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RESEARCH

Habitat selection and movement patterns of the Raccoon dog (*Nyctereutes procyonoides*) in Denmark using GPS telemetry data

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Abstract

The Asiatic raccoon dog (*Nyctereutes procyonoides)* has successfully colonized Northern, Eastern, and Central Europe, following 20th century introductions. While subject to eradication campaigns, its ecological impacts remain incompletely understood and debated. This study aims to examine the habitat preference and movement patterns of raccoon dogs in Denmark using GPS telemetry data. Habitat selection patterns were examined seasonally using Jacob's electivity index. Movement intensity (travel speed) was examined according to temporal and environmental predictors such as time of day, time of year and habitat type. Raccoon dogs showed an overall preference for peatbogs, marshes, and broadleaf tree cover, and an overall avoidance of water bodies (per se), artificial surfaces and constructions, natural material surfaces (e.g., river pebble banks, beaches, sand dunes), cultivated areas, coniferous tree cover and herbaceous vegetation, and a close to neutral selection pattern for moors and heathland. Habitat usage was generally consistent throughout the seasons for all habitat types, apart from minor shifts observed, particularly from November to February. The raccoon dog exhibited a unimodal nocturnal activity pattern throughout all seasons, with highest mean travel speeds occurring during spring and lowest during winter. Prolonged periods of higher mean daily speeds were observed during autumn. Mean speed levels also varied according to habitat type, with raccoon dogs moving slower in habitats they preferred and faster in those they did not prefer. These results indicate that raccoon dogs in Denmark adjust their habitat selection and movement patterns throughout the year, with a general preference for moist and high tree coverage areas. This information can be utilized in forecasting models for their potential future range and area use in different regions.

Keywords Raccoon dog · *Nyctereutes procyonoides* · Habitat · Travel speed · Telemetry

Introduction

The raccoon dog (*Nyctereutes procyonoides,* Grey 1834), a medium-sized omnivorous canid, indigenous to East Asia, was introduced to the former USSR in the mid-1900s, where it rapidly established and spread throughout Central and Northern Europe at a rate of approximately 40 km per year, and occasionally up to 120 km per year (Lavrov 1971). In Denmark, the first raccoon dog was recorded in 1980 on the Jutland peninsula (Baagøe and Ujvári 2007), and since then the raccoon dog has established populations throughout Jutland but not yet on the remaining island regions of Eastern Denmark (Miljøstyrelsen 2020), although observations have been made on Funen (Pers. Comm. Mariann Chriél).

Following an increased presence of the raccoon dog across EU member states, the European Union classified the species as invasive in 2017, due to its estimated threat to native biodiversity (European Union 2017). Primary concerns regarding their threat to biodiversity revolve around the negative impacts that the raccoon dog may have on native mesopredator and prey species; particularly regarding the predation of threatened bird and amphibian populations. In addition, the

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potential for disease transmission exists, such as the rabies virus, tapeworm (*Echinococcus multilocularis*), roundworm (*Trichinella spiralis*) and sarcoptic mange (*Sarcoptes scabiei)* (Kauhala and Kowalczyk 2011), however, there are no known pathogens that have been newly introduced by the raccoon dog to Europe (Pagh and Chriél 2017). The raccoon dog may locally predate ground nesting bird colonies (Koshev et al. 2020; Salewski and Schmidt 2019; Viksne et al. 2011), and may successfully scare away nesting birds as large as graylag geese (*Anser anser*) (Dahl and Åhlén 2019). This is particularly concerning as ground-nesting bird populations are in severe decline across Europe (McMahon et al. 2020). Amphibian species, particularly those with vulnerable isolated populations are another topic of concern (Miljøstyrelsen 2017; Mulder 2013) as amphibians and their spawn are a common occurrence in the raccoon dog diet, especially during the spring and summer months (Elmeros et al. 2018; Sutor et al. 2010). Nevertheless, there is no evidence that these organism groups are doing worse in parts of Europe long occupied by raccoon dogs than elsewhere. Various studies have examined the niche overlap between the raccoon dog and native mesopredators in Europe, such as the red fox (*Vulpes vulpes*), badger (*Meles meles*), pole cat (*Mustela putorius*), and pine marten (*Martes martes*) (Baltrunaité 2010; Drygala and Zoller 2013a, c; Elmeros et al. 2018; Kauhala et al. 1998b; Sidorovich et al. 2000a). They were found to indeed have niche overlap, particularly dietary, however, differences in diet were variable enough that only minor competition may occur when resources are plentiful (Drygala and Zoller 2013b; Elmeros et al. 2018; Jędrzejewski et al. 1989; Kauhala et al. 1998a; Sidorovich et al. 2000b). In times of limited resources, and in areas where the raccoon dog does not display winter passivity, competition with native predators could potentially occur (Watabe and Saito 2022). Raccoon dogs may utilize badger setts and fox dens for shelter and pup rearing, and have been observed to peacefully cohabitate with badgers and foxes (Kowalczyk et al. 2008). Although evidence of localized influence on prey species and niche overlap with other mesopredators exists, the general impact that the raccoon dog has on Europe's native biodiversity remains unclear.

The raccoon dog is an opportunistic generalist, having a wide dietary niche (Castelló 2018; Elmeros et al. 2018), a high reproductive capacity (Helle and Kauhala 1995; Kauhala 1996b; Kowalczyk et al. 2009; Pagh et al. 2020), effective dispersal (Drygala et al. 2010; Herfindal et al. 2016), and an ability to hibernate (Kauhala and Saeki 2004; Mustonen et al. 2007; Ward and Wurster-Hill 1990); all of which collectively attribute to their successful establishment of novel areas. In general, they prefer habitats such as meadows, moist deciduous and mixed forests with abundant understory, river valleys, lakeshores, marshes, and moist heath. However, they are also known to occupy other habitats such as woodlands and agricultural areas (Castelló 2018). Habitat use by raccoon dogs can be affected by the availability of food (Castelló, 2018), shelter and suitable den sites. Raccoon dogs are largely nocturnal; however, they may also be quite active during the day but typically only if they have thick vegetation as refuge (Ikeda et al. 2016; Kauhala et al. 2007; Schwemmer et al. 2021; Zoller and Drygala 2013). In Finland, periods of highest seasonal activity are between March and April, potentially due to the mating season and in response to an increase in food availability. Periods of lowest activity are between November and February (Kauhala et al. 2007), associated with a period of winter dormancy or intermittent wintertime passivity (Mustonen et al. 2007; Süld et al. 2017). During the autumn months, raccoon dogs accumulate extensive fat stores (Korhonen et al. 1991), in preparation for winter dormancy (Kauhala and Saeki 2004; Ward and Wurster-Hill 1990).

Scientific research examining raccoon dog ecology in Denmark is limited, and ecological assessments in different ecoregions will allow for more accurate and effective risk assessments regarding the species' impact on native biodiversity. Therefore, this study aimed to examine relevant ecological traits of the raccoon dog in Denmark, including habitat preferences and movement patterns such as travel speed, using GPS-based telemetry data, to provide a better understanding of the role that the raccoon dog plays in the ecosystem. Habitat preferences were examined according to the biological seasons, and travel speed was examined according to time of day, time of year and habitat type. Further examination of travel speed was made according to the time of day across biological seasons. Referring to results from similar studies in Europe, we hypothesized that the raccoon dog in Denmark would exhibit distinct shifts in their:

(i) Selection of habitat types according to the biological seasons, with an overall preference for high-coverage forests and habitats closely associated with water,
(ii) Travel speed according to the time of day between the biological seasons, by exhibiting a unimodal nocturnal activity pattern, and higher speeds during the spring and summer months, and lower speeds during the winter denning months, and
(iii) Travel speed according to habitat type, by exhibiting lower speeds in preferred habitats and higher speeds in avoided habitats.

Methods

Study area

The study area includes the Danish peninsula of Jutland as well as the neighboring island region of Funen (56.2639°N, 9.5018°E) (Appendix A – Fig. 6). This is the region of Denmark where raccoon dogs are known to be established. The study area spans approximately 32,800 km^2 and shares a border with Germany. The land is heavily cultivated with 65.8% of the land area being dedicated to agricultural practices (Bank 2018), and the remaining proportion of natural land primarily consisting of coniferous and deciduous forests, wetlands, coastal dunes, grasslands, and moors and heathlands. Denmark is low in elevation with average elevation being 31 m above sea level, and has a temperate climate with an average annual temperature of 9.1 °C and extreme temperatures of -23.1 °C and 34 °C (2011–2020) (Danmarks Meteorologiske Institut 2021).

Telemetry data preparation

The telemetry data used in this study was collected via GPS-based satellite transmitters in the form of radio-collars which were placed on feral raccoon dogs that were trapped and released back into Danish nature on both Jutland and Funen for monitoring purposes over the course of 10 years (2011–2020). All trapping, collaring, and handling of raccoon dogs occurred prior to the commencement of this study. The collared raccoon dogs were released into areas that were deliberately chosen by the monitoring program and were also manually moved from place to place on occasion. This monitoring of raccoon dogs is part of a national program run by the Environmental Protection Agency—Ministry of Environment of Denmark (Naturstyrelsen 2010). The primary objective of this monitoring effort was to utilize the knowledge of raccoon dog monogamous pairing behavior to locate others to facilitate more effective eradication efforts. Individuals that were collared were adults and the sex of the individual was only recorded if they were used on a long term basis. The geospatial telemetry data was collected via an enterprise known as "FollowIt" (Followit 2018).

The geographic location of each collar was recorded at various time intervals with the majority being recorded at 10-min, 2-h and 3-h time intervals. The coordinates were registered in decimal degrees formatting, in addition to the date and time of point registration. The coordinates were converted to UTM format prior to analysis and mapped in qGIS (version 3.1). Before using the raw coordinate data, coordinate duplicates, points registered outside Jutland and Funen (except those registered in northern Germany, indicating movement between Denmark and Germany), locations where raccoon dogs were known to be handled, and if the interfix speed exceeded 20 km per hour (indicating car travel), were removed.

Habitat selection

Telemetry and land cover data preparation

For the habitat selection analysis, telemetry data registered within Denmark only was used, and the first three days of each individual raccoon dog's telemetry data were removed from the dataset to minimize bias in habitat choice associated with the deliberate human placement of the individual. To categorize habitat types, a land cover raster layer of Denmark was acquired from the Sentinel-2 Global Land Cover project (Malinowski et al. 2020). In Denmark, 10 land cover classes were present: artificial surfaces and constructions, cultivated areas, broadleaf tree cover, coniferous tree cover, herbaceous vegetation, moors and heathland, marshes, peatbogs, natural material surfaces (f.ex. river pebble banks, sand dunes, beaches), and water bodies (full descriptions found in Appendix A - Fig. 5). The overall accuracy of this land cover estimation was estimated at 94% (Malinowski et al. 2020). To limit the raster layer to only include areas that raccoon dogs can physically access, the layer was cropped further to the size of the Danish land mass with a 3 km coastal buffer, which included portions of the ocean and fjords (see Appendix A - Fig. 6). The buffer range of 3 km was chosen because there were a few telemetry points located within this distance from the coastline, specifically within the fjords.

Analysis

Habitat selection was analyzed across four seasons, which were defined according to previous literature (Drygala et al. 2008; Zoller and Drygala 2013). The seasons include oestrus and gestation (OG, March – April), birth and cub-rearing (BCR, May—July), extensive foraging and fat accumulation (EF, August – October) and reduced activity (RA, November – February). To determine if any particular habitat type was being either selected or avoided, an electivity index (Jacob's D) was calculated for each individual within each habitat type (Manly et al. 1993). The formula used for calculating this index is as follows:

$$D = \frac{(r - p)}{r + p - 2rp}$$

where r represents the proportion of habitat used, and p represents the proportion of habitat available. The electivity index (D) may range from -1 to + 1, where negative values indicate avoidance and positive values indicate selection. A value of 0 indicates neutrality, with neither selection nor avoidance. The proportion of habitat available (p) was calculated uniquely to each individual based on the proportion of each habitat type found within their unique utilization distribution (UD). The UD was calculated using kernel density estimation, using a 95% isopleth level and reference bandwidth. To ensure an accurate UD estimation, only individuals with a minimum of 40 telemetry points were included in this analysis (Kauhala et al. 2010; Seaman et al. 1999), resulting in a total of 129 individuals with the mean number of telemetry points per individual being 1,900, the minimum being 41 and the maximum being 5,992. To ensure that the UD represented areas raccoon dogs could realistically access, the UD was cropped to have the same boundaries as the land cover raster with a 3 km coastal buffer (see Appendix A - Fig. 7b). A land cover raster layer was created for each individual that corresponded to their UD size, and the proportion of each habitat type available was determined by extracting the raster values from their unique raster layers and dividing the number of each habitat's raster cells by the total number of raster cells. This method assumes that all geographic areas within the individual's UD are equally accessible to the individual. Each individual's telemetry data was subset according to season and the UD was estimated according to this data (for an example, see Appendix A - Fig. 8). For individuals monitored over multiple years, the seasonal data was pooled together for all years.

The proportion of habitat used (r) was defined as the number of telemetry points for each individual found within each habitat type, divided by the total number of telemetry points of that individual. Only the telemetry points found within the individual's UD were used. Once the proportion of habitat used and available were calculated, the electivity index was calculated for each habitat and individual separately.

Statistical analysis

To determine if habitat use was selective or random, the selection index value for each habitat type across four seasons was tested for being significantly different from the value of 0. The Anderson–Darling test was used to test for normality, and a One Sample T-test was used for normally distributed data, and a Wilcoxon Signed Rank test was used for non-normal data.

To determine if the selection pattern for each habitat type varied according to season, linear mixed effect models were built for each habitat type separately (see Appendix A - Table 3 and *Statistical modelling* for model details and methodology). To test if the fixed effect *Season* had a significant influence on the response variable *Selection Index,* Wald Chi-Square tests were performed when normality assumptions were met, whereas the Kruskal Wallis Rank Sum Test was used when normality assumptions were not met. If significant, Multiple Comparisons of Means with Tukey Contrasts was used for the normal data, and the Dunn test for the non-normal data, to determine which seasons differed from one another.

Travel speed

Telemetry data preparation

For the analysis of travel speed the first three days of data collection and the data acquired from individuals that traveled between Denmark and Germany's border were included. To examine each individual's path of movement, a 'track' was built using the *make_track* function of the *amt* package using R software. This track consisted of all registered fixes placed in consecutive order by time per individual. The track for each individual was converted into a 'step' format, using the *steps* function of the *amt* package which compiles two consecutive telemetry points into one 'step' using 'step length (straight-line distance)' and 'step time duration' (hereafter referred to as 'interfix time' (IT).

Analysis

We used the animal's rate of travel (speed, in meters/hour) to infer overall activity patterns according to (Ensing et al. 2014; Merrill and Mech 2003; Owen-Smith and Goodall 2014; Palomares and Delibes 1993). Through the examination of movement intensity, we can generally infer the type of activity that the animal is executing, with slower speeds indicating rest, or intense foraging and higher speeds indicating directional movement activities, such as dispersal. For each individual, the rate of travel was calculated for each step of their track. The rate of travel for each step was calculated as follows:

$$Speed = \frac{step\ length\,(m)}{interfix\ time\,(hr)}$$

The IT was chosen based on prioritizing the lowest possible IT to optimize accuracy of speed calculations while still maintaining a high enough sample size for further analysis. The majority of the telemetry data was collected using ITs of 3 h, 1 h, 6 h and 10 min (in that order). There was a 2-min buffer around each IT, therefore the ITs included in this analysis are of a 2-min range (see Appendix B - Fig. 9 and Table 7). Only individuals with a minimum of 50 'steps' were used in the analysis.

Travel speed was examined according to two main predictors: the *time of day between seasons* (defined by 24 h across four seasons) and *habitat type* (defined by 10 habitat types). The seasons were defined according to the raccoon dog's biological seasons. Due to sample size constraints, the seasons for this analysis were redefined as OG (April), BCR (July), EF (October) and RA (January).

To optimize the analysis in response to sample size constraints, different ITs were used according to the hypothesis being tested. To choose the most appropriate IT for each hypothesis, priorities were given to choosing that i) which was lowest, ii) provided a high enough overall sample size, iii) and provided a relatively well-balanced design. For examining *Speed* according to *time of day between seasons*, an IT of 10 min was used (Appendix B - Tables 8 and 9), according to *habitat type* an IT of 3 h was used (Appendix B - Table 10). To understand the methodology behind these choices please refer to Appendix B (*Methodology*).

The *habitat type* variable represented the same ten land cover categories as in the habitat selection analysis and was developed by extracting the raster values from the land cover raster for each corresponding 'step' that was used to calculate each speed value. Since each 'step' used to estimate speed is comprised of two consecutive telemetry points, one of the telemetry points was chosen to extract the raster values to. It was determined that using either the first or last telemetry point of the 'step' did not make a difference in the percent variation explained of the *Speed* variable, so the habitat type of the first telemetry point of the 'step' was used to create the variable.

Statistical analysis

All models used in this analysis were linear mixed effects models (see Appendix B - Table 11 and *Statistical modelling* for model details and methodology). The residuals of all models were not normally distributed; therefore, response variables were log10 transformed to meet the assumptions of a linear mixed effects model. Post hoc pairwise comparisons for the model terms of interest were performed by estimating the least square means (otherwise known as estimated marginal means) for the fixed effect term of interest and then performing pairwise comparisons on these means (using the *ls_means* function of the *lmerTest* package (Kuznetsova 2020)). Least square means were used due to the unbalanced nature of the experimental groups and to account for the presence of other influential variables within the model (Mangiafico 2016).

Results

Habitat selection

Availability and usage of habitat types

The largest proportion of land area was cultivated areas (37.3%), water bodies (19.6%) and herbaceous vegetation (19.3%). While the most raccoon dog telemetry points were found in peatbogs (24.5%), marshes (21.2%), cultivated areas (17.6%), herbaceous vegetation (14.4%), and broadleaf tree cover (11.3%) (Fig. 1, Appendix A – Table 1).

Selection according to season

Throughout the year, the raccoon dog consistently preferred peatbogs, marshes, and broadleaf tree cover and consistently avoided water bodies, natural material surfaces, cultivated areas, and artificial surfaces and constructions. The degree of preference or avoidance of these habitat types varied only slightly between the seasons. In contrast, the raccoon dog's selection patterns in coniferous tree cover and herbaceous vegetation varied between preference and avoidance throughout the year, with these habitats being avoided during the summer months and preferred or neutral during the winter months (Fig. 2, Appendix A – Tables 2, 3, 4 and 5).

Overall variation in the median selection or avoidance of habitats observed between the seasons was highest in coniferous tree cover (ΔSI 0.62), followed by moors and heathland (ΔSI 0.57), cultivated areas (ΔSI 0.43), herbaceous vegetation (ΔSI 0.35), broadleaf tree cover (ΔSI 0.20), artificial surfaces and constructions (ΔSI 0.13), peatbogs (ΔSI 0.11), marshes (ΔSI 0.08), water bodies (ΔSI 0.02), and lastly natural material surfaces (ΔSI 0.0). Overall selection patterns across all habitats were most similar between the BCR and EF seasons, and most dissimilar between BCR and RA (Appendix A - Table 6).

Travel speed

Raccoon dogs traveled with an overall mean speed of 402 m/h ± 799 SD (IT: 10 min, $N = 30$), 229 m/h ± 467 SD (IT: 1 h, $N = 115$), and 280 m/h ± 500 SD (IT: 3 h, $N = 111$) (Appendix B – Table 7).

Time of day

The time of day played a significant role in explaining variation in travel speed (Appendix B – Table 12), with there being a unimodal nocturnal trend. Nocturnal behaviour was observed consistently throughout each biological season with minor variations; the most notable occurring during the peak hours of movement. Daily travel speeds were lowest during RA, followed by EF, then BCR, and highest during OG. Higher speed levels persisted for longer during EF, and significantly higher speeds occurred during the peak hours of BCR and OG, particularly when compared to RA (Fig. 3, Appendix B – Tables 13, 14 and 15).

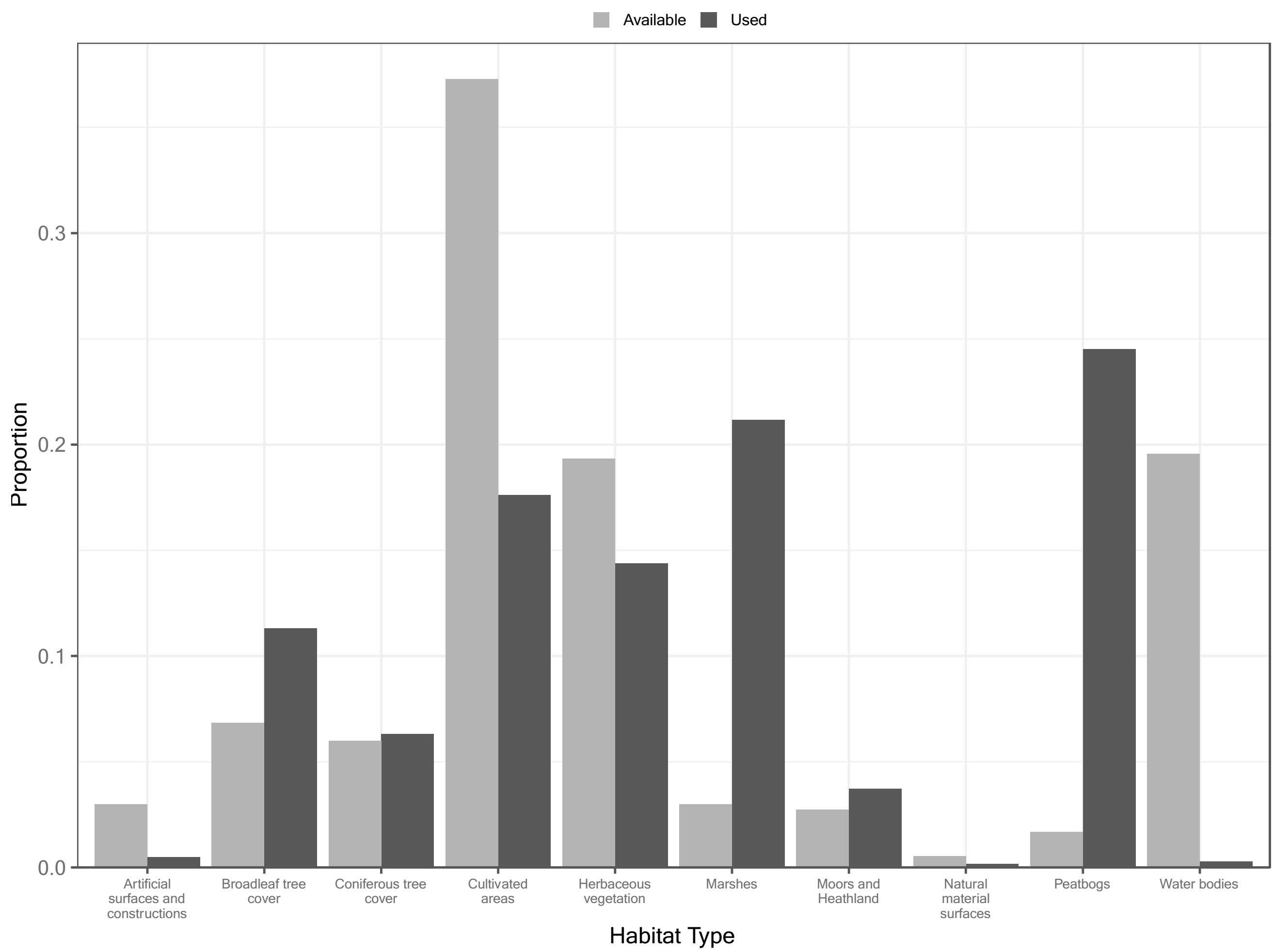

Fig. 1 Proportions for each habitat type that is available and used by the raccoon dog according to the entire study region in Denmark and entire telemetry dataset. Habitat available represents the proportion of the land cover raster that is represented by each habitat type and the habitat used represents the proportion of telemetry points found within each habitat type from the entire telemetry dataset

Habitat type

Raccoon dog travel speed varied significantly between habitat types, with the highest mean speeds being in artificial surfaces and constructions, water bodies, natural material surfaces and cultivated areas, and the lowest speeds being in peatbogs and marshes. (Fig. 4, Appendix B – Tables 16, 17, 18 and 19).

Discussion

Reliability of the method

Habitat selection

Autocorrelation of the telemetry points may be a challenge in telemetry data, however, studies have found that the benefits associated with controlling for autocorrelation, do not outweigh the costs of not controlling for autocorrelation, as it can severely reduce the sample size and also limit the biological significance of the analysis (De Solla et al. 1999; Fieberg 2007). Lastly, the inability to analyze differences in habitat selection patterns according to sex, was another limitation, as there was a limited number of individuals that were sexed within the dataset, and there was also a strong bias of males being monitored as opposed to females.

Travel speed

The complications associated with interpreting speed values estimated at different IT´s lie with making accurate distance traveled estimates between the telemetry points used to estimate speed. The distance traveled between the two points is measured as a straight-line distance, which often is not representative of the actual trajectory that the animal

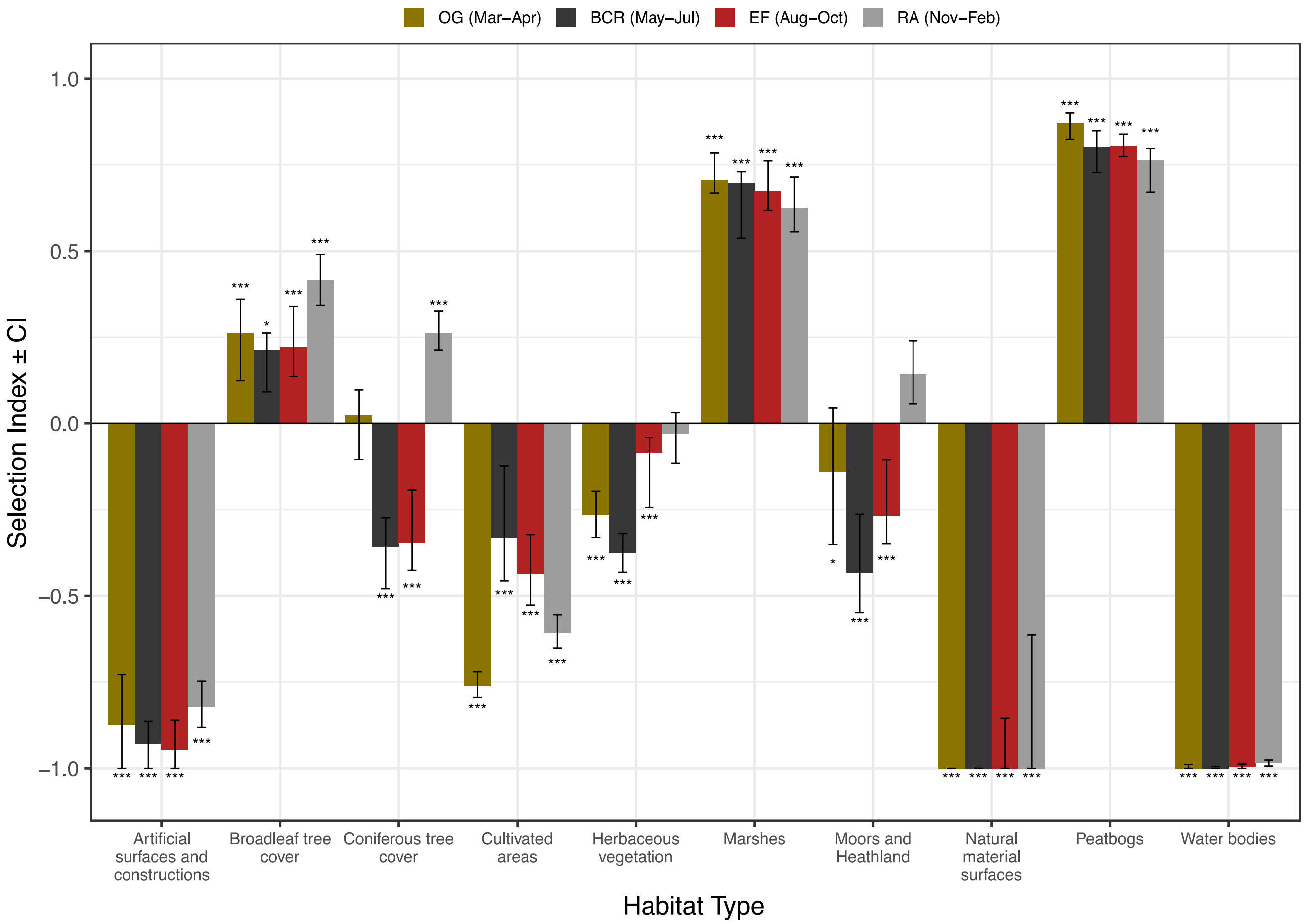

Fig. 2 Median habitat selection index of the raccoon dog in Denmark observed in 10 habitat types across four seasons. Seasons are defined by four main distinctions in raccoon dog ecological behaviors: OG = oestrus and gestation, BCR = birth and cub-rearing, EF = extensive foraging and fat accumulation, and RA = reduced activity. Index values above 0 indicate preference of the habitat, whereas values below 0 indicate avoidance, and values at 0 indicate neutrality. Error bars indicate 95% confidence intervals. Significance is indicated by asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and indicates if the index value significantly differs from 0

travels. Common biases associated with straight-line distance estimation is the sampling frequency of the points, and tortuosity of the path traveled – which can vary incredibly according to various factors. Animals with more directional movements (lower tortuosity), may be in the process of dispersing, whereas an animal with nondirectional movements (higher tortuosity), may be considered established (Herfindal et al. 2016). The straight-line distance traveled can vary substantially according to the sampling frequency used where distance traveled is increasingly underestimated, and that several fixes per minute are required to achieve tolerably accurate estimates (Noonan et al. 2019; Rowcliffe et al. 2012; Sennhenn-Reulen et al. 2017). Research has shown that with a one minute sampling interval, distance was underestimated by 6.3% on average, and with a 2 h sampling interval, distance was underestimated by 32.3% (Sennhenn-Reulen et al. 2017). It was therefore a priority to use the lowest IT possible if sample size allowed.

Habitat selection

The preference for peatbogs, marshes and broadleaf tree cover corresponds to various other studies within the raccoon dogs introduced range (Baltrunaité 2010; Kauhala and Auttila 2010; Melis et al. 2015; Mustonen et al. 2012). Preference for these habitats was observed year-round, indicating their importance throughout the year as habitats that are providing their main source of food. The overall avoidance of artificial surfaces and constructions, and water bodies corresponds to other research (Drygala et al. 2008; Sutor and Schwarz 2013). Overall selection patterns across all habitats were most similar between the birth and cub rearing and extended foraging seasons, and most dissimilar between birth and cub rearing and reduced activity seasons. This dissimilarity was expected, as in Denmark—resource availability is highest during the months of birth and cub rearing and lowest during the months of reduced activity. During periods of lower resource availability,

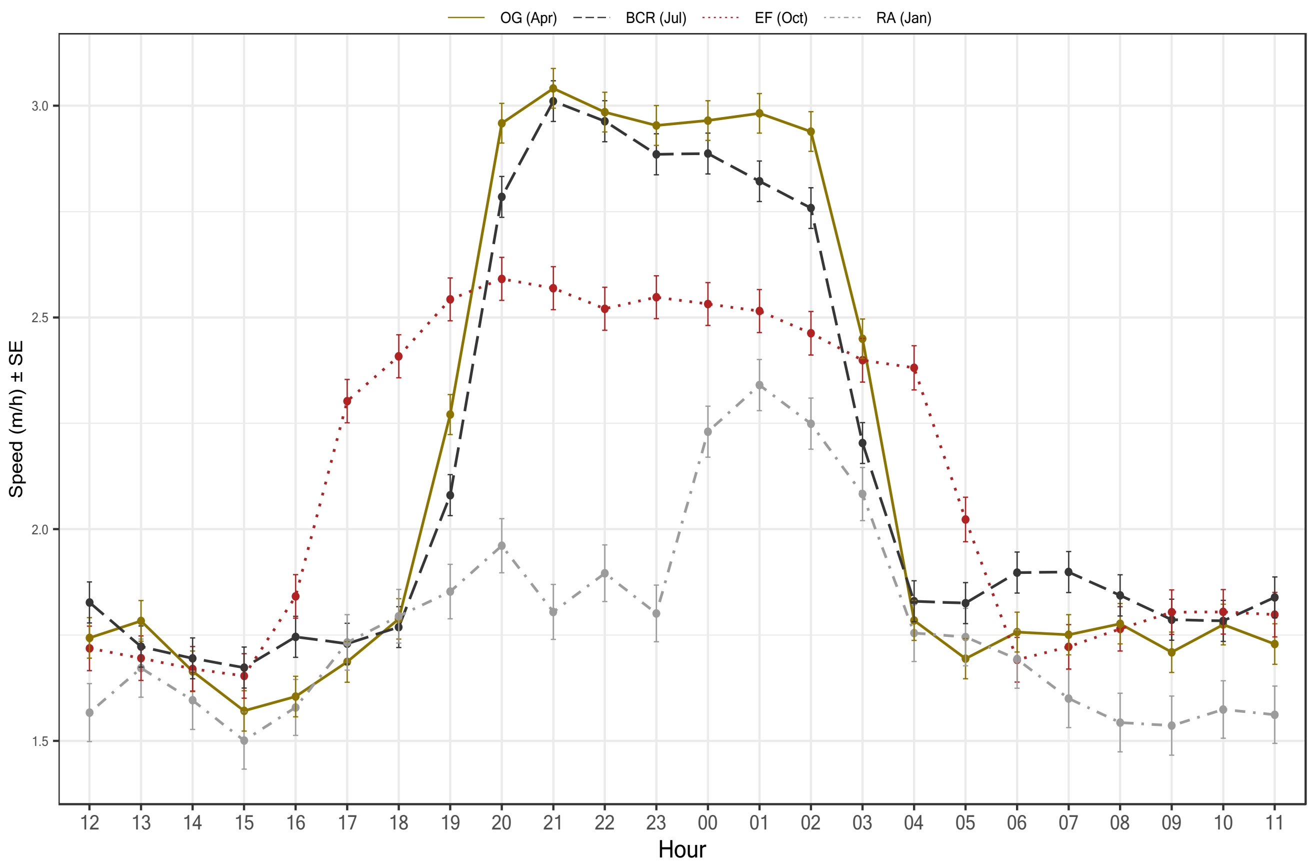

Fig. 3 Mean speed (least square) of raccoon dog movement in Denmark in meters per hour according to time of day across four seasons. Seasons are defined by four main distinctions in raccoon dog ecological behaviors: OG = oestrus and gestation, BCR = birth and cub-rearing, EF = extensive foraging and fat accumulation, and RA = reduced activity. Data was collected using an interfix time of 10 min. Least square mean values are in the log-10 scale. Error bars indicate standard error values

it would be most advantageous for the raccoon dog to broaden its habitat selection patterns to optimize sufficient resource and shelter acquisition.

During the reduced activity season, raccoon dogs showed markedly different selection patterns compared to the other seasons, specifically within four habitats: broadleaf tree cover, coniferous tree cover, herbaceous vegetation, and moors and heathland. They used these habitat types more during the winter than during the other three seasons. Similar preferences for coniferous and deciduous forests during winter were found in Germany, Finland, and Lithuania. The higher preference for broadleaf and coniferous tree cover during winter in Denmark may indicate that they are utilizing this habitat type for denning, shelter and resting purposes as well as for food, considering these forests offer berries year round, which are known to be a reliable food source prior to and throughout winter (Elmeros et al. 2018; Kauhala 1993; Sutor et al. 2010). In Sweden, the raccoon dog selected coniferous forests during winter but selected against the habitat during the rest of the year (Melis et al. 2015). In Germany, raccoon dogs were observed utilizing abandoned badger setts in coniferous forests all year round, for the purpose of daytime resting places, shelter from bad weather, winter resting, and for cub-rearing (Sutor and Schwarz 2012), and in Poland, an increased use of burrows and hollow trees (which are primarily found in forests) as den sites occurred as mean daily temperature decreased (Kowalczyk and Zalewski 2011). In Denmark, used badger setts are more likely to be found in areas of high forest coverage (Jepsen et al. 2005).

The shift from avoidance to an almost neutral selection pattern for herbaceous vegetation and moors and heathland during the winter indicates that during times of lower resource availability, these habitat types become useful to the raccoon dog. In Finland, raccoon dogs preferred moist heaths during the winter months due to the availability of berries (Kauhala 1996a), and in Sweden the raccoon dog showed a neutral selection pattern for heathlands and meadows during the winter but selected against these habitats

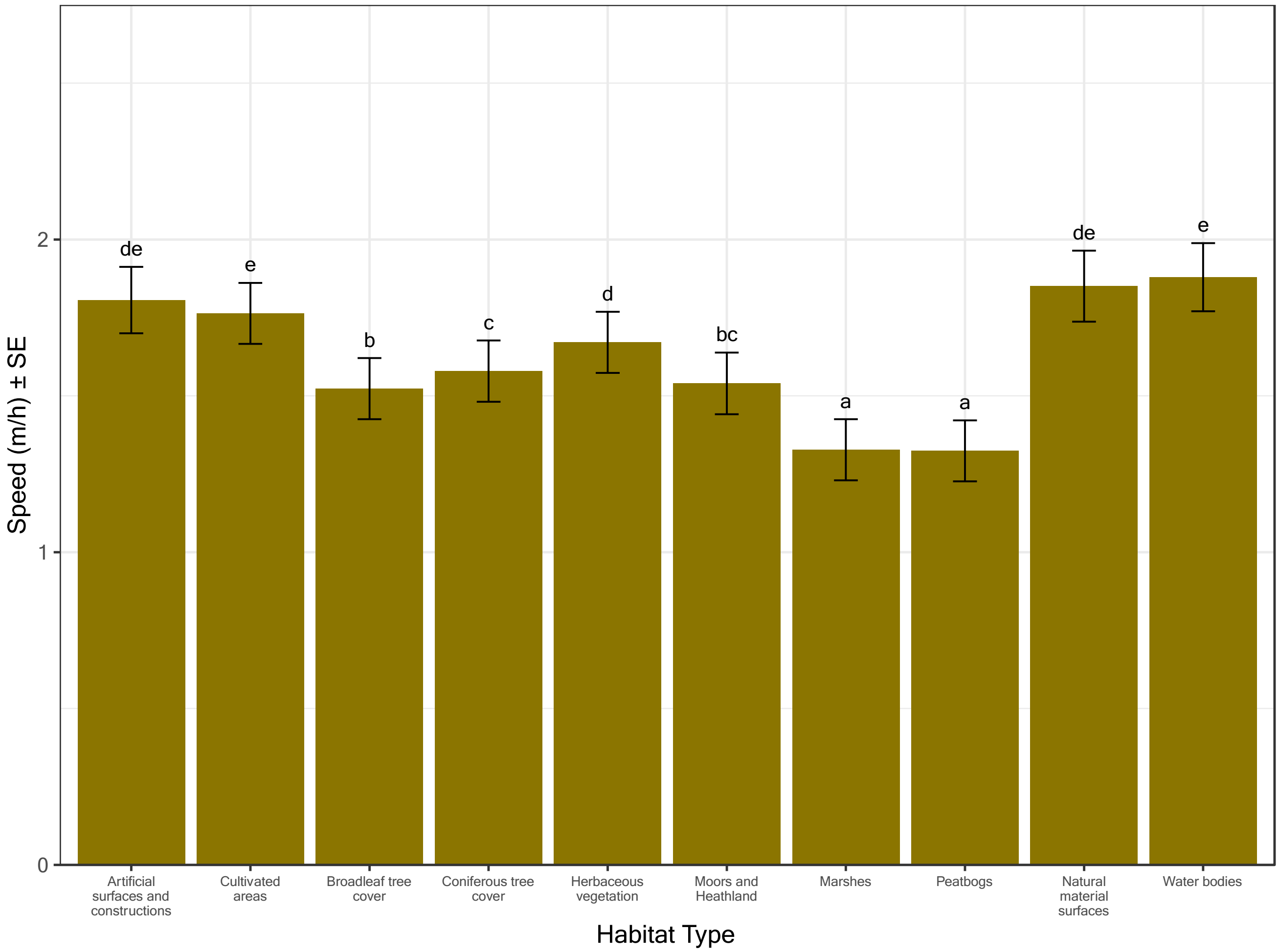

Fig. 4 Mean speed (least square) of raccoon dog movement in Denmark in meters per hour according to habitat type. Data was collected using an interfix time of 3 h. Least square mean values are in the log-10 scale. Error bars indicate standard error values. Letters indicate significant differences between habitat types

during the rest of the year (Melis et al. 2015). In Germany, it was found that grasslands were a preferred habitat throughout the year, as these conditions are suitable for various prey species of the raccoon dog, such as small mammals, birds and invertebrates (Sutor and Schwarz 2013). Certain insectivores (primarily shrews) and birds are frequently consumed prey items during the winter in Denmark (Elmeros et al. 2018), which may explain the shift to neutral selection pattern of herbaceous vegetation in our study. This shift in preference may indicate an increased use of areas located closer to human settlements, such as mowed yards and gardens. Artificial surfaces, which was classified largely as human settlement areas and major highway systems, were also utilized slightly more during the winter months. This slight increase in usage of artificial surfaces during the winter may be due to the opportunistic foraging of carrion occurring near human settlement areas. In Finland, (Mustonen et al. 2012) found that anthropogenic areas such as gardens, roads, and railroads were all preferred habitats of the raccoon dog during winter. The preference for gardens was supported by their winter diet analysis which indicated consumption of anthropogenic food sources, which has been observed in other areas of Europe (Mustonen et al. 2012; Süld et al. 2017; Sutor et al. 2010).

During the birth/cub-rearing season, four habitats; broadleaf tree cover, coniferous tree cover, herbaceous vegetation and moors and heathland, saw an overall decrease in usage. The opposite trend was observed within cultivated areas where usage during birth and cub rearing increased, however it was still avoided. In Germany, a similar result was found, where raccoon dogs avoided farmland areas except during the cub-rearing season where there was a neutral selection pattern for the habitat, and a slight difference between the sexes was found with selection of cereal fields where females preferred this habitat and males did not (Drygala et al. 2008). Cultivated areas may become a more useful habitat for females during the cub-rearing season, while she is out foraging to maintain her milk supply, or it may simply be a matrix habitat that may be located near the den-site. During cub-rearing, habitat preference may not only depend on rich habitats in relation to basic diet, but also the need for a place of refuge for the cubs. The need for a safe denning place may limit habitat use to be more local around the den.

Travel speed

We predicted that the raccoon dog in Denmark would display a unimodal nocturnal activity pattern with minor shifts throughout the year, with lower speeds during the winter and higher speeds during the spring/summer. Our results showed that the raccoon dog indeed displayed such patterns, with peak speeds occurring at night, and minimal movement occurring during the day, across all four seasons. This has been observed in a variety of studies across the raccoon dog's introduced range (Drygala et al. 2001; Kauhala et al. 2007; Schwemmer et al. 2021; Zoller and Drygala 2013), and native range (Ikeda et al. 2016; Seki and Koganezawa 2011, *N. viverrinus* subspecies). Diurnal activity was observed as well, although much less frequently. Changes in diurnal activity has been observed between the seasons in other studies, where the proportion of daytime movements increased as mean daily air temperatures decreased (Seki and Koganezawa 2011), and where diurnal activity was more prevalent during the cub-rearing season and correlated positively with increasing day length (Zoller and Drygala 2013). We observed an increase in diurnal activity during the birth/cub-rearing season where speed was significantly higher than all the other seasons during hours 06, 07 and 12, which corresponds to other studies (Ikeda et al. 2016; Ogurtsov et al. 2018; Zoller and Drygala 2013). This increased level of diurnal activity is likely due to the 24-h care associated with rearing cubs. Other minor variations in daily movement patterns were observed seasonally, with the lowest speed levels occurring during the reduced activity season, and highest occurring during oestrus/gestation and birth/cub-rearing seasons. Mating can occur between February – March (Helle and Kauhala 1995; Miljøstyrelsen 2020), when male spermatogenic cells (Qiang et al. 2003) and testosterone (Rudert et al. 2011) reach their peak levels. This increased travel speed during the month of April relative to the other months may be a result of mating behavior. Raccoon dogs may also exhibit an increase in foraging activity following an extended period of reduced activity over winter. During the extensive foraging/fat accumulation season higher speed levels were maintained for a longer period, which is likely due to an increase in time spent foraging in a 24-h period, in preparation for winter.

We predicted that the raccoon dog would travel slower in habitats that were preferred and faster in habitats that were avoided, when compared to the habitat selection analysis. According to 'area restricted search' behavior, an animal will remain in an area longer where resources are high as opposed to areas where resources are low, and will also move more slowly and tortuously in such high resource areas (Turchin 1998). Our results correspond well with this theory and our prediction, with raccoon dogs moving faster within their avoided habitats and slower within their preferred habitats. In Japan, a similar pattern was observed, where the raccoon dog displayed slower speeds in habitats that were favored (Saeki et al. 2007). Our results provide indirect evidence of raccoon dog habitat preferences and supports the results from our habitat selection analysis.

Conclusion

In conclusion, the raccoon dog in Denmark possesses ecological traits that are similar to their conspecifics found elsewhere in their introduced range. They prefer moist habitats and high coverage forests year-round and will additionally favor coniferous forests and heathlands during winter. They exhibit a unimodal nocturnal activity pattern throughout the year with highest speeds occurring during spring and summer and lowest during winter. They are capable of shifting their habitat use and movement intensity according to season in response to environmental stimulus, and with a gradually warming climate, these patterns may shift during the milder winters to come. With their overall level of ecological plasticity, the raccoon dog is likely capable of adapting to the ongoing climatic changes locally in much of Europe and expand their current distribution even further. Having a detailed understanding of how the raccoon dog interacts with its environment on a local scale can inform assessments regarding their likely future presence and space use as well as any associated ecological effects in the study region and potentially also more broadly.

Appendix A – Habitat selection

Methodology

Statistical modelling

Variable descriptions Linear mixed effect models were built for each habitat type to determine if there were significant shifts in habitat selection between the seasons (Table 3). The response variable, *Selection Index* (*SI*) associated with each habitat type was represented as a continuous variable, and the two predictor variables; *Season* (fixed effect) and *ID* (random effect) as categorical. The *ID* variable represented the identification number of each individual, as the categorical random intercept to account for individuals being observed across more than one season.

$$lmer\,(SI \sim Season + (1\,|\,ID))$$

In the case where model fit improved, *Season* was included as a random slope in addition to the *ID* random intercept, to account for the variation of impact *Season* may have on the *Selection Index* according to each individual.

$$lmer\,(SI \sim Season + (1 + Season\,|\,ID))$$

Model selection To determine which random effect structure fit the data best, models with different random effect structures were compared to one another by

LAND COVER TYPE	DESCRIPTION
Artificial surfaces and constructions	All surfaces where landscape has been changed by or is under influence of human construction activities by replacing natural surfaces with artificial abiotic constructions or artificial materials.
Broadleaf tree cover	Land covered with broadleaved tree canopy that loses leaves seasonally.
Coniferous tree cover	Land covered with needle-leaved tree canopy that do not lose needles seasonally.
Cultivated areas	Cultivated areas managed by human that include non-irrigated and irrigated arable land with different crops and land under rice cultivation. It also includes temporary bare soils (e.g. fallow lands).
Herbaceous vegetation	Lands covered by herbaceous vegetation including both natural low productivity grassland and managed grassland used for grazing and/or mowing.
Marshes	Low-lying areas covered with non-woody vegetation distinguished by the presence of water at the surface (waterlogged) either permanent or temporary, due to high precipitation rates or flooding by fresh or sea water.
Moors and Heathland	Low growing vegetation with closed cover and with predominately shrub and bushy vegetation (limited herbaceous species allowed).
Natural material surfaces	Any kind of surface material that remains in its natural state or form, including consolidated surfaces, which are in most parts impervious for water, formed by natural material and with a solid surface. It may have been modified through different man-made processes (e.g. extraction sites). It also includes any surface with loose mineral particles of any size range, either as an outcome of natural physical sedimentation processes or human activiy, e.g. mountain slope debris, glacier moraines, river pebble banks, beaches, sand dunes (unvegetated) or quarries.
Peatbogs	Peatlands with deposit of decomposed moss or other dead plant material (including exploited peatlands).
Water bodies	Water in liquid state of aggregation regardless of location, shape, salinity and origin (natural or artificial).

Fig. 5 Land cover category descriptions of those found in Denmark from the land cover raster layer developed by the Sentinel-2 Global Land Cover project. Figure adapted from (Malinowski et al. 2019)

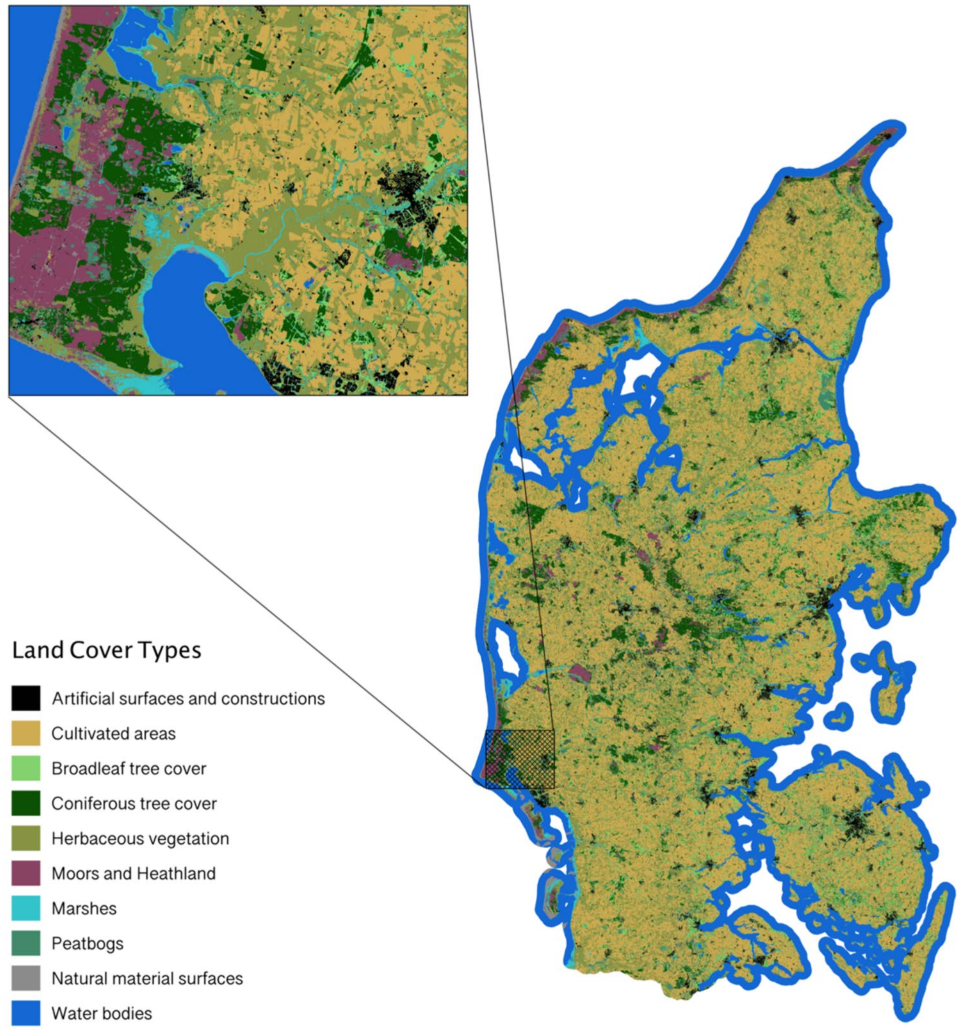

Fig. 6 The overall study area, in the form of a land cover raster of Denmark clipped to the Jutland/Funen regions with a 3 km coastal buffer. Zoomed in portion is to present land cover types on a larger scale

examining their Akaike Information Criterion (AIC) values and the model with the lower AIC value was determined to have the better random effect structure. To determine if each fixed effect term contributed to explaining variation in the response variable, an Analysis of Deviance Table (Type II) was developed by using the *Anova* function on the full mixed effect model. Each model's AIC and coefficient of determination (conditional & marginal R^2) values were examined when comparing models. Residuals of each model were examined and if assumptions of normality were not met, the response variable was transformed.

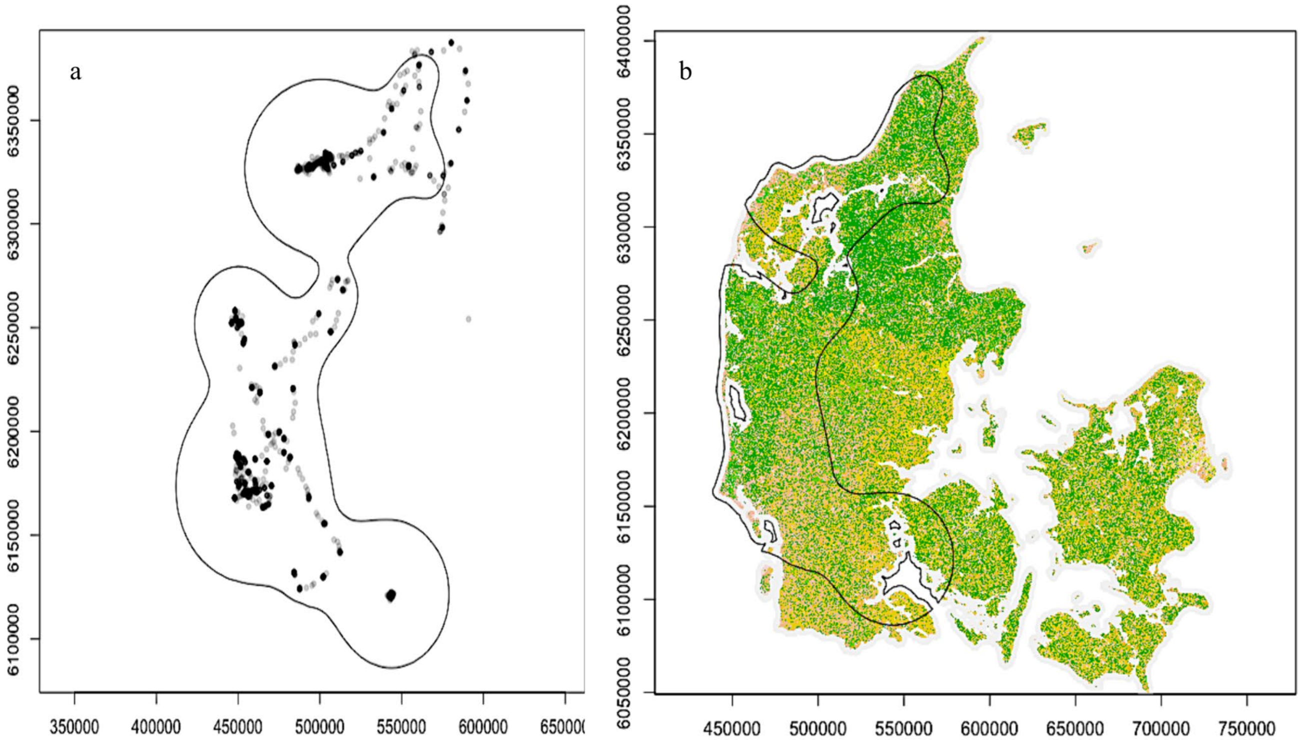

Fig. 7 **a** Estimated UD of one individual and their respective telemetry points from the entire study period **b** Same individual's UD overlayed and clipped to the size of the land cover raster

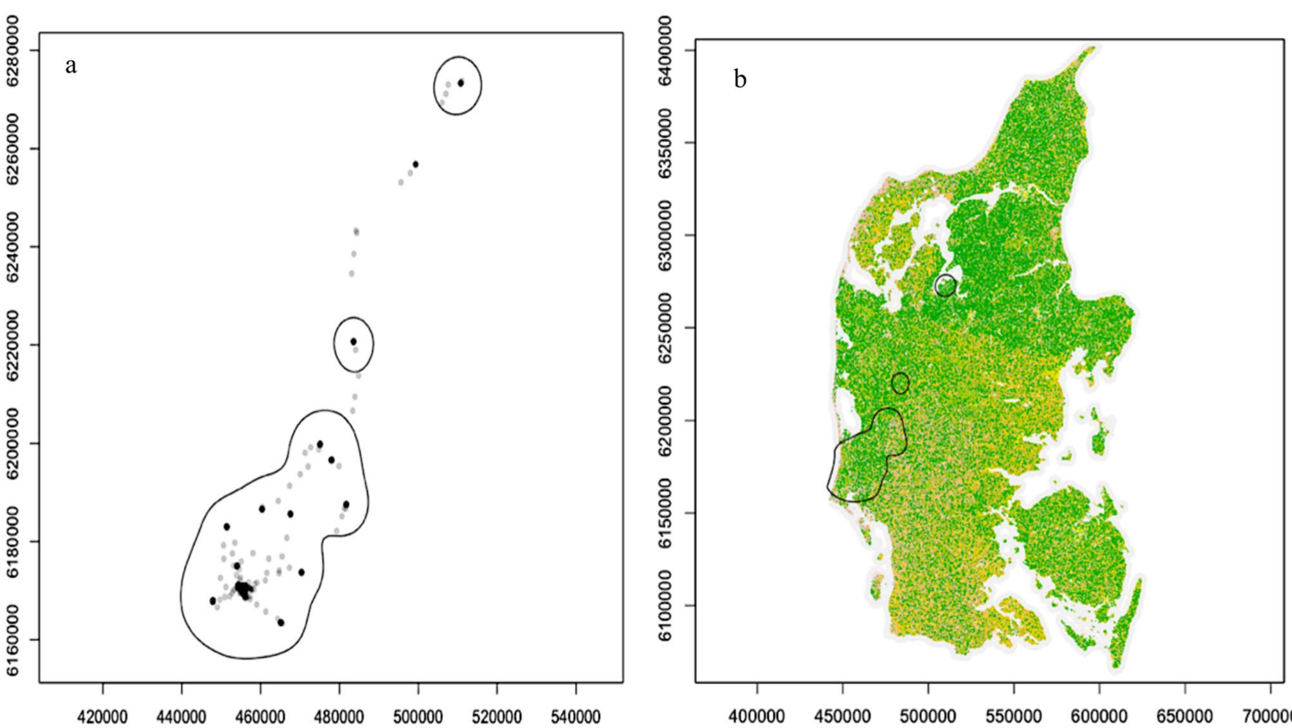

Fig. 8 **a** Estimated UD of same individual as in Fig. 7 and their respective telemetry points from the 'Oestrus/Gestation (March–April)' Season **b** Same individual's UD overlayed and clipped to the size of the land cover raster

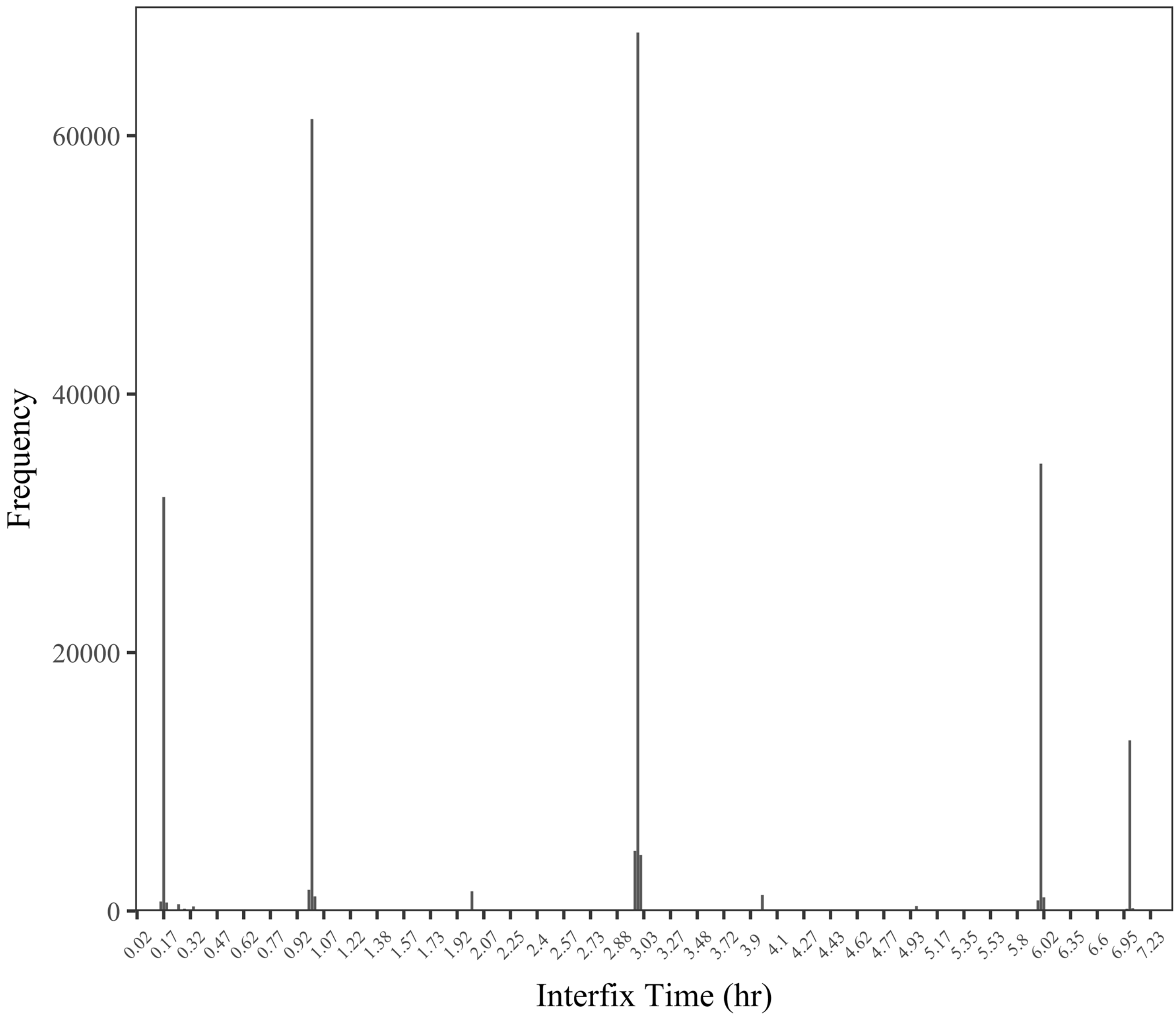

Fig. 9 The frequency of GPS collar interfix times used to monitor collared racoon dogs in Denmark for the entire dataset. Only interfix times below 7 hours were included in this figure

Table 1 Proportions for each habitat type that is available and used according to the entire study region and entire telemetry dataset. Habitat available represents the proportion of the land cover raster that is represented by each habitat type and the habitat used represents the proportion of telemetry points found within each habitat type from the entire telemetry dataset

Habitat	Type	Proportion
Artificial surfaces and constructions	Used	0.005
	Available	0.030
Cultivated areas	Used	0.176
	Available	0.373
Broadleaf tree cover	Used	0.113
	Available	0.068
Coniferous tree cover	Used	0.063
	Available	0.060
Herbaceous vegetation	Used	0.144
	Available	0.193
Moors and heathland	Used	0.037
	Available	0.027
Marshes	Used	0.212
	Available	0.030
Peatbogs	Used	0.245
	Available	0.017
Natural material surfaces	Used	0.002
	Available	0.005
Water bodies	Used	0.003
	Available	0.196

Table 2 Median and 95% CI selection index values for each habitat type across all seasons, as well as the statistical tests and results for testing if the index value for each habitat type within each season significantly differed from 0

Habitat Type	Season	Median SI	LCI	UCI	ΔSI	Test	Statistic	Df	*p*-value
Artificial surfaces and constructions	OG	-0.87	-1	-0.73	0.13	WSR	47	-	4.56E-15 ***
	BCR	-0.93	-1	-0.86		WSR	18	-	1.49E-17 ***
	EF	-0.95	-1	-0.86		WSR	6	-	4.86E-19 ***
	RA	-0.82	-0.88	-0.75		WSR	161	-	1.46E-16 ***
Broadleaf tree cover	OG	0.26	0.12	0.36	0.20	WSR	2550	-	2.51E-04 ***
	BCR	0.21	0.09	0.26		WSR	2858	-	1E-02 *
	EF	0.22	0.14	0.34		WSR	3805	-	8.41E-05 ***
	RA	0.41	0.34	0.49		WSR	4650	-	1.45E-11 ***
Coniferous tree cover	OG	0.02	-0.1	0.1	0.62	WSR	1625	-	4.77E-01
	BCR	-0.36	-0.48	-0.27		WSR	710	-	3.4E-09 ***
	EF	-0.35	-0.43	-0.19		WSR	976	-	2.17E-08 ***
	RA	0.26	0.21	0.33		WSR	3742	-	1.98E-04 ***
Cultivated areas	OG	-0.76	-0.79	-0.72	0.43	WSR	31	-	5.27E-15 ***
	BCR	-0.33	-0.46	-0.12		WSR	872	-	1.04E-07 ***
	EF	-0.44	-0.53	-0.32		WSR	344	-	1.63E-14 ***
	RA	-0.61	-0.65	-0.55		WSR	0	-	1.85E-18 ***
Herbaceous vegetation	OG	-0.27	-0.33	-0.2	0.35	OST	-8.03	83	5.7E-12 ***
	BCR	-0.38	-0.43	-0.32		OST	-14.1	95	5.13E-25 ***
	EF	-0.08	-0.24	-0.04		OST	-4.68	102	8.8E-06 ***
	RA	-0.03	-0.12	0.03		OST	-1.01	101	3.15E-01

Table 2 (continued)

Habitat Type	Season	Median SI	LCI	UCI	ΔSI	Test	Statistic	Df	*p*-value
Marshes	OG	0.71	0.67	0.78	0.08	WSR	3296	-	1.62E-11 ***
	BCR	0.70	0.54	0.73		WSR	4099	-	9.8E-11 ***
	EF	0.67	0.62	0.76		WSR	5207	-	8.9E-17 ***
	RA	0.63	0.56	0.71		WSR	4933	-	1.38E-14 ***
Moors and heathland	OG	-0.14	-0.35	0.04	0.57	WSR	1251	-	1.73E-02 *
	BCR	-0.43	-0.55	-0.26		WSR	604	-	2.95E-10 ***
	EF	-0.27	-0.35	-0.11		OST	-4.61	102	1.16E-05 ***
	RA	0.14	0.06	0.24		WSR	3089	-	1.23E-01
Natural material surfaces	OG	-1	-1	-1	0.00	WSR	52	-	5.54E-15 ***
	BCR	-1	-1	-1		WSR	39	-	1.17E-17 ***
	EF	-1	-1	-0.86		WSR	114	-	4.22E-17 ***
	RA	-1	-1	-0.61		WSR	308	-	1.54E-14 ***
Peatbogs	OG	0.87	0.82	0.9	0.11	WSR	3475	-	4.89E-14 ***
	BCR	0.80	0.73	0.85		WSR	4265	-	1.48E-12 ***
	EF	0.80	0.77	0.84		WSR	5136	-	6.22E-16 ***
	RA	0.76	0.67	0.8		WSR	4846	-	1.29E-13 ***
Water bodies	OG	-1	-1	-0.99	0.02	WSR	1	-	6.63E-16 ***
	BCR	-1	-1	-0.99		WSR	0	-	7.39E-18 ***
	EF	-1	-1	-0.99		WSR	1	-	4.47E-19 ***
	RA	-0.98	-0.99	-0.98		WSR	0	-	1.08E-18 ***

ΔSI indicates the variation in selection index values throughout the four seasons for each habitat type. This was calculated by taking the difference between the lowest and highest median selection indices for each habitat

Abbreviations for Seasons: *OG* Oestrus/Gestation (March–April), *BCR* Birth/Cub-Rearing (May–July), *EF* Extensive Foraging/Fat Accumulation (Aug-Oct), *RA* Reduced Activity (Nov-Feb); Abbreviations for Tests: *WSR* Wilcoxon signed rank, *OST* One-sample t-test

Table 3 The statistical linear mixed effect models used to determine the relationship between the selection index of each habitat type relative to season - and their associated AIC and Coefficients of Determination values

Habitat	Model	AIC	Coefficient of Determination (R^2) Conditional	Marginal
Artificial surfaces and constructions	lme(sqrt(SI + 1.01) ~ Season + (1 + Season | ID))	226.84	0.84	0.03
Broadleaf tree cover	lme(1/(max(SI + 1.01)—SI)) ~ Season + (1| ID))	-423.27	0.30	0.05
Coniferous tree cover	lme(SI ~ Season + (1| ID))	463.45	0.31	0.17
Cultivated areas	lme(sqrt(SI + 1.01) ~ Season + (1 + Season | ID))	-46.79	0.89	0.13
Herbaceous vegetation	lme(SI ~ Season + (1| ID))	145.25	0.27	0.16
Marshes	lme(1/(max(SI + 1.01)—SI)) ~ Season + (1 + Season| ID))	-344.64	0.87	0.01
Moors and Heathland	lme(SI ~ Season + (1| ID))	570.84	0.23	0.08
Natural material surfaces	lme(log10(SI + 1.01) ~ Season + (1| ID))	970.36	0.13	0.03
Peatbogs	lme(1/(max(SI + 1.01)—SI)) ~ Season + (1| ID))	-359.89	0.32	0.02
Water bodies	lme(log10(SI + 1.01) ~ Season)	422.35	-	0.03

Table 4 Statistical tests and results for testing if selection indices for each season are significantly different from one another within each habitat type

Habitat Type	Wald chi-sq		Kruskal–Wallis	
	X^2	Pr(> Chisq)	X^2	*p*-value
Artificial surfaces and constructions	12.74	0.0052 **	11.582	0.009*
Broadleaf tree cover	23.912	2.6e-05 ***	-	-
Coniferous tree cover	89.629	< 2.2e-16 ***	-	-
Cultivated areas	61.6	2.7e-13 ***	-	-
Herbaceous vegetation	81.473	< 2.2e-16 ***	-	-
Marshes	4.795	0.1874	5.413	0.1439
Moors and heathlands	39.625	1.28e-08 ***	-	-
Natural material surfaces	-	-	10.272	0.0164 *
Peatbogs	8.190	0.0422 *	12.193	0.0068 *
Water bodies	-	-	10.626	0.0139 *

Table 5 Post Hoc tests and results of pairwise comparisons of Seasons within each habitat type

Habitat Type	Pairwise Comparison	Dunn Test			Tukey Contrasts	
		z	p-unadj	p-adj	z	Pr(> |z|)
Artificial surfaces and constructions	BCR – EF	0.212	0.832	0.832	-0.195	0.997
	BCR – OG	-1.292	0.196	0.393	1.545	0.405
	EF – OG	-1.517	0.129	0.517	1.756	0.290
	BCR – RA	-2.758	0.006 **	0.029 *	2.782	0.027 *
	EF – RA	-3.023	0.003 **	0.015 *	3.490	0.003 **
	OG – RA	-1.352	0.176	0.529	1.261	0.582
Broadleaf tree cover	BCR – EF	-	-	-	0.900	0.805
	BCR – OG	-	-	-	1.632	0.360
	EF – OG	-	-	-	0.782	0.863
	BCR – RA	-	-	-	4.571	< 0.001 ***
	EF – RA	-	-	-	3.763	< 0.001 ***
	OG – RA	-	-	-	2.787	0.027 *
Coniferous tree cover	BCR – EF	-	-	-	1.191	0.632
	BCR – OG	-	-	-	4.484	< 0.001 ***
	EF – OG	-	-	-	3.380	0.004 **
	BCR – RA	-	-	-	8.546	< 0.001 ***
	EF – RA	-	-	-	7.496	< 0.001 ***
	OG – RA	-	-	-	3.735	0.001 **
Cultivated areas	BCR – EF	-	-	-	-0.446	0.969
	BCR – OG	-	-	-	-6.461	< 0.001 ***
	EF – OG	-	-	-	-4.111	< 0.001 ***
	BCR – RA	-	-	-	-7.038	< 0.001 ***
	EF – RA	-	-	-	-5.469	< 0.001 ***
	OG – RA	-	-	-	3.070	0.011 *
Herbaceous vegetation	BCR – EF	-	-	-	5.430	< 0.001 ***
	BCR – OG	-	-	-	2.570	0.050 *
	EF – OG	-	-	-	-2.623	0.044 *
	BCR – RA	-	-	-	8.639	< 0.001 ***
	EF – RA	-	-	-	3.303	0.005 **
	OG – RA	-	-	-	5.745	< 0.001 ***

Table 5 (continued)

Habitat Type	Pairwise Comparison	Dunn Test z	p-unadj	p-adj	Tukey Contrasts z	Pr(>|z|)
Moors and heathland	BCR – EF	-	-	-	2.343	0.088
	BCR – OG	-	-	-	3.122	0.010 **
	EF – OG	-	-	-	0.900	0.805
	BCR – RA	-	-	-	6.201	< 0.001 ***
	EF – RA	-	-	-	3.945	< 0.001 ***
	OG – RA	-	-	-	2.841	0.023 *
Natural material surfaces	BCR – EF	-1.014	0.311	0.621	-	-
	BCR – OG	0.145	0.885	0.885	-	-
	EF – OG	1.118	0.264	0.791	-	-
	BCR – RA	-2.726	0.006 **	0.032 *	-	-
	EF – RA	-1.732	0.083	0.333	-	-
	OG – RA	-2.756	0.006 **	0.035 *	-	-
Peatbogs	BCR – EF	-0.569	0.569	0.569	0.954	0.776
	BCR – OG	-2.131	0.033 *	0.166	1.921	0.219
	EF – OG	-1.616	0.106	0.319	1.015	0.741
	BCR – RA	1.331	0.183	0.366	-0.792	0.858
	EF – RA	1.933	0.053	0.213	-1.766	0.290
	OG – RA	3.445	0.0006 ***	0.003 **	-2.686	0.036 *
Water bodies	BCR – EF	-1.391	0.164	0.492	-	-
	BCR – OG	-0.892	0.373	0.745	-	-
	EF – OG	0.435	0.664	0.664	-	-
	BCR – RA	-3.166	0.002 **	0.009 **	-	-
	EF – RA	-1.820	0.069	0.275	-	-
	OG – RA	-2.154	0.031 *	0.156	-	-

Abbreviations for Seasons: *OG* Oestrus/Gestation (March–April), *BCR* Birth/Cub-Rearing (May–July), *EF* Extensive Foraging/Fat Accumulation (Aug-Oct), *RA* Reduced Activity (Nov-Feb)

Table 6 Season pairs ranked by their level of similarity to one another according to their habitat selection patterns, with rank 1 being most similar and rank 6 being most dissimilar. The similarity of seasons is defined by the number of habitat types where the selection pattern for each season was significantly different from the other using Table 5

Rank	Season Pair	No. Habitat Types	Habitat Types
1	BCR – EF	1	HV
2	EF – OG	3	CA, CTC, HV
3	BCR – OG	4	CA, CTC, HV, MH
4	EF – RA	6	ASC, BTC, CA, CTC, HV, MH
5	OG – RA	7	BTC, CA, CTC, HV, MH, NMS, PB
6	BCR—RA	8	ASC, BTC, CA, CTC, HV, MH, NMS, WB

Abbreviations for seasons: *OG* Oestrus/Gestation (March–April), *BCR* Birth/Cub-Rearing (May–July), *EF* Extensive Foraging/Fat Accumulation (Aug-Oct), *RA* Reduced Activity (Nov-Feb); Abbreviations for habitat types: *ASC* Artificial surfaces and constructions, *BTC* Broadleaf tree cover, *CTC* Coniferous tree cover, *CA* Cultivated areas, *HV* Herbaceous vegetation, *MA* Marshes, *MH* Moors and heathland, *NMS* Natural material surfaces, *PB* Peatbogs, *WB* Water bodies

Table 7 Number of steps within each grouping of ITs after outlier removal (20,000 m/h). A step is defined as a pair of consecutive geographic coordinates. Number of individuals are those within each subset of data with greater than 50 steps

Interfix Time	# of Steps	# of Individuals	# of Steps per Individual (mean ± SD)	Step Length (m) (mean ± SD)	Speed (m/h) (mean ± SD)
0.15 – 0.18 hr	33,423	30	1113 ± 641	67 ± 134	402 ± 799
0.98 – 1.02 hr	64,049	115	555 ± 497	229 ± 467	229 ± 467
2.98 – 3.02 hr	76,954	111	689 ± 624	839 ± 1501	280 ± 500

Table 8 Between-group sample sizes of Hours for each subset of data according to the IT

	Interfix Time (hr)		
Hour	0.15 – 0.18	0.98 – 1.02	2.98 – 3.02
0	1510	167	8712
1	1547	475	3
2	1489	502	1
3	1458	478	21629
4	1373	19382	7354
5	1349	26227	6
6	1341	11703	2660
7	1347	381	1
8	1326	379	3
9	1338	382	7320
10	1319	383	4
11	1323	384	0
12	1310	374	7225
13	1301	379	1
14	1319	372	9
15	1332	383	7210
16	1356	114	1
17	1373	134	1
18	1432	172	7152
19	1453	558	1
20	1476	182	1
21	1474	181	7660
22	1442	181	0
23	1435	176	0

Results

Appendix B – Travel speed

Methodology

Summarisation of the three different datasets corresponding to different interfix times (10 min, 1 hr, 3 hrs):

10 minutes:

- Lowest overall sample size of the three datasets (Table 6)
- Data is evenly spread throughout the day (Table 8)
- Data is not evenly spread throughout the year (only includes data for months Jan, Apr, Jul & Oct) (Tables 7 and 9)

1 hour:

- Second highest overall sample size of the three datasets (Table 6)
- Data is not evenly spread throughout the day, with the majority of fixes being collected during hours 04, 05, & 06 (Table 8)
- Data is evenly spread throughout the year, with the majority of fixes being collected during hours 04, 05, 06 across all 12 months (Tables 7 and 9)

3 hours:

- Highest overall sample size of the three datasets (Table 6)
- Data is relatively evenly spread throughout the day, with the majority of fixes being collected every 3 hours (Table 8)

- Data is relatively evenly spread throughout the time of year, with the majority of fixes being collected every 3 h consistently throughout the 12 months, with the exception of the summer months (Apr-Sep) where data was not collected during hour 04 (Tables 7 and 9)

Time of day between Seasons

Due to sampling constraints, the decision to use the 10-min IT dataset for this analysis was straight forward as this was the only dataset with consistent data throughout the day at hourly intervals.

Habitat type

Given the higher sample sizes of the 1-hour and 3-hour IT datasets, the results of these two datasets were compared to observe any differences. The results from the 3-h IT dataset were most similar to those of the habitat selection analysis performed in this study with slower speeds corresponding to habitats that were selected for and higher speeds corresponding to habitats that were avoided.

Statistical modelling

Variable descriptions The response variable, *Speed* (m/h), was represented as a continuous variable, and the three predictor variables; *Hour, Season and Habitat* were represented as categorical. *Hour* was represented by each hour of the day, *Season* by the four seasons and *Habitat* by ten unique habitat types. The *Speed* variable was log10 transformed for all models. The random effect structure consists of the categorical variable *ID* which represents the identification number of each individual raccoon dog, and the categorical variable *Year* which represents the years that the observations took place. This random effect structure controls for the fact that speed measurements taken from each individual raccoon dog are not independent, and that individuals monitored in the same year may show similar movement patterns to one another. The variable *ID* is nested within *Year* as individuals were monitored over several years but not all individuals were monitored over every single year.

Model selection To determine which random effect structure fit the data best, models with different random effect structures were compared to one another by examining their AIC values and the model with the lower AIC value was determined to have the better random effect structure. To determine if each fixed effect term contributed to explaining variation in the response variable, an Analysis of Deviance Table (Type II) was developed by using the *Anova* function on the full mixed effect model. If a model term was insignificant, starting with the interaction terms, it was removed from the model, and the *anova* function was applied to the old and reduced model together to determine which model was a better fit. Each model's AIC and coefficient of determination (conditional & marginal R^2) values were examined when comparing models.

Results

Table 9 Between-group sample sizes of hours between each month of the year for each subset of data according to the IT

		Interfix Time (hr)		
Hour	Month	0.15–0.18	0.98–1.02	2.98–3.02
00	Jan	148	13	426
01	Jan	161	33	0
02	Jan	163	37	1
03	Jan	143	33	416
04	Jan	114	222	1155
05	Jan	111	1321	1
06	Jan	106	1152	126
07	Jan	107	18	0
08	Jan	105	20	0
09	Jan	102	21	182
10	Jan	111	20	1
11	Jan	112	19	0
12	Jan	108	13	175

Table 9 (continued)

Hour	Month	Interfix Time (hr)		
		0.15–0.18	**0.98–1.02**	**2.98–3.02**
13	Jan	107	14	0
14	Jan	106	14	2
15	Jan	112	16	174
16	Jan	121	2	0
17	Jan	125	7	0
18	Jan	140	15	178
19	Jan	132	45	0
20	Jan	134	19	0
21	Jan	129	18	295
22	Jan	117	17	0
23	Jan	117	14	0
00	Feb	2	0	543
01	Feb	0	13	0
02	Feb	0	14	0
03	Feb	0	12	559
04	Feb	0	402	1343
05	Feb	0	1655	0
06	Feb	0	1328	132
07	Feb	0	6	0
08	Feb	0	6	0
09	Feb	0	6	326
10	Feb	0	6	0
11	Feb	0	6	0
12	Feb	0	6	319
13	Feb	0	6	0
14	Feb	0	5	0
15	Feb	0	5	319
16	Feb	0	0	0
17	Feb	2	0	0
18	Feb	0	0	307
19	Feb	0	53	0
20	Feb	0	0	0
21	Feb	0	0	388
22	Feb	0	0	0
23	Feb	0	0	0
00	Mar	0	4	876
01	Mar	0	31	2
02	Mar	0	33	0
03	Mar	0	34	870
04	Mar	1	543	1858
05	Mar	0	2255	3
06	Mar	0	1960	319
07	Mar	0	35	0
08	Mar	0	35	0
09	Mar	0	35	642
10	Mar	0	35	0
11	Mar	0	35	0
12	Mar	0	35	635
13	Mar	1	34	0
14	Mar	0	34	0
15	Mar	0	34	638
16	Mar	0	5	0

Table 9 (continued)

		Interfix Time (hr)		
Hour	**Month**	**0.15–0.18**	**0.98–1.02**	**2.98–3.02**
17	Mar	0	5	0
18	Mar	0	5	619
19	Mar	0	58	0
20	Mar	0	6	0
21	Mar	0	5	667
22	Mar	0	5	0
23	Mar	0	5	0
00	Apr	527	9	725
01	Apr	551	36	0
02	Apr	524	40	0
03	Apr	527	38	2968
04	Apr	494	2538	0
05	Apr	491	2392	0
06	Apr	496	399	244
07	Apr	482	38	0
08	Apr	473	38	0
09	Apr	474	37	591
10	Apr	450	37	0
11	Apr	457	38	0
12	Apr	460	37	591
13	Apr	450	37	0
14	Apr	459	36	0
15	Apr	467	37	587
16	Apr	458	8	0
17	Apr	451	9	0
18	Apr	473	8	584
19	Apr	502	18	0
20	Apr	523	8	0
21	Apr	529	8	576
22	Apr	525	8	0
23	Apr	516	8	0
00	May	16	0	739
01	May	0	29	0
02	May	0	30	0
03	May	0	29	2855
04	May	0	2593	1
05	May	0	2642	0
06	May	0	527	281
07	May	0	30	0
08	May	0	29	0
09	May	0	30	753
10	May	0	30	0
11	May	0	30	0
12	May	0	31	736
13	May	0	30	0
14	May	0	28	1
15	May	0	30	730
16	May	0	0	0
17	May	0	0	1
18	May	0	1	724
19	May	0	25	0
20	May	0	0	0

Table 9 (continued)

		Interfix Time (hr)		
Hour	**Month**	**0.15–0.18**	**0.98–1.02**	**2.98–3.02**
21	May	0	0	683
22	May	0	0	0
23	May	0	0	0
00	Jun	1	15	792
01	Jun	0	27	1
02	Jun	0	28	0
03	Jun	0	28	2748
04	Jun	0	2637	0
05	Jun	1	2721	0
06	Jun	0	646	296
07	Jun	0	27	0
08	Jun	0	26	0
09	Jun	0	26	883
10	Jun	0	26	0
11	Jun	0	26	0
12	Jun	0	27	846
13	Jun	0	27	0
14	Jun	0	27	0
15	Jun	0	27	811
16	Jun	0	15	0
17	Jun	0	14	0
18	Jun	0	14	799
19	Jun	0	41	0
20	Jun	0	14	0
21	Jun	0	14	778
22	Jun	0	14	0
23	Jun	0	14	0
00	Jul	412	0	775
01	Jul	446	0	0
02	Jul	437	0	0
03	Jul	430	0	2579
04	Jul	425	2473	0
05	Jul	421	2585	0
06	Jul	418	636	221
07	Jul	425	1	0
08	Jul	416	0	0
09	Jul	423	0	818
10	Jul	427	0	0
11	Jul	426	0	0
12	Jul	416	0	775
13	Jul	412	0	0
14	Jul	427	0	0
15	Jul	420	0	765
16	Jul	418	0	0
17	Jul	423	1	0
18	Jul	431	0	799
19	Jul	426	28	0
20	Jul	432	0	0
21	Jul	431	0	752
22	Jul	413	0	0
23	Jul	414	1	0
00	Aug	12	17	745

Table 9 (continued)

		Interfix Time (hr)		
Hour	Month	0.15–0.18	0.98–1.02	2.98–3.02
01	Aug	0	18	0
02	Aug	0	18	0
03	Aug	0	18	2444
04	Aug	0	2395	0
05	Aug	0	2397	0
06	Aug	0	635	169
07	Aug	0	18	0
08	Aug	0	18	0
09	Aug	0	18	724
10	Aug	1	18	0
11	Aug	1	17	0
12	Aug	1	17	713
13	Aug	0	18	0
14	Aug	0	17	0
15	Aug	0	16	724
16	Aug	0	16	1
17	Aug	0	18	0
18	Aug	0	18	759
19	Aug	0	19	0
20	Aug	0	17	0
21	Aug	0	18	773
22	Aug	0	18	0
23	Aug	0	18	0
00	Sep	12	26	932
01	Sep	12	56	0
02	Sep	10	68	0
03	Sep	12	66	2654
04	Sep	12	2558	0
05	Sep	12	2563	0
06	Sep	10	807	220
07	Sep	12	60	0
08	Sep	12	62	0
09	Sep	12	61	886
10	Sep	12	63	0
11	Sep	12	65	0
12	Sep	12	65	877
13	Sep	13	67	0
14	Sep	12	65	0
15	Sep	17	64	908
16	Sep	16	30	0
17	Sep	18	30	0
18	Sep	18	30	893
19	Sep	18	58	0
20	Sep	18	29	0
21	Sep	15	28	865
22	Sep	12	28	0
23	Sep	12	27	0
00	Oct	368	30	880
01	Oct	377	88	0
02	Oct	355	90	0
03	Oct	346	85	2306
04	Oct	327	2238	258

Table 9 (continued)

		Interfix Time (hr)		
Hour	**Month**	**0.15–0.18**	**0.98–1.02**	**2.98–3.02**
05	Oct	313	2458	0
06	Oct	311	844	235
07	Oct	321	79	1
08	Oct	320	82	1
09	Oct	323	82	708
10	Oct	318	82	0
11	Oct	315	80	0
12	Oct	313	77	732
13	Oct	318	79	1
14	Oct	315	82	3
15	Oct	316	85	734
16	Oct	343	22	0
17	Oct	354	21	0
18	Oct	370	25	694
19	Oct	374	69	0
20	Oct	369	29	0
21	Oct	370	29	794
22	Oct	375	31	0
23	Oct	376	32	0
00	Nov	12	29	755
01	Nov	0	78	0
02	Nov	0	76	0
03	Nov	0	75	738
04	Nov	0	502	1476
05	Nov	0	1852	1
06	Nov	0	1619	261
07	Nov	0	51	0
08	Nov	0	45	0
09	Nov	4	45	537
10	Nov	0	47	3
11	Nov	0	49	0
12	Nov	0	48	547
13	Nov	0	49	0
14	Nov	0	47	2
15	Nov	0	50	549
16	Nov	0	12	0
17	Nov	0	15	0
18	Nov	0	23	526
19	Nov	0	75	1
20	Nov	0	27	0
21	Nov	0	29	671
22	Nov	0	29	0
23	Nov	0	29	0
00	Dec	0	24	524
01	Dec	0	66	0
02	Dec	0	68	0
03	Dec	0	60	492
04	Dec	0	281	1263
05	Dec	0	1386	1
06	Dec	0	1150	156
07	Dec	0	18	0
08	Dec	0	18	2

Table 9 (continued)

		Interfix Time (hr)		
Hour	**Month**	**0.15–0.18**	**0.98–1.02**	**2.98–3.02**
09	Dec	0	21	270
10	Dec	0	19	0
11	Dec	0	19	0
12	Dec	0	18	279
13	Dec	0	18	0
14	Dec	0	17	1
15	Dec	0	19	271
16	Dec	0	4	0
17	Dec	0	14	0
18	Dec	0	33	270
19	Dec	1	69	0
20	Dec	0	33	1
21	Dec	0	32	418
22	Dec	0	31	0
23	Dec	0	28	0

Table 10 Between-group sample sizes for the Habitat variable of each subset of data according to the IT

	Interfix Time (hr)		
Habitat	**0.15 – 0.18**	**0.98 – 1.02**	**2.98 – 3.02**
Artificial surfaces and constructions	201	150	234
Broadleaf tree cover	4043	7323	7592
Coniferous tree cover	1677	4234	4000
Cultivated areas	3953	9976	12611
Herbaceous vegetation	4097	6612	11235
Marshes	6728	14797	17709
Moors and heathlands	897	2283	2854
Natural material surfaces	106	46	154
Peatbogs	11033	17938	19069
Water bodies	93	151	298

Table 11 The statistical linear mixed effect models used to determine the relationship between the speed of the raccoon dog in Denmark relative to each of the predictor variables using different ITs of 10 minutes, and 3 hours - and their associated AIC and Coefficients of Determination values

			Coefficient of Determination (R^2)	
Interfix Time	**Model**	**AIC**	**Conditional**	**Marginal**
10 minutes	lmer(log10($Speed_{10min}$) ~ Hour * Season + Habitat + (1 |Year/ID)	57426	0.518	0.463
3 hours	lmer(log10($Speed_{3hr}$) ~ Month * Habitat + Hour + (1 | Year/ID)	158439	0.593	0.566

Table 12 Analysis of Deviance Table using Type II Wald chi-square tests for the mixed effects model built to represent speed estimated using a 10-minute IT. Speed was log10 transformed. Model: $lmer\left(Speed_{10min} \sim Hour \ * \ Season + Habitat + (1 \mid Year/ID)\right)$

Variable	**Chisq**	**Df**	**Pr(> Chisq)**
Hour	16250.30	23	< 2.2e-16 ***
Season	543.46	3	< 2.2e-16 ***
Habitat	1589.46	9	< 2.2e-16 ***
Hour:Season	2821.20	69	< 2.2e-16 ***

Table 13 Observed mean, standard error (SE) and sample size (N) for speed (m/h) according to time of day between the four seasons, estimated using an IT of 10 minutes

Hour	Season	N	Mean	SE
0	OG	526	1295.58	51.87
0	BCR	428	1081.72	60.85
0	EF	392	687.41	46.49
0	RA	162	698.97	71.03
1	OG	551	1236.26	45.05
1	BCR	446	899.05	41.05
1	EF	389	677.00	48.32
1	RA	161	751.36	69.83
2	OG	524	1159.33	56.53
2	BCR	437	720.42	33.96
2	EF	365	590.79	37.28
2	RA	163	630.63	66.37
3	OG	526	563.49	51.27
3	BCR	429	331.27	36.98
3	EF	357	590.73	42.82
3	RA	143	557.37	67.63
4	OG	494	159.57	29.65
4	BCR	425	110.06	12.05
4	EF	338	614.89	46.51
4	RA	114	280.06	56.39
5	OG	490	83.05	14.21
5	BCR	421	99.07	10.35
5	EF	325	288.62	31.25
5	RA	111	130.44	26.21
6	OG	496	85.04	5.91
6	BCR	418	124.85	21.40
6	EF	321	97.62	15.21
6	RA	106	106.54	18.85
7	OG	482	82.59	5.37
7	BCR	425	125.12	19.32
7	EF	333	68.19	5.76
7	RA	107	70.51	10.75
8	OG	473	79.73	5.68
8	BCR	416	101.39	8.57
8	EF	332	109.02	34.06
8	RA	105	49.34	6.71
9	OG	474	71.44	4.83
9	BCR	423	85.68	6.70
9	EF	335	82.00	8.85
9	RA	102	42.05	4.95
10	OG	450	125.17	39.88
10	BCR	427	75.01	6.78
10	EF	330	93.94	11.96
10	RA	110	95.75	34.32
11	OG	457	82.06	13.58
11	BCR	425	92.66	10.57
11	EF	327	92.85	12.27
11	RA	112	52.94	8.18
12	OG	460	105.33	21.13
12	BCR	416	106.23	10.75
12	EF	325	138.47	53.10
12	RA	108	42.87	5.04
13	OG	450	136.82	34.00
13	BCR	412	56.62	4.06
13	EF	327	77.48	10.23
13	RA	107	65.45	8.14
14	OG	459	61.98	4.74
14	BCR	427	62.24	5.99
14	EF	327	70.04	7.29
14	RA	106	51.80	7.22
15	OG	467	50.55	4.30
15	BCR	420	144.72	48.22
15	EF	333	78.09	18.47
15	RA	112	44.03	5.22
16	OG	458	51.09	3.11
16	BCR	418	118.73	34.68
16	EF	359	135.82	13.40
16	RA	121	83.00	13.97
17	OG	451	73.37	6.28
17	BCR	423	74.86	7.02
17	EF	372	532.51	72.67
17	RA	125	187.32	39.55
18	OG	473	98.98	10.08
18	BCR	431	105.14	9.28
18	EF	388	487.15	30.22
18	RA	140	250.83	35.92
19	OG	502	411.81	33.01
19	BCR	426	222.95	17.32
19	EF	392	575.11	30.01
19	RA	132	241.92	28.47
20	OG	523	1105.16	48.43
20	BCR	432	683.81	29.84
20	EF	387	760.98	70.99
20	RA	134	349.98	47.87
21	OG	529	1265.47	43.34
21	BCR	431	1146.39	49.55
21	EF	385	622.92	32.82
21	RA	129	248.84	36.56
22	OG	525	1256.45	43.41
22	BCR	413	1090.65	45.79
22	EF	386	690.60	55.61
22	RA	117	448.12	64.04
23	OG	516	1208.42	47.43
23	BCR	414	992.09	43.56
23	EF	388	689.20	36.80
23	RA	117	298.09	54.17

Abbreviations for Seasons: *OG* Oestrus/Gestation (April), *BCR* Birth/Cub-Rearing (July), *EF* Extensive Foraging/Fat Accumulation (Oct), *RA* Reduced Activity (Jan)

Table 14 Least square mean and standard error (SE) for speed (m/h) (log10 transformed) according to time of day between the four seasons. Estimated using a mixed effect model with speed as the response variable using an IT of 10 minutes

Hour	Season	lsmean	SE
0	OG	2.97	0.047
0	BCR	2.89	0.048
0	EF	2.53	0.050
0	RA	2.23	0.060
1	OG	2.98	0.047
1	BCR	2.82	0.048
1	EF	2.52	0.051
1	RA	2.34	0.060
2	OG	2.94	0.047
2	BCR	2.76	0.048
2	EF	2.46	0.051
2	RA	2.25	0.060
3	OG	2.45	0.047
3	BCR	2.20	0.048
3	EF	2.40	0.052
3	RA	2.08	0.063
4	OG	1.78	0.047
4	BCR	1.83	0.048
4	EF	2.38	0.052
4	RA	1.75	0.067
5	OG	1.69	0.047
5	BCR	1.83	0.048
5	EF	2.02	0.053
5	RA	1.75	0.068
6	OG	1.76	0.047
6	BCR	1.90	0.048
6	EF	1.69	0.053
6	RA	1.69	0.069
7	OG	1.75	0.047
7	BCR	1.90	0.048
7	EF	1.72	0.052
7	RA	1.60	0.069
8	OG	1.78	0.048
8	BCR	1.84	0.048
8	EF	1.76	0.052
8	RA	1.54	0.069
9	OG	1.71	0.048
9	BCR	1.79	0.048
9	EF	1.80	0.052
9	RA	1.54	0.070
10	OG	1.77	0.048
10	BCR	1.78	0.048
10	EF	1.80	0.053
10	RA	1.57	0.068
11	OG	1.73	0.048
11	BCR	1.84	0.048
11	EF	1.80	0.053
11	RA	1.56	0.068
12	OG	1.74	0.048
12	BCR	1.83	0.048
12	EF	1.72	0.053
12	RA	1.57	0.068
13	OG	1.78	0.048
13	BCR	1.72	0.049
13	EF	1.70	0.053
13	RA	1.67	0.069
14	OG	1.66	0.048
14	BCR	1.69	0.048
14	EF	1.67	0.053
14	RA	1.60	0.069
15	OG	1.57	0.048
15	BCR	1.67	0.048
15	EF	1.65	0.053
15	RA	1.50	0.068
16	OG	1.60	0.048
16	BCR	1.75	0.048
16	EF	1.84	0.051
16	RA	1.58	0.066
17	OG	1.69	0.048
17	BCR	1.73	0.048
17	EF	2.30	0.051
17	RA	1.73	0.065
18	OG	1.79	0.048
18	BCR	1.77	0.048
18	EF	2.41	0.051
18	RA	1.79	0.063
19	OG	2.27	0.047
19	BCR	2.08	0.048
19	EF	2.54	0.051
19	RA	1.85	0.064
20	OG	2.96	0.047
20	BCR	2.78	0.048
20	EF	2.59	0.051
20	RA	1.96	0.064
21	OG	3.04	0.047
21	BCR	3.01	0.048
21	EF	2.57	0.051
21	RA	1.80	0.065
22	OG	2.98	0.047
22	BCR	2.96	0.048
22	EF	2.52	0.051
22	RA	1.90	0.067
23	OG	2.95	0.047
23	BCR	2.89	0.048
23	EF	2.55	0.051
23	RA	1.80	0.067

Abbreviations for Seasons: *OG* Oestrus/Gestation (April), *BCR* Birth/Cub-Rearing (July), *EF* Extensive Foraging/Fat Accumulation (Oct), *RA* Reduced Activity (Jan)

Table 15 Post hoc pairwise comparison results for the least square means of speed according to time of day between the four seasons

Hour	Seasonal Pairwise Comparisons	Estimate	SE	df	t value	lower	upper	Pr(>|t|)
00	BCR - EF	0.355	0.045	20782.745	7.976	0.268	0.443	1.6E-15
00	BCR - RA	0.657	0.054	32225.906	12.124	0.551	0.763	9.4E-34
00	EF - RA	0.301	0.058	20361.856	5.216	0.188	0.415	1.9E-07
00	OG - BCR	0.078	0.038	32645.980	2.065	0.004	0.152	3.9E-02
00	OG – EF	0.433	0.044	15594.559	9.928	0.348	0.519	3.7E-23
00	OG - RA	0.735	0.053	32131.261	13.877	0.631	0.838	1.2E-43
01	BCR - EF	0.307	0.044	20365.181	6.900	0.220	0.394	5.3E-12
01	BCR - RA	0.481	0.054	32442.517	8.954	0.376	0.587	3.6E-19
01	EF - RA	0.175	0.058	19624.248	2.996	0.060	0.289	2.7E-03
01	OG - BCR	0.160	0.037	32643.412	4.337	0.088	0.233	1.5E-05
01	OG – EF	0.467	0.044	14954.312	10.714	0.382	0.552	1.1E-26
01	OG - RA	0.642	0.053	32497.275	12.222	0.539	0.745	2.8E-34
02	BCR - EF	0.295	0.045	20942.300	6.542	0.207	0.384	6.2E-11
02	BCR - RA	0.509	0.054	32224.960	9.446	0.404	0.615	3.8E-21
02	EF - RA	0.214	0.059	19490.459	3.632	0.098	0.329	2.8E-04
02	OG - BCR	0.181	0.038	32647.668	4.805	0.107	0.254	1.6E-06
02	OG – EF	0.476	0.045	15840.950	10.690	0.389	0.563	1.4E-26
02	OG - RA	0.690	0.053	32232.871	13.056	0.586	0.793	7.4E-39
03	BCR - EF	-0.196	0.046	21531.939	-4.285	-0.285	-0.106	1.8E-05
03	BCR - RA	0.121	0.057	32519.523	2.133	0.010	0.231	3.3E-02
03	EF - RA	0.316	0.061	21429.517	5.148	0.196	0.436	2.7E-07
03	OG - BCR	0.246	0.038	32645.311	6.521	0.172	0.320	7.1E-11
03	OG – EF	0.051	0.045	16231.821	1.130	-0.037	0.139	2.6E-01
03	OG - RA	0.367	0.055	32562.880	6.628	0.258	0.475	3.5E-11
04	BCR - EF	-0.552	0.046	21568.398	-11.904	-0.642	-0.461	1.4E-32
04	BCR - RA	0.075	0.061	32623.440	1.217	-0.046	0.195	2.2E-01
04	EF - RA	0.626	0.066	23965.072	9.434	0.496	0.756	4.3E-21
04	OG - BCR	-0.045	0.038	32648.303	-1.175	-0.120	0.030	2.4E-01
04	OG – EF	-0.597	0.046	16778.613	-12.982	-0.687	-0.507	2.4E-38
04	OG - RA	0.030	0.061	32657.389	0.490	-0.089	0.148	6.2E-01
05	BCR - EF	-0.198	0.047	21991.365	-4.226	-0.289	-0.106	2.4E-05
05	BCR - RA	0.080	0.062	32653.325	1.294	-0.041	0.202	2.0E-01
05	EF - RA	0.278	0.067	25602.099	4.146	0.146	0.409	3.4E-05
05	OG - BCR	-0.131	0.039	32645.835	-3.402	-0.207	-0.056	6.7E-04
05	OG – EF	-0.329	0.046	17111.784	-7.090	-0.420	-0.238	1.4E-12
05	OG - RA	-0.051	0.061	32674.910	-0.835	-0.171	0.069	4.0E-01
06	BCR - EF	0.206	0.047	22435.204	4.385	0.114	0.298	1.2E-05
06	BCR - RA	0.204	0.063	32651.853	3.233	0.080	0.328	1.2E-03
06	EF - RA	-0.002	0.068	26116.426	-0.024	-0.135	0.132	9.8E-01
06	OG - BCR	-0.141	0.039	32644.243	-3.649	-0.216	-0.065	2.6E-04
06	OG – EF	0.065	0.046	17304.493	1.406	-0.026	0.156	1.6E-01
06	OG - RA	0.064	0.062	32673.815	1.023	-0.058	0.186	3.1E-01
07	BCR - EF	0.176	0.046	22006.554	3.807	0.086	0.267	1.4E-04
07	BCR - RA	0.299	0.063	32652.596	4.753	0.176	0.422	2.0E-06
07	EF - RA	0.122	0.068	26216.631	1.807	-0.010	0.255	7.1E-02
07	OG - BCR	-0.148	0.039	32643.032	-3.830	-0.224	-0.072	1.3E-04
07	OG – EF	0.028	0.046	16962.036	0.615	-0.062	0.119	5.4E-01
07	OG - RA	0.151	0.062	32671.142	2.423	0.029	0.272	1.5E-02
08	BCR - EF	0.079	0.047	21756.017	1.691	-0.013	0.171	9.1E-02

Table 15 (continued)

Hour	Seasonal Pairwise Comparisons	Estimate	SE	df	t value	lower	upper	Pr(>|t|)
08	BCR - RA	0.300	0.063	32653.401	4.734	0.176	0.425	2.2E-06
08	EF - RA	0.221	0.068	26142.599	3.241	0.087	0.355	1.2E-03
08	OG - BCR	-0.067	0.039	32648.665	-1.718	-0.143	0.009	8.6E-02
08	OG – EF	0.012	0.047	17198.744	0.260	-0.079	0.103	7.9E-01
08	OG - RA	0.233	0.063	32670.552	3.718	0.110	0.356	2.0E-04
09	BCR - EF	-0.018	0.047	21639.212	-0.384	-0.109	0.073	7.0E-01
09	BCR - RA	0.250	0.064	32653.179	3.901	0.124	0.376	9.6E-05
09	EF - RA	0.268	0.069	26261.660	3.888	0.133	0.403	1.0E-04
09	OG - BCR	-0.077	0.039	32647.401	-1.975	-0.153	-0.001	4.8E-02
09	OG – EF	-0.095	0.046	17006.017	-2.034	-0.186	-0.003	4.2E-02
09	OG - RA	0.173	0.063	32670.337	2.730	0.049	0.298	6.3E-03
10	BCR - EF	-0.021	0.047	22031.094	-0.455	-0.112	0.070	6.5E-01
10	BCR - RA	0.209	0.062	32491.927	3.363	0.087	0.331	7.7E-04
10	EF - RA	0.231	0.067	23749.805	3.426	0.099	0.362	6.1E-04
10	OG - BCR	-0.009	0.039	32646.735	-0.222	-0.086	0.068	8.2E-01
10	OG – EF	-0.030	0.047	17665.042	-0.637	-0.122	0.062	5.2E-01
10	OG - RA	0.201	0.062	32514.941	3.235	0.079	0.322	1.2E-03
11	BCR - EF	0.041	0.047	21793.186	0.873	-0.051	0.133	3.8E-01
11	BCR - RA	0.277	0.062	32136.091	4.482	0.156	0.399	7.4E-06
11	EF - RA	0.236	0.067	22562.478	3.524	0.105	0.368	4.3E-04
11	OG - BCR	-0.110	0.039	32647.667	-2.817	-0.187	-0.034	4.9E-03
11	OG – EF	-0.069	0.047	17408.801	-1.472	-0.161	0.023	1.4E-01
11	OG - RA	0.167	0.062	32140.577	2.716	0.047	0.288	6.6E-03
12	BCR - EF	0.109	0.047	22094.391	2.308	0.016	0.201	2.1E-02
12	BCR - RA	0.260	0.063	32652.611	4.155	0.138	0.383	3.3E-05
12	EF - RA	0.152	0.068	26310.756	2.242	0.019	0.285	2.5E-02
12	OG - BCR	-0.084	0.039	32648.746	-2.141	-0.161	-0.007	3.2E-02
12	OG – EF	0.025	0.047	17630.219	0.522	-0.068	0.117	6.0E-01
12	OG - RA	0.176	0.062	32668.137	2.837	0.055	0.298	4.6E-03
13	BCR - EF	0.027	0.047	21818.928	0.581	-0.065	0.120	5.6E-01
13	BCR - RA	0.051	0.063	32653.603	0.807	-0.073	0.174	4.2E-01
13	EF - RA	0.023	0.068	25984.974	0.345	-0.110	0.157	7.3E-01
13	OG - BCR	0.061	0.040	32648.708	1.531	-0.017	0.138	1.3E-01
13	OG – EF	0.088	0.047	17416.082	1.863	-0.005	0.180	6.2E-02
13	OG - RA	0.111	0.063	32670.592	1.781	-0.011	0.234	7.5E-02
14	BCR - EF	0.025	0.047	21675.966	0.527	-0.067	0.116	6.0E-01
14	BCR - RA	0.099	0.063	32651.744	1.570	-0.025	0.222	1.2E-01
14	EF - RA	0.074	0.068	25958.167	1.091	-0.059	0.208	2.8E-01
14	OG - BCR	-0.031	0.039	32648.157	-0.784	-0.107	0.046	4.3E-01
14	OG – EF	-0.006	0.047	17287.242	-0.127	-0.098	0.086	9.0E-01
14	OG - RA	0.068	0.063	32670.589	1.090	-0.054	0.191	2.8E-01
15	BCR - EF	0.020	0.047	21350.602	0.421	-0.072	0.111	6.7E-01
15	BCR - RA	0.172	0.062	32641.427	2.785	0.051	0.294	5.4E-03
15	EF - RA	0.153	0.067	25125.054	2.283	0.022	0.284	2.2E-02
15	OG - BCR	-0.102	0.039	32651.407	-2.618	-0.179	-0.026	8.8E-03
15	OG – EF	-0.082	0.047	17158.042	-1.767	-0.174	0.009	7.7E-02
15	OG - RA	0.070	0.061	32666.093	1.144	-0.050	0.190	2.5E-01
16	BCR - EF	-0.096	0.046	20245.854	-2.087	-0.185	-0.006	3.7E-02
16	BCR - RA	0.167	0.060	32627.747	2.765	0.049	0.285	5.7E-03

Table 15 (continued)

Hour	Seasonal Pairwise Comparisons	Estimate	SE	df	t value	lower	upper	Pr(>|t|)
16	EF - RA	0.262	0.065	22788.911	4.057	0.136	0.389	5.0E-05
16	OG - BCR	-0.141	0.039	32650.049	-3.591	-0.218	-0.064	3.3E-04
16	OG – EF	-0.237	0.046	15934.492	-5.160	-0.326	-0.147	2.5E-07
16	OG - RA	0.026	0.060	32666.080	0.430	-0.091	0.143	6.7E-01
17	BCR - EF	-0.573	0.046	20445.847	-12.591	-0.662	-0.484	3.2E-36
17	BCR - RA	-0.003	0.059	32637.676	-0.051	-0.120	0.114	9.6E-01
17	EF - RA	0.570	0.064	23075.785	8.926	0.445	0.695	4.7E-19
17	OG - BCR	-0.043	0.039	32650.715	-1.093	-0.120	0.034	2.7E-01
17	OG – EF	-0.616	0.046	16201.543	-13.469	-0.706	-0.526	3.9E-41
17	OG - RA	-0.046	0.059	32671.489	-0.777	-0.162	0.070	4.4E-01
18	BCR - EF	-0.639	0.045	20394.686	-14.245	-0.727	-0.551	8.0E-46
18	BCR - RA	-0.026	0.057	32551.074	-0.447	-0.138	0.087	6.5E-01
18	EF - RA	0.614	0.062	21167.033	9.973	0.493	0.735	2.3E-23
18	OG - BCR	0.019	0.039	32649.239	0.498	-0.057	0.095	6.2E-01
18	OG – EF	-0.620	0.045	15893.726	-13.824	-0.708	-0.532	3.2E-43
18	OG - RA	-0.006	0.057	32604.013	-0.112	-0.118	0.105	9.1E-01
19	BCR - EF	-0.462	0.045	20245.568	-10.314	-0.550	-0.375	7.0E-25
19	BCR - RA	0.228	0.058	32584.036	3.894	0.113	0.342	9.9E-05
19	EF - RA	0.690	0.062	21842.793	11.042	0.568	0.813	2.9E-28
19	OG - BCR	0.190	0.038	32651.831	4.970	0.115	0.265	6.7E-07
19	OG – EF	-0.272	0.044	15350.297	-6.147	-0.359	-0.185	8.1E-10
19	OG - RA	0.418	0.058	32615.954	7.262	0.305	0.531	3.9E-13
20	BCR - EF	0.194	0.045	20098.694	4.317	0.106	0.282	1.6E-05
20	BCR - RA	0.824	0.058	32547.113	14.199	0.710	0.938	1.3E-45
20	EF - RA	0.630	0.062	21366.724	10.123	0.508	0.752	5.0E-24
20	OG - BCR	0.174	0.038	32644.694	4.600	0.100	0.248	4.3E-06
20	OG – EF	0.368	0.044	14674.872	8.319	0.281	0.454	9.7E-17
20	OG - RA	0.998	0.057	32580.271	17.494	0.886	1.109	3.3E-68
21	BCR - EF	0.442	0.045	20367.431	9.839	0.354	0.530	8.6E-23
21	BCR - RA	1.206	0.059	32531.447	20.432	1.091	1.322	3.3E-92
21	EF - RA	0.765	0.063	21738.179	12.107	0.641	0.888	1.2E-33
21	OG - BCR	0.030	0.038	32638.987	0.799	-0.044	0.104	4.2E-01
21	OG – EF	0.472	0.044	14681.515	10.697	0.385	0.558	1.3E-26
21	OG - RA	1.237	0.058	32575.304	21.329	1.123	1.350	3.0E-100
22	BCR - EF	0.443	0.045	20117.993	9.762	0.354	0.532	1.8E-22
22	BCR - RA	1.067	0.062	32596.275	17.321	0.947	1.188	6.5E-67
22	EF - RA	0.625	0.065	22780.635	9.559	0.497	0.753	1.3E-21
22	OG - BCR	0.022	0.038	32646.756	0.566	-0.053	0.096	5.7E-01
22	OG – EF	0.464	0.044	14591.026	10.492	0.378	0.551	1.2E-25
22	OG - RA	1.089	0.060	32622.281	18.048	0.971	1.207	1.8E-72
23	BCR - EF	0.338	0.045	20198.074	7.464	0.249	0.426	8.7E-14
23	BCR - RA	1.084	0.061	32601.024	17.639	0.964	1.205	2.6E-69
23	EF - RA	0.747	0.065	22771.385	11.459	0.619	0.875	2.6E-30
23	OG - BCR	0.068	0.038	32644.302	1.776	-0.007	0.143	7.6E-02
23	OG – EF	0.406	0.044	14639.902	9.154	0.319	0.492	6.2E-20
23	OG - RA	1.152	0.060	32635.392	19.105	1.034	1.271	6.3E-81

Abbreviations for Seasons: *OG* Oestrus/Gestation (Apr), *BCR* Birth/Cub-Rearing (Jul), *EF* Extensive Foraging/Fat Accumulation (Oct), *RA* Reduced Activity (Jan)

Table 16 Analysis of deviance table using type II Wald chi-square tests for the mixed effects model built to represent speed estimated using a 3-hour IT. Speed was log10 transformed. Model: $lmer\left(Speed_{3hr} \sim Month * Habitat + Hour + (1 \mid Year/ID)\right)$

Variable	Chisq	Df	Pr(> Chisq)
Month	670.27	11	< 2.2e-16 ***
Habitat	2845.40	9	< 2.2e-16 ***
Hour	60484.41	20	< 2.2e-16 ***
Month:Habitat	1084.33	99	< 2.2e-16 ***

Table 17 Observed mean speed (m/h), 95% confidence interval (CI) and sample size (N) of dataset using an IT of 3 hours, according to habitat type

Habitat	N	Mean	95% CI
Artificial surfaces and constructions	284	824.30	172.38
Cultivated areas	13411	396.44	9.47
Broadleaf tree cover	6701	250.85	9.23
Coniferous tree cover	3540	338.51	16.81
Herbaceous vegetation	13141	423.55	10.18
Moors and Heathland	2833	356.98	20.49
Marshes	16985	182.46	5.56
Peatbogs	17893	132.17	4.26
Natural material surfaces	175	700.45	109.78
Water bodies	269	697.92	84.61

Table 18 Least square mean speed (m/h) and standard error values (SE) according to habitat type. Estimated using a mixed effect model with speed as the response variable using an IT of 3 hours. Least square means and error values are in log-10 form

Habitat	LS Mean	SE
Artificial surfaces and constructions	1.81	0.11
Cultivated areas	1.76	0.10
Broadleaf tree cover	1.52	0.10
Coniferous tree cover	1.58	0.10
Herbaceous vegetation	1.67	0.10
Moors and Heathland	1.54	0.10
Marshes	1.33	0.10
Peatbogs	1.32	0.10
Natural material surfaces	1.85	0.11
Water bodies	1.88	0.11

Table 19 Post hoc pairwise comparison results of the least square means of speed according to habitat type using an IT of 3 h

Habitat Pairwise Comparisons	Estimate	SE	df	t value	lower	upper	Pr(>|t|)
ASC - CA	0.042	0.043	75028.74	0.979	-0.042	0.127	3.278e-01
ASC - BTC	0.283	0.044	75047.75	6.498	0.198	0.368	8.187e-11
ASC - CTC	0.227	0.044	75037.23	5.127	0.140	0.314	2.949e-07
ASC - HV	0.135	0.043	75019.77	3.137	0.051	0.219	1.705e-03
ASC - MH	0.266	0.045	75026.08	5.930	0.178	0.354	3.040e-09
ASC - MA	0.478	0.043	75035.87	11.109	0.394	0.563	1.198e-28
ASC - PB	0.482	0.043	75039.22	11.179	0.397	0.567	5.468e-29
ASC - NMS	-0.045	0.072	74966.02	-0.618	-0.186	0.097	5.364e-01
ASC - WB	-0.073	0.064	74976.52	-1.139	-0.200	0.053	2.545e-01
CA - BTC	0.241	0.011	75033.19	21.117	0.218	0.263	1.082e-98
CA - CTC	0.185	0.014	75071.48	13.118	0.157	0.213	2.877e-39
CA - HV	0.093	0.009	74953.36	9.779	0.074	0.111	1.431e-22
CA - MH	0.224	0.016	74844.40	13.945	0.193	0.256	3.847e-44
CA - MA	0.436	0.010	73836.64	45.370	0.417	0.455	0.000e + 00
CA - PB	0.440	0.010	73810.27	44.822	0.421	0.459	0.000e + 00
CA - NMS	-0.087	0.059	74924.36	-1.479	-0.202	0.028	1.392e-01
CA - WB	-0.116	0.049	74963.99	-2.363	-0.212	-0.020	1.815e-02
BTC - CTC	-0.056	0.015	75081.04	-3.689	-0.085	-0.026	2.256e-04
BTC - HV	-0.148	0.011	74984.53	-13.315	-0.170	-0.126	2.114e-40
BTC - MH	-0.017	0.017	74878.73	-0.971	-0.050	0.017	3.316e-01
BTC - MA	0.195	0.011	74386.57	17.696	0.174	0.217	6.298e-70
BTC - PB	0.199	0.011	74632.91	18.049	0.178	0.221	1.156e-72
BTC - NMS	-0.327	0.059	74927.88	-5.552	-0.443	-0.212	2.826e-08
BTC - WB	-0.356	0.049	74978.16	-7.229	-0.453	-0.260	4.924e-13
CTC - HV	-0.092	0.014	75086.22	-6.697	-0.119	-0.065	2.138e-11
CTC - MH	0.039	0.019	75086.88	2.097	0.003	0.076	3.601e-02
CTC - MA	0.251	0.014	74988.43	18.296	0.224	0.278	1.306e-74
CTC - PB	0.255	0.014	75056.29	18.499	0.228	0.282	3.127e-76
CTC - NMS	-0.272	0.060	74915.45	-4.565	-0.388	-0.155	4.999e-06
CTC - WB	-0.301	0.050	74976.45	-6.014	-0.398	-0.203	1.823e-09
HV - MH	0.131	0.016	75057.33	8.379	0.101	0.162	5.448e-17
HV - MA	0.343	0.009	74874.86	37.830	0.326	0.361	3.126e-310
HV - PB	0.347	0.009	74958.34	37.570	0.329	0.365	4.801e-306
HV - NMS	-0.180	0.059	74906.03	-3.065	-0.294	-0.065	2.175e-03
HV - WB	-0.208	0.049	74964.59	-4.265	-0.304	-0.113	1.998e-05
MH - MA	0.212	0.016	74920.69	13.568	0.181	0.243	6.910e-42
MH - PB	0.216	0.016	75016.90	13.795	0.185	0.246	3.084e-43
MH - NMS	-0.311	0.060	74925.69	-5.188	-0.428	-0.193	2.133e-07
MH - WB	-0.211	0.060	63046.15	-3.487	-0.329	-0.092	4.89e-04
MA - PB	0.013	0.009	63079.88	1.362	-0.006	0.032	1.73e-01
MA - NMS	-0.704	0.113	62841.31	-6.242	-0.925	-0.483	4.33e-10
MA - WB	-0.524	0.059	63043.39	-8.924	-0.640	-0.409	4.62e-19
PB - NMS	-0.717	0.113	62839.91	-6.357	-0.938	-0.496	2.07e-10
PB - WB	-0.537	0.059	63048.82	-9.136	-0.653	-0.422	6.69e-20
NMS - WB	0.179	0.127	62892.83	1.415	-0.069	0.428	1.57e-01

Abbreviations for habitat types: *ASC* Artificial surfaces and constructions, *CA* Cultivated areas, *BTC* Broadleaf tree cover, *CTC* Coniferous tree cover, *HV* Herbaceous vegetation, *MH* Moors and Heathland, *MA* Marshes, *PB* Peatbogs, *NMS* Natural material surfaces, *WB* Water bodies

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Availability of data and material Access to data may be achieved by contacting the corresponding author and with permission from the Danish Ministry of Environment.

Declarations

Ethics approval No ethical approval was required from an institutional or national ethics review board. The study complies with current Danish Laws, as a part of the of the regular surveillance and culling of raccoon dogs in Denmark by the Danish Ministry of the Environment. This study did not include the trapping, collaring, or handling of animals.

Competing interests The authors declare no competing interests.

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