Habitat preferences of juvenile Scottish ospreys (*Pandion haliaetus*) at stopover and wintering sites

Ruth E. Crawford[1], Jed A. Long[1*]

*Corresponding Author Email: jed.long@st-andrews.ac.uk

[1]School of Geography & Geosciences
University of St Andrews
St Andrews, Fife, UK

Submitted to: Ringing and Migration

Date submitted: 08/07/2016

SUMMARY

We use satellite tracking data, from five juvenile Scottish ospreys, to explore habitat preferences of ospreys at stopover and wintering sites. Daily activity patterns were analysed using a binomial generalized linear model (GLM). 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 osprey showed preference for landscape and land cover variables and for protected areas. Autumn migration strategies varied between individuals, with ospreys using stopovers sites in France, Spain and Morocco and wintering in West Africa. Activity levels of ospreys were variable throughout the day, with localized peaks at 1100 and 1500. Ospreys preferred to be near to water features (rivers, lakes, ocean) while avoiding urban areas. Individual differences were observed in preference for forest and open-area land cover classes. Overall, ospreys did not preferentially use protected areas. Our research confirms well established preference for aquatic habitats, but preference or avoidance for other habitats and protected areas varied dependent on individual. We highlight the potential of combing satellite tracking data with environmental data sources to explore the spatial ecology of migratory birds at stopover and wintering sites abroad.

Keywords: Space use, use vs available habitat, Satellite telemetry, movement ecology, stopover ecology

INTRODUCTION

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 animal space use (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 matches 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 datasets (e.g., those generated from remote sensing) is a powerful ecological tool that has not yet reached its full potential in movement ecology research (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; Lohmus 2001; Toschik et al. 2006; Bai et al. 2009) informing conservation strategies at breeding sites, for example guiding the width of disturbance buffer zones around nests; identifying priority areas for reserves and informing the location of artificial nesting structures (Lohmus 2001; Toschik et al. 2006; Bai et al. 2009; Rodriguez et al. 2013). Such a focus on the breeding season is disproportionate as 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 (Kjellen et al. 1997; Kjellen et al. 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 2010; Galarza & Dennis 2009). 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 (i.e., variations across space and time) which lead to an improved understanding of species movement ecology and behaviour. An understanding of habitat selection by ospreys at stopover sites and winter ranges is needed to further inform effective conservation strategies along migratory routes. Conservation is most commonly realized through the designation of protected areas, however it is unknown if and how the current arrangement of protected areas are utilized 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 are: i) to determine the seasonal migration and daily movement patterns; ii) to identify habitat preferences, and iii) to investigate use of protected areas of the five tracked osprey originating from Scotland.

METHODS

Satellite tracking data

Satellite tracking data on five juvenile Scottish ospreys was collected by the Scottish Wildlife Trust (SWT) from 2012-2016 (, Table 1). Juvenile osprey were ringed following standard ringing procedures, while at the same time GPS harnesses (Argos/GPS PTT-100, Microwave Telemetry Inc., Columbia, Maryland) were fitted on each of three 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 one hour between 04:00 and 23:00). Those recorded as ‘no fix’ or ‘low voltage’ were removed from the dataset, along with those fixes where the GPS location recorded an error.

< Table 1 here >

Delineating Migration and Stopover Sites

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

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% isopleth contours were obtained from the resulting kernel surface and used delineate core use areas at the stopover and wintering ranges. We chose 70% level for delineating the stopover ranges as 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 if 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 (1st June- 31st October) and the dry season (1st November to 31st May).

Daily activity patterns

For every observed osprey location, the activity status (active versus inactive) of the osprey was defined. An osprey was considered to be active, i.e. foraging or flying, if the flight speed, provided by the transmitter, was > 0 knots (Washburn et al. 2014). For the pooled osprey data, the daily activity levels were analysed at 1 hr intervals from 07:00 to

21:00 (when the most data were available) using a binomial generalized 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 osprey.

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). A use vs available 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 as 5967 m, as this was the average daily stopover distance. To define available habitat at wintering ranges, the minimum convex polygon (MCP) encompassing the winter range of tracking data was used (Johnson 1980; Liminana et al. 2012; Popp et al. 2013). Ocean area 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 osprey literature (Table 2). Data sources were chosen for their extent, resolution and suitability in relation to the habitat characteristic of interest. All variables were represented as 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.

< Table 2 here >

We tested for significant differences between the observed used locations and expected available habitat locations using a non-parametric Mann-Whitney U test (for continuous variables; e.g., Oppel et al. 2004) and a chi-square test (for categorical landcover variables; Byers et al. 1984). For the continuous habitat variables, we perform repeated statistical tests on the data associated with each individual, which is subject to issues of multiple-testing and increased Type I error rates (Cabin 2000). To account for this effect, we used the Bonferroni correction which is a *post hoc* adjustment of the critical value and is considered to be a conservative approach to reducing the Type I error rate. 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, if 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 proportion of usage lay below the calculated confidence intervals then a significant preference for that land cover type was inferred.

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 was not provided, but the central geographic point and the extent of the protected area was available, a circular buffer around the central geographic point was calculated, the radius of which was derived so as to result in the correct protected area extent (Liminana et al. 2012). Chi-squared tests were used to determine if 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 of protected area boundaries. This analysis was repeated, comparing if ospreys used protected areas designated for the protection of birds and/or wetlands to the number of expected locations within these protected areas.

RESULTS

Migration Patterns

Three ospreys experienced satellite transmitter failure and one osprey was found dead in Guinea Bissau at the end of 2013, thus data was only available for four autumn migrations, three wintering periods and one spring migration (Table 1; Table 3). Only data on Blue YD was available for a complete wintering period. Departure dates for autumn migration ranged from 17th August to 9th September (Table 3). Total autumn migration distance ranged from 5227.2km to 6432.6km and average travel day speed during autumn migration ranged from 242.8km/day to 307.5km/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 less than 100km a 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 between 6-52 days (Table 4). Three ospreys passed primarily over land during autumn migration, whilst Blue YZ and Blue YD crossed over the ocean west of France (Figure 1). Arrival dates at wintering sites ranged from 30th September to 10th October (Table 4). Ospreys wintered in West Africa (Senegal, The 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.

<Table 3 here>

<Table 4 here>

<Figure 1 here>

Daily activity patterns

Activity levels varied throughout the day by the osprey tracked in our study, and we found a bi-modal 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 times 09:00– 18:00 all showed significantly higher levels of activity by the tracked osprey, 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 significantly more active (i.e., BlueYD and FR4). We also found evidence that behaviour at wintering sites is associated with of higher levels of activity, suggesting that time-of-day is not the only important predictor of activity levels.

< Figure 2 here >

< Table 5 here >

Space use and habitat preferences

Fixed kernel density estimates of core use areas ranged from 43.4 km^2 to 208.1 km^2 at stopover sites (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 had a smaller core use area in the dry season (Table 6).

< Table 6 here >

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 preferences shape habitat preference. For example, Blue YD was found to avoid lakes during stopover, while 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 wintering, whereas urban areas were avoided by the other ospreys. Blue 44 and FR3 showed a preference for areas near to major roads, while the other individuals avoided major roads (and preferred habitat near minor roads). Boxplots 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.

< Table 7 here >

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) $x^2(3) = 164.9$, $p < 0.001$; Site S2 (Blue YZ) $x^2(4)=127.5$, $p <0.001$; Site S3 (Blue YD) $x^2(2)=653.9$, $p < 0.001$; Site S4 (FR3) $x^2(2)=19.9$, $p < 0.001$. Land cover data was not available at a high enough resolution for analysis 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 but 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-square 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) x^2 (3) = 1417.6, p<0.001; Site W2 (FR3) x^2(4)=272.7, p < 0.001; Site W3 (FR4 x^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 8 here >

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 of protected areas Table 9). At two wintering sites, individuals showed a preference of protected areas designated for wetland and bird protection whilst there was avoidance at three other sites (Table 9).

< Table 9 here >

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 research made sea crossings to north Spain. Dennis (2008) notes that Scottish osprey are more likely to make longer sea crossings than their continental counterparts – particularly from Ireland down to the north of Spain – due to the geography of their migration routes, which 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; Kjellen 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; Kjellen et al. 2001). This is possible as 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 (Kjellen et al. 1997). In our analysis, osprey FR3 took a brief second stopover in Morocco before passing over the Sahara desert which 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, which may explain why this stopover was short.

The wintering sites of Scottish ospreys was in line with the wintering range of Northern European ospreys in existing research, illustrating the importance of tropical West Africa as a wintering location for ospreys (Osterlof 1977; Prevost 1982; Hake et al. 2001; Dennis 2008). The duration of Blue YD's wintering period was similar to those of other recorded juvenile ospreys (Hake et al. 2001). Juvenile ospreys remain at wintering sites, maturing for up to three years, before departing for the breeding grounds (Osterlof 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 their 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 (Flemming & Smith 1990; Boshoff & Palmer 1983). 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 initial daily foraging activity was often delayed by fog, which could explain why the first activity peak was not until late morning. We also found that activity levels at wintering sites was 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 during at midday (Etkins 2004). Thermals can assist osprey in reducing flight energy expenditure by soaring 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 (i.e., 70% KDE 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 may be localised to maximise refuelling rates in preparation for the rest of the migratory journey (Galarza & Dennis 2009). In contrast, space use areas at the wintering sites were generally larger (as defined by the 70% kernel density estimate contour) than during stopover and breeding periods. The large wintering areas contrast with existing 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 forthcoming winters.

Space use by the wintering ospreys varied seasonally during time spent in West Africa. During the West African rainy season, many species of fish migrate upriver and disperse into tributaries for spawning and reproduction, whilst during the dry season, marine estuaries in West Africa peak in abundance of fish biomass (Winemiller & Jepsen 1998; Guillard et al. 2004). Space use by osprey likely vary 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 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), which may reflect 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; which support previous research on wintering ospreys by Casado and Ferrer (2005) who suggest 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, which again supports 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, which could be because the variety in agricultural canopy height may offer prominent trees that provide suitable roosting and resting sites (Saurola 1997; Galarza & Dennis 2009), or may suggest habituation to agricultural practices due to their prominence on 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 wintering ospreys in

West Africa rest on trees, shrubs and other perches close to water during the day, whilst at night ospreys roost in tall, prominent trees to avoid predators.

Overall, we found ospreys to avoid urban areas, which supports existing literature identifying 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 Canarain opsreys avoided human settlements and access routes, indicationg that human settlements limit ospreys habitat use. However, Casado and Ferrer (2005) found wintering ospreys in Spain selected water bodies closer to urban centres. Similarly, Bierregaard *et al*. (2014) and Washburn *et al*. (2014) argue 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 studied ospreys. 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 in disturbance tolerance between the ospreys (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. However protected areas are commonly designated for their terrestrial properties, 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. However, expansion of protected areas is unlikely to occur in wintering regions, due to socioeconomic conditions (McDonald & Boucher 2011). Therefore, the protection of wintering ospreys may need to rely on management and conservation efforts outside of protected areas. Education programmes, alongside collaboration between conservationists throughout the geographic ranges at important stopover and wintering locations will be vital in ensuring that ospreys are protected in their habitats throughout their annual cycle.

Importantly, this research illustrates the applicability of using 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, which is a common problem in satellite tracking studies owing to the high cost of the devices and logistics of fitting them to the individuals. The combination of satellite tracking data and freely available environmental datasets 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 to prioritize habitat and locations used by species that range over large spatial distances.

ACKNOWLEDGEMENTS

The authors would like to thank Will Cresswell and Urska Demsar for invaluable discussions about avian migration ecology and spatial analysis. We are grateful to the Scottish Wildlife Trust (SWT), in particular Emma Rawlings, Rab Potter, and Charlotte Flemming for providing and assisting with processing the osprey satellite data. Also thanks to Roy Dennis and Keith Brockie who are responsible for performing the ringing and satellite tagging procedures that enabled this data to be collected.

REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**, 140–160.

Africa Infrastructure Knowledge Program (2012) Senegal and Mauritania roads. Available at: http://www.infrastructureafrica.org [Accessed February 16, 2015].

Alerstam, T., Hake, M. & Kjellen, N. (2006) Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal Behaviour* **71**, 555–566.

Bai, M.L. & Schmidt, D. (2012) Differential migration by age and sex in central European Ospreys Pandion haliaetus. *Journal of Ornithology* **153**, 75–84.

Bai, M.L., Schmidt, D., Gottschalk, E. & Mohlenberg, M. (2009) Distribution pattern of an expanding osprey ({Pandion} haliaetus) population in a changing environment. *Journal of Ornithology* **150**, 255–263.

Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M.S. & Matthiopoulos, J. (2010) The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B* **365**, 2245–2254.

Bierregaard, R.O., Poole, A.F. & Washburn, B.E. (2014) Ospreys (Pandion haliaetus) in the 21st century: populations, migration, management, and research priorities. *Journal of Raptor Research* **48**, 301–308.

Boshoff, A.F. & Palmer, N.G. (1983) Aspects of the biology and ecology of the osprey in the cape province South Africa. *Ostrich* **54**, 189–204.

Bustamante, J. (1995) The duration of the post-fledging dependence period of Ospreys Pandion haliaetus at Loch Garten Scotland. *Bird Study* **42**, 31–36.

Byers, C.R., Steinhorst, R.K. & Krausman, P.R. (1984) Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* **48**, 1050–1053.

Cabin, R.J. (2000) To Bonferonni or not to Bonferonni: When and how are the questions. *Bulletin of the Ecoloical Society of America* **81**, 246–248.

Cadahia, L., Urios, V. & Negro, J.J. (2007) Bonelli's Eagle Hieraaetus fasciatus juvenile dispersal: hourly and daily movements tracked by GPS. *Bird Study* **54**, 271–274.

Carss, D.N. & Brockie, K. (1994) Prey remains at Osprey nests in Tayside and Grampian 1987-1993. *Scottish Birds* **17**, 132–145.

Casado, E. & Ferrer, M. (2005) Analysis of reservoir selection by wintering ospreys (Pandion haliaetus haliaetus) in Andalusia Spain: A potential tool for reintroduction. *Journal of Raptor Research* **39**, 168–173.

Clancy, G.P. (2005) Feeding behaviour of the osprey Pandion haliatus on the north coast of new south wales. *Corella* **29**, 91–96.

Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., Weiskopf, D. & Weibel, R. (2015) Analysis and visualisation of movement: an interdisciplinary review. *Movement Ecology* **3**, 5.

Dennis, R. (2008) *A Life of Ospreys*, Dunbeath, UK: Whittles Publishing.

Dickson, B.G., Jenness, J.S. & Beier, P. (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management* **69**, 264–276.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S.C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D. & Wikelski, M. (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology* **1**, 3.

EEA (2006) CORINE land cover 2006 seamless vector data. *European Environment Agency*. Available at: http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-3 [Accessed January 30, 2015].

EEA (2012) European catchments and river network system (v1). *European Environment Agency*. Available at: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3#tab-gis-data [Accessed March 12, 2015].

Etkins, N. (2004) *Weather and Bird Behaviour* 3rd ed., London: Third Edition.

FAO (2014) Rivers of Africa (Derived from HydroSHEDS), Version 2. *Food and Agriculture Organization of the United Nations*. Available at: http://www.fao.org/nr/water/aquamaps/ [Accessed February 13, 2015].

Flemming, S.P. & Smith, P.C. (1990) Environmental influences on osprey foraging in northeastern Nova Scotia. *Journal of Raptor Research* **24**, 64–67.

Galarza, A. (2010) Fishing behaviour of the Osprey Pandion haliaetus in an estuary in the northern Iberian Peninsula during autumn migration. *Revista Catalana d'Ornitologia*, 56–60. Available at: https://ornitologia.org/ca/queoferim/divulgacio/publicacions/rco/26_56_60.pdf.

Galarza, A. & Dennis, R.H. (2009) A spring stopover of a migratory osprey (Pandion haliaetus) in northern Spain as revealed by satellite tracking: implications for conservation. *Animal Biodiversity and Conservation* **32**, 117–122.

Gaston, K.J., Jackson, S.F., Cantu-Salazar, L. & Cruz-Pinon, G. (2008) The Ecological Performance of Protected Areas. *Annual Review of Ecology, Evolution, and Systematics* **39**, 93–113.

Geofabrik (2015) OpenStreetMap (roads). Available at: http://download.geofabrik.de/europe.html [Accessed March 12, 2015].

Glass, K.A. & Watts, B.D. (2009) Osprey diet composition and quality in high-and low-salinity areas of lower Chesapeake Bay. *Journal of Raptor Research* **43**, 27–36.

Green, R. (1976) Breeding behaviour of Ospreys Pandion haliaetus in Scotland. *Ibis* **118**, 475–490.

Guillard, J., Albaret, J.J., Simier, M., Sow, I., Raffray, J. & de Morais, L.T. (2004) Spatio-temporal variability of fish assemblages in the Gambia Estuary (West Africa) observed by two vertical hydroacoustic methods: moored and mobile sampling. *Aquatic*

Living Resources **17**, 47–55.

Hake, M., Kjellen, N. & Alerstam, T. (2001) Satellite tracking of Swedish Ospreys Pandion haliaetus: autumn migration routes and orientation. *Journal of Avian Biology* **32**, 47–56.

Hardey, J., Crick, H., Wernham, C., Riley, H., Etheridge, B. & Thompson, D. (2006) *Raptors: A Field Guide to Survey and Monitoring* T. S. Box, ed., Stationery Office Books.

Hebblewhite, M. & Haydon, D.T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B* **365**, 2303–2312.

IUCN & UNEP (2015) The World Database on Protected Areas (WDPA). *International Union for Conservation of Nature and United Nations Environment Program*. Available at: www.protectedplanet.net [Accessed January 26, 2015].

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002) A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* **12**, 1840–1860.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.

Kjellen, N., Hake, M. & Alerstam, T. (1997) Strategies of two Ospreys Pandion haliaetus migrating between Sweden and tropical Africa as revealed by satellite tracking. *Journal of Avian Biology* **28**, 15–23.

Kjellen, N., Hake, M. & Alerstam, T. (2001) Timing and speed of migration in male, female and juvenile Ospreys Pandion haliaetus between Sweden and Africa as revealed by field observations, radar and satellite tracking. *Journal of Avian Biology* **32**, 57–67.

Lehner, B. & Doll, P. (2004) Global lakes and wetlands databse. Available at: https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database [Accessed February 10, 2015].

Liminana, R., Soutullo, A., Arroyo, B. & Urios, V. (2012) Protected areas do not fulfil the wintering habitat needs of the trans-Saharan migratory Montagu?s harrier. *Biological Conservation* **145**, 62–69.

Lohmus, A. (2001) Habitat selection in a recovering Osprey Pandion haliaetus population. *Ibis* **143**, 651–657.

Martell, M., Henny, C., Nye, P. & Solensky, M. (2001) Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *Condor* **103**, 715–724.

McCullagh, P. & Nelder, J. (1989) *Generalized Linear Models*, London: Chapman and Hall.

McDonald, R.I. & Boucher, T.M. (2011) Global development and the future of the protected area strategy. *Biological Conservation* **144**, 383–392.

METI & NASA (2011) The Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM), Version 2. *Ministry of Economy, Trade, and Industry of Japan and The National Aeronautics and Space Administration*. Available at: http://gdem.ersdac.jspacesystems.or.jp/ [Accessed

February 22, 2015].

Millspaugh, J.J., Kesler, D.C., Kays, R., Gitzen, W., Schulz, J.H., Rota, C.T., Bodinof, C.M., Belant, J.L. & Keller, B.J. (2012) Wildlife radiotelemetry and remote monitoring. In N. Silvy, ed. *The Wildlife Techniques Manual*. Baltimore: The John Hopkins University Press, pp. 258–283.

National Geomatics Center of China (2010) GlobeLand30. Available at: http://www.globallandcover.com/GLC30Download/index.aspx [Accessed September 16, 2015].

Neu, C.W., Byers, C.R. & Peek, J.M. (1974) A technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**, 541–545.

NOAA (2015) Global Self-consistent, Hierarchical, High-resolution Geography Database. *National Oceanic and Atmospheric Administration*. Available at: http://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html [Accessed February 28, 2015].

Oppel, S., Schaefer, H.M., Schmidt, V. & Schröder, B. (2004) Habitat selection by the pale-headed brush-finch (Atlapetes pallidiceps) in southern Ecuador: implications for conservation. *Biological Conservation* **118**, 33–40.

Osterlof, S. (1977) Migration, wintering areas, and site tenacity of the European Osprey Pandion haliaetus (L.). *Ornis Scandinavica* **8**, 61–78.

Poole, A.F. (1989) *Ospreys: A Natural and Unnatural History*, Cambridge: Cambridge University Press.

Popp, J.N., McGeachy, D.N. & Hamr, J. (2013) Elk (Cervus elaphus) seasonal habitat selection in a heterogeneous forest structure. *International Journal of Forestry Research* **415913**, 1–7.

Prevost, Y.A. (1982) *Wintering ecology of ospreys in Senegambia*. The University of Edinburgh.

Rodriguez, B., Rodriguez, A., Siverio, M. & Siverio, F. (2013) Conservation implications of past and present nesting habitat selection of the endangered Osprey Pandion haliaetus population of the Canary Islands. *Ibis* **155**, 891–897.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G. & Fuller, R.A. (2014) Conserving mobile species. *Frontiers in Ecology and the Environment* **12**, 395–402.

Sarasola, J.H. & Negro, J.J. (2005) Hunting success of wintering {Swainson}'s hawks: environmental effects on timing and choice of foraging method. *Canadian Journal of Zoology* **83**, 1353–1359.

Saunders, D.L., Meeuwig, J.J. & Vincent, A.C.J. (2002) Freshwater protected areas: strategies for conservation. *Conservation Biology* **16**, 30–41.

Saurola, P. (1997) The osprey (Pandion haliaetus) and modern forestry: a review of population trends and their causes in Europe. *Journal of Raptor Research* **31**, 129–137.

Strandberg, R. & Alerstam, T. (2007) The strategy of fly-and-forage migration illustrated for the osprey (Pandion haliaetus). *Behavioural Ecology and Sociobiology* **61**, 1865–1875.

Strandberg, R., Klaassen, R.H. & Thorup, K. (2009) Spatio-temporal distribution of migrating raptors: a comparison of ringing and satellite tracking. *Journal of Avian*

Biology **40**, 500–510.

Swenson, J.E. (1979) Factors affecting status and reproduction of ospreys in Yellowstone National Park. *Journal of Wildlife Management* **43**, 595–601.

Swenson, J.E. (1978) Prey and foraging behavior of ospreys on Yellowstone Lake Wyoming. *Journal of Wildlife Management* **42**, 87–90.

Thorup, K., Alerstam, T., Hake, M. & Kjell?n, N. (2006) Traveling or stopping of migrating birds in relation to wind: an illustration for the osprey. *Behavioural Ecology* **17**, 497–502.

Toschik, P.C., Christman, M.C., Rattner, B.A. & Ottinger, M.A. (2006) Evaluation of Osprey habitat suitability and interaction with contaminant exposure. *Journal of Wildlife Management* **70**, 977–988.

Urbano, F., Cagnacci, F., Calenge, C., Dettki, H., Cameron, A. & Neteler, M. (2010) Wildlife tracking data management: a new vision. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**, 2177–85.

Washburn, B.E. (2014) Human-osprey conflicts: industry, utilities, communication, and transportation. *Journal of Raptor Research* **48**, 387–395.

Washburn, B.E., Martell, M.S., Jr, B., O., R., Henny, C.J., Dorr, B.S. & Olexa, T.J. (2014) Wintering ecology of adult North American Ospreys. *Journal of Raptor Research* **48**, 325–333.

Winemiller, K.O. & Jepsen, D.B. (1998) Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* **53**, 267–296.

Worton, B. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.

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	02/07/2012	Transmitter failure: Nov. 2012
Blue YD	Male	May 2012	17/07/2012	Transmitter failure: May 2014
Blue YZ	Female	June 2013	15/07/2013	Died: Nov. 2013
FR3	Male	May 2015	29/06/2015	Still receiving data
FR4	Female	May 2015	29/06/2015	Transmitter failure: December 2015

Table 2. Data sources and description of habitat variables. All habitat variables were derived from the original source using a geographic 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	A Global Self-consistent, Hierarchical, High-resolution Geography shoreline Database (NOAA 2015)	A Global Self-consistent, Hierarchical, High-resolution Geography 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	ASTER GDEM (METI & NASA 2011)	ASTER GDEM (METI & NASA 2011)
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 land cover data was aggregated into five land cover classes: Urban area, Water body, Forests, Open, Sparse/Agricultural trees.

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

[1] Blue 44 died during autumn migration so calculations are included until date of death

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	08/09/2012		62	10	2582.3	2221.9	222.2
Blue YZ	Autumn	05/09/2013	18/10/2013	43	20	6432.6	6096.6	304.8
Blue YD	Autumn	12/09/2012	30/09/2012	18	18	5298.4	5298.4	294.4
FR3	Autumn	17/08/2015	11/10/2015	55	23	6161.9	5584.0	242.8
FR4	Autumn	01/09/2015	18/09/2015	17	17	5227.2	5227.2	307.5
Blue YD[2]	Spring	24/04/2014		27	22	5835.1	5781.8	262.8

[2] Blue YD experienced transmitter failure during spring migration so calculations are included until date of transmitter failure

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	15/09/2012	06/11/2012	52	605
S2	Blue YZ	South West Spain	Stopover	11/09/2013	04/10/2013	23	315
S3	Blue YD	North East France	Stopover	12/05/2014	17/05/2014	5	89
S4	FR3	West France	Stopover	25/08/2015	20/09/2015	26	317
S5	FR3	North Morocco	Stopover	26/09/2015	02/10/2015	6	82
W1	Blue YD	Senegal/ Mauritania	Wintering	30/09/2012	24/04/2014	571	7566
W2	FR3	Senegal/ Gambia	Wintering	11/10/2015		324[1]	4173
W3	FR4	Senegal/Gambia/ Guinea Bissau	Wintering	18/09/2015		94[1]	1178

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

Table 5 Core use areas (70% UD) 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

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

	Estimate	Std Error	*p-value*	
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	*
BlueYD	1.210	0.196	0.000	*
BlueYZ	0.362	0.206	0.080	
FR3	0.072	0.189	0.704	
FR4	0.969	0.212	0.000	*

*Significant at $\alpha = 0.05$.

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.

Variable	Site	Variable mean		p	Preference (+) Avoidance (-)
		Observed	Expected		
Distance to river (m)	S1	391.0	2163.7	<0.001*	+
	S2	694.0	1147.6	<0.001*	+
	S3	808.3	1274.7	0.009	
	S4	230.5	1028.1	<0.001*	+
	S5	3115.9	2917.3	0.293	
	W1	2316.5	3715.5	<0.001*	+
	W2	13988.4	4655.1	<0.001*	-
	W3	2706.4	5409.8	<0.001*	+
Distance to lake (m)	S1	232.3	8187.8	<0.001*	+
	S2	1163.5	9969.7	<0.001*	+
	S3	12663.1	8689.8	<0.001*	-
	S4	17460.8	18977.7	<0.001*	+
	S5	6876.4	9448.3	0.015	
	W1	17454.6	31434.8	<0.001*	+
	W2	1225.0	15567.2	<0.001*	+
	W3	22749.8	21149.5	0.068	
Distance to coast[1] (m)	W1	68209.7	103287.5	<0.001*	+
	W2	7439.0	17964.3	<0.001*	+
	W3	10360.2	18555.1	<0.001*	+
Distance to urban area (m)[2]	S1	1745.0	1785.3	<0.001*	-
	S2	8592.8	5232.5	<0.001*	-
	S3	1542.6	765.6	<0.001*	-
	S4	1364.9	2898.5	<0.001*	+
	W1	8537.7	9470.2	<0.001*	-
	W2	1897.8	4638.5	<0.001*	+
	W3	6053.1	5083.0	<0.001*	-
Distance to major road (m)	S1	671.4	1334.3	<0.001*	+
	S2	6339.3	2133.7	<0.001*	-
	S3	886.3	532.6	<0.001*	-
	S4	447.1	584.0	0.349	
	S5	1134.4	1516.3	0.111	
	W1	6334.7	6232.3	<0.001*	-
	W2	1802.8	4607.2	<0.001*	+
	W3	6356.3	4093.4	<0.001*	-
Distance to minor road (m)	S1	634.7	931.6	<0.001*	-
	S2	869.0	2349.1	<0.001*	+
	S3	116.6	207.3	0.002*	+
	S4	165.7	161.9	0.006*	-
	S5	1170.5	904.4	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	200.94	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 = $\alpha/m = 0.05/7 = 0.00714$

[1]Coast areas were not relevant at stopover sites.[2]High resolution urban area data was not available for analysis at stopover site E

Table 8. Bonferroni confidence intervals calculated for land cover categories at stopover and wintering sites.

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

*Significant at $\alpha = 0.05$, with Bonferroni confidence intervals.

[1]At the wintering site (W), agricultural trees were not identifiable from the data; sparse trees was 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.

Site	Osprey ID	Within Protected Area (%) Observed	Expected	x^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 $\alpha = 0.05$

Figure Captions

Figure 1. Migratory tracks of five juvenile osprey: Blue44, BlueYZ, BlueYD, FR3 and FR4, originating from Scotland. Stopover and wintering sites identified and used to examine habitat preferences are shown.

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

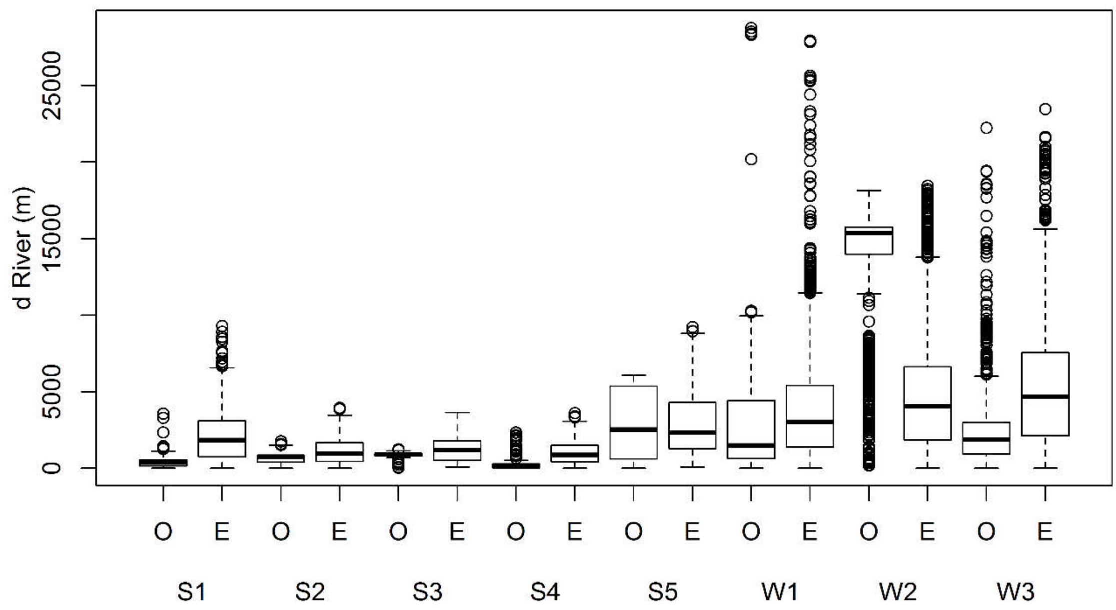
Appendix I: Aggregation of land cover classes.

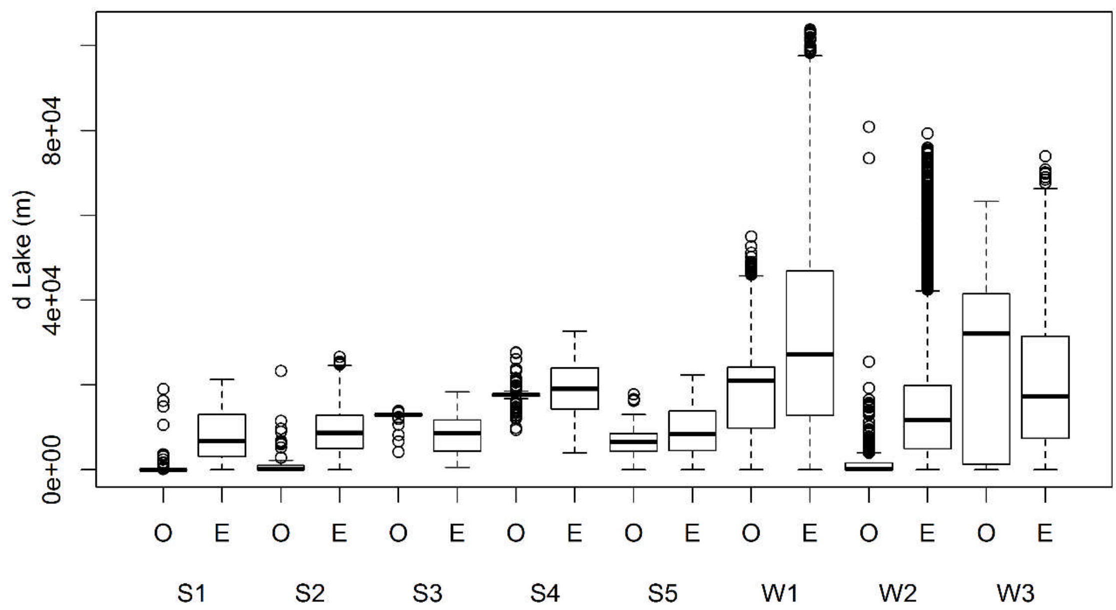
Corine (2006b) land cover categories for stopover sites in Europe	
Corine land cover category code and label	**Aggregated category**
111 Urban fabric 112 Urban fabric 121 Industrial, commercial and transport units 122 Industrial, commercial and transport units 123 Industrial, commercial and transport units 124 Industrial, commercial and transport units 131 Mine, dump and construction sites 132 Mine, dump and construction sites 133 Mine, dump and construction sites 141 Artificial, non-agricultural vegetated areas 142 Artificial, non-agricultural vegetated areas	Urban
311 Broad-leaved forest 312 Coniferous forest 313 Mixed forest	Forest
221 Vineyards 222 Fruit trees and berry plantations 223 Olive groves 244 Agro-forestry areas	Agricultural trees
511 Water courses 512 Water bodies 521 Coastal lagoons 522 Estuaries 523 Sea and ocean	Water bodies
211 Non-irrigated arable land 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	Open

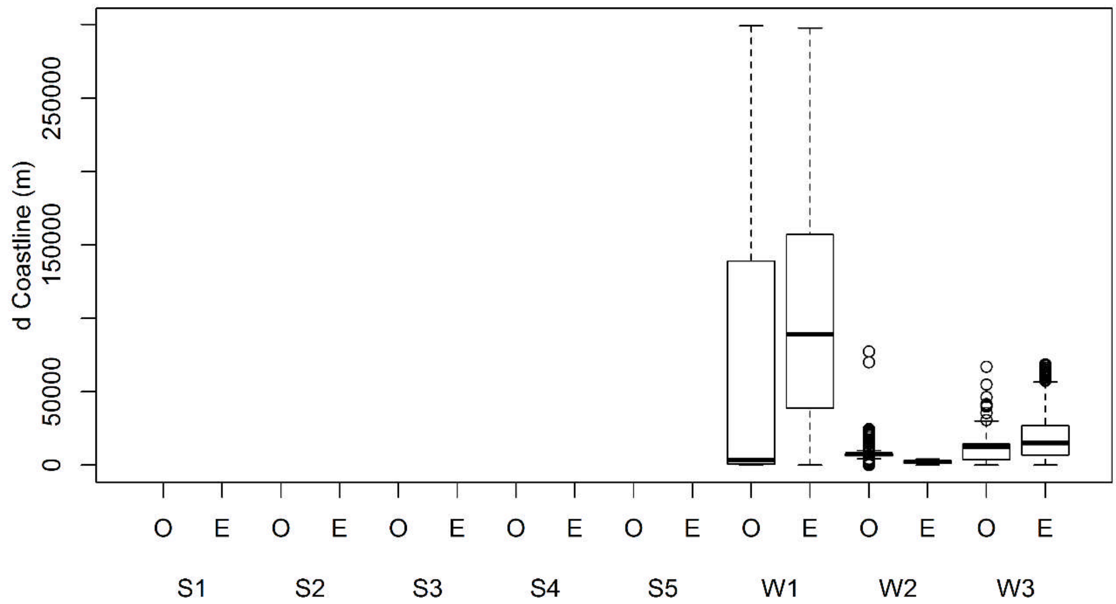
Aggregation of GlobeLand30 (National Geomatics Center of China, 2010) land cover categories for wintering sites in West Africa	
GlobeLand30 Category	**Aggregated category**
80 Artificial surfaces	Urban
20 Forest	Forests
40 Shrub lands	Sparse trees
60 Water bodies	Water bodies
10 Cultivated land 30 Grasslands	Open

50 Wetland 70 Tundra 90 Bareland 100 Permanent snow and ice	

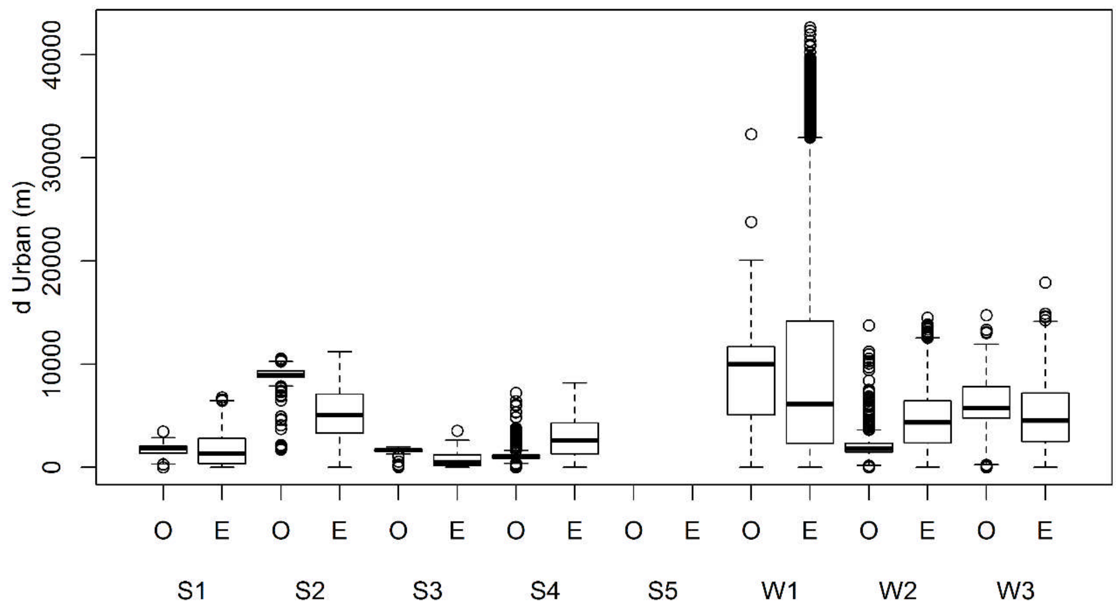
Appendix II: Boxplots showing the distribution comparisons for each stopover and wintering site, for each individual, for each continuous variable investigated. These can be used to assist in interpreting the results presented in Table 7 in the manuscript. Note that for the distance to minor roads vs distance to coastline, this was separate for stopover (distance to minor roads) and wintering (distance to coastline) periods. Also, there was no data to facilitate a distance to urban calculation for stopover 5 which occurred in Morocco.



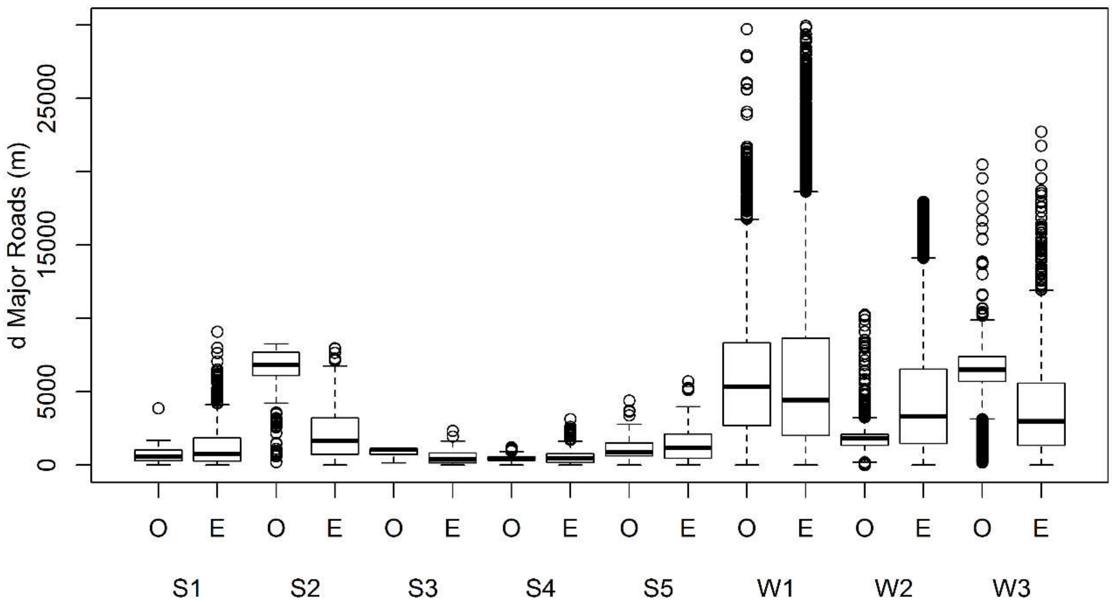


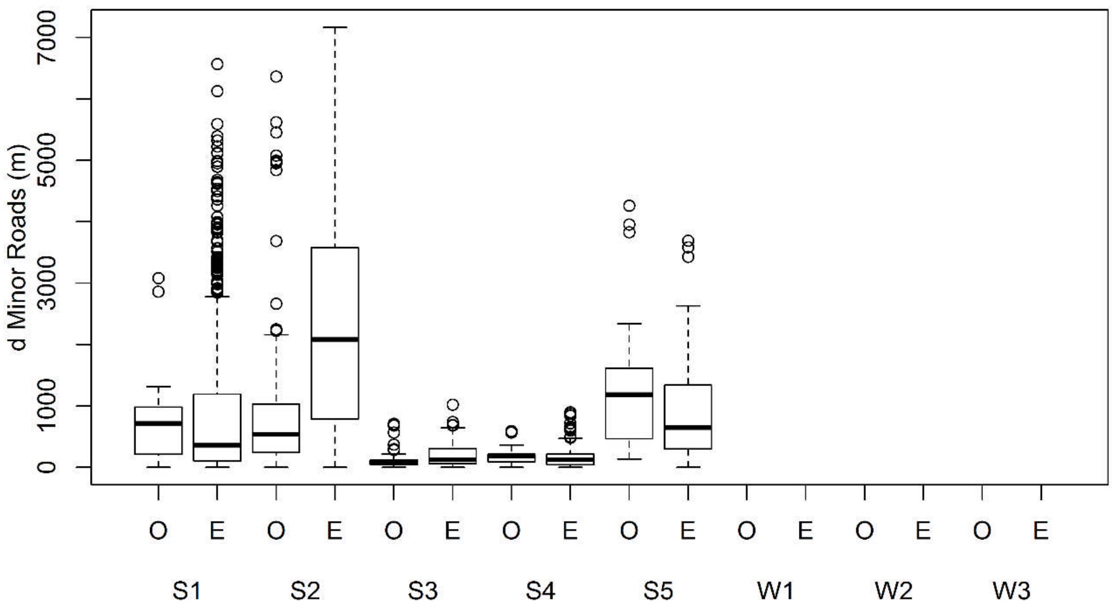


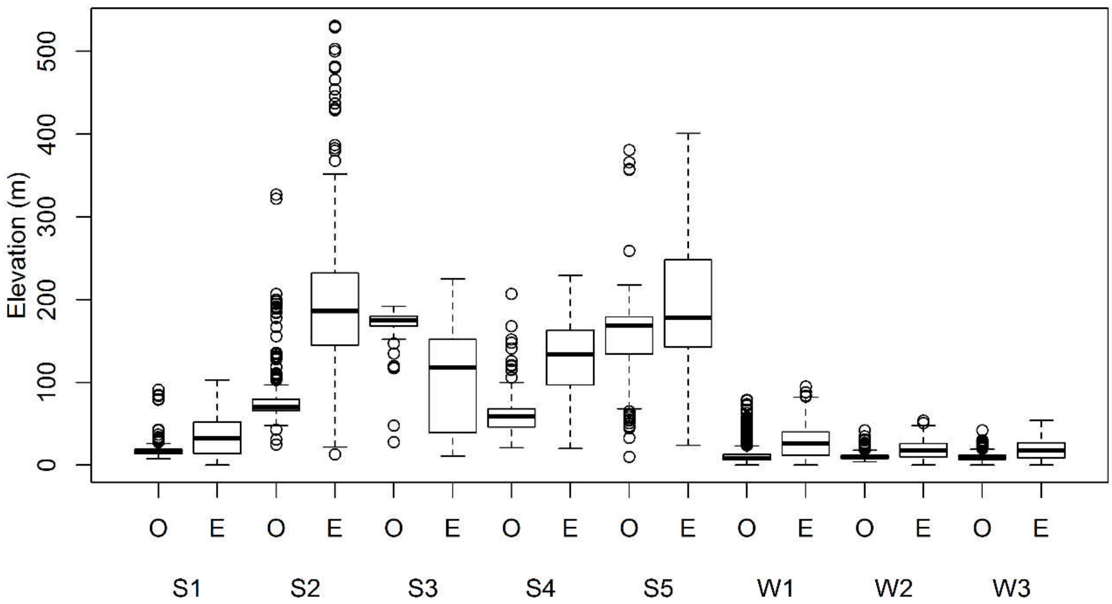
d Coastline (m)
0
50000
150000
250000
O
E
S1
S2
S3
S4
S5
W1
W2
W3

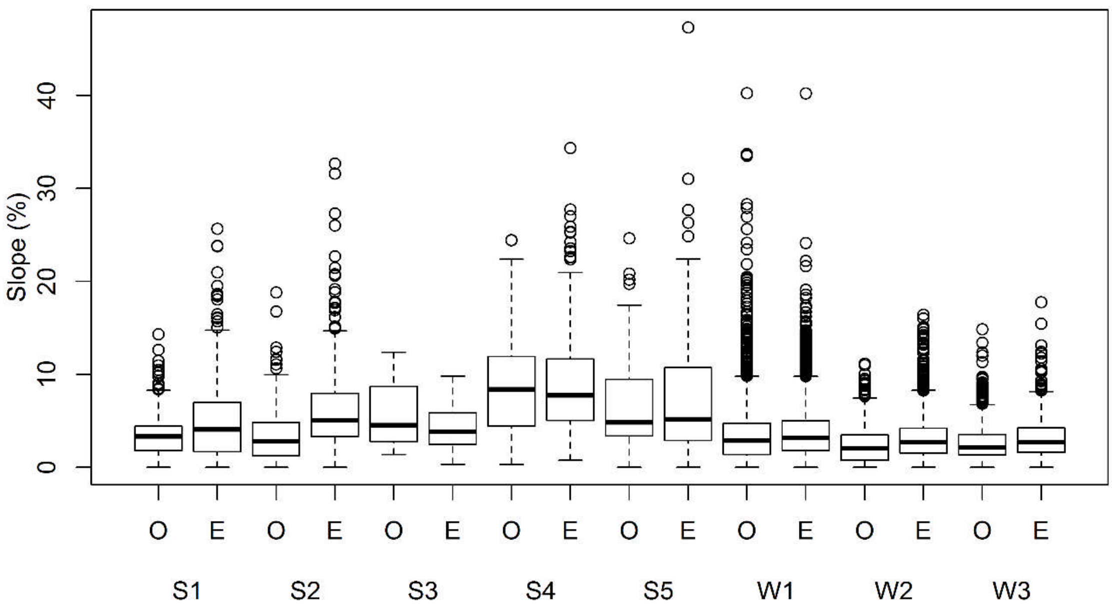


d Urban (m)
0
10000
20000
30000
40000
O
E
S1
S2
S3
S4
S5
W1
W2
W3


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