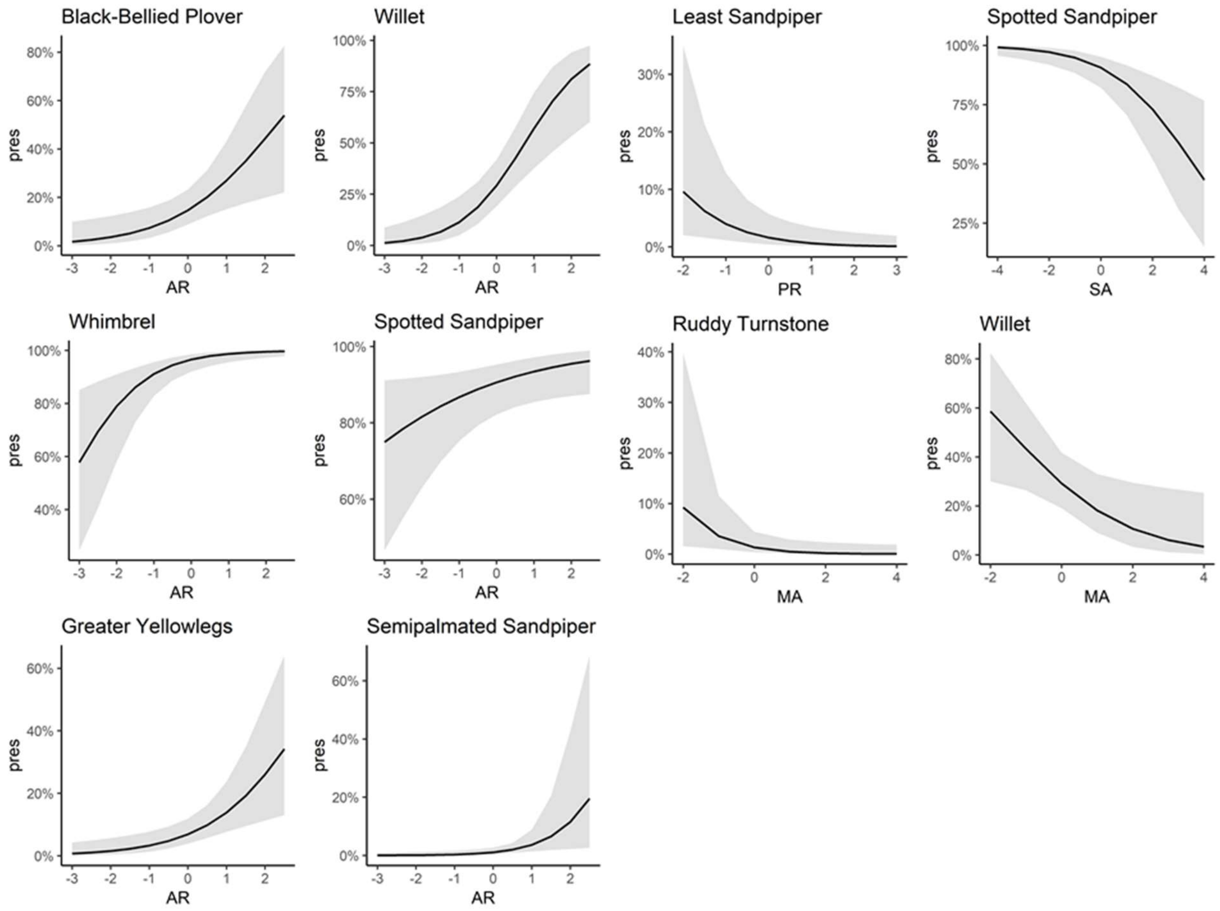


Figure 4.5. **Probability of presence of shorebirds in tidal flats of Sanquianga-Iscuandé, southwestern Colombia, 2012 - 2017, in relation to habitat variables (AR = Area, MA = Marine, SA = Safety, PR = Productivity) from top models. Graphs display model-averaged predictions and 95% confidence intervals from top models. Only informative variables are shown while other variables were held at their median values.**

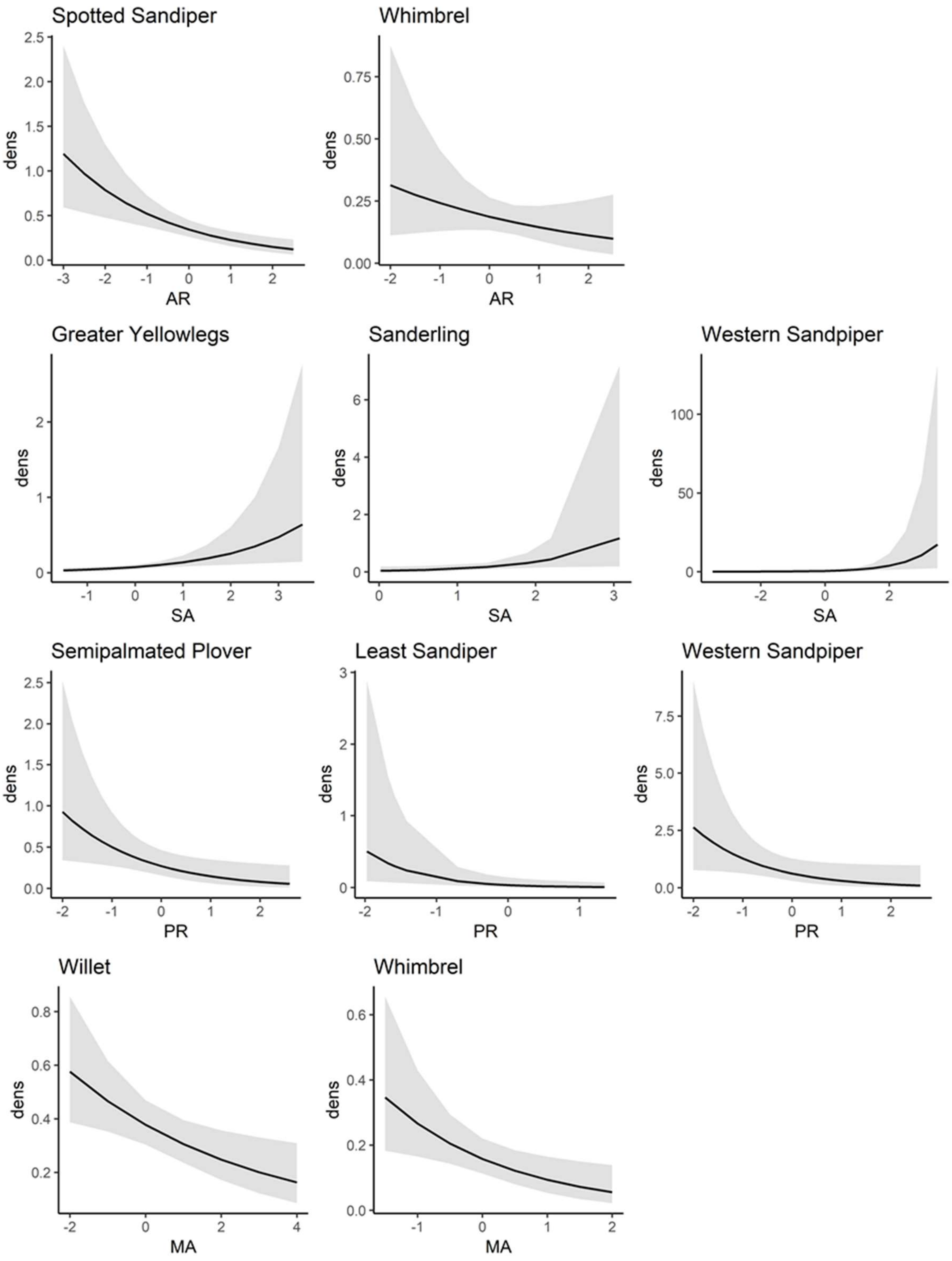


Figure 4.6. **Marginal plots of mean predicted effect of area, safety, productivity, marine gradient on density of non-breeding shorebird species. Only species with significative predictors from full Linear Mixed Models shown. Shading represent 95% CI**

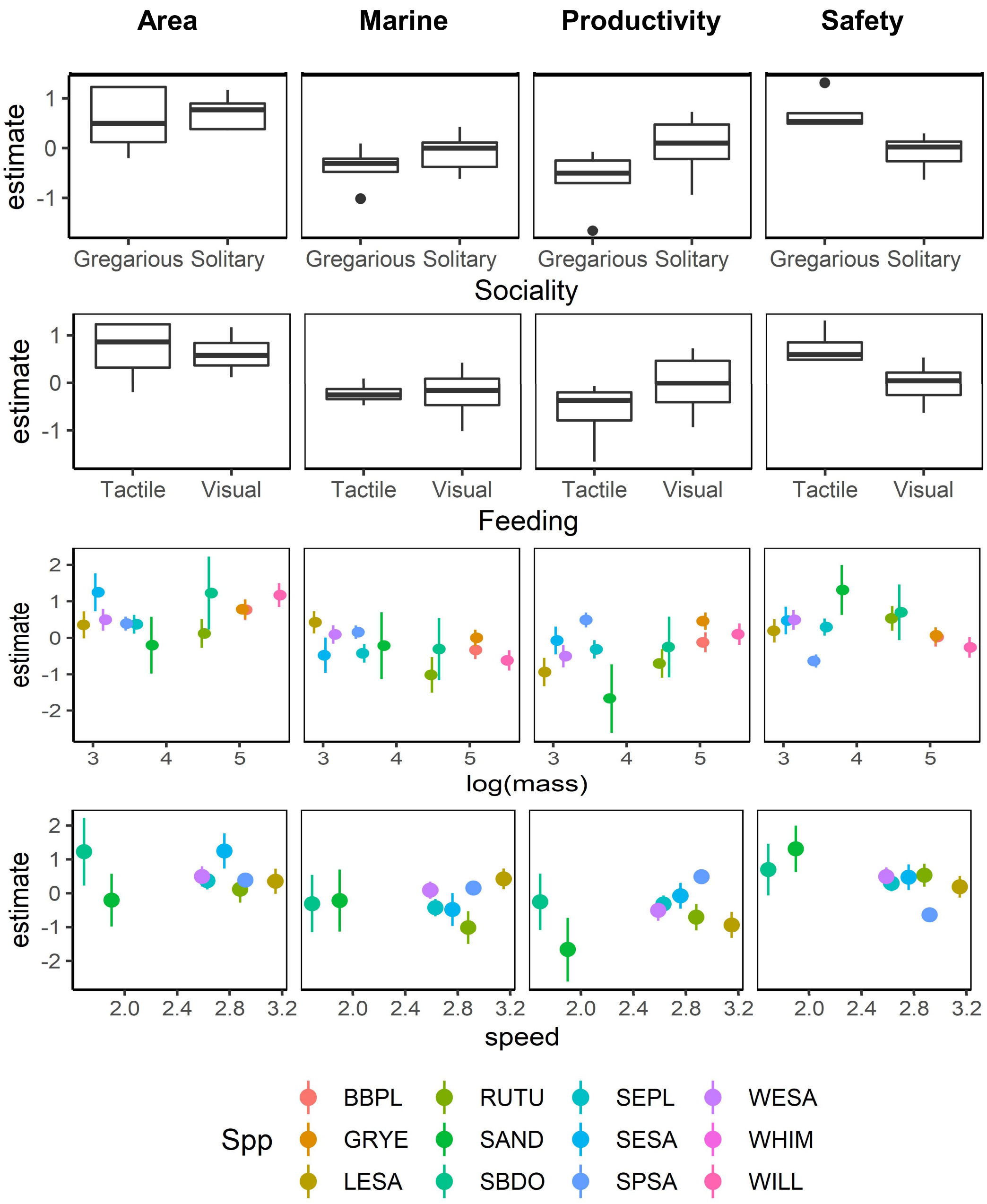


Figure 4.7. **Standardized slopes and 95% CI of the effect of habitat variables (AR = Area, MA = Marine, SA = Safety, PR = Productivity) on the presence of twelve shorebird species in relation to four ecological traits: sociality, feeding mode, log of body mass and take off speed**

4.5. Discussion

Surveys of the rich shorebird community across the Sanquianga-Iscuandé delta complex provided a robust database for examining species-specific predictors of distributions and the applicability of conceptual models addressing trade-offs in habitat choice based on habitat safety and escape performance, food availability, foraging mode and sociality. One size did not fit all; species varied in the factors accounting for their distributions. Because of this variation, we can now describe several broad patterns or syndromes of covarying traits that emerge from these analyses and compare these with our initial predictions about individual factors expected to drive distributions, based on first principles and previous literature. It is important to keep in mind that the effects being discussed are based on coefficients calculated as averages of sets of similarly parsimonious models for each species.

As expected based on previous work at migration and a few non-breeding sites, safety, defined as openness, was prioritized as a predictor of presence, with the prominent exception of the more territorial species (see below). Previous studies signal that shorebirds avoid foraging close to vegetation or manmade structures (Pomeroy et al., 2006; Verkuil and de Goeij, 2003). Early detection of predator attacks by shorebirds could be impaired while foraging in proximity to those visual obstructions. In some studies, those distances have been estimated to range from a few dozen up to few hundred meters (Pomeroy, 2006). If the same behavioural rules apply to mangroves, a large majority of the tidal habitat in our study area will be classified as dangerous. Even with high productivity, foraging opportunities will be lowered by proximity to cover in all but a few sections within this coastal landscape.

In contrast to the preference for safer sites, I found unexpected generally negative relationships with productivity. Combined with generally positive safety results this implies that the delta habitat is structured such that open areas are in general less productive, at least when also taking area and marine position into account. Such an intrinsic habitat trade-off has been suggested or implied in previous studies of shorebird foraging location trade-offs (e.g. Ydenberg et al., 2002, Pomeroy et al. 2006,2008, Duijns et al., 2009; Rourke et al., 2018). This study substantially expands the potential generality of such an environmental feature over a suite of species and at a new geographic scale. The shorebird species that face this trade-off have generally biased themselves towards safety. I infer that the marginal cost of additional danger is not offset by the benefits of additional resource availability. Our study was done on overwintering birds that were prioritizing survivorship over e.g. preparation for migration or breeding. Greater prioritization of foraging in richer patches could occur when life history considerations shift priorities towards more efficient resource acquisition, such as during pre-migratory periods.

The prediction that solitary species would more strongly utilize safer habitats was opposite to what I observed. Since territoriality intrinsically involves foregoing the safety of many eyes, and of selfish-herd effects, I hypothesized that these species would more strongly prefer more open habitat. The two most territorial species form an identifiable subgroup with common distributional features, as dramatically visible in a comparison of species-specific mean presence and density values (Fig. 4.2). Whimbrels and Spotted Sandpipers are thinly spread across the entire delta, and in contrast to most of the other species, have negative relationships with the habitat safety index and positive relationships with productivity (Fig. 4.3). The two species have similar environmental factor profiles for density as well (Fig. 4.4), which they also shared somewhat with Willets and Black-bellied plovers, the two next most territorial species (Fig. 4.2). Foraging in richer habitats could increase intake rate, and thereby provide both species greater time for individual vigilance. These would be cases were more efficient foraging provided an offsetting safety advantage. Foraging and vigilance rates could be examined empirically.

The large body size of Whimbrels may provide intrinsic protection against smaller avian predators. Spotted Sandpipers have the strongest negative relationship with the safety index, suggesting that it is a misnomer for this species. Spotted Sandpipers typically forage along water edges, and take advantage of rapid take-off speeds to fly into mangroves when threatened by predators, analogous to the behaviour of many ground-feeding passerines that prefer to forage closer to bushes (e.g. Walther and Gosler, 2001). This behaviour highlights an important difference between mangroves as visual barriers or edges and the features used to define distance to cover in studies at temperate sites. Mangrove forest provide porous edges that can provide safety from avian predators within them, in contrast to dykes or even salt marsh edges recognized in most previous studies of food-safety trade-offs in shorebirds. Thus, part of the counterintuitive results for at least these territorial species may reflect the forest nature of these edges.

Flight speeds may trade-off generally against prioritization of the use of open habitat (Fig. 4.7, bottom right corner). Although measurements were available for only 8 species, the two slowest species, Short-billed Dowitchers and Sanderlings had the highest coefficients for safety, while the two fastest species, Spotted and Least Sandpipers, had the lowest values. If such a relationship is real, it implies that the two tactics trade-off against each other in the species' overall danger management strategies (Lind and Cresswell 2006, Cresswell, 2008, Fernández and Lank, 2010).

Foraging mode showed relationships as predicted with safety, with more probing species favouring more open habitat. Body mass may show the pattern I predicted, with both large and small species having a lower prioritization of open habitats (Fig. 4.7). There may be a quadratic relationship.

4.6. Summary

I found support for all predictions with respect to prioritization of safety, with some caveats. Safety was the second informative variable, after an area effect, which can itself also be a measure of safety (Pomeroy et al., 2008) or represent other habitat features. Tactile foragers showed stronger relationships with safety gradients than visual forages, as did species with lower escape performance or intermediate size. Large species were most tolerant to danger and their distribution in general was affected by other factors. This contrasts with a lack of prioritization, and indeed generally negative relationships with respect to productivity, with the prominent exception of territorial species. The latter may favor utilizing more productive habitat to provide more efficient foraging opportunities that enable them to spend more time in vigilance. It is also the case, however, that the porous nature of mangroves alters the relationship between visual obstruction and safety as, since for some species mangroves provide protective cover from aerial predators

Chapter 5.

Joint distributions of migratory shorebirds: role of species interactions and shared environmental response on tidal flats in Southern Colombia

5.1. Abstract

Species distributions may be explained by dispersal ability, responses to the environment, and the outcome of biotic interactions (competition, commensalism, facilitation). Environmental and biotic filters can operate in the same or in contrasting directions and disentangling their role in the assembly of biological communities represents an active challenge in ecology. Migratory bird distributions are likely less by differential dispersal limitations and provide an opportunity to isolate the effects of the environment and biotic interactions on community structure. I used co-occurrence analysis to explore the randomness of species-pairs distribution and joint distribution modelling to compare the importance of environmental factors and species interactions on the assembly of migratory shorebird communities in mangroves of southern Colombia.

I showed that many pairs of shorebird species associate in a non-random, predominantly positive pattern. The variation in multivariate distribution is not explained by environment alone, but by a combination of environment and residual variation interpreted as attributable to interactions among the species themselves). In contrast with previous studies of community assembly, our study shows a larger role of residual variation. This result suggests that in addition to shared environmental responses, biotic interactions, particularly heterospecific attraction, play an important role in the assembly of non-breeding shorebird communities. Shared responses to safety-productivity gradients could be enhanced by heterospecific attraction to bias the distribution of shorebirds towards places with the presences of other species. As an alternative, species could share responses to an unknown environmental factor that was not included in the model. Co-occurrence and joint distribution modelling could be extended

to improve the understanding of the assemblage of migratory bird communities and to improve predictive modelling along global migratory flyways.

5.2. Introduction

The distribution of species is affected by climate and topography, habitat types, dispersal ability and geographic barriers, and species interactions (MacArthur 1958). Communities are assembled and species may co-occur when species can tolerate local environmental conditions (Kraft et al., 2015), and direct and indirect interactions with competitors and predators. Disentangling the role of multiple environmental and biotic filters on the composition of biological communities presents a conceptual and analytical challenge and remains an active pursuit within ecology (Pollock et al., 2014).

Traditional mechanistic models have focused on “assembly rules” that structure biological communities (Diamond, 1975). Environmental filters restrict community membership to species with specific functional traits (Kraft et al., 2015). Biotic filters may then explain the existence of forbidden pairs, perhaps because of competitive exclusion. In turn, the prevalence of some species combinations may emerge because they make efficient use of resources or facilitate the presence of each other (Brown et al., 2000; Wilson, 1999). However shared or contrasting responses to environmental filters can mask biotic interactions and complicate interpretation of community assembly patterns (Royan et al., 2016). Species could segregate in space because of competitive exclusion or simply because they inhabit different niche-space. Similarly, species could aggregate due to facilitation or mutualistic interactions or because they share responses to the environment (Cazelles et al., 2016).

An alternative model has been proposed that posits that species co-occurrence and community composition simply emerge as an outcome of random processes (Gotelli and Graves, 1996; Hubbell, 2005). Null models have been used to describe these non-deterministic patterns of species association (Gotelli et al., 2010, 1997). Null models make use of data on presence/absence (Ulrich, 2004) or abundance (Ulrich and Gotelli, 2010) data to build randomized matrices of species presence or abundance that can be compared with observed patterns. Connor and Simberloff (1979) used a null model to re-examine Diamond’s island bird communities and argued that patterns previously suggested to result from competitive exclusion could have emerged from random patterns of colonization and extinction. Similarly, Gotelli et al. (1997) used a null model to argue that assembly rules based on competition between species of the same genus were not needed to explain bird community assemblages in Australia. More recent implementations of null models use probabilistic modelling instead of matrix randomization (Veech, 2013b). Using this type of co-occurrence analysis, Royan et al. (2016) showed that 19 bird species on 100 waterways of Great Britain, segregated in a non-random pattern, with bird communities structured on riparian, slow-flowing and fast-flowing rivers. Although null models based on matrices or probabilistic model allow exploratory assessment and visualization of species associations, neither model the relationships between species explicitly (Royan et al., 2016) and both lack the ability to discriminate between the role of environment and biotic interactions (Ulrich, 2004).

Recent studies have employed a new approach, joint species distribution modelling (JSDM), to disentangle the effect of environment and biotic interactions on community structure (Warton et al., 2015). JSDMs are similar to traditional multivariate statistics in that they quantify relationships between species, but also incorporate species relationships with environmental variables (Warton et al., 2015). An additional advantage of JSDMs is their flexibility, in that they can use presence/absence or abundance data with a range of distributions (e.g. normal, Poisson, zero-inflated Poisson) and incorporate complex spatial and temporal structure in data ((Clark et al., 2016). JDSMs have now been used to assess the role of the environment and biotic interactions on the community assembly of birds (Sebastián-González et al. 2010, Royan et al. 2016), frogs (Pollock et al., 2014), fishes (Thorson et al., 2017, 2015), butterflies (Thorson et al., 2016), and soil bacteria (Niku et al., 2017). However, to date there is no consensus on the relative importance of biotic interactions and the environment in community assembly (Thorson, 2019).

Migratory birds are an ideal group to explore the role of environmental filters and biotic interactions in the assemblage of biological communities. Dispersal limitations relevant to plant communities (Wilson, 1999), animals on islands (Nakamura et al., 2015), and some other iconic examples of biological communities (Brown et al., 2000), simply do not apply to migratory birds. Migratory birds can occupy locations across large latitudinal, climatic and habitat gradients (Tellería et al., 2014). However, despite their dispersal abilities, migratory birds can have smaller wintering than breeding ranges (La Sorte et al., 2017), suggesting that local environmental or biotic interactions restrict their non-breeding distributions. Community ecologists have traditionally emphasized the importance of competition in the assembly of bird communities (Cody, 1974; Diamond, 1975; Gotelli and Graves, 1996). However, recent null models (Gotelli et al., 1997) and JSDM approaches (e.g. Sebastián-González et al. 2010) suggest that positive interactions may be more important in the structure of some bird communities. Positive associations could arise because birds use the presence of other species as a cue to asses habitat quality (Mönkkönen et al., 1997, 1990, Valone, 2007, 1989) Alternatively, the presence of heterospecifics could provide direct benefits associated with predator monitoring and dilution risk (Beauchamp, 2014).

In this study I examine the composition of the shorebird community that winter on the tidal flats of southern Columbia. I assess the strength of evidence for environmental filters and species interactions in driving non-breeding shorebird community assemblages. Using shorebird surveys at tidal flats within a large geographic area (ca. 1000 km^2) conducted between 2012 and 2017, I (i) examine whether patterns of species co-occurrence are random, or show evidence of negative or positive associations, (ii) use JDSMs to assess the role of environmental filters and species interactions on community assembly, and (iii) use correlation matrices and network diagrams to visualize the strength, direction and membership of associations between species pairs before and after controlling for environmental variables. I discuss the implications of my results for understanding the community assembly of migratory bird communities.

5.3. Methods

5.3.1. Shorebird occupancy and abundance

I conducted shorebird surveys at 136 tidal flats in Sanquianga National Park and Iscuande River Mouth, Nariño Department, southern Colombian Pacific Coast. The surveys that were conducted over six years (2012–2017) recorded the abundance of 18 shorebird species using standardized methods (Chapter 4). I excluded occasional species that were present in only 1–2 survey years (Collared Plover, Red Knot and Marbled Godwit), and those found in fewer than five sites (American Oystercatcher and Lesser Yellowlegs). I also excluded 9 sites where no shorebirds were observed.

5.3.2. Environmental drivers of species co-occurrence and shorebird community composition

For each of the 127 tidal flats, I collated data on environmental gradients known to influence presence and abundance of shorebirds in the study area (Chapter 4) and other shorebird studies (Guadagnin et al., 2009; Kober and Bairlein, 2009; Martínez-curci et al., 2015; Matthew E Reiter et al., 2015). These variables were: the area of the tidal flat (1.5–1800 ha); the distance from the center of the tidal flat to the nearest vegetation (0–660m), which provides an index of safety from predators; distance from the center of the tidal flat to the coastline (0–30 km), which represents the estuarine-marine gradient; and productivity measured as a 5-Year (2013–2017) Normalized Difference Vegetation Index (NDVI). NDVI is a common metric in assessing the productivity of terrestrial biomes (Alatorre et al., 2016) and tidal flats (Kim et al., 2014; Kromkamp et al., 2006). Variables were calculated using spatial analysis tools in QGIS software (QGIS Development Team, 2015) using a habitat classification map of the tidal flats generated with Google Earth Engine (Gorelick et al., 2017). In chapter 4 I presented additional details with respect to generation of the tidal flat map and environmental variables.

5.3.3. Modelling probability of Co-occurrence

I initially used a probabilistic modelling approach (see Veech 2013) to assess the probability of random, positive and negative co-occurrence between pairs of shorebird species, based on the overall presence/absence (present at least one year) data for 127 sites. This approach uses the probability of occurrence of each species to calculate the probability that species pairs co-occur, assuming that the distribution of each species is independent of others and compares these expected values with those observed. The model classifies species pairs as random or significant associations based on an alpha threshold of 0.05. I ran these analysis in R software (R Core Team, 2017b) using the package cooccur (Griffith et al., 2016).

5.3.4. Modelling co-occurrence and co-abundance in relation to environment

Co-occurrence modelling allows exploratory assessment and visualization of associations, but not modelling the relationship with environment (Royan et al., 2016). I used a Generalized Linear Latent Variable Model to examine the multivariate occurrence or abundance of shorebirds in relation to environment variation and residual variation attributed to species interactions and other sources (Warton et al., 2015). Generalized Linear Latent Variable Models (GLLVM) are joint distribution models, that, like ordination techniques, summarize multivariate data into a lower number of dimensions, in this case “latent variables”. Latent variables store the relationships between species and these can be compared between “species-only” models (“residual” models in JSDM terminology), and models that also include the effects of the environmental variables.

I fitted GLLVMs to the multivariate data of 6-Year presence/absence or abundance (adjusted by sample size and rounded to the nearest digit) of thirteen shorebird species across 127 sites. The models examining the presence/absence data were fitted using a binomial distribution, while those examining abundance were fitted using a zero-inflated Poisson distribution. Models fitted with a zero-inflated Poisson distribution outperformed those fitted with a negative binomial distribution with a better fit (lower AIC_c) and more uniform distribution of residuals than models with Poisson (Appendices G, H). All models included tidal flat as a fixed site effect. Each model set included a “species-only” model and a model that included both species and the environmental variables (area, safety, productivity and estuarine gradient). In “species-only” models, the latent variable is constructed using the multivariate response (either binomial or abundance) constrained by fixed tidal flat effects. In “environment” models, the latent variables are also constrained by the environmental variables. I assessed the support for the two models within each set by comparing the AIC_c, corrected for small sample sizes The log-likelihood functions used to calculate the AIC_c for the models were calculated using variance approximation and Laplace approximation, as recommended for binomial presence/absence data and over dispersed GLLV respectively (Niku et al., 2017). GLLV models were implemented with the gllvm package for R (Niku et al., 2018, 2017).

Species (residual) correlations and environmental correlations were extracted from the relevant presence ((GLLVM-binomial with fixed site effects) and abundance (GLLVM-ZIP with fixed site effects) models. Multivariate species (residual) correlations were visualized using correlograms and circular diagrams. Species (residual) correlations were extracted from the presence (GLLVM-binomial with fixed site effects) and abundance (GLLVM-ZIP with fixed site effects) and visualized using correlograms and circular diagrams. Correlograms show the strength (R) and direction of the correlations (positive, negative) between pairs of species. Circular diagrams are a type of network diagram (Gu et al., 2014) that in addition to showing the directionality and magnitude of the associations, highlight the change in multivariate connections between nodes (species) in different correlation matrices. I use these methods of visualizing the results of the analyze to (i) elucidate the positive, negative and random patterns in community structure, (ii) illustrate the effect of including environment on these patterns and (ii) and explore the strength and directionality of relations between species. Visualizations were done in R, using corrplot for correlograms (Taiyun Wei and Simko, 2017), and circlize package (Gu et al., 2014) for circular diagrams.

5.4. Results

5.4.1. Co-occurrence modelling

A probabilistic model of co-occurrence of shorebirds in southern Colombia revealed that a large proportion of species associations were positive (n = 52, 66.7%), many were random (n = 25, 32%), and only one was negative (n = 1, 1.3%, Fig. 5.1a). Whimbrel and Spotted Sandpiper have the largest numbers of random associations, 100% in the first case and 93% in the second, while other species have less than 50% random associations. Overall only a fraction of associations was random (33%), while a large proportion (67%) showed non-random co-occurrences (Fig. 5.1a). The species-pairs that occurred together more than expected by chance included the three species of plovers (Black-bellied, Wilson’s and Semipalmated), some (but not all) of the small sandpipers (e.g. Western Semipalmated Sandpipers and Sanderling), and two of the three tringines (Willet and Greater Yellowlegs. Interestingly, co-occurrence patterns of species pairs involving the two most common species in the study area (Whimbrel and Spotted Sandpiper) were predominantly random. The only species pair that occurred less than expected by chance was the Spotted Sandpiper and Sanderling (Fig. 5.1b). Taken together the results from co-occurrence analysis indicate that (i) the species composition of shorebird communities largely followed non-random patterns of community assembly, (ii) non-random pattern of community assembly were largely due to positive associations between species, and (iii) many positive associations were between species that shared physical traits.

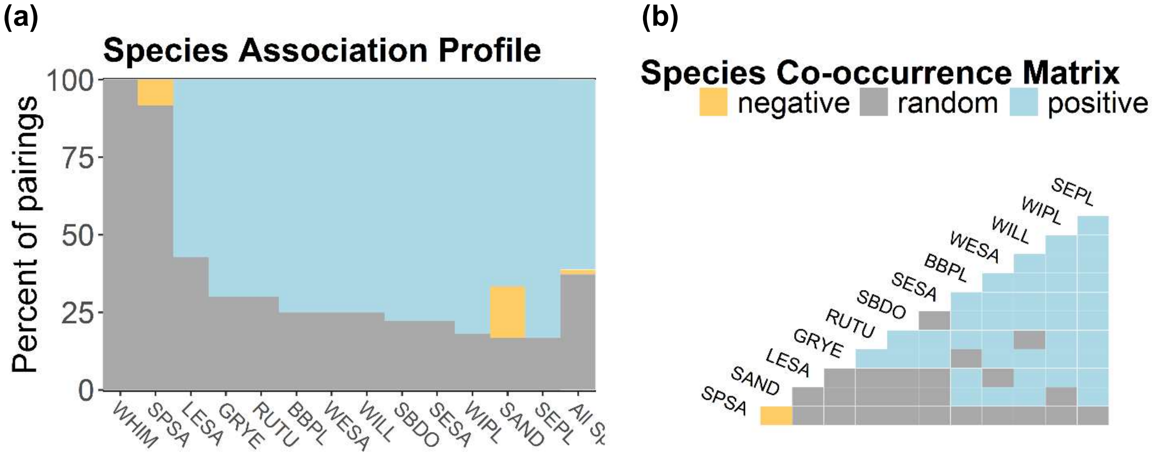


Figure 5.1. **Species association profile for 13 species of shorebirds occupying 127 tidal flats in southern Colombia. The species association profile (a) shows the percentage of species-pairs that are random, positive or negative, while the species co-ocurrence matrix (b) shows the association between each species-pair. Excluding Whimbrel for which all pairings are random, Sanderling and Spotted Sandpiper are the only pair with a negative association (percent of pairings appear larger in Sanderling, because this species is less frequent, i.e. has less pairing than Spotted Sandpiper).**

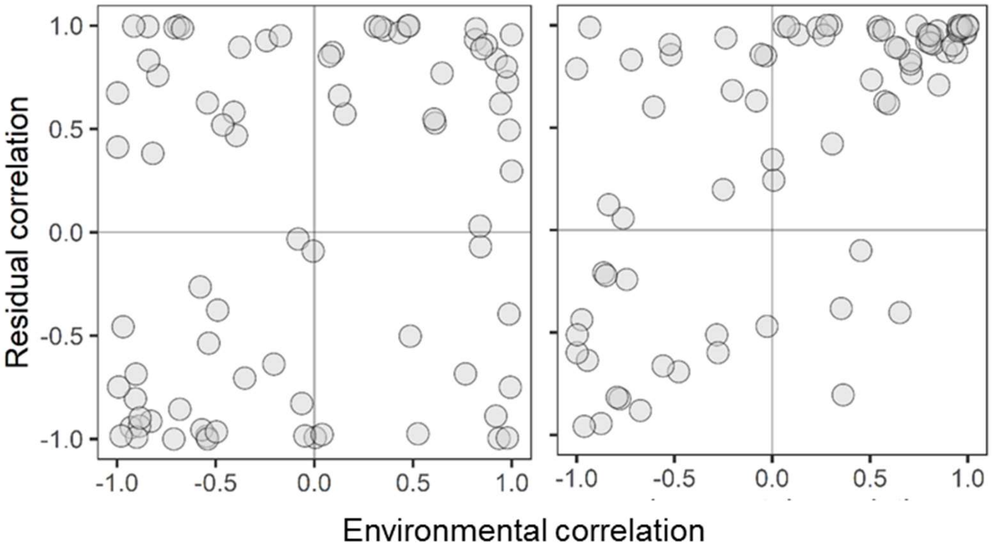
5.4.2. Co-occurrence and co-abundance in relation to environment

The GLLV models examining multivariate presence and abundance of shorebirds showed that species interactions and environmental responses were both involved in the assembly of these communities. The models including species and environmental variables receive far more support that the species-only models (presence, species + environment (Appendix G).

The GLLV model examining multivariate presence/absence data provided evidence for positive and negative associations between species. Residual correlations ranged widely and divergently, with the majority being higher than 0.5 or lower than -0.5 (Fig. 5.2a). Species responses to the environment were also divergent, with species -

pairs being equally likely to show shared (environmental correlations >0.5) and opposing (environmental correlations <-0.5) responses to the environment. Therefore, species co-occurred because of positive species interactions and shared environmental responses (29% of species-pairs are in the top right quadrant of Fig. 5.2a) and did not co-occur because of negative species interactions and opposing environmental responses (30% of species-pairs are in the bottom left quadrant).

In contrast, the GLLV model examining multivariate abundance data provides evidence that species associations are more likely to be positive than negative (Fig. 5.2b). Residual correlations are more likely to be >0.5 than <-0.5. However, species responses to the environment were as likely to be shared (>0.5) as opposed (<-0.5;). Consequently, species co-abundance was frequently high because of positive species interactions and shared environmental responses (45% of species-pairs are in the top right quadrant of Fig. 5.2b), and co-abundance was only occasionally low because of negative species interaction and opposing environmental responses (5% of species pairs are in the bottom left quadrant)



(a) **(b)**

Figure 5.2. **Modelled environmental and residual correlations after GLLVM on presence (a) and abundance (b) multivariate data of 13 shorebird species on 127 tidal flats. Each dot represents a species pair**

Taken together, the residual correlations from GLLV models show that (i) positive and negative interactions are prevalent in determining the composition of shorebird communities, but that (ii) positive interaction between species play a more important role in determining covariation in abundance.

Correlograms that provide a visualization of the strength of correlations between 78 pairs of shorebird species confirm that the assembly of shorebird communities is predominantly driven by non-random processes (Fig. 5.3). GVLM species-only models examining multivariate presence/absence (Fig. 5.3a) suggest negative and positive associations between species pairs are equally likely. In these models, the strength of the residual correlations is reduced after controlling for the environment (Fig. 5.3b) demonstrating that some positive and negative patterns of co-occurrence are driven by shared or opposing responses to the environment.

GVLM species-only models examining multivariate abundance also suggest that the non-random processes drive the abundance of species in shorebird communities but suggest that positive associations are more prevalent than negative associations (Fig. 5.3c). The strength of the positive residual correlations is reduced, and negative residual correlations strengthened after controlling for the environment, illustrating that shared responses to the environment can exaggerate positive species interactions and mask negative species interactions.

Taken together these correlations can be used to investigate the direction and strength of associations between species with different functional or taxonomic membership. For example, 3 plovers (Semipalmated, Wilson’s, Black-bellied) and 2 sandpipers share the largest number of positive interactions, in all, but particularly in “species-only models” (Figs. 5.3a–5.3c). Several of those relationships reduce in strength but remain similar in direction with the inclusion of environmental variables. These results could be interpreted as assembly mechanisms regulating joint-presence and joint-abundance shared across sets of species (e.g. plovers and sandpipers). Meanwhile Whimbrel and Spotted Sandpiper had the largest proportion of negative associations with other shorebirds species, particularly in abundance models (Figs. 5.3c–5.3d). Many of these negative associations may result from differential patterns of distribution, suggesting a role for shared environmental responses between these two species and opposed to other species (Chapter 4).

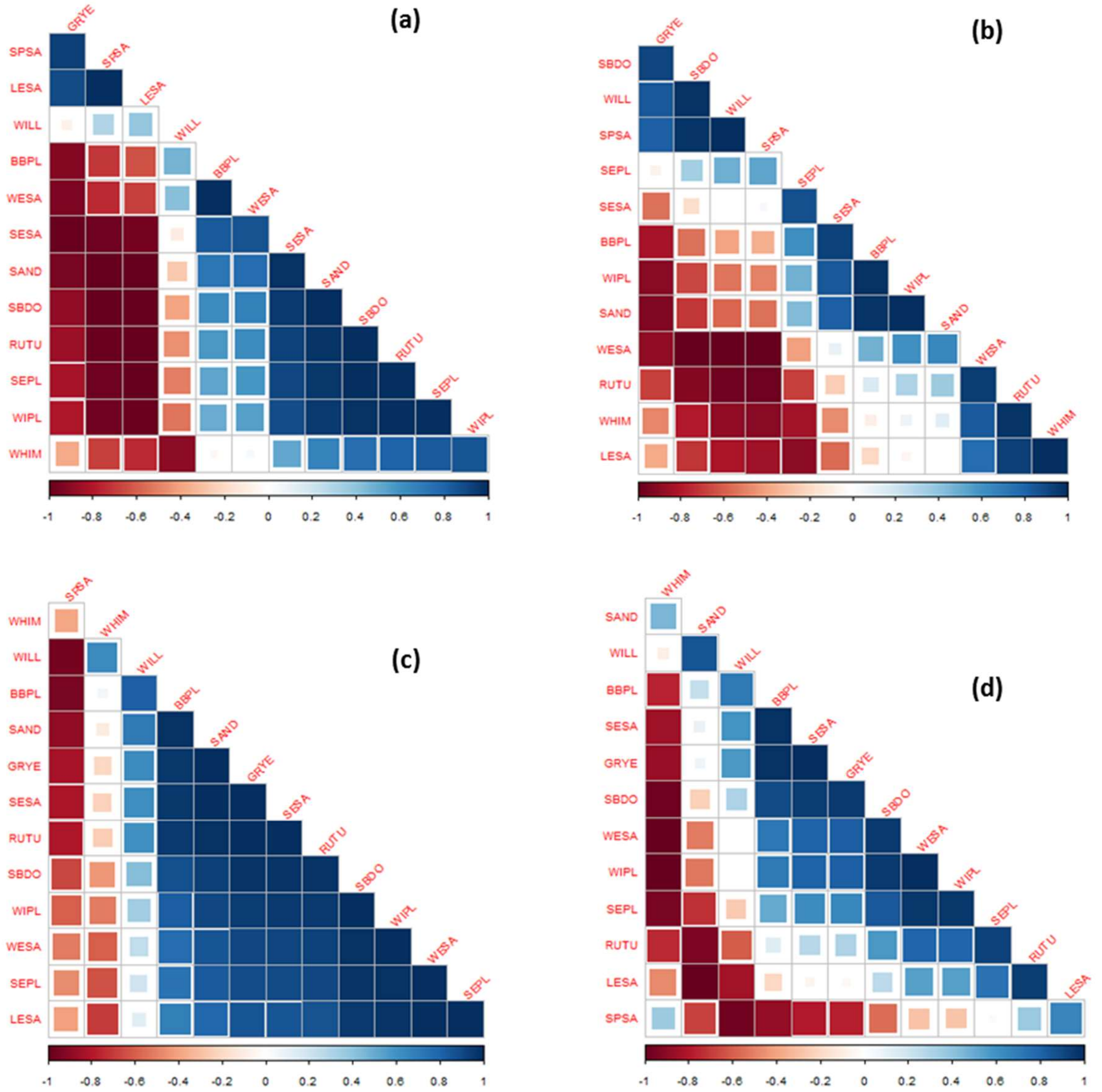


Figure 5.3. **Correlation Matrices after fitting Binomial (a+b) and Zero-inflated Poisson (c+d) GLLV models to multivariate presence and abundance data for 13 shorebird species. On the left (a and c) "species-only" models and on the right (b and d) species and environment. All models include fixed effects of sampling site. Stronger correlations are represented by darkerdarker red (negative) ordarker blue (positive) shading. Species are ordered by factor score, such that positively correlated species tend to be close together.**

Circular network diagrams built from residual (species-only) and environmental (species and environment) correlation of multivariate presence and abundance confirm the importance of non-random processes in the assembly of shorebird communities (Figs. 5.4 and 5.5). Correlations from GVLM species only models of multivariate presence/absence data suggest that there are strong positive and negative associations between species (Figs. 5.4a, c). Correlations from GVLM species only models of multivariate abundance data suggest strong positive associations between species are more common (Figs.5.5a, c).

Controlling for shared or opposing responses to the environment does not radically alter conclusions about the role of positive and negative species interactions in patterns of shorebird co-occurrence (c.f. Figs.5.4a, b and Figs.5.4c, d). In contrast, controlling for species responses to the environment alters the strength and direction of species interactions (they become weaker and more negative; c.f. Figs. 5.5a, c and Figs. 5.5c, d). This result illustrates that shared responses to the environment can mask negative interactions between shorebird species.

Overall, the results from correlations extracted from the GVLM models showed that: (i) models based presence of shorebirds have more divergent patterns of non-random assembly, with stronger and more negative interactions than patterns based on abundance; (ii) species abundance was strongly and positively correlated, a pattern that remains after including environmental variation; (iii) shared environmental responses may drive many of the positive associations and mask the negative associations found between shorebird species abundance; (iv) some sets of species with similar associations (e.g. positive association between plovers and some species of sandpipers) were stable after the inclusion of environmental variation; and (v) the most common species (Whimbrel, Spotted Sandpiper) do not have strong interactions or have predominantly negative interactions with other shorebird species.

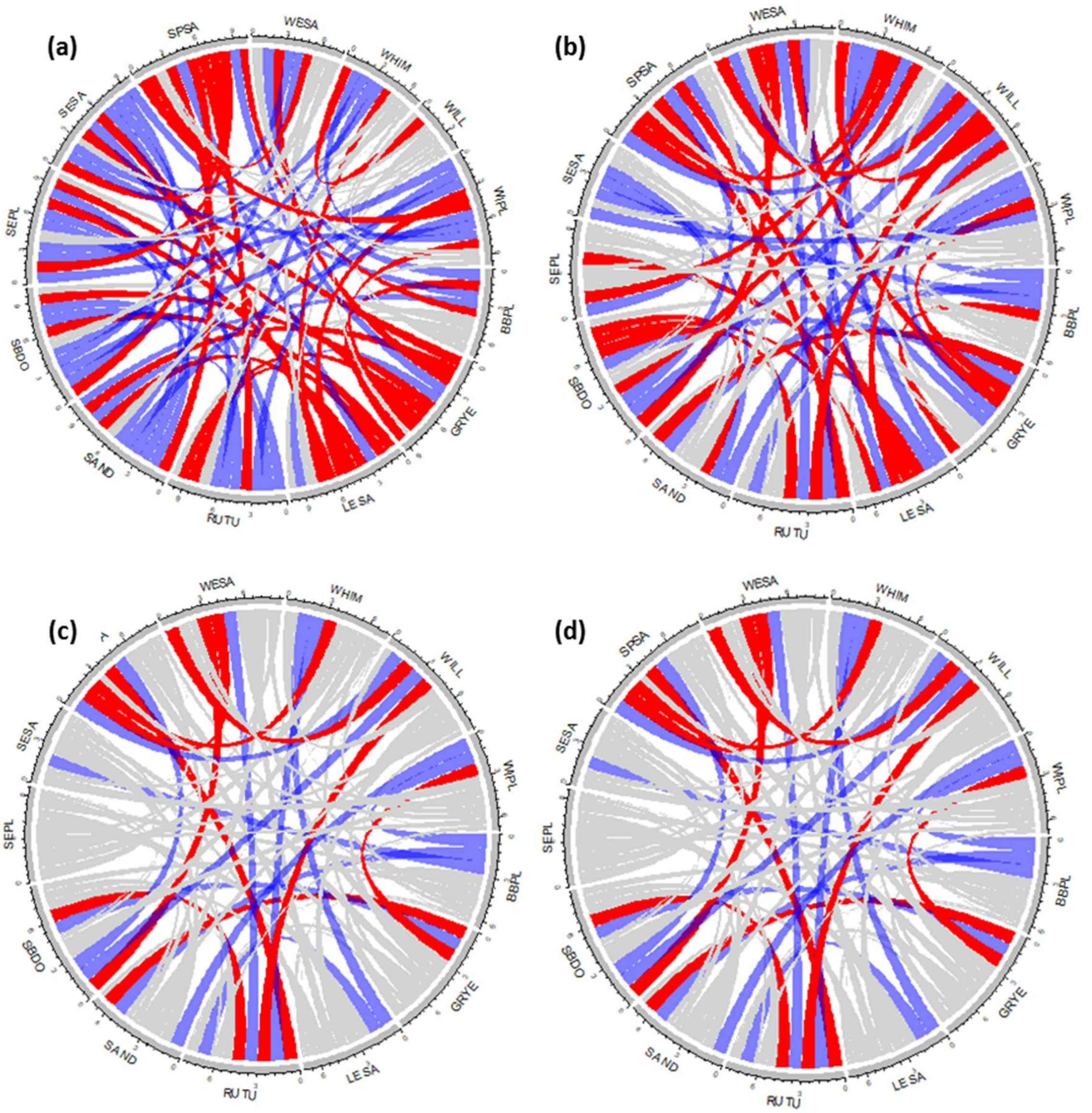


Figure 5.4. Circular diagrams with connections (ribbons) between nodes (shorebird species) showing positive (blue) and negative (red) correlations after GLLVM models of multivariate presence. Top diagrams (a, b) highlight correlations with R < -7 or R > -7 while bottom plots (c, d) increase the threshold to R < -9 or R > -9. Left panels (a, c) represent “species only” models and right panels (b, d) models constrained by environment.

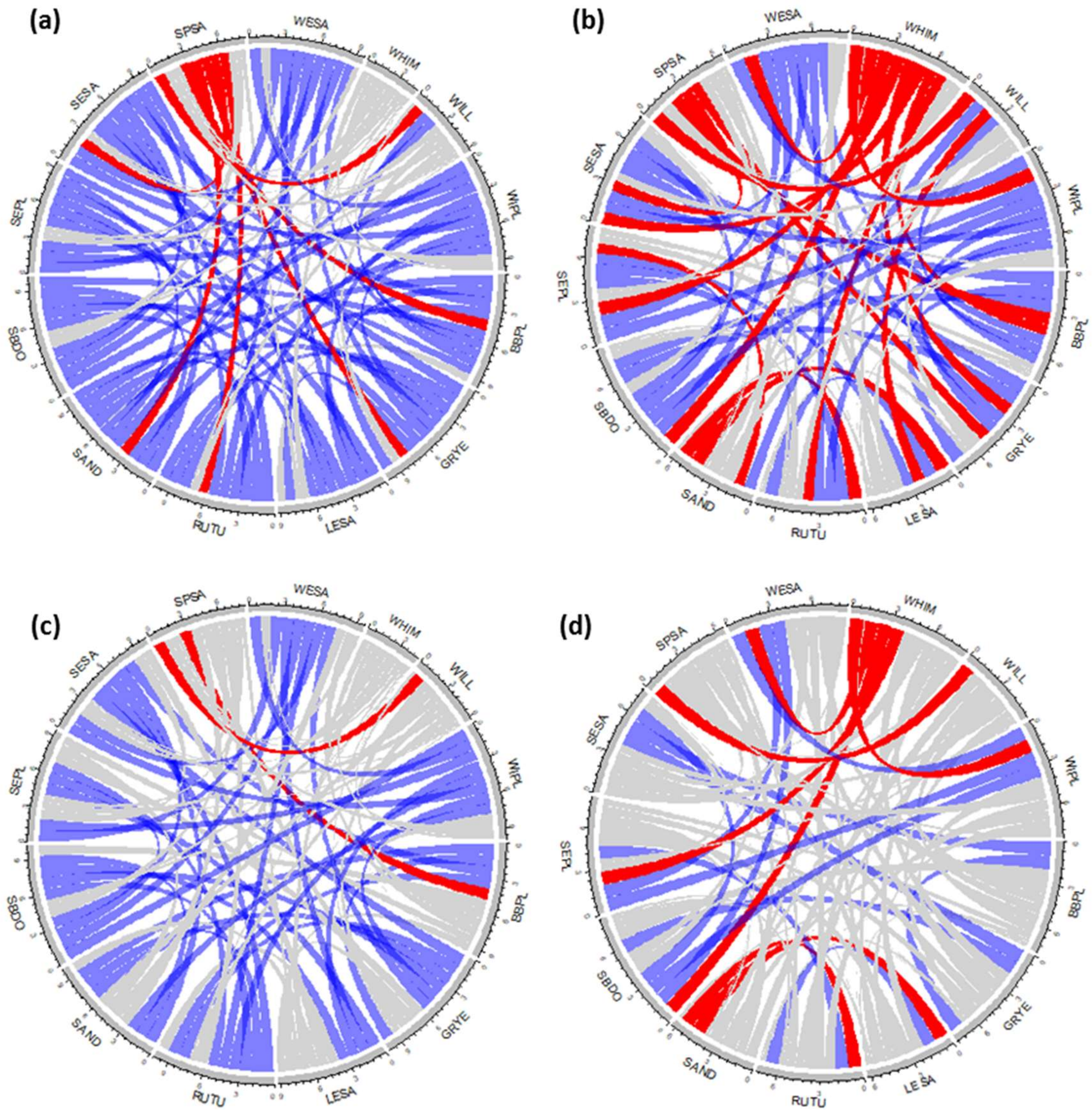


Figure 5.5. **Circular diagrams with positive (blue) and negative (red) correlations between shorebird species after GLLVM models of multivariate abundance. Left panels (a, c) represent "species only" models and right panels (b, d) models constrained by environment. Top diagrams (a, b) highlight correlations with R < -7 or R > -7 while bottom plots (c, d) increase the threshold to R < -9 or R > -9.**

5.5. Discussion

Using a large-scale survey and a novel technique to model the covariation of species distributions I examined the relative importance of shared or opposing responses, competition and positive species interaction in structuring non-breeding shorebird communities. First, I found that many shorebird species exhibit non-random patterns of co-occurrence and co-abundance in tidal flats of southern Colombia, which in most cases involved positive associations. Second, I found that while environmental predictors contributed to the multivariate distribution of shorebirds, residual variation, attributed to species interactions or unaccounted environmental variation, was similar of perhaps stronger, suggesting that positive species interactions could play a role in the assembly of nonbreeding shorebird communities in tidal flats of southern Colombia.

Null models have been used to evaluate the hypothesis that communities are assembled at random (Gotelli and Graves, 1996). In this study I found evidence of the prevalence of non-random patterns of distribution between communities of non-breeding shorebirds. Several pairs of species were more likely to occur than would be expected by chance. My results contrast with other studies that suggest than random patterns are prevalent within avian communities (Gotelli, 1999; Gotelli et al., 1997). My results are however consistent with more recent studies that have shown non-random patterns of co-occurrence in river bird communities in the UK (Royan et al., 2016), and buntings in Spain (Bastianelli et al., 2017a). Null models do not allow the role of species interactions and species response to environmental variables to be partitioned.

Joint Species Distribution modelling provides a new statistical tool to identify the contribution of species interactions and environmental filters in species distribution and assembly of communities. Using this approach, I confirmed the presence of non-random associations between species pairs and found that shared responses to the environment play an important role, but that species interactions also contribute. Several species appear to make habitat selection decision based on environmental variables that reduce predation risk (area of the tidal patch and distance to cover) as seen in Chapter 4. I found that several species of shorebirds, particularly sandpipers and small plovers were positively associated with each other, and most of these associations could be attributed to shared environmental responses. Previously (chapter 4) I have shown strong correlated response of the same groups of shorebirds to gradients of productivity and safety.

The JDSM approach also provides evidence for a pluralistic model of community assembly in overwintering shorebirds. Most associations that could not be attributed to shared responses to the environment were positive (Fig. 5.4 and Fig 5.5). These results contrast with early studies that show a larger contribution of either shared environmental responses (Royan et al., 2016) or of species interactions (Sebastián-González et al., 2010, Bastianelli et al., 2017b). In congeneric species of granivorous birds (Bastianelli et al., 2017b), negative interactions were predominant, but positive interactions were common across waterbird species (Sebastián-González et al., 2010). My results support a dual explanation for the joint distribution of non-breeding shorebirds involving both, shared environmental responses and species interactions, mostly positive.

These results were aligned with previous studies of bird communities were positive associations are prevalent (Ovaskainen et al., 2017; Sebastián-González et al., 2010) and suggest that heterospecific attraction (Mönkkönen et al., 1997, 1996) could provide fitness benefits and play a role in the patterns of community assembly in nonbreeding shorebird communities. In addition to potential benefits from predator monitoring and avoidance associated to multispecies flocks (Terborgh, 1990), species looking for places to forage can exploit public information about the location and behaviour of other foraging birds (Valone, 2007, 1989). Shorebirds co-occurring with individuals of other species could increase their relative feeding gain while potentially reducing costs of interference with conspecifics (Thomson et al., 2003). Environmental factors linked to safety and positive interactions between species related to safety may both play a role in these positive patterns of non-breeding shorebird assembly.

I found some evidence of negative associations between shorebird species in southern Colombia. Avian communities have traditionally been thought to be structured by competition. Although negative interactions were not as immediately obvious as the positive interactions, I found evidence for negative interactions between Spotted Sandpiper and Whimbrel, the most frequent species in the study area, with at least 6 species each (Fig 5.4 and 5.5). While most shorebirds are biased toward large open sites, these two species are dwellers of small tidal flats associated with mangrove forests (Johnston-González and Abril, 2018; Reed et al., 2013; Zharikov and Milton, 2009). Divergent environmental responses then could explain those contrasting patterns. An alternative explanation is that those species are excluding other shorebirds from these sites, which are also more productive (Chapter 4). Both Whimbrel and Spotted Sandpiper are highly territorial (Reed et al., 2013; Skeel and Mallory., 1996) and in the study area there is evidence of agonistic interactions toward conspecific (Abril, 2011) and heterospecifics (Ruiz-Guerra, 2004). Constraining GLLVM (Fig. 5.3d) by environment to species-only models, some of these negative associations flip direction (i.e. Spotted vs. Least sandpiper and Whimbrel) and some other associations appear (Spotted Sandpiper and Willet), suggesting that some negative associations could be masked by shared environmental responses.

In this chapter I have compared the importance of the environment and species interactions in the assembly of non-breeding shorebird communities in southern Colombia. I used two novel modeling frameworks: probabilistic species co-occurrence modelling and joint distribution modelling to assess the proportion of the variation in distribution of communities attributed to environmental variables versus species interactions. I showed that shorebird species associated in non-random, mostly positive patterns and that some of these associations occur in species sharing functional traits (e.g., plovers, sandpipers). Co-occurrences and co-abundance of species could be attributed to a combination of shared environmental responses, but also to species interactions. This chapter highlights the potential role of heterospecific attraction in the assembly of shorebird communities in contrast with other groups where shared responses to the environment or negative interactions appear to play a stronger role. Joint distribution modelling offers the potential for improving species distribution modeling and understanding assembly patterns of biological communities.

Chapter 6.

General discussion

Habitat selection in shorebirds involves a hierarchy of decisions that operate at different spatial scales (Jones, 2001b; Pickens and King, 2014) and incorporates information from multiple dimensions, including environmental gradients (Cardoso et al., 2013), heat and water balance (Rogers et al., 2006), food availability(English et al., 2017), safety from predators (Lank et al., 2003), parasites (Alerstam et al., 2003; Gaidet et al., 2012), and the abundance of hetero- and conspecifics (Taylor et al., 2010). Piersma (2012) summarized these axes of habitat selection in four dimensions: safety, food, heat-water balance and social aspects. Safety from predators has been found to influence habitat selection of shorebirds in the breeding grounds (e.g. Colwell et al., 2011; Cunningham et al., 2016; Laidlaw et al., 2015) and on migration (e.g. Hope et al., 2011; Pomeroy et al., 2006). In comparison, the role of safety from predators has been generally overlooked in studies examining habitat selection on the wintering grounds (Cardoso et al., 2013; Kober and Bairlein, 2006; Tavares et al., 2015). Exceptions include studies in the Tagus estuary in Portugal (Martins et al., 2015), Banc d'Arguin, Mauritania (van den Hout et al., 2009), and Baja California, Mexico (Fernández and Lank, 2010).

This thesis explores the influence of predation risk in the distribution of shorebirds in an important non-breeding location in southern Colombia. I have focused attention on two components of 'predation risk': (1) vulnerability - a characteristic of individual shorebird and species related to their ability to detect and escape predators; and (2) habitat danger - features of the environment that facilitate or impede detection of predators (Lank and Ydenberg, 2003). I explore how differences in vulnerability inherent to body size, feeding mode and escape performance could affect the vulnerability of shorebirds (Chapter 3), compared the role of habitat danger with other environmental drivers in the distribution of species (Chapters 2 and 4) and contrast the role of danger and other environmental features with that of species interactions in the distribution of species and assembly of non-breeding shorebird communities (Chapter 5).

6.1. Main findings

In Chapter 2, I assessed how the location of Whimbrel nocturnal roosting sites could be explained by the interplay between food and danger landscapes. Nocturnal roosts were located on mangrove islands isolated from the mainland, in the center of this extensive tropical delta with ready access to a larger area of tidal mudflats, and thus feeding territories, compared with potential alternative locations. Food-danger landscapes accounted for the geographic distribution of the roosts, but not for the large number of individuals in single locations. The large concentration of Whimbrels at a particular site could mean that individuals make the same decision given the same environmental information or that some individuals use the presence of conspecifics when selecting a roost site (Nocera et al., 2006; Stamps, 1988).

In the next Chapter I expanded to the entire non-breeding shorebird community and studied the allometry of escape performance. I showed that wing loading increases with body mass (within species) and with log body mass (between species). Species with lower wing loading have faster take-off flights, but there is high variation in the slopes of the interspecific relationships. Species with lower escape performance (i.e. heavier wing load and slower take off speed) were expected to show higher flight initiation distance (FID). Although mean flight initiation distance tends to decrease with higher take-off speeds, there was considerable overlap in the magnitude of these responses and the evidence for a relationship with take-off speed was weak. Wing load was a better predictor of FID but did not explain all the variation on these responses. Other factors not addressed in the experimental setup, including social context (presence and distance to other individuals), distance to cover and habitat quality could account for some of those results.

In Chapter 4, features of the environment linked to safety from predation (i.e. tidal flats with larger area and distance to cover) were found to be important predictors for occupancy by and the density of shorebirds. Interestingly, these habitats were used despite being less productive, emphasising the importance of safety compared to food availability in habitat selection by wintering shorebirds. The few species that did not conform included Whimbrel and Spotted Sandpiper. The first species is large and perhaps less vulnerable to the avian predators present in the area (Peregrine Falcon, Merlin), while the second has faster take-off speeds that aid in escape into nearby mangroves. Such use of mangroves as protective cover from predators that predominantly hunt in the open may be an alternative non-exclusive explanation for species being able to inhabit sites near the cover.

Chapter 5 summarized the patterns of joint distribution between pairs of shorebird species. I took advantage of the multi-year dataset on occupancy and abundance from Chapter 4, but instead of focusing on single-species responses, I studied the multivariate response of the whole community to environmental variation. I used two relatively novel techniques: (1) co-occurrence analysis and (2) joint distribution modelling, to identify random associations of species pairs, and to partition patterns of environmental versus residual variation. I confirmed the importance of non-random processes in structuring the distribution of shorebirds and showed that habitat selection by shorebirds is influenced by environmental features related to the safety from predators, and to positive and negative interactions with heterospecifics. Positive interactions appeared more important than negative interactions in the structure of non-breeding shorebird communities. Positive interactions could arise due to the exploitation of public information (i.e. presence of heterospecifics used as cues about habitat quality), or due to benefits associated with vigilance and dilution of predation risk. Negative interactions likely due to competitive exclusion were sometimes masked by species having shared responses to the environment.

6.2. Significance

Understanding how changes in habitat affect the range and persistence of species is central to the science and practice of conservation. The degradation of the non-breeding habitats that extend across temperate and tropical regions is one of the main hypothesis for the population declines of birds across migratory flyways (Pearce-Higgins et al., 2017; Senner et al., 2016a; Sutherland et al., 2012). Assessing this hypothesis requires information on the spatial extent of habitats (Murray et al., 2014), and the reliance of species on them (Studds et al., 2017). Thus, identifying factors that influence habitat use and reflect habitat quality from the perspective of shorebirds (e.g. resources, danger, social interactions) will help us predict the consequences of habitat change. A first step includes gathering information on the location and quality of remaining habitats, and proactively identifying key non-breeding areas, using predictive modelling. Remote sensing of shorebird habitat will help to fill this gap. The recent availability of tidal maps with global coverage (Murray et al., 2018), pre-compiled open-source analysis routines (Kwok, 2018) and user-friendly spatial analysis platforms (Murray et al., 2017) opens a new world of possibilities for large-scale description and analyses of tidal habitats, replacing time-consuming and expensive ground-based approaches.

I highlight two results from this thesis can be incorporated into mapping exercises to inform conservation effort. Both suggest that a fuller understanding of habitat selection decisions requires consideration of predators. First, using distribution and behavioural data, I have shown that shorebird species with different morphologies and escape performances react differently to environmental gradients (Chapter 3). Beyond area per se, the safety gradient weights habitat decisions by these migratory shorebirds heavily enough such that primary productivity, a proxy for food availability, turned out negatively associated with their distributions. Most shorebird species and functional groups responded to the effects of all those gradients combined. However, several species distributed preferentially towards some of those axes. Second, I found positive interactions that suggest that predators also act on behavioural decisions reflected in distribution patterns (Chapter 5). The direct implication is that shorebird management should consider a stronger focus on community rather than the species level. Management of shorebird communities requires the development of joint distribution models that in addition to environmental features (as in traditional species distribution modelling) can capture the direction and strength of interactions between species.

Joint distribution models are an alternative to species-distribution models to capture the multivariate nature of survey data and highlight some potentially relevant interactions between species. Here I showed how joint species-distribution models that incorporate presence/absence and abundance data could be used to infer the overall response of the community to environmental drivers, but also the strength and direction of associations between species, and hence a potential role for biotic interactions in structuring communities (chapter 5). Such interactions are determinant in shaping current distribution of migratory birds and understanding their future changes (Austin and Rehfisch, 2003). Responses of species to current and future habitat changes could be the product of direct environmental effects and those mediated through the interactions with other species. We have come a long way in this direction, but the next step to fully understand the response of shorebirds to habitat changes, beyond the direct response to the environment, could be to incorporate related species using joint distribution models.

6.3. Future directions

Predation has direct fitness consequences and shorebirds are expected to maximize habitat decisions that account for it (Cooper and Frederick, 2007). Predation danger (habitat) and vulnerability to predators (intrinsic) are two key components of risk management by shorebirds (Lank and Ydenberg, 2003). By choosing a habitat that reduces predation danger or increase chances to detect and escape predators, shorebirds could maximize their fitness. But different predators could exert pressure in multiple directions, or in other words, could create multiple predator landscapes that overlap in the same area. Similarly, multiple shorebird species could respond to these predator landscapes with an array of antipredator strategies suited to their own morphology and escape performance (Barbosa, 1995).

One example of these multiple habitat decisions is offered by the Whimbrel. At night this species gets extremely concentrated in few locations, roosting within mangrove islands (Johnston-González and Abril, 2018). By roosting on the roots of Red Mangrove trees, a substrate that offer high structural complexity, Whimbrels could prevent attacks from Owls or from Falcons hunting at dawn and dusk. Through the large stretches of water between the roosts and the mainland, Whimbrels could prevent an incursion from terrestrial predators (i.e. possums, feral and wild felids and dogs) (Chapter 2). These nocturnal distributions, sometimes involving 60% of the local population in a single stretch of few hectares of mangrove forest (Johnston-González et al., 2006) contrast heavily with the widespread pattern exhibited during the day. Whimbrel is the most abundant shorebird (6500–8000 individuals) in the mangroves of southern Colombia and it occupies the most tidal flat patches (>85%) of any other shorebird in the area. How this species became so widely distributed in the area and why its feeding distribution is so contrasting between day and night could exemplify principles of risk management. In the Banc d’Arguin, Whimbrel and other large bodied species were targeted and killed by large falcons more frequently than expected by their abundance (Van Den Hout et al., 2008). But the diversity, abundance and size of falcon species in Mauritania is larger than in Sanquianga-Iscuande (Ruiz-Guerra et al., 2007). We lack observations of attack rates for the study area, but predator encounter rates of

Merlin and Peregrine Falcon are low (0.2 birds/h) and concentrated in the large open tidal flats, while close to zero in the extensive mangrove network where Whimbrel abound (personal observations)). There are several forest falcons in the study area (Márquez et al., 2005), but there is no evidence that suggest they target whimbrels or other shorebirds. By using areas near the cover (Chapter 3), Whimbrels in Sanquianga-Iscuande could avoid being targeted by falcons, which traditionally hunt in the open (Buchanan, 2012; Buchanan et al., 1988; Dekker and Ydenberg, 2004). This could also be the case of smaller size species that dwell in sites with complex vegetation, including Spotted and Least Sandpipers. But to the extent to which cover can be involved in shorebird antipredator strategies remain to be tested.

Another key result from my thesis was the importance of positive interactions (Chapter 5) between species that share similar escape performance (Chapter 3). Part of these associations could be explained by shared responses to the safety gradient (Chapter 4), but many of those associations (especially those involving residual correlations from abundance data, Fig. 5.5) were maintained after controlling for the environment. These residual correlations suggest that either other environmental features were not captured or that there are positive associations, in other words those species are attracted to each other. Coasts are dynamic places and organisms tracking coastal resources must have several layers of decision-making associated to their habitat choices. Before selecting patch, shorebirds must process several information sources to track areas of higher productivity and safety. For inexperienced birds, but also for more experienced, public information (e.g. location or foraging intake of other individuals) can play a role in the selection of a patch. We found a strong signal for a role of heterospecific attraction in the distribution of shorebirds, a role that has been highlighted previously and even is part of the folk tradition of shorebird hunting using decoys. Behavioural assays targeting responses of shorebirds to environments with and without social imprints could be used to assess the asymmetry of these relationships and how important is heterospecific attraction for distribution and assembly of shorebird communities.

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Appendix A.

Maximum number of individuals and habitat features of occupied Whimbrel roosts in Sanquianga National Park

	Number of individuals, centrality and feeding area					Isolation and disturbances					
Roost Site	Whimbrel max count (Individuals)	Distance to Centre (km)	Distance to River (km)	Tida flats 12km radius (km^2)	Avg. distance to tidal in 12km radius (km)	Island size (km^2)	Distance to village (km)	Distance to waterway (km)	Human density (Persons in 1 km radius)	% water in 1 km radius	% mangrove in 1 km radius
El Parguero 4	2938	2,38	2,68	50,15	7,77	0,12	2,25	2,85	0	0,71	0,07
Aguacatal	280	10,77	6,55	31,71	6,1	1,53	2,52	3,03	0	0,35	0,53
El Parguero 1	111	5,47	5,84	47,87	8,08	0,5	5,18	3,04	0	0,59	0,18
Estero El Carmen	63	2,72	2,66	47,53	7,32	0,65	1,7	1,51	0	0,37	0,32
El Parguero 7 (7-8)	52	4,46	2,8	46,27	7,34	1,13	1,65	5,62	0	0,31	0,54
Conguero	38	6,92	3,57	56,31	7,16	0,13	0,7	5,62	166,48	0,47	0,18
El Parguero 9 (6-9)	37	1,57	3,3	53,04	7,67	10,13	2,13	1,29	0	0,17	0,6
El Parguero 2	29	3,56	3,73	50,47	7,93	0,22	3,32	2,91	0	0,52	0,09
Punta Isla Grande	28	4,41	6,23	53,56	7,78	0,74	2,31	1	0	0,5	0,29
Islas Cocal	26	9,36	1,39	53,24	6,86	0,05	0,6	4,08	0	0,52	0,26
Campo Alegre	8	8,14	2,39	53,2	7,06	0,36	0,43	2,73	0	0,39	0,33
El Parguero 5	7	2,51	1,63	48,89	7,65	0,26	1,87	3,77	0	0,75	0,1
El Parguero 3	4	3,29	2,89	49,63	7,83	0,03	2,83	3,63	0	0,63	0,07

Appendix B.

Mudflat area (km2) accumulated around occupied and potential Whimbrel roosting sites

Table B1. **Mudflat area (km2) accumulated around occupied and potential Whimbrel roosting sites in concentric buffers of 1 km radius. Median, minimum and maximum value and results of Mann-Whitney U test.**

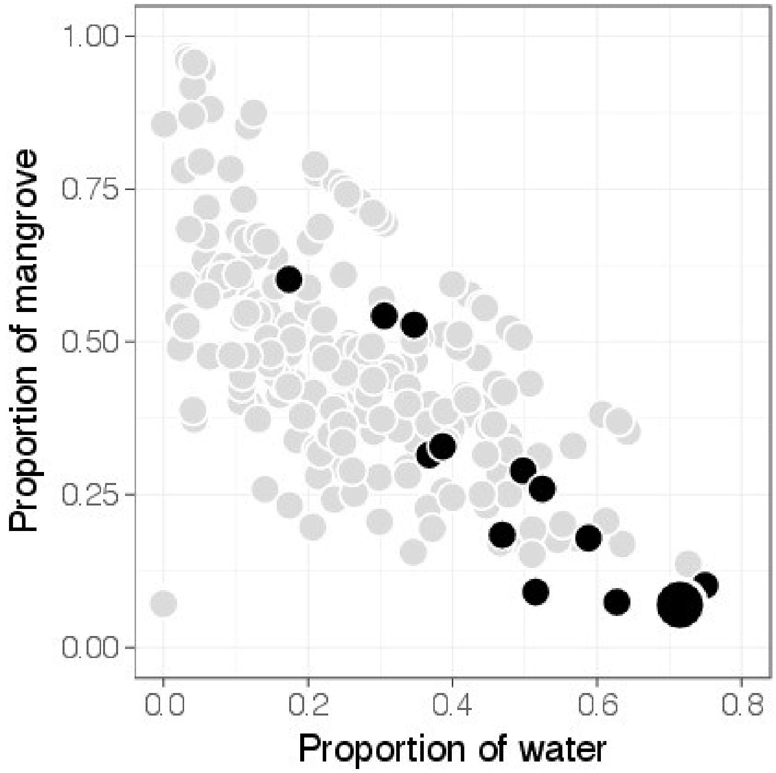
Radius (Km)	Occupied (*n* = 13)			Potential (*n* = 209)			Mann-Whitney test	
	median	min	max	median	min	max	U	p.value
1	0,5	0,2	2,3	0,9	0,0	3,1	1244	0,107
2	2,8	1,2	3,9	2,3	0,2	5,8	1149,5	0,678
3	5,5	3,7	8,9	4,7	0,4	9,3	917	0,066
4	9,2	7,3	14,1	8,0	0,5	13,5	892	0,04
5	13,1	11,3	20,5	12,0	1,9	20,2	840	0,022
6	19,0	14,2	27,2	16,7	2,9	29,0	896	0,04
7	27,1	18,0	33,8	21,3	3,3	34,8	804	0,014
8	33,9	24,0	41,1	27,2	4,2	42,7	721	0,005
9	41,5	26,3	51,4	35,2	9,9	53,3	624	0,001
10	50,8	32,5	60,3	42,0	12,8	61,9	533	<0.001
11	60,7	38,4	68,3	47,8	15,0	70,0	489	<0.001
12	70,3	42,7	75,2	53,3	19,0	76,8	442	<0.001
13	77,5	47,7	84,9	59,1	24,7	83,2	371	<0.001
14	84,2	57,7	92,4	65,7	28,8	89,3	321	<0.001
15	92,8	62,4	99,5	72,3	33,8	95,7	339	<0.001
16	97,8	67,0	104,5	79,3	40,8	102,0	341	<0.001
17	105,9	74,3	110,5	85,2	46,4	109,4	349	<0.001
18	110,4	82,8	115,3	89,6	53,2	114,7	375,5	<0.001
19	109,9	100,4	116,7	95,3	57,9	114,9	288	<0.001
20	113,6	102,4	118,1	102,1	66,1	123,4	388	<0.001
21	116,6	105,5	118,3	106,6	72,5	132,2	457	0,003
22	119,0	110,6	123,7	110,6	79,2	138,8	551,5	0,005
23	119,8	115,3	138,8	113,9	86,8	140,3	622,5	0,015
24	120,8	118,0	139,1	116,7	93,2	143,6	570,5	0,027
25	123,9	118,3	141,4	119,7	96,9	147,2	740	0,016
26	140,5	120,8	143,9	122,1	99,9	149,9	593	0,052
27	142,6	124,6	153,0	124,3	103,2	154,3	610	0,01
28	144,0	126,2	144,7	125,9	106,3	158,8	303,5	0,099
29	147,2	128,9	149,5	127,1	110,2	161,6	482	0,016
30	145,4	128,9	155,1	129,1	111,8	162,2	428,5	0,234

Radius (Km)	Occupied (*n* = 13)			Potential (*n* = 209)			Mann-Whitney test	
	median	**min**	**max**	**median**	**min**	**max**	**U**	**p.value**
31	150,4	130,5	161,9	130,1	116,9	167,8	475,5	0,019
32	152,8	130,1	154,1	139,4	122,0	168,8	529	0,235
33	154,9	132,7	163,0	140,5	124,4	172,9	668	0,073
34	159,5	133,2	162,0	152,7	126,1	173,9	279	0,251
35	160,0	152,7	165,1	154,3	129,8	176,2	420,5	0,367

Appendix C.

Proportion of mangrove and water in 1 km radius from occupied and potential Whimbrel roost sites

The main roost is indicated by a larger circle.



Appendix D.

Shorebird Surveys

Table D1. Number of sampling units, sampled area and individual shorebirds counted on seven surveys in Sanquianga-Iscuandé.

Year	Sampled mudflats	Sampled Area (ha)	Individuals
*2009	62	2647	838
2012	80	2474	34220
2013	57	2306	9197
2014	93	3945	4806
2015	98	4210	3559
2016	61	3271	6457
2017	69	3433	6093

*2009 Was a pilot year with methods still in development and not included in the final analysis

Table D2. Number of sampled sites per basin in seven shorebird surveys in Sanquianga-Iscuandé (2009, 2012-2017).

Year	Salango	Guascama	Sanquianga	Amarales	Tapaje	Iscuande
09	10	17	11	13	11	
12	8	19	18	20	13	2
13	7	8	18	13	9	2
14	9	19	29	22	12	2
15	9	15	30	23	15	6
16	8	13	17	11	5	7
17	5	16	20	14	11	3

Appendix E.

Environmental predictors

Habitat features

Our 162 sampled tidal flats represent the entire spectrum of habitat variability in size, productivity, safety and marine gradients within the >7000 tidal patches estimated for the study area. The size of sampled patches ranged from 1.5 ha to 956 ha. Productivity and safety gradients were slightly correlated (>0.5) in their untransformed form (Table D1) but uncorrelated after transformation. Average productivity was higher near cover and lower in open tidal flats. Neither of them correlated with marine influence.

Table E1. Correlation between environmental predictors.
Pearson correlation coefficients between pairs of habitat predictors in their raw, transformed and standardized forms (center and scaled). Correlation between Area and distance to cover decrease when area is transformed.

	NDVI	Distance to coast (km)	Distance to cover (m)	Area (ha)	Log10 (Area (ha))
NDVI	1	0.25	-0.22	-0.21	-0.12
Distance to coast		1	-0.28	-0.13	-0.11
Distance to cover			1	0.51	0.14
Area (ha)				1	0.57
Log10 (Area (ha))					1

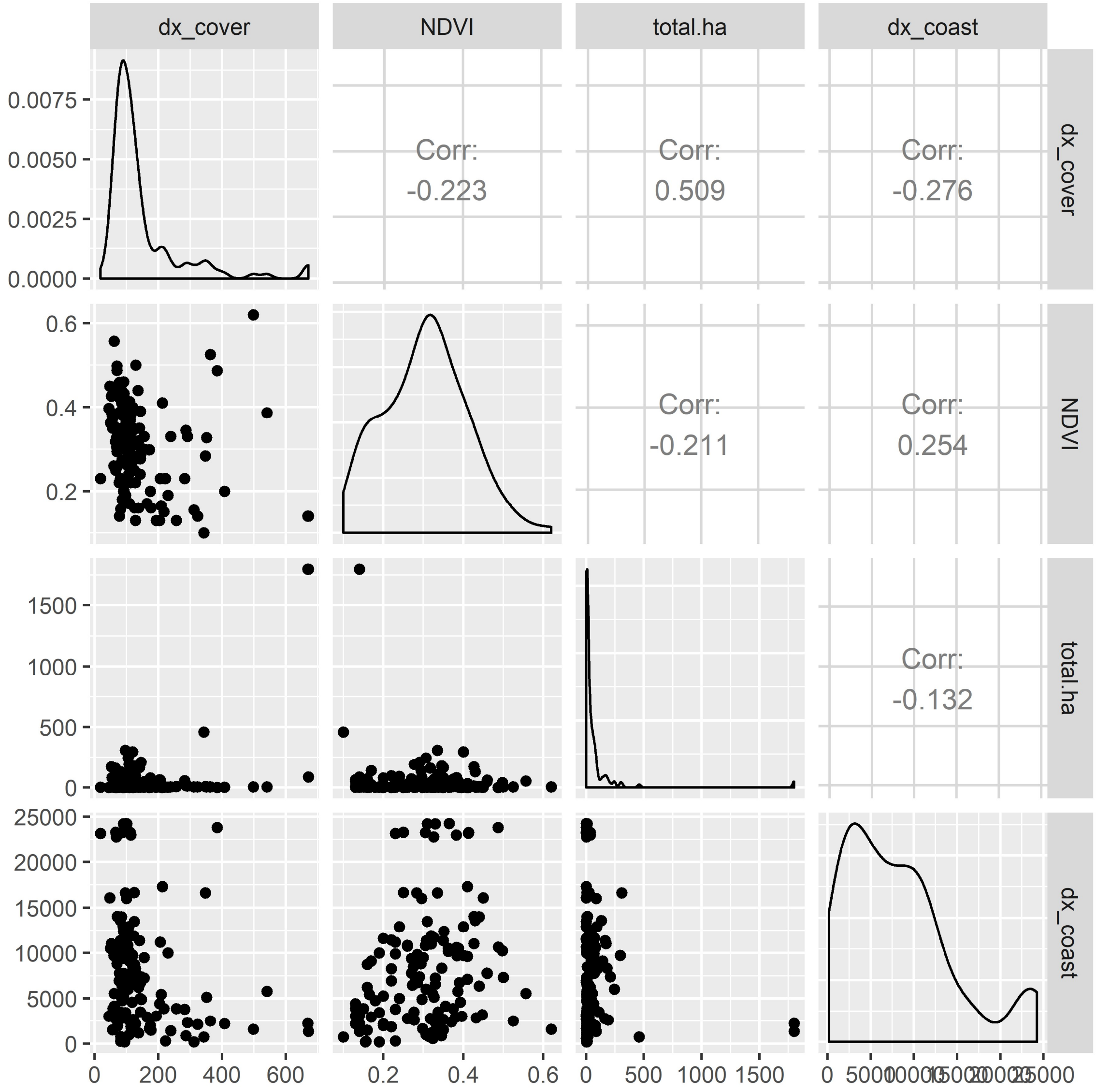


Figure E1. **Correlation and distribution of environmental predictors – Raw. Pearson correlation coefficients and scatterplots between environmental predictors**

Total area of the tidal patch (total.ha) and distance to cover (ds_cover) have a positive correlation >0.5. Other variables as distance to coast (dx_coast) and NDVI have weaker correlations. Some variables have several some influential points

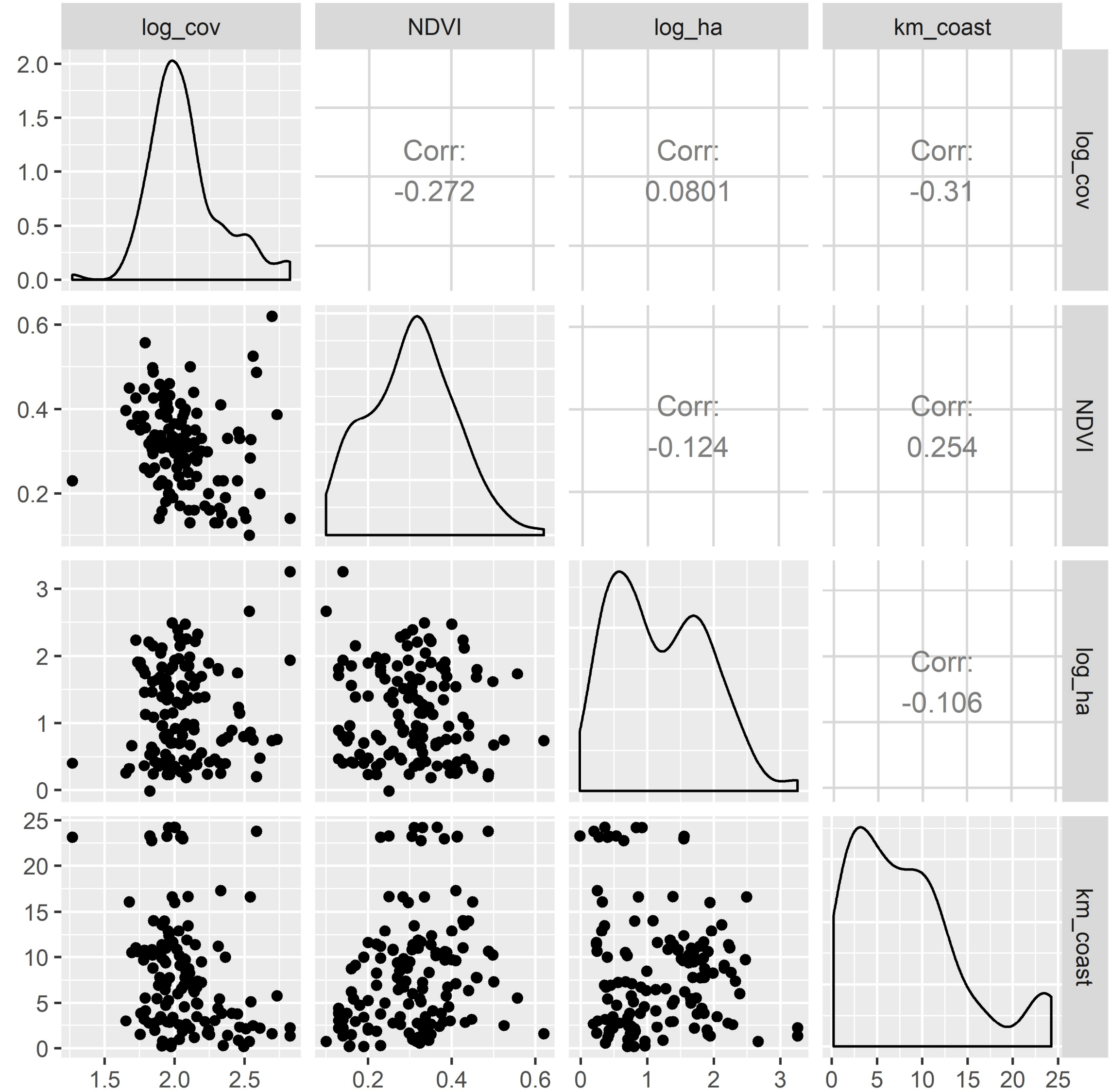


Figure E2. Correlation and distribution of environmental predictors – Transformed.

Pearson correlation coefficients of habitat variables of tidal patches of southern Colombia. Log10 transformation improves normality of two variables: distance to cover and area of the patch, and reduces correlation between them. Distance to coast was rescaled to km. (dx_coast= Distance to coast (km) , NDVI= 5-Y averaged normalized difference vegetation index, log10_ha is Log10 of area of the patch (ha), log_cov = log10 of distance to cover (m).

Appendix F.

Occupancy and abundance of shorebirds

Shorebird species in the study are have different patterns of distribution. Whimbrel, Willet and Spotted Sandpiper were widespread while Black Bellied Plover, Semipalmated Plover and Wilson’s Plover occupy a lower proportion of sites. Collared Plover and Marbled Godwit were recorded in only few locations (Fig F1).

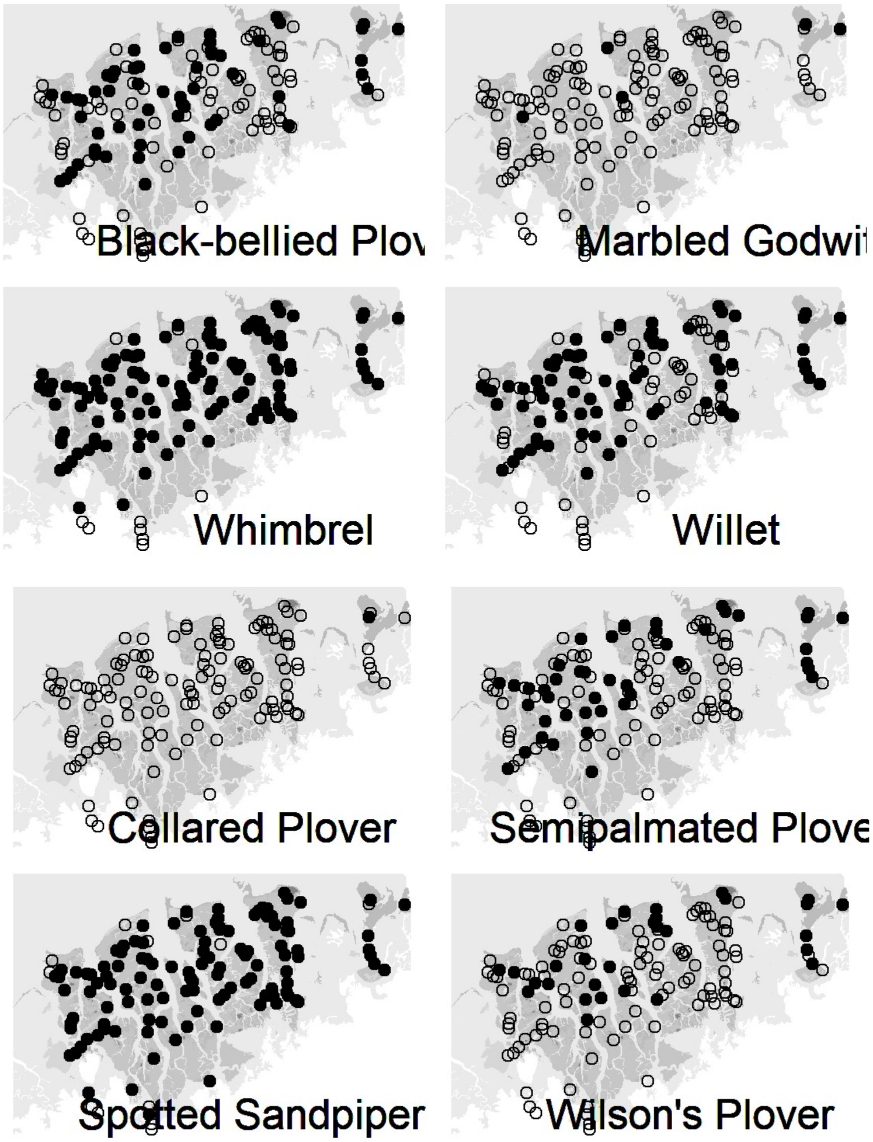


Figure F1. **Sites occupied (black) and unoccupied (blank) by 18 shorebird species during surveys (2012-2017)**

For all shorebird species most sites had between one and 10 individuals and except for Western Sandpiper and short-Billed Dowitcher, all species have abundances below 100 individuals per site. Large shorebirds (Whimbrel, Willet, Black bellied Plover) were more frequent than small shorebirds in all abundance classes **(**Fig F2)**.**

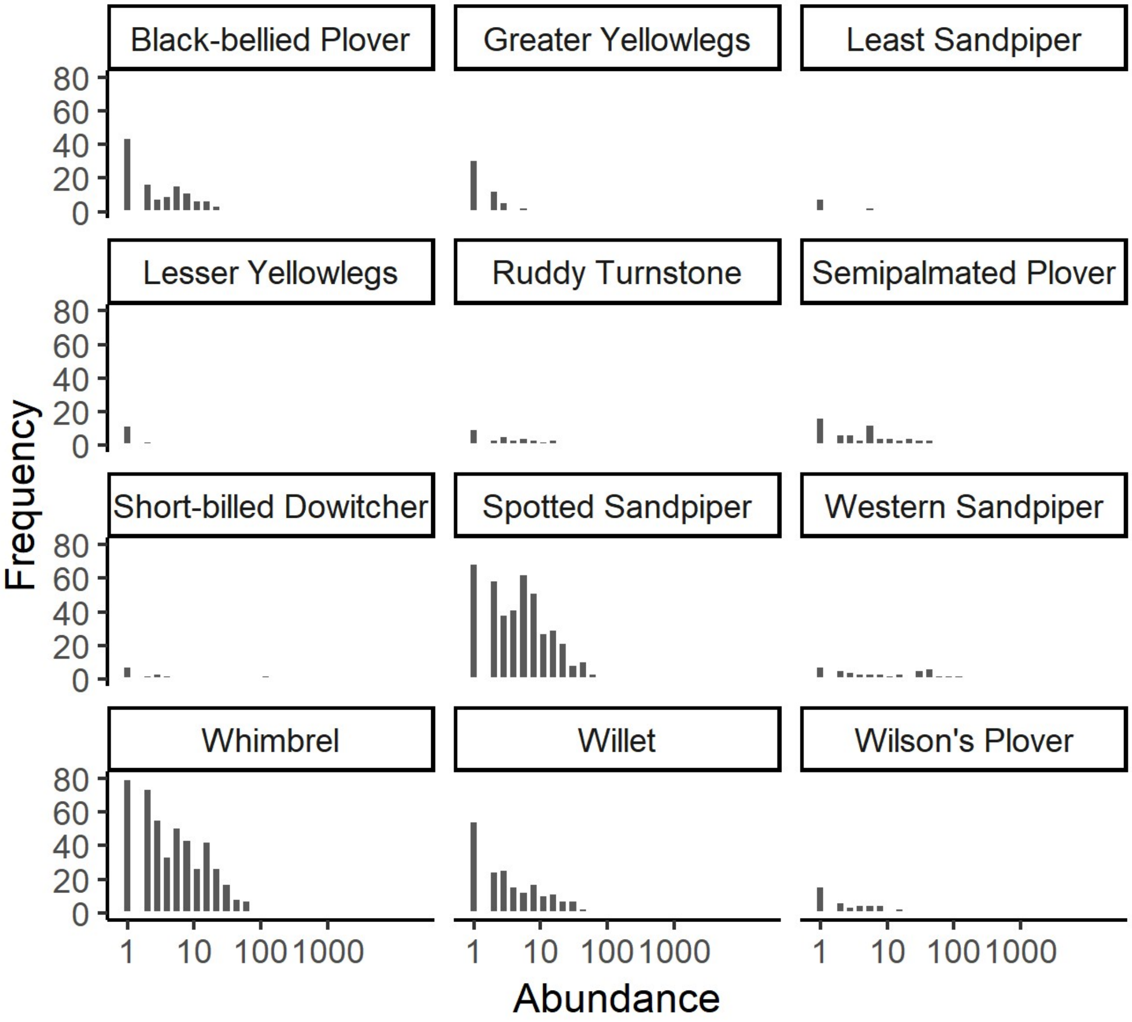


Figure F2. Histogram of abundance (log scale) of the 12 most common species in shorebird surveys of tidal flats in Northern Nariño, Colombia.

Shorebird species exhibit different patterns of aggregation of individuals across sites (Fig. F3). The slopes of medium and small size shorebirds were most pronounced, suggesting that a larger number of individuals were found in small number of sites. Short-Billed Dowitchers showed the more extreme pattern, with more than 50% of the total abundance accumulated in a single site. In the other hand, Large species (Whimbrel, Willet, Black Bellied Plover) show less pronounced slopes, suggesting a more even distribution of the abundance across the surveyed sites. Spotted Sandpiper is the only small shorebird exhibiting an even distribution. There was some variation in the slopes, but the general pattern of accumulation of abundance within each species was consistent across years.

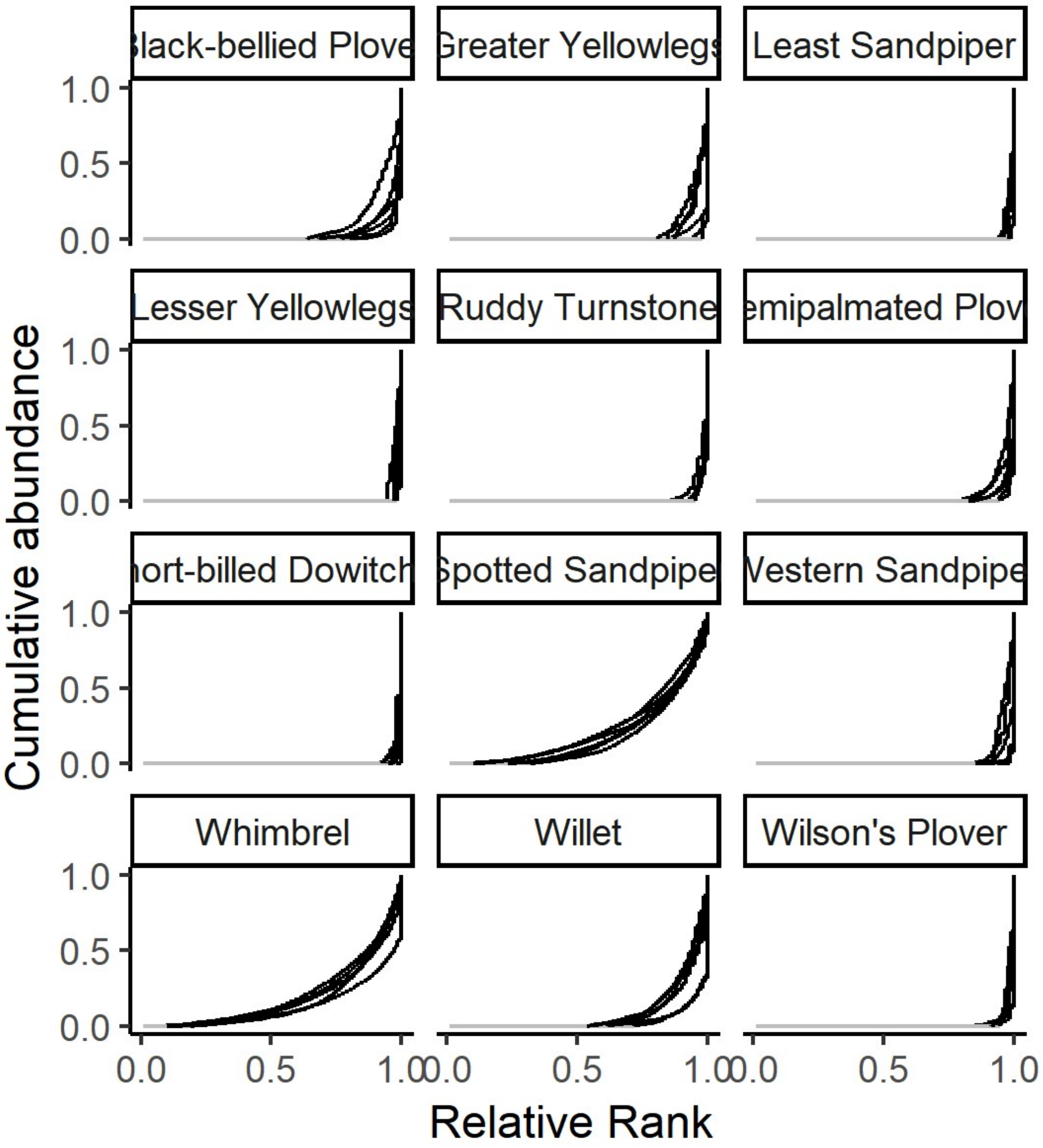


Figure F3. **Cumulative distribution of abundance of 12 common shorebird species vs. the relative rank of each site 3surveyed (rank/total sites). Grey horizontal line indicates the zeroes and black lines the accumulation of abundance on surveyed sites on each of the surveyed years.**

Appendix G.

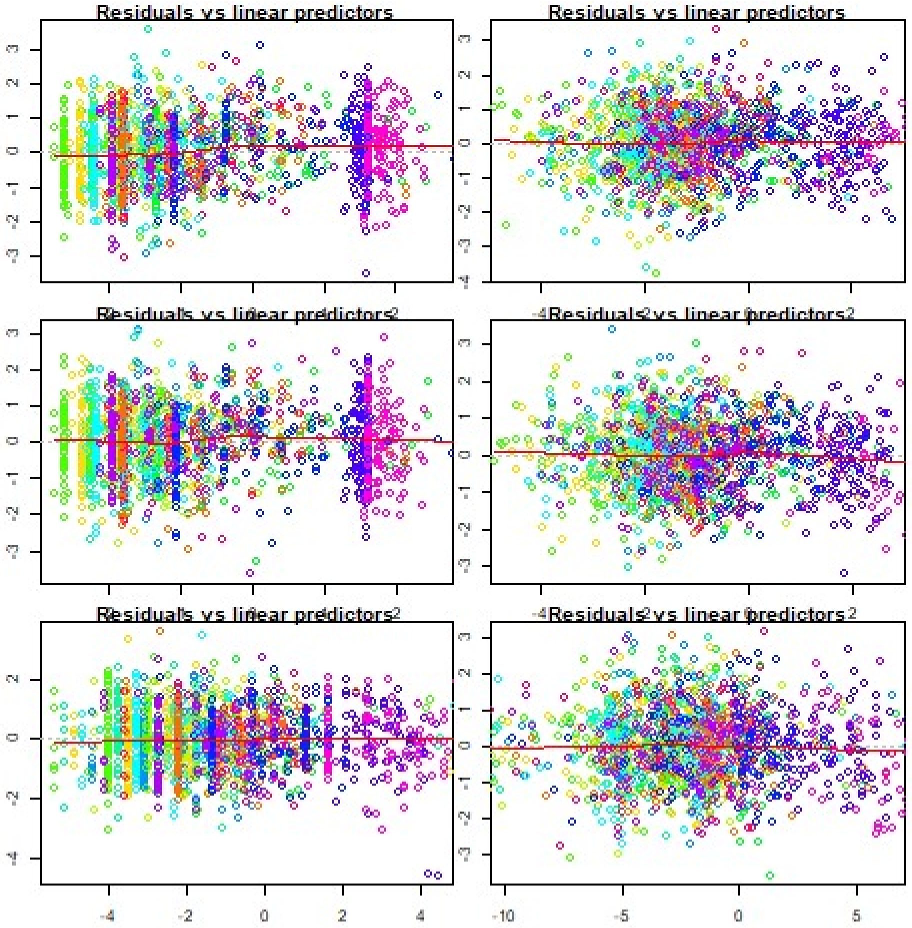
Values of AICc for GLLVMs for multivariate Presence (Binomial) and abundance

Values of AICc for GLLVMs for multivariate Presence (Binomial) and abundance (Poisson, Zero-Inflated Poisson and Negative binomial) of shorebirds in tidal flats of Southern Colombia. Models with site included as fixed effect (+Site (F)) have a better fit than models that include Site as a fixed effect (+Site (R)) or that do not include site effects for both Species Only and Species + Environment. Models with environmental data have a better fit that "Species Only' models. Within abundance models, ZIP and Poisson outperformed Negative Binomial in all but species-only models. Poisson was outperformed by ZIP in species-only models and species+ environment and site(R), but in other instances AICc were very similar.

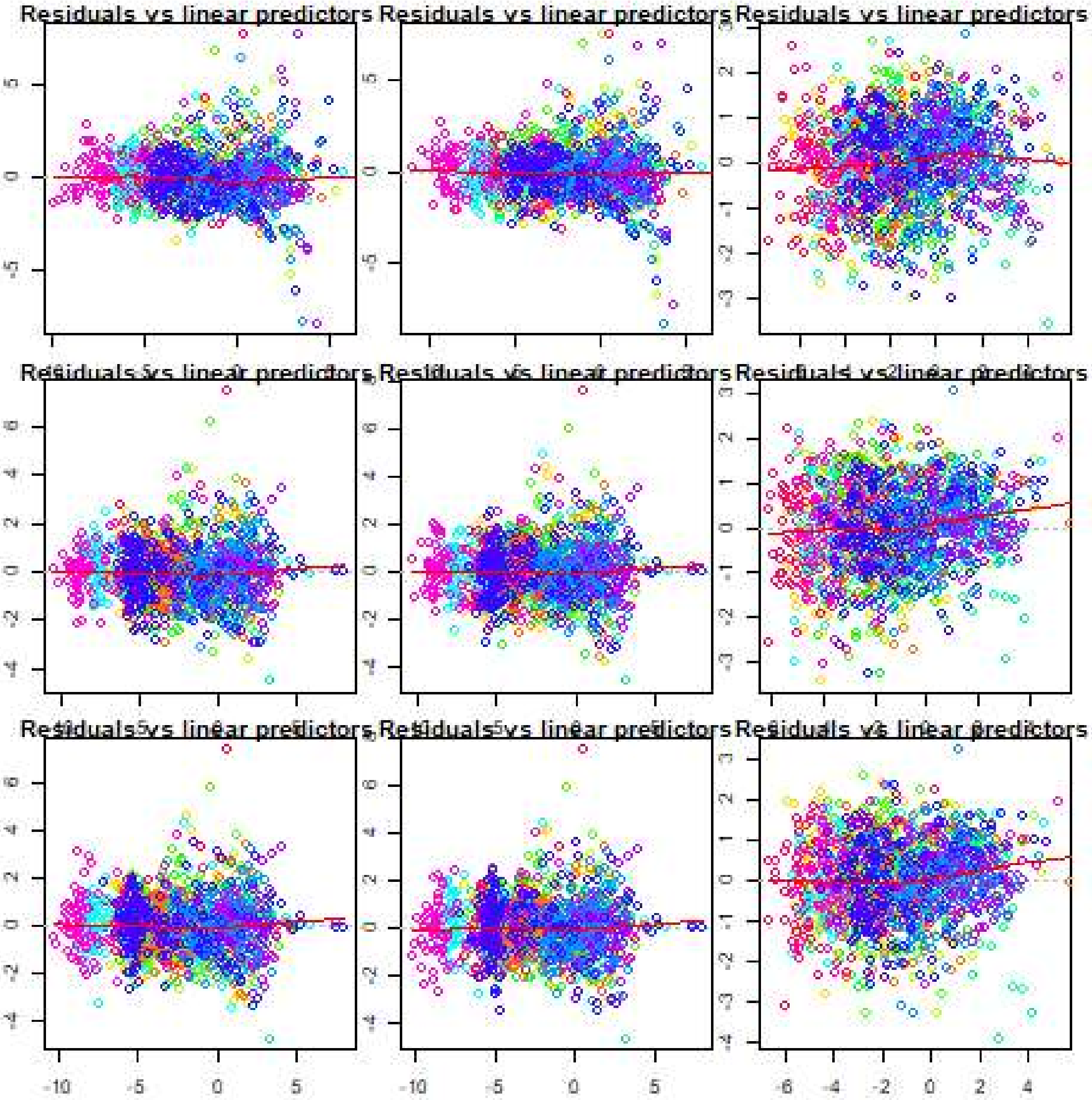
	Presence	**Abundance**		
Model	**Binomial**	**Poisson**	**Zero-Inflated Poisson**	**Negative-Binomial**
Species Only	1390.2903	4903.037	4799.310	4107.735
+Site (R)	1518.2588	4034.766	4034.752	4292.642
+Site (F)	**981.1149**	**3576.391**	**3576.390**	**3648.431**
Species +Environment	1204.3187	3690.754	3690.754	3857.907
+ Site (R)	1333.2473	3706.086	3689.509	4060.256
+ Site (F)	**824.2231**	**3211.411**	**3211.384**	**3459.361**

Appendix H.

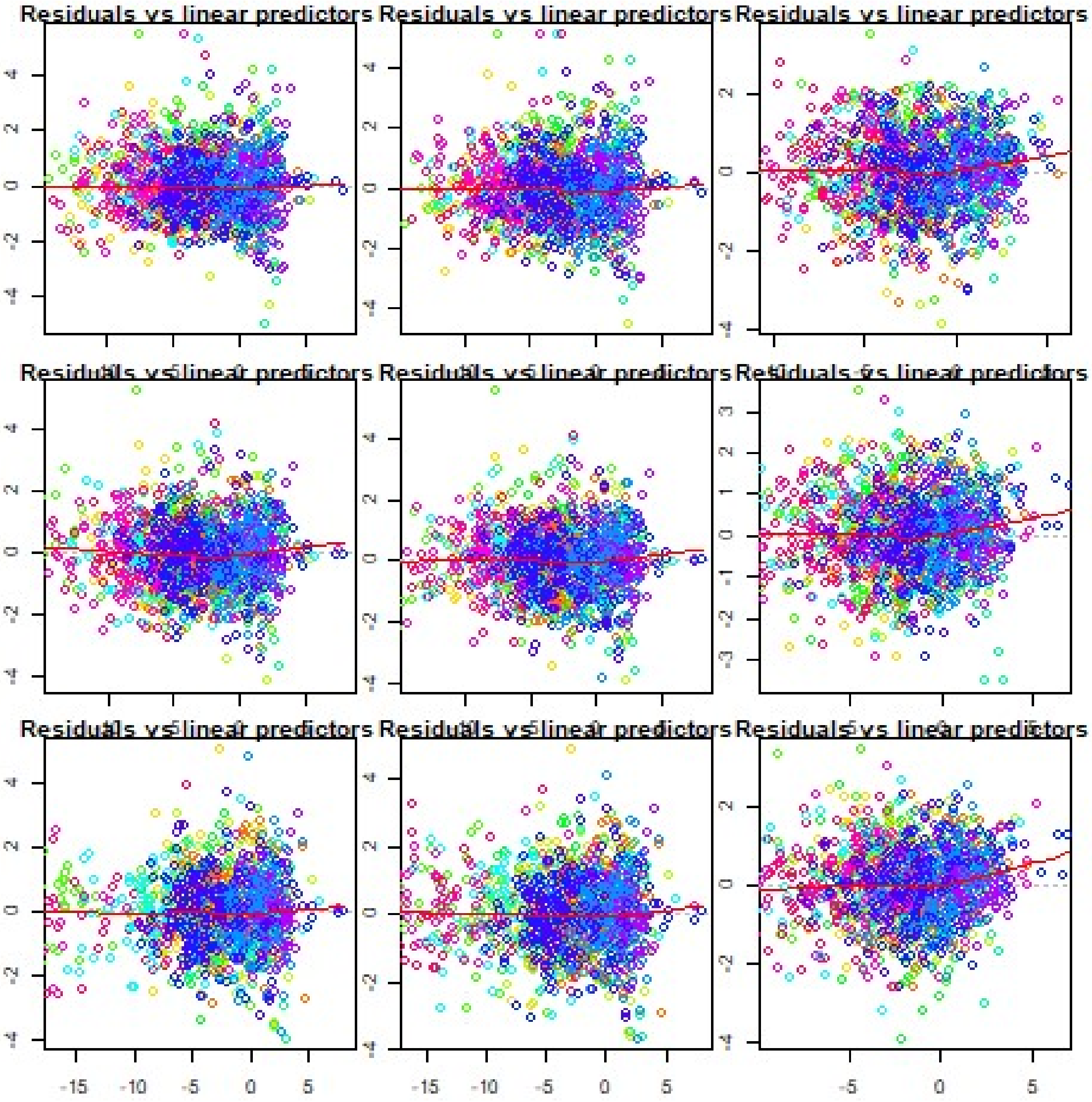
Dunn-Smyth residuals from GLLVM models



Dunn–Smyth residuals against linear predictors of Binomial GLLVM for multivariate presence of shorebirds. Each colour represents one species and the Line the LOESS fit of the residuals. Left plots represent “species only” models and “species and environment” are on the right. Models without site effects are on top and with site effects as random (middle) or fixed effects (bottom).



Dunn–Smyth residuals against linear predictors for GLLVMs without covariates, with species-only models (top) and the inclusion of random site effects (middle) or fixed site effects (bottom). Poisson (left) and ZIP (center) models without random site effects show Dunn–Smyth with fan shapes while residuals given under negative binomial (right) are more uniformly distributed around zero indicating a more appropriate fit to the data. LOESS line suggests light skewness towards extreme values more marked in Negative Binomial. The ZIP model with covariates and fixed site effects (middle bottom) had the best fit showing a more uniform distribution of residuals and lower skewness. Dots are individual sites and each colour represents one species.



Dunn–Smyth residuals against linear predictors for GLLVMs without covariates (top), all covariates (middle) and covariates and random effects (bottom). Poisson (left) and ZIP (center) models without random site effects show more dispersion of Dunn–Smyth residuals with fan shapes while residuals given under negative binomial (right) are more uniformly distributed around zero indicating a more appropriate fit to the data. However, LOESS lines suggest more skewness towards extreme values more marked in Negative Binomial. The ZIP model with covariates and fixed site effects (middle bottom) had the best fit showing a more uniform distribution of residuals and lower skewness. Dots are individual sites and each colour represents one species.