



# Movement ecology and minimum density estimates of red foxes in wet grassland habitats used by breeding wading birds

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## Abstract

The red fox (*Vulpes vulpes*) is a widely distributed generalist meso-predator implicated in declines of wading bird populations. In the wet grassland habitats where waders breed, wildlife managers work to mitigate fox predation risk to waders during the nesting period through lethal and non-lethal control methods. However, limited knowledge on fox movement ecology in these habitats makes it difficult to design effective management strategies. We used GPS telemetry to understand fox home range size, daily activity and movement patterns, and how these metrics may vary among wet grassland sites with different management. We caught and GPS-tagged 35 foxes in the March–June wader nesting period on two wet grassland sites in central southern England; Britford during 2016/17 and Somerley during 2018/19. We estimated home range areas from location data using local convex hulls, and from these estimates we derived the minimum fox density at each site and year. Daily activity patterns and movement behaviour of each fox were obtained using both telemetry and trail camera data. Mean fox home range area at Britford (0.21 km<sup>2</sup>, SE=0.025) was significantly smaller than at Somerley (0.68 km<sup>2</sup>, SE=0.067), and estimated minimum densities were around four times higher (Britford=10.6 foxes/km<sup>2</sup>, Somerley=2.4 foxes/km<sup>2</sup>). Foxes were more active and moved faster during twilight and night hours, but both telemetry and camera data indicate they were also active for one-third of daylight hours. Distances moved per day were variable between foxes but generally smaller at Britford. We also found evidence for dispersal during spring, with movements of up to 19 km per day. Home ranges at both wet grassland sites were smaller than comparable sites elsewhere. These indicated foxes were living at exceptionally high densities at Britford, where there is no fox control, increased food availability and where waders no longer breed. Spatio-temporal movement patterns were closely related to home range metrics, with higher levels of fox activity at Somerley, where home ranges were larger. The movements of itinerant and dispersing foxes during the nesting period suggests that lethal control would need to be very intensive to be effective. The likely anthropogenic food subsidy of fox density at Britford suggests that controlling access to similar food resources would help reduce predation pressure on breeding waders.

**Keywords** *Vulpes vulpes* · GPS telemetry · Home range · Activity patterns · Movement behaviour · Breeding waders · Wader predation · Nesting period · Avon Valley

## Background

The long-term population decline of some wading bird species in Europe, e.g. northern lapwing (*Vanellus vanellus*) and redshank (*Tringa totanus*), has been relatively well documented, but is still poorly understood. In common with other ground-nesting bird species, population growth appears to be prevented by high levels of nest and chick

predation (Macdonald and Bolton 2008; Roos et al. 2018; McMahon et al. 2020). Breeding density, and sometimes productivity in terms of chicks fledged, of lapwing and redshank are greatest in wet grassland habitats (Wilson et al. 2005; Merricks 2010; Silva-Monteiro et al. 2021), but it is not clear whether this is because of food availability for chicks, partial protection from predators afforded by the high water table or some other effect. High predation rates have been recorded in most studies in these habitats, and although a wide spectrum of predator species is involved, the red fox (*Vulpes vulpes*) figures prominently in almost every study (Teunissen et al. 2008; Mason et al. 2018; Kaasiku et al. 2022). While waders make up only a small component of fox

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diet and do not appear to be specifically targeted by foraging foxes (Meisner et al. 2014), incidental predation from foxes is evidently an important factor in wader population declines (Mason et al. 2018; Roos et al. 2018; Zielonka et al. 2019).

The fox is an adaptable and opportunistic generalist meso-predator (Voigt and Macdonald 1984; Cavallini 1996; Macdonald and Reynolds 2004; Devenish-Nelson et al. 2013) distributed across the northern hemisphere in habitats as diverse as tundra, desert, forest and agricultural land, as well as in urban areas (Macdonald and Reynolds 2004). Territory-holding fox groups are typically dominant breeding pairs, often with non-breeding females (Macdonald 1979; von Schantz 1981; Reynolds and Tapper 1995), but both the number of non-breeding females and territory size vary with food availability (Voigt and Macdonald 1984; Iossa et al. 2009). This plasticity means that fox density can vary considerably among different parts of a given landscape (Heydon et al. 2000; Webbon et al. 2004; Sidorovich et al. 2006; Scott et al. 2014), with implications for the amount of dispersal between different areas. Fox movement behaviour has been widely studied (Macdonald and Reynolds 2004), but understanding of fox group structure, density and home range use in and around wet grassland habitats remains poor. It has been studied in the coastal regions of Denmark, Germany and the Netherlands (Mulder 1985; Meisner et al. 2014; Schwemmer et al. 2021), but not elsewhere in Europe. This knowledge gap limits the development of management aimed at the conservation of waders.

Historically, efforts to recover wader populations have focused on increasing the availability and quality of breeding habitats on farmland, particularly through agri-environment measures across western Europe (Smart et al. 2014; McMahon et al. 2020). However, given continued declines (Smart et al. 2013; Franks et al. 2018; Heldbjerg et al. 2018), it has become clear that wader breeding productivity remains poor without parallel predation management (Smart et al. 2014; McMahon et al. 2020; Laidlaw et al. 2021). Predation risk may be reduced to varying extents, either directly through lethal control of predators (Tapper et al. 1996; Fletcher et al. 2010; Smith et al. 2010; Baines et al. 2023), exclusion fencing (Rickenbach et al. 2011; Smith et al. 2011; Malpas et al. 2013), nest enclosures (Isaksson et al. 2007) or other non-lethal methods (Selonen et al. 2022); or indirectly through habitat management (Laidlaw et al. 2019). Lethal control of both foxes and corvids can substantially benefit ground-nesting bird productivity (Tapper et al. 1996; Fletcher et al. 2010), but may not always be so effective. The impact of culling on fox density varies considerably due to both site and operator effects (Porteus et al. 2019). Removal of foxes can lead to compensatory nest and chick predation by avian or smaller mammalian predators that are harder to control, e.g. stoat (*Mustela erminea*), with no reduction in overall predation rate (Holy and Belting 2019).

Lethal control is also controversial on ethical grounds (Fall and Jackson 2002). Non-lethal methods such as exclusion fencing around preferred nesting sites can reduce direct predation pressure from foxes during the nesting season but require regular maintenance and do not protect against avian predators (Laidlaw et al. 2021). A better understanding of fox ecology—density, home range size, habitat use and dispersal—in the vicinity of key wet grassland habitats would help to design effective management strategies.

We studied fox ecology during the wader nesting season at two contrasting wet grassland sites within a river valley in central southern England. The two sites were thought to differ in the availability of food resources for foxes other than waders and in the intensity of fox culling. Although the extent of the floodplain differed, both sites had short swards in March–April with shallow wet channels and small pools and patches of sedge and rush, i.e. good-quality nesting and chick-rearing habitat for lapwing and redshank, but at one site waders no longer bred successfully. We sought (1) to quantify fox home range sizes; (2) to describe typical fox movement behaviour, home range overlap, daily activity patterns during the wader breeding season and the extent of extraordinary movements outside normal home ranges; and (3) to estimate minimum fox population density.

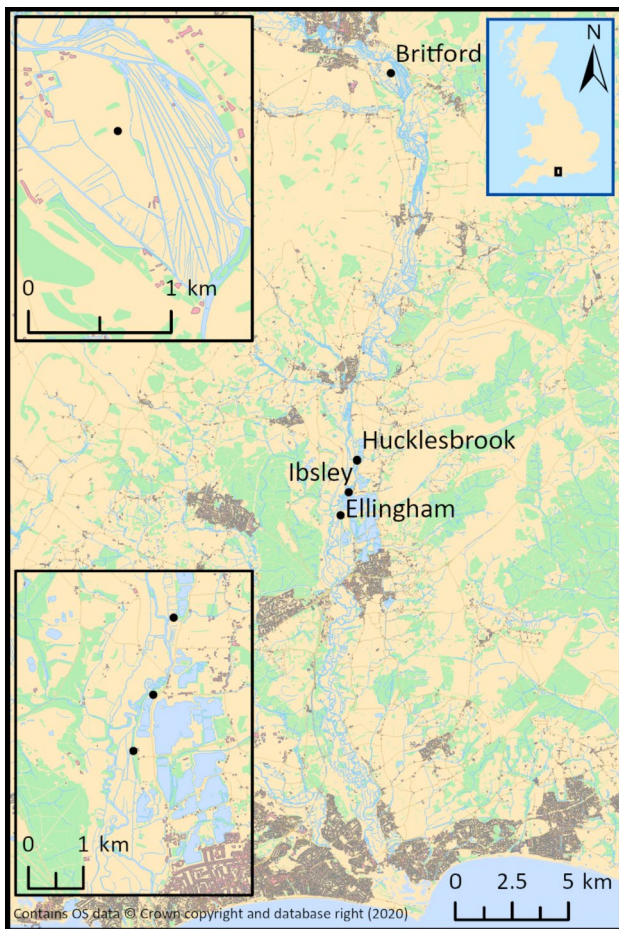
## Methods

### Study areas

This study took place between 2015 and 2019 on two representative wet grassland sites in the River Avon Valley in central Southern England (Fig. 1). The Avon Valley is both a Special Area of Conservation designated under the EU Habitats Directive and a Special Protection Area under the EU Birds Directive. It covers ~26 km<sup>2</sup> of floodplain grassland and the most numerous breeding waders are lapwing and redshank, but five other species breed in low numbers and four frequent the valley to feed prior to breeding elsewhere. In 1982, the valley supported the fourth highest density of breeding waders of all lowland wet grassland sites in England, but by 2002 was the site which had suffered the greatest percentage decline (Wilson et al. 2005).

### Britford

In 2016–2017, foxes were caught on a small privately owned farm (c. 100 ha) bounded by the village of Britford to the west and the River Avon to the east. The landscape is predominantly wet grassland (floodplain grazing marsh and lowland meadow) and pasture interspersed with semi-natural woodland. Fields are generally small and enclosed by hedgerows, ditches and barbed wire fences. Typical of



**Fig. 1** Location of the study sites within the River Avon Valley in central southern England. Britford (upper left zoomed inset) is in the upper valley, close to the city of Salisbury (population: 42,000). Somerley (lower left zoomed inset) is in the lower valley (composed of Hucklesbrook, Ibsley and Ellingham wet grasslands), close to the town of Ringwood (population: 14,000). Map shows conurbation (pink with grey outline), woodland (green), water courses (blue) and roads (brown); all other land classification shown as yellow

the upper valley, there is a system of relict water meadows (Cook and Williamson 2007) comprising ridges and furrows, water carriers and drains, which on the neighbouring farm downstream are traditionally managed, with the grassland periodically flooded using a system of hatches and sluice gates, to encourage grass growth. The wet grasslands here are c. 0.6 km at their widest point. Across the site, grassland fields are rotationally and seasonally grazed by cattle, some are left as hay crops each spring and some are sheep paddocks. The site includes a commercial fish farm, of which there are three throughout the Avon Valley. Habitat management measures to help breeding waders, including autumn mowing and grazing to improve grass growth, ditch maintenance and willow pollarding, have been implemented through agri-environment schemes. Historically, lapwing, redshank and common snipe (*Gallinago gallinago*) have

all bred at Britford, with three to four breeding pairs in 1990–1996, but none recorded on surveys since 2010 (GWCT, unpublished data). There was no concerted fox control effort since 2000.

### Somerley

In 2018–2019, foxes were caught at Somerley, a large (c. 3000 ha) privately owned country estate which supports several tenanted farms around the Hampshire village of Harbridge, adjacent to and west of the New Forest. The estate includes three contiguous wet grassland systems (Hucklesbrook, Ibsley and Ellingham) which run north–south along the River Avon ~24 km downriver from Britford. The wet grasslands are wider (up to 0.75 km) and wetter than Britford, and prone to late-winter flooding. The Hucklesbrook wet grasslands are managed as flood-marsh and provide low-intensity grazing for horses and cattle. The Ibsley and Ellingham wet grasslands are predominantly grazed by cattle, with some fields left for hay crops. The river corridor has an open aspect with few trees. Fields are generally bound by wire fence lines and water courses. Above the floodplain, the landscape includes pastoral farmland and estate parkland interspersed with residential properties, gravel extraction pits and mixed woodland where pheasants (*Phasianus colchicus*) are annually released at low density for recreational shooting. Although with relatively low effort compared to other nearby estates, foxes are routinely culled by night-shooting in autumn and winter to prevent conflict with game and sheep management objectives, with up to 20 foxes removed annually. The estate ceased culling efforts during spring while we caught and tracked foxes. The wet grassland fields supported an estimated 15 pairs of lapwing and 7 pairs of redshank during 1990–1996, with numbers increasing slightly to averages of 19 and 9 pairs, respectively, in the early 2010s (GWCT, unpublished data). As part of a parent project to increase wader productivity (see Funding), chick-rearing habitats were improved in 2015–2017 and temporary electric fencing was installed opportunistically to protect specific nesting lapwing (GWCT 2020).

### Fox capture and tagging

Our aim was to understand the movements of foxes during the wader nesting season, which we defined to be 15 March to 15 June based on systematic records of local egg-laying and chick fledging dates (GWCT, unpublished data). We began fox tagging effort at the start of March and continued either until early May or all available tags were in use. Fox capture and tagging were conducted under a UK Government Home Office licence in accordance with the *Animals (Scientific Procedures) Act* (1986). Fox capture was initially attempted using live-capture cage traps (XL Heavy Duty



Fox Trap; JDA Engineering Ltd, UK), but following zero captures all foxes were subsequently caught using passive neck snares (DB snare; Perdix Wildlife Supplies, UK). Contrary to widespread misconception, live-catch neck snares (also known as Humane Cable Restraints) catch and restrain foxes without serious injury provided they are well-designed and carefully used (Defra 2012; Short et al. 2012), i.e. in accordance with the Defra Code of Practice on fox snares (Defra 2016). The DB snare includes designed-in technical components both to facilitate fox capture, and to allow non-target species like roe deer (*Capreolus capreolus*) and badger (*Meles meles*) to self-release (Short et al. 2012). We used trail cameras (Ltl Acorn 5310) set along linear features and at water crossing points, e.g. tracks, fence lines and foot bridges, at a height of 1–2 m to detect foxes and avoid non-targets, e.g. badger and otter (*Lutra lutra*). Up to 20 cameras were set at any one time and were typically moved between locations every couple of weeks. After tagging effort was complete, cameras remained in key locations to record tagged and untagged fox activity. These data and field observations, including searching for scats, tracks and breeding earth (den) locations, were used to identify locations where foxes were active and to minimise risk of capture of non-target species, especially badger and otter. Snares were set only in areas known to be visited by untagged foxes, or to recapture specific foxes to replace a collar, and were inspected early morning and late afternoon. Snare use was influenced by fox and non-target activity, presence of livestock and by water levels: snares can only be set on fields where livestock are absent and when the ground is dry enough for snares to be tethered to secure ground-anchors.

Once captured, foxes were restrained by ‘scruffing’ them—holding securely by the loose skin at the back of the neck—and examined for visible external injuries and to assess general body condition. Any physical injuries (e.g. skin abrasions or pre-existing bite wounds) were treated in accordance with an agreed Home Office licence protocol. Professional veterinary advice was always available by telephone if required. We recorded sex and reproductive condition, but to minimise handling stress, we did not weigh foxes. All foxes caught were judged to be adults and to weigh > 5 kg. For captured foxes not requiring veterinary consultation (17/18 timed events), the average time to assess physical condition, fit a collar and release the fox was 6 min 13 s. All foxes were released where caught.

We used Tellus Ultra-Light GPS collars (215 g; Followit, Sweden) which have 22 GPS channels, activity sensors and a remote drop-off device. We conducted tests of the GPS location accuracy and confirmed that 90% of fixes were within 10–15 m for an active animal (Appendix 2). Collars were programmed to attempt a location fix every 10 min, but there were circumstances in which we switched them

remotely to a 60-min schedule to conserve battery life, for instance, following dispersal events away from the wet grassland sites. For all resident foxes, the 60-min schedule was adopted following initial data collection on a 10-min schedule, either during daytime (0800–1800) or for 4-day periods within each week; this allowed data recording during more of the nesting period. We programmed collars to search for available satellites for up to 90 s, after which time the collar turned itself off until the next scheduled attempt. When conditions allowed, collar data were uploaded automatically to the Followit Tellus server on an hourly basis, and we reviewed it daily. Besides monitoring tagged animals for any abnormal behaviour, e.g. prolonged lack of movement or dispersal events, this also allowed the remote drop-off to be activated when battery voltage fell to a critical level. Collars were retrieved using an integrated VHF antenna activated upon drop-off, and data were downloaded from the internal memory for analysis. In six cases where the remote drop-off failed, attempts were made to recover collars by shooting the fox from a high seat located in the area where the fox had been active. For two collars which were not retrieved due to drop-off failure, we used the data uploaded to the server. It is unknown whether any foxes were tagged in successive years as they were not permanently marked.

## Data preparation

We filtered out inaccurate fixes by visual assessment of estimated locations, also removing 2D fixes based on only three satellites and those with negative or outlier altitude values. There was no relationship between high horizontal degree of precision (HDOP) values and obvious outlier locations, so HDOP was not used to filter fixes. Fixes were converted from latitude–longitude to British National Grid for analysis in metres.

## Home range size estimation

In a social and territorial species like the red fox, concepts of individual or group home-range, territorial defence and exclusivity are easily confounded. In this paper, we use the term ‘home range’ to mean the subset of geographic space where a particular individual is most likely to be found based upon its observed movements (Hooten et al. 2017).

We limited our home range analysis to resident tagged foxes, defined as those that remained on the wet grassland sites for the duration each was tagged within the wader nesting season and showed a stationary spatial distribution. We did not analyse data from foxes that were (1) tagged for < 14 days ( $n=2$ ); (2) itinerant, defined as those that moved away from the wet grassland sites within a day of capture and spent most of their time away from them, suggesting they were caught on exploratory movements from elsewhere

( $n=3$ ); and (3) dispersers, defined as those that were initially present on the wet grassland sites but moved away within weeks of capture and subsequently resided elsewhere ( $n=3$ ). One male fox moved from Ibsley on the day of capture but subsequently remained exclusively on the Ellingham wet grasslands within the Somerley site. We assumed he was a resident given the early capture date (1 March) and size of his resident home range; it is likely that when caught, he was a territorial male making an excursion at the end of the mating season (Macdonald 1987).

We derived home ranges using the local convex hull (LoCoH) method (Getz et al. 2007). LoCoH has been used elsewhere for deriving fox home ranges as they perform better than the Minimum Convex Polygon (MCP) method where there are distinct boundaries that may limit movement, e.g. geographic or physiographic features, so are more suitable for animals with territory boundaries that follow hard-edged features such as roads and rivers (Walton et al. 2017). The  $k$ -LoCoH method subsets the data by selecting the  $k-1$  nearest neighbours of each reference location, then constructs the local convex polygon (i.e. local hull) around each to produce a set of non-parametric kernels whose union is the utilisation distribution (UD) (Getz et al. 2007). We took initial estimates of  $k$  for each fox as the square root of the number of locations, then evaluated by examining diagnostic plots of area covered by the UD against the value of  $k$  (Getz et al. 2007; Lyons et al. 2013). We examined sensitivity of area to selection of the  $k$ -value and found little difference for values  $\pm 5$  of the initial estimate. LoCoH home ranges were derived using the *adehabitatHR* package v0.4.19 (Calenge 2006) in R v4.0.4 (R Core Team 2021). We obtained both the 95% and 100% isopleths and examined correlations between the home range areas and perimeters for each.

To calculate minimum fox density of resident and total (i.e. resident plus itinerant and disperser foxes), we first calculated combined area of all resident fox home range areas in each year. We then determined the resident and total fox numbers tagged in each year and divided each of these numbers by the combined home range area to estimate the minimum density of the resident and total fox population, respectively, during the tagging periods. We used two-way ANOVA with Type-III sums of squares to examine the effect of site and sex on 95% LoCoH home range areas of resident foxes. To determine the extent of social relationships between the resident tagged foxes in each year, we constructed an intersection matrix of the percentage overlap of each fox with the individual home ranges of all other foxes.

## Movement behaviour

We determined the movement trajectory of each fox using the *adehabitatLT* package (Calenge 2006) in R v4.3.1, based

on 10-min fixes. For periods when individual collars had been switched to a 60-min fix schedule to conserve battery life, regular interval trajectories were created by interpolating missing values at the intervening 10-min intervals when fixes were not collected. We considered only active fixes so that phantom movements due to GPS fix inaccuracies while foxes were resting did not enter the calculation, e.g. while underground at earths. For each fox, we summarised the mean and maximum distance moved in 10 min, and for whole days where fixes were on a 10-min schedule, the mean and maximum distance moved in a day. Using the distance moved per 10-min fix event, we then calculated the speed of movement between successive fixes and related this to hour of day. We used two-way ANOVA to examine the effect of site and sex on mean daily movement distance. We examined the mean distances moved by each fox in relation to home range area and perimeter to determine whether foxes that have larger home ranges move further to patrol them. In addition, we examined fix locations in each successive day post-release in relation to the estimated home range to determine whether capture influenced movement behaviour.

## Activity patterns

Each collar recorded activity as the time it was moving in either the  $x$ - or  $y$ -plane during each scheduled 90-s fix attempt. We set the activity sensor at the most sensitive setting to ensure movements were not missed. Based upon tests with static collars, a collar was 'active' during a fix event (i.e. the fox was not resting) if there was a total  $\geq 2$  s of activity in each plane during the event. Choice of this threshold was supported by the presence of long periods ( $> 4$  h) within each 24 h where 'activity' as judged by this criterion was zero, indicating periods of rest. Activity was recorded regardless of fix success, giving a continuous sample for each fox during its tagged period. Active hours were defined as the hours in each day in which there was  $\geq 1$  active fix.

We used generalised linear mixed models (GLMMs) to examine activity patterns in relation to time of day, month of year, sex and study site. The response variable was the activity status of each fox (active or inactive) at each fix attempt, modelled assuming binomial errors with a logit link function. Fox ID was included as a random effect, to allow for individual variation in behaviour and collar fit. All other variables were converted to factors and included as fixed effects. We examined for interactions between time of day and month as foxes may increase daily activity during the spring to resource cubs.

A time-of-day factor was included as either (1) the hour or (2) diel period in which each fix attempt was made. As there was a change from GMT to BST during the study period, we analysed fox activity against both GMT and local time to determine whether fox activity aligned more closely

with astronomical time or human activity. We divided time into discrete non-overlapping diel periods: day, night and twilight. Day was defined as the time between sunrise and sunset, occurring when the sun is level with the horizon. We divided twilight into two periods likely to reflect ways in which human activity might influence fox behaviour. During Civil Twilight (sun  $< 6^\circ$  below the horizon), humans can carry out outdoor activities without artificial light (USNO 2020). During Nautical Twilight (sun  $6$  to  $12^\circ$  below the horizon), terrestrial objects are still distinguishable by humans, but artificial light is required for outdoor activity. Initial examination of fox activity data by hour indicated that the start of activity around sunset was more synchronous than the cessation of activity around sunrise, so we also distinguished AM and PM twilight periods. Night was defined as the diel period between evening Nautical Twilight and morning Nautical Twilight. This resulted in a six-level diel period factor (morning Nautical Twilight, morning Civil Twilight, Day, evening Civil Twilight, evening Nautical Twilight, Night).

We fitted GLMMs using the *lme4* package v1.1–26 (Bates et al. 2015) in R v4.0.4. We compared models using Akaike's Information Criterion (AIC). Animals do not randomly switch between activity and rest; however, GLMMs including temporal autocorrelation failed to converge, so we were unable to test the assumption of independence in activity status between fixes.

We supplemented GPS data on activity patterns using trail camera images of foxes. Cameras were primarily used to guide fox tagging effort and were frequently moved between locations within the sites before and during the nesting period to monitor mammalian predators, but nonetheless at each site provided information on the timing of fox activity during this period. For each fox detection, we recorded age (adult or juvenile), sex (if obvious) and whether it was tagged or not. Detections of foxes  $< 5$  min apart were considered as a single visit to the location (Kämmerle et al. 2019; Fiderer et al. 2019). Only images showing adult foxes were used to avoid bias from high levels of juvenile activity around breeding earth locations. Each detection event was categorised into the diel periods described above. For each site, a fox detection rate was calculated based on the number of hours cameras were operating within each diel period.

## Results

### Tagging effort

In total, 3454 snare-days resulted in 47 fox captures (including 10 recaptures) and 5 non-target captures, excluding animals that self-released. During the typical local wader nesting period (15 March–15 June), we recorded location data

for 19 foxes (8F, 11M) at Britford (2016–17, Table A1 in Appendix 1) and 16 foxes (8F, 8M) at Somerley (2018–19, Table A2 in Appendix 1). One Britford fox was tagged for  $< 24$  h as the collar became detached on a livestock fence during a movement event away from the study site, so we only used data from the 34 foxes tagged for  $> 1$  week for analysis. Overall mean data period for foxes was 45.0 days (range: 8.9–80.6 days); during the nesting period only it was slightly shorter at 41.1 days (range: 8.9–66.3 days). The number of fixes recorded by collars before battery life expired was variable, with some recording  $> 6000$  fixes. Collars on which the battery failed before reaching 3000 fixes were typically attached to female foxes who spent a lot of time underground at breeding earths: we assume their batteries depleted attempting to contact satellites. While most fixes were obtained on a 10-min schedule, a mean of 8.6% of fixes (range: 0.6–29.8%) for 28 foxes were from a 60-min schedule. Filtering removed 19,061 fixes (12.6%) from the total number of 151,822 fix attempts. Also, 47.3% of successful fixes were active fixes.

Collars were recovered from 33 foxes, with the fate of two foxes unknown after remote drop-off failures. We recorded an unidentified tagged fox on a trail camera at Britford on 18 July 2019; this indicated no obvious adverse effect on condition  $> 2$  years post-release. Ten foxes died while tagged: three from natural causes (according to veterinary pathology reports: two from sepsis; one from thoracic injuries following a suspected attack by a nesting mute swan *Cygnus olor*); three were shot on the study areas to recover collars after remote drop-off failures; and four were shot by wildlife managers outside the study areas following dispersal events.

### Home range size and density estimates

The estimates of resident fox home range showed variable differences between 95 and 100% LoCoH isopleths (Table 1). For some foxes, 100% LoCoH isopleths included areas with no fix locations that were never used (Figs. A1 and A2 in Appendix 1). 95% LoCoH isopleths followed hard-edged features and included fewer unused areas compared to 100% isopleths, such as static water bodies and specific fields in which there were no locations (Figs. 2 and 3). However, for some foxes the 95% LoCoH isopleths consisted of multiple polygons, had convoluted shapes or had holes indicating unused areas in the middle of the polygon. This complicated both estimation and interpretation of 95% LoCoH home range perimeters. The correlation between home range perimeter and home range area for LoCoH 100% isopleths was stronger ( $r = 0.88$ ) than for 95% isopleths ( $r = 0.59$ ). We therefore present both 95% and 100% LoCoH home range area estimates but only 100% LoCoH perimeter estimates (Table 1).

**Table 1** Home range estimates determined as the 95% and 100% isopleths of the utilisation distribution given by local convex hulls (LoCoH)

Fox	<i>k</i>	Area 95% (km <sup>2</sup> )	Area 100% (km <sup>2</sup> )	Perimeter 100% (m)
B16F01	29	0.23	0.35	2677
B16F02	49	0.23	0.38	2718
B16F03	46	0.38	0.67	3956
B16M02	53	0.33	0.79	4856
B16M05	44	0.13	0.21	2124
B16M06	45	0.13	0.22	2221
B17F01	25	0.15	0.19	2349
B17F03	51	0.29	0.40	3509
B17F04	48	0.23	0.35	3596
B17F05	44	0.21	0.47	3448
B17M01	31	0.14	0.23	2212
B17M05	42	0.12	0.37	3711
S18F01	37	0.59	1.15	4612
S18F02	49	0.81	1.28	5270
S18M02	39	0.66	0.86	5134
S18M03	51	1.24	1.61	6759
S18M04	46	0.80	1.19	4936
S19F01	58	0.64	0.90	4419
S19F03	26	0.51	0.66	5338
S19F04	47	0.23	0.78	3828
S19F05	44	0.82	1.29	4910
S19F06	39	0.47	0.72	3424
S19M01	45	1.01	1.45	4990
S19M02	61	0.62	0.87	3797
S19M03	58	0.45	1.20	5455
S19M04	41	0.72	1.15	4566

The number of nearest neighbour polygons (*k*) used in LoCoH estimation is shown. Only foxes determined to have a stationary distribution, i.e. resident, are included. Each fox was assigned a unique code using site (B=Britford, S=Somerley), year, sex (F=female, M=male) and number, e.g. B16F01 identifies female fox number 1 tagged at Britford in 2016

Home ranges at Somerley were larger than those at Britford (mean and range 0.68 km<sup>2</sup>, 0.23–1.24 km<sup>2</sup>, and 0.21 km<sup>2</sup>, 0.12–0.38 km<sup>2</sup> respectively; ANOVA  $F_{1,22} = 12.03$ ,  $P = 0.002$ ). Although male home ranges were mostly larger across both sites, sex was not significant. However, the

interaction between site and sex approached significance ( $F_{1,22} = 3.87$ ,  $P = 0.062$ ) due to female home ranges being larger than male home ranges at Britford, but males having larger home ranges at Somerley. The combined home range areas differed between years at each site due to the number and sex composition of foxes tagged, which resulted in variable minimum resident and total density estimates (Table 2). Nonetheless, minimum densities were over three times higher at Britford compared to Somerley. Averaged across both years, the minimum resident density at Britford was 7.0 foxes/km<sup>2</sup> compared to 2.1 foxes/km<sup>2</sup> at Britford. Including the itinerant and disperser foxes tagged at each site, the minimum total density at Britford was 10.6 foxes/km<sup>2</sup> compared to 2.4 foxes/km<sup>2</sup>. The home range overlap matrix between resident foxes (Fig. A3 in Appendix 1) showed that high percentage overlaps (> 80%) were most frequent for male–female combinations. It was also common for females to share some home range area with other females, indicating presence of social groups. Males generally had low percentage overlaps with other male home ranges, but there were two high-percentage male–male combinations, also indicating social group structure.

**Movement behaviour**

Across all 34 foxes, the mean distance moved per day was 4.65 km (SE=0.33). The maximum distance moved in a day was 19.46 km, during a dispersal movement away from Somerley. Daily movement distance of foxes at Britford was lower (mean = 3.4 km/day, SE=0.34) compared to Somerley (mean = 6.1 km/day, SE=0.35). Across both sites and years, female foxes moved further per day (mean = 5.1 km/day, SE=0.41) than males (mean = 4.3 km/day, SE=0.50). There was a significant interaction between the effects of site and sex on daily distance moved (ANOVA  $F_{1,30} = 4.36$ ,  $P = 0.045$ ) as females moved further each day than males at Britford, but males moved further than females at Somerley. The mean distance moved in an active 10-min interval was 105 m (SE=6.2). Mean movement distance per 10-min interval for resident foxes was positively related to both home range area and perimeter from 100% LoCoH isopleths (Fig. 4). Movement speeds were highest during night and twilight hours,

**Table 2** Combined home range area of resident foxes tagged in each year, estimated using the 95% isopleths obtained from local convex hulls

Site	Year	<i>N</i> resident foxes	Resident home range (km <sup>2</sup> )	Minimum resident density (foxes/km <sup>2</sup> )	Minimum total density (foxes/km <sup>2</sup> )
Britford	2016	6 (3F, 3M)	1.03	5.83	8.74
	2017	6 (4F, 2M)	0.73	8.23	12.35
Somerley	2018	5 (2F, 3M)	3.26	1.53	1.84
	2019	9 (5F, 4M)	3.45	2.61	2.90

These areas were used to estimate the minimum resident density and minimum total (resident + itinerant + disperser) density given numbers of tagged adult foxes



with females moving at faster speeds than males, particularly during daylight (Fig. 5). The maximum distance moved in a 10-min interval was 1.14 km, implying an average speed of 6.8 km/h during that 10 min.

Movement behaviour of resident foxes in the first week post-release was similar to their later behaviour (Figs. A4 and A5 in Appendix 1). While some appeared to spend part of the initial day following capture outside of their home range (i.e. B17F03, B17M05, S18F01, S19M03), this may reflect the tendency to catch foxes at or near their home range boundary because similar excursions occurred at other times. The exception was S18M02, who was resident > 2 km from the capture location and never revisited it.

We recognised two aberrant patterns of behaviour, which we interpreted as ‘itinerancy’ and ‘dispersal’. ‘Itinerants’ moved away from the capture locations in wet grasslands within 1 day. A male from each site moved immediately upon release to locations 1–3 km away and resided within small wooded areas (< 0.15 km<sup>2</sup>), from where over several weeks they made repeated movements direct to the wet grasslands and close to their capture sites. For the Britford male, this included visits to the Britford fish farm where dead fish were available to scavenge. The frequency of return visits dropped during the period each itinerant fox was tagged. A Somerley female moved 20 km to a new location in the first night post-capture, spent 2 weeks exploring rural and urban areas around this location then moved 22 km back to a wet grassland area important for breeding waders just south of Somerley, where she was shot by the site wildlife manager about a week later. ‘Dispersers’, all Britford males, resided on the wet grasslands for up to a month after being tagged, before dispersing to new locations away from them. One fox made weekly visits back to the fish farm, despite residing for over a month in an area (< 5 ha) of woodland 4 km from Britford. All dispersers were subsequently shot by wildlife managers on the new areas within 2–8 weeks of arrival.

### Activity patterns

The number of hours per day in which there were active fixes was greater for female foxes (mean = 18.6 h/day, SE = 0.55) than male foxes (mean = 16.7 h/day, SE = 0.42). One female fox was recorded active in every hour, for a mean of 23.2 in each 24-h period (SE = 0.17). Foxes were more active at Somerley (mean = 18.6 h/day, SE = 0.51) compared to Britford (mean = 16.6 h/day, SE = 0.43). The percentage of total fixes that were active was also higher at Somerley (Fig. 6). Although foxes were more active during twilight and night hours, they remained active on one-third of fixes during daylight hours, with total levels of activity increasing during the spring and into summer months (Fig. 6). The model which best explained the activity data included diel period, month,

site and an interaction between diel period and month (Table 3). The effect of site indicated that the probability of a fox being active during a location fix at Somerley was 34% higher ( $\beta = 0.29$ , SE = 0.09,  $P < 0.01$ ) than at Britford. The significant ( $P < 0.05$ ) interaction effect between diel period and month, for all levels except one, indicates that activity in each diel period is different in each month; from March through June, the activity during twilight and night increased (Fig. A6 in Appendix 1).

Cameras were operated at Britford in 14 locations in 2016 (363 camera days) and 20 locations in 2017 (589 camera days), and at Somerley in 22 locations in 2018 (812 camera days) and 43 locations in 2019 (1048 camera days, Table 4). Across both sites, fox detection rate per hour was highest during evening twilight periods and lowest during daylight (Fig. 7). Daylight detection rate was 23% of detection rate during evening civil twilight hours and 38% of detection rate at night. Cameras located at earths increased detection rates at both sites. With those detections excluded, the pattern of activity among diel periods was the same at both sites (Fig. 7). Fox detection rates were higher in all periods at Britford compared with Somerley, if detections at earths were excluded; with earth detections included, detection rate was highest in morning nautical and civil twilight at Somerley (Fig. 7).

### Discussion

Our study determined fox home range size and movement patterns in wet grassland habitats important to breeding wading birds. Our estimates of mean home range size in the Avon Valley were 0.21 km<sup>2</sup> at Britford and 0.68 km<sup>2</sup> at Somerley. Previous estimates of home range size in the UK show wide variation among rural habitats (Voigt and Macdonald 1984; Hewson 1986; Reynolds and Tapper 1995; Baker and Harris 2008). Among previous studies, the most local to the Avon Valley is the estimate of 2.7 km<sup>2</sup> from a drier farmland site with mixed agriculture about 16 km away (90% harmonic mean contour; Reynolds and Tapper 1995). This compares to wet grassland habitat estimates of 1.05–2.0 km<sup>2</sup> from the coastal dunes of the Netherlands (estimator not reported; Mulder 1985), 2.5 km<sup>2</sup> from the coastal polders of southwest Denmark (95% MCP; Meisner et al. 2014) and 4.4 km<sup>2</sup> from a wetland area of central Germany (95% MCP; Fiderer et al. 2019). To make meaningful comparisons, the model and isopleth used to estimate home range area should be the same, and unfortunately there is no consensus for choice of home range estimation method (Laver and Kelly 2008; Fieberg and Börger 2012; Seidel et al. 2018). Nevertheless, some fox home range areas in the Avon Valley were less than one-tenth the size of comparable estimates elsewhere. Indeed, our estimates were more similar to previous



UK urban fox home range estimates (e.g. Doncaster and Macdonald 1991; White et al. 1996; Scott et al. 2018).

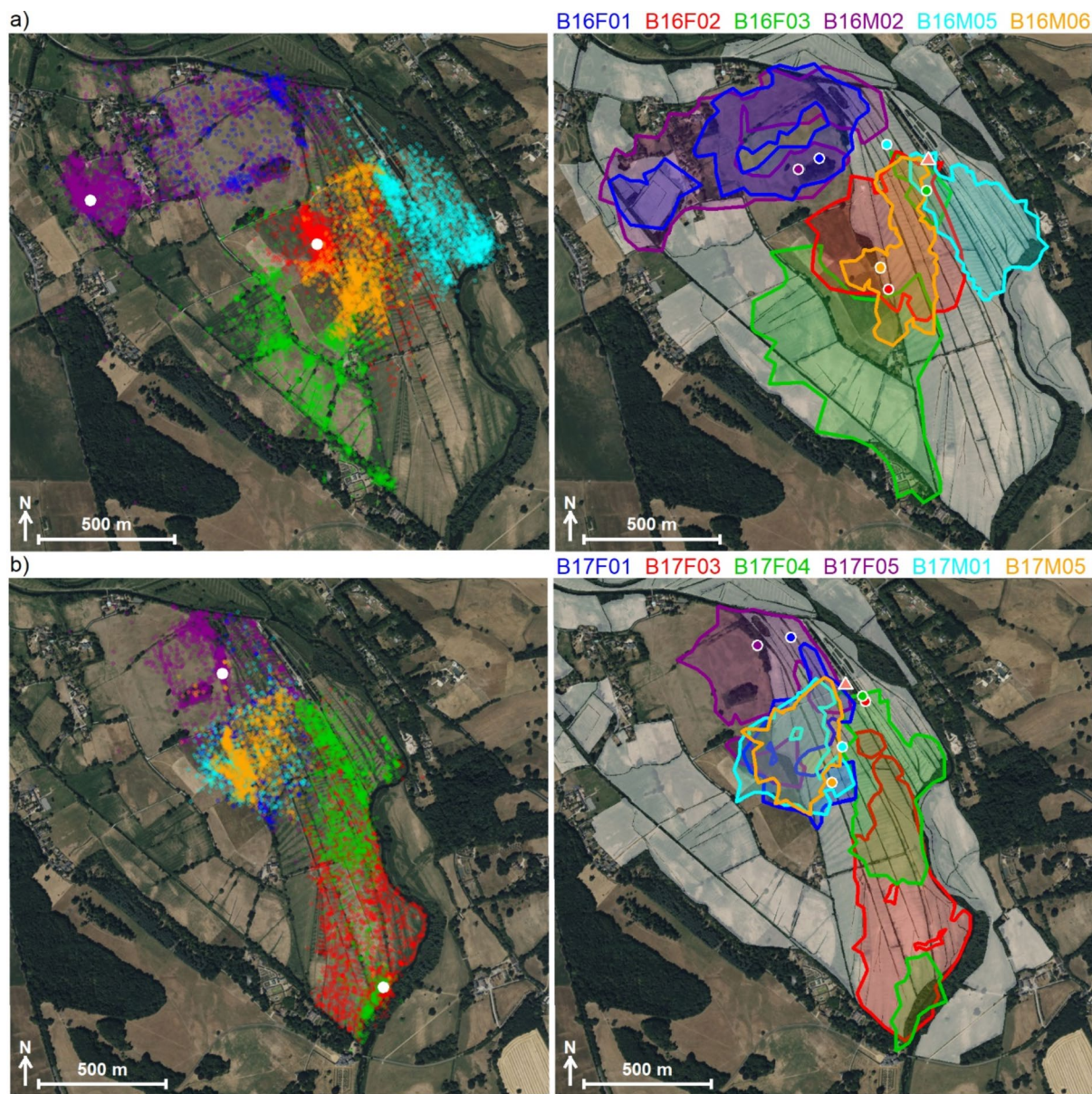
LoCoH home range boundaries followed features that could be expected to be important to territory-holding foxes but were not in themselves barriers to movement. These included river channels, carriers, ditches, roads, tracks and field boundaries. Even the main channel of the river Avon at Ellingham was frequently crossed by tagged foxes, indicating no physical barrier to their movement. Nevertheless, there was minimal overlap of activity by social groups with home ranges on opposite sides of these linear features so they can be interpreted as territory boundaries. As expected, we found male–female and female–female overlaps within shared territories. However, we also found multiple male foxes living within the same home ranges at both wet grassland sites, something that has previously been noted only in urban habitats (Harris and Smith 1987).

Although LoCoH estimates typically represent the areas utilised by each fox closely, some 100% LoCoH isopleths included unavailable areas, e.g. S19M03 home range included a small lake that was excluded from the 95% LoCoH isopleth. Also, 95% LoCoH home range areas at Somerley were three times the size of those at Britford, but the estimated minimum fox densities were less than a quarter of those at Britford. Trail camera detection rates away from earths also support higher densities at Britford. True density is likely to be higher than these minimum estimates due to the known presence of untagged foxes. A more complete estimate of density incorporating DNA evidence from the same study will be attempted in the future. Previous estimates of spring fox density in rural UK landscapes range from 0.16 to 2.23 foxes/km<sup>2</sup> (Heydon et al. 2000; Webbon et al. 2004). While Britford densities were very high, estimated minimum densities at Somerley were within the confidence intervals of fox densities estimated both locally and in similar pastoral habitats (Webbon et al. 2004; Porteus et al. 2019).

The smaller home ranges and thus higher densities at Britford may be explained by two main factors: culling pressure and food availability. At Somerley, foxes were removed by culling each autumn and winter, which must have lowered spring fox density. Even with replacement through immigration (Lieury et al. 2015; Porteus et al. 2018), all of the 22 fox culling operations studied by Porteus et al. (2019) resulted in suppression of spring density, with density on average 47% (range 20–90%) of estimated carrying capacity. The absence of fox control at Britford means the fox population was probably closer to carrying capacity. Food availability, and thus carrying capacity, may also be higher at Britford than Somerley. The wet grassland management in the upper Avon valley coupled with multiple drainage channels on water meadows leads to vegetation growth expected to benefit vole populations (*Microtus* spp. and *Arvicola*

*amphibius*) which tend to cycle. Vole densities may have been especially high at Britford during the study period because a subsidiary study found they were the principal prey items identifiable in fox faeces by macroscopic analysis (Sadoff 2017). Dead fish from the fish farm provided an abundant anthropogenic food resource that was regularly replenished during the nesting season, and numerous foxes (tagged and untagged) were photographed utilising it in 45 separate images. Utilisation of this fish resource by breeding vixens feeding cubs could explain why female home ranges were larger than male home ranges at Britford, though we caution that apparent differences in home range size between sexes will also reflect the social status of the foxes caught. Camera data also hint at higher food availability at Britford as the difference in detection rates between evening twilight and night periods, and morning twilight periods, was much greater than at Somerley, suggesting that food requirements were met within a shorter activity period each night at Britford. This interpretation is in line with the global finding that increased food availability from anthropogenic sources results in smaller fox home ranges (Main et al. 2020). A further factor that could explain differences in fox home range on wet grassland sites is the availability of suitable breeding earth locations. At Britford, the river valley is narrower and there are more dry locations suitable for earths on adjacent farmland (Fig. 2). At Somerley, further downstream, the wet grasslands are wider and therefore dry earth locations above the river terrace are necessarily further away (Fig. 3). Breeding adults at Somerley that regularly used the wet grasslands had further to travel between them and earth locations, resulting in larger home ranges.

Repeated movements to the fish farm location within and between home ranges highlight its importance to the Britford fox population. Such recursive use of resource locations has been shown to shape fox home ranges (McKeown et al. 2020); our results provided evidence of foxes remembering and revisiting such a resource in the weeks after dispersal to new areas several kilometres away. Return movements were not limited to Britford dispersers, as non-resident Somerley foxes also regularly returned to the wet grassland sites. Although the age of dispersing foxes was not determined, they were most likely young adults from the previous year who were pushed out of territories when new cubs were born. All dispersers were noticeably subordinate and docile when handled for tagging, compared to the resident foxes, with the most aggressive fox (B16M02) having a much larger home range than other resident male foxes at Britford. The new areas settled by dispersers were typically very small, and the male fox (S18M01) which secured the largest area post-dispersal made the least frequent returns to the wet grassland sites. The frequencies of return visits by each dispersing fox decreased over time, presumably as they developed a cognitive map of predictable food resource



**Fig. 2** Britford fox fix locations and estimated home ranges in **a** 2016 and **b** 2017. Fixes (left panels) are shown using transparent colours so denser colour indicates areas with greater use. Known or suspected breeding earth (den) locations are shown by solid white circles. Home ranges (right panels) determined as the 95% isopleth of the utilisation

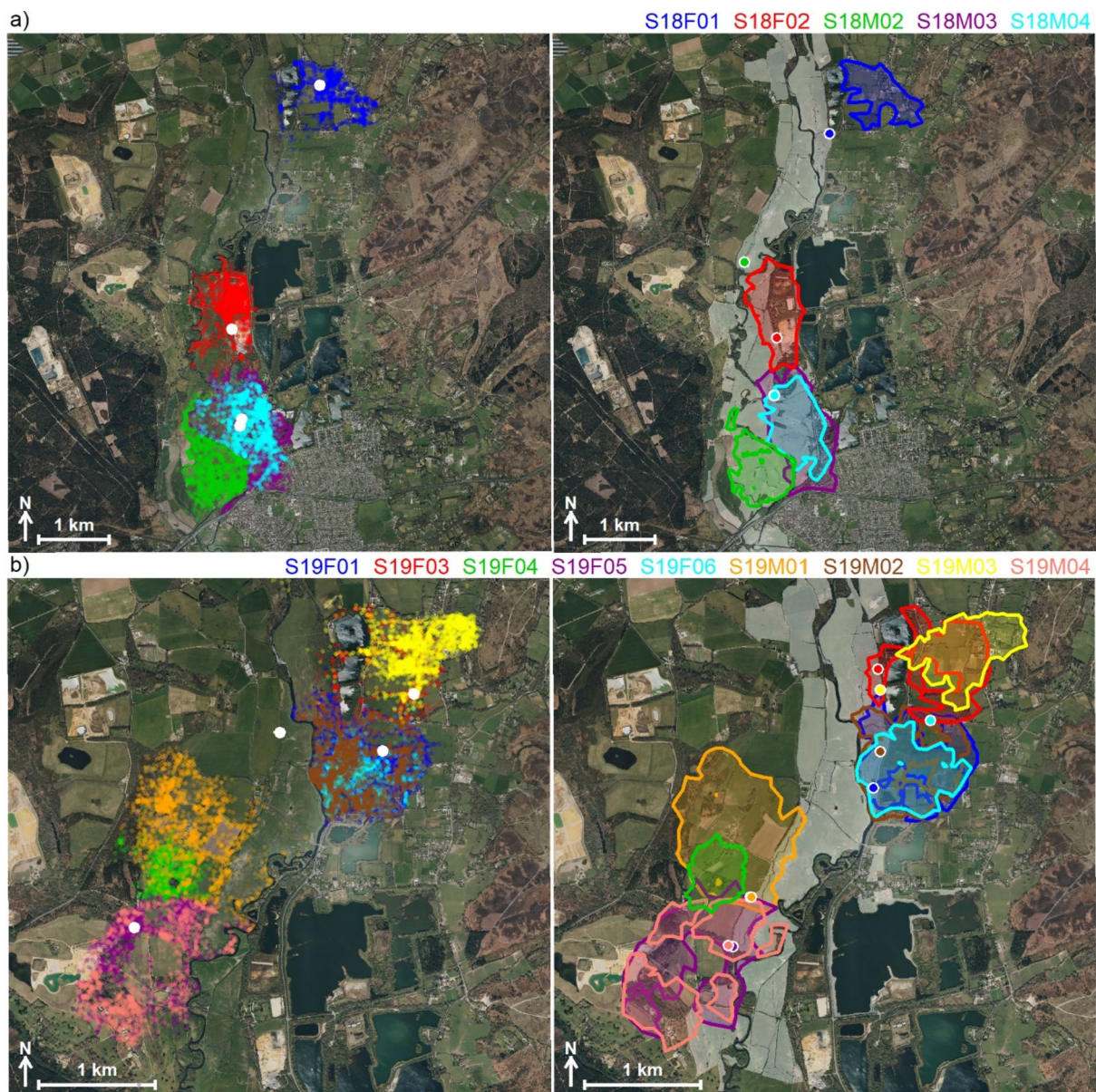
distribution given by local convex hulls. Wet grassland habitats are shown in transparent white. Capture locations for each fox are shown by matching coloured circles with a white outline. The fish farm is shown by a salmon-coloured triangle with a white outline. Contains Bing imagery (©Microsoft Corporation 2022)

locations in their new home ranges. Due to collar battery lifespan and because most dispersing foxes were killed within weeks, we do not know for how long these return movements persisted, but similar dispersal patterns have been described elsewhere (Mulder 1985).

Autumn and winter are the main dispersal period for foxes (Macdonald and Reynolds 2004), but we observed several dispersal events during the spring nesting season. Three of these events were at Britford in 2017, when fox density was high, but we cannot say whether these unusual

events were density related as we did not have all foxes tagged at each site in each year. All dispersers were male foxes, consistent with female philopatry and male-biased dispersal (Macdonald and Reynolds 2004; Walton et al. 2021). However, location fixes of captured and tagged foxes showed that itinerant foxes of both sexes were also present on wet grassland sites during this spring period. Movements of non-resident foxes across the landscape, even where there is no culling to perturb territory structure (Macdonald and Bacon 1982; Carter et al. 2007), are





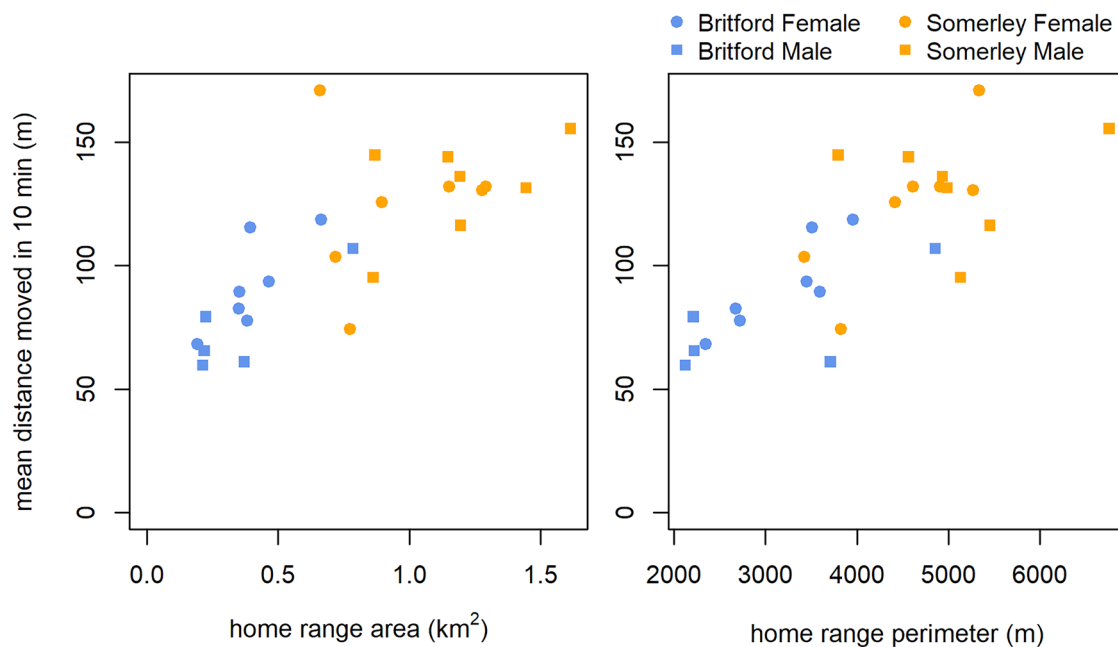
**Fig. 3** Somerley fox fix locations and estimated home ranges in **a** 2018 and **b** 2019. Fixes (left panels) are shown using transparent colours so denser colour indicates areas with greater use. Known or suspected breeding earth (den) locations are shown by solid white circles. Home ranges (right panels) determined as the 95% isopleth

of the utilisation distribution given by local convex hulls. Wet grassland habitats are shown in transparent white. Capture locations for each fox are shown by matching coloured circles with a white outline. Contains Bing imagery (©Microsoft Corporation 2022)

likely to increase predation pressure on nesting waders at a critical time of year.

At Somerley, larger home ranges meant on average those resident foxes moved almost twice as far and were active for an additional 2 h each day compared to foxes at Britford. Increased area means lengthier home range perimeters, and—if home ranges can be equated with territories—imply additional time must be spent patrolling and defending their boundaries. Together with smaller social group sizes, territory defence could explain why male foxes at Somerley

moved greater daily distances. Female foxes were active for more hours each day and also moved at faster speeds than males. During the wader nesting season, vixens have increased food requirements due to rearing of cubs. In the UK, cubs are born between mid-March and mid-April (Lloyd 1980). The additional female food required per cub during lactation is around 25% of female food requirement (Sargeant 1978), meaning a typical litter of four cubs (Reynolds and Tapper 1995) will require each breeding female to double the amount of prey captured. Once cubs



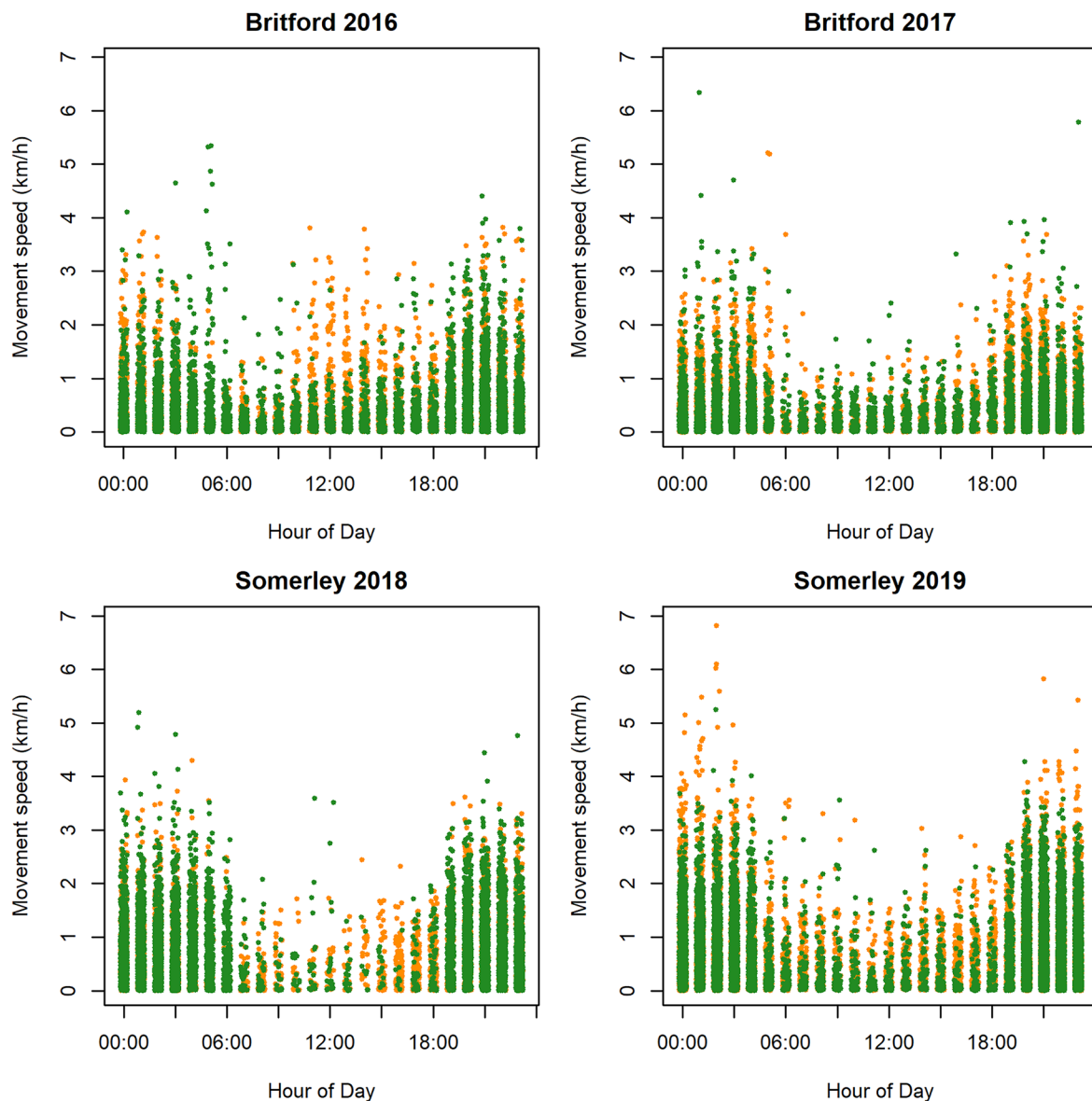
**Fig. 4** Relationship between mean distance moved in each 10-min interval and **a** home range area and **b** home range perimeter as determined by the LoCoH 100% isopleths for each fox. Symbols and colours represent different sexes and sites, respectively

are weaned, they then require an increasing amount of prey to be provisioned during the remainder of the nesting season (Sargeant 1978). An extreme example from our data was S19F03, who was active in almost all hours of the day and night. Although this level of activity seems unsustainable, our active hours metric means that a fox recorded as active in two consecutive hours could be resting for much of that time. As that collar was only used on S19F03, we also cannot rule out that it was oversensitive to activity compared to other collars. Trail cameras at that earth confirmed she was tending a litter of two cubs, but other than a tagged male (S19M03) no other foxes were detected, implying that there was no help with food provisioning from non-breeding foxes. Increased activity may also relate to earths being further from the wet grasslands, where we hypothesise that food availability was greater than around the natal earth locations. We observed S19F01 relocating cubs to the Hucklesbrook wet grasslands once they were weaned and active above ground. Although foxes in smaller home ranges did not travel so far each day, the higher density of foxes implies a greater predation risk for wader species, as suggested by the lack of recent wader breeding events at Britford.

Fox activity increased overall during the wader nesting season, and activity during twilight and night hours increased month by month, presumably related mainly to the need to provision growing cubs. Previous studies have reported that nocturnal activity patterns of foxes are related

to human presence during daylight (Díaz-Ruiz et al. 2016; Kämmerle et al. 2020). Human activity can be assumed to be linked more to clock time than to sunrise–sunset, so our finding that fox activity was better predicted by GMT than daylight-adjusted time suggests that human activity patterns were not such an important influence on fox activity on these wet grassland sites. Foxes were two to three times more likely to be active and moved faster during twilight and night hours compared with day, with highest activity in evening nautical twilight, supporting the understanding that fox foraging behaviour is chiefly crepuscular and nocturnal (Reynolds and Tapper 1995; Díaz-Ruiz et al. 2016; Kämmerle et al. 2020). Nevertheless, in contrast to those studies and similar to findings from a study in coastal polder regions (Schwemmer et al. 2021), foxes at wet grassland sites were active on about 30% of daylight fixes. Camera detection rates also showed a day–night difference (daylight rate was 23–38% of other periods), and daylight detections accounted for almost 40% of total detections. Average movement speeds during daylight hours were slower than during other periods, but routes and speeds > 1 km/h suggest some daylight foraging as well as smaller movements around den sites. This level of daylight activity highlights that it is unsafe to assume that daylight predation events are due to other predator species as foxes represent a threat to breeding waders during daylight hours as well as during twilight and night periods (Mason et al. 2018).

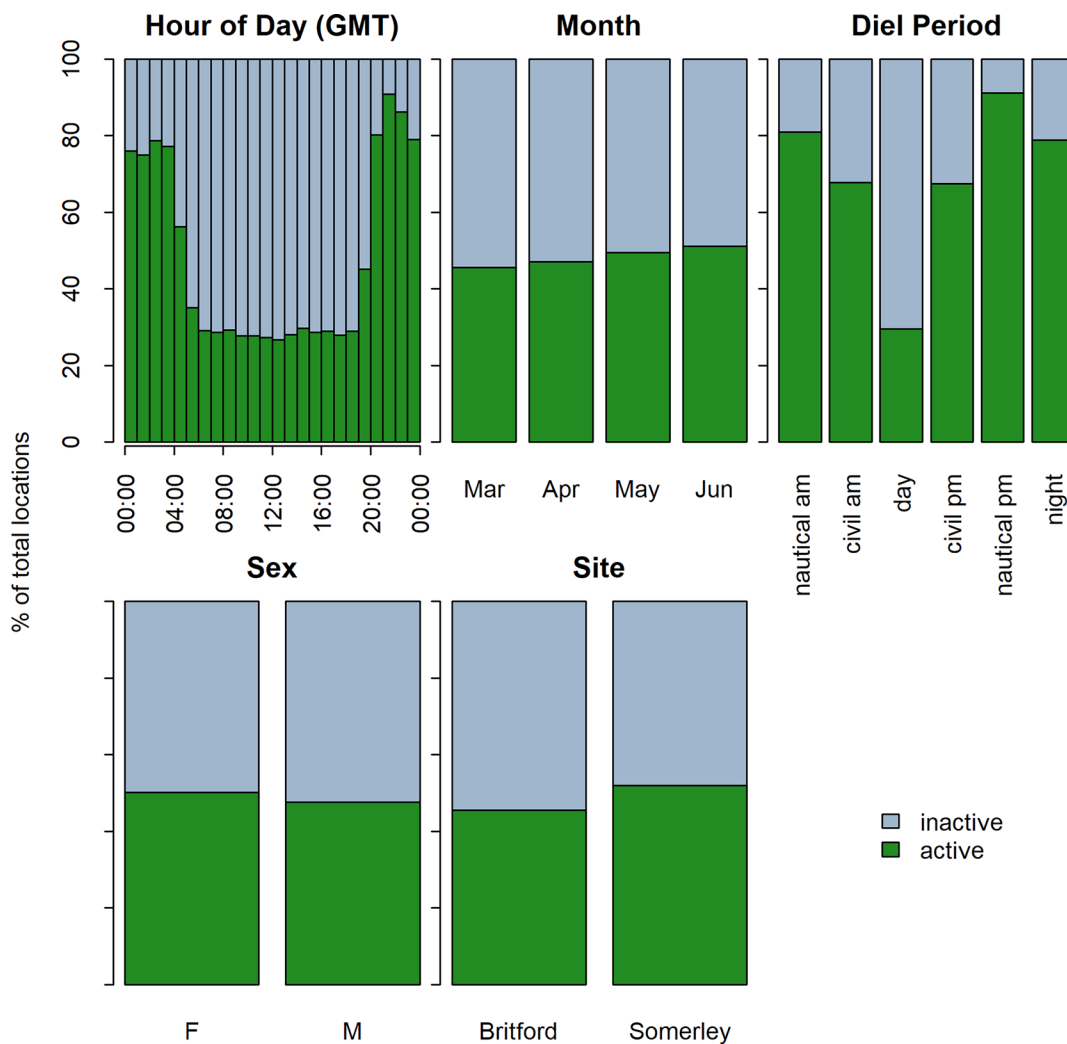




**Fig. 5** Movement speed of foxes between successive 10-min fixes in relation to the hour of day, grouped by site and year. Data are jittered on each hour and male fox data (green) are shown overlaid on female fox data (orange)

Capture locations were mostly at or near what later appeared to be the home range boundary, which supports that they are more vulnerable to capture in snares on unfamiliar ground (Reynolds and Tapper 1995). In contrast to other studies that have used them successfully in other habitats (e.g. Walton et al. 2017), cage traps were ineffective at capturing foxes in wet grassland habitats as we had no fox captures in them, and no evidence of baits in cages being taken by foxes. This suggests that

snares can be a uniquely successful capture device in this environment. Our experience in this and previous studies (Reynolds and Tapper 1995) suggests rapid recovery of red fox from capture in cable restraints, given the methodological safeguards practised here. This is supported by evidence from other canids, as Gese et al. (2019) found that wolves (*Canis lupus*) recover normal movement behaviour more quickly after capture in cable restraints compared to foothold traps.



**Fig. 6** Activity levels of tagged foxes 2016–2019 in relation to time of day, month, diel period (day, night, nautical twilight, civil twilight), sex and site

**Table 3** Activity pattern model comparisons using AIC

Model	Variables included	AIC	ΔAIC	n parameters
1	Diel6 <sup>a</sup> + Month + Site + Diel6:Month (+ FoxID)	168,570.4	0.0	26
2	Diel6 + Month + Site (+ FoxID)	169,301.5	731.1	11
3	Diel6 + Month + Site + Sex (+ FoxID)	169,301.5	731.1	12
4	Diel6 + Month (+ FoxID)	169,307.3	736.8	10
5	Diel6 + Site (+ FoxID)	169,705.4	1134.9	8
6	Diel6 (+ Site/FoxID)	169,711.0	1140.6	8
7	Diel6 + Sex (+ FoxID)	169,713.3	1142.8	8
8	Diel6 (+ FoxID)	169,713.9	1143.4	7
9	HourGMT <sup>b</sup> + Month + Site (+ FoxID)	170,522.9	1952.4	29
10	HourGMT <sup>b</sup> (+ FoxID)	170,605.6	2035.2	25
11	Hour <sup>b</sup> + Month + Site (+ FoxID)	170,978.6	2408.1	29
12	Hour <sup>b</sup> (+ FoxID)	171,061.6	2491.2	25
13	Month (+ FoxID)	208,073.7	39,503.3	5
14	Site (+ FoxID)	208,108.6	39,538.1	3
15	Sex (+ FoxID)	208,119.2	39,548.7	3

Variables in parentheses were included as random effects. ‘.’ indicates an interaction and ‘/’ indicates nested terms. All other variables were included as fixed effects

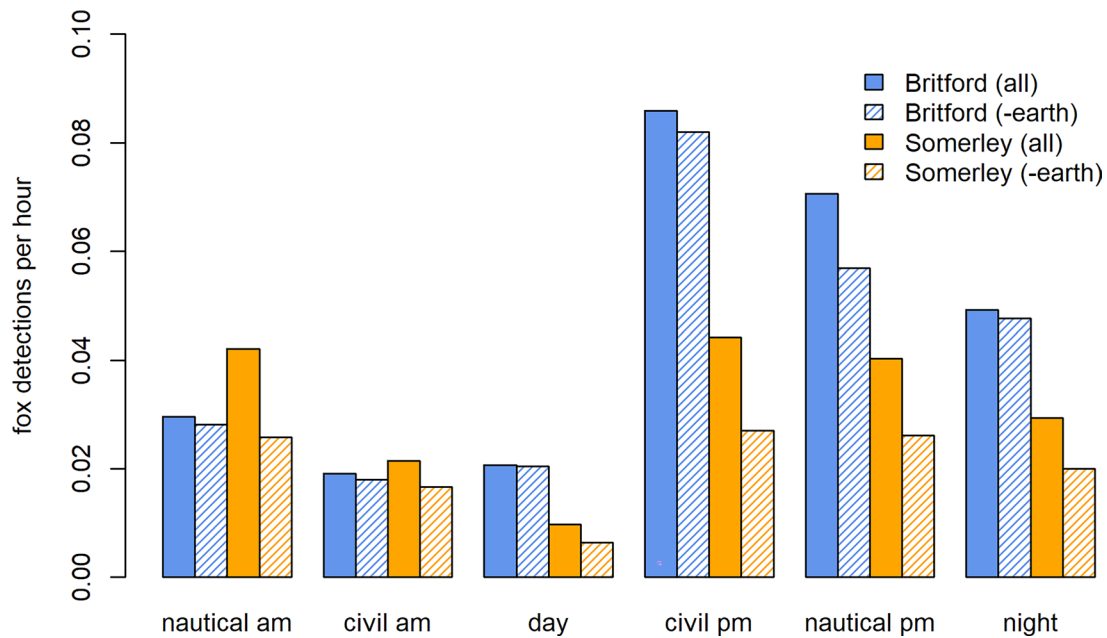
<sup>a</sup>Diel6 = 6-level factor (night, nautical twilight AM, civil twilight AM, day, civil twilight PM, nautical twilight PM)

<sup>b</sup>HourGMT = GMT time, Hour = daylight-adjusted time

**Table 4** Summary of camera trapping effort during the mid-March to mid-June nesting period

Site	Year	Number of camera locations (with fox detections)	Days operational	Number of fox detections		Mean fox detections camera <sup>-1</sup> day <sup>-1</sup>	
				Tagged	Untagged	Tagged	Untagged
Britford	2016	14 (13)	25.9 (2.4–69.7)	29	342	0.08	0.94
	2017	20 (17)	29.5 (8.1–86.6)	60	302	0.10	0.51
Sommerley	2018	22 (21)	36.9 (9.2–79.2)	16	303	0.02	0.37
	2019	43 (33)	24.4 (6.0–89.2)	126	441	0.12	0.42

The numbers of fox detections reflect adult foxes (not cubs at cameras located near earths) detected > 5 min apart



**Fig. 7** Adult fox detection rates of both tagged and untagged foxes during each of the six diel periods (nautical twilight am, civil twilight am, day, civil twilight pm, nautical twilight pm, night) on trail

cameras located at Britford (2016–2017) and Sommerley (2018–2019), for all camera locations at each site ('all', solid colours) and for those that were not situated at breeding earths ('-earth', hatched)

### Conclusions

We found very different fox home range size on two wet grassland sites within the same river catchment. Based solely on the subset of foxes captured and tagged, minimum fox density at both sites was greater than expected from other studies in rural areas, and at one site (Britford) was comparable only with urban UK fox densities. This was plausibly explained by the absence of lethal fox control and subsidy by a significant anthropogenic food resource. The presence of multiple males in some territories and the spring dispersal of some of these fits this interpretation. In turn, high fox density may explain the near absence of waders at this site and their failure to breed there despite suitable habitat.

Spatio-temporal movement patterns of resident foxes were closely related to home range metrics, in that larger home-ranges involved more daily travel. Larger home-ranges at Sommerley may have reflected lower resource availability and lower population density than at Britford, but landscape structure, i.e. a wider floodplain at Sommerley, may also have played a part in obliging foxes to den further from wetland food resources. The need to provision cubs led to increased fox activity in all diel periods, including daylight hours. At both sites, some foxes made regular use of villages and conurbations, presumably exploiting anthropogenic food resources.

Several findings of this study will be helpful in focusing fox management for waders. First, the use of anthropogenic

food resources by foxes suggests the desirability of reducing their availability, where obvious sources of food are identified and are amenable to control. Reducing the availability of food from anthropogenic sources has been shown to increase fox home range sizes, driven by reduced survival rates lowering fox density (Bino et al. 2010). Second, it was apparent that wet grassland was an attractive habitat for foxes at both sites, and certain individuals resided largely or entirely within this habitat. Discussion with landowners and game managers suggested that lethal control efforts were focused within neighbouring habitats where access and visibility were more favourable. Our findings suggest that this would be likely to target the wrong foxes, leading to poor success and loss of faith in the approach, even though in upland habitat, effective lethal control of key predators has been shown to make the difference between wader population decline and population increase (Fletcher et al. 2010). However, wet grassland is not an easy habitat for either lethal or non-lethal management. Lethal methods are limited by the flat topography and poor vehicular access, which constrain safe shooting opportunities. Rough vegetation and flooding in wet grasslands also limit the effectiveness of electric fencing to protect nests and chicks against foxes. At best, temporary electric fences are a deterrent (White and Hirons 2019; Laidlaw et al. 2021; Verhoeven et al. 2022; Jellesmark et al. 2023), and the willingness of foxes to breach them may be related to the significance of the habitat and its food resources in their daily lives. The successful use of cable restraints, combined with trail cameras, to catch foxes for tagging in this study shows that these tools can be uniquely effective in wet grassland habitat if lethal control is considered.

Understanding how mobile the fox population is during the wader nesting season itself is also important. We already knew that culled foxes can be replaced rapidly through immigration (Porteus et al. 2019); these new results suggest that potential replacement foxes can arrive overnight from 19 km away, greatly extending what we might consider to be source populations. Although intensive culling efforts can reduce the fox population locally during the wader nesting season and provide short-term relief (Porteus et al. 2019), it may be more appropriate to consider the cause of wader decline and its longer-term solution at a much larger scale (Roos et al. 2018).

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10344-023-01759-y>.

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**Author contribution** All authors designed the study; MJS collected the data; TAP managed the data, performed the analysis and wrote the initial draft of the manuscript; all authors contributed to the revisions of the manuscript, read and approved the final manuscript.

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**Availability of data and materials** The datasets generated and analysed in the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.304>.

## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethics approval** Fox capture and tagging was conducted in compliance with UK Home Office regulations under the *Animals (Scientific Procedures) Act 1986* (project licence PPL30/3273). All associated field work was subject to review and approval by the GWCT’s Animal Welfare and Ethical Review Body (AWERB).

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