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Habitat preferences of juvenile Scottish Ospreys *Pandion haliaetus* at stopover and wintering sites

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ABSTRACT
In this study, we use satellite-tracking data from five juvenile Scottish Ospreys *Pandion haliaetus* to explore habitat preferences at stopover and wintering sites. Daily activity patterns were analysed using a binomial generalised linear model. Kernel density estimation was used to identify core areas at stopover sites and seasonal ranges at the wintering site. A 'use versus available habitat' study design was implemented to test whether Ospreys showed preference for a variety of landscape and land-cover variables and for protected areas. Autumn migration strategies varied between individuals, with some Ospreys using stopover sites in France, Spain and Morocco. Ospreys wintered at sites in West Africa. Activity levels varied through the day, with localised peaks at 11:00 and 15:00 h. Ospreys preferred to be near to water features (rivers, lakes, ocean) while avoiding urban areas. Individual differences were observed when considering preference for forest and open-area land-cover classes. Overall, Ospreys did not preferentially use protected areas. Our research confirms already well-established preferences for aquatic habitats, but preference for or avoidance of other habitats, including protected areas, varied between individuals. We highlight the potential of combining satellite-tracking data with environmental data sources to explore the spatial ecology of migratory birds at stopover and wintering sites abroad.

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Effective conservation relies on an understanding of the geographical spaces important to a species for fulfilling different aspects of its life cycle, such as foraging and shelter. This is particularly important for migratory species that use a range of different habitats throughout their annual cycle (Runge *et al* 2014). Ring-recovery analysis has provided coarse locational information on the spaces used by some migratory avian species. However, ring-recovery research provides little information on the temporal and spatial details of space use at these sites (Strandberg *et al* 2009). Recent advances in satellite-tracking technology have revolutionised the study of migratory species, providing researchers with fine-scale spatial and temporal data on animal movements, facilitating more detailed analysis of space use by animals throughout their life cycle (Hebblewhite & Haydon 2010).

Habitat characteristics play an important role in shaping patterns of space use by animals (Aarts *et al* 2008, Beyer *et al* 2010). Consequently, identifying important habitat for a given species is crucial in informing conservation and management strategies. Habitat analysis is often constrained by the limited availability of habitat attribute data that match the fine spatial and temporal resolution of satellite-tracking data (Hebblewhite & Haydon 2010, Urbano *et al* 2010). While field methods for generating habitat data can be costly and time consuming, recent developments in remote sensing are leading to a growing number of environmental databases that contain spatial and temporal information on habitat characteristics (Urbano *et al* 2010). Combining satellite-tracking data with available environmental data sets (*eg* those generated from remote sensing) is a powerful ecological tool that has yet to reach its full potential in research into movement ecology (Dodge *et al* 2013, Demšar *et al* 2015).

The Osprey *Pandion haliaetus* is a long-distance migratory raptor that is widely distributed across the northern hemisphere. Research on Ospreys worldwide has often focused on the breeding season (Green 1976, Bustamante 1995) and informing conservation strategies at breeding sites, *eg* guiding the width of disturbance-buffer zones around nests, identifying priority areas for reserves and informing the location of artificial nesting structures (Lőhmus 2001, Toschik *et al* 2006, Bai *et al* 2009, Rodríguez *et al* 2013). Such a focus on the breeding season is disproportionate, as

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northern European Ospreys spend over half of their year away from the breeding grounds on migration and at wintering sites in tropical West Africa (Hake *et al* 2001, Alerstam *et al* 2006, Dennis 2008, Bai & Schmidt 2012). Mortality during the non-breeding season is common, with threats including the pollution of habitats, hunting, fishing, fish farming and collision with power lines (Hake *et al* 2001, Dennis 2008).

The introduction of satellite telemetry has enabled the collection of detailed data on Ospreys during the non-breeding season. To date, most of this research has focused on timings, routes and speed of migration, outlining differences in strategies between individuals, males, females, adults and juveniles (Kjellén *et al* 1997, 2001, Hake *et al* 2001, Martell *et al* 2001, Alerstam *et al* 2006). There has been little empirical research examining the migrations of Scottish breeding Ospreys using modern satellite telemetry (but see Dennis 2008 for a detailed historical account).

Many European Ospreys make one or more stopovers during migration in order to satisfy energy demands required for long migratory journeys (Hake *et al* 2001, Alerstam *et al* 2006). Stopover sites adjacent to ecological barriers are especially important in preparing Ospreys for these difficult crossings (Dennis 2008). Furthermore, Ospreys can return to familiar stopover sites, making notable detours to reach these locations (Alerstam *et al* 2006). Although the use of stopover sites has been recognised, very little research has been conducted into the ecology and behaviour of Ospreys during stopovers (Galarza & Dennis 2009, Galarza 2010). Research on the behaviour and ecology of European Ospreys at wintering sites is similarly limited. Studies using field-based observations of Ospreys at wintering sites in West Africa and Spain provide only a snapshot of habitat use and activities, lacking spatial and temporal detail on individual Ospreys (Prevost 1982, Casado & Ferrer 2005).

Satellite tracking can be used to identify patterns in movement activity (*ie* variations across space and time) which lead to an improved understanding of a species' movement ecology and behaviour. An understanding of habitat selection by Ospreys at stopover sites and winter ranges is needed to design effective conservation strategies along migratory routes. Conservation is most commonly realised through the designation of protected areas; however it is unknown whether and how the current arrangements of protected areas are utilised by migrating Ospreys (Gaston *et al* 2008). In this paper, we use satellite-tracking data to investigate the habitat preferences of five juvenile Ospreys, hatched in Scotland, at their stopover and wintering sites. The aims of this research were: to determine the seasonal migration and daily movement patterns; to identify habitat preferences; and to investigate use of protected areas of the five tracked Osprey originating from Scotland.

Methods

Satellite-tracking data

Satellite-tracking data were collected by the Scottish Wildlife Trust during 2012–16 for five juvenile Scottish Ospreys (Table 1). Juvenile Ospreys were ringed following standard ringing procedures, while at the same time GPS harnesses (Argos/GPS PTT-100, Microwave Telemetry Inc., Columbia, Maryland) were fitted to each of five individuals. The GPS trackers were programmed to record the geographical position, speed, course and altitude of the Ospreys at regularly programmed intervals (one attempted fix every hour between 04:00 and 23:00). Those recorded as 'no fix' or 'low voltage' were removed from the data set, along with those fixes where the GPS recorded a location error.

Delineating migration and stopover sites

Date of departure on migration was defined by a marked movement of >100 km/day. Migration distance was calculated by summing the distance between all fixes during migration in the WGS 1984 World Mercator Projection. An Osprey was considered to be at a stopover site if it travelled <100 km/day, within a 24-h interval, during migration (Hake *et al* 2001). Arrival and departure at wintering sites was defined by a travelling distance of <100 km/day at the end and start of migration.

Table 1. Description of the Scottish Wildlife Trust's satellite-tracking data of five juvenile Ospreys hatched in Scotland.

Osprey ID	Sex	Hatched	Date tagged	Status
Blue 44	Male	May 2012	2 July 2012	Transmitter failure: Nov 2012
Blue YD	Male	May 2012	17 July 2012	Transmitter failure: May 2014
Blue YZ	Female	June 2013	15 July 2013	Died: Nov 2013
FR3	Male	May 2015	29 June 2015	Still receiving data
FR4	Female	May 2015	29 June 2015	Transmitter failure: Dec 2015

Stopover and winter ranges were delineated using fixed-bandwidth kernel density estimation (Worton 1989). Kernel density estimation requires the estimation of the bandwidth parameter which controls the shape of the resulting density surface. Here we used the reference method (Worton 1989) for automatically selecting the bandwidth for each stopover and wintering range. The 70% isopleths were obtained from the resulting kernel surface and used to delineate core-use areas at the stopover and wintering ranges. We chose 70% for delineating the stopover ranges because the 70% level represented a compromise between larger and smaller stopover ranges, and was the best level for delineating stopover ranges based on comparing different values ranging from 50% to 95% (Millspaugh *et al* 2012). To explore whether winter ranges moved according to season, we computed winter ranges, following the procedure outlined above, using data separated into the two West African seasons relevant to Osprey ecology, defined as the rainy season (1 June to 31 October) and the dry season (1 November to 31 May).

Daily activity patterns

For every Osprey location observed, the activity status (active versus inactive) of the bird was defined. An Osprey was considered to be active, *ie* foraging or flying, if the flight speed, provided by the transmitter, was >0 knots (Washburn *et al* 2014). For the pooled data, the daily activity levels were analysed at hourly intervals from 07:00 to 21:00 (when most data were available) using a binomial generalised linear model (McCullagh & Nelder 1989). We treated the hourly time of day as a categorical factor, along with the individual, and whether the Osprey was at a stopover or wintering site. Using this model, we tested whether different times of day had increased activity levels. From the model output, we computed Wald tests to assess which times of day were associated with increased activity by Ospreys.

Habitat preferences

A 'use versus available' study design was employed to determine habitat preferences of Ospreys at stopover and wintering sites (Beyer *et al* 2010). Such a study design involves comparing the value of habitat variables at observed Osprey locations, as determined from the satellite-tracking data, to the value of habitat variables at points located randomly within defined 'available' habitat. To define available habitat at stopover sites, a spatial buffer was generated around the movement path (defined as the sequence of fixes comprising the stopover) for each Osprey (Johnson *et al* 2002, Dickson *et al* 2005). The buffer distance was set to 5967 m, as this was the average daily stopover distance. To define available habitat at wintering ranges, we used the minimum convex polygon encompassing the winter range of tracking data (Johnson 1980, Limiñana *et al* 2012, Popp *et al* 2013). Ocean that was >2 km from the coast was excluded from the available habitat area, as Ospreys cannot rest, roost or forage in deep water (Dennis 2008).

Random points were generated within the defined available habitat, where the number of random points (hereafter 'expected') was equal to the number of Osprey satellite-tracking fix locations (hereafter 'observed') at that site. Nine habitat variables that are potentially important to Ospreys were identified from existing literature (Table 2). Data sources were chosen for their extent, resolution and suitability in relation to the habitat character of interest. All variables were represented in a grid (raster) format with a spatial resolution of 30 m. The value of each habitat variable was extracted at both observed and expected locations for statistical comparison.

We tested for significant differences between the observed, used locations and the expected available

Table 2. Data sources and description of habitat variables. All habitat variables were derived from the original source using a geographical information system (GIS).

Variable	Data source	
	European sites	African sites
Distance to river	European catchments and rivers network system (EEA 2012)	Rivers of Africa (derived from HydroSHEDS) (FAO 2014)
Distance to lake	CORINE land cover seamless vector data: water bodies (EEA 2006)	Global Lakes and Wetland Database (Lehner & Doll 2004)
Distance to coast	Global Shoreline Database (NOAA 2015)	Global Shoreline Database (NOAA 2015)
Distance to urban area[1]	CORINE land cover seamless vector data: artificial surfaces (EEA 2006)	GlobeLand30 (National Geomatics Center of China 2010)
Distance to major road	OpenStreetMap (Geofabrik 2015)	Senegal, Mauritania and The Gambia Roads (Africa Infrastructure Knowledge Program 2012); OpenStreetMap (Geofabrik 2015)
Distance to minor road	OpenStreetMap (Geofabrik 2015)	OpenStreetMap (Geofabrik 2015)
Elevation, Slope	ASTER GDEM (METI & NASA 2011)	ASTER GDEM (METI & NASA 2011)
Land cover[1]	CORINE land cover raster data (EEA 2006)	GlobeLand30 (National Geomatics Center of China 2010)

[1]See Appendix I for details on how data were aggregated into five land-cover classes.

Table 3. Timing, distance and speed of migrations (see Figure 1).

Osprey ID	Migration	Departure	Arrival	Duration (days)	Travel days	Total distance (km)	Distance (excluding stopover km)	Travel-day speed (km/day)
Blue 44[1]	Autumn	8 Sep 2012		62	10	2 582.3	2 221.9	222.2
Blue YZ	Autumn	5 Sep 2013	18 Oct 2013	43	20	6 432.6	6 096.6	304.8
Blue YD	Autumn	12 Sep 2012	30 Sep 2012	18	18	5 298.4	5 298.4	294.4
FR3	Autumn	17 Aug 2015	11 Oct 2015	55	23	6 161.9	5 584.0	242.8
FR4	Autumn	1 Sep 2015	18 Sep 2015	17	17	5 227.2	5 227.2	307.5
Blue YD[2]	Spring	24 Apr 2014		27	22	5 835.1	5 781.8	262.8

[1]Blue 44 died during autumn migration so calculations are included until date of death.
[2]Blue YD experienced transmitter failure during spring migration so calculations are included until date of transmitter failure.

habitat locations using a non-parametric Mann–Whitney *U* test (for continuous variables; *eg* Oppel *et al* 2004) and a chi-square test (for categorical land-cover variables; Byers *et al* 1984). For the continuous habitat variables, we performed repeated statistical tests on the data associated with each individual, a method which is subject to issues of multiple testing and increased Type I error rates (Cabin & Mitchell 2000). To account for this effect, we used the Bonferroni correction which is an adjustment of the critical value post hoc and is considered to be a conservative approach to reducing the rate of Type I errors. The Bonferroni correction requires that the multiple tests be grouped in some way, and here we grouped the tests performed on each individual (and in the case of Blue YD and FR3, separated into stopover and wintering sites) for each of the continuous habitat variables. For the categorical land-cover variables, where the difference was significant, Bonferroni confidence intervals were calculated, following Neu *et al* (1974), to determine which land-cover types were significantly preferred or avoided. If the expected proportion of usage for a land-cover type lay above the calculated confidence interval, then a significant avoidance of that land-cover type was inferred. Similarly, if the expected usage lay below the confidence interval then a significant preference was inferred for that land-cover type.

Use of protected areas

The spatial boundaries of protected areas at stopover and wintering study sites were obtained from the World Database on Protected Areas (IUCN & UNEP 2015). Where data on the spatial boundary of a protected area were not provided, but the central geographic point and the extent of the protected area were available, a circular boundary around the central point was calculated, set to result in the given extent of protected area (Limiñana *et al* 2012). Chi-squared tests were used to determine whether the Ospreys preferentially used protected areas, by comparing the number of observed locations to the number of expected locations, for each individual, within and outside protected-area boundaries. This analysis was repeated, comparing Ospreys observed using protected areas designated for the protection of birds or wetlands to the number of expected locations within these protected areas.

Results

Migration patterns

Three satellite transmitters failed and one Osprey was found dead in Guinea-Bissau at the end of 2013; thus data were available only for four autumn migrations, three wintering periods and one spring migration (Tables 1 & 3). Data were available for a complete wintering period only for Blue YD. Departure dates for autumn migration ranged from 17 August to 9 September (Table 3). Total autumn migration distance ranged from 5 227.2 km to 6 432.6 km and average travel-day speed during autumn migration ranged from 242.8 km/day to 307.5 km/day (Table 3). During autumn migration, two individuals made a stopover in Europe, one individual made two stopovers (in Europe and Morocco) and two individuals made no stopovers (Figure 1). FR3 travelled <100 km/day whilst passing over Wales and England but travel remained southwards, so this period was not included in stopover analysis. Stopover duration in autumn lasted 6–52 days (Table 4). Three Ospreys passed primarily over land during autumn migration, whilst Blue YZ and Blue YD crossed the ocean west of France (Figure 1). Arrival dates at wintering sites ranged from 30 September to 10 October (Table 4). Ospreys wintered in West Africa (Senegal, Gambia, Guinea-Bissau and Mauritania) (Figure 1). Blue YD remained within the wintering region for 571 days, returning during spring migration in April 2014 (Table 4). On spring migration, Blue YD took a five-day stopover in northern France.

Daily activity patterns

Activity levels of the Ospreys tracked in our study varied throughout the day, and we found a bimodal

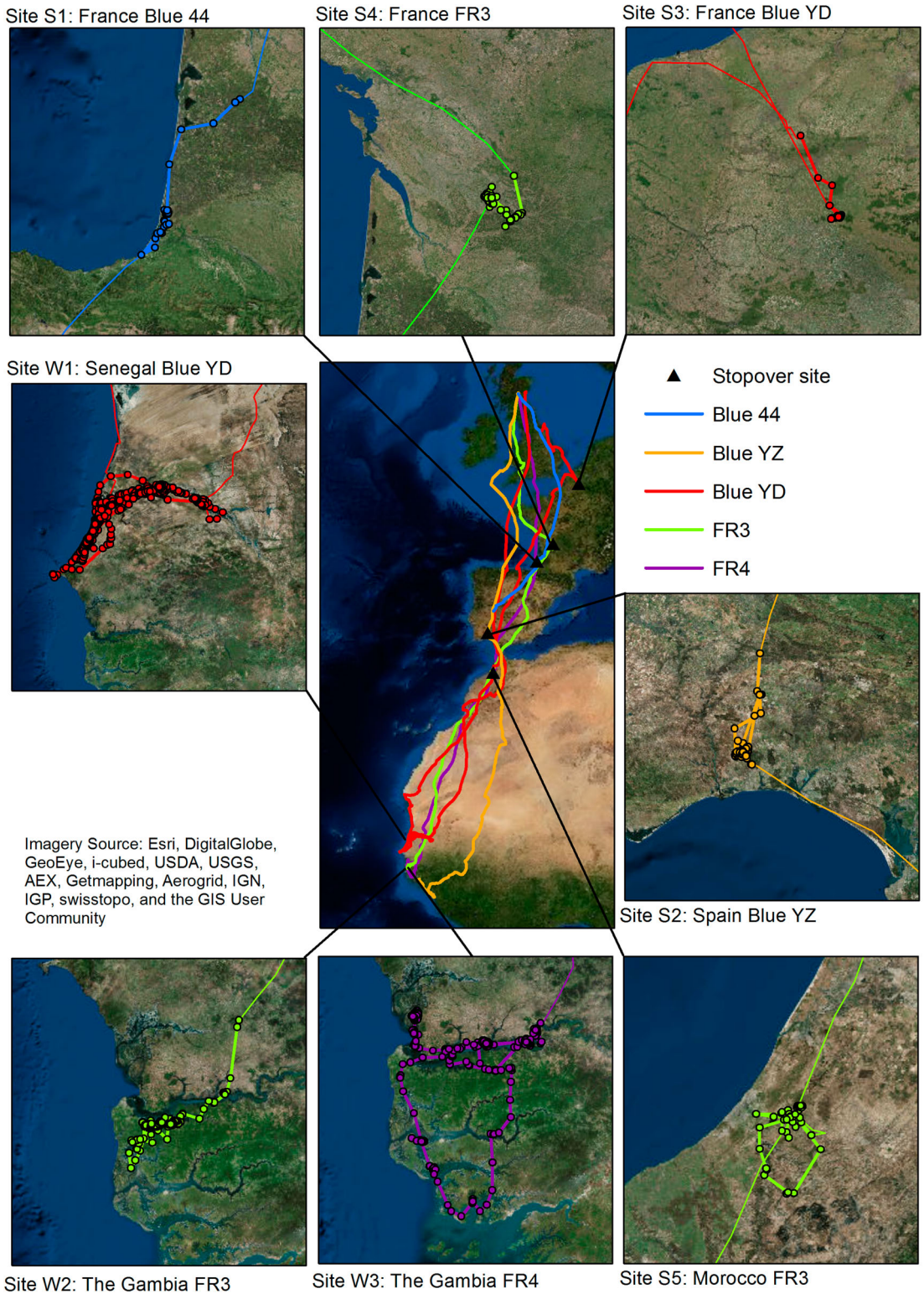

Figure 1. Migratory tracks of five juvenile Ospreys originating from Scotland: Blue 44, Blue YZ, Blue YD, FR3 and FR4. Stopover and wintering sites identified and used to examine habitat preferences are shown.

distribution, with peaks at 11:00 and 15:00 (Figure 2). Based on the GLM analysis, we found that, relative to the reference time of 07:00, the hours 09:00–18:00 all showed significantly higher levels of activity by the tracked Ospreys, when accounting for individual and stopover or wintering (Table 5). We also found the times 20:00 and 21:00 to have significantly less activity, relative to 07:00. Some individuals were

Table 4. Location and duration of stopover and wintering periods (see Figure 1).

Site ID	Osprey ID	Location	Site type	Arrival	Departure	Days	Fixes
S1	Blue 44	South-west France	Stopover	15 Sep 2012	6 Nov 2012	52	605
S2	Blue YZ	South-west Spain	Stopover	11 Sep 2013	4 Oct 2013	23	315
S3	Blue YD	North-east France	Stopover	12 May 2014	17 May 2014	5	89
S4	FR3	West France	Stopover	25 Aug 2015	20 Sep 2015	26	317
S5	FR3	North Morocco	Stopover	26 Sep 2015	2 Oct 2015	6	82
W1	Blue YD	Senegal/Mauritania	Wintering	30 Sep 2012	24 Apr 2014	571	7566
W2	FR3	Senegal/Gambia	Wintering	11 Oct 2015		324[1]	4173
W3	FR4	Senegal/Gambia/Guinea-Bissau	Wintering	18 Sep 2015		94[1]	1178

[1]Represents number of days studied, as wintering periods are incomplete.

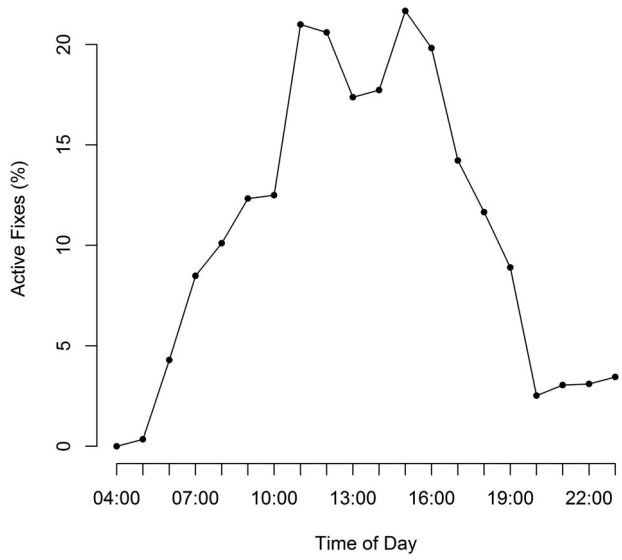

Figure 2. Daily activity pattern during stopovers and wintering: percentage of satellite fixes where Ospreys were active at hourly intervals throughout the day. Most data were available for hours between 07:00 and 21:00.

significantly more active (BlueYD and FR4). We also found evidence that behaviour at wintering sites is associated with higher levels of activity, suggesting that time of day is not the only important predictor of activity levels.

Table 5. Core-use areas (70% kernel) at stopover sites and seasonal core-use areas at wintering sites.

Site	Osprey ID	Period/season	Core-use area (km^2)
S1	Blue 44	Stopover	43.4
S2	Blue YZ	Stopover	68.4
S3	Blue YD	Stopover	102.1
S4	FR3	Stopover	85.5
S5	FR3	Stopover	208.1
W1	Blue YD	Rainy 2012	442.0
		Dry 2012/13	1279.4
		Rainy 2013	850.5
		Dry 2013/14	1201.6
W2	FR3	Rainy 2015	1071.8
		Dry 2015/16	50.2
		Rainy 2016	115.2
W3	FR4	Rainy 2015	194.3
		Dry 2015	5065.6

Space use and habitat preferences

Fixed kernel density estimates of core-use areas at stopover sites ranged from 43.4 km^2 to 208.1 km^2 (Table 6). At wintering sites, seasonal core-use areas ranged from 50.2 km^2 to 5065.6 km^2 (Table 6). Blue YD and FR4 used smaller core areas during the rainy seasons compared to the dry seasons, whilst FR3 used a smaller core area in the dry season (Table 6).

Individual preferences shaped habitat selection, although we do see some general trends (Table 7). At the majority of sites there was a preference for areas close to rivers and lakes, a preference for low elevations and shallow slopes and an avoidance of urban areas. At all wintering sites, there was a preference for habitat near coastal areas. With many variables, we begin to see individual differences shape habitat preference. For example, Blue YD was found to avoid lakes during stopover, whereas preference for lakes was observed at the other stopover sites and at Blue YD's wintering site. FR3 displayed a preference for locations near urban areas during stopover in France and during

Table 6. Results from a generalised linear model testing activity levels against time of day (TOD), stopover site status, and individual.

	Estimate	SE	*P*
Intercept	-2.622	0.176	0.000*
TOD 08:00	0.196	0.167	0.240*
TOD 09:00	0.427	0.161	0.008*
TOD 10:00	0.448	0.161	0.005*
TOD 11:00	1.081	0.149	0.000*
TOD 12:00	1.058	0.149	0.000*
TOD 13:00	0.846	0.152	0.000*
TOD 14:00	0.879	0.152	0.000*
TOD 15:00	1.133	0.149	0.000*
TOD 16:00	1.014	0.151	0.000*
TOD 17:00	0.597	0.158	0.000*
TOD 18:00	0.361	0.162	0.026*
TOD 19:00	0.055	0.172	0.747*
TOD 20:00	-1.287	0.249	0.000*
TOD 21:00	-1.112	0.242	0.000*
Stopover	-0.685	0.146	0.000*
Blue YD	1.210	0.196	0.000*
Blue YZ	0.362	0.206	0.080*
FR3	0.072	0.189	0.704*
FR4	0.969	0.212	0.000*

*Significant at $\alpha = 0.05$.

wintering, whereas urban areas were avoided by the other Ospreys. Blue 44 and FR3 showed a preference for areas near to major roads, but the other individuals avoided major roads and preferred habitat near minor roads. Box plots of the distributions of each continuous habitat variable (for observed and expected locations are presented in Appendix II, and provide further evidence that may assist in interpreting the results from Table 7.

At stopover sites, chi-square goodness-of-fit tests showed that the frequency of observed Osprey locations in each land-cover category differed significantly from the expected frequency: site S1 [Blue 44] $\chi^2_3 = 164.9$, $P < 0.001$; site S2 [Blue YZ] $\chi^2_4 = 127.5$, $P < 0.001$; site S3 [Blue YD] $\chi^2_2 = 653.9$, $P < 0.001$; site S4 [FR3] $\chi^2_2 = 19.9$, $P < 0.001$. Land-cover data were not available at a high-enough resolution for analysis of stopover site E. Again, some general trends emerge from the stopover analysis, along with individual preferences (Table 8). There was avoidance of urban areas by Blue 44, Blue YZ and Blue YD at their stopover sites. At site S4, FF3 showed neither preference nor avoidance of urban areas. Blue 44, Blue YD and FR3 preferentially used forested areas during stopovers whereas Blue YZ avoided forests and preferred agricultural trees. Blue 44 and Blue YZ showed a preference for water bodies at stopover sites. Open land-cover areas were avoided by Blue YD, Blue 44 and FR3 but Blue YZ showed neither preference nor avoidance of open land cover. Similarly, at wintering sites, chi-squared goodness-of-fit tests showed that the frequency of observed locations in each land-cover category differed significantly from the expected frequency: site W1 [Blue YD] $\chi^2_3 = 1\,417.6$, $P < 0.001$; site W2 [FR3] $\chi^2_4 = 272.7$, $P < 0.001$; site W3 [FR4] $\chi^2_4 = 263.2$, $P < 0.001$. Urban areas were significantly avoided at all wintering sites (Table 8). During wintering, FR3 and FR4 preferred open land cover and avoided habitat associated with forests and sparse trees, whereas Blue YD preferred habitat associated with sparse trees and water bodies and avoided open land cover.

Table 7. Results for Mann–Whitney *U* tests for continuous habitat variables, showing observed and expected mean values for each variable at stopover and wintering sites. Also see box plots in Appendix II.

Variable	Site	Mean value: Observed	Mean value: Expected	*P*	Preference (+) Avoidance (-)
Distance to river (km)	S1	0.391	2.164	<0.001*	+
	S2	0.694	1.148	<0.001*	+
	S3	0.808	1.275	0.009	
	S4	0.231	1.028	<0.001*	+
	S5	3.115	2.917	0.293	
	W1	2.316	3.716	<0.001*	+
	W2	13.988	4.655	<0.001*	-
	W3	2.706	5.410	<0.001*	+
Distance to lake (km)	S1	0.232	8.188	<0.001*	+
	S2	1.164	9.970	<0.001*	+
	S3	12.663	8.690	<0.001*	-
	S4	17.461	18.978	<0.001*	+
	S5	6.876	9.448	0.015	
	W1	17.455	31.435	<0.001*	+
	W2	1.225	15.567	<0.001*	+
	W3	22.750	21.150	0.068	
Distance to coast[1] (km)	W1	68.210	103.288	<0.001*	+
	W2	7.439	17.964	<0.001*	+
	W3	10.360	18.555	<0.001*	+
Distance to urban area[2] (km)	S1	1.745	1.785	<0.001*	-
	S2	8.593	5.233	<0.001*	-
	S3	1.543	0.766	<0.001*	-
	S4	1.365	2.899	<0.001*	+
	W1	8.538	9.470	<0.001*	-
	W2	1.898	4.639	<0.001*	+
	W3	6.053	5.083	<0.001*	-
Distance to major road (km)	S1	0.671	1.334	<0.001*	+
	S2	6.339	2.134	<0.001*	-
	S3	0.886	0.533	<0.001*	-
	S4	0.447	0.584	0.349	
	S5	1.134	1.516	0.111	
	W1	6.335	6.232	<0.001*	-
	W2	1.803	4.607	<0.001*	+
	W3	6.356	4.093	<0.001*	-
Distance to minor road (km)	S1	0.635	0.932	<0.001*	-
	S2	0.869	2.349	<0.001*	+
	S3	0.117	0.207	0.002*	+
	S4	0.166	0.162	0.006*	-
	S5	1.171	0.904	0.008	
Elevation (m)	S1	17.6	34.1	<0.001*	+
	S2	84.3	192.6	<0.001*	+
	S3	168.0	104.1	<0.001*	-
	S4	61.1	130.2	<0.001*	+
	S5	157.4	200.9	0.006*	+
	W1	9.8	27.0	<0.001*	+
	W2	10.6	18.3	<0.001*	+
	W3	10.3	19.0	<0.001*	+
Slope (%)	S1	3.5	4.9	<0.001*	+
	S2	3.5	6.3	<0.001*	+
	S3	5.8	4.2	0.003*	-
	S4	9.3	8.9	0.402	
	S5	6.9	7.8	0.863	
	W1	3.4	3.7	<0.001*	+
	W2	2.5	3.1	<0.001*	+
	W3	2.7	3.1	<0.001*	+

*Significant at $\alpha = 0.05$, with Bonferroni correction, critical value (α/m, where m is the number of tests performed for a given site).
[1]Coastal areas were not relevant at stopover sites.
[2]No high-resolution urban-area data were available for analysis at stopover site 5.

Use of protected areas

We found that the use of protected areas was site and individual specific during stopover, with preference shown at two stopover sites, avoidance at one site and no significant preference or avoidance shown at two sites (Table 9). During wintering, two individuals showed avoidance and one individual showed a preference for protected areas (Table 9). At two wintering sites, individuals showed a preference for protected areas designated for wetland and bird protection whilst there was avoidance at three other sites (Table 9).

Table 8. Observed, with Bonferroni confidence intervals, and expected usage by Ospreys of land-cover categories at stopover and wintering sites.

		Proportion of use		
Land cover	Site	Observed (CI)	Expected	Preference* (+) Avoidance* (-)
Urban	S1	0.002 (0–0.006)	0.096	-
	S2	0 (0–0)	0.006	-
	S3	0.011 (0–0.037)	0.112	-
	S4	0.003 (0–0.011)	0.009	
	W1	0.002 (0.001–0.003)	0.006	-
	W2	0 (0–0)	0.005	-
	W3	0.001 (0–0.003)	0.005	-
Forest	S1	0.585 (0.535–0.635)	0.512	+
	S2	0.054 (0.022–0.086)	0.190	-
	S3	0.865 (0.782–0.948)	0.090	+
	S4	0.461 (0.388–0.533)	0.344	+
	W1	0	0	
	W2	0 (0–0)	0.0002	-
	W3	0 (0–0)	0.005	-
Agricultural trees[1]	S1	0	0	
	S2	0.384 (0.316–0.453)	0.305	+
	S3	0	0	
	S4	0	0	
	W1	0.192 (0.181–0.204)	0.117	+
	W2	0.060 (0.051–0.070)	0.119	-
	W3	0.093 (0.071–0.114)	0.248	-
Water bodies	S1	0.255 (0.210–0.299)	0.127	+
	S2	0.083 (0.044–0.121)	0.016	+
	S3	0	0	
	S4	0	0	
	W1	0.091 (0.082–0.099)	0.031	+
	W2	0.042 (0.034–0.050)	0.079	-
	W3	0.026 (0.014–0.038)	0.089	-
Open	S1	0.159 (0.122–0.196)	0.264	-
	S2	0.479 (0.425–0.565)	0.483	
	S3	0.124 (0.043–0.204)	0.798	-
	S4	0.536 (0.464–0.608)	0.647	-
	W1	0.715 (0.702–0.728)	0.846	-
	W2	0.898 (0.886–0.910)	0.796	+
	W3	0.880 (0.856–0.905)	0.656	+

*Significant at α = 0.05, with Bonferroni confidence interval.
[1]At the wintering site (W), 'Agricultural trees' were not identifiable from the data and 'Sparse trees' were substituted.

Table 9. Percentage of observed and expected locations within protected areas and wetland/bird protected areas and chi-square test results at stopover and wintering sites.

		Within protected area (%)				
Site	Osprey ID	Observed	Expected	χ^2	*P*	Preference* (+) Avoidance* (-)
All protected areas						
S1	Blue 44	25.5	26.6	0.210	0.647	
S2	Blue YZ	17.1	11.1	4.723	0.030*	+
S3	Blue YD	3.40	51.7	52.07	<0.001*	-
S4	FR3	82.6	23.3	223.8	<0.001*	+
S5	FR3	0	0			
W1	Blue YD	16.7	21.3	57.59	<0.001*	-
W2	FR3	0.10	11.0	473.4	<0.001*	-
W3	FR4	39.3	14.8	179.7	<0.001*	+
Wetland/bird protected areas only						
S1	Blue 44	0.2	1.3	5.485	0.019*	-
S2	Blue YZ	0	1.3	4.026	0.045*	-
S3	Blue YD	0	2.3	2.023	0.155	
S4	FR3	0	0			
S5	FR3	0	0			
W1	Blue YD	16.6	1.8	986.5	<0.001*	+
W2	FR3	0	3.8	162.1	<0.001*	-
W3	FR4	38.5	2.8	457.3	<0.001*	+

*Significant at α = 0.05.

Discussion

We found that Ospreys can avoid passing extensive water bodies during autumn migration, travelling through Europe and crossing the Mediterranean Sea at southern Spain. This supports existing research that Ospreys show some level of avoidance of risks when migrating (Hake *et al* 2001). However, two Ospreys in this study made sea crossings to northern Spain. Dennis (2008) notes that Scottish Ospreys are more likely to make longer sea crossings than their continental counterparts – particularly from Ireland south to northern Spain – due to the geography of their migration routes, and this increases their chances of becoming lost at sea. The use of a migratory stopover by northern European Ospreys in this study is consistent with existing literature (Hake *et al* 2001, Kjellén *et al* 2001, Alerstam *et al* 2006). Although most European Ospreys make one or more stopovers during their autumn migration, previous research presents examples of Ospreys that, like Blue YD and FR4, make no stopovers, navigating directly to their wintering range (Hake *et al* 2001, Kjellén *et al* 2001). This is possible because Ospreys can use a fly-and-forage migration strategy, foraging opportunistically whilst covering distance on migration (Strandberg & Alerstam 2007). Ospreys may use a fly-and-forage migration strategy, without any stopovers, to arrive early at wintering sites, giving them access to high-quality wintering territories (Kjellén *et al* 1997). In our analysis, Osprey FR3 took a brief second stopover in Morocco before passing over the Sahara Desert: this may demonstrate resting before crossing a difficult ecological barrier (Dennis 2008). Blue YD's stopover was brief during spring migration: Ospreys are driven to fly quickly to the breeding grounds to find a mate and suitable nest site, and this may explain why this stopover was short.

The wintering sites of Scottish Ospreys were in line with the wintering range of northern European Ospreys defined by previous research, illustrating the importance of tropical West Africa as a wintering location for Ospreys (Österlöf 1977, Prevost 1982, Hake *et al* 2001, Dennis 2008). The duration of Blue YD's wintering period was similar to those recorded for other juvenile Ospreys (Hake *et al* 2001). Juvenile Ospreys remain at wintering sites, maturing for up to three years, before departing for the breeding grounds (Österlöf 1977).

Space use was localised at stopover sites, but was wide ranging and seasonally variable at the wintering site. Generally, undisturbed tree cover, close to water bodies, was preferred at stopover sites and undisturbed open cover, close to water bodies, was preferred at the wintering site. Finally, protected areas were only preferentially used at three stopover and wintering sites. Knowledge of this kind will be important in guiding the conservation of this iconic species throughout its migratory cycle.

Ospreys were most active during early morning, midday and late afternoon at stopover sites. Peaks in activity in the morning and late afternoon have been observed previously, and have been attributed to active foraging to compensate for the nocturnal non-feeding period (Boshoff & Palmer 1983, Flemming & Smith 1990). Such a high level of activity may reflect intensive foraging activity during stopovers to accumulate energy in preparation for the rest of the migratory journey.

During wintering, activity peaked in the late morning and late afternoon. Prevost (1982) observed that daily foraging was often delayed initially by fog, which could explain why the first activity peak was not until late morning. We also found that activity levels at wintering sites were higher than during stopover. A further possible explanation for high activity during the late morning and at midday is that the Ospreys were taking advantage of thermals, which are strongest around midday (Elkins 2004). Thermals can assist Osprey in reducing energy expenditure by allowing them to soar on columns of rising air to gain altitude (Thorup *et al* 2006). Research on other raptor species has also found higher levels of midday activity associated with the use of thermals (Sarasola & Negro 2005, Cadahia *et al* 2007).

We found the size of the areas used as stopover sites (*ie* 70% kernel-density isopleths) was similar to sizes of space use during the breeding season, when Scottish Ospreys usually range within a localised area (10–15 km of the nest; Hardey *et al* 2006, Dennis 2008). However, use of habitat within these areas was not uniform and reflects the configuration of individual habitat characteristics at different stopover sites, such as the location of water bodies (Bai *et al* 2009). Space use during stopover periods might be localised to maximise refuelling rates in preparation for the rest of the migratory journey (Galarza & Dennis 2009). In contrast, areas used at the wintering sites were generally larger (as defined by the 70% kernel-density contour) than during stopover and breeding periods. The large sizes of wintering areas contrast with previous research that reports localised space use by adult Ospreys wintering in America and in West Africa (Hake *et al* 2001, Washburn *et al* 2014). However, a potential explanation for this discrepancy may be related to differences in space use at different life

stages. The research here studied juvenile Ospreys and Hake *et al* (2001) suggest that juveniles range across a wider space than wintering adults, as they search for high-quality wintering habitat to return to in subsequent winters.

Space use by the wintering Ospreys varied seasonally during time spent in West Africa. During the rainy season, many species of fish migrate upriver and disperse into tributaries to spawn and reproduce, whilst fish biomass in coastal estuaries in West Africa peaks during the dry season (Winemiller & Jepsen 1998, Guillard *et al* 2004). Space use by Ospreys likely varies with the seasonal abundance and movement of prey species in different West African aquatic habitats, as wintering Ospreys show temporally variable preferences for foraging habitats that are most profitable (Prevost 1982).

We found Ospreys used areas close to water bodies at both stopover and wintering sites, which is unsurprising given that Ospreys forage primarily on fish (Poole 1989). Preference for these habitats may be magnified by the fact that resting close to foraging sites allows Ospreys to maximise energy conservation (Galarza & Dennis 2009). Here we found Ospreys to use a diverse set of aquatic habitats, illustrating their dietary plasticity (Swenson 1978, Glass & Watts 2009). However, individual preferences for different water-body types were evident. For example, despite available coastal habitat, Blue 44 preferred to be close to freshwater sites during stopover. This may reflect behaviour learnt in breeding grounds in Scotland, where Ospreys forage primarily on freshwater species (Green 1976, Carss & Brockie 1994).

We found that Ospreys show variable habitat preferences between stopover and wintering sites. For example, Blue YD selected rivers during stopover but used lakes, rivers and marine habitat when wintering in West Africa. Ospreys are known to exhibit variety in their foraging habitat preferences when wintering (Washburn *et al* 2014, Prevost 1982), perhaps reflecting the quality and availability of prey resources. Overall, it is evident that foraging habitat preferences are complex, and more research is needed to explore preference variation over time and space of wintering Ospreys in West Africa.

The results here suggest Ospreys preferred sites with low elevation and shallow slopes during the non-breeding period, supporting previous research on wintering Ospreys by Casado & Ferrer (2005), who suggested that water bodies at lower elevations have greater fish productivity due to high exchange rates between the entry and exit of water. Forested landscapes were preferred by three of the juveniles, and open landscapes were avoided during stopovers, again supporting previous observations (Galarza & Dennis 2009). One explanation for this pattern is that forested areas provide safe and quiet resting and roosting stopover habitat, facilitating refuelling rates and increasing survival chances (Galarza & Dennis 2009). Blue YZ showed a preference for areas of agricultural trees, perhaps because the variety in agricultural canopy height may offer prominent trees that provide suitable roosting and resting sites (Saurola 1997, Galarza & Dennis 2009), or it may suggest habituation to agricultural practices due to their prominence in the landscape (Bai *et al* 2009).

At wintering sites, we found that two Ospreys preferred open land cover, which could reflect a preference for habitat that commands clear visibility of water for foraging and perch hunting (Clancy 2005). Blue YD showed an avoidance of open landscapes at the wintering site, selecting areas with sparse tree cover. Prevost (1982) suggests that Ospreys wintering in West Africa rest on trees, shrubs and other perches close to water during the day, whilst at night they roost in tall, prominent trees to avoid predators.

Overall, we found that Ospreys avoided urban areas, which supports previous literature showing that Ospreys prefer habitat with low human disturbance during the non-breeding season (Galarza & Dennis 2009, Washburn *et al* 2014). Similarly, Rodríguez *et al* (2013) found that nesting Canarian Ospreys avoided human settlements and access routes, indicating that human settlements limit habitat use by Ospreys. However, Casado & Ferrer (2005) found that Ospreys wintering in Spain selected water bodies closer to urban centres. Similarly, Bierregaard *et al* (2014) and Washburn *et al* (2014) argued that Ospreys are highly adaptable to human disturbance and are increasingly prospering in urban and peri-urban spaces. Disturbance tolerance was not uniform throughout the Ospreys studied. For example, Blue 44 and FR3 illustrated a higher tolerance of major roads than the other Ospreys, whereas Blue YZ and Blue YD were observed near minor roads during stopovers. FR3 also showed a higher tolerance to urban areas at both stopover and wintering sites, compared to other Ospreys. Differing degrees of habituation to human activity may explain differences between Ospreys in their tolerance of disturbance (Swenson 1979). The avoidance of human activities by the Ospreys at stopover and wintering sites could have several implications. Human–Osprey conflicts may not be a large issue in stopover and wintering regions if Ospreys maintain an avoidance of urban areas (Washburn 2014). However, recent expansion in tourism,

recreation, agriculture and other human activities could have serious implications for the suitability of habitat at stopover and wintering sites.

Protected areas are one of the core management strategies used to conserve species (Gaston *et al* 2008). However, at only three sites out of eight did Ospreys preferentially use protected areas. This may be because the distribution of protected areas throughout Europe and in West Africa is not homogeneous. At two wintering sites Ospreys preferentially used protected areas designated for the protection of birds and wetlands. Protected areas are commonly designated for their terrestrial properties, however, overlooking aquatic habitats that are important for Ospreys (Saunders *et al* 2002). Increasing the network of protected areas to encompass a greater proportion of the habitats preferred by Ospreys could improve protection of this species during the non-breeding season. Expansion of protected areas is unlikely to occur in wintering regions, however, due to socioeconomic conditions (McDonald & Boucher 2011). Therefore, the protection of wintering Ospreys may need to rely on management and conservation efforts outside protected areas. Education programmes, alongside collaboration between conservationists throughout the geographical range, will be vital in ensuring that Ospreys are protected in their habitats at important stopover and wintering locations and throughout their annual cycle.

Importantly, this research illustrates the applicability of satellite-tracking data to explore the habitat preferences of highly mobile species. However, a limitation of our work is the small number of individuals tracked: this is a common problem in satellite-tracking studies, owing to the high cost of the devices and the logistics of fitting them to the individuals. The combination of satellite-tracking data and freely available environmental data sets provides a powerful analytical framework to study the spaces used by migratory species, and one that complements ongoing field-based observations. The methodological approach applied here can be used with other species, to help inform conservation and management strategies and to prioritise habitat and locations used by wide-ranging species.

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APPENDIX I. Aggregation of land-cover classes for Europe and West Africa.

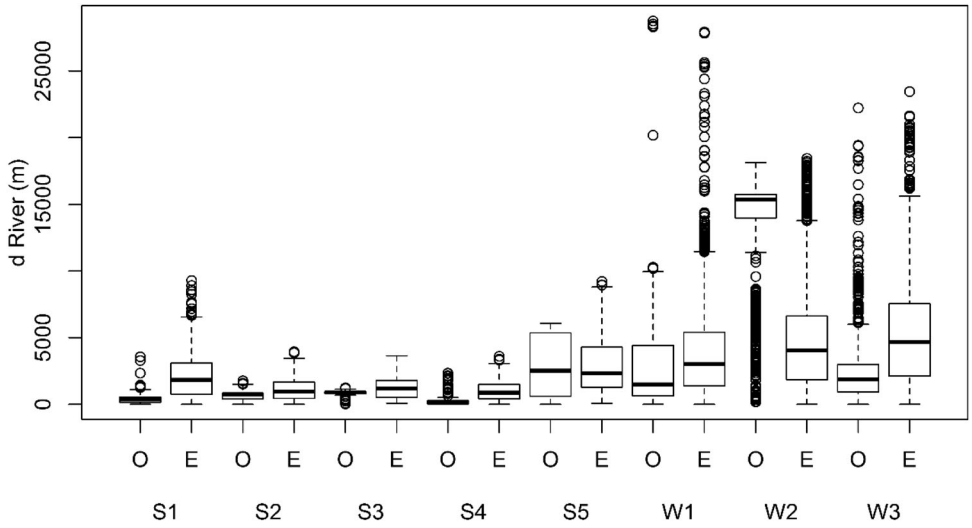
A: CORINE (EEA 2006) land-cover categories for stopover sites in Europe.

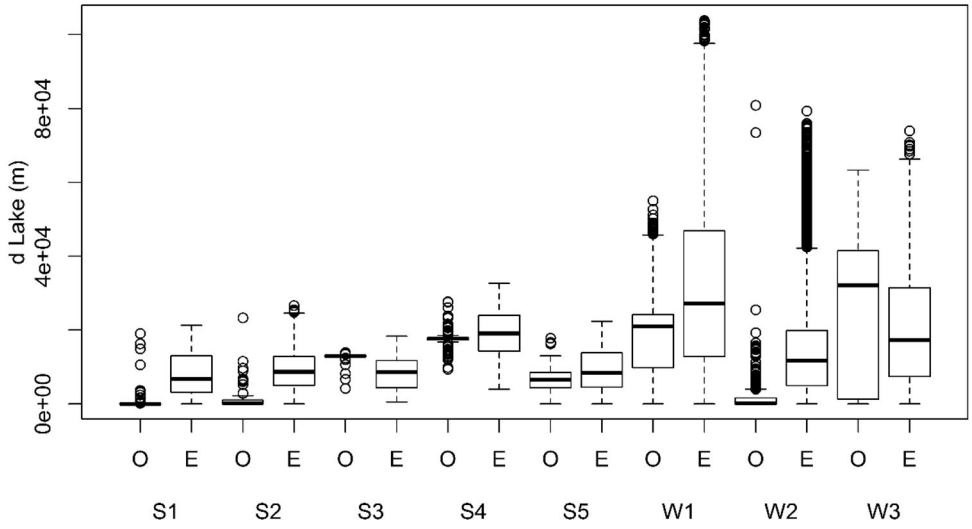
CORINE land-cover category code and label		Aggregated category
111–112	Urban fabric	Urban
121–124	Industrial, commercial and transport units	
131–133	Mine, dump and construction sites	
141–142	Artificial, non-agricultural vegetated areas	
311	Broad-leaved forest	Forest
312	Coniferous forest	
313	Mixed forest	
221	Vineyards	Agricultural trees
222	Fruit trees and berry plantations	
223	Olive groves	
244	Agro-forestry areas	
511	Water courses	Water bodies
512	Water bodies	
521	Coastal lagoons	
522	Estuaries	
523	Sea and ocean	
211	Non-irrigated arable land	Open
212	Permanently irrigated land	
213	Rice fields	
231	Pastures	
241	Annual crops associated with permanent crops	
242	Complex cultivation patterns	
243	Land principally occupied by agriculture, with significant areas of natural vegetation	
321	Natural grasslands	
322	Moors and heathland	
323	Sclerophyllous vegetation	
324	Transitional shrub	
331	Beaches, dunes, sands	
332	Bare rocks	
333	Sparsely vegetated areas	
334	Burnt areas	
335	Glaciers and perpetual snow	
411	Inland marshes	
412	Peat bogs	
421	Salt marshes	
422	Salines	
423	Intertidal flats	

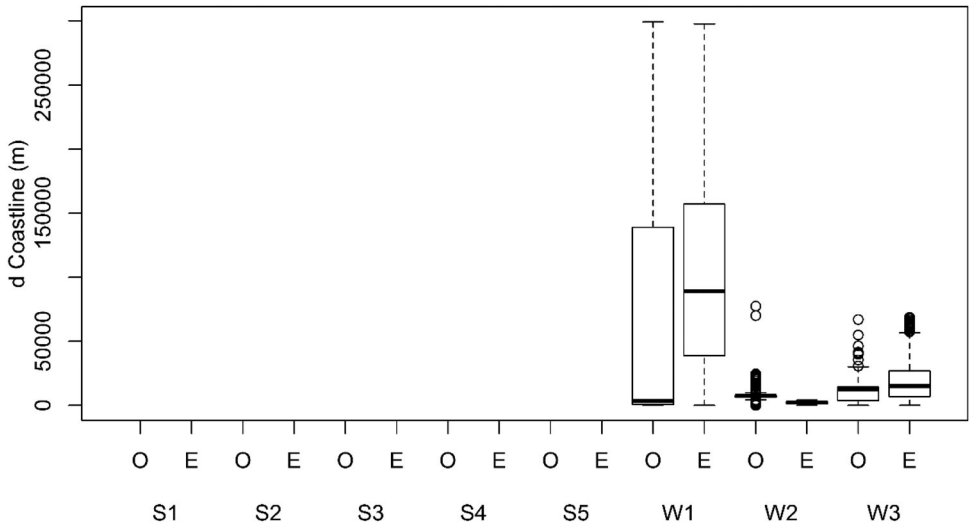
B: Aggregation of GlobeLand30 (National Geomatics Center of China 2010) land-cover categories for wintering sites in West Africa.

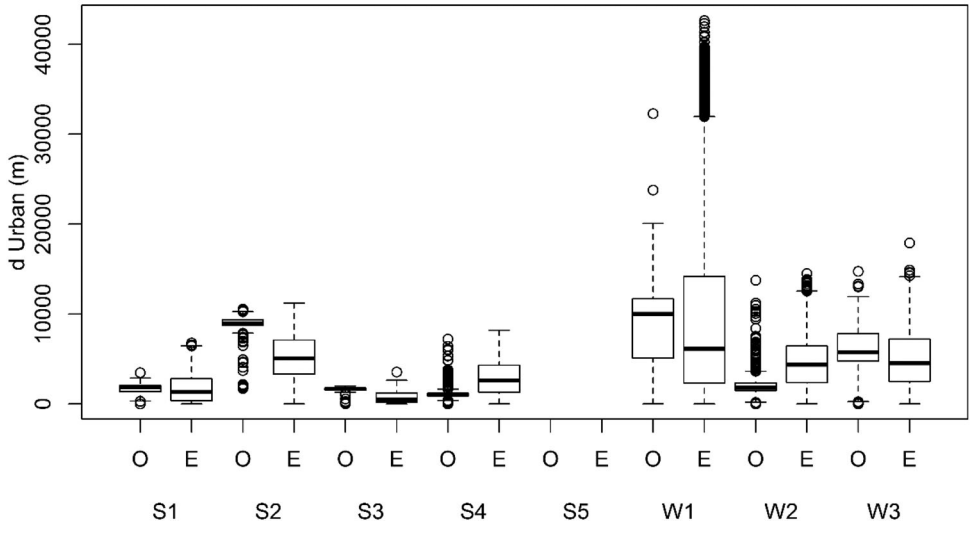
GlobeLand30 category		Aggregated category
80	Artificial surfaces	Urban
20	Forest	Forests
40	Shrub lands	Sparse trees
60	Water bodies	Water bodies
10	Cultivated land	Open
30	Grasslands	
50	Wetland	
70	Tundra	
90	Bare land	
100	Permanent snow and ice	

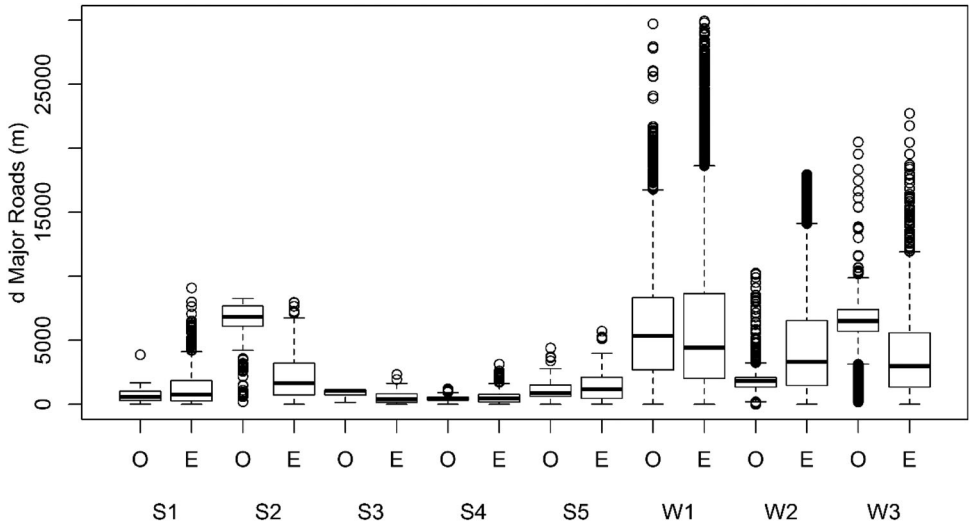
APPENDIX II. Box plots showing the distribution comparisons for each stopover and wintering site, for each individual and for each continuous variable investigated. These can be used to assist the interpretation of results presented in Table 7. Note that for the distance to minor roads *v* distance to coastline, this was separate for stopover (distance to minor roads) and wintering (distance to coastline) periods. Also, there were no data to facilitate a distance-to-urban calculation for stopover 5, which occurred in Morocco.

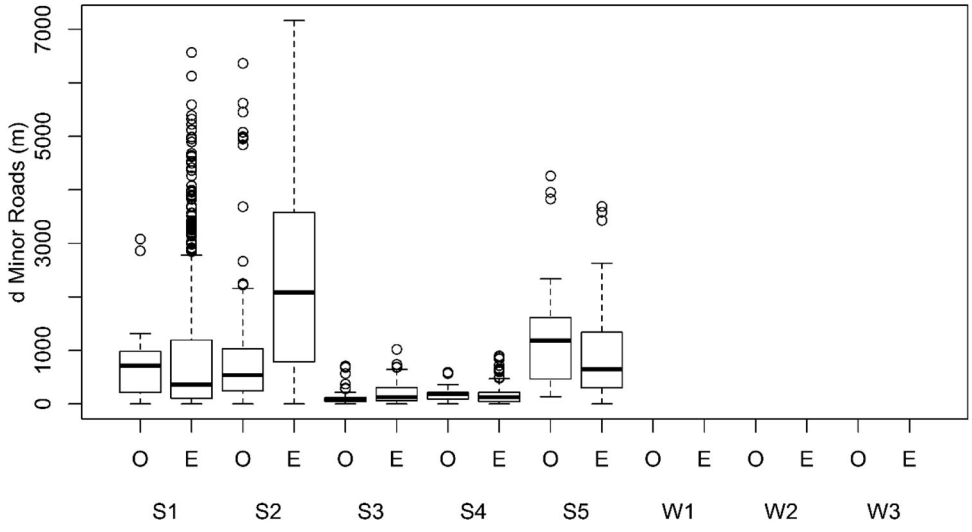


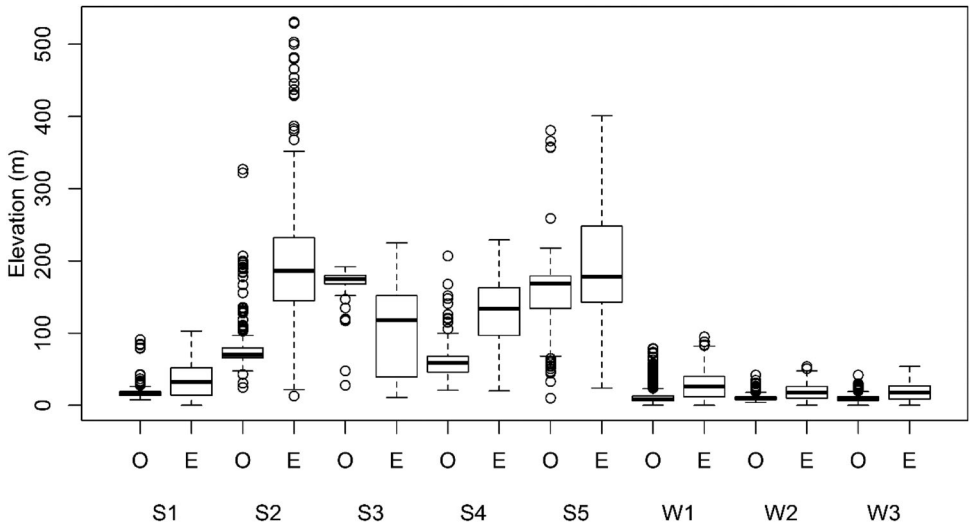


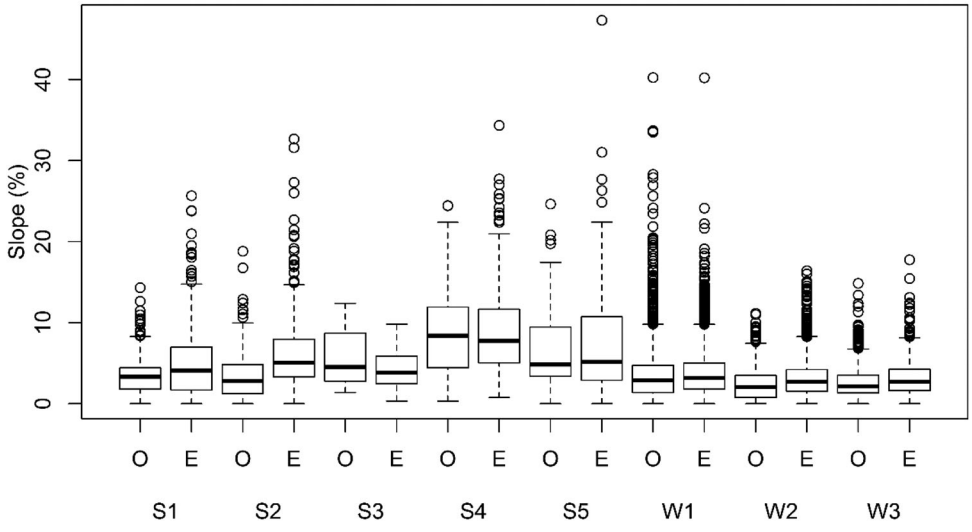

d Coastline (m)
0
50000
150000
250000
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3


d Urban (m)
0
10000
20000
30000
40000
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3


d Major Roads (m)
0
5000
15000
25000
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3


d Minor Roads (m)
0
1000
3000
5000
7000
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3


Elevation (m)
0
100
200
300
400
500
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3


Slope (%)
0
10
20
30
40
O E O E O E O E O E O E O E O E
S1 S2 S3 S4 S5 W1 W2 W3