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## Individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Eurasian Curlews *Numenius arquata*

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### ABSTRACT

**Capsule:** Eurasian Curlews *Numenius arquata* were faithful to foraging and roosting areas on their coastal wintering grounds, including a habitat creation site. Home range sizes were greater at night than during the day, and showed high inter-individual variability which was not related to sex.

**Aims:** To examine factors affecting variation in the winter home range size of the largest European wader species: the near-threatened Eurasian Curlew *Numenius arquata*.

**Methods:** We examined individual, sexual and temporal (day/night, seasonal and annual) variation in the size of the home ranges of 18 GPS tagged Curlews captured at two sites on the Humber Estuary, UK.

**Results:** Home ranges were small (mean  $\pm$  SD = 555.5  $\pm$  557.9 ha) and varied slightly in size through the non-breeding season (September–March). We found some annual differences in home range size, and there was some evidence that home range size was greater at night compared to daytime. There was strong inter-individual variation in home range size, which was not related to the species' sexual size dimorphism and thus potential differences in resource use.

**Conclusions:** Our results highlight that wintering Curlews on the Humber Estuary maintain small home ranges which vary strongly between individuals. Knowledge of the home range size of wintering waders is vital to inform management responses to the potential impacts of environmental changes such as sea-level rise and improving the efficacy of compensatory habitats.

### ARTICLE HISTORY

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Wader populations are facing long-term declines because of the direct and indirect effects of human activities (Sutherland *et al.* 2012). The Numeniini, which include curlews and godwits, are the focus of both scientific research and conservation efforts because of rapidly declining trends across several flyways (Pearce-Higgins *et al.* 2017). This group contains 13 species, of which two are possibly extinct and several others endangered or threatened. In the United Kingdom (UK), the population and breeding range of the near-threatened Eurasian Curlew *Numenius arquata* (hereafter Curlew) have declined dramatically since the mid-1990s (Balmer *et al.* 2013, Brown *et al.* 2015, EBCC 2020, Harris *et al.* 2020). There is also evidence of declining trends in some parts of northwest Europe (EBCC 2020). In the UK, evidence points to low reproductive success as the likely demographic driver of these population declines (Brown *et al.* 2015). A large-scale analysis of Breeding

Bird Survey (BBS; jointly managed by the British Trust for Ornithology, the Joint Nature Conservation Committee, and the Royal Society for the Protection of Birds) data showed adverse effects of intensive agriculture, forestry, the increase in generalist predator populations, and climate warming on breeding Curlews (Franks *et al.* 2017). While UK birds are generally resident, the UK over-wintering population is inflated by the arrival of birds from Fennoscandia in winter, particularly along the east coast (Bainbridge & Minton 1978, Wernham *et al.* 2002). With an overwintering population of 120,000 Curlew, the UK plays a vital role in the species' conservation across the East Atlantic flyway. Numbers wintering in the UK increased during the 1980s, following the cessation of hunting, although they have declined since the 1990s, reflecting UK and European breeding population trends (Massimino *et al.* 2019, EBCC 2020). There has been evidence that wintering survival was reduced by mechanized cockle

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harvesting and hunting in North Wales, UK (Taylor & Dodd 2013). Recent analyses showed that increases in winter survival in some areas of the UK appeared to coincide with the hunting ban (Cook *et al.* 2021).

With increasing sea-level rise due to climate change, there has been considerable effort to create new intertidal habitats to compensate for the current and future losses of intertidal habitats in estuaries, but the approaches used remain in development and sites largely confined to northwest Europe (ABPmer 2021). In the process of managed realignment, farmland habitats adjacent to the estuary can be converted into intertidal habitats by lowering or breaching the sea walls (Esteves 2014). Managed realignment has proved to be a successful approach for the re-creation of intertidal habitats for waders (Atkinson *et al.* 2004, Mander *et al.* 2007, 2021). Where existing farmland is already extensively used by Curlews as a foraging ground, the effect of habitat creation can be a double-edged sword. Whilst suitable foraging terrestrial habitats (e.g. agro-ecosystems) are lost to the estuary, new intertidal habitats are created. Curlews predominantly feed on estuarine intertidal flats during the non-breeding season, but also use terrestrial fields. It has not been demonstrated whether all birds in a population use both intertidal and terrestrial habitats or if individuals specialize in certain habitat types. However, this information is crucial to understanding the balance in value between terrestrial and intertidal habitats, and determining the extent of the areas in which birds reside (i.e. home range), forage and rest, and the factors affecting this, is key. Measuring home range, which is used to define the vital space that an animal uses over a given time (Burt 1943), is important to many ecological studies. Knowledge of the use of space and habitat underpins effective conservation measures for a range of taxa (Zeale *et al.* 2012, Pop *et al.* 2018, Godet *et al.* 2018). In ecological modelling (e.g. using individual-based models: IBMs), assumptions about animal movements are often made using *a priori* information on space use and habitat use. Where IBMs are used to predict the effect of environmental changes and human activities on waders (Stillman *et al.* 2000), determining the home range size and making realistic assumptions about movements are needed to accurately predict the effect of environmental change on wader populations.

The foraging decisions that Curlews make on their wintering grounds aim to maximize their food intake rate to maintain their fitness (i.e. body condition and ability to survive) (Stillman *et al.* 2000). For example, waders may forage at night on intertidal flats if they have been unable to meet their daily energy

requirements during the day (supplementary feeding hypothesis of McNeil *et al.* 1992). Conversely, they may prefer foraging at night because it is more profitable or safer from predators (preference hypothesis of McNeil *et al.* (1992). The Curlew is one of a number of wader species that uses both intertidal flats and non-estuarine habitats to forage over the wintering period (Milsom *et al.* 1998, Navedo *et al.* 2013, Townshend 1981a). Non-estuarine habitats, such as coastal pasture close to intertidal areas, can be used as an alternative foraging ground or a supplementary foraging area (Navedo *et al.* 2013). For example, Curlews have the ability to feed in terrestrial habitats to supplement their diet when the intertidal habitats are covered at high tide. Alternatively, they may switch to feed in terrestrial habitats when it is more profitable to do so (Bowgen 2016). There is evidence from colour-ringing studies that individual Curlews within the same population may have different patterns of habitat use (Townshend 1981b), which could be driven in part by sexual dimorphism. Some waders, especially godwit and curlew species, exhibit differences between males and females such as bill length and body size (Van de Kam *et al.* 2004). Sexual dimorphism in Black-tailed Godwits *Limosa limosa* has been shown to drive spatial segregation on the intertidal flats in estuaries, linked to the accessibility of prey between individual males and females (Alves *et al.* 2013). From observations of colour-ringed birds, Townshend (1981a) found a difference in foraging habitat use and rate of foraging in cold weather between male and female Curlews, with longer-billed female Curlews preferentially foraging on intertidal flats and shorter-billed males on grassland.

To date, studies of the local winter movements of waders have been based on radio telemetry and/or ringing and colour-ringing. Such studies have been used to determine site fidelity, home ranges and the habitat preferences of several wader species (Leyrer *et al.* 2006, Taft *et al.* 2008, Lindström *et al.* 2010, Verkuil *et al.* 2010, Mittelhauser *et al.* 2012). Radio telemetry has also shown differences in the diurnal and nocturnal use of intertidal habitats (Burton & Armitage 2005, Leyrer *et al.* 2006). Recently, advancements in modern telemetry (e.g. global positioning system (GPS) tracking technology) have enabled researchers to follow waders for more extended periods and obtain data remotely. One such study, deployed GPS tags to follow a small sample of Curlews through their annual cycle, and their movements between breeding, staging, and overwintering sites, demonstrating the species' strong site-fidelity (Schwemmer *et al.* 2016), and confirming

findings of mark-recapture studies (Rehfishch *et al.* 2003). High-resolution GPS devices have also been recently used on Curlews to examine the factors affecting the timing of their departure from, and arrival at, their wintering sites (Schwemmer *et al.* 2021). Through GPS tracking there is potential to gain far more comprehensive information on the scale of animal space-use, i.e. an individual's home range size, through the day and night and across seasons. Whilst colour-marking studies have focussed on the influence of sexual dimorphism on Curlew movements (Townshend 1981a), home range variation in response to sexual dimorphism has not been examined. Furthermore, although GPS tags equipped with accelerometers have also been used to determine the behaviour of waders (van der Kolk *et al.* 2019), studies have not evaluated behaviour from the GPS data alone. It is possible to infer bird behaviour from path track characteristics (e.g. step length and the angle of direction) using state-space models, such as Hidden Markov models (HMMs); these approaches have been used extensively to identify the behaviours of seabirds (Dean *et al.* 2013, Trevail *et al.* 2019, Zhang *et al.* 2019).

Here, we assess individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Curlew wintering on the Humber Estuary Special Protection Area (SPA), and use GPS tracking data alone to examine the main pattern of activity. We hypothesized that (i) home range size may change through the non-breeding season as a function of resource depletion and (ii) between winters, reflecting changes in resource availability. Home range size may increase in response to prey depletion on intertidal flats which may force the birds to explore other patches. We also hypothesized (iii) that home range size may be driven by individual strategies related to sexual dimorphism, and thus that home range sizes may differ between males and females. We further hypothesized that (iv) home range might be smaller at night because of the greater risk of predation in intertidal and terrestrial habitats.

## Methods

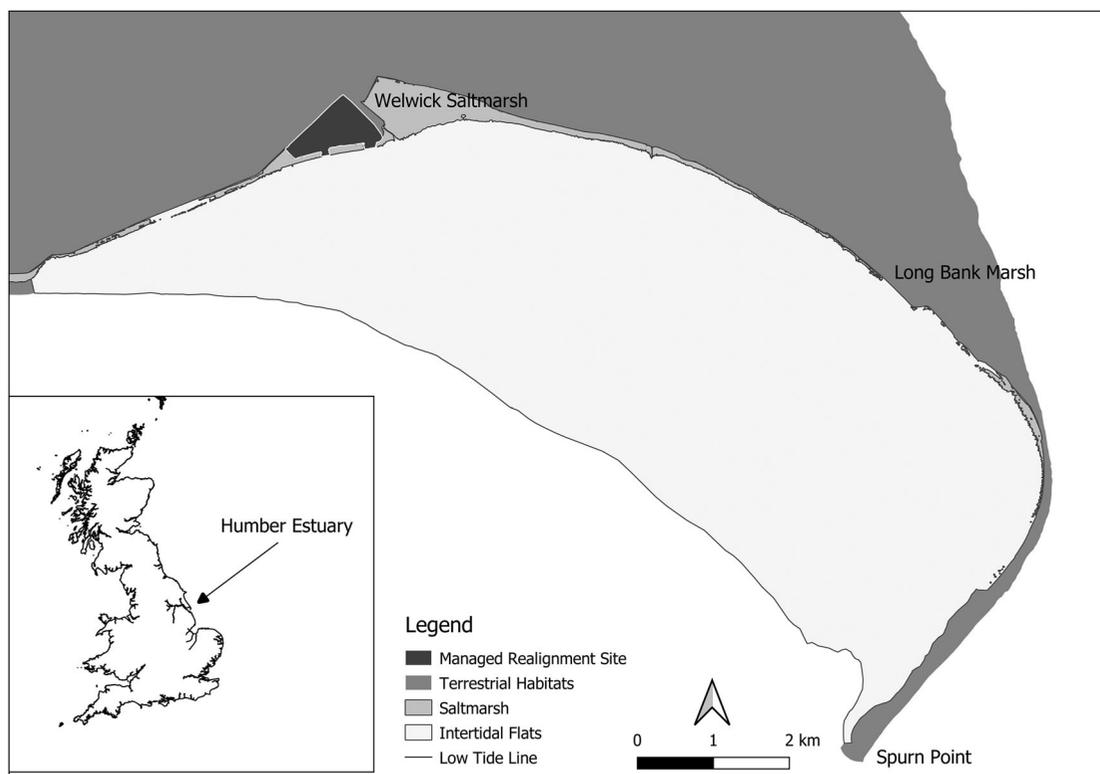
### Catching and GPS tagging Curlew

The work was carried out at two sites on the Humber Estuary: Welwick Saltmarsh (53.64°N 0.02°E), which is contiguous to the Welwick managed realignment site (53.64°N 0.00°E), and Long Bank Marsh (53.62°N 0.12°E) (Figure 1). The Welwick managed realignment site was created in 2007 through a breach of the flood defence. The 54 ha site was designed to offset the loss

of habitats due to port development in the Humber Estuary. Adult Curlews are present on their wintering sites, such as the Humber Estuary, from early July to mid-April (Frost *et al.* 2021, pers. obs.). According to the Wetland Bird Survey (WeBS), 2787 Curlews (latest five-year average) overwinter in the Humber Estuary (Frost *et al.* 2021). Long Bank Marsh and Welwick Saltmarsh (including the managed realignment site) support regular roosts of approximately 300 and 700 individuals, respectively (Mander & Stone 2020, Spurn Bird Observatory 2022,). Curlews were caught in the winters of 2015/2016, 2017/2018, 2018/2019 and 2019/2020, between late September and late February. At the Welwick Saltmarsh site, Curlews were caught using mist-nets set in saltmarsh pools, used as night-time roosts. At Long Bank Marsh, a wet grassland with standing water used by roosting birds, birds were caught using mist-nets at night and with cannon nets at dawn. Twenty-two Curlews were captured over nine catches across the four winters (online Table S1). Aging of the Curlews was based on plumage characteristics as described in Baker (2017). The bill-length (mm), wing-length (mm) and body mass (g) of all individuals were measured and the sex of adult birds determined based on the bill-length equation derived by Summers *et al.* (2013). Adult birds were positively assigned to a sex category (male or female) when their biometrics placed them above a probability threshold of 95%. Five males, eight females, five adult birds of unassigned sex, and four first-winter birds were included in the sample of 22 birds (Table S1).

All birds caught were fitted with a numbered metal-ring, a unique set of colour-rings for subsequent re-identification in the field, and a GPS/UHF tag. The Pathtrack nanoFix® GEO + RF tag used nano Fix® technology with low power UHF technology (Pathtrack, Otley, UK) for downloading data to a base station. To test their accuracy, eight of the tags were activated prior to deployment to record hourly GPS position for a period of up to 24 h. The tags were placed at a height of approximately 0.20 m above ground in a range of habitats (e.g. bare ground, exposed mud in small pools, low saltmarsh vegetation and high saltmarsh vegetation) across the upper shore. The mean ( $\pm$  SD) distance between observed and actual location of the tags was  $25 \pm 13$  m. According to the manufacturer, GPS xy position for these tags has an error of up to 20 m in good conditions (G. Brodin, PathTrack pers. comm.).

The GPS/UHF tags were glue-mounted to feathers (trimmed to 5 mm) on the back of birds, between the scapulars (following Warnock & Warnock (1993)). Glue-mounting was preferred over the use of



**Figure 1.** Study site showing the capture sites at Welwick Saltmarsh and at Long Bank Marsh.

harnesses for welfare reasons. While the use of harnesses may provide long-term data over different stages of birds' annual cycles, their use may potentially have impacts on the birds' condition, breeding success or even survival, depending on the method used and species (Geen *et al.* 2019). In contrast, there appears to be little if any long-term effect from glue-mounted devices which fall off at, or prior to, the next body moult. Long-term deployments beyond the wintering period were not required for this study, but at least one individual was observed without its tag three months after deployment. The tags were set to record the position of the bird every 90 min and to attempt to download data to a base station in the field every 60 min, using a one-way remote UHF data communication. This sampling regime gave an expected battery lifespan of at least 28 days (and 448 fixes) for tags deployed in 2016, which covered two spring-neap-spring tidal cycles. Battery lifespan increased to at least 56 days (896 fixes) from 2017 as a result of manufacturing improvements. However, we found that battery lifespan declined if the deployment was delayed for more than a year from manufacturing, resulting in a reduction in the number of fixes obtained for six individuals. Base stations were positioned within 200 m of the roosts and were checked weekly to retrieve the data and ensure regular downloads. All tags successfully downloaded fixes to

the field-based base stations, with the exception of one tag deployed at the Welwick Saltmarsh for which no data fixes were recorded. The tags weighed between 4.9 and 5.1 g which was below the 1% threshold of the mean ( $\pm$  SD) body mass of known females and males captured in our study, respectively 922 ( $\pm$  65 g) and 792 ( $\pm$  77 g). Ringing and GPS tagging activities were undertaken under licence from the Special Methods Technical Panel of the British Trust for Ornithology. All fieldwork activities were subject to ethical approval from the University of Hull.

### Home range estimation

All analyses were carried out using R software version 3.6.0 (R Core Team 2019). Comparing estimates of home ranges between studies can be problematic due to differences in data collection and analytical methods. Here, therefore, we initially explored two approaches – Kernel Density Estimator (KDE) and Kernel Brownian Bridge (KBB); techniques that are described in the 'adehabitatHR' package (Calenge 2019). The KDE is a commonly applied home-range estimator in which a kernel distribution (i.e. three-dimensional hill or kernel) is placed on each location. An estimation of the Utilisation Distribution (UD) is then generated across the area of interest (Worton 1989). The calculation of the UD is sensitive to the

bandwidth selection (i.e. smoothing parameter) of the kernels, which determines the resolution of the UD. Errors resulting from over-smoothing or under-smoothing can occur when estimating home-range sizes. There are standard methods to compute the smoothing parameter: ‘reference bandwidth’ and Least Square Cross Validation (LSCV). As individual Curlews can spend several hours at the same position while roosting at high tide, many duplicate fixes in the data prevented the use of the LSCV. Instead, the smoothing was determined by a ‘reference bandwidth’.

The Kernel Brownian Bridge approach is an extension of the KDE method which considers the time dependence between successive locations. The Kernel Brownian Bridge method places a kernel function above each step (a straight line connecting two consecutive locations). As a result, the Brownian Bridge is conditioned by the start and end time of the step, the animal’s speed and the precision of the tag (Horne *et al.* 2007). Therefore, the Brownian movement model requires the input of sig1: a first smoothing parameter related to the speed of animals; sig2: a second smoothing parameter related to the imprecision of the location data. Sig1 was estimated from the data using a maximum likelihood estimate with the ‘liker’ function in the package *adehabitatHR* (Calenge 2019). Sig2 is similar to the smoothing parameter *h* of the classical kernel method, and is therefore related to the imprecision of the relocations (i.e. the spatial resolution of the tag).

Of 22 individuals GPS tagged, core (50%) and total (90%) home ranges were estimated for a total of 18 individuals with data collected using an identical sampling regime (one fix for every 90 min) but with a varying sampling duration. We excluded three individuals from the analysis for which fewer than 224 fixes were obtained (less than 14 days), and one individual for which no movement data were obtained from the tag. A mean of 691 fixes (range = 260–1115) was obtained for the 18 individuals, equating to a period of 43 days (range = 16–69) (Table S2). There were no significant differences in core range sizes (one-way Anova,  $F_{1,34} = 2.744$ ,  $P > 0.05$ ) or total home range sizes (one-way Anova,  $F_{1,34} = 1.18$ ,  $P > 0.05$ ) between the two estimators. Because the two approaches provided similar estimates of both core (50%) and total (90%) home ranges, we chose to use the KDE to examine space use and variation in home range size.

### Habitat use

We examined the proportions of different habitats in core and total home ranges for individuals captured at Long

Bank Marsh ( $n = 4$  individuals) and Welwick Saltmarsh ( $n = 14$  individuals). Individual core (50%) and total (90%) home ranges were calculated using the Kernel Density Estimator (KDE). Using open-source layers on saltmarsh extent from [environment.data.gov.uk](http://environment.data.gov.uk), and boundary-lines for high and low tide from [digimap.edina.ac.uk](http://digimap.edina.ac.uk), we determined the extent of broad habitat types in QGIS. Boundary-lines of the managed realignment site were sourced from Associated British Port (ABP). Broad habitats were categorized into four categories. The land behind the sea defences which bordered the study area was classed as the ‘terrestrial habitat’. Terrestrial habitat was dominated by arable land with rotation and, therefore, crops were likely to change between winters. Some fields were left fallow in winter 2019/2020 due to preparation work for two proposed additional managed realignment sites near the Welwick Saltmarsh. Three broad habitat types were identified on the intertidal areas: ‘intertidal flats’, ‘saltmarsh’, and the ‘managed realignment site’, the latter created in 2007 through the breaching of flood defence. We calculated for each individual the proportions of core and total home ranges which overlapped with broad habitat types. Finally, we averaged the proportions of different habitats in core and home range for individuals captured at Long Bank Marsh and the Welwick Saltmarsh.

### Examining factors driving home range size

We examined the factors affecting variation in home range size by producing total (90%) KDE home range estimations for periods of 14 days, starting from the highest spring tide and finishing on the subsequent highest spring tide in the next spring tidal cycle. This standardization enabled us to account for the effect of the variation of the tidal amplitude. Home range estimations were produced for day and night – based on civil twilight – and calculations were made using the R package ‘*suncalc*’. A total of 48 periods (each 14 days) were considered in the analysis for 18 individuals. The home range estimation from the KDE method was used as a dependent variable in a generalized additive model (GAM) (‘*gam*’ function in *mgcv*) that evaluated the influence of date (number of days from 1st September), diurnal cycle (day/night), age/sex, winter and site. Number of days from 1st September was included as a predictor using thin-plate regression splines as a smoothing function (Wood 2003). The date was calculated from the 1st September for the start of each 14 days period. Diurnal cycle, age/sex, winter were included as fixed effects, while individual identity (ID) was included as

a random effect. Although we could not properly assess annual changes, given that individuals were ‘nested’ within year, we included winter of capture as a fixed-effect in the model. Following assessment of residual diagnostics using simulated residuals (DHARMA package, Hartig & Lohse 2021) we chose to use a Gamma distribution to model home range size. We found no evidence of auto-correlation ( $DW = 1.8543$ ,  $P = 0.4691$ ) or over-dispersion (dispersion = 0.86236,  $P = 0.76$ ) in the simulated residuals. The full model is presented with each term assessed on level of significance.

### Determining movement behaviour

We used a HMM to identify the movement behaviour of Curlews using the package `move` ‘HMM’ in R (Michelot *et al.* 2016). We used a two-states model with state 1 defined as ‘roosting’ and state 2 defined as ‘other’ behaviour (including travelling and foraging). We used the gamma structure for the step length, the turning angle distribution was von Mises and we employed the Viterbi algorithm to define the states (Michelot *et al.* 2016). Tidal height (as metres above chart datum) was incorporated as a covariate in the model. Tide height data for Immingham were sourced from the British Oceanographic Data Centre (BODC) at a 15 min interval which matched with our GPS sampling frequency. Model fit was assessed through inspection of pseudo-residuals. Both pseudo-residuals of step and angle were tested for normality using the Jarque–Bera tests for normality.

The daytime feeding intensity of Curlews was measured to verify the HMM predictions. Monthly scan sampling was undertaken over a half-tidal cycle between October 2019 and March 2020 at the Welwick managed realignment site which supports roosting Curlew flocks, and on the fronting intertidal flats where the birds foraged. Scan sampling was also undertaken on nearby agricultural land, which supported Curlew flocks of 100 or more individuals over the winter of 2019/2020 to account for the field feeding activity. We recorded individual bird behaviour (categories: foraging, roosting and loafing/preening) every 20 min. Scan sampling was undertaken at least twice per month, and covered rising and falling tides during spring and neap conditions to account for the variability in feeding intensity over a range of tidal heights. On rising tides, scan sampling started at low tide when the mudflat fronting the realignment site was fully exposed and finished at high water when the tide covered the area, and all birds had joined the roost in the realignment

site. Conversely, on falling tides, scan sampling covered the high to low water period and finished when the mudflat was fully exposed. The percentage of time spent foraging (number feeding/total numbers) was averaged across the scan samples collected ( $n = 147$ ) during the available feeding period.

## Results

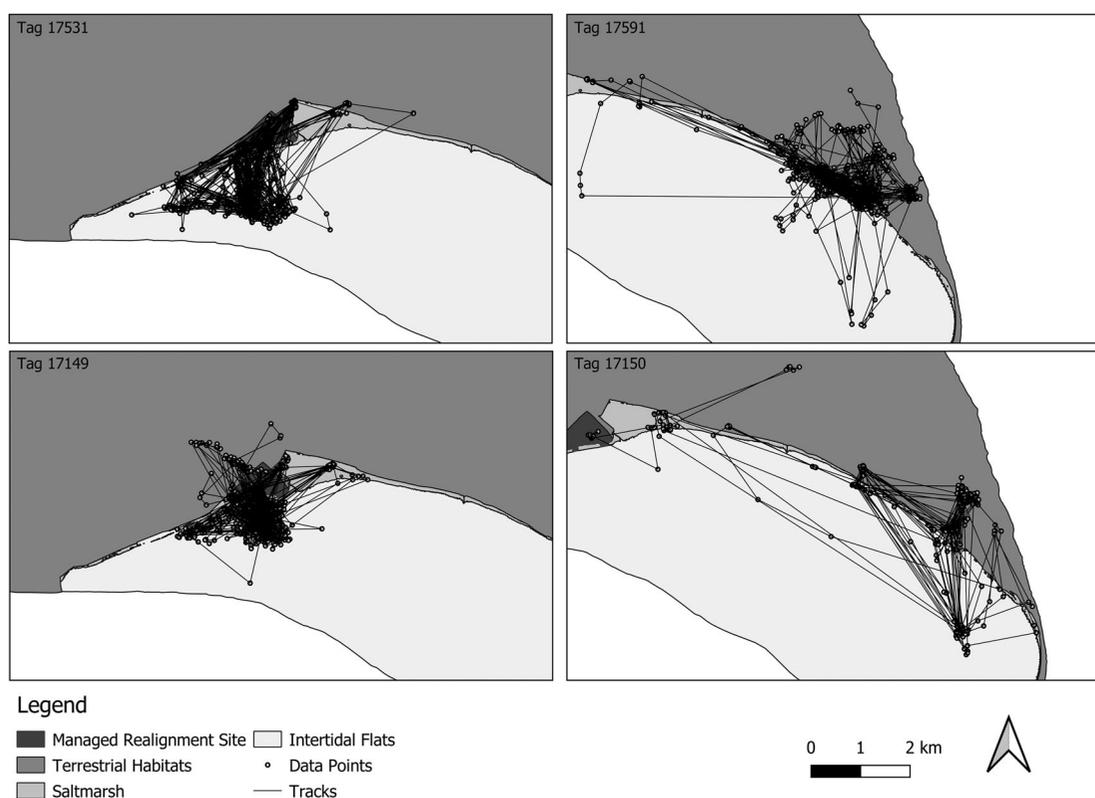
### Feeding and roosting-site fidelity

Movement data of all 17 Curlews captured and tagged at the Welwick Saltmarsh are presented. All individuals were faithful to the area during the non-breeding season (Figure 2; Figure S1). In four winters of tracking, individuals did not switch roosts and remained faithful to their foraging areas on adjacent intertidal flats. While Curlews used the Welwick Saltmarsh and the re-created intertidal areas of the Welwick realignment site to roost, they predominantly fed on the intertidal flats and in fields immediately contiguous to the Humber Estuary. Very occasionally individuals were tracked in farmland habitats up to 3.5 km from the shoreline (Figure S1). Six individuals only used intertidal habitats, while the remaining 11 individuals made movements between the intertidal and terrestrial habitats.

In two winters of tracking, the four Curlews captured and tagged at Long Bank Marsh were predominantly site-faithful to their roosting site, but three individuals switched roosts intermittently to Welwick Saltmarsh and adjacent fields (Figure 2; Figure S1). For one bird (Tag 17150), the switch coincided with an exceptional cold weather event in March 2018. Two further birds (Tag 17582 and Tag 17590) captured in January 2020 regularly switched roosts to the Welwick Saltmarsh site through February and March 2020, predominantly using fields that had been flooded following periods of heavy rain. Inland movements were more prominent in individuals captured at Long Bank Marsh, with fields within 2 km from the intertidal flats regularly used (Figure S1). All four individuals made movements between the intertidal and terrestrial habitats during the non-breeding season.

### Home range size estimates

Core (50%) and (90%) home ranges were estimated for a total of 18 individuals for which there were sufficient data. Both core (50%) range and total (90%) home range sizes varied markedly between individuals. For example, the estimated total home range size produced with the KDE varied between 60.0 ha (260



**Figure 2.** Example of GPS tracks of wintering Curlew captured at Welwick Saltmarsh (tag 17531 and tag 17149) and Long Bank Marsh (Tag 17591 and Tag 17150).

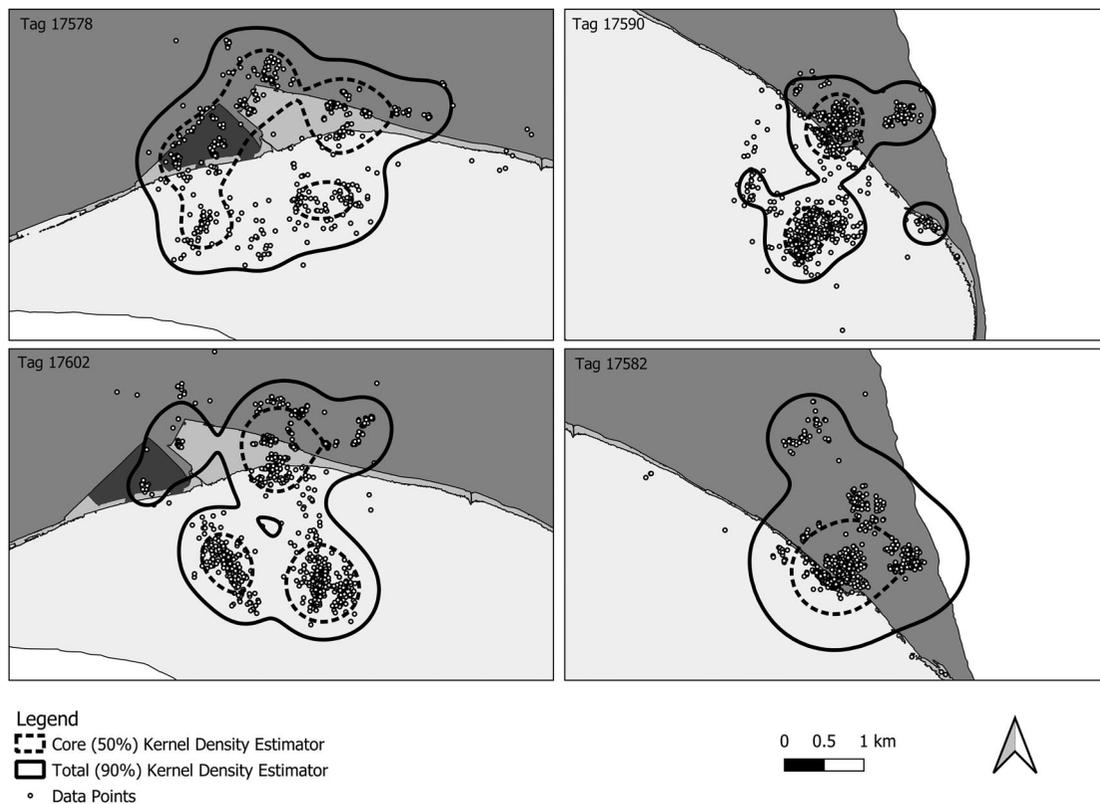
fixes) and 802.3 ha (521 fixes). The average home range size was 555.5 ha (691 fixes) and 76.1 ha, respectively, at the 90% and 50% level (Table S2). Examples of the spatial extent of the Curlew home ranges are given in Figure 3.

### Habitat use

The proportions of different habitats in core and total home ranges varied between the capture sites, i.e. Long Bank Marsh ( $n=4$  individuals) and Welwick Saltmarsh ( $n=14$  individuals) (Table 1). The home ranges of individuals captured and tagged at the Welwick Saltmarsh predominantly overlapped with the intertidal flats of the Humber Estuary, and Curlews showed little use of the terrestrial habitat, with respectively 15% and 17% of their total home and core ranges overlapping with this habitat. By contrast, individual GPS tagged Curlews from Long Bank Marsh made more extensive use of the terrestrial habitat (Table 1). This habitat made up 55% and 52% of their core and total home ranges, respectively. Long Bank Marsh, which is a wet grassland with standing water, is a key roost for Curlews on the outer Humber Estuary.

### Individual, age/sex and temporal variation in home range size estimates

Results of the full model that included all factors affecting variation in estimated total (90% KDE) home range sizes (ha) of wintering Curlews are shown in Table 2. The full model explained 56.1% of the deviance. The estimates from this model indicate that total (90% KDE) home range sizes were typically greater during the night than during the day. No evidence was found for a difference in ranges between sites. There was, however, a difference between years, with smaller home range sizes found during the third winter of tracking. Variation in home range sizes across individuals (and thus between sexes and winters) and between the day and night is shown in Figure S2, with example of individual movements shown in Figure S3. There was a slight relationship between the number of days since the start of the wintering season and home range sizes, suggesting that home range sizes slightly decrease through the non-breeding season (Figure 4). We rejected the hypothesis that home range size was linked to sexual dimorphism: we could not identify any differences in home range size between adult males, adult females, adult birds of unassigned sex, and first-winter birds.



**Figure 3.** Examples of Kernel Density Estimator (KDE) estimated core (50%) and total (90%) home range sizes for individual Curlews captured at Welwick Saltmarsh (Tag 17578 and 17602) and Long Bank Marsh (Tag 17590 and 17582).

### Movement behaviour

HMMs distinguished two distinct behaviour modes, which equated to resting (overall mean  $\pm$  sd step length:  $20.8 \pm 14.9$  m) and other behaviours ( $579.6 \pm 660.0$  m). According to the most likely state sequence under the fitted model, Curlew spent 22% of their time resting and 78% engaged in other behaviours. At night, Curlew spent 31% of their time resting versus 13% of the time during the day. This means that a greater proportion of Curlews were undertaking other behaviours in the daytime, presumably foraging. Visual observations carried out across the intertidal flats (including the managed realignment site) and the terrestrial habitats between October 2019 and March 2020 indicated that Curlews spent 62% of the time foraging during hours of daylight. As expected, the visual observations indicated the proportion of foraging Curlews varied during the tidal cycle. The median was below 70% around 2 h on either side of

high water, but there was considerable variation in the range of values. By contrast, there was little variation three hours on either side of low water with a median between 80% and 100% (Figure 5).

### Discussion

Our understanding of the habitat and space use of non-breeding waders that is needed to set effective conservation measures is limited. Here, we focus on the space use of the near-threatened Curlew, which uses both intertidal and terrestrial habitats of estuaries in winter. Previous work has documented that Curlews are very faithful to roosting areas during the non-breeding season (Rehfishch *et al.* 2003, Schwemmer *et al.* 2016) and are known to make extensive use of land surrounding the estuary, especially coastal grasslands (Townshend 1981a, Milsom *et al.* 1998, Navedo *et al.* 2013). We examined individual, sexual

**Table 1.** Percentage of averaged Curlew home ranges overlapping with broad habitat types (range is given in brackets).

Capture Site	Home Range	Terrestrial Habitat	Realignment Site	Saltmarsh	Intertidal Flats
Welwick Saltmarsh	Core	15% (0–53)	17% (0–36)	16% (5–38)	52% (0–75)
	Total	17% (5–38)	13% (4–25)	17% (8–39)	52% (31–64)
Long Bank Marsh	Core	55% (43–68)	0% (0–0)	1% (0–3)	43% (31–57)
	Total	52% (38–65)	0% (0–2)	7% (2–12)	41% (24–59)

**Table 2.** Model coefficient estimates for the full model assessing factors affecting variation in estimated total (90% KDE) home range sizes (ha) of wintering Curlew. Standard errors, *t*-values and *P* for the MGCV GAM.

Parameter	Estimates	SE	t value	<i>P</i>
Intercept	6.55	0.46	14.41	0.001
Nycthemeral (night)	0.21	0.10	2.08	0.040
Site (Welwick Saltmarsh)	-0.54	0.37	-1.45	0.150
Winter 2	-0.12	0.42	-0.28	0.779
Winter 3	-1.42	0.47	-2.99	0.003
Winter 4	-0.33	0.34	-0.95	0.344
Adult (male)	-0.05	0.32	-0.16	0.869
Adult (unassigned)	0.23	0.35	0.67	0.504
First Winter (unassigned)	0.67	0.36	1.87	0.065
Smoother	df	F	<i>P</i> -value	
S(days)	1	6.727	0.011	
S(id)	6.39	4.631	0.001	

and temporal (day/night, seasonal and annual) variation in the home range size of 18 Curlews tagged over four winter seasons at two sites on the Humber Estuary, UK. To our knowledge, this is the first study to investigate the variation in home range size of Curlews throughout the non-breeding season.

### Seasonal and annual variation

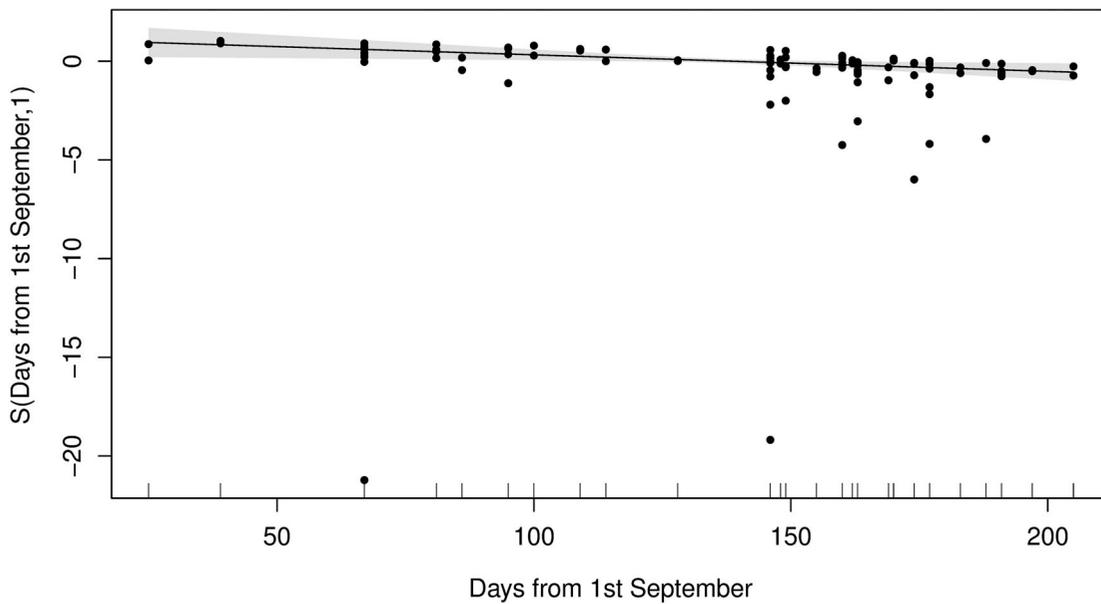
We hypothesized that home range size may change through the non-breeding season as a function of resource depletion on the intertidal flats. We detected only slight variation in home range size through the winter period. There were, however, small annual differences in home range size, but it must be acknowledged that we tracked different individuals in each winter, at different times during those winters. The numbers of birds tagged per winter were variable and dependent on successful catches. For most birds, home range size varies through the annual life cycle and food availability regulates home range dynamics (Rühmann *et al.* 2019), however, variation in home range size during the non-breeding season has not been well studied in wader populations. Townshend (1981a) found seasonal changes in the use of tidal flats and terrestrial habitats by individual colour-ringed Curlews wintering on the Tees Estuary, UK. In radio-tracked Western Sandpipers *Calidris mauri*, Warnock & Takekawa (1996) found no evidence of seasonal variation in overall home range size through the winter and spring in the San Francisco Bay Estuary, USA, but core areas were smaller in spring than in early or late winter. In our study, the lack of expansion or retraction of the home range in winter is likely to reflect the high quality of resources on the intertidal habitats.

Despite being the largest European shorebird, our study shows that Curlews occupied very small home

and core ranges in comparison with waders of lower body mass. Smaller wader species such as Red Knot *Calidris canutus* may occupy larger home ranges, and show large variability in wintering home range size along the East Atlantic Flyway. Although core and home ranges were not calculated in the following studies, the size of area used by radio-tagged Red Knots ranged from 1600 ha or less at a tropical wintering area along the Sahara coast, the Banc d'Arguin, Mauritania (Leyrer *et al.* 2006) to 80,000 ha in the Western Wadden Sea, The Netherlands (Piersma *et al.* 1993). Radio-tracking studies found large home ranges for Dunlin *Calidris alpina*, with home range calculated as a 95% Minimum Convex Polygon (MCP) or fixed kernel 95% Utilisation Distribution (UD) varying between 1290 and 56,500 ha depending on geographical areas and habitats (Sanzenbacher & Haig 2002, Shepherd & Lank 2004, Taft *et al.* 2008, Choi *et al.* 2014). Within the Numeniini group, there is evidence of small (<600 ha) feeding core ranges (KDE) for GPS tagged Bar-tailed Godwits *Limosa lapponica* ( $n=6$ ) (Jourdan *et al.* 2021). In comparison, our study found the mean core range to be even smaller for Curlews (<100 ha). Among other species of Curlew, the home range (95% Minimum Convex Polygon) of a single radio-tagged Long-billed Curlew *Numenius americanus* was estimated to be 2441 ha along the Gulf of Mexico, Florida, USA (Gabbard *et al.* 2001). In our study, only one individual had a home range size exceeding 2400 ha (90% KDE) and mean ( $\pm$  sd) home range size was  $555.5 \pm 557.9$  ha. Although there is an allometric relationship between home range size and body mass in mammals (McNab 1963) and such relationships also exist in birds (Newton 1979, Ottaviani *et al.* 2006), the relationship may differ between the non-breeding and breeding season.

### Variation in relation to sexual dimorphism

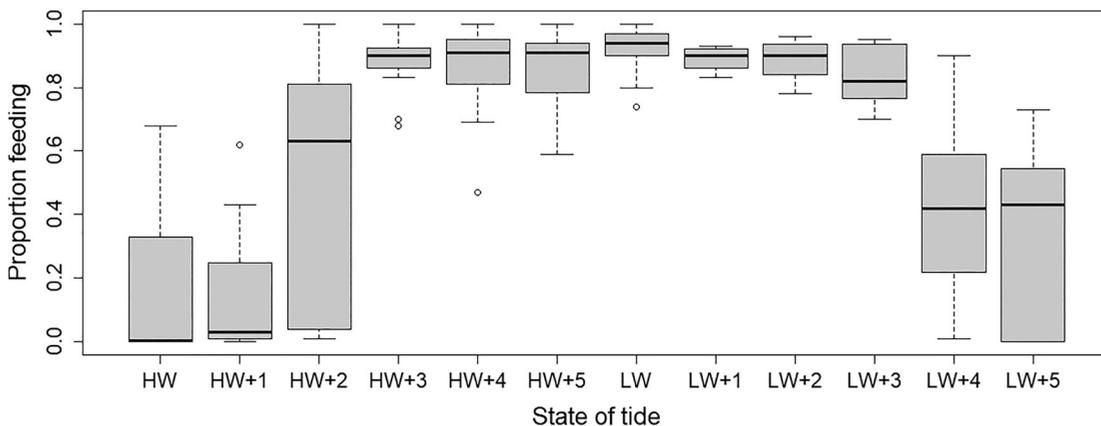
We also hypothesized that home range size may be driven by individual strategies related to sexual dimorphism, and thus that home range size may differ between males and females. In our study, the sex of adult Curlews did not account for variability in the home range size at the individual level. During the non-breeding season, intersexual competition in dimorphic wader species, such as godwits, drives small-scale spatial segregation on tidal flats (Alves *et al.* 2013, Both *et al.* 2003), which might result in differences in home range. Townshend (1981a) found colour-ringed male and female Curlews to distribute differently between terrestrial and intertidal habitats.



**Figure 4.** The relationship between (90% KDE) home range sizes (ha) of individual wintering Curlews and date within the winter (days from 1st September) as shown by GAM smoothing temporal terms (line) fitted to centre of gravity data. Shaded area and points represent pointwise confidence bands (SE) and partial residuals respectively.

Males moved to fields in winter because of decreasing feeding rates on tidal flats, resulting from the decreased availability of *Nereis* worms (Townshend 1981a). Rolando (2002) argued that food availability is the only true factor controlling home range ecology in birds, and that intraspecific competition cannot be considered as a controlling factor. To maximize their access to resources and reduce intraspecific competition on the intertidal flats, waders adopt different feeding strategies, typically either actively defending a feeding territory or moving in flocks while maintaining their distance from other individuals to reduce interference competition (Goss-

Custard 1980, Van de Kam *et al.* 2004). Territoriality has been observed in Curlews during the non-breeding season (Ens 1979, Ens & Zwarts 1980, Townshend 1981b, Colwell 2000, Colwell & Mathis 2001). Although we did not detect difference between males and females in our study, the high inter-individual variation in home range size observed may reflect feeding strategies (e.g. territoriality) or individual specialization (Durell & Dit 2000). Individual variation makes populations and species less susceptible to environmental changes, and contributes to promoting ecological success (Forsman & Wennersten 2016).



**Figure 5.** Medians representing the proportion of wintering Curlews foraging across the tide during the day, as derived from monthly scan sampling undertaken over a half-tidal cycle between October 2019 and March 2020 at the Welwick realignment site, on the fronting intertidal flats and adjacent terrestrial fields.

### Diurnal variation

We hypothesized that home ranges might be smaller at night because of the greater risk of predation. Although the nocturnal activity of waders has been investigated using radio telemetry (Burton & Armitage 2005) and more recently using GPS tags (Jourdan *et al.* 2021), little is known about the nocturnal home range of Curlews in winter. Our study provided evidence that nocturnal ranges were greater than diurnal ranges, although there was much individual variation. Differences in the nocturnal and diurnal use of feeding and roosting areas by wintering waterbirds may be linked to the density/activity of prey, disturbance and predation (Sitters *et al.* 2001, Piersma *et al.* 2006). Burton & Armitage (2005) found that individual wintering Common Redshanks *Tringa totanus* had larger home ranges at night than during the day. However, that study focused solely on the areas used during the intertidal foraging period. In contrast, Jourdan *et al.* (2021) found that nocturnal feeding core areas of Bar-tailed Godwits to be even more restricted and mostly spatially distinct from the daytime ones on the tidal flats. Whilst there was evidence that nocturnal ranges were greater, we did not investigate habitat use in relation to diurnal cycle. As Curlews feed by sight and touch (Davidson & Evans 1986), the difficulty in visually detecting earthworms – the primary food source for Curlews in coastal grassland (Navedo *et al.* 2020) – might influence the use of terrestrial fields at night. As artificial illumination has a positive effect on the nocturnal foraging of wader (Santos *et al.* 2010), lunar phase may also influence nocturnal foraging activity in terrestrial habitats. Using GPS data alone we found Curlews spent 22% of their time resting and 78% engaged in other behaviours during the non-breeding season, but only 69% of their time feeding at night compared to 87% during the day. Large waders usually forage for 70–85% of the time (Van de Kam *et al.* 2004) in winter. To our knowledge, this is the first study to infer wader behaviour from path track characteristics (e.g. step length and the angle of direction) using state-space models such as HMMs.

### Limitations

The biggest limitations in this study related to tag attachment, battery lifespan and the distribution of the capture sites in the outer estuary. Firstly, to minimize welfare concerns we did not consider using harnesses to attach tags. As an alternative, it is now possible to use leg loops which support the GPS tag for a longer

period (Jiguet *et al.* 2021), although it is important to evaluate the potential effects of such deployments. As we were principally interested in movement data solely from within the winter period and not across other times of the birds' annual cycles, and due to limited battery life of the GPS tags used, we used glue-mounting to deploy the tags that then detached from the birds after approximately three months. Hence, we were only able to track the same individual over a single winter. Thus, we could not examine the individual inter-annual variability in home range sizes. The relatively short battery life of the GPS with UHF download also meant that a trade-off had to be made between the sampling regime and the tracking duration to cover the tidal rhythm and ensure representative coverage of the non-breeding season. At least 56 days of data were expected with the trade-off, but performance of the tag over the four winters was not equal and thus resulted in a variable number of fixes per individual. With the continuous miniaturization of tags, GPS/GSM technology is now available for birds the size of a Curlew; individuals can be tracked over the full non-breeding season (from early July to early April) and for up to several years (Schwemmer *et al.* 2021). In this study, we only sampled individuals from roosts in the outer estuary where the large intertidal flats offered a long feeding window compared to the intertidal flats of the upper and middle estuary, which are narrower and thus quickly submerged. The decreasing availability of intertidal flats in other parts of the estuary could drive differences in movement behaviour or habitat use (i.e. habitat functional response).

### Conclusions

Using fine-scale GPS tracking data, this study provides new insight into the winter home ranges of Curlews. To our knowledge, there are no published studies examining the home range size of Curlews and highlighting the inter-individual variation. The relatively small home range size and its lack of variation through the non-breeding season are relevant for the conservation of this near-threatened species. Knowledge of the home range size and movements of wintering waders in relation to the diurnal cycle is vital to informing management responses to environmental changes such as sea-level rise, and thus in improving the efficacy of compensatory habitats such as provision of coastal grasslands and managed realignment sites. Furthermore, knowledge of home range area and behaviour patterns can improve mechanistic models of survival (e.g. IBMs, Stillman *et al.* 2000), which

themselves can inform management decisions in the estuary. However, it is important to note that our results may be site-specific and reflect the birds' available habitats and resources on the Humber Estuary. Variation in home range size through the non-breeding season might occur at sites where the available intertidal resources are insufficient for individuals to meet their daily energy requirements, forcing some to switch to feeding in terrestrial fields more frequently. The unexplained inter-individual variability in home range size thus requires further attention.

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