Dynamic Space Use of Andalusian Rice Fields by Overwintering Lesser Black-Backed Gulls is Driven by Harvest-Related Flooding

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Research

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Abstract

Background: Research on the space use and behavior of waterbirds—as highly mobile of wetland habitats—yields important insights on human-wildlife interactions of ecological and societal importance under global change. The extent to which dynamic (within-season) changes in anthropogenic landscapes affects these interactions is poorly understood. Lesser black-backed gulls (*Larus fuscus*) are prominent biovectors of biological and artificial materials, and have exhibited large population increases in parts of southern Europe in recent decades.

Methods: We combined GPS tracking, earth observation, accelerometry and field observations to study the space use of overwintering in a mixed rice field landscape in Andalusia, Southern Spain. We used Manly selectivity metrics and classified remote sensing imagery to directly evaluate space use and habitat selection for these gulls and how it changed throughout the rice harvest cycle.

Results: Analysis of over 45,000 GPS fixes and 14 classified remotely-sensed images from winter 2016-17 showed dynamic space use driven by the harvest-related flooding across the rice harvest cycle. Prior to harvest, gulls foraged in rice paddies during the day and roosted in adjacent waterbodies (the River Guadalquivir, and fish ponds) at night. During harvest, they spent nearly 100% of their daily cycle within the rice fields, foraging in harvested paddies and roosting in post-harvest, flooded paddies. After harvest, they roosted in flooded fields at night and foraged at landfills in the surrounding landscape.

Conclusion: Gull space use at landscape and paddy scales was closely linked to dynamic land and water management over the rice agricultural cycle, illustrating the detailed scales at which human activities influence the movements of ecologically important, human-associated biovectors like gulls. The frequent early-spring movement patterns of these increasingly numerous gulls between landfills and agricultural fields an important biotransport link for potentially toxic materials between waste sites and places where food is grown for human consumption.

1. Background

Anthropogenic landscape change is the leading driver of biodiversity loss in the 21st century and a major mechanism of continued global environmental change (Sala et al., 2000; Foley et al., 2005; Di Marco et al., 2018). Research on human-dominated landscapes is thus an important field of study in ecology and conservation, yielding insights for predicting and understanding interactions between biodiversity and human systems in the Anthropocene. This is especially true in wetland environments, which are highly dynamic and strongly affected by local topography and hydrology. Natural wetlands have been reduced considerably in global extent while being replaced by anthropogenic wetlands such as ricefields and reservoirs (Davidson et al. 2018). As highly mobile animals that readily practice habitat supplementation (using multiple habitat types during their daily or life cycle), birds, and waterbirds especially, are important ecological connectors in heterogeneous landscapes (Green and Elmberg, 2014; Şekercioğlu et al., 2016). The movement behavior and space use of waterbirds in human-dominated landscapes can thus have important implications for ecology, conservation, and human health (Sakoda et al., 2012; Martín-Veléz et al., 2019; Navarro et al. 2019).

Many species in the white-headed gull complex (*Larus spp.*), are well adapted to human-dominated landscapes given their broad ecological flexibility and ability to take advantage of resources made available by a variety of human activities (Van Toor et al., 2017). They have consequently benefitted from the increasing development of many areas within their global distribution, exhibiting rapidly increasing population trends in anthropogenic areas across their range (Calladine 2004; Eaton et al., 2015; Boertmann and Frederiksen, 2016). Population-level studies on mitochondrial genetic diversity in the Lesser black-backed gull (*Larus fuscus*; LBBG) in Europe indicate rapid population expansion in the twentieth century (de Knijff et al., 2001; Liebers and Helbig, 2002; Ross-Smith et al., 2014), while abundance is decreasing at several coastal breeding colonies, leading to the red listing of some subspecies (Ross-Smith et al., 2014; Eaton et al., 2015; Hario and Rintala, 2016). The increased availability of human refuse as a food resource due to the cessation of trash-burning processes in parts of Europe, and decreased availability of fisheries discards from altered fishing practices have led to a larger dependence of gulls on terrestrial and anthropogenic foods (Harris, 1965; Camphuysen, 1995; Oro, 1996). The spatial shift in *Larus* gulls and their growing use of food resources associated with humans raises concerns about their environmental and societal impacts, especially given their known role as biovectors, linking terrestrial and aquatic as well as anthropogenic and ecological systems (Martín-Veléz et al., 2019, 2020). For example, increased availability of terrestrial food in anthropogenic landscapes has led to roosting of large numbers of gulls on inland water bodies, with important impacts on water quality (Byappanahalli et al. 2015, Winton & River 2017).

LBBG overwintering in the vicinity of Doñana National Park in southwestern Spain have shown a ten-fold increase in abundance in the last 50 years (Rendón et al., 2008) and are observed in large numbers in and around nearby water bodies and rice fields throughout the winter season. Rice field landscapes are increasingly well-studied anthropogenic wetland habitats that comprise a variety of land uses and resources including irrigation ditches, grasslands, forests, natural marshes, and rice-growing paddies (King et al., 2010). These landscapes are highly dynamic across the annual harvest cycle (Fasola and Ruiz, 1997), and are heavily used by waterbirds of diverse taxa (Pernollet et al. 2015, Ramo et al. 2013, Rendón et al. 2008).

LBBG winter inland across Andalusia in southern Spain, but a combination of movement and census data suggest that in the first half of the winter they concentrate in the extensive rice field area (up to 38,000 ha.; Ramo et al. 2013) adjacent to the Doñana wetlands. These rice fields are the node with the greatest centrality within the network of important habitat sites for LBBG across the region (Martín-Vélez et al. 2020). During the rice harvest period, they feed on invasive crayfish exposed as rice plants are harvested, as well as on spilled rice grain (Lovas-Kiss et al., 2018). Individual gulls may spend many days in the rice fields during this time of the year (Martín-Vélez et al. 2020) and intra-seasonal changes in rice field use and travel to and from other habitats are thought to be linked to resource availability within the rice fields (Toral and Figuerola, 2010; Toral et al., 2011). However, this hypothesis has not been examined based on actual spatial resource availability in the rice fields, nor has the space-use of individual LBBG in response to changes in rice field habitats been studied. The movement behavior of LBBG, especially during the under-studied overwintering season, is considered a research priority for their conservation and management (Ross-Smith et al., 2014).

We combined high-resolution spatiotemporal GPS tracking and accelerometry data with remote sensing and field observations to investigate the space use and movement behavior of LBBG overwintering in a rice field landscape in Andalusia, Southwest Spain. Our objectives were to 1) quantify the spatiotemporal changes in the availability of different habitats within rice paddies throughout the harvest cycle, and determine how this influences gull behavior and habitat selection within rice paddies, 2) determine changes in the selection of rice fields over nearby alternative habitats within the Guadalquivir river delta during the winter period, and whether these are driven by rice field management, 3) establish the relationship between behavior and habitat use, using data from field observations and accelerometers.

2. Methods

2.1 Study Area

We conducted data collection and analysis at three scales, 1) the larger rice field landscape, 2) the local rice field complex, and 3) the interior of rice paddies (Figure 1). The larger rice field landscape is a rectangular 4200km^2 area centered around the rice fields but which includes the Doñana National and Natural parks, Veta la Palma aquaculture ponds, and adjacent agricultural areas within the Guadalquivir river delta (Figure 1); this area encompassed >90% of all LBBG GPS fixes during the study period, and was used as the study area for all static habitat selection analysis. The rice field complex is a zone of intensive rice cultivation to the Northeast of Doñana National Park, and is the largest rice production area in Spain. It lies within a Biosphere Reserve (Green et al. 2018) and comprises several hundred small (4-35 ha) polygonal paddies divided by dikes, small roads, and irrigation canals and portions of the Guadalquivir river. The rice field complex includes all landcover falling within a 250m buffer of rice paddy edges. It also includes larger urban settlements, fragments of shrubland and forest, relict natural marshland and extensive areas of dryland agriculture including cotton fields and fruit orchards. Finally, we examined habitat features in the interior of individual paddies, which we defined as the area at least 45m interior of the paddy edge (Toral et al., 2011). We used this analytical scale for our dynamic habitat analysis of space use with respect to within-paddy condition.

Habitat availability in rice paddies follows a consistent pattern according to the annual rice harvesting cycle, which we divided into three phases. During the pre-harvest stage, all paddies contain unharvested rice. The active harvest phase begins with rice harvest starting in late September and early October, and paddies are tilled or plowed after harvest, and finally flooded. Flooded conditions in rice paddies persist from October to December or January, depending on ambient precipitation and evaporation rates (Toral et al., 2011). The active harvest phase is marked by high heterogeneity in habitat types, because the harvest, tilling, and flooding occur in a spatiotemporally staggered and piecemeal fashion because of limited harvesting equipment, leading to asynchronous transitions between within-paddy conditions (Toral et al., 2011). The post-harvest phase begins in mid- to late-January, when all fields have typically been harvested; for the purposes of this study, the post-harvest phase of the overwintering season ends with the departure of overwintering LBBG in mid-March.

2.2 GPS Tracking Data

We used data on the movements of LBBGs tracked using Global Positioning System (GPS) trackers (University of Amsterdam Bird Tracking System, UvA-BiTS, Bouten et al., 2013) from breeding colonies in north-west Europe. The GPS trackers measured spatial position (mean position error of 3m for 60s intervals, 30m for 600 second intervals) and acceleration (tri-axial accelerometer; Bouten et al., 2013). Birds were captured and fitted with trackers under license on their breeding grounds in Northern Europe (United Kingdom, Thaxter et al. 2019; Belgium, Stienen et al., 2016; the Netherlands, Shamoun-Baranes et al., 2017). The UvA-BiTS data are stored in a centralized database (http://www.uva-bits.nl; Bouten et al. 2013). Prior to analyses, all GPS data were checked for erroneous velocity measurements (>80km/hr, the upper limit observed for this species; Shamoun-Baranes et al., 2017), potentially unreliable fixes (with fewer than 4 satellites used for geopositioning), and bursts (periods of sampling where a large number of fixes were taken over a short period of time), to avoid biasing estimates of space use. Erroneous or unreliable data points were excluded. We examined the fix interval (duration between fixes) for all GPS trackers in the database to investigate temporal structure in sampling, and sub-sampled the data to a common interval (20 minutes) to avoid bias in habitat selection calculations (Shamoun-Baranes et al., 2011); this filtering step retained ~80% of fixes (Additional File 1). We estimated the Haversine distance (spherical distance between geographical coordinates of GPS fixes) between each consecutive point, and examined the mean and total daily distance traveled for all gulls throughout the overwintering period for seasonal patterns. Finally, we calculated trajectory speed as distance/duration.

We selected data for the 2016-2017 winter season because that year had a relatively high number of tracked birds appearing in the study area (n=18), more low cloud-cover satellite images available than other years, and precipitation levels close to the average values of the past 20 years. We used all GPS data for the period of August 15, 2016 to March 15 2017 (hereafter overwintering period) within our study area, omitting all individuals with less than 1000 GPS fixes prior to data filtering and subsampling. These individuals were removed because they either had a small number of days (<14) present in the rice field landscape during the study period or in one case had sampling intervals that were temporally coarse (>3 hr) yielding poor information on fine-scale habitat use and movement patterns. In total, excluded individuals accounted for <4% of all fixes recorded in the rice field landscape during the 2016-2017 overwintering season, while the remaining dataset contained >45,000 GPS fixes from 6 individual gulls (five individuals tagged in Zeebrugge, Belgium and one on Skokholm island, U.K.).

We created two data subsets based on GPS fixes that coincided with the dates of available imagery for our dynamic habitat analysis. The first of these consisted only of data collected on the same day as each available remotely sensed image (24-hour window), and consisted of 3,082 fixes, and the second (expanded dataset) included fixes from one day before and one day after each image (72-hour window), for a total of 9,185 fixes; this is slightly less than three times as many as the 24-hour window dataset, because two images were two days apart from the proceeding image, leading to an overlap in their 72-hour windows. The 24-hour window dataset has a lower probability that harvest status changed between image collection and a given GPS fix within that window but has reduced statistical power due to a smaller sample size, while the 72-hour window dataset increases sample size and statistical power but at slightly increases the risk of including GPS fixes collected under different harvest conditions.

For each of the 6 remaining birds, we also used the UvA-BiTS virtual lab (Bouten, 2018) online client to project and visually check trajectories of unfiltered data for each gull prior to quantitative analysis. This was done by subsampling data points to 3-hour intervals and then visually examining GPS trajectories for coarse-scale movement behavior within the rice field landscape (e.g., movements between the rice paddies and other landscape features, or repeated daily movements to features outside of the rice field landscape). Any forays outside of the rice field landscape (Fig. 1) were visually examined at a 20-minute interval resolution to identify additional destinations during the overwintering season.

2.3 Remote-sensing Imagery, Classification, and Ancillary Spatial Data

We downloaded and classified a total of 14 images (ten from Landsat 5, 7 and 8 and four from Sentinel-1), with dates ranging from 2 September 2016 to 17 February 2017 (days 7 to 175) to detect and quantify the dynamic availability of habitat resources for gulls at the rice paddy scale throughout the overwintering period (hereafter “dynamic habitat analysis”). All images were geometrically and radiometrically corrected according to Aragonés et al. (2005). We classified harvest status landcover types within each paddy in the rice field complex for each available image date. Following Toral et al. (2011), we restricted the classification of rice paddies to the interior of each paddy by excluding a 45m buffer inwards from their outer edge to avoid spectral confusion with land-cover categories that are not found within paddies (e.g. shrubland, roads). Notably, this means that use of features outside of paddy interiors (e.g., dikes and roads between paddies) were quantified only in our static habitat analysis.

We classified these clipped images using K-means unsupervised classifications with the RStoolbox package (Leutner et al., 2019) in R 3.5.2 (R Core team, 2019). We chose a value of K based on the largest consensus among a suite of 30 indices using the Nbclust package (Charrad et al., 2015) in R. Where no clear consensus among metrics was available, the parsimonious (smallest K) competing value was chosen. We used the resulting image with the highest number of habitat classes present as the basis for thematic classes used in all other classified images. We attempted at minimum to classify harvest status conditions that were relevant to habitat use by gulls (see also Martín Vélez et al. 2020), specifically green vegetation or unharvested rice (low-density foraging activity), recently harvested rice (large amounts of active foraging), tilled rice (active foraging), and flooded areas (loafing, sleeping, and occasional foraging). These classes were assigned using knowledge from field visits and reference images.

We detected 7 thematic classes for harvest status within rice paddies: bare ground, dry tilled, wet tilled, deep flooded, shallow flooded, harvested rice, and green vegetation (either pre-harvest rice or other plants colonizing fields post-harvest). Deep-flooded and shallow-flooded paddies were detected based on spectral signatures, wherein deep-flooded fields showed a signature strongly indicative of water, while shallow-flooded paddies showed some mixture of water and bare ground, indicating that land was reflecting some light through a shallow layer of water; water depth in neither case likely exceeds 30cm, so the terms ‘deep’ and ‘shallow’ are based only on relative differences in water depth.

In addition to image-based classifications of harvest status, we generated an additional map of habitat resources that were unlikely to change throughout the wintering season for an analysis of static habitat features at the rice field landscape scale. For this we used a reclassified version of landcover data from the SIPNA database (Sistema de Información sobre el Patrimonio Natural de Andalucía, Junta de Andalucia, REDIAM, 2019), which included rivers and dikes, roads, non-rice agriculture, urban areas, natural and artificial ponds, and other more permanent features in the larger rice field landscape. We simplified thematic classifications for this dataset to match behaviorally-relevant habitat types for LBBG for a final habitat map of the larger rice field landscape (for extent, see Fig. 1). This involved combining classes that presumably had no impact on gull biology into single classes, for example, combining industrial and residential development into “urban”, and different types of fruit orchards into “non-rice agriculture”. Areas known to be rice paddies were lumped into a single class, “Unclassified Rice” to reflect birds using rice paddy interiors in our static habitat analysis (for days without imagery and subsequent harvest status information; Additional File 2). Finally, we generated a shapefile consisting of a 250m buffer around all rice paddies, to be used for determining whether or not given GPS fixes were occurring within the rice field complex or in another part of the rice field landscape (e.g., landfills, more distant sections of the Guadalquivir river, aquaculture ponds or natural marshes, Fig. 1).

2.4 Accelerometer Data

Tri-axial accelerometer data (1-second segments of acceleration data in three dimensions collected concomitantly with GPS fixes at 20hz frequency) were available for four of the tagged gulls. We removed accelerometer segments with more or less than 1-second of data to avoid bias, yielding a dataset of 10,641 accelerometer segments. We converted all accelerometer measurements to G’s (equivalent to gravity at the Earth’s surface, 9.8m/s^2), and calculated mean and standard error along each directional axis for each segment in order to calculate dynamic acceleration. Finally, we calculated overall dynamic body acceleration (ODBA) as the sum of all dynamic accelerations for each segment (Wilson et al., 2006; Nathan et al., 2012). We classified accelerometer data using the random forest model and behavioral classes for LBBG generated by Shamoun-Baranes et al. (2016). These classes were terloco (terrestrial locomotion, walking), flap, exflap (rapid, active flapping), soar (gliding flight), manouvre (flapping and soaring combined), peck, , sit/stand (resting or inactive with the body level), walk, float, and boat (resting on a moving object). We associated exflap, peck, and terloco with feeding and food-searching related behaviors, flap, manouvre, and soar with travel, and boat, float, and sit/stand with resting. These accelerometry-based behavioral classifications differ from those outlined for field observations (below), which were based only on visual identification and observation. We validated accelerometer classifications by checking the correspondence of classified behaviors with other spatial characteristics of the associated GPS fix for a subset of 100 fixes (e.g., whether floating was associated with points in water, or whether instantaneous velocity was high enough for points classified as soaring or flying).

2.5 Field Observation Data

We conducted behavioral observations of overwintering LBBG in the rice field complex to complement and validate the GPS and accelerometer data. We collected observational data between 0900 and 1800 hours from early November to the end of January during the 2018-2019 overwintering period (days 75-157). We constructed an ethogram of seven behaviors that were readily distinguishable in the field: walking, searching-foraging, flying, swimming, bathing, sitting, and standing. We classified all observations according to these mutually exclusive behavior classes. Behavioral data consisted of instantaneous scans as well as focal bird observations. We performed instantaneous scans on paddies that contained LBBG and scanned the entire paddy (including surrounding dikes and airspace above it) for a 1-minute interval and counted the number of gulls performing a certain behavior. To reduce the potential for temporal autocorrelation in behaviors, repeated instantaneous scans in the same site were conducted no less than 10 minutes apart. For observations of focal birds, a single individual was monitored for up to 30 minutes, recording the amount of time spent on each behavior. Observations were ended if line of sight of the bird was lost. We also recorded time of day, harvest status (unharvested, actively being tilled, or harvested, and not flooded, partially flooded, or flooded), weather, and GPS location of the approximate paddy centroid. We conducted 142 instantaneous scans and 22 focal follows (totaling approximately 10h of observation) across 70 locations and 7 days of observation.

2.6 Space Use Analyses

We classified all GPS points according to whether they fell inside or outside of the rice field complex, and whether they occurred during the day or night (according to daily sunrise and sunset times, using the R package RchivalTag (Bauer, 2018). We additionally classified all points by land use based on our static habitat map (rice field landscape scale) using a simple overlap point extraction (R package ‘raster’; Hijmans & van Etten, 2012). For our dynamic habitat analysis, we classified all fixes that fell within the interior of rice paddies by harvest status using the same method. We conducted this analysis for both the 24-hour and 72-hour window data subsets. Accordingly, all GPS fixes received a static habitat classification, and our imagery-based subsets (24- and 72-hour windows) received specific information on harvest status at the paddy scale for our dynamic habitat analysis. We converted all date-time stamps of GPS fixes to a “day after arrival”, where day 1 was the day of the first bird’s arrival into the rice field landscape (for the 2016/2017 overwintering season, this was 27 August, such that 1 January 2017 was day 128). We present all results in both calendar date and day after arrival.

We conducted space use analyses at population and individual scales, using simple overlays and point-selection functions. The relatively small position error for fixes filtered for quality (~3m) lends credence to this type of analysis, although such errors could result in biases against detecting space use in thin, linear features like smaller roads and dikes. We conducted separate analyses for GPS fixes during the day and night to examine differences in gull behavior across the daily cycle. We also conducted analyses on data that were subset according to the three phases of the overwintering harvest cycle: pre-harvest (days 1-50, or August to mid-October), active harvest (days 50-140, or mid-October to mid-January) and post-harvest (days 140-202, or mid-January to mid-March, when the last bird left the rice field landscape), based on Toral et al. (2011), our own remote sensing datasets, and field observations across years.

We used the static habitat (rice field landscape scale) map to compare the selection of rice field habitats vs. non-rice field habitats and investigate the role of non-paddy habitat features embedded in the rice field complex, while we used the image-based data subsets for a dynamic analysis of how rice paddy harvest status influenced the use of the rice paddy interiors by LBBG. For both analyses, we calculated Manly selection ratios for habitat types following Fletcher and Fortin (2018) and using the widesII function in the package AdehabitatH*S* (Calenge and Basille, 2019). We calculated availability by randomly sampling 10,000 points from our habitat layers using the sampleRandom function in package Raster for classified remotely-sensed images (Hijmans et al., 2019) and the over function in package sp for our vector-based static habitat dataset (Pebesma et al., 2018). Availability and selection were calculated on a by-image (thus 24-hour or 72-hour) basis for the dynamic (image-based) habitat dataset. We calculated separate selection ratios by phase of the overwintering season and day versus night, as well as their factorial combination. Manly selectivity ratios were considered significant when their 95% confidence intervals did not overlap zero. Because results for dynamic habitat selection analyses were not qualitatively different between our 24- and 72-hour window data subsets, all results for habitat selection among paddies of different harvest status are presented using the 72-hour window subset (~10,000 GPS fixes).

2.7 Abundance Data

We assessed the abundance of LBBG in the rice field complex using two independent time series of LBBG abundance. First, we used aerial survey data collected monthly during 2016-17 by the monitoring team of the Doñana Biological Station (EBD-CSIC), following the methods explained in Rendón et al. (2008). Briefly, counts of the Doñana wetlands are performed by a single trained observer during a ~3 h flight in a small plane along a ~450km planned route at 40-250m elevation, including about 60% of the rice field complex on the west side of the Guadalquivir river (Mañez et al., 2012). We included only count data from August to March. From the air, Yellow-legged gull (*Larus michahellis*) and LBBG cannot accurately be separated, but the numbers of Yellow-legged gulls in rice fields are comparatively trivial during winter (CBvR & AJG, pers. obs), averaging <10% of all counted gulls during winter. . Yellow-legged gulls make up <1% of all gulls counted in river surveys within the rice field complex (see below), making aerial counts a reliable index of LBBG abundance.

We also analyzed data from weekly daytime (0800 to 1700 hours) counts of gulls that were made via line transects on a boat along the Guadalquivir river from Spring 2008 to Fall 2009 (the only period for which these survey data were available). We selected only those survey observations collected within the rice field complex and calculated total daily abundances for each survey date during the 2008-2009 overwintering period.

2.8 Analyses of Behavior

We analyzed the prevalence of different behaviors within the rice fields and throughout the overwintering season using classified accelerometer data (in 2016-17), protocols of focal birds (in 2018-2019) and instantaneous scans in the field. We used chi-squared tests to detect significant relationships between paddy-scale harvest status and behavior prevalence and then used correspondence analysis (using the packages FactoMineR; Husson et al., 2019) to visualize these relationships in low-dimensional space. For behavioral data collected in the field, behavior prevalence was measured by all gulls engaging in a certain behavior (focal birds), or the number of gulls performing that behavior at given point in time (instantaneous scan). For accelerometer data, behavioral prevalence was the proportion of fixes (among all fixes that had classified accelerometer data, controlled for sampling interval) classified as that behavior. We assessed the potential for autocorrelative bias in behavior by repeating calculations with instantaneous scan data including and excluding replicates from the same day and site. For accelerometer data, we conducted analyses separately using our static habitat dataset (landscape-scale, all data points) and our dynamic habitat dataset based on available imagery (paddy-scale, 24- and 72-hour subsets).

3. Results

3.1 Remote sensing of changing conditions in rice paddies

Remotely-sensed thematic classes within rice paddies changed progressively in their representation throughout the winter season (Fig. 2). Green vegetation and bare ground were the predominant thematic classes early in the winter season prior to harvest (days ~1-60), with the appearance of harvested rice and flooded paddies as harvest and tilling proceeded starting in early October. The greatest thematic class diversity within ponds was observed between late November and mid-December (day 90-110), where green vegetation, bare ground, dry and wet tilled, and shallow and deep flooded paddies were simultaneously available within the rice field complex. This time period coincided with peak use of the rice field complex by GPS-tracked gulls (see Fig. 3) and peak LBBG abundance from aerial surveys (Additional File 3). By late December, most paddies were deeply flooded after harvest, while beginning in January (post-harvest phase) water levels began to fall, resulting in a greater prevalence of shallow flooded and dry tilled paddies.

3.2 GPS Tracking Data

Arrival dates to the rice field landscape ranged from August 27 (day 1) to November 7 2016 (day 73). Space use patterns with respect to the rice field complex were distinct between the three phases of harvest (pre-harvest, active harvest, and post-harvest; Figs. 2-4). Two gulls did not arrive to the rice field landscape until the beginning of the active harvest phase, so tracking data are limited to four individuals for the pre-harvest phase. In this phase, individuals spent time in rice field complex during the day, but tended to roost outside the complex at night, typically in aquatic habitats like artificial fish ponds at Veta la Palma, natural marshes within Doñana National Park, or the Guadalquivir river.

In the active harvest phase, which started on October 15 (day 50), individual gulls began also spending nights in the rice field complex. Birds then spent almost the entire 24-hour cycle inside the rice field complex until December 19-29 (day 115-125), at which point they began commuting with increasing frequency to locations outside of the rice field complex (Figs. 3 & 4). Notably, these patterns were very consistent across sampled individuals (Fig. 4). These locations were, without exception, landfills at 22-67km distance from the rice field complex. In December and January, gulls normally returned to the complex at night, but occasionally spent evenings in nearby water bodies, other flooded areas, or sections of the Guadalquivir river that were upstream or downstream of the rice field complex. Daily distance traveled (including all movements, regardless of direction), averaged across all gulls, was 55.53 ± 3.04km, reaching a maximum on day 201 (March 15; 364.4km) and a minimum on day 71 (5 November, 10.6km). Mean daily distance traveled was greatest during the pre- and post-harvest stages of the overwintering season and reached its minimum during the active harvest phase (Fig. 3). The last tracked gull still present in the study area departed on Spring migration on March 16 (day 202).

3.3 Abundance Estimates

Total gull abundance in the nearby Guadalquivir river in the winter of 2008-2009 showed two peaks around days 30 and 150, which corresponds to the timing of transition into and out of the active harvest phase observed in the winter of 2016-2017. Gull abundance in the river reached its lowest numbers during the active harvest phase, when, according to GPS data, all birds were within the rice field complex and rice paddies (Additional File 3).

Aerial counts of gulls inside the rice field complex during 2016-2017 followed the opposite trend to those observed in the Guadalquivir river. The number of gulls reached a maximum of 3750 on day 83, remaining high until day 115 and then declining steeply thereafter, corresponding with the pattern we found in the tracked individuals. This corresponds with peak selection and use of the rice field complex by tracked gulls in our study during the same winter (Additional File 3).

3.4 Habitat selection

Static habitat analysis

A Manly selectivity analysis showed strong evidence for habitat selection both at the landscape scale (static analysis) and at the population scale (n=6 individuals; χ^2>5000, p < 0.00001). Rice paddies were selected significantly more than expected by chance at this scale (Table 1). Other habitats were used proportionally to their availability, even when data were subset by day and night (Table 1; Additional Files 4-15). When analyses were further split into the three wintering phases, the Manly selectivity analysis showed that rice paddies were selected during the active- and post-harvest phases but not in the pre-harvest phase. During the pre-harvest phase, dikes and roads in the rice field complex were also selected by gulls at the population level (Additional Files 4-15). At the individual level, most LBBG (three out of four individuals during the pre-harvest phase, four of six during the active phase, and six of six during the post-harvest phase) showed very high selectivity ratios for the Guadalquivir river during day and night, but due to large individual differences this was not significant at the population level despite a very high magnitude of selection (Table 1).

In the pre-harvest phase, several individuals showed preferences for the Veta la Palma fishponds and rice paddies, but similarly, individual differences were large leading to confidence intervals overlapping zero at the population level (Additional Files 4-15). At the landscape scale, all individuals showed strong selection for rice paddies during the active harvest phase, both during the day and at night, but the use of dikes and canals, artificial ponds, and roads strongly differed between individuals (Additional Files 4-15). The strongest selection for rice paddies was observed at night during the post-harvest phase. Significant diurnal selection for rice paddies was still evident in that phase, although the gulls spent most of their time at landfills outside of the rice field landscape (Additional Files 4-15). Among all static habitat classes, rice paddies were the most used feature, accounting for >79% of fixes on the rice field landscape, with small dikes and canals (7.2%) and non-rice open space (fallow fields and other non-crop undeveloped areas; 5.6%) as the next most used features regardless of availability (Table 1).

Dynamic habitat selection

In our dynamic habitat analysis based on classified images of rice paddy interiors (images summarized in Fig. 2), during the pre-harvest phase, gulls showed a significant preference for green vegetation and unharvested rice as opposed to bare ground, even as the latter increased in availability (10 September – 4 October, Table 2 and Additional Files 16-18). In the first image falling within the active harvest phase, day 89 (23 November), flooded paddies had become available and gulls showed a strong and significant preference for this habitat type. Gulls showed significant preferences for deep flooded and wet tilled paddies throughout the active harvest phase. Gulls continued to show significant selection for deep flooded paddies in the post-harvest phase until these habitats were no longer available on Day 175 (17 February; Table 2; Additional Files 16-18). At this point, gulls showed significant selection for dry and wet-tilled habitats and avoided green vegetation.

3.5 Analysis of Accelerometer data

Behavioral time budgets of the gulls remained relatively constant throughout the overwintering season. Gulls spent the majority (72%) of time resting (behavioral class sit/stand), with terrestrial locomotion (7.8%), flapping (6.1%), and feeding and behaviors related to food-searching and foraging (peck, exflap; total 5.7%) as the next most prevalent behaviors. ODBA showed no clear seasonal pattern, but peaks in ODBA occurred around dawn and dusk. All individuals spent more time on behaviors related to food-searching, foraging and locomotion (terloco, peck, manouvre, flap, soar) during the day and more time standing still during the night, with increased flapping at dusk and dawn (Additional File 19) but with no obvious seasonal trends (Additional Files 19-21; but see daily distance traveled, Fig. 3).

Chi-squared analyses indicated a statistically significant association between behaviors and both static and dynamic (within-paddy) habitat features during the day (χ^2=1417, p < 0.00001) and night (χ^2=820, p < 0.00001). Floating was predictably restricted to aquatic habitats (artificial wetlands, rivers and streams) and resting occurred in marshlands, roads, and dikes within the rice field complex (Additional Files 22-27). Food-searching and foraging-related behaviors (terloco/walk, peck) were mainly observed inside rice paddies at all stages of harvest, especially in shallow flooded and wet-tilled paddies. During the active- and post-harvest phases, non-rice open areas were associated with flap and soar behaviors.

During the day, non-rice agriculture and open space were associated with flying and maneuvering, and dikes, canals and paddy interiors were associated with sitting and resting during the entire overwintering season. Shallow flooded ponds were associated with food-searching and foraging-related behaviors (peck and terrestrial locomotion/walk) and artificial ponds and rivers and streams were associated with floating. During the night, most habitats were associated with sitting and resting, especially roads and dikes and deep-flooded paddies, and rivers and streams and artificial ponds were associated with floating (Additional Files 22-27).

3.6 Field Observations of Behavior

For instantaneous scan data, we found no qualitative difference in results when including replicate site visits in the same day. The number of gulls in an instantaneous scan ranged from one to several hundred, although the scan typically only resulted in the sampling of up to ~70 individuals per scan due to the one-minute time limit. The maximum number of replicate scans for the same site and day was three, and scans conducted per day ranged from 9-34. Ethograms of focal birds and instantaneous scans largely corresponded with one another, showing that the majority of time was spent in resting behaviors (sitting and standing; 58% and 51%, respectively in ethograms and scans). Active behaviors were observed less frequently (flying 13% and 5%, respectively, walking 4% and 12%, and swimming 9% and 13%). The amount of time spent foraging amounted to 11% and 14%, respectively. Chi-squared analyses indicated significant deviations from behavioral patterns expected under random behavior in rice fields (focal follow: χ^2=42300, $p < 0.00001$; instantaneous scan: χ^2=913, $p < 0.00001$), and correspondence analysis of both datasets showed clear associations between flooded fields and bathing, swimming, and preening behaviors (Additional File 28). Partially flooded fields were more used for foraging and walking, while dry fields were associated with flying (travel) and foraging. Standing showed no strong association with any flooding pattern and sitting was more associated with flooded or partially flooded fields (Additional File 28).

4. Discussion

We analyzed the space use of LBBGs in the Andalusian rice field landscape and changes in habitat characteristics within rice paddies across time to examine the fine-scale drivers of movement behavior in this important and widespread taxon. Our spatial analyses show clear, consistent, and highly structured changes in LBBG use of the rice paddies throughout the overwintering season. These changes correspond with three phases of the harvest cycle, and the spatiotemporal patterns of abundance. They are likely driven by the availability of spatial resources (i.e., foraging and roost sites), specifically with respect to the proximity and reliability of food resources, a major driver of LBBG space use in anthropogenic landscapes during the breeding season (Spelt et al., 2019). These patterns were highly consistent among sampled individuals and were strongly supported by field observations of abundance and behavior during the same and different years. The use of and behavior in rice fields showed strong differences between day and night (diurnal feeding and nocturnal resting) as well as the between the different phases of harvest at the landscape scale. Rice paddies were used more often when recently harvested and when flooded. Gulls used recently harvested paddies for daytime foraging and loafing, which parallels Spelt et al. (2019)'s observations that LBBG sought terrestrial prey after plowing and other disturbance in other types of agricultural fields. Rice paddy interiors were most used during the active harvest phase when a wide range of paddy conditions occurred, making both foraging and resting habitats simultaneously available. During that period, all birds spent 100% of their recorded time (day and night) within the rice field complex. Daily movements were strongly reduced during that phase, as birds reduced commuting time by finding all of their resources within the rice field complex (Figure 3; Clark et al., 2016). Martín-Veléz et al. (2020) also showed the importance of these same rice fields for gulls at a regional scale, with rice fields acting as the central node in the connectivity network of habitats across Andalusia.

Aerial and boat-based surveys complemented the patterns observed through GPS telemetry and showed peak abundances of gulls inside the rice field complex when rice paddy interiors showed the greatest diversity of available conditions (active harvest phase), while gulls stayed more in the rivers when only one habitat type was prevalent (pre- and post-harvest phases). These findings are consistent with previous studies at a broader scale which found that gull numbers peak at harvest time as birds exploit crayfish (*Procamburus clarkii*) and other resources that are exposed during and immediately after harvest (Rendón et al. 2008, Lovas-Kiss et al. 2018). This is in accordance with the reported importance of rice fields for other bird populations that overwinter in Andalusia (Lourenço and Piersma 2008; Toral et al., 2012). From December onwards, many of these LBBG disperse to other areas of Andalusia outside of the rice field landscape where they forage in landfills and roost in reservoirs and natural lakes (Martín-Vélez et al. 2019, 2020, this study). Accelerometer data indicate that the gulls spend most of their overwintering time budget resting in water bodies inside and outside the rice field complex, at similarly high proportions as gulls in the breeding season (Spelt et al., 2019). This aligns well with other observations that gulls prefer to sleep and rest in open water (Baker, 2009; Clark et al., 2016), although especially during the harvesting phase gulls also often rested on dikes in the rice field complex.

The strong selection for rice paddies during active harvest in combination with the presumably unchanging availability of alternative resources (landfills) strongly suggest that changing conditions in rice paddies (Fig. 2) are a primary driver of space use for overwintering gulls in the Andalusian rice field landscape. Both alternative roosting sites (bodies of open water like rivers and wetland ponds) and feeding sites (landfills) were consistently available throughout the overwintering season, but were not selected for until such resources were not available in the rice field complex. Dynamic space use of LBBG has been observed on anthropogenic landscapes during the breeding season (Thaxter et al., 2015; Spelt et al., 2019), supporting the notion that overwintering LBBG are similarly selecting spatial resources based on predictability and proximity. Curiously, ODBA, which is often used as a proxy for energy expenditure and activity (e.g. Sotillo et al 2019), as well as the proportion of time spent on different behaviors, did not change during overwintering period, despite an increase in daily commute distances. This implies there were no substantial differences in the bird's dietary or metabolic needs during the overwintering season, and that changes in behavior are driven by harvest dynamics and the resulting shifts in resource availability within rice paddies. This consistency in behavioral frequency across the overwintering season also contrasts strongly with studies on breeding gulls, which show substantial shifts in time-activity budgets over the course of the breeding season (Spelt et al., 2019).

Preference of LBBG for artificial wetlands other than ricefields was also strong at the individual scale. Artificial fishponds were selected strongly by a subset of tracked gulls, whereas the natural marshes of Doñana National Park, so important for many other waterbird species (Rendon et al. 2008), were avoided by LBBG. The selectivity index for rivers was extremely high for most gulls, showing that the Guadalquivir river provided a preferred roosting site when flooded paddies were not available, probably due to the safety it provides from predators, and its central position within the ricefield complex.

LBBG are an important focal taxon for movement research due to their ability to link elements of the biosphere and anthroposphere, strong ties to human land use and large population increases in Europe in recent decades (Calladine 2004; Eaton et al., 2015; Boertmann and Frederiksen, 2016). Their growing prevalence on anthropogenic landscapes, especially agricultural fields and bodies of water, gives their movement behavior and space use important implications for local ecology and human health. The landscape-scale movements of gulls, and how it changes within a season is especially worthy of careful consideration. Gulls moving within as well as to and from the rice paddies are important biovectors of nutrients, weeds, exotic species and other organisms, as well as potential pollutants (Lovas-Kiss et al. 2018; Martín-Vélez et al. 2019, 2020). Gulls are also likely to disperse genes for antimicrobial resistance into rice fields, both when feeding at landfills or when roosting in the nearby river, which is contaminated with urban wastewaters (Ahlstrom et al. 2019).

Our study shows that LBBG traveled daily to landfills most often during the post-harvesting phase and that they did so during daylight, suggesting that their role as biovectors in rice fields is largely restricted to this phase and that deposition of potentially harmful materials in areas of human concern occurs during roosting, which is predominantly at night. Indeed, at the Andalusian scale Martín-Veléz et al. (2020) showed that LBBG strongly increased their time spent at landfills, leading to increased connectivity between landfills and other habitats such as rice fields during the same time period across several overwintering seasons. The present study illustrates the fine-scale dynamics behind this pattern, including a shift to using rice fields almost exclusively for roosting and landfills for foraging. This pattern could result in major influxes of other contaminants (e.g., heavy metals and plastics) into fields where food for human consumption will be grown throughout the following spring and summer, a phenomenon observed in other roosting areas for landfill-feeding gulls (Winton and River, 2017; Seif et al., 2018; Martín-Veléz et al., 2019). They are even likely to disperse genes for antimicrobial resistance into rice fields, both when feeding at landfills or when roosting in the nearby river, which is contaminated with urban wastewaters (Martin et al. 2011, Ahlstrom et al. 2019).

Our study included detailed space use analyses of six individual LBBG, representing a small sample of the large numbers that inhabit the rice fields during the overwintering season. The gulls which remained in the rice field landscape during the chosen overwintering season were almost all breeding in Belgium with one in the UK, which could cause geographical biases in the conclusions of this study. However, the results of our space use analyses using GPS tracking data are strongly consistent with and supported by other work in the region across years (Martín-Veléz et al., 2020) and additional data collated for this study, including field observations from 2018-2019 and time series of abundance collected in the field during 2008-09 and 2016-17. Thus, though small in sample size, our study provides an in-depth, individual-scale perspective on the mechanisms driving larger LBBG movement and abundance patterns being observed at the landscape scale in Andalusia.

Implications for Management and Conservation

LBBG are a species of conservation concern in the EU and on the Amber list of birds in the UK (Calladine 2004; Eaton et al., 2015; Boertmann and Frederiksen, 2016), having shown dramatic population declines in some coastal breeding areas. Their coincident population increases in urban areas, by contrast, are a significant source of human-wildlife conflict (Rock, 2005). Accordingly, the mechanistic understanding of space use and movement decisions made by overwintering LBBG in this study is important progress in the complicated conservation and management context of this species (Ross-Smith et al., 2014; Spelt et al., 2019). Their growing prevalence on anthropogenic landscapes, especially agricultural fields and water bodies, likely important implications for local ecology and human health. Changes in the habitat preferences and subsequent movement patterns of the gulls are therefore especially worthy of careful consideration.

Conclusions

We found that overwintering LBBG occupying an anthropogenic rice agriculture landscape change their movement patterns and space use over the course of the winter according to the habitat resources available in rice-growing paddies across a winter harvesting cycle. Behavioral observations in the field and using classified accelerometer data indicated that these changes in space use were to find habitats for food acquisition and resting, and that metabolic needs and behavioral time budgets did not change over the course of the winter. LBBG's rapid increase in anthropogenic landscapes and potential for transporting diverse materials including agents potentially harmful to human health makes a mechanistic understanding of their movement behavior important and relevant to management and conservation.

List Of Abbreviations

LBBG – Lesser black-backed gull

UK – United Kingdom

GPS – Global Positioning System

ODBA – Overall Dynamic Body Acceleration

Declarations

Ethical approval and consent to participate: This study involved no human participants, human data or human tissues. All procedures performed on the tagged individuals and their brood complied with the standards of experimentation and welfare for vertebrate animals established under Belgian (Royal Decree of 6 April 2010), Dutch (Dutch Act on animal health and welfare 1992) and European Law (Directive 2010/63/EU), and were approved by the University of Antwerp Ethical Committee (project Ethics Committee number 2013–73). Birds in the UK were tagged under license, with approval by the independent Special Methods Technical Panel of the UK Ringing Scheme.

Consent for publication: All authors have reviewed the draft submitted herein and consented to its review and publication.

Availability of Supporting Data: See supplementary materials. All GPS location data used in this study are managed by the UvA-BiTS Team (http://www.uva-bits.nl/).

Competing interests: The authors declare no conflict of interest.

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Author Contributions: CBvR conducted statistical analyses and behavioral field observations in the field, created figures, and wrote the manuscript. DA assisted with spatial analyses, conducted pre-processing of remotely-sensed images, and improved spatial figures. WB conducted behavioral classifications of behavioral data and created the UvA-BiTS database. CBT and EWMS both deployed trackers on birds used in this study, and helped with writing the manuscript. JB and AJG helped with study design and writing of the manuscript.

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Tables

Table 1: Population-level Manly selectivity ratios for tracked Lesser black-backed gulls (*Larus fuscus*) in the broader rice field landscape (static habitat analysis). Habitat availability was determined using a regional land cover dataset. Percent availability values are for the entire rice field landscape (Fig.1).

Asterisks (*) indicate significant relationships where the 95% CI does not overlap 0. All values are calculated for the entire overwintering season using data from all 6 tracked gulls.

Habitat Type	Availability (%)	Use (%)	Manly Selectivity Ratio (μ ± SE)
Artificial Ponds	0.9	2.0	2.16 ± 1.21
Small dikes and Canals	5.8	7.2	1.27 ± 0.52
Natural Marshland	11.9	1.5	0.13 ± 0.06
Non-rice agriculture	3.05	1.6	0.53 ± 0.2
Non-rice open space	32.6	5.6	0.17 ± 0.07
River margin	1.1	0.5	0.43 ± 0.32
Rivers and streams	0.01	2.0	143.93 ± 161.52
Roads and large dikes	2.7	0.58	0.22 ± 0.0.15
Rice paddy	39.4	79.1	2.01 ± 0.09*
Urban	1.8	0	0.00

Table 2: Representative population-level Manly selectivity ratios for tracked Lesser black-backed gulls (*Larus fuscus*) using rice paddy interiors across the overwintering season (dynamic habitat analysis), excluding dates with redundant availability and selection results. Habitat availability was determined using classification of remotely-sensed images of paddy interiors. Percent availability values are relative to other habitat resources within rice paddies only. Data are shown for a subset of days with analyzed imagery (see Fig. 1 for all days). Dates are given in day-month and day after arrival in parentheses. Day after arrival is based on the time since the arrival of the first bird to the rice field landscape (27 August). Asterisks (*) indicate significant relationships where the 95% CI does not overlap 0.

Date	Habitat Type	Gulls (n)	Availability (%)	Use (%)	Manly Selectivity Ratio (μ ± SE)
10 Sept (day 15; pre-harvest)	Green Vegetation / Unharvested rice	2	84.5	100%	1.2 ± 0.01*
	Bare ground / Harvested	“ ”	15.5	0.0	0.00
24 Sept (day 29; pre-harvest)	Green Vegetation / Unharvested rice	3	85.4	100%	34.1 ± 6.88*
	Bare ground / Harvested	“ ”	14.6	0.0	
26 Sept (day 31; pre-harvest)	Green Vegetation / Unharvested rice	3	81.7	100%	5.5 ± 0.11*
	Bare ground / Harvested	“ ”	18.3	0.0	
4 Oct (day 39; pre-harvest)	Green Vegetation / Unharvested rice	3	70.7	40.9	3.3 ± 2.07
	Bare ground / Harvested	“ ”	29.3	59.1	11.6 ± 5.02
23 Nov (day 89; active harvest)	Green Vegetation / Unharvested rice	6	9.9	0.0	0.00
	Bare ground / Harvested	“ ”	14.6	0.0	0.00
	Deep flooded	“ ”	75.4	100	7.7 ± 0.2*
29 Nov (day 95; active harvest)	Green Vegetation / Unharvested rice	6	4.5	0.0	0.00
	Bare ground / Harvested	“ ”	9.6	0.0	0.00
	Deep flooded	“ ”	37.3	64.2	9.7 ± 1.67*
	Wet tilled	“ ”	25.4	17.1	3.8 ± 1.19*
	Dry Tilled	“ ”	15.3	9.8	3.6 ± 1.89
	Shallow flooded	“ ”	7.9	8.8	6.28 ± 3.43
7 Dec	Green Vegetation / Unharvested rice	6	3.8	0.0	0.00

(day 103; active harvest)					
	Bare ground / Harvested	“ ”	9.33	0.0	0.00
	Deep flooded	“ ”	60.9	86.1	7.73 ± 0.45*
	Dry Tilled	“ ”	16.5	6.4	2.15 ± 0.82
	Shallow flooded	“ ”	9.9	7.6	4.3 ± 2.01
23 Dec (day 119; active harvest)	Green Vegetation / Unharvested rice	6	24.7	0.0	0.00
	Deep flooded	“ ”	75.3	100	7.46 ± 0.42*
31 Dec (day 127; active harvest)	Green Vegetation / Unharvested rice	6	32.3	0.0	0.00
	Deep flooded	“ ”	67.7	100	7.40 ± 0.42*
2 Jan (day 129; active harvest)	Green Vegetation / Unharvested rice	6	5.3	0.0	0.00
	Bare ground / Harvested	“ ”	17.5	7.9	3.37 ± 1.56
	Deep flooded	“ ”	60.2	91.7	8.95 ± 0.68*
	Dry tilled	“ ”	17.0	0.3	0.12 ± 0.137
24 Jan (day 151; post harvest)	Green Vegetation / Unharvested rice	6	7.5	0.0	0.00
	Deep flooded	“ ”	32.9	89.6	15.9 ± 1.89*
	Dry tilled	“ ”	60.7	10.3	1.0 ± 0.66
17 Feb (day 175; post-harvest)	Green Vegetation / Unharvested rice	3	6.8	0.0	0.00
	Dry Tilled	“ ”	58.5	48.2	4.46 ± 0.82*
	Wet Tilled	“ ”	34.7	51.8	8.03 ± 1.46*

Figures

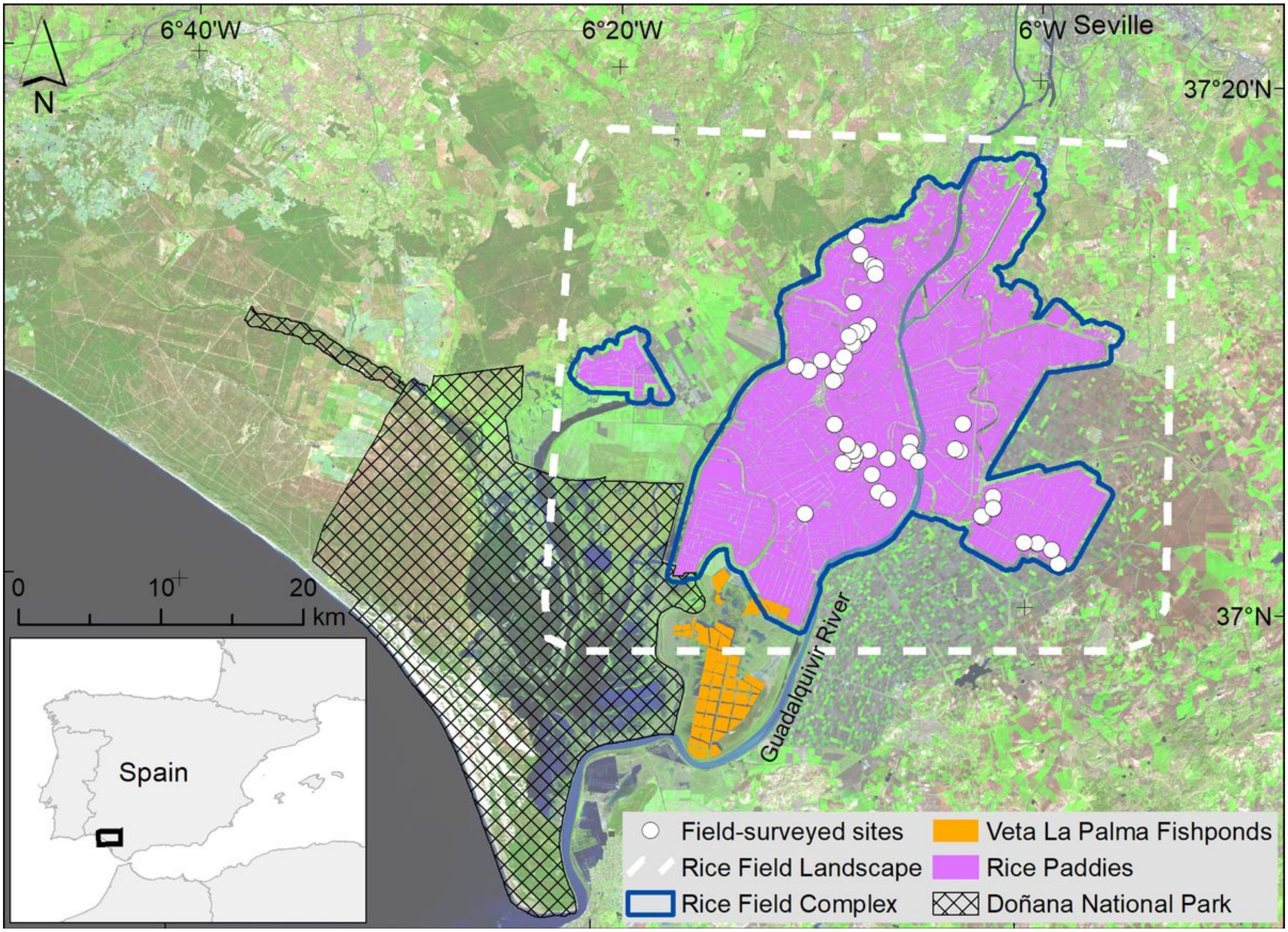

Figure 1

A false-color infrared photograph of the study area, showing the rice field landscape (the total area for which all land cover types were classified for our static habitat analysis), the rice field complex, and the interior of the rice paddies (where within-paddy habitat availability was assessed using remotely-sensed imagery). The protected wetlands of Doñana National Park and the nearby Veta la Palma fishponds are also shown.

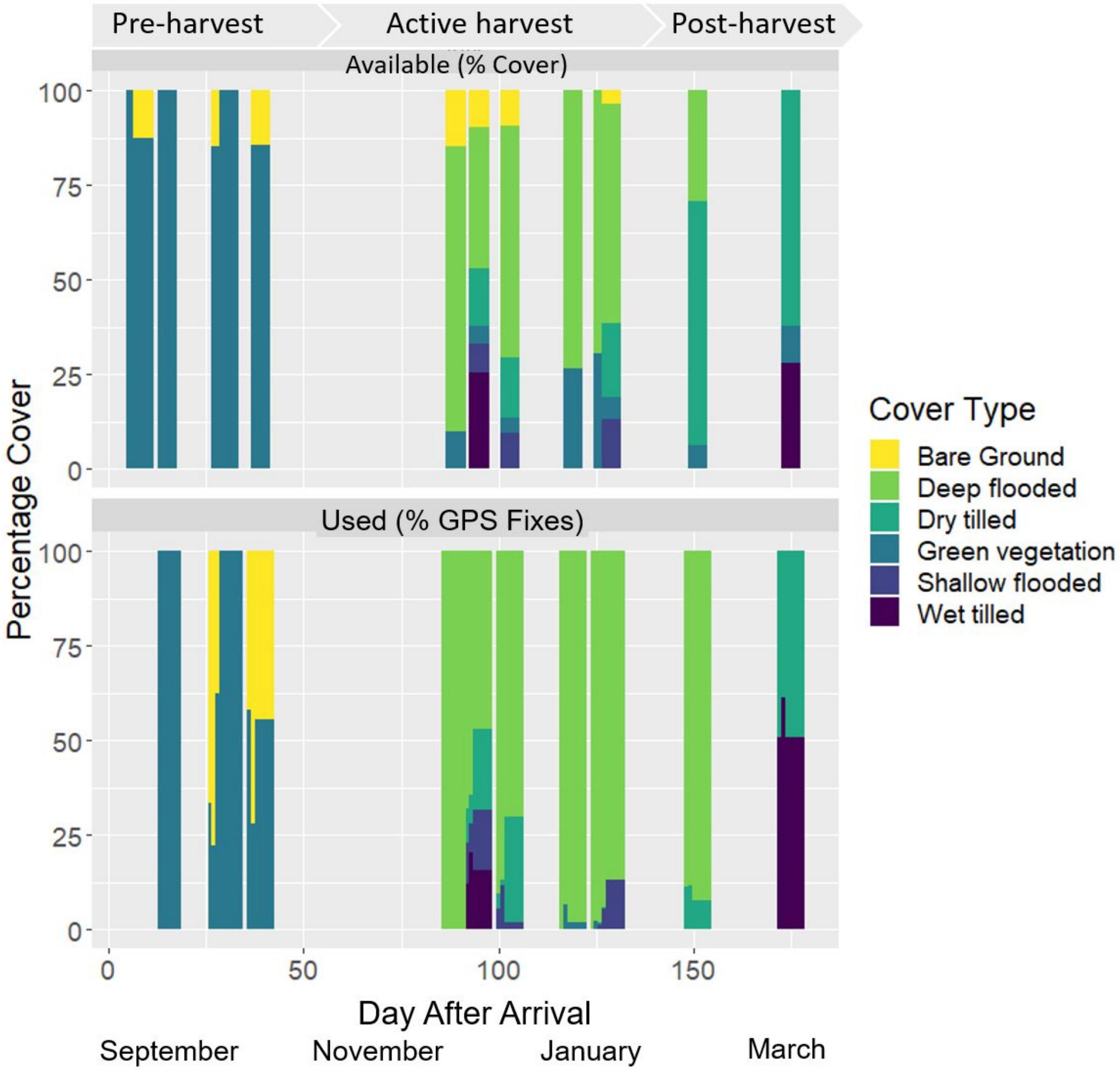

Figure 2

The availability (percent cover) and use (% gull daily time within) of rice paddies in different conditions across the course of the season, based on classified remotely-sensed images of the rice paddy interiors. Both availability and use are assessed at the paddy scale; see Table 1 for landscape-scale habitat use. The phases of the gull overwintering season, demarcated by changes in commuting behavior, are shown at the top, and months of the year below the Y-axis. Day after arrival is based on the time since the arrival of the first bird to the rice field landscape (27 August).

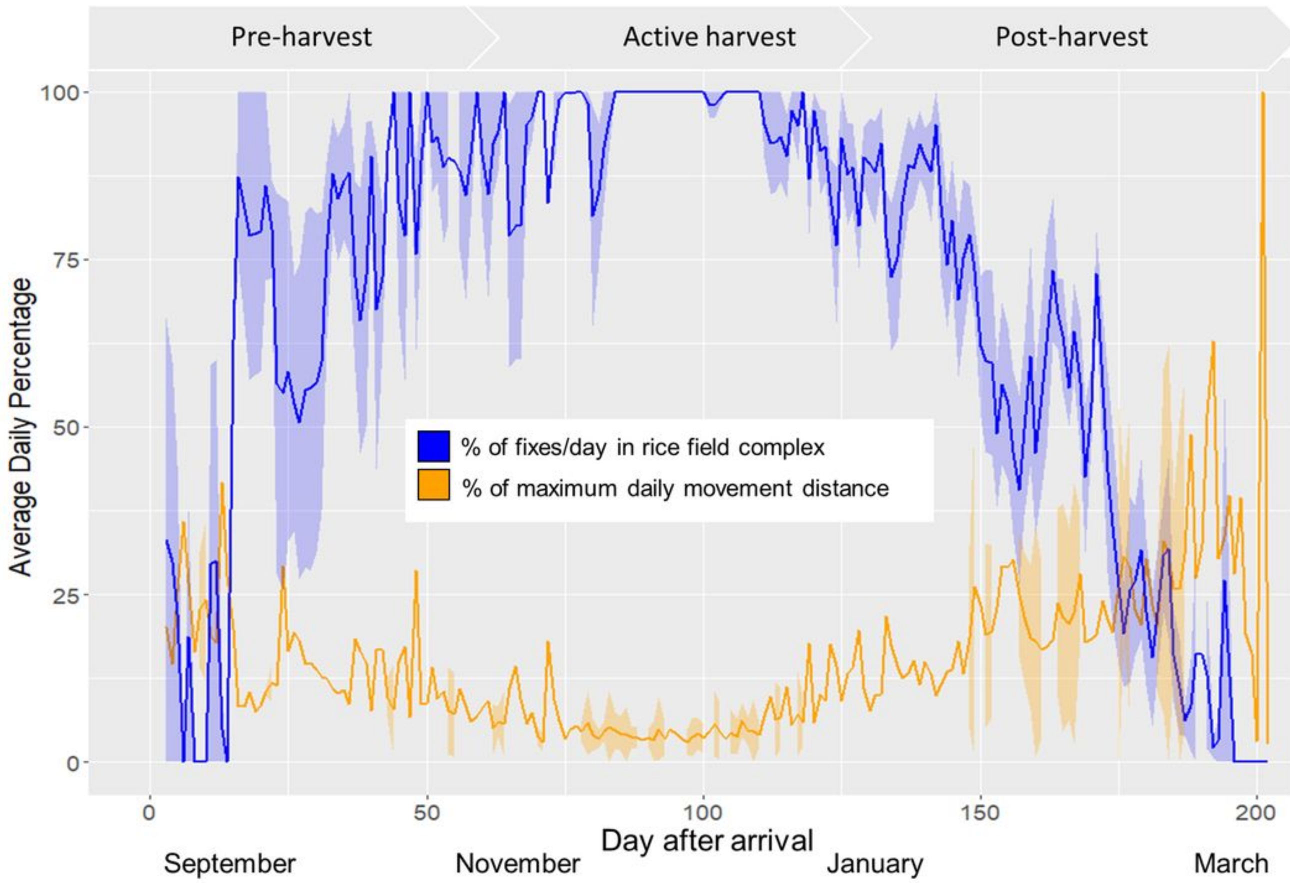

Figure 3

Time series of Lesser black-backed gull behavior within the rice field landscape across the entire overwintering season. The average daily percentage of time/day (a proxy for time budget; blue) spent within the rice field complex increased during the pre-harvest phase, reached a maximum during the active harvest phase, and declined during the post-harvest phase. The average percentage of maximum daily movement distance (a proxy for relative daily movement; orange) followed an opposite trend, with the lowest daily movements during the active harvest phase. Shaded areas represent 95% confidence intervals for mean estimates. Day after arrival is based on the time since the arrival of the first bird to the rice field landscape (27 August).

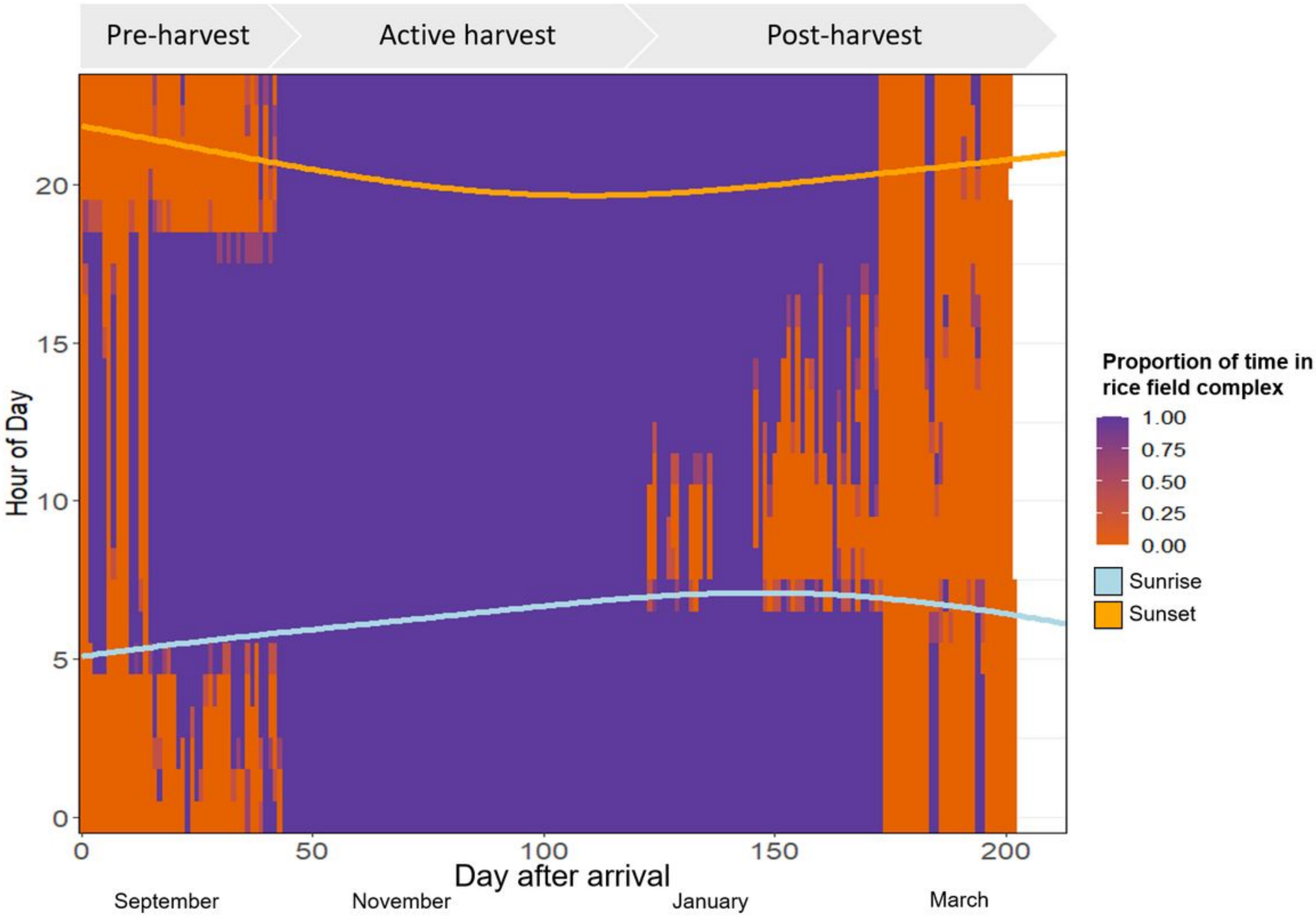

Figure 4

The hourly proportion of time spent in the rice field complex averaged across all birds for each day of the overwintering cycle. Birds switched from spending daylight hours in the complex and roosting elsewhere in the rice field landscape (pre-harvest phase), to spending 100% of their daily cycle in the complex (active harvest phase), to roosting in the complex but spending daytime hours outside (post-harvest phase). Day after arrival is based on the time since the arrival of the first bird to the rice field landscape (27 August).

Supplementary Files

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- AdditionalFile24FigS7C312020.tiff
- AdditionalFile23FigS7B312020.tiff

- AdditionalFile22FigS7A312020.tiff
- AdditionalFile21FIGS6B312020.png
- AdditionalFile20FIGS6A312020.png
- AdditionalFile19FigS5312020.tiff
- AdditionalFile18FigS4C4262020.tif
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- AdditionalFile16FigS4A4262020.tif
- AdditionalFile15FigS3FCIS4262020.tiff
- AdditionalFile14FigS3F4262020.tiff
- AdditionalFile13FigS3ECIS4262020.tiff
- AdditionalFile12FigS3E4262020.tiff
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