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## RESEARCH ARTICLE

# Land-use intensity impacts habitat selection of ground-nesting farmland birds in The Netherlands

Yuhong Li<sup>1</sup>  | Theunis Piersma<sup>1,2</sup>  | Jos C. E. W. Hooijmeijer<sup>1</sup> | Ruth A. Howison<sup>1,3</sup> 

<sup>1</sup>Conservation Ecology Group, Groningen Institute for Evolutionary Life Science (GELIFES), University of Groningen, Groningen, The Netherlands

<sup>2</sup>NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, Den Burg, The Netherlands

<sup>3</sup>Knowledge Infrastructures Department, Campus Fryslân, University of Groningen, Groningen, The Netherlands

## Correspondence

Yuhong Li

Email: [yuhong.li@rug.nl](mailto:yuhong.li@rug.nl)

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## Abstract

1. Agricultural intensification has modified grassland habitats, causing serious declines in farmland biodiversity including breeding birds. Until now, it has been difficult to objectively evaluate the link between agricultural land-use intensity and range requirements of wild populations at the landscape scale.
2. In this study of Black-tailed Godwits *Limosa limosa*, we examined habitat selection and home range size during the breeding phase in relation to land-use intensity, at the scale of the entire Netherlands. From 2013 to 2019, 57 breeding godwits were tracked with solar-Platform Transmitter Terminals (26–216 locations [mean: 80] per bird per breeding phase) and used to estimate their core (50%) and home ranges (90%). Of these, 37 individuals were instrumented in Iberia and therefore unbiased toward eventual breeding locations. The tracks were used to analyse habitat selection by comparing the mean, median and standard deviation of land-use intensity of core and home ranges with matching iterated random samples of increasing radii, that is, 500 m (local), 5 km (neighbourhood), 50 km (region) and the whole of The Netherlands.
3. Land-use intensities of the core and home ranges selected by godwits were similar to those at the local and neighbourhood scales but were significantly lower and less variable than those of the region and the entire country. Thus, at the landscape scale, godwits were selected for low-intensity agricultural land.
4. The core range size of godwits increased with increasing land-use intensity, indicating high agricultural land-use intensity necessitating godwits to use larger areas.
5. This is consistent with the idea that habitat quality declines with increasing land-use intensity. This study is novel as it examines nationwide habitat selection and space use of a farmland bird subspecies tracked independently of breeding locations. Dutch breeding godwits selected areas with lower land-use intensity than what was generally available. The majority of the Dutch agricultural grassland (94%) is managed at high land-use intensity, which heavily restricts the viability of breeding possibilities for ground-nesting birds. The remote sensing methodology

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described here illustrates the potential to study entire wild populations from the local field level to their whole spatial range.

#### KEYWORDS

agricultural intensification, Argos, black-tailed godwit, home range, meadow bird, remote sensing, Sentinel-1, space use

## 1 | INTRODUCTION

Post-war intensification of agriculture has extensively modified the countryside of Europe, transforming most semi-natural grassland habitats into homogeneous fields, characterized by mechanization, deep drainage and the increasing use of artificial fertilizers and agrochemicals (Benton et al., 2003; Emmerson et al., 2016), and unfavourable to farmland birds that require varied habitat structures for breeding, refugia and food resources (Donald et al., 2001; Newton, 2004, 2017; Stoate et al., 2009). The diversity and abundance of insects, the main food of farmland birds during the breeding season, are significantly lower in high-intensity farmland compared to low-intensity farmland (Seibold et al., 2019). Moreover, intensive agricultural practices contribute to soil degradation by lowering groundwater tables and mechanically injecting manure, which intensifies soil desiccation and results in a hard top soil layer impenetrable for soil probing birds (Gilroy et al., 2008; Onrust & Piersma, 2019; Onrust, Wymenga, Piersma, et al., 2019). Furthermore, frequent mechanical mowing coinciding with the birds' breeding season reduces the reproductive success of farmland birds (Kentie et al., 2015; Kleijn et al., 2010; Kruk et al., 1997; Roodbergen & Teunissen, 2019).

To better conserve threatened animals with their habitats, it is important to understand their space use in relation to the characteristics of their habitats (He et al., 2019). Based on the ideal-free distribution which assumes that there are no competitive asymmetries and that all individuals are equally 'free' to occupy any space in the habitat (Fretwell, 1969; Sutherland, 1996), the size of an animal's home range is expected to be negatively correlated with the quality and abundance of resources. In other words, the home range size of an animal is smaller in areas with rich resources and larger in areas with poor resources (Fretwell, 1969; Sutherland, 1996). This has been found in a variety of bird species, such as Tengmalm's Owl *Aegolius funereus* (Kouba et al., 2017), Eurasian Eagle-owl *Bubo bubo* (Lourenço et al., 2015), Bluethroat *Luscinia svecica* (Godet et al., 2015, 2018) and Wild Turkey *Meleagris gallopavo* (Thogmartin, 2001).

For farmland birds, habitat quality, denoting resource quality and quantity, has been found inversely related to agriculture management intensity (Newton, 2017). Advances in objectively quantifying large-scale agricultural land-use intensity have been made using remote sensing imagery, in which a land-use intensity index is quantified by the standard deviation of changes in vegetation height throughout the growing season (Howison, Piersma, et al., 2018). Intensively managed farmland is characterized by fast vegetation growth combined with frequent mowing or harvesting, resulting in high magnitude of the standard deviation, whereas low-intensity

farmland has more stable vegetation height due to slower vegetation growth and less frequent harvesting (Howison, Piersma, et al., 2018). Thereby, the land-use intensity index can be used to assess the impact of agricultural management on farmland bird populations at the landscape scale.

Almost all ground-nesting farmland bird populations breeding in The Netherlands have shown drastic population declines since 1960s, probably as a consequence of nationwide agricultural intensification (Roodbergen & Teunissen, 2019). Among them, the Dutch population of continental Black-tailed Godwit *Limosa limosa* (afterwards called 'godwit') is one of the most well-studied (sub-)species and can serve as a representative of Dutch farmland birds as it historically shares breeding habitats with many other farmland birds (Howison, Belting, et al., 2018; Roodbergen & Teunissen, 2019). The Dutch population of godwits, which comprises 87% of the East-Atlantic Flyway population, has declined by ~70% since the late 1960s (Gill et al., 2007; Kentie et al., 2016), attributed to reproduction that does not compensate the annual losses (Kentie et al., 2018; Loonstra et al., 2019). Low recruitment reflects low nest and chick survival as a result of habitat degradation and intensive farming-associated disturbance during the breeding season (Groen & Hemerik, 2002; Kentie et al., 2013). Godwit breeding ecology and how it has been impacted by intensive agriculture management has been well documented at local scales (e.g. Groen & Hemerik, 2002; Kentie et al., 2014; Roodbergen & Klok, 2008; Verhoeven et al., 2020). However, given the nationwide scale of agricultural intensification (Open Government Data, 2016) and the nationwide range of godwit breeding sites, it is of great importance to expand the scale of studies to the entire country of The Netherlands.

In this research, we investigated, at the scale of the entire Netherlands, how godwits select habitats in relation to agricultural land-use intensity at three different spatial scales (0.5, 5 and 50 km) that represent a sequence of hierarchical decisions they make for nesting and foraging sites (Kentie et al., 2014), and examined the consequences for their core and home range sizes during breeding. From 2013 to 2019, 57 breeding godwits instrumented with Argos Platform Transmitter Terminals (PTTs) were tracked; of these, 37 individuals were instrumented in Iberia, thus independent of known breeding locations in The Netherlands. The independent sample of the 37 individuals was used to examine the hypothesis that godwits actively select for low-intensity agricultural land from the available area. The tracks from all 57 individuals were used to test the hypothesis that godwits breeding in more intensive agricultural land would have larger home ranges than those breeding in less intensively managed fields.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This study involved all agricultural land and nature reserves in The Netherlands that accounted for 2,224,651 ha and 53.6% of the land surface of the country (Open Government Data, 2016). These habitats are managed at the parcel scale, ranging from 0.01 to 37,282 ha (Open Government Data, 2016). Of these habitats, 36% of the area consisted of arable land, 46% agricultural grassland, 16% nature reserves and 2% others (Open Government Data, 2016). Although arable fields are not the primary habitat of godwits, they were included since these fields usually occur in a mosaic with grassland. Any management that takes place in arable fields would affect neighbouring grasslands, for example, irrigation, lowered water table and use of chemical herbicides, pesticides and fungicides (De Felici et al., 2019; de Jong et al., 2008; Gramlich et al., 2018).

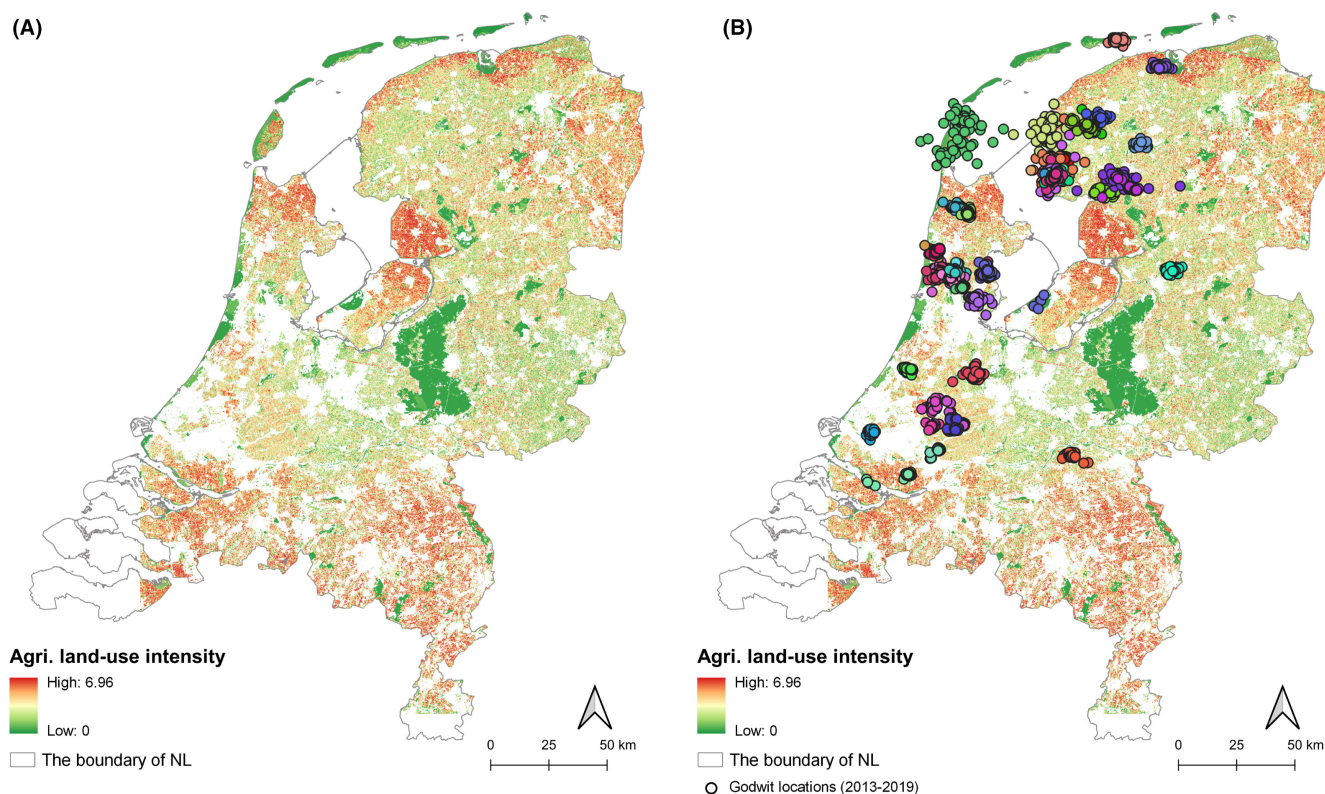
### 2.2 | Agricultural land-use intensity

The agricultural land-use intensity index summarizes the variation in vegetation height throughout the growing season that is captured by C-band synthetic aperture radar (C-SAR) instruments on the

Sentinel-1 satellite (Howison, Piersma, et al., 2018). C-SAR imagery from two scenes (31 March 2016 to 22 August 2016 at 12-day intervals and  $10 \times 10 \text{ m}^2$  resolution) covering 96% of the land surface of The Netherlands were downloaded from the ESA Copernicus Scientific Data Hub (<https://scihub.copernicus.eu/dhus/#/home>).

The spatial data processing was carried out in SNAP 6.0 and ArcMap 10.5.1. (see Figure S1 for the workflow diagram, see Howison, Piersma, et al., 2018 for detailed description). A small area of 4% of The Netherlands land surface falling outside of the two downloaded scenes, namely Zeeland and South Limburg, was left out of the analysis because no tracked godwits bred in these areas and due to the disproportionate amount of time needed to include these areas in the land-use intensity analysis. The land use pattern derived in 2016 in Figure 1A was used for the whole study period (2013–2019) since 2016 was representative of typical seasonal field conditions and preceded the severe dry years that followed in 2017, 2018 and 2019.

The effectiveness of the applied land-use intensity index in representing different agricultural land use categories, that is, arable land, agricultural grassland (including conventionally managed grassland and agri-environmental schemes) and managed reserves, was examined with a one-way analysis of variance (ANOVA). The land-use intensity index significantly differed among the three types of land use with arable land having the highest values, agricultural grassland the intermediate and managed reserve the lowest (Figure S2, one-way



**FIGURE 1** (A) Radar remotely sensed agricultural land-use intensity, The Netherlands, calculated from C-SAR time series 31 March to 22 August 2016. (B) Radar remotely sensed agricultural land-use intensity map with the recorded locations (LC 3, 2, 1) from the 57 tracked godwits during the study period with a colour representing an individual. To show the land-use intensity of the godwit breeding areas, we present the land-use intensity maps with and without godwit tracking locations.



ANOVA:  $F_{(2, 5697)} = 1658, p < 0.001$ ). Accordingly, arable land constitutes the upper end of the land-use intensity gradient whereas managed meadow bird reserves make up the lower end and agricultural grassland constitutes the intermediate part.

## 2.3 | Tracking data

From 2013 to 2019, 57 adult godwits were instrumented with solar-powered PTT-100 satellite transmitters (Microwave Telemetry, Inc.), transmitting for at least one complete breeding season (the information on legal justification of bird capturing and tagging is provided in the Acknowledgement). Of these, 37 individuals were tagged outside of their breeding range in Extremadura, Spain (39.0364°N, 5.9112°W) and Tejo estuary, Portugal (38.8525°N, 8.9695°W) between January and February, of which breeding sites were shown to be spread out across The Netherlands (Figure 1B), and 20 individuals were instrumented in their breeding grounds in southwest Friesland, The Netherlands (52.9600°N, 5.4830°E) between April and June (Senner et al., 2015, 2019). The transmitters weighing 5.0 g or 9.5 g represented  $2.14 \pm 0.14\%$  and  $3.43 \pm 0.22\%$  of an individual's mass at the time of capture (see Senner et al., 2019 for more details).

The duty cycles programmed in satellite transmitters varied with years: '10h-on & 48h-off' (2013, 2014, 2015), '8h-on & 24h-off' (2015, 2016, 2017), '6h-on & 36h-off' (2019) and 'continuous on' (2019). All locations were retrieved via the CLS tracking system ([www.argos-system.org](http://www.argos-system.org)). In this study, we used the highest-quality tracking data, location qualities LC 3, 2 and 1 accurate to 250, 500 and 1500 m, respectively (CLS, 2016), to analyse habitat selection and home range. We included the locations of LC1 with spatial error of 1500 m in the analyses because including or excluding them does not quantitatively change the main results (Tables S1 and S2).

Locations of an individual recorded within the boundary of The Netherlands from March to July were packaged as a breeding event. Locations recorded less than 1 h from the previous location were removed to minimize autocorrelation and avoid overrepresentation of these areas (Cresswell & Smith, 1992). In full, this study consisted of 57 individual godwits capturing 94 breeding events, as some individuals were tracked in consecutive years (see below for statistical treatment of repeat measures).

## 2.4 | Assigning the breeding period

Godwits arrive in The Netherlands from mid-March to mid-April to start their breeding season (Lourenço et al., 2011; Verhoeven et al., 2019). The breeding season can be divided into three phases: pre-breeding (territory establishment), breeding (egg laying to fledging) and post-breeding (fledging to migration; Loonstra et al., 2019; Roodbergen & Klok, 2008; Senner et al., 2015, 2019; Verhoeven et al., 2020).

In this study, we focused on the breeding phase of godwits, including the egg laying, incubation and chick-rearing, during which godwits remain close to their nest sites (van den Brink et al., 2008).

The breeding phase of godwits was assigned individually through visual inspection of the tracking data with the following steps. First, the breeding phase was coarsely defined based on the well-studied godwits' breeding timing: pre-breeding phase is before 20 April; breeding phase is from 21 April to 20 June (including 3 days for egg laying, 23 days for incubation and 35 days for chick rearing); post-breeding phase is after 21 June (Loonstra et al., 2019; Roodbergen & Klok, 2008; Senner et al., 2015; Verhoeven et al., 2020). Second, if the tracking data indicated a godwit stayed around its breeding site after 21 June, we prolonged the breeding phase till it permanently left its breeding location that year. This is because almost half of the godwits fail in their first clutch due to increasing predation or frequent agriculture-related disturbance, and replacement clutches would lead to an extension of the pre-defined breeding period (Verhoeven et al., 2020). Third, if a godwit left its breeding site prior to 21 June, a situation considered as an early breeding phase, we advanced the start of its breeding phase. The earliest possible start date was set as 7 April (Lourenço et al., 2011; Senner et al., 2015). After filtering, the number of locations per bird per breeding season ranged from 26 to 216, with the mean of 80, and the duration of the breeding phase ranged from 32 to 101 days with a median of 57 days. The short breeding events (<50 days) might imply a breeding failure. However, we included all breeding events in the further analyses as excluding or including them did not change the results statistically.

## 2.5 | Home range estimation

Adapted from its original definition (Burt, 1943), the home range is denoted by the area that a godwit uses during its breeding phase. The size of the home range was estimated by two widely used approaches: minimum convex polygon (MCP) and kernel density estimator (KDE) with the fixed smoothing parameter  $h$  determined by least squares cross-validation method (Mohr, 1947; Worton, 1989). To minimize the unwanted influence of the outermost locations on home range estimate, we calculated 90% and 50% MCP and KDE. The area delimited by 50% MCP and KDE was defined as the core range, and the area corresponding to 90% of MCP and KDE was defined as home range. Both approaches were implemented in R 3.6.2 with the ADEHABITATHR package (Calenge, 2011). For further analysis, the realized home range was calculated by masking out cities, roads, infrastructure and water bodies from the core and home range polygons.

To quantify the land-use intensity of individuals' breeding sites, we calculated the median land-use intensity index of centred buffers with radii of 500 m and 1000 m, corresponding to the core range and home range, assuming that godwit nests were located at the centre of their MCP core range.

## 2.6 | Habitat selection

To avoid bias towards favourable breeding locations, 20 individuals instrumented in The Netherlands were removed from the habitat

selection analysis. The remaining 37 individuals were tagged in the Iberian Peninsula and therefore unbiased to eventual breeding locations. First-time breeders choose their breeding sites from the whole Netherlands, while older individuals return to previous sites ( $\pm 7$  km; Kentie et al., 2014). Following territory and nest site establishment, godwits choose to forage in specific sites surrounding their eventual nest locations (van den Brink et al., 2008). Accordingly, we investigated habitat selection at local, neighbourhood and regional scales by building 0.5, 5 and 50 buffers, respectively, surrounding each godwit's assumed nest location.

To characterize the land-use intensity of the 0.5, 5 and 50km buffers, we generated point arrays with points spaced of 30, 300 and 3000m apart, respectively, over the buffers. To ensure a thorough random sampling of the surrounding landscape, the arrays were sampled with the same number of recorded locations of the individual godwit within the MCP core range, with 2000 random sampling iterations. We calculated the mean, median and standard deviation land-use intensity index of each buffer by averaging the corresponding parameter of the 2000 samples to characterize the available land. In addition, we calculated the same parameters for land-use intensity of recorded locations within MCP core and home ranges to represent the selected land.

## 2.7 | Statistical analyses

For the habitat selection, one-way ANOVA models were used to examine the difference of the mean, median and standard deviation of land-use intensity index between recorded locations of individual adult godwits within their core and home range areas and the available areas (0.5 km buffers, 5 km buffers, 50km and country scale buffers).

Generalized linear mixed models were used to assess how land-use intensity affected home range size of godwits during the breeding phase (Cnaan et al., 1997). Duty cycle differed between the transmitters and was added as a fixed variable in the models. Variables used for the models were the log-transformed range size (MCP core range and home range, and KDE core range and home range) as the response variable, the median land-use intensity index of buffers (500 and 1000m buffers) and duty cycle as the fixed variables, individual identity and year as the random variables, and the number of locations as an offset. The random variables that were found to explain no variation in a model were removed.

## 3 | RESULTS

### 3.1 | Habitat selection

The recorded locations for both MCP core range and home range showed similar mean land-use intensity index to the index of the available area at the local (0.5 km) and neighbourhood scales (5 km); however, they showed significantly lower mean intensity index than the regional (50km) and national scales (Figure 2A,

one-way ANOVA:  $F_{(5, 558)} = 32.4, p < 0.001$ ). A similar pattern was also found in median land-use intensity index (Figure 2B, one-way ANOVA:  $F_{(5, 558)} = 23.7, p < 0.001$ ). Land-use intensity index of the recorded locations for both MCP core range and home range had similar standard variation to the local scale (0.5 km), but had significantly less variation than the neighbourhood (5 km), region (50km) and nation scales did (Figure 2C, one-way ANOVA:  $F_{(5, 558)} = 212.8, p < 0.001$ ).

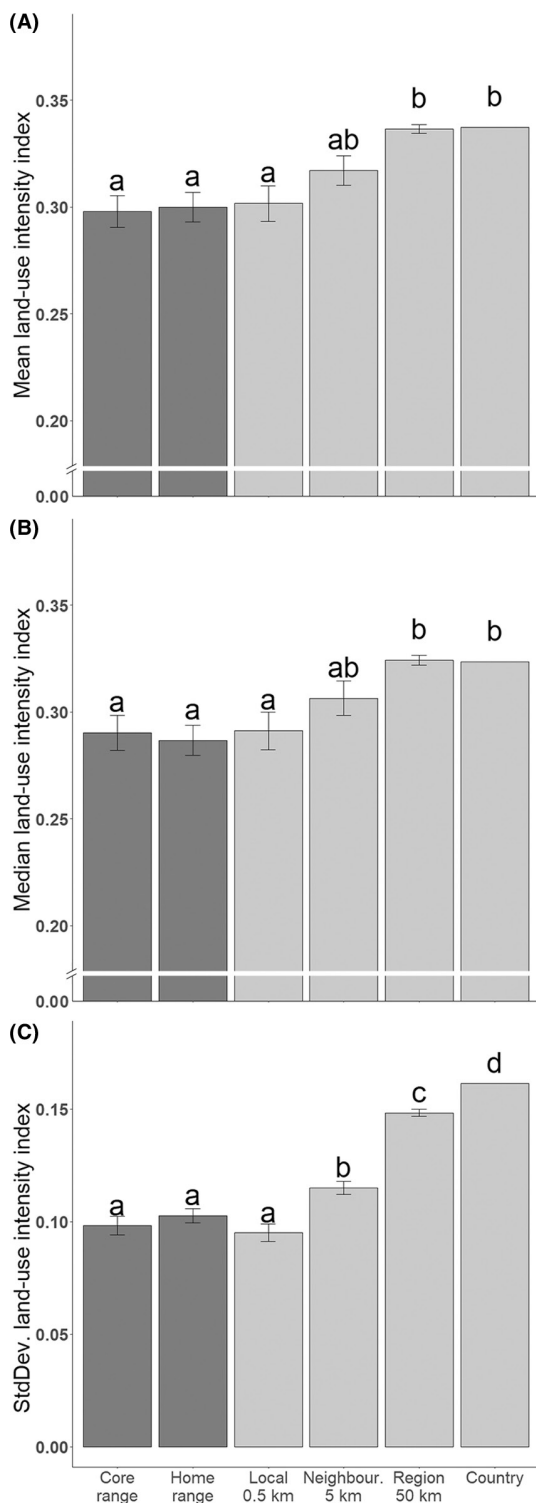
### 3.2 | Home range size and agricultural land-use intensity

Over the 7 years, the mean size of core range of godwits during their breeding phase calculated according to MCP was  $163.1 \pm 711.6$  ha ( $\pm$ SD) with a median value of 49.1 ha. The mean home range was about four times as large, that is,  $632.5 \pm 1685.5$  ha ( $\pm$ SD) with a median size of 265.1 ha. Using the KDE approach, the mean core range size was  $192.6 \pm 408.0$  ha ( $\pm$ SD) with a median of 79.7 ha, and the mean home range was  $773.0 \pm 1287.1$  ha ( $\pm$ SD) with a median of 366.7 ha. The large standard deviation of the estimates was due to eight breeding events where extremely large core and home ranges (over five times larger than the medians) were found. Calculated by the mean of the medians of the MCP and KDE estimates, godwits breeding in high-intensity agricultural land had a median core range of 73.8 ha and a median home range of 306.6 ha, which is, respectively, 1.7 times and 1.1 times larger than godwits whose core range centred on managed reserves (Table S3).

We found that the core range sizes estimated by both MCP and KDE increased strongly with the increasing land-use intensity of 500m buffers (Table 1, Figure 3A,C). MCP core range size was also positively affected by the land-use intensity of 1000m buffers (Table 1, Figure 3B). None of the home range sizes was found to have a significant relation with the land-use intensity of either 500m or 1000m buffers (Table 1, Figure 3E-H; for full modelling results, see Table S1).

## 4 | DISCUSSION

In this study, we investigated the breeding space use of godwits based on the Argos tracking system. We are fully aware of the location accuracy limitation of this tracking system and its implication on our analyses and interpretation of the results. However, the substantial sample size of 57 individual godwits, that were equipped away from the breeding area, permits independent study of godwit space use at the nationwide scale and avoids bias of observer time and travel limitations. Despite the location accuracy limitation, we found that adult godwits chose agricultural land with low-intensity management compared to the available area at broad scales, and that their core range size significantly increased with the increasing land-use intensity of habitats. This



**FIGURE 2** The comparison of (A) mean, (B) median and (C) standard deviation of land-use intensity index between recorded locations within the MCP core and home ranges of individual adult godwits (dark grey), and available area at different scales (light grey). Error bars represent SE, and bars with different letters are significantly different (Tukey HSD,  $p < 0.05$ ).

evidence supports our hypotheses that godwits actively choose low-intensity fields and that godwits breeding in more intensive grassland need larger habitats.

#### 4.1 | Habitat selection

Adult godwits choose lower land-use intensity habitats from the available land at the regional and nationwide scales, suggesting that low-intensity or conserved grasslands contain resources that are not, or no longer, available in the majority of the grasslands. This outcome is consistent with the nationwide intensive agricultural land management in The Netherlands: 94% of grasslands are managed at high intensity use and only 6% grasslands maintained at low agricultural intensity or preserved in reserves (Open Government Data, 2016).

No difference was detected between the land-use intensity of the recorded locations of individual godwits and that of the immediate surroundings of the breeding sites (0.5 km and 5 km scales). This suggests that the neighbourhood scale (5 km) might be the spatial level at which godwits select their habitats based on land-use intensity and in space finer than this scale no strong habitat selection occurs or habitat selection was made on other cues, such as social factors that can make individuals choose to breed at sites synchronized with their migration group (Helm et al., 2006; Lourenço et al., 2011). However, this may also highlight the limitation of detecting the selection at a fine scale, attributed to the spatial error of the Argos PTT tracking system. In fact, habitat-quality-based habitat selection might occur at the neighbourhood scale. Kentie et al. (2014) found that a higher proportion of godwits transited from monocultures to meadows than in the opposite direction when choosing their breeding sites within 7 km of their previous one.

#### 4.2 | Home range size

To our knowledge, it is the first attempt to estimate the breeding home range of this threatened species among all populations, despite the probability of an overestimate caused by the limited spatial accuracy of the Argos tracking system (Thomson et al., 2017). The breeding space use of godwits estimated here is considerably larger (MCP home range: 265.1 ha), compared to other ecologically similar species (i.e. ground-nesting waders feeding on invertebrates) and we can find information for: Northern Lapwing *Vanellus vanellus* (MCP home range: 0.68–0.80 ha; Johansson & Blomqvist, 1996; Verhulst et al., 2007), Common Redshank *Tringa totanus* (MCP home range: 0.56 ha; Verhulst et al., 2007), Eurasian Golden Plover *Pluvialis apricaria* (MCP home range: 41 ha; Pearce-Higgins & Yalden, 2004) and Eurasian Curlew *Numenius arquata* (MCP home range: 45.2 ha; Berg, 1992). Such a conspicuous difference in home range sizes between their studies and ours might have a methodological basis in addition to the limited tracking accuracy in this study: their estimates were based on either field observation or radio telemetry tracking, methods constrained by observation efforts and specific study site characteristics. Nevertheless, the comparatively substantial breeding home range size derived here still fits in the movement range of godwit families with chicks till fledging: they can travel farthest up to 1.6 km from the nest site (Schekkerman & Müskens, 2000), leading to a potential 804 ha foraging area. Meanwhile, the same study

**TABLE 1** Results of the general linear mixed models examining the relation between land-use intensity and godwits' core/home range size during the breeding phase

Response variable	Fixed variable <sup>a</sup>	Random variable	Coefficient	SE	t-value	p-value
MCP core range	500m	id	5.30	1.60	3.32	<0.01**
	1000m	id	5.60	2.14	2.62	<0.05*
KDE core range	500m	id	3.18	1.47	2.17	<0.05*
	1000m	id	2.76	1.95	1.41	0.163
MCP home range	500m	id	1.92	1.38	1.40	0.167
	1000m	id	2.10	1.86	1.13	0.261
KDE home range	500m	id	1.72	1.32	1.31	0.197
	1000m	id	1.60	1.73	0.93	0.358

Abbreviations: KDE, kernel density estimator; MCP, minimum convex polygon.

<sup>a</sup>The radius of the buffers where the median land-use intensity was calculated.

showed that godwit families spent half of their time within a distance of 250m to their nest (Schekkerman & Müskens, 2000), which leads to a 20ha core range that is at the same magnitude of the core range size we derived (49.1 ha). Overall, to better understand the space use of this species during the critical breeding phase, it is necessary and urgent to use tracking systems with high spatial accuracy, for example, GPS, to record their movements.

The majority of godwit breeding events occurred within a narrow gradient range of intermediate land-use intensity and only a few observations were found at the upper and lower end of the land use gradient (Figure 3). In fact, the significant relation between core range and land-use intensity is driven by the observations at extremely low or high land-use intensity as removal of them (observations with land-use intensity either lower than 0.15 or higher than 0.45) leads to insignificant relationships (Table S4), except the relation between MCP core range and land-use intensity within a 500m buffer. Such a narrow, middle-situated, concentrated occupation of godwits on the land-use intensity gradient, along with another finding in this study (godwits selected lower land-use intensity habitats at the national scale), strongly demonstrates the fact that the land-use intensity of the majority of the agricultural landscape is too high for godwits to use, and godwits try their best to select the intermediately managed land from the pervasive, intensively managed land. Although this finding has been revealed abundantly at local scales (Groen et al., 2012; Howison, Piersma, et al., 2018), this study provides the clear evidence that it also happens at the countrywide scale.

Godwits breeding in intensively managed grasslands required larger core ranges, which might be a means to compensate for the insufficient resources present in intensive grasslands. Due to the limited food availability, foraging rate of chicks, defined as the number of prey items ingested per minute, was found 31% lower in intensive agricultural fields than in reserve fields, suggesting a considerable decrease in foraging success and efficiency caused by foraging in intensive fields (Schekkerman & Beintema, 2007). In response to the lowered prey abundance, chicks increase their walking speed (steps per minute) by 17% in agricultural grassland compared to that in reserve meadows (Schekkerman & Beintema, 2007), thus probably leading to larger core ranges. As chicks are accompanied by their parents during the fledging period (Groen & Hemerik, 2002; Kentie et al., 2013), increased chicks'

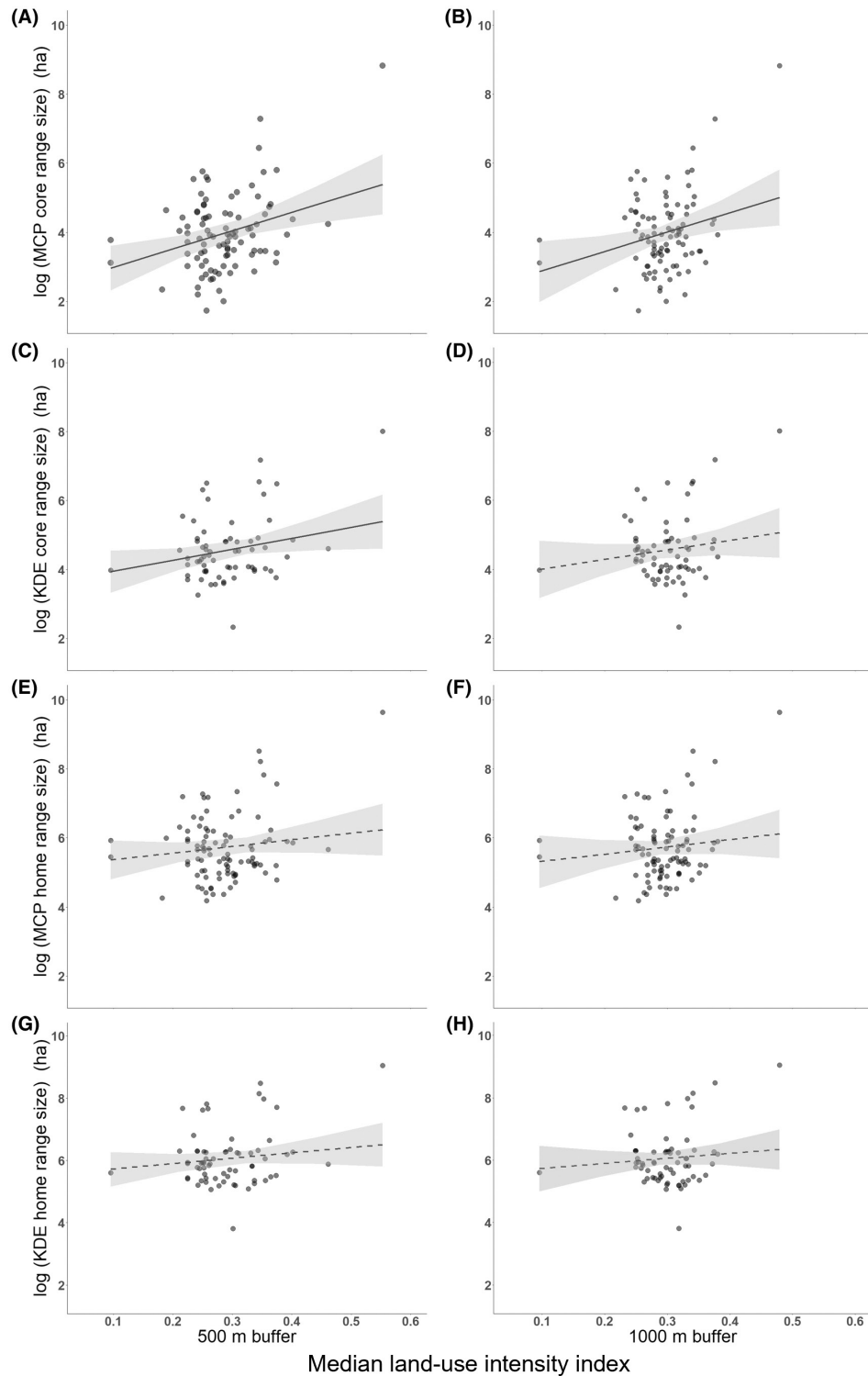
foraging movements in intensive agricultural land imply increased adults' movements that have not been well studied yet.

Unlike core range size, home range size was not found to be significantly related to land-use intensity. Core range, by definition, concentrating half of their movements might represent the range over which godwit adults accompanying their precocial, flightless chicks forage meticulously (Groen & Hemerik, 2002; Kentie et al., 2013). Therefore, food resources in the core range are expected to be intensively exploited. In contrast, locations occurring outside the core range might reflect godwit adults' exploratory movements made by flights, and thus in such an area the food resources are less exploited. Hence, it is expected that core range size is closely related to habitat quality whereas home range size is less linked to land-use intensity. However, such a difference in the effects of land-use intensity on core range size and home range size needs to be further tested with tracking data of higher accuracy.

### 4.3 | Conservation perspective

Many declining ground-nesting farmland birds occupy the same type of breeding habitats and use similar food resources (soil-macrodetrivores for adults and insects for chicks) as Black-tailed Godwits, for example, Northern Lapwing, Common Snipe *Gallinago allinago* and Ruff *Calidris pugnax* (Howison, Belting, et al., 2018; Roodbergen & Teunissen, 2019). The impacts of increasing landscape-level agricultural land-use intensity on habitat use of breeding godwits identified in this study are generally applicable to them as well. Recovery of godwits and other ground-nesting farmland birds necessitates the creation of high-quality habitats that are characterized by high openness, diverse herbs, heterogeneous swards, high groundwater levels, low fertilization levels and late mowing (Groen et al., 2012; Howison, Piersma, et al., 2018). By examining nationwide habitat selection and space use of godwits tracked independently of breeding locations, this research provided strong evidence that the land-use intensity of the majority of Dutch agricultural land is too high for godwits to inhabit. This urgently calls for conservation action in agricultural landscapes. In addition, this study provides an estimate of ca. 400ha continuous





**FIGURE 3** Median land-use intensity based on different scales in relation to core and home range size estimates. The relation of median land-use intensity index of (A) 500m buffers and (B) 1000m buffers to MCP core range size. The relation of median land-use intensity index of (C) 500m buffers and (D) 1000m buffers to KDE core range size. The relation of median land-use intensity index of (E) 500m buffers and (F) 1000m buffers to MCP home range size. The relation of median land-use intensity index of (G) 500m buffers and (H) 1000m buffers to KDE home range size. The solid lines represent significant effect while the dashed lines mean non-significant effect.

protected area that can encompass most of godwits' home range during their breeding phase. This estimate can be used in future landscape designs prioritizing increasing numbers of breeding godwits. Implementing these structural and well-documented changes

to agricultural management will benefit the functioning of the entire wet-grassland ecosystem that supports a rich assemblage of vegetation, insects and birds, and high-quality food production (Howison, Belting, et al., 2018; Onrust, Wymenga, & Piersma, 2019).

The intensification of agriculture has spread through farmlands at a global scale. Currently, 75% of the earth's terrestrial surface has undergone conversion to serve the needs of the human population and 63% can be attributed to agriculture, which has been followed by drastic farmland biodiversity loss (Díaz et al., 2019). Evaluating the impacts of agricultural intensification on communities or single organisms ranging from large mammals, birds, invertebrates, plants and the soil biome that may be influenced by human land modification and management is essential for designing future landscapes prioritizing the recovery of biodiversity. Using a novel combination of remotely sensed land-use intensity and continuous animal-tracking, we investigated the space use of a farmland bird subspecies over the most important part of its breeding range using long-term unbiased tracking data recorded from the individuals tagged away from their breeding sites. Thereby, we provided a template for ecologists who study other species to use these methods to understand the effects of land-use intensity on other species or whole communities.

#### AUTHOR CONTRIBUTIONS

Yuhong Li, Ruth A. Howison and Theunis Piersma conceived the ideas and designed the methodology; Jos C. E. W. Hooijmeijer collected the data; Yuhong Li analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/2688-8319.12201>.

#### DATA AVAILABILITY STATEMENT

Data available from the University of Groningen Research Data Repository <https://doi.org/10.34894/BZ9GTR> (Li et al., 2022).

#### ORCID

Yuhong Li  <https://orcid.org/0000-0001-7822-6817>

Theunis Piersma  <https://orcid.org/0000-0001-9668-466X>

Ruth A. Howison  <https://orcid.org/0000-0001-6470-6131>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1** Workflow diagram of the software, tools and steps used to calculate the land-use intensity index from C-SAR time series from 31 March to 22 August 2016.

**Figure S2** Mean agricultural land-use intensity index of three agricultural land use types. Error bars represent SE and bars with different letters are significantly different (Tukey HSD for both tests,  $p < .05$ ). When examining the difference of the index among the three land-use types, to avoid spatial autocorrelation and balance the size of each category, we applied cross validation and one-way ANOVA with a post hoc Tukey test (Picard & Cook, 1984). The data was divided into 50% training and 50% testing datasets. Welch's ANOVA was conducted as an addition to the one-way ANOVA, to account for the residual deviation from normality (Tomarken & Serlin, 1986). The results show that the land-use intensity index of arable land was the highest among the three land use types, whereas the index of agricultural grassland was intermediate and that of managed reserve was the lowest (one-way ANOVA:  $F_{(2, 5697)} = 1658$ ,  $p < .001$ , Welch's ANOVA:  $F_{(2, 3716)} = 1302$ ,  $p < .001$ ,  $R^2 = 0.35$ , RMSE = 0.12). The test model was similar to the training model ( $R^2 = 0.36$ , RMSE = 0.12), suggesting a good fit.

**Table S1** Results of the general linear mixed models examining the relationships between land-use intensity and core/home range sizes estimated with recorded locations of quality LC 3, 2 and 1.

**Table S2** Results of the general linear mixed models examining the relationships between land-use intensity and core/home range sizes estimated with recorded locations of quality LC 3 and 2.

**Table S3** The median core/home range sizes of godwits grouped by the land-use intensity levels of their breeding areas (the 500 m buffer zone). The determination of land-use intensity levels follows Howison et al. (2018).

**Table S4** Results of the general linear mixed models examining the relationships between land-use intensity and core/home range sizes estimated with recorded locations of quality LC 3, 2 and 1, excluding observations with extremely low (< 0.15) and high (> 0.45) land-use intensity.

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