Spatio-temporal movement patterns and habitat choice of red foxes (*Vulpes vulpes*) and racoon dogs (*Nyctereutes procyonoides*) along the Wadden Sea coast

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Abstract

Wetlands such as the World Heritage Site in the Wadden Sea include important habitats for breeding waterbirds. Its saltmarshes and adjacent conservation polders are used by thousands of breeding birds. However, some alarming population declines have been recorded during recent decades and previous studies found indications that predation pressure from red foxes (*Vulpes vulpes*) and more recently from invasive racoon dogs (*Nyctereutes procyonoides*) played an important role. The current study aimed to assess habitat utilisation by foxes and racoon dogs along the coast of the Wadden Sea. We equipped 21 foxes and seven racoon dogs with GPS collars and recorded a total of 37,586 (mean: 2,088) GPS fixes during a total of 2,617 (mean: 145) equipment days for red foxes and 3,440 (mean: 573) GPS fixes during a total of 272 (mean: 45) equipment days for racoon dogs. Foxes showed high individual variability in Kernel 95% home range sizes, with a mean of 172.2 ha (range: 3 to 824 ha) and little overlap among territories. Males had significantly larger home ranges than females, and there were no differences in home range sizes between adults ($n = 14$) and young ($n = 4$). Racoon dogs had smaller home ranges than foxes (mean: 52.8 ha). The preferred habitat type of both predators during daytime was the conservation polders along the Wadden Sea, while foxes also selected saltmarshes during the night. In contrast, both species avoided farmland areas. Foxes showed 20% of their activity during daylight hours and spent this time largely in areas with dense vegetation cover. None of the tagged individuals entered areas with particularly high bird densities (i.e. Wadden Sea islands or Halligen). However, our data suggest that foxes and racoon dogs frequently make use of linear structures such as dykes and dams and patrol along the tide line for carcasses. This suggests that at least single individuals of both species are prone to enter islands that are connected by dams to the mainland.

Keywords Home range · habitat use · GPS telemetry · activity · wetland

Introduction

Wetlands are among the most important habitats for breeding waterbirds worldwide (e.g. Wetlands International 2006; Long et al. 2007; Williamson et al. 2013). However, ground-nesting birds have demonstrated poor reproductive success in various regions around the globe, including bird-related Special Protection Areas (SPAs), often attributed to

predation pressures by mammals (e.g. Meisner et al. 2014; Mason et al. 2018; Fiderer et al. 2019).

This situation exists in one of the Europe's largest and most important SPAs in the Wadden Sea, extending from the eastern North Sea at south Denmark across Germany to The Netherlands. Thousands of pairs of 35 different bird species breed on the saltmarshes on the mainland (including the adjacent conservation polders), islands and Halligen (inhabited marsh islands regularly inundated during storm surges) (Bruns et al. 2001; Koffijberg et al. 2015). However, alarming population declines have been reported for most breeding birds, including rare and common species, in most regions of the Wadden Sea (Schwemmer et al. 2014; Koffijberg et al. 2015, 2017). The reasons for these declines vary, but in addition to flooding, predation by terrestrial mammals is one of the main factors affecting the breeding success of ground-nesting birds (Thorup and Koffijberg 2016; Leyrer

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et al. 2019). Previous studies showed that 30–40% of the clutch losses along the Wadden Sea coast could be attributed to red foxes and up to 30% to racoon dogs (Cimiotti and Klinner-Hötker 2019; Salewski and Schmidt 2019; Salewski et al. 2019). Given the strong population declines caused by both predator species, conservation agencies along the Wadden Sea are currently discussing management options (Leyrer et al. 2019). However, currently basic information on spatio-temporal movement patterns, habitat selection and home range sizes of red foxes and racoon dogs along the Wadden Sea coast are missing. The main aim of this study was thus to collect basic information on the spatio-temporal patterns of these predators along the Wadden Sea coast using highly precise GPS telemetry, to facilitate the management of important NATURA 2000 bird-breeding sites (e.g. by predator control or suitable habitat management measures; JMBB – Joint Monitoring Breeding Bird Group 2013; Leyrer et al. 2019). Our study was not designed to investigate direct effects of both predators on ground-breeding birds.

Red foxes (*Vulpes vulpes*; referred to as “foxes” below) are native to Central Europe and frequently prey on ground-nesting birds, according to various dietary studies (e.g. Goldyn et al. 2003; Dell’Arte et al. 2007; Rickenbach et al. 2011; Meisner et al. 2014; Elmeros et al. 2018). Although hunting intensity varies among years, annual numbers of hunted foxes reported to the German federal state of Schleswig-Holstein roughly reflect the potential population trends of red foxes (MELUND - Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung des Landes Schleswig-Holstein 2018). After a vaccination programme against rabies in Germany during the 1980s, the hunting bag of foxes in Schleswig-Holstein increased to a maximum of around 20,000 individuals at the beginning of the 1990s, and recent numbers have since levelled off at around 15,000 hunted individuals (Fig. 1).

In contrast to red foxes, racoon dogs (*Nyctereutes procyonoides*) have an even broader dietary niche, including higher proportions of invertebrates and vegetation, but also including birds, particularly during the breeding season (e.g. Sutor et al. 2010; Kauhala and Ihalainen 2014; Elmeros et al. 2018; Salewski and Schmidt 2019). The diet choice of racoon dogs has been described as opportunistic, and individuals often select superabundant prey types (Kauhala et al. 1993; Sutor et al. 2010). Racoon dogs invaded Central Europe after introduction into the European part of Russia between 1929 and 1955, with the first records in eastern Germany in 1964 (Nowak 1973). Several studies using ear tags and radio telemetry have documented this species’ strong dispersal ability (e.g. Sutor 2008; Drygala et al. 2010). Following a southeast to northwest movement, racoon dogs have also invaded the federal state of Schleswig-Holstein (Schmüser et al. 2019) and are now abundant along the Wadden Sea coast. The hunting bag of racoon dogs in Schleswig-Holstein reflects the strong population increase of this invasive species (Fig. 1). The first racoon dog in Schleswig-Holstein was recorded in 1974 (Heidemann 1975) and the first individual was shot in 1982 (MELUR 2018), while the hunting bag of racoon dogs has increased exponentially since the beginning of the twenty-first century (Fig. 1).

Although habitat use by foxes has already been studied using telemetry at various inland sites (e.g. Bischof et al. 2018; Fiderer et al. 2019), according information in coastal areas is scarce. A pilot study in Denmark analysed the spatial behaviour of three individuals close to the coast (Meisner et al. 2014). So far, this is the only available study on movement patterns of red foxes in a polder system along the Wadden Sea coast.

Similar to foxes, the activity patterns of racoon dogs have mostly been analysed in inland systems using VHF telemetry (Drygala et al. 2008a, 2008b, 2008c; Sutor 2008; Drygala

Fig. 1 Hunting bags of foxes and racoon dogs caught in the federal state of Schleswig-Holstein, north Germany (data source: MELUND - Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung des Landes Schleswig-Holstein 2018)

et al. 2010; Drygala and Zoller 2013; Zoller and Drygala 2013), while information on habitat use by this species along the coast, adjacent to one of the Europe's most important SPAs, is still missing.

The Wadden Sea coastline consists of a mosaic of different habitat types (i.e. islands, saltmarshes, conservation polders (embanked land now mainly used for nature conservation) and areas with intensive farming). Suitable breeding habitat for coastal birds in the Wadden Sea has declined as a result of ongoing sea level rises, coastal protection measures and intensive agriculture (e.g. Hofstede 2019). This coastal squeezing effect is further amplified by intensive predation pressures from terrestrial mammals such as foxes and the invasive racoon dog (Leyrer et al. 2019; Salewski and Schmidt 2019; Salewski et al. 2019). Coastal protection measures, such as the reinforcement of dams connecting Halligen (i.e. highest density areas for breeding birds) to the mainland, have increased the predation of breeding birds by foxes (Drost 2013; Schiffler et al. 2018; Leyrer et al. 2019). On Hallig Oland, severe losses among gulls and terns occurred and a spoonbill (*Platalea leucorodia*) colony on the Hallig got extinct since ground predators were able to regularly visit the Hallig (Schiffler et al. 2018; Leyrer et al. 2019). The occurrence of non-endemic terrestrial mammals on the islands and Halligen has been listed as an indicator within the Marine Strategy Framework Directive by the OSPAR commission (<https://www.ospar.org/>; OSPAR 2013). However, the movements, activity budgets and home range sizes of foxes and racoon dogs within the habitat mosaic of the Wadden Sea coast are insufficiently known (but see Meisner et al. 2014 for a preliminary study with 3 tagged foxes along the coast of south Denmark). Therefore, we investigated how foxes and racoon dogs utilised the coastal zone of the Wadden Sea, including the vast saltmarsh areas behind the sea dyke and the numerous adjacent conservation polders and the intensively farmed landscape. The aim of this study was to gather basic information on the spatio-temporal patterns and habitat use of both species to facilitate recommendations for upcoming conservation management plans.

Methods

Study area

Employing a large-scale study design, foxes and racoon dogs were caught in various places along the Wadden Sea coast in the German federal states of Schleswig-Holstein (north of river Elbe) and Lower Saxony (south of river Elbe), in the direct vicinity of the saltmarshes and nature conservation polders (Fig. 2), which provide breeding sites for various bird species. In Schleswig-Holstein, foxes and racoon dogs were caught in four different sub-areas: (1) the island of Sylt, which has been

connected to the mainland via a railway dam since the 1920s and which has high numbers of breeding foxes and racoon dogs (yearly hunting bag: about 150 foxes and 60 racoon dogs (B. Fink hunting district Sylt, pers. comm.)) and includes the large conservation polder “Rantum Becken” as an important site for around 250 breeding pairs of 20 birds species, particularly avocets (*Recurvirostra avosetta*) and black-headed gulls (*Chroicocephalus ridibundus*) (Walter 2020; Fig. 2a); (2) the peninsula of Nordstrand and the adjacent conservation polder “Beltringharder Koog” (Fig. 2b); (3) the region “Wurster Küste”, including a large summer polder system adjacent to the saltmarshes of the Wadden Sea (Fig. 2c); and (4) a polder system in the mouth of the Elbe river (Fig. 2d).

Catching and tagging of foxes and racoon dogs

Foxes and racoon dogs were caught in live traps along the Wadden Sea coast by hunters year-round. The traps were mainly placed within small passes between two water bodies and consisted of concrete tubes and a dark wooden box where the caught animal was kept until it was treated. All traps were either controlled two times per day by a hunter or were equipped with a remote system raising an alarm via a SIM card when the trap closed (Trapmaster, EPV Electronics, Germany). The traps met EU regulations, and catching permits were provided by the Obere Jagdbehörde Schleswig-Holstein and the National Park Administration of Lower Saxony. Prior to deployment, all individuals were weighed, sexed, aged (adults were differentiated from immatures < 1-year-old based on tooth abrasion) and anaesthetised by intramuscular injection of 0.3–0.5 ml medetomidine (Dormitor®; Orion Corporation, Espoo, Finland; injection volume depended on body weight) and kept in a cage until full muscle relaxation. After deployment of the GPS collars (see below), the same volume of Atipamezole (Antisedan®; Orion Corporation, Espoo, Finland) was injected as an antagonist. All animals were released immediately following deployment. Handling of all animals was in accordance with the permission provided by Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung (MELUND) and by Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit (LAVES).

GPS collars

We used GPS collars from three different companies. (1) “1C-heavy” collars (weighing 190 g) were obtained from e-obs GmbH (Grünwald, Germany). These collars stored all data until they were transferred to a base station via a VHF connection. The device schedule was informed by an accelerometer, i.e. devices adopted a low-resolution logging interval when the animal was resting (Brown et al. 2012). This feature enabled us to use the data to compute activity budgets for the foxes (see below). The five e-obs devices used were only

Fig. 2 Study area. Large-scale map: location of study area in Middle Europe; bold rectangle in large-scale map: study area along the eastern Wadden Sea coast including four sub-areas where foxes and racoon dogs were caught. **a)** Island of Sylt with the conservation polder Rantum Becken; **(b)** peninsula of Nordstrand adjacent to the conservation polder

of Beltringharder Koog; **(c)** Wurster Küste including the summer polder system adjacent to the saltmarshes of the Wadden Sea. Yellow polygons: conservation polders; red polygons: saltmarshes. Sources of satellite images: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

applied for foxes (two immature females, one immature male, two adult males; Table 1). (2) “Tellus Ultra Light” collars (weighing 220 g) obtained from Followit (Lindesberg, Sweden) were equipped with a GSM module and transferred all recorded data via a mobile phone network to a data server after a minimum of eight logs were recorded. (3) “Felis” collars (weighing 77 g) by Ecotone Telemetry (Sopot, Poland) also had a GSM module that allowed about half of the dataset to be transferred to a server via a mobile phone network, while the other half of the recorded data was stored on the collar and could be downloaded using a base station positioned within the home range of the equipped animal. Ecotone devices also had a solar panel to recharge the battery.

The logging schedules of all three device types could be reprogrammed via either a GSM network or a VHF connection to a base station. The schedules were thus adjusted to a logging interval of 20 minutes (shortest time intervals) to 6 hours, depending on the battery status and time of year. We aimed to

collect most data during the bird-breeding season (March to June) and adjusted the schedule to broader intervals outside the breeding season to conserve battery power. All recorded data were stored on the online portal www.movebank.org.

We equipped 21 foxes, including eight e-obs, seven Followit and six Ecotone devices. However, three of the eight e-obs devices failed to return any data and 18 datasets (11 females, including 3 immatures, and 7 males, including 1 immature) were therefore analysed in this study. Of the 18 datasets, six were generated in the sub-area Beltringharder Koog, one in “Neufeld”, seven in Wurster Küste and four on the island of Sylt (Table 1). Five foxes were caught in saltmarshes (27.8%), five in conservation polders (27.8%) and eight individuals in farmland (44.4%; see Table 1 for catching location of each individual).

We tagged seven racoon dogs, four with Followit and three with Ecotone devices. However, one Followit collar malfunctioned, and we therefore analysed six datasets in this

Table 1 Equipment location and period, age, sex, home range (minimum convex polygon and kernel 95%) and time spent in the three major habitat types for foxes

ID	Tag type	Tagging location	Sub-area	Equipment period	No of equipment days	No of fixes	Sex	Age	MCP (ha)	Kernel 95% (ha)	Time spent in saltmarsh (%)	Time spent in conservation polder (%)	Time spent in farmed area (%)
3524.1 ^(a)	e-obs	Cons. polder	Nord-strand	08.08.2014 - 02.03.2015	207	8661	f	im	629.3	227.4	0.9	66.6	32.5
3525	e-obs	Farmland	Nord-strand	21.06.2015 - 28.04.2016	343	5497	f	im	162.6	30.3	4.0	92.6	3.4
FI6064	Followit	Saltmarsh	Wurster Küste	22.07.2017 - 27.10.2017	98	843	f	im	387.4	148.7	2.1	3.2	94.7
Decu8	Ecotone	Cons. polder	Nord-strand	05.08.2015 - 11.09.2015	38	1697	f	ad	284.2	30.1	0.0	70.4	29.6
Decu10.1	e-obs	Saltmarsh	Neufeld	25.04.2016 - 17.07.2016	84	937	f	ad	246.9	22.3	2.0	-	98.0
Decu10.2	e-obs	Saltmarsh	Wurster Küste	04.04.2017 - 11.07.2017	99	502	f	ad	363.1	101.8	22.9	74.3	2.8
FI6136	Followit	Saltmarsh	Wurster Küste	01.03.2018 - 01.06.2018	93	1121	f	ad	786.4	90.9	27.1	29.6	43.3
FI6134	Followit	Saltmarsh	Wurster Küste	05.03.2018 - 14.03.2018	10	103	f	ad	161.5	41.3	52.4	40.8	6.8
Decu18	Ecotone	Farmland	Wurster Küste	01.04.2018 - 28.04.2018	27	182	f	ad	73.1	19.3	0.0	0.0	100.0
FI6324	Followit	Farmland	Sylt	11.10.2018 - 13.10.2019	368	1203	f	ad	287.0	47.4	12.0	0.0	88.0
Decu28	Ecotone	Cons. polder	Sylt	18.03.2019 - 26.05.2019	70	3256	f	ad	31.6	3.0	0.0	87.2	12.8
4844 ^(a)	e-obs	Cons. polder	Nord-strand	06.07.2016 - 26.10.2016	113	3193	m	im	1424.8	361.8	6.8	58.5	34.8
4843	e-obs	Farmland	Nord-strand	01.06.2016 - 28.01.2018	607	3491	m	ad	2077.6	824.2	1.0	34.6	64.4
FI6135	Followit	Farmland	Wurster Küste	16.02.2018 - 23.05.2018	97	781	m	ad	314.3	73.1	0.0	0.0	100.0
FI6322	Followit	Farmland	Wurster Küste	27.03.2018 - 25.06.2018	91	2072	m	ad	364.7	74.0	0.0	0.0	100.0
3524.2	e-obs	Farmland	Nord-strand	06.02.2018 - 24.02.2018	19	61	m	ad	551.2	427.3	0.0	0.0	100.0
FI6137	Followit	Farmland	Sylt	31.01.2018 - 05.07.2018	156	3472	m	ad	88.6	20.0	0.0	0.2	99.8
Decu17 ^(a)	Ecotone	Cons. polder	Sylt	16.02.2018 - 23.05.2018	97	514	m	ad	2482.7	555.9	23.7	20.0	56.2
Mean										595.4 (± 677.1)	8.6 (± 13.8)	34.0 (± 33.4)	59.3 (± 37.7)

^(a) Foxes were partly migratory. According excursion was excluded prior to computing home ranges

MCP minimum convex polygon; Cons polder conservation polder; f female; m male, im immature; ad adult

study (three immature males and three adult females). Three datasets were generated in the sub-area Beltringharder Koog, two in Wurster Küste and one on the island of Sylt (Table 2). Two racoon dogs were caught in saltmarshes (33.3%), three in conservation polders (50%) and one in farmland (16.7%); see Table 2 for catching location of each individual).

Data analyses and statistics

Movement patterns for all foxes (except the single fox caught in the Neufeld sub-area) and racoon dogs that returned data were visualised using the Geographical Information System (GIS) ArcGIS 10.3 (Environmental System Research Institute (ESRI) 2011). Home ranges were computed using 95% fixed kernel distributions (K95) and minimum convex polygons (MCPs100) in the Home Range Tools extension for ArcGIS (Rodgers et al. 2007). The home ranges were computed by excluding excursions (following Burt 1943) which were found in one adult and two immature foxes to explore new territories. We tested for differences in the K95 (response variable) among age and sex (predictors) for foxes using additive linear models (LMs) (Korner-Nievergelt et al. 2015). Because of the small sample size and the uneven sex/age distribution ($n = 6$), we did not perform according tests for racoon dogs. Models were checked for heteroscedasticity by plotting standardised residuals against fitted values. We also visually inspected QQ plots of the residuals to check for normality of the error distribution. No transformation of the response variable was necessary. Finally, we visually inspected the autocorrelation structure of the models using ACF plots. This indicated randomness of the response variable (K95) allowing to test for differences among age and sex using plain LMs.

We computed the proportion of time that a fox or racoon dog, respectively, spent within the three habitat types, “saltmarsh” (i.e. grazed or ungrazed areas between the dyke line and the intertidal flats of the Wadden Sea), “conservation polder” (including the dyke line but excluding water bodies) and “farmed area” (including all types of fields, pastures, bushy areas and small woodlands), based on the aerial images provided by the Nationalpark administration Schleswig-Holsteinisches Wattenmeer and satellite imagery provided by the GIS base map. Because this study aimed to analyse habitat use by foxes and racoon dogs at a large spatial scale covering the entire eastern Wadden Sea coast, we did not analyse habitat choice within the fine-scale habitat mosaic (e.g. in relation to different field types or vegetation management), but rather focussed on the relevance of the above three broad-scale habitat types.

We computed a habitat preference index, as suggested by Jacobs (1974), which has previously been used successfully to analyse habitat preference by racoon dogs at a German terrestrial site (Drygala et al. 2008c). We created a resource

selection function by determining the overall area of available habitat for each fox and racoon dog, respectively, using the smallest polygon that included all K95 home ranges (Kazmaier et al. 2001; Silva et al. 2009). We then computed the proportions of the three habitat types that fell into the polygons and finally determined the proportion of time that an individual spent within each habitat type. Following Jacobs (1974), the habitat preference was computed using the symmetrical index:

$$P_i = (U - V) / (U + V - 2UV), \quad (1)$$

where U was the proportion of habitat used and V was the proportion of available habitat type i . p varied from -1 to $+1$, with values close to $+1$ indicating strong habitat preference, values close to -1 indicating avoidance and values around zero indicating that the respective habitat was used in proportion to its availability.

Differences in preference among the three habitat types were tested using LMs following Tukey’s test with Bonferroni correction of the p value (Korner-Nievergelt et al. 2015). Models were checked in the same way as stated above.

All statistical tests were performed using R 3.5.1 (R Core Team 2018).

To determine diurnal activity patterns, all GPS fixes were classified as either “day” (i.e. all daylight hours, including the time of civil twilight) or “night” (i.e. the hours of darkness) using the R-package “suncalc” (Thieurmél and Elmarhraoui 2019). Examples of spatial differences in habitat use between day and night were plotted on a map for three foxes and one racoon dog, to illustrate circadian movement behaviours and space use.

The data generated by the five e-obs devices were finally used to compute activity budgets for the foxes. These devices were controlled by an accelerometer to switch from a high- to a low-resolution logging interval when the animal was resting (Brown et al. 2012). We computed the mean proportion of time ($\pm$ SD) in low-resolution mode for each hour of the day to illustrate the diurnal activity patterns of the foxes.

Results

Home ranges and spatial patterns

The 18 foxes showed highly variable home ranges with K95 ranging from 3 ha in an adult female to 824 ha in an adult male (Table 1). The mean K95 home range for all foxes was 172.2 ha, but the standard deviation was large ($\pm$ 221 ha; Table 1; Fig. 3). All but three foxes, which performed exploratory excursions (Decu 17 in Fig. 3a, 3524.1 and 3525 in Fig. 3b), showed stable home ranges during the whole tagging period.

Table 2 Equipment location and period, age, sex, home range (minimum convex polygon and kernel 95%) and time spent in the three major habitat types for racoon dogs

ID	Tag type	Tagging location	Sub-area	Equipment period	No of equipment days	No of GPS fixes	Sex	Age	MCP (ha)	Kernel 95% (ha)	Time spent in saltmarsh (%)	Time spent in conservation polder (%)	Time spent in farmed area (%)
Decu9	Ecotone	Cons. polder	Nord-strand	04.12.2015 - 30.12.2015	27	138	f	ad	76.4	51.5	1.4	94.2	4.3
Fl6063	Followit	Saltmarsh	Wurster Küste	13.08.2017 - 04.09.2017	23	170	f	ad	62.4	14.5	0.0	0.0	100.0
Fl6364	Followit	Cons. polder	Sylt	03.10.2019 - 27.02.2020	147	709	f	ad	295.3	129.9	0.0	86.5	13.5
Decu7	Ecotone	Cons. polder	Nord-strand	25.07.2015 - 26.08.2015	33	2019	m	im	200.8	52.1	0.9	99.0	0.1
Decu24	Ecotone	Farmland	Nord-strand	09.11.2016 - 05.12.2016	27	154	m	im	56.6	45.0	0	46.2	53.8
Fl6065	Followit	Saltmarsh	Wurster Küste	09.08.2017 - 23.08.2017	15	326	m	im	80.5	23.6	0.6	0.0	99.4
							Mean		128.7 (± 89.1)	52.8 (± 37.3)	0.5 (± 0.6)	54.3 (± 42.0)	45.2 (± 42.3)

For abbreviations, see Table 1

In total, 13 out of 18 individuals had a territory in the direct vicinity of the sea dyke at the edge of the Wadden Sea (Fig. 3). The Wadden Sea islands (except for Sylt) and Halligen were not used by the studied foxes (Fig. 3b), and most individuals spent most of their time in farmed areas and conservation polders. Males had significantly larger K95 home ranges (median: 361.8 ha) than females (median: 41.3 ha; LM: $t = 2.8$, degrees of freedom (df) = 15, $p = 0.013$) (Fig. 4a), but there was no significant difference in home range size between age classes (LM: $t = 1.6$, df = 15, $p = 0.14$) (Fig. 4b). The explained variance of the whole model was 30%. The territories of foxes equipped with GPS collars in the same region showed little overlap (Fig. 5a).

Raccoon dogs had smaller home ranges than foxes (mean K95 home range 52.8 ha, with a large standard deviation of 37.3 ha; range 14.5 ha (one adult female) to 129.9 ha (another adult female)) (Table 2). Given the low number of equipment days compared with foxes (Tables 1 and 2), the results for racoon dogs should be interpreted with caution. However, racoon dogs appeared to use similar sites to foxes (Fig. 3), with almost complete overlap of territories with foxes in some cases (Fig. 5b).

Habitat selection and temporal patterns

Overall, foxes spent most of their time in farmed areas (mean: $59.3 \pm 37.7\%$), followed by conservation polders (mean: $34.0 \pm 33.4\%$) and saltmarshes (mean: $8.6 \pm 13.8\%$) (Table 1). However, when relating habitat use to habitat availability, the preference index differed significantly among the three habitat classes (ANOVA: $F = 8.9$, df = 2, $p < 0.001$), and post-hoc tests indicated that foxes significantly selected conservation polders over farmed areas during day and night and saltmarshes only during the day (Fig. 6a). Furthermore, saltmarsh was selected over farmed areas during the night, but not during the day (Fig. 6a). Significant differences of habitat preferences among day and night within the same habitat type could only be found for conservation polders (i.e. higher preference of conservation polders during the day).

Raccoon dogs spent most of their time in conservation polders (mean: $54.3 \pm 42.0\%$) and nearly as much time in farmed areas (mean: $45.2 \pm 42.3\%$), whereas saltmarshes were used very little (mean: $0.5 \pm 0.6\%$) (Table 2). Habitat preference of racoon dogs differed significantly among the three habitat types (ANOVA: $F = 97.1$, df = 2, $p < 0.001$), and post-hoc tests indicated that racoon dogs significantly preferred conservation polders over farmed areas, both during day and night, and over saltmarshes during day, but not during night (Fig. 6b). Furthermore, there were no significant differences in the use of saltmarsh and farmed areas during the night or during the day (Fig. 6b). Significant differences of habitat preferences between day and night within the same habitat type could be found for conservation polders (i.e. higher preference during

Fig. 3 Spatial patterns of red foxes and racoon dogs in three of the four sub-areas (see Fig. 2 for locations in the overall study area). RD = Racoon dog, ad = adult, im = immature, m = male, f = female, BHK = Beltringharder Koog. Sources of satellite images: see Fig. 2

Fig. 4 Kernel 95% home range sizes of female vs. male (a) and adult vs. immature foxes (b). Bold line: median; box: 25% confidence interval; dashed line: 95% confidence interval; open circles: outliers. *** = $p < 0.001$; n.s. = not significant

the day) and for saltmarshes (i.e. higher preference during the night).

Diurnal activity was recorded for five foxes. Foxes were most active during the night and at dusk and dawn (mean proportionate activity time 45–85%) (Fig. 7). In contrast, activity clearly decreased around noon, to a mean value of around 20%. All foxes were active for at least some time throughout the daylight hours.

Foxes mainly used open areas during the night but mainly selected sub-areas with high vegetation cover during the day.

For example, female immature fox 3524.1 clearly preferred a corn field with high vegetation cover during the day (yellow polygon in Fig. 8a; only data from 9 August to 1 November 2014 shown), but spent most of its time in the adjacent grazed pasture northwest of the corn field and on the grazed dyke line to the west at night. Female immature fox 3525 mainly used the grazed sea dyke and the pioneer zone of the saltmarsh with low vegetation cover at night, but mainly used a reed bed in the centre of the conservation polder during the day (Fig. 8b; data from the whole equipment period 21 June 2015 to 28 May 2016 shown). Female adult fox Decu10.2 mainly used an ungrazed part of the summer polder during the day (yellow polygon in Fig. 8c) and the grazed part during the night (data from the whole equipment period 4 April to 17 June 2017 shown).

Similar spatio-temporal patterns were found for racoon dogs. For example, racoon dog FI6364 made excursions to the open farmland area and the dyke line separating the conservation polder Rantum Becken from the farmed area at night, but spent most of the daylight hours in either the reed beds in the conservation polder or in dense shrub areas just north of the conservation polder (Fig. 8d; only data from 3 October to 31 December 2019 shown).

Discussion

Territories and home ranges

All foxes tagged simultaneously in our study site showed distinct intraspecific avoidance behaviour with exclusive territories, in accordance with the behaviour of foxes elsewhere (e.g. Coman et al. 1991). Carter et al. (2012) stated that there was greater home range overlap between sub-adults than between adult foxes, especially at the cores of their home ranges. The same was found for foxes at an inland site in Germany, close to Berlin (Fiderer et al. 2019), and this was confirmed in the current study.

A review of nine previous studies presenting K95 home range sizes for European red foxes in a variety of landscapes (mainly urban areas and open land) derived a mean size of 131.1 ha (Fiderer et al. 2019). The overall mean of 172.2 ha in the present study would have ranked as the third highest value among these nine studies, indicating that the home ranges of foxes along the Wadden Sea were relatively large. To the best of our knowledge, no previous study has been conducted at a similar coastal site, with only two studies in coastal areas. A study of 24 foxes in an area of sand dunes north of The Hague reported a K95 home range size of 107.5 ha (Dekker et al. 2001), which was significantly smaller than that in the current study. In contrast, another study by Meisner et al. (2014) of three foxes in a coastal polder system found an adaptive K95 home range of 314 ha, which was about twice as large as that

Fig. 5 Examples of spatial overlap among three fox territories (a) and between one fox and one racoon dog territory (b). Sources of satellite images: see Fig. 2

in our study; however, comparisons should be made with care because of the use of different kernel methods and the low sample size ($n = 3$).

The home ranges of racoon dogs in our study were very small and, on average, only about a quarter the size of those of foxes. However, a study at an inland site in northeastern Germany found considerably larger home ranges (i.e. 382 ha for females and 352 ha for males; Drygala et al. 2008a), and a previous study comparing the home ranges of foxes and racoon dogs showed similar average home range sizes in both species (Drygala and Zoller 2013). Given that racoon dogs have smaller home ranges during the cubbing season and after birth (Drygala et al. 2008b), the low values found in our study may have been caused by the small sample size and the comparatively short tagging period for most of the racoon dogs. Our sample size was also too small to draw any conclusions about intraspecific overlap of territories among racoon dogs. However, a radio-tagging study of more individuals at an inland site in Germany suggested that racoon dogs did not have exclusive territories (Drygala et al. 2008a).

Foxes are known to use linear (anthropogenic) structures such as roads and forest edges, as well as settlements (Silva et al. 2009; Janko et al. 2011; Towerton et al. 2016; Bischof et al. 2018), which could explain why many individuals in the current study travelled along the sea dykes or old inland dyke lines separating the conservation polders from the farmed mainland areas. Furthermore, the preference of linear structures might explain why some foxes (though not recorded in our study) might make use of dams connecting islands or

Halligen to the mainland (Schiffler et al. 2018). The remains of dead birds or other animals along the tide line on linear dykes and dams connecting islands and Halligen to the mainland may also increase their use by red foxes, similar to their utilisation of roads to feed on animal carcasses hit by cars (Silva et al. 2009). Foxes along the Wadden Sea coast have been documented to feed on seal carcasses (T. Rosenberger, Seal Station Friedrichskoog, pers. comm.). To the best of our knowledge, there are currently no data on the use of linear structures by racoon dogs; however, this study now suggests that at least some racoon dogs may also use such linear structures, similar to foxes.

Previous studies in Australia and Europe found no significant differences in the home ranges of male and female red foxes (Meek and Saunders 2000; Drygala and Zoller 2013). This contradicts the results of the present study, which found significantly larger home ranges in males compared with females. However, given that male foxes might share their home range with several vixens (e.g. Reynolds and Tapper 1995), larger home ranges in males can be expected. Although we caught the foxes year-round, most females were tracked during the cubbing season, and it is possible that female foxes restricted their activity to areas close to the den during this period and thus had smaller home ranges. However, in most cases, the overall telemetry period for females was longer than the cubbing season, suggesting that female foxes did indeed have smaller home ranges than males.

Drygala and Zoller (2013) found that female racoon dogs had larger K95 home ranges than female foxes, while male

Fig. 6 Habitat preference of foxes (a) and racoon dogs (b). For explanation of the box plots, see Fig. 4. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$; n.s. = not significant

racoon dogs had smaller home ranges than male foxes. Although our sample size of racoon dogs was too small to differentiate between the sexes, we found clear indications that racoon dogs had smaller home ranges than foxes of either sex.

Former studies also found similar dispersal distances for immature male and female racoon dogs (e.g. Drygala et al. 2010). Given the biased sex and age distribution of racoon dogs in our study, we were not able to show similar patterns.

Our findings indicated that the home ranges of racoon dogs and foxes overlapped with no strong interaction or competition between the two species. This was supported by a study in

northeast Germany, which showed a low degree of interaction between these two species (Drygala and Zoller 2013).

Temporal patterns

Our study clearly demonstrated that foxes showed a crepuscular and nocturnal activity peak. However, in contrast to previous studies (e.g. Meek and Saunders 2000; Carter et al. 2012), all individuals in this study also showed high levels of diurnal activity, particularly in areas of dense vegetation. Our findings suggest that foxes took the opportunities to hide in

Fig. 7 Diurnal activity patterns of five foxes. Bars represent mean proportions of activity; error bars depict standard deviation

the nature conservation polders and ungrazed saltmarshes that offer high vegetation structure throughout the year.

Although our sample size of racoon dogs was too small to draw any conclusions regarding their hourly circadian activity budget, our data clearly suggest that racoon dogs were active almost exclusively at night and spent the daylight hours hidden in dense vegetation (mainly in conservation polders). The more open saltmarshes were used significantly more during the night. This matches the findings for racoon dogs equipped with VHF telemetry devices in northeastern Germany, where the authors found that 87% of activity occurred at night (Zoller and Drygala 2013). However, in contrast to former studies that found opportunistic use of different habitat types by racoon dogs with no clear temporal pattern (Drygala et al. 2008c), our results clearly suggest that the tagged individuals spent most of their time (particularly during daytime) preferably within conservation polders with abundant reed beds that offer dense vegetation that racoon dogs are known to use as shelter against cold, predation and human disturbance (Kowalczyk and Zalewski 2011).

Habitat use along the Wadden Sea coast

Given that foxes and racoon dogs showed a limited home range, the habitat choice of both species needs to be interpreted against the background of the catching location. However, we were able to equip similar numbers of both species across all three habitat types and additionally all individuals were caught in direct vicinity of all three habitat types. Therefore, our study design should provide correct results on habitat preferences.

The current results showed that both foxes and racoon dogs significantly preferred conservation polders adjacent to the coast, compared with saltmarshes and farmland. Anthropogenic activities and management measures in these

conservation areas are usually low and predators can therefore hide easily in the vast reed beds, while these conservation sites also usually include high densities of ground-nesting birds (e.g. Bruns et al. 2001), potentially explaining the importance of these areas for both study species, particularly during the daylight hours. According to studies using nest cameras (Salewski and Schmidt 2020), red foxes were responsible for 46% and racoon dogs for 28% of the predation events of black-tailed godwits (*Limosa limosa*) nests in conservation polders along the Wadden Sea coast, whereas polecats (*Mustela putorius*) were recorded in 18% and other mammal or bird species only in < 10% of the cases (Salewski and Schmidt 2019; Salewski et al. 2019).

In a similar study at a mainland site, Fiderer et al. (2019) equipped nine racoons (*Procyon lotor*) and five foxes over a 22-month period. They showed that racoon activity mostly overlapped with reed and swamp areas, indicating high overlap with waterfowl-breeding sites in reed beds, while foxes preferred woodlands, with little overlap in home ranges between foxes and racoons. Fiderer et al. (2019) suggested that foxes exerted high predation pressure on ground-nesting birds in grassland close to woodland. In the absence of woodlands in our study area, the core home ranges of many individuals in our study were in reed areas within nature conservation polders, and the tagged foxes appeared to prefer this habitat type. A preference of foxes for dense vegetation such as shrubs, forests or reed beds has been found in other studies at different sites in the northern hemisphere (e.g. van Etten et al. 2007; Fiderer et al. 2019).

The management schemes (grazing by cattle or mowing) and vegetation structures of conservation polders and saltmarshes are not easily compared. However, since a moderately high proportion of mainland saltmarshes are no longer grazed or mowed (Esselink et al. 2017), their vegetation structure (in terms of hiding possibilities for foxes and racoon

Fig. 8 Examples of spatio-temporal activity patterns of three foxes (a–c) and one raccoon dog (d) (using data from 3 October 2019 to 31 December 2019). Yellow polygon in (a): corn field (data from 9 August to 1 November 2014); yellow polygon in (c): ungrazed area in summer polder. Sources of satellite images: see Fig. 2

dogs) in some respects resembles that in conservation polders. It is therefore surprising that our study did not show similarly high preferences of either foxes or racoon dogs for these two habitat types. However, there was a significant indication that foxes preferred saltmarshes over farmlands during the night (suggesting better foraging options in saltmarshes during this time), whereas racoon dogs showed similar preferences for these two habitat types during day and night.

Whether foxes and racoon dogs deliberately select areas with high bird densities remains to be proven, although a previous study found no evidence to support such a relationship (Meisner et al. 2014). While foxes were found to significantly impact bird populations, the role of racoon dogs as nest predators seems to be strongly site-specific. While studies from northern Europe found only low predation pressure on ground-breeding birds (Opermanis et al. 2001; Kauhala 2004; see review in Kauhala and Kowalczyk 2011), a recent study carried out in one of our study sites using nest cameras revealed that red foxes and racoon dogs were the most significant nest predators in breeding areas of black-tailed godwits suggesting that both species might prefer areas with high nest densities (Salewski and Schmidt 2019). Future studies conducted at smaller spatial scales are needed to shed light on the link between numbers of breeding birds and the spatial activity patterns of the two predators. However, the availability of other prey resources, such as mice, might help to explain the habitat preferences of foxes and racoon dogs. Previous studies have shown the importance of small rodents in the diets of both species, together with cereals and fruits for racoon dogs (Kauhala et al. 1993; Dell'Arte et al. 2007; Sutor et al. 2010; Elmeros et al. 2018). Although no monitoring data are available, the availability of such prey types is likely to be low in saltmarshes (as a consequence of regular inundation during storm tides, which will not be tolerated by many rodents) compared with conservation polders and farmland areas, particularly outside the breeding season.

Nevertheless, our results suggest that areas within the coastal habitat mosaic that offer high vegetation cover are used over-proportionally by both foxes and racoon dogs, particularly at daytime (see examples for corn field and ungrazed pasture within the summer polder in Fig. 8c).

Conclusions

This study clearly shows that foxes and racoon dogs use the mosaic of the coastal landscape in a sophisticated way. Home ranges of foxes along the Wadden Sea coast were among the largest recorded in Europe, so far. Overlap of home ranges of the two species indicates that a co-existence in the same territories is possible. The results highlight the important role of conservation polders, including large reed beds, for foxes and

racoon dogs particularly during daytime. These are also the sites where many losses among ground-breeding birds by the two species were recorded (Salewski and Schmidt 2019; Salewski et al. 2019). Although most foxes along the coast seem to prefer habitat types other than saltmarshes (where the highest numbers of ground-nesting birds can be found; Koffijberg et al. 2017), some foxes also showed a preference for saltmarshes particularly during the night. While direct effects of foxes and racoon dogs on ground-breeding birds within this habitat type remain to be proven by systematically designed studies (e.g. by using nest cameras), the results of our study show that both predators were using linear structures such as flood lines in the tidal area, along dykes and dams suggesting that the tagged individuals made use of carcasses. The attraction effect by carcasses along dams can play an important role for individual predators entering areas with high densities of breeding birds, such as saltmarshes on islands and Halligen (Schiffler et al. 2018), which could have important effects on the populations of ground-nesting birds (e.g. Mason et al. 2018), with potentially severe effects on breeding success (Salewski and Schmidt 2019).

Although the current study was designed to unravel the different importance of three major habitat types along the Wadden Sea coast for foxes and racoon dogs using a broad-scale approach, we could clearly show that diurnal activity patterns of foxes and racoon dogs also differed on a small spatial scale (i.e. use of areas with dense vegetation during the day and areas with short vegetation during the night). Future work may now focus on exploring the habitat selection patterns at finer spatial scales, e.g. to determine the preferred vegetation types within conservation polders, crop types in the farmed areas and management regimes within the saltmarsh areas.

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Data Availability Tracking data of foxes and racoon dogs are archived at Movebank (<https://www.movebank.org>).

Declarations

Ethics approval Permission to catch and equip foxes and racoon dogs with GPS collars in the federal state of Schleswig-Holstein was provided

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Conflicts of interest/competing interests The authors declare no conflict of interests and no competing interest.

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