The Amazon Basin's rivers and lakes support Nearctic-breeding shorebirds during southward migration

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ABSTRACT

Identifying the migration routes and stopover sites used by declining species is critical for developing targeted conservation actions. Long-distance migratory shorebirds are among the groups of birds declining most rapidly, yet we frequently lack detailed knowledge about the routes and stopover sites they use during their hemisphere-spanning migrations. This is especially true for species that migrate through mid-continental regions in the Western Hemisphere. We therefore used satellite transmitters to track 212 individuals of 6 shorebird species during their southward migrations—*Pluvialis dominica* (American Golden-Plover), *Limosa haemastica* (Hudsonian Godwit), *Tringa flavipes* (Lesser Yellowlegs), and *Calidris subruficollis* (Buff-breasted Sandpiper), *C. melanotos* (Pectoral Sandpiper), and *Bartramia longicauda* (Upland Sandpiper)—as they crossed the Amazon Basin of South America, a region from which reports of shorebird numbers are increasing but remain relatively rare. Our results make clear that the Amazon Basin provides stopover habitat for a large number of shorebirds: more than 74% of individuals tracked crossing the Amazon Basin stopped over in the region for an average of 2–14 days, with some spending the entire nonbreeding season there. All species selected stopover sites along the region's many rivers and lakes, while within stopover sites each species exhibited distinct habitat preferences. The timing of stopovers within sub-basins of the Amazon Basin also coincided with periods of low water, when the muddy, shallow water habitats preferred by most shorebirds are likely plentiful. Together, our results highlight the need for detailed investigations into shorebird abundance and distribution within the Amazon Basin, threats to shorebirds within particular subbasins, and links between shorebird conservation efforts and those targeting the myriad other species that inhabit this dynamic, hyper-diverse region.

Keywords: Amazon Basin, migration, shorebirds, stopover sites

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LAY SUMMARY

- Long-distance migratory shorebirds are declining worldwide. For many of these species, we lack essential information about their habitats throughout the year, including the stopover sites they use during migration.
- In the Western Hemisphere, information is particularly lacking for the midcontinent of South America, a region that several shorebird species may cross during their southward migrations.
- We examine satellite tracking data from six shorebird species to show that stops in the Amazon Basin are surprisingly common, occurring in more than 74% of southward migratory tracks.
- Shorebirds selected stopover sites along rivers and lakes and exhibited distinct local-scale habitat preferences. These results highlight the need for detailed investigations into shorebird abundance and stopover site characteristics within the Amazon Basin, as well as potential links to broader conservation efforts.

Las cuencas y lagos de la cuenca amazónica sustentan a las aves playeras que se reproducen en el Neártico durante la migración hacia el sur

RESUMEN

Identificar las rutas migratorias y los sitios de parada utilizados por las especies en declive es crucial para desarrollar acciones de conservación específicas. Las aves playeras migratorias de larga distancia están entre los grupos de aves que disminuyen más rápidamente, pero con frecuencia carecemos de conocimientos detallados sobre las rutas y los sitios de parada que utilizan durante sus migraciones de magnitud hemisférica. Esto es especialmente cierto para las especies que migran a través de las regiones medio-continentales del Hemisferio Occidental. Por lo tanto, utilizamos transmisores satelitales para rastrear a 212 individuos de 6 especies de aves playeras durante sus migraciones hacia el sur—*Pluvialis dominica*, *Limosa haemastica, Tringa flavipes*, *Calidris subruficollis*, *C. melanotos* y *Bartramia longicauda*—mientras cruzaban la cuenca amazónica de América del Sur, una región en la cual los estudios sobre el número de aves playeras están aumentando, pero siguen siendo relativamente raros. Nuestros resultados dejan claro que la cuenca amazónica proporciona hábitat de parada para un gran número de aves playeras: más del 74% de los individuos rastreados que cruzaron la cuenca amazónica se detuvieron en la región durante un promedio de 2 a 14 días, y algunos pasaron toda la temporada no reproductiva allí. Todas las especies seleccionaron sitios de parada a lo largo de los numerosos ríos y lagos de la región, mientras que dentro de los sitios de parada cada especie mostró preferencias de hábitat distintas. El momento de las paradas dentro de las subcuencas de la cuenca amazónica también coincidió con períodos de aguas bajas, cuando los hábitats de aguas poco profundas y fangosas preferidos por la mayoría de las aves playeras son probablemente abundantes. En conjunto, nuestros resultados destacan la necesidad de investigaciones detalladas sobre la abundancia y distribución de las aves playeras dentro de la cuenca amazónica, las amenazas a las aves playeras dentro de subcuencas particulares, y los vínculos entre los esfuerzos de conservación de las aves playeras y aquellos dirigidos a la miríada de otras especies que habitan esta región dinámica y de gran diversidad.

Palabras clave: aves playeras, cuenca amazónica, migración, sitios de parada

INTRODUCTION

Long-distance migratory shorebirds are exhibiting some of the most rapid population declines among all bird species. In recent decades, estimates indicate that their populations in North America have declined by >50% (Rosenberg et al. 2019, Smith et al. 2023), mirroring those in other flyways globally (Kentie et al. 2016, Studds et al. 2017). These declines are caused by myriad, simultaneous changes occurring throughout their distributions, ranging from habitat degradation and loss to the pervasive effects of global climate change (Pearce-Higgins et al. 2017). One of the biggest challenges facing conservation efforts aimed at reversing shorebird declines is the fact that, despite years of intensive study, we still lack detailed knowledge about many species' whereabouts over the course of the year (Scarpignato et al. 2023). This hinders our ability to both identify the most relevant conservation threats and determine the best approaches to mitigate those threats (Chan et al. 2019).

In the Western Hemisphere, underlying our lack of knowledge about shorebird movements have been 2 key factors: the immense distances covered by many species during their migrations and the geography of the hemisphere itself. The combination of color banding, stable isotopes, and tracking studies have slowly begun to fill in the gaps in our knowledge about exactly how far shorebirds are capable of flying and where they might be stopping over (Myers et al. 1990, Bishop and Warnock 1998, Atkinson et al. 2005, Gill et al. 2009, Gratto-Trevor et al. 2012, Johnson et al. 2016, Ruthrauff et al. 2019, Lagassé et al. 2020, Huysman et al. 2022). Many of these studies focused on species that predominantly use coastal ecosystems, however, where predictably abundant resources attract large assemblages of shorebird species during migration (González et al. 1996, Atkinson et al. 2007, Carmona et al. 2008). The hemisphere's mid-continental regions, on the other hand, are frequently characterized by isolated, ephemeral habitats whose extent and distribution are difficult to predict from year to year (Skagen and Knopf 1994, Davis and Smith 1998, Skagen 2006). This makes developing systematic studies to characterize species' migration patterns difficult. Thus, while mid-continental regions support a tremendous number and diversity of shorebirds, the migrations of the species using them remain less well-documented than those of species migrating along coastal routes (McCarty et al. 2015; Wright et al. 2020; Lamarre et al. 2021).

The Amazon Basin of South America—one of the world's largest river drainages, covering ~7,000,000 km^2—is paramount among these lesser-studied mid-continental regions. Although nearly two dozen shorebird species that breed in North America potentially overfly the Amazon Basin during migration en route to nonbreeding sites in southern South America (Morrison and Ross 1989), our knowledge of shorebirds in the region has generally been limited to infrequent reports of small numbers of individuals (Antas 1983, Lanctot et al. 2002, Serrano 2010). More recently, the emergence of community science-driven databases (eBird 2023, WikiAves 2023) and the proliferation of miniature tracking devices have begun to change this situation, putting the Amazon Basin's potential importance for shorebirds in focus. On-the-ground counts in the Beni Province of Bolivia, for instance, recently led to the establishment of the Amazon Basin's first Western Hemisphere Shorebird Reserve Network site (Barba Azul Nature Reserve; WHSRN 2015), while tracking studies of *Calidris subruficollis* (Buff-breasted Sandpiper) and *Limosa haemastica* (Hudsonian Godwit) using light-level geolocators suggest that significant proportions of both species' populations stop in the region (Senner et al. 2014, Lanctot et al. 2016). These recent developments indicate that the Amazon Basin may host large numbers of shorebirds and that different portions of the region may be important for different populations and species. Unfortunately, the imprecision of the tracking devices employed thus far (Rakhimberdiev et al. 2016), as well as the paucity of on-the-ground observations relative to the size of the region, largely preclude drawing firm conclusions about where most shorebirds are stopping or what habitats they might be using.

The rapid rates at which long-distance migratory shorebirds are declining suggest that determining how they are using the Amazon Basin should be a top priority for shorebird conservation efforts. The dramatic changes taking place in the region underscore this urgency: the past decade has seen rapid deforestation and development (Silva Junior et al. 2020), as well as increasingly frequent anthropogenically-driven forest fires (da Silva Junior et al. 2022). Future disturbances may include the construction of more than 200 hydroelectric dams on tributaries of the Amazon River (Timpe and Kaplan 2017), increased resource extraction activities (Villacís et al. 2016, Martins et al. 2022), and difficult-to-predict changes to the region's climate that will have global implications (Duffy et al. 2015). Without more specific information about shorebird habitat use in the region, it is impossible to forecast how these environmental changes will affect shorebird populations, or to discern how populations may have already been affected.

Here we use GPS and Argos satellite transmitters to investigate stopover occurrence for 6 species of long-distance migratory shorebirds traveling across the Amazon Basin during their southward migrations—*L. haemastica*, *Tringa flavipes* (Lesser Yellowlegs), *C. subruficollis*, *C. melanotos* (Pectoral Sandpiper), *Bartramia longicauda* (Upland Sandpiper), and *Pluvialis dominica* (American Golden-Plover). Specifically, we address 4 objectives: (1) determine the proportion of tagged birds of the above species migrating to southern South America that stop in the Amazon Basin; (2) identify the location and duration of their Amazonian stopovers; (3) characterize the habitat features associated with their Amazonian stopovers; and, (4) quantify the availability of these habitat features throughout the year. Ultimately, this project will help facilitate on-the-ground efforts to document in more detail how shorebirds use the Amazon Basin, as well as develop targeted conservation actions focused on a suite of declining species in a rapidly changing region.

METHODS

Study Region

We examined shorebird migrations across South America and particularly across the inland region of the Amazon Basin. To define this region, we used the "Amazon Basin" polygon in the basin Level 1 shapefile from the Amazon Waters Initiative (AWI; Venticinque et al. 2016; Figure 1), which includes the Amazon, Tocantins, Guianas, Orinoco, and Paranaiba River basins and the Paraná headwaters. Within the region, we used the AWI Basin Level 3 shapefiles to identify 39 major inland tributary basins (hereafter, "subbasins"; see Figure 2) and the AWI 6th-11th order river shapefile to identify major rivers.

Tracking Data

We compiled shorebird movement datasets that (1) were collected from species known to migrate across the Amazon Basin, (2) relied on satellite transmitters, and (3) contained at least one track with locations within the Amazon Basin region. These datasets reflect movement by six Nearctic-breeding shorebird species and, to our knowledge, represent a large proportion of the datasets that meet our three criteria to date. Neotropical-breeding shorebird species may also use the Amazon Basin, but exceedingly few of them have been tracked and, among those that have, none has entered or crossed

the Amazon Basin (Faria et al. 2023). Data were collected between 2016 and 2022 using Argos Platform Terminal Transmitters (PTTs; Microwave Telemetry, Inc.) or Pinpoint GPS Argos transmitters (Lotek, Inc.). All devices were deployed at sites outside the Amazon Basin (Table 1) and relayed location information to orbiting satellites. *Limosa haemastica* and some *C. subruficollis* deployments occurred at nonbreeding sites south of the Amazon Basin; *T. flavipes*, *P. dominica*, *C. melanotos*, *B. longicauda*, and some *C. subruficollis* deployments occurred at breeding sites or migratory stopover sites in North America (see Kempenaers and Valcu 2017, Hill et al. 2019, Tibbitts et al. 2021, Linscott et al. 2022, McDuffie et al. 2022 for more details).

The accuracy of location estimates varied with location type (Argos or GPS). Argos locations were estimated during programmed duty cycles or incidentally whenever a device's battery voltage and satellite overpasses aligned. We performed standard quality filtering on Argos locations, including Kalman filtering in Movebank (CLS 2014, Wikelski et al. 2024), inspecting for extreme outliers using visual checks, and (for PTT-only transmitters) passing locations through a "best hybrid" Douglas Argos filter with a maximum redundancy distance of 10 km (see Douglas et al. 2012 for details). We retained only "valid" Argos locations (i.e., location quality classes [LC] 3, 2, 1, 0, A, or B) for which the error radius is anisotropic and generally ranges from <250 m to 18 km (Douglas et al. 2012, CLS 2014). GPS locations were estimated at programmed intervals ranging from 2 hours to 14 days. We manually removed extreme GPS outliers and retained only locations calculated from >2 satellite fixes, which have higher accuracy (i.e., location classes 2D or 3D) and an approximately isotropic error radius of <100 m (Kaplan and Hegarty 2006). For a detailed listing of per-species tag types, location types, and sampling intervals, see Table 1.

For most species, satellite transmitters captured only southward-moving migrations across South America. We therefore focused on these southward movements, selecting for analysis only individuals tracked at least as far south as the northern boundary of the Amazon Basin during the window of southward migration, which occurs during the latter half of the year (July to December). To estimate the routes that individuals traveled, we generated straight-line movement tracks between locations using the R package *sf* (Pebesma 2018). We calculated the proportion of these tracks that appeared to follow inland routes across the Amazon Basin, as opposed to those that bypassed the region to the west or followed the coastline of the Atlantic Ocean to the east. In some instances, a track entered the Amazon Basin but ended prematurely when the device's battery failed. We manually inspected each track for battery failure, which was apparent when a track ended in a cluster of locations with no subsequent movement. In these cases, we removed all locations associated with the final cluster to avoid conflating tag loss, device malfunction, or bird mortality with a stopover event.

Stopover Identification

Our primary goal was to identify and describe stopover events during southward migration to the best of our ability for each tracked species. Although many popular methods for identifying behaviors in animal movement tracks begin with standardization (i.e., prior filtering or interpolation of location estimates to ensure regular and equivalent sampling intervals), we performed no standardization to avoid introducing biases that would run counter to our goal. When sampling regimes are diverse, standardization *via* filtering may remove events from more frequently sampled movement tracks, while standardization *via* interpolation may inadvertently generate unsubstantiated events in less frequently sampled tracks. Instead, we used a more flexible method that could identify stopovers within the original sampling frequency of each track. In this way, we focus on describing broad

patterns of stopover occurrence rather than precise comparisons of stopover behavior across species or individuals.

Our method for identifying stopovers involved two steps: first, identifying empirical locations indicative of a stationary movement pattern and then grouping these stationary locations into discrete stopover events. In the first step, we annotated each location within a movement track as "stationary" or "non-stationary" using Expectation-Maximization Binary Clustering (EMbC), a general-purpose unsupervised clustering method built on the maximum likelihood estimation of a Gaussian mixture model. In an animal movement context, EMbC generates binary partitions for high versus low travel velocity and high versus low turning angle (Garriga et al. 2016). We applied the EMbC algorithm to movement tracks aggregated for each species, maximizing the available training data for the algorithm—which was especially critical for individuals with sparse location data—while also allowing for species-specific variation in movement. To ensure that partitions were informed by realistic movements rather than overt location errors, we used an EMbC speed limit of 40 ms^{-1}, which excludes locations that exceeded the flight speed of shorebirds (Grönroos et al. 2012) from the clustering process. We labeled all locations in the low-velocity cluster as "stationary" behavior, regardless of their turning angles, to better isolate locations associated with foraging and resting (van Toor et al. 2018, Wilkinson et al. 2019). We labeled all other locations as "non-stationary." We performed no smoothing on these behavioral assignments since periods of foraging and resting may be interspersed with long-distance relocations or large location errors. EMbC provided an efficient, flexible, and consistent way to isolate locations of interest for stopover analysis, even across a diverse set of irregularly sampled and often error-prone movement tracks. We used the *EMbC* package (Garriga et al. 2019) to apply this algorithm in the R Programming Environment (v.4.1.3; R Core Team 2022).

In the second step, we grouped stationary locations into stopover events. After exploring several possible spatiotemporal "rules" for joining stationary locations into single events, we chose to define stopovers as groups of locations separated by no more than 10 km and lasting at least 12 hr. This definition allowed us to join locations indicative of intensive, local resource use into a single stopover while not over-splitting events each time an individual relocated to a nearby foraging patch (Neima et al. 2020) We then applied a sequence of filters and checks: (1) we extracted groups within our Amazon Basin shapefile using the R package *sf* (Pebesma 2018) and selected those that began between July and December; (2) if movement tracks indicated that an individual also remained within the region during the nonbreeding season (January to June), we discarded groups of locations that occurred after southward movement had ceased; (3) to ensure a reasonable degree of location confidence, particularly for habitat selection analyses (see below), we discarded a small number of groups ($n = 4$) that consisted only of locations with unbounded error estimates (i.e., only Argos 0, A, or B); and, (4) we checked that the last location in a group adequately reflected the end of the stopover event. This final filter was necessary because EMbC occasionally failed to include an otherwise plausible last location when its velocity was slightly above the partition for stationarity. This may occur when velocity to the next location is averaged over a period that spans both continued stopover and recommencement of higher-speed migratory flight, producing a moderately elevated average velocity. We opted to include these last locations when their velocity was generally low (<5 ms^{-1}) and they were within the vicinity (<5 km) of the previous location. We manually checked all additions to ensure their locations and turning angles were consistent with continued stopover (i.e., not a southward movement). This check ensured that our estimated stopover durations accurately reflected the empirical data, without altering stopover counts. We considered the resulting groups of

stationary locations to represent discrete stopover events within the Amazon Basin during southward migration.

We calculated approximate arrival and departure dates for each stopover event using the timestamps of the first and last locations and assessed variation in duration using the R package *lubridate* (Grolemund and Wickham 2011). We report these and all sample statistics with their interquartile ranges (IQR). Because location sampling intervals varied across tag types, we caution that these durations should be considered minimum estimates and are not comparable across individuals or species. We used a logistic regression to evaluate the influence of temporal resolution on stopover occurrence, using the mean interval between location estimates for each individual during the migratory window. Finally, we calculated an approximate centroid for each stopover using the R package *sf* (Pebesma 2018). We found that Argos class 0, A, and B locations occasionally had a large, distorting effect on centroids, particularly when stopovers consisted of only a few locations—an observation consistent with the known higher variability in error radius for these "low" Argos LCs (Douglas et al. 2012). Therefore, we used only locations with lower variability (GPS and Argos LC 3, 2, and 1) for centroid estimation. While Argos location classes are not always reliable predictors of the size of location error (Witt et al. 2010), our checks were a simple and minimal way to improve confidence in stopover site locations across differently structured movement tracks.

Geographic Patterns

To evaluate the spatial distribution of shorebird stopovers within the Amazon Basin, we calculated species richness and stopover density within the 39 subbasins (see Figure 2). We defined the per-subbasin stopover density as n/A, where n = the number of observed stopover centroids within a subbasin and A = area of the subbasin in km^2. We compared this value to densities from a Complete Spatial Randomness (i.e., homogenous Poisson point process; 'CSR') null model generated by randomly distributing an equivalent number of points throughout the region using Monte Carlo simulations. We ran 99 simulations and performed a per-subbasin confidence envelope test that rejected CSR (at $\alpha = 0.02$) when the observed density was greater than the maximum simulated density or less than the minimum simulated density (Baddeley et al. 2014). To evaluate potential associations with the major drainage network of the Amazon Basin, we calculated stopover density within 1 and 5 km of AWI river centerlines and, *via* a similar confidence envelope test, compared results with the simulated density of a CSR null model. These distances were selected to capture aggregations in relation to narrow tributaries and main river channels—like the Amazon/Solimões—which may span several kilometers in width. Finally, for individuals tracked over more than one southward migration, we inspected their tracks for returns to the same stopover site using the pairwise Euclidian distance of all stopover-associated locations.

Habitat Selection

Because habitat selection involves decision-making at multiple hierarchical scales, we evaluated the selection of stopover sites within the broader landscape (analogous to 2nd order selection) and finer-scale selection of areas within stopover sites (analogous to 3rd order selection; Johnson 1980) using a suite of remote sensing data layers. We used high-resolution (<5 m $pixel^{-1}$), optical Planet-NICFI imagery (Planet 2017, NICFI 2021) for visual overviews of landscape structure, as well as annual land use and land cover ('LULC') data from MapBiomas Amazonía (Colección 4.0,

https://amazonia.mapbiomas.org/), which is generated using supervised classification of spectral Landsat 4–8 imagery at a 30-m spatial resolution. To assess the freshwater resources that shorebirds may have selected, we used the Joint Research Commission ('JRC') Global Surface Water "occurrence" layer, generated from Landsat 5, 7, and 8 imagery from 1984–2021 (Pekel et al. 2016). JRC occurrence quantifies the long-term frequency of surface water presence across this time period from 0–100% at a 30-m spatial resolution, with monthly averaging to offset seasonal bias in the number of valid observations due to cloud cover (Pekel et al. 2016). To assess the use of highland versus lowland biomes, we also included digital elevation data (meters above sea level) from NASA's Shuttle Radar Topography Mission, also at a 30-m spatial grain (Farr et al. 2007). All remote sensing data layers were pre-processed and obtained through Google Earth Engine (Gorelick et al. 2017).

[LEVEL HEADING 3] Site selection

We first investigated the large-scale landscape configurations that may influence shorebird decisions to stop. We began by visually inspecting biannual Planet-NICFI imagery basemaps matched to shorebird stopover locations and the period associated with shorebird arrival. For a quantitative examination of site selection, we fit species-specific resource selection functions to the areas surrounding stopover sites in a used-available framework, contrasting the environmental 'neighborhoods' (Addicott et al. 1987) around used stopover sites with the neighborhoods around available sites. Used and available neighborhoods were defined by placing a fixed-width buffer around each stopover site centroid. Since we did not have prior information about the scales at which shorebirds evaluate potential stopover sites, we explored a range of buffer sizes (2, 5, 10, 15, and 20 km) using a pseudo-optimized moving window approach and selected the best-performing "characteristic" scale for each variable and species (see Supplementary Methods; McGarigal et al. 2016, Zeller et al. 2017). Available neighborhoods were randomly distributed across the region at a 500:1 (available:used) ratio. To avoid edge effects and an overrepresentation of areas that populations may rarely or never cross, we randomly distributed available neighborhoods no less than 20 km from the Amazon Basin boundary and only in subbasins crossed by the straight-line movement tracks of corresponding individuals.

Next, we compared environmental variables within used and available neighborhoods. We focused on five MapBiomas LULC classes that reflect and extend the known habitat preferences of shorebirds: "forest", "farming", "grassland", "wetland", and "rivers, lakes, and oceans" (hereafter, we refer to this last class as "rivers & lakes" for our inland region). Both "farming" and "forest" are aggregate, higher-order categories defined by MapBiomas: "forest" includes the "forest formation", "open forest/savannah formation", and "flooded forest" classes, while "farming" includes "pasture", "agriculture", and "mosaic use" (mixed pasture and agriculture) classes. For site-level selection, we classified JRC surface water occurrence into 4 categories, reflecting permanently (≥97%), frequently (22–96%), occasionally (1–21%), and never (0%) inundated pixels, using thresholds selected by an a priori inspection of occurrence quantiles across the study region. We summarized categorical LULC and JRC variables as within-neighborhood proportions and continuously varying elevation as a within-neighborhood mean.

We estimated selection coefficients using "infinitely weighted" univariate logistic regressions, assigning large a priori weights of 10^3 to available points. Infinite weighting in this way helps to minimize the sampling bias inherent in finite availability data and facilitates faster computations, particularly over areas as large as the Amazon Basin (Aarts et al. 2012, Fithian and

Hastie 2013). Environmental variables were *z*-standardized and checked for co-linearity using Pearson correlations. As a result of these checks, the proportions of permanent inundation and dry land, which were often closely correlated with the proportion of rivers & lakes ($r > 0.7$), were not evaluated. Models were fit separately to each species and variable at its characteristic scale. Since some individuals stopped more than once during southward migration and/or were tracked over multiple years—potentially introducing spatial autocorrelation into the site selection process—we calculated robust confidence intervals for each coefficient using track-level (i.e., per-individual, per-year) clustering via the *sandwich* package (Zeileis et al. 2020). In resource selection functions, variable coefficients reflect the relative strength of selection (RSS) for sites one standard deviation of the variable away from the mean and are reported as log odds, or exp(β), with associated robust confidence intervals (Fieberg et al. 2021). We confirmed coefficient stability by fitting models with increasing numbers of available neighborhoods and checking for convergence on stable values at our available:used ratio.

[LEVEL HEADING 3] Within-site selection

To examine the selection of environmental variables at finer spatial scales (i.e., within a stopover site), we used step-selection functions fit to subsets of movement tracks. Step-selection functions can offer more specific insights into the habitats and resources that individuals use (Thurfjell 2014), but they can be challenging to fit for avian stopover events, which are often brief and composed of a small number of coarsely sampled and/or low-accuracy locations. While these limitations made fitting individual step-selection functions infeasible, we used a modified form of this function, pooling higher-accuracy steps at the species level to examine the resources selected most frequently by our focal species.

For each species, we first created stopover-associated subsets of movement tracks. We used only stopover-associated locations in order to restrict inference to movements with comparable correlation structures and filtered these to retain only GPS locations and Argos LC 3 locations with associated Kalman-derived error ellipse information. This analysis did not include Argos locations without associated error ellipse information from 37 *C. melanotos* and 6 *B. longicauda* tracked with Argos PTT devices. We then identified used step "endpoints" (i.e., locations that followed another location within the same stopover event). We generated 5 available endpoints using theoretical step length and turning angle distributions for each used endpoint. For more information on the parameterization of these distributions, see the Supplementary Methods.

We compared environmental features—namely, LULC and surface water occurrence—at used and available step endpoints. Because we were interested only in identifying the most influential features, we used the LULC class distributions (Supplementary Material Figure S4) to identify up to 4 frequently selected LULC classes for each species and reclassified all others into a general reference category. Values were compared in a stratified case-control design, implemented *via* the R package *survival* (Therneau 2022). When model results indicated quasi-separation or non-convergence, we reclassified lower-performing LULC classes into the reference category. We then added continuous surface water occurrence values, allowing for linear and quadratic terms. We selected the best performing LULC/occurrence model for each species using AIC_c (Burnham and Anderson 2002), preferring simpler models when these values were comparable ($\Delta AIC_c \leq 2$). Variable coefficients are reported in log odds with robust confidence intervals.

Finally, because all telemetry-derived locations remain only estimates (rather than "true" locations), we explored the influence of location error on our selection coefficients. We used informative error priors, state-space models, and Monte Carlo simulations to identify plausible alternatives for used endpoints. We used the *ctmm.select* function from the R package *ctmm* to identify the best-fitting continuous-time state-space models for each track (Fleming and Calabrese 2022) and the *predict* function to generate 99 alternative "used" locations for each observed used location. We then evaluated the number of times the coefficients of selected or avoided variables changed signs, or their robust confidence intervals crossed one. For more information on these steps, see the Supplementary Methods.

RESULTS

Stopover Incidence

We identified 212 shorebirds that were tracked at least as far south as the Amazon Basin during southward migration. Several individuals (n = 17) undertook this journey multiple times, producing a total of 233 southward migratory tracks. Nearly all of these tracks appeared to follow inland routes across the Amazon Basin. The only exceptions were 5 *T. flavipes* that followed the Atlantic coast south, intersecting the region only in the Amazon River estuary (i.e., at its easternmost extreme). Of the 228 tracks that took inland routes, 10 ended abruptly before recording a stopover event or nearing the region's southern boundary. Because we did not have sufficient data to determine use of the region for these individuals, we discarded their tracks from further counts and proportions, leaving 218 southward tracks across the inland Amazon Basin from 202 unique individuals (Table 2).

We found that 74.3% of tracks crossing the Amazon Basin recorded at least 1 stop in the region, while 24.0% contained 2 or more stops. Per-species proportions of tracks with stopovers ranged as high as 90.5% in *C. melanotos* and 80.0% in *C. subruficollis*, and as low as 57.7% in *B. longicauda*. We caution, however, that these proportions should be interpreted as minimums: tracks with lengthy intervals between locations may not necessarily have been continuous over the region, even if no stopover events were recorded. Indeed, stopover occurrence was significantly associated with the sampling interval: each additional hour between locations was associated with a 0.8% decrease in the odds of observing a stopover event (OR = 0.992, 95% CI [0.987, 0.996], $p < 0.001$; Supplementary Material Figure S1). Several tracks in which stopovers were not observed were sampled at multi-day intervals (e.g., 14-day intervals for some *B. longicauda* and *T. flavipes*). Several others contained unexpected and pronounced reporting gaps that may have been a result of declining battery performance during long deployments (e.g., >2 days for some *T. flavipes*, *C. melanotos*, and *L. haemastica*).

We also noted several individuals—in total, 3 *T. flavipes*, 3 *B. longicauda*, and 1 *C. melanotos*—that migrated to and subsequently spent part or all of their nonbreeding seasons within the region, often moving across sequences of stationary sites. Of the 17 individuals tracked for 2 southward migrations, 9 stopped in the region in both years (1 *L. haemastica*, 7 *C. melanotos*, and 1 *C. subruficollis*), and none returned to the same stopover site(s).

Geographic Patterns

Three of 39 hydrological subbasins in the region had higher stopover densities (stops km^{-2}) than expected for their size under CSR: the Amazon Floodplain, Mamoré, and San Miguel. Eight subbasins had lower densities than expected, including the Araguaia, Iriri, Japurá-Caquetá, Juruena, Negro, Tocantins, Trombetas, and Xingu (Figure 2A). Species richness was highest in the Amazon Floodplain, where at least 1 individual from each species stopped, and was also high in the Mamoré subbasin, where individuals from 5 species stopped (Figure 2B). In total, 27.6% of stopover centroids were within 1 km and 60.0% were within 5 km of major river centerlines, generating observed near-river stopover densities higher than those generated by all random simulations.

Temporal Patterns

Arrivals at stopover sites primarily occurred during September (59.3%) and October (21.5%; Figure 3A), a period that coincides with falling or low water throughout much of the region (Supplementary Material Figure S2). Subbasin dates of first arrival (i.e., an individual's first stopover within a subbasin) were generally similar across the region but slightly later in the east and south (Figure 3B). Across species, the earliest stopover occurred in *C. melanotos* (5 August), while in *P. dominica*, the earliest stopover was more than a month later (10 September). Minimum stopover durations lasted from 0.6 to 83.9 days, with *L. haemastica* stopping for the shortest periods (median: 1.7 days; IQR: 1.2–2.2 days) and *B. longicauda* the longest (median: 12.0 days; IQR: 8.2–26.4 days), though these values were likely influenced by interspecific variation in transmitter location frequency (Figure 4) and, in some cases, by the proximity of stopover sites to longer-term nonbreeding sites.

Habitat Selection

[LEVEL HEADING 3] Site selection

Shorebirds stopped over in various hydrological landscapes, including river bars, oxbows, ria lakes, river islands, river floodplains, interfluvial grasslands, and aquacultural and agricultural sites (Supplementary Material Figure S3). All species selected for (RSS > 1) sites with a higher proportional cover of grassland, wetland, rivers & lakes, and frequent or occasional inundation (Figure 5). All species also selected against (RSS < 1) sites with higher proportional forest cover. Coefficients and robust confidence intervals are reported in Supplementary Material Table S2.

[LEVEL HEADING 3] Within-site selection

We evaluated step-selection functions on a total of 798 stopover step endpoints, taken from 4 *L. haemastica*, 23 *T. flavipes*, 22 *P. dominica*, 9 *B. longicauda*, 13 *C. melanotos*, and 37 *C. subruficollis* southward migrations. We found that nearly all species selected for rivers & lakes within their stopover sites, except *B. longicauda*, which selected grasslands and mosaics of pasture and agriculture (Figure 6; Supplementary Material Table S3). For more details on model fitting, see the Supplementary Results. Including a linear surface water occurrence term marginally improved the

model for *L. haemastica*, indicating a selection of sites that are more frequently inundated throughout the year; for other species' models, including surface water occurrence made no significant improvement. Selected or avoided coefficient estimates were robust to location error, retaining their signs in all cases and their strictly positive or negative robust confidence intervals in all but one case: the grassland coefficient for *B. longicauda*, whose robust confidence interval crossed one in 17% of simulations.

DISCUSSION

Our study makes clear that the Amazon Basin provides stopover habitat for the majority of individuals from 6 Nearctic-breeding shorebird species en route to southern South America. We found that while the stopovers of these individuals spanned much of the Amazon Basin, most were concentrated in a few regions and made use of a specific suite of habitat features. In particular, habitats along or near the Amazon Basin's many rivers and lakes were preferred by most species. Taken together, our results indicate the Amazon Basin likely provides important habitat for many shorebirds and that shorebird conservation should be considered alongside that of the incredible array of other species found in the region.

Stopover Incidence

We found that at least 74% of our tracked individuals stopped in the Amazon Basin, including large proportions of *C. melanotos* and *C. subruficollis*. On average, stopovers were relatively short, although individuals from several species stopped over for considerably longer periods. Some individuals of three species even spent their entire nonbreeding periods in the region (see also Hill et al. 2019). In combination, these results far exceeded our expectations for the number of birds stopping over in the region based on its size alone. A number of the species we tracked, for instance, are known to regularly fly over similarly sized inland regions (Senner et al. 2014, Lanctot et al. 2016, Hill et al. 2019) and other large, well-studied inland regions support few important shorebird stopover sites (Delany et al. 2009). As the lifetime performance of satellite tracking devices improves, future work should also investigate the importance of the region throughout the annual cycle, including during the nonbreeding season and northbound migration. Because a number of Nearctic-breeding shorebird species have yet to be the subject of tracking studies but are known to spend the nonbreeding season either in or south of the Amazon Basin—including *C. fuscicollis* (White-rumped Sandpiper), *C. bairdii* (Baird's Sandpiper), *C. himantopus* (Stilt Sandpiper), *Actitis macularius* (Spotted Sandpiper), and *T. solitaria* (Solitary Sandpiper)—future work may further increase our estimates of the importance of the region to shorebirds.

Stopover Geography, Habitat Use, and Water-level Fluctuations

North America is characterized by migratory flyways that funnel birds passing through the continent around major barriers and into areas with sufficient stopover habitat (Buhnerkempe et al. 2016). Similar flyways have yet to be described from South America, although clear corridors of movement along both the Atlantic and Pacific coasts have been described, as have connections between the Amazon Basin and Patagonia (Antas 1983, Morrison 1984, Jahn et al. 2013, 2016). Our results

suggest that the Amazon Basin should not be considered a single unit, as some shorebird species tended to stop in distinct portions of the region. *Calidris subruficollis*, *C. melanotos*, and *B. longicauda* largely stopped over in the western portion of the Amazon Basin; whereas *P. dominica*s tended to stop in the eastern portion. *Tringa flavipes* and *L. haemastica* were somewhat less constrained, using both the western and eastern portions, as well as much of the area in between. As a result, only 3 subbasins within the Amazon Basin exhibited high stopover intensities and species diversity—the Amazon River Floodplain and the San Miguel and Mamoré Rivers in Bolivia—while most other subbasins hosted only 1 or 2 species. Nonetheless, because we were unable to gather tracking data from across the entire breeding and nonbreeding ranges of each species, it is possible that other subbasins might be used more heavily by yet-to-be-tracked populations of our study species.

Irrespective of where they stopped over within the Amazon Basin, the shorebirds we tracked selected a similar suite of "open" habitat features. First and foremost, all species selected stopover sites close to the region's rivers and lakes. They also preferred sites with higher proportions of grassland, pasture, and impermanent surface water, while avoiding sites with higher proportional forest cover. At finer scales, many species also preferred areas with rivers and lakes within their stopover sites. Only *B. longicauda* did not exhibit this behavior, preferring instead interfluvial areas of natural or modified grasslands. Taken together, our results emphasize the importance of Amazonian riverine habitats for shorebirds. Such habitats are used by shorebirds in other mid-continental regions globally (Albenese and Davis 2015), but are often heavily managed, resulting in significant habitat loss (Taft and Haig 2003) and reductions in quality where they do remain (Kozik et al. 2022).

Notably, riverine habitats may not always be available to shorebirds, even where they continue to exist. Historical on-the-ground observations in the Amazon Basin, for example, have documented shorebirds using the muddy shores and interiors of riverine islands that are only available during limited portions of the year (Serrano 2010). Accordingly, Antas (1983) hypothesized that regional variation in rainfall might determine where and when shorebirds stop within the Amazon Basin. Our data corroborate this hypothesis, as the arrival of our tracked individuals coincided with the dry season in much of the region and regional variation in stopover timing roughly corresponded with variation in the timing of periods of lower water (Latrubresse et al. 2017). Whether shorebirds are actively choosing to migrate through specific regions when water levels are low requires further investigation, but shorebird movements in other inland regions are similarly timed and, in fact, predicated on the existence of ephemeral shallow water habitats (Skagen et al. 2008, Pedler et al. 2017). Though we found no consistent pattern in the long-term (1984–2021) frequency of surface water occurrence in the areas that shorebirds selected, long-term trends may also be insufficient to capture the local conditions that shorebirds experience at stopover sites. Surface water distribution, in particular, is highly variable across years and can change rapidly during southward migration, especially along river networks. Future work may need to rely on remote sensing imagery captured at high spatial and temporal resolutions in order to link shorebird arrival with the dynamic hydrology that dominates much of the region.

Conservation Implications

The Amazon Basin is a naturally dynamic region, with water levels that can vary dramatically across seasons and years, resulting in pulses of water that intermittently flood areas, shift the course of rivers, and alter both small- and large-scale ecological processes (Countinho et al. 2019, Marca-Zevallos et

al. 2022). Superimposed on this natural dynamism are the myriad anthropogenic changes that have occurred in the region in recent decades, including rapid rates of deforestation (Silva Junior 2020), human population growth and urbanization (Richards and VanWey 2015), agricultural intensification (Marin et al. 2022), and hydrodynamic regime alteration (Latrubesse et al. 2017). What these anthropogenic changes mean for the future ecological integrity of the Amazon Basin is uncertain, but many studies predict rapid rates of habitat and biodiversity loss (Latrubesse et al. 2020), coupled with dramatic changes to the regional and global climate (Duffy et al. 2015).

At the same time, shorebird populations are declining faster than those of nearly any other group of birds, with declines being especially pronounced in long-distance migrants (Rosenberg et al. 2019). In fact, the average rate of decline across the 6 species tracked here exceeds 70% over the past 4 decades (Smith et al. 2023). In this context, the incredible rates of environmental change occurring in the Amazon Basin represent an unknown but likely significant threat to the shorebird populations that use the region. In particular, the large number of proposed hydroelectric dams within the Amazon Basin (Timpe and Kaplan 2017) could profoundly influence the timing of the availability of the riverine habitats that are clearly important to shorebirds. Development and implementation of an integrated research and monitoring program in the Amazon Basin would support understanding: (1) whether the areas of high shorebird diversity and stopover intensity that we identified are also associated with large aggregations of shorebirds—such as have recently been found in the Beni Province of Bolivia (WHSRN 2015)—or if they represent areas of extensive available habitat that enable shorebirds to remain at low densities; (2) how shorebirds use the variety of habitats they select within stopover sites and, especially, if some habitats are used only for certain activities or at specific times of the day; (3) the degree to which intra- and interannual variation in water levels determine where in the Amazon Basin shorebirds stop and when they stop there; (4) the degree to which shorebirds use the Amazon Basin during northward migration when water levels are higher (Antas 1983) and winds may be more beneficial along other migratory routes (Linscott et al. 2022); and (5) how populations differ in vulnerability according to the countries and subbasins they visit within the Amazon Basin, which may have differing hunting regulations and magnitudes of habitat loss/change. This research agenda, coupled with policy-based efforts to link shorebird conservation with efforts targeted at other Amazonian biodiversity, would support expedited and efficient conservation.

It is important to note, however, that shorebirds may be resilient to some changes in the Amazon Basin. Although natural habitats were selected for more strongly by all species, *B. longicauda*, *P. dominica*, and *T. flavipes* also selected agricultural and mosaic use areas within their stopover sites. These preferences are in line with these species' habitat use during other periods of the year (Lehnen and Krementz 2013, Stodola et al. 2014, Alfaro et al. 2019, Hill et al. 2019), as well as being corroborated by anecdotal on-the-ground observations from the Peruvian and Bolivian portions of the Amazon Basin (Lesterhuis and Angarita 2022). Nonetheless, the successful use of agricultural habitats by shorebirds often requires specific management practices (e.g., Golet et al. 2022), and it will be important to adapt and develop methods specific to this region that can benefit both humans and shorebirds.

Conclusion

Successful conservation measures depend on accurate information about where species occur and what pressures may influence their ability to survive and reproduce. For species that migrate long distances, tracking devices that remotely provide data on individual movements often offer the only feasible way to gather such information (Navedo and Piersma 2023). Our use of tracking data here follows in the footsteps of other recent studies by filling in holes in our scientific knowledge of the migratory strategies of otherwise relatively well-studied Northern Hemisphere breeding species (Chan et al. 2019, van Bemmelen et al. 2019, Verhoeven et al. 2020). The continued existence of such gaps points to the urgent need for movement data from other understudied species (Scarpignato et al. 2023), availability of these data for direct conservation action, and updating of conservation priorities as new information is acquired. We hope that our study can thus simultaneously spur conservation action for the benefit of shorebirds and other taxa in the Amazon Basin, as well as accelerate efforts to characterize the migrations of the remaining yet-to-be-studied Nearctic and, especially, Neotropical shorebird species (e.g., Faria et al. 2023).

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Ethics statement

Shorebird trapping and transmitter attachment were conducted following recommended procedures in the Guidelines to the use of Wild Birds in Research of the Ornithological Council. All projects were conducted under appropriate government permits.

Conflict-of-interest statement

The authors have no conflicts of interest to report.

Author contributions

JL, EB, RB, and NRS conceived of the project; all authors collected the data; JL carried out the analyses; JL and NRS wrote the manuscript; all authors contributed edits.

Data availability

Movement data for *Bartramia longicauda* (Upland Sandpipers; 2 populations) and *Tringa flavipes* (Lesser Yellowlegs) have been archived at Movebank (www.movebank.org). Data for *B. longicauda* from the Great Plains and New England are available as Upland Sandpiper Annual Life Cycle Ecology (Movebank ID: 176770813, Hill and Renfrew 2019). Data for *T. flavipes* are available as USFWS Lesser Yellowlegs (*Tringa flavipes*) migratory movements (Johnson and McDuffie 2024). Movement data for *Calidris subruficollis* (Buff-breasted Sandpiper) are available as Tracking data for Buff-breasted Sandpipers (*Calidris subruficollis*) (Tibbitts et al. 2023). Movement data for *Limosa haemastica* (Hudsonian Godwits), *Pluvialis dominica* (American Golden-Plovers), *C. melanotos* (Pectoral Sandpiper), and *B. longicauda* (Alaska population) are stored on Movebank and available upon request to the data owners. For *L. haemastica,* see "Migration of Hudsonian Godwits. Linscott et al." (Movebank ID: 950270455). For *P. dominica*, see "Fall movement of American golden-plovers from the Seward Peninsula and North Slope, 2022. Bathrick et al." (Movebank ID: 2220666774) and “Arctic shorebird migration tracking study - American Golden-Plover. Lanctot et al.” (Movebank ID: 565443496). For *C. melanotos*, see “Arctic shorebird migration tracking study – Pectoral Sandpiper. Lanctot et al.” (Movebank ID: 560144617). For all species, movement data within the Amazon Basin are archived at the Zonodo digital repository (doi: 10.5281/zenodo.12802304), and sample code used for habitat analyses is available at: http://www.github.com/jalinsco/AB_Shorebird_Stopovers

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Table 1. Shorebird tracking projects that contributed data for analysis of stopovers in the Amazon Basin during southward migration. Counts (*n*) reflect the number of tracked individuals in each project that traveled at least as far as the northern boundary of the Amazon Basin. Telemetry devices were manufactured by Microwave Telemetry, Inc. (Argos PTTs) or Lotek, Inc. (PinPoint Argos). Median observed location intervals are calculated across all individuals considered for analysis, with interquartile range (IQR) in parentheses.

Species	*n*	Years	Telemetry device	Programmed location intervals	Observed location intervals	Deployment locations	Reference
Pluvialis dominica (American Golden-Plover)	9	2022	4-g PinPoint Argos-75	2 days	2.0 days (IQR: 2.0–2.0)	Alaska, USA	Bathrick et al., see Acknowledgments
	27	2019–2020, 2022	4.8-g PinPoint Argos-120	2 days	2.0 days (IQR: 2.0–2.0)	Alaska, USA or Canada	Lanctot et al., see Acknowledgments
Calidris subruficollis (Buff-breasted Sandpiper)	6	2017–2020	2-g Argos PTT	Incidental	2.1 hr (IQR: 1.0–5.4)	Texas, USA or Uruguay	Tibbitts et al. (2023)
	45	2016–2019	4-g PinPoint Argos-75	2 days (GPS); Incidental (Argos)	2.0 days (IQR: 1.71–2.0)	Texas or Alaska, USA	Tibbitts et al. (2023)
Limosa haemastica (Hudsonian Godwit)	1	2019–2020	5-g Argos PTT	Incidental for 5 hours/ 24 hours off	0.5 hr (IQR: 0.3–1.7)	Chiloé Archipelago, Chile	Linscott et al. (2022)
	4	2019–2021	6.6-g PinPoint Solar	2 hr (GPS); Incidental (Argos)	2.0 hr (IQR: 0.8–2.3)	Chiloé Archipelago, Chile	Linscott et al. (2022)
Tringa flavipes (Lesser Yellowlegs)	43	2019–2021	4-g PinPoint Argos-75	2 or 14 days (GPS); Incidental (Argos)	2.0 days (IQR: 2.0–4.0)	Alaska, USA or Canada	Johnson and McDuffie (2024)
Calidris melanotos (Pectoral Sandpiper)	37	2016–2020	5-g Argos PTT-100	Incidental	1.6 hr (IQR: 0.6–7.5)	Alaska, USA	Kempenaers and Valcu (2017, and personal communication)
	16	2018–2021	4-g PinPoint Argos-75	24 hr (GPS); Incidental (Argos)	24 hr (IQR: 24.0–24.0)	Alaska, USA	Lanctot et al., see Acknowledgments
Bartramia longicauda (Upland Sandpiper)	2	2016–2018	5-g Argos PTT	Incidental	0.9 hr (IQR:0.5–2.0)	Kansas or Massachusetts, USA	Hill et al. (2019)
	5	2016–2017	4-g PinPoint Solar	7 or 14 days	8.0 days (IQR: 7.0–14.0)	Kansas or Massachusetts, USA	Hill et al. (2019)
	6	2021–2022	2-g Argos PTT	Incidental	0.8 hr (IQR: 0.4–1.9)	Alaska, USA	Gesmundo and Johnson, personal communication
	11	2021–2022	4-g PinPoint Argos-75	3, 5, or 7 days (GPS): Incidental (Argos)	3.0 days (IQR: 3.0–4.5)	Alaska, USA	Gesmundo and Johnson, personal communication

Table 2. Per-species counts of individual shorebirds that were analyzed for stopover events in Amazon Basin during southward migration. Track counts reflect that some individuals were tracked over multiple migrations. For all species, the majority of tracks included at least one stopover event.

Species	Individuals	Southward tracks	Southward tracks with stopover(s)	Total stopovers
American Golden-Plover	33	33	22 (66.7%)	25
C. subruficollis	48	50	40 (80.0%)	65
Hudsonian Godwit	4	8	5 (62.5%)	8
Lesser Yellowlegs	43	38	23 (60.5%)	33
Pectoral Sandpiper	51	63	57 (90.5%)	100
Upland Sandpiper	23	26	15 (57.7%)	15
Total	202	218	162 (74.3%)	246

Figure 1. Shorebird stopovers occurred throughout the Amazon Basin during southward migration. Centroids of stopover events (points) and corresponding movement tracks (lines) are shown (**A**) for all species and (**B**) for each species separately. White polygon depicts the extent of the inland Amazon Basin. Shorebirds were tracked using satellite transmitters in 2016–2022.

Figure 2. Shorebird stopover density and species richness vary within major hydrological subbasins of the Amazon Basin during southward migration. Variations in color indicate (**A**) subbasins with higher or lower density than expected under a Complete Spatial Randomness (CSR) null model, and (**B**) the number of species that stopped in each subbasin.

Figure 3. Shorebird dates of arrival at stopover sites within the Amazon Basin are generally later to the south and east. (**A**) Stopover event centroids (points) are colored by the month of arrival and shown in relation the major river network (gray lines; Venticinque et al. 2016). (**B**) Julian date of arrival is shown for 5 major subbasins, as indicated on the map: Ucayali, the Upper Amazon/Solimões floodplain (west of the confluence with the Rio Negro), the Lower Amazon floodplain (east of the confluence with the Rio Negro), Mamoré, and Purus. Corresponding boxplots show the distribution of dates of first arrival for individuals that stopped in the subbasin. Hinges are first and third quantiles, with a point indicating an outlier.

Figure 4. Stopover durations (green boxplots) and the intervals between location estimates (gray boxplots) vary for species migrating southward across the Amazon Basin. Boxplot hinges are the first and third quantiles of distributions for 6 species: *Pluvialis dominica* (AMGP), *Calidris subruficollis* (BBSA), *Limosa haemastica* (HUGO), *Tringa flavipes* (LEYE), *C. melanotos* (PESA), and *Bartramia longicauda* (UPSA). Points represent outliers, with extreme outliers and corresponding durations/intervals indicated in text.

Figure 5. Relative selection strength ('RSS') for broad-scale stopover site characteristics within the Amazon Basin during southward migration. Coefficients (points) reflect the RSS of proportional land use/land cover and surface water occurrence classes and elevation for each shorebird species. Robust 95% confidence intervals (horizontal lines) are given in log-odds and are black when confidence intervals do not cross one (vertical dashed line), indicating either selection or avoidance of the characteristic. Missing estimates indicate non-convergence or quasi-separation.

Figure 6. Relative selection strength ('RSS') for fine-scale land use/land cover ('LULC') and surface water occurrence classes within shorebird stopover sites in the Amazon Basin during southward migration. Coefficient estimates (points) and robust confidence intervals (horizontal lines) are given in log-odds and are black when confidence intervals do not cross one (vertical line), indicating either selection or avoidance of the class. LULC classes with no estimates were re-classified into the reference category.

Figure 1

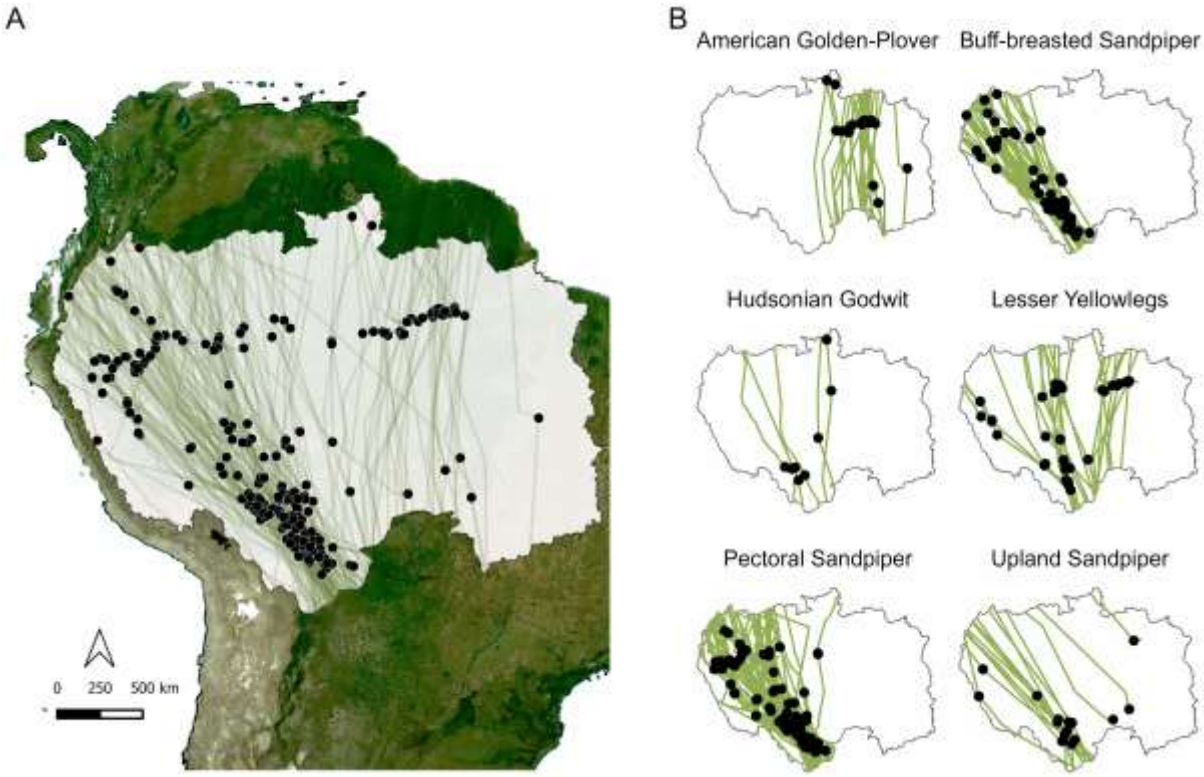

Figure 2

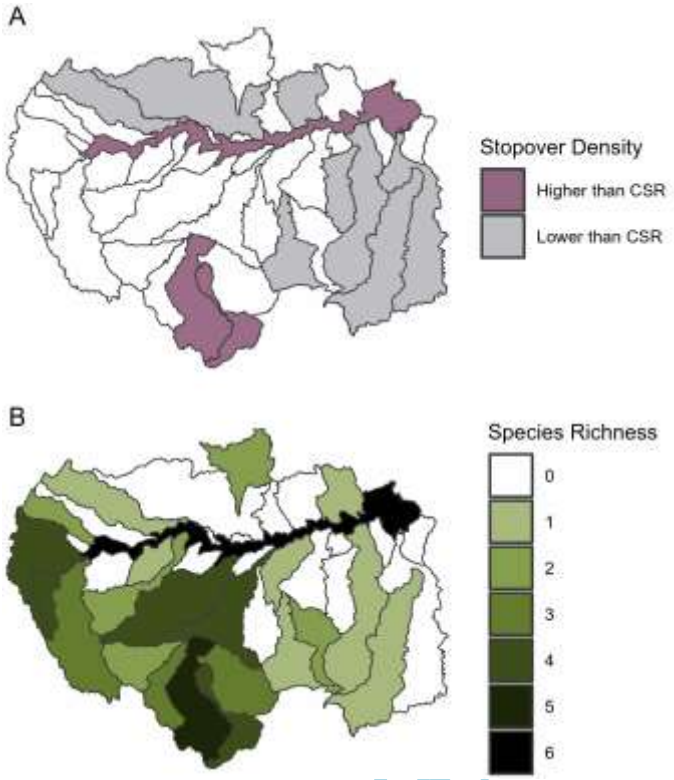

Figure 3

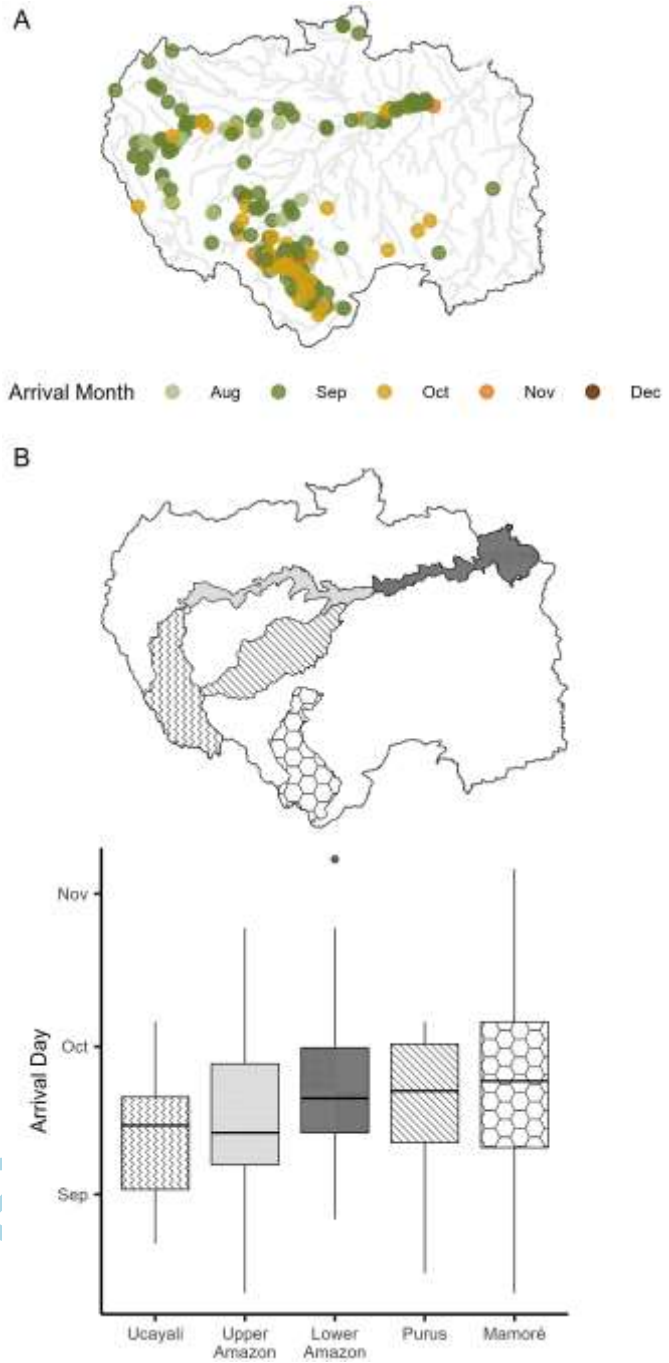

Figure 4

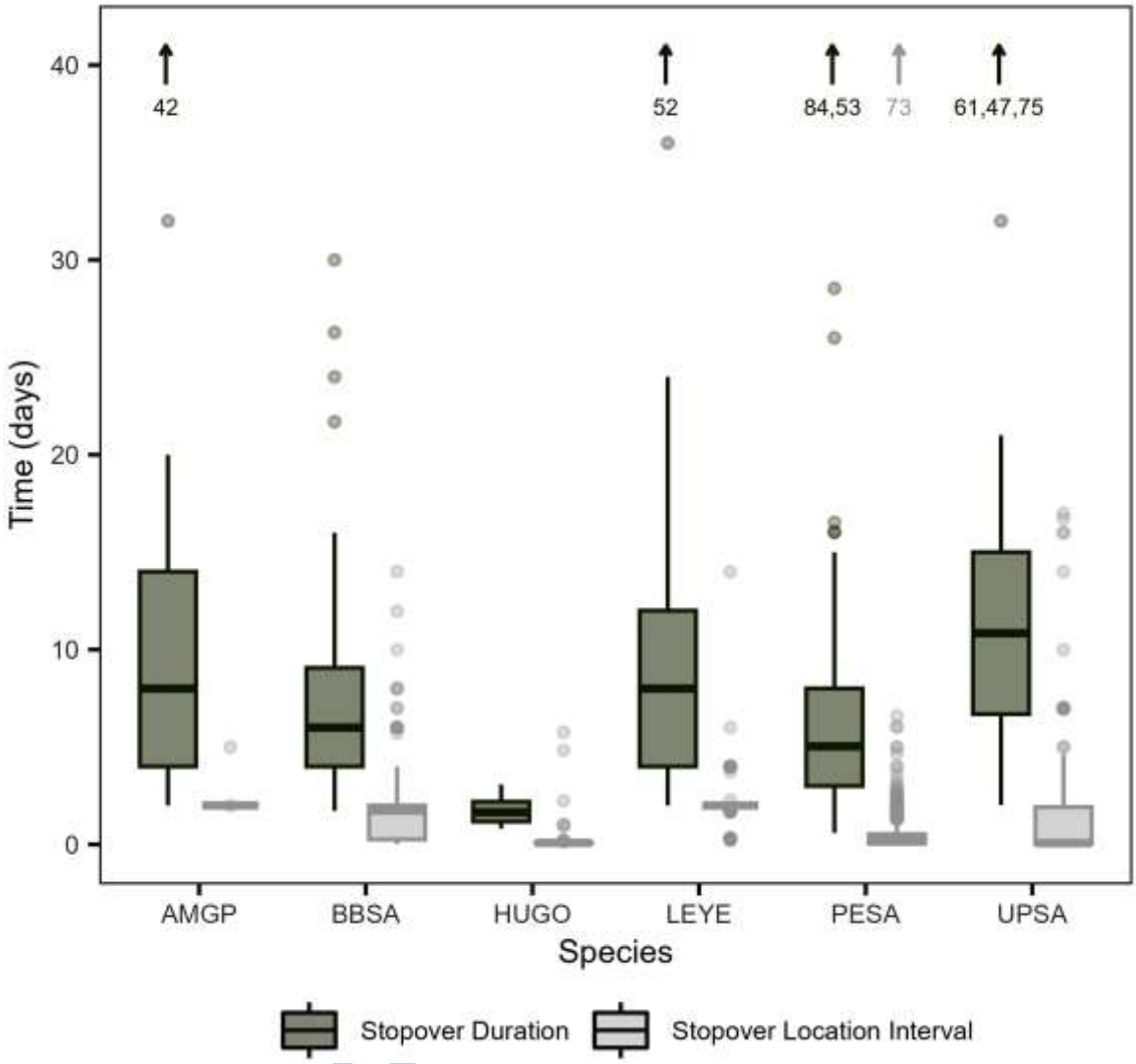

Figure 5

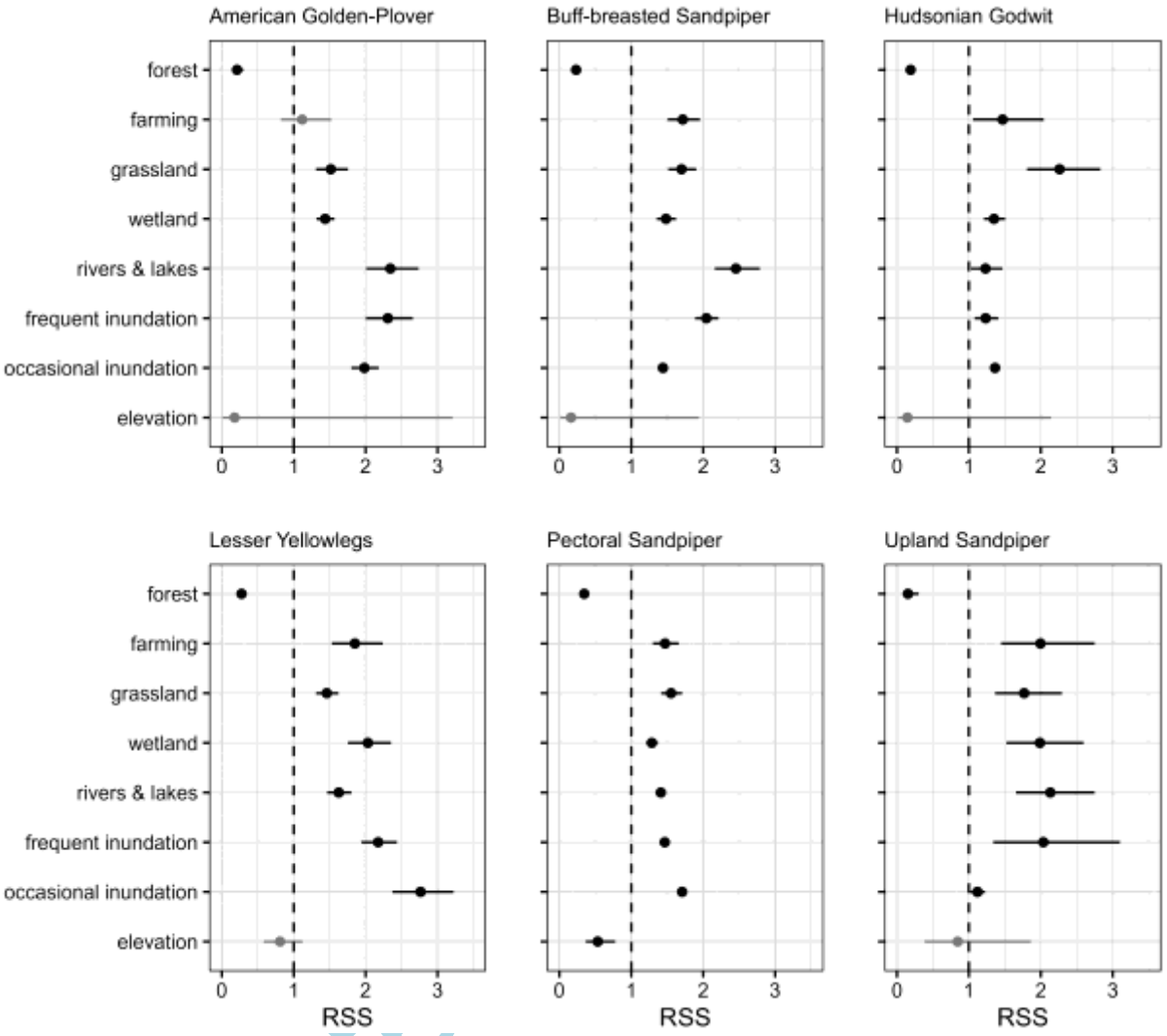

Figure 6