



**Inland Norway  
University of  
Applied Sciences**

Faculty of Applied Ecology and Agricultural Sciences

Kim van Kooten

**Master thesis**

**The effect of kinship on dynamic interactions  
and foraging behaviour in female red fox  
(*Vulpes vulpes*)**

Master in Applied Ecology

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## Abstract

The spatial organization of animals is a key concept in ecology and plays a crucial role in understanding animal behavior. Yet, much remains unknown regarding how individuals of the same, and of different, species interact on a daily basis. For the elusive red fox, few data relating to the dynamics of interactions or relatedness of individuals sharing space are available. Using high-resolution GPS-data combined with genetic kinship data, I analyzed the spatial and foraging behavior of female red foxes by calculating their overlap of home ranges (i.e. static interaction) combined with temporal overlap (i.e. dynamic interaction). Closely related individuals showed a considerably higher temporal overlap compared to others, indicating partitioning of resources was low. Distantly related individuals showed spatial overlap in ranges similar to those that were closely related, but surprisingly, unrelated individuals showed range overlap higher than related individuals. In both cases, low temporal overlap indicated a high degree of resource partitioning to be present. This indicates that female red foxes who are sharing space display variable tolerance towards each other and suggests that resource availability and kinship have a synergetic effect on red fox spacing behaviour. Though more data is undoubtedly needed, this study provides the first steps of filling the gap in knowledge of red fox interactions and social structure.

**Keywords:** *Vulpes vulpes*, kinship, resource partitioning, dynamic interaction, Global Positioning System (GPS)

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## Sammendrag

Den romlige fordelingen av dyr er et nøkkelbegrep innen økologi og spiller en avgjørende rolle i å forstå dyrs atferd. Likevel er lite kjent om hvordan individer av samme art, og av ulike arter, samhandler på daglig basis. For rødreven, en flyktig art, finnes det lite data relatert til hvordan individer som deler hjemmeområder er i slekt, eller hvordan dynamikken i deres interaksjoner er. Ved hjelp av kort tidsintervall GPS-data kombinert med genetisk slektskapsdata analyserte jeg bevegelser og furasjerersatferd til revetisper. Dette gjorde jeg ved å beregne deres overlapp i hjemmeområder (som kalles for «static interaction») kombinert med overlapp i tid («dynamic interaction»). Individer som var nær i slekt viste betraktelig høyere overlapp i tid sammenlignet med andre, som indikerer at de benyttet seg av ressurser samtidig. Individer som var i mindre grad beslektet viste områdeoverlapp lik de som var nær beslektet, mens individer som ikke var i slekt viste overraskende større områdeoverlapp enn de som var i slekt. I begge disse tilfellene var det derimot lite overlapp i tid, som indikerer at de ikke brukte ressurser samtidig. Dette tyder på at revetisper som deler sine hjemmeområder viser variabel toleranse mot hverandre, og antyder at tilgjengelighet av ressurser og slektskap har en samvirkende effekt på rødrevens romlige fordeling. Selv om flere data uten tvil er nødvendig, danner dette studiet de første steg for å fylle kunnskapshullet om rødrevens interaksjoner og sosiale struktur.

**Nøkkelord:** *Vulpes vulpes, slektskap, ressursdeling, dynamic interaction, Global Positioning System (GPS)*

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# 1. Introduction

The spatial organization of animals is a key concept in ecology and plays a crucial role in understanding animal behavior (Emlen & Oring, 1977). Within a population of animals sharing space, interactions among individuals are likely to occur. The degree to which individuals interact with each other is highly dependent on the availability of resources, competition for these resources and the species' social system (Burt, 1943, Ostfeld, 1990). How animals respond to each other, whether it is by showing tolerance, attraction or avoidance, will influence where animals are in space and time, thus modifying both population and community structure and organization (Mattisson et.al., 2011). It is therefore of great interest to better understand how individuals interact both within and across species.

As resource competition is the primary interaction regulating and structuring populations (Kneitel, 2008), the dispersion and availability of resources (referred to as the 'resource dispersion theory') fundamentally influences spacing behavior in many animals, including carnivores (Macdonald, 1983). Species can develop different strategies to obtain necessary resources, such as having territories. Territoriality can be defined as the occupation of a defended or exclusive area (Cavallini, 1996), and theory predicts this results in home ranges which overlap less than expected by chance (Macdonald, 1983). Individuals can inhabit territories alone or with one or more conspecifics depending on the available resources, meaning resource dispersion also influences sociality. However, even if individual ranges overlap substantially, resource partitioning might be present by concentrating foraging activities in different parts (Doncaster, 1990), which means intraspecific competition can also influence individual foraging strategies (Dorning & Harris, 2017). For solitary animals, the resource dispersion hypothesis predicts that territorial species may overlap where resource richness is highest even while individuals remain behaviorally solitary (Elbroch, Lendrum, Quigley & Caragiulo, 2016).

Additionally, kinship or relatedness can play an important role in social behavior and tolerance towards other individuals (Lukas & Clutton-Brock, 2018). Hamilton (1964) proposed that individuals could gain inclusive fitness benefits by 'helping out' relatives, known as the kin selection or kinship theory. This theory predicts related individuals to be more tolerant towards each other, or even cooperate together, than non-related individuals (Smith, 2014, Elbroch et.al., 2016). In many carnivore species living in groups, group members consist of related individuals (Macdonald, 1983). These members are often philopatric (i.e. staying in the area they are born after reaching maturity, Waser & Jones,

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1983), and can even exhibit alloparental behavior by caring for young that are not their own (Macdonald, 1983).

The red fox (*Vulpes vulpes*) is a species that is flexible both spatially and socially. They can have home ranges from  $< 2 \text{ km}^2$  to well over  $30 \text{ km}^2$  (Doncaster & Macdonald, 1981, Walton, Samelius, Odden & Willebrand, 2017), and exhibit variable territoriality as they can live solitary, in pairs or in social groups (Macdonald, 1981). Due to its adaptive nature, the red fox has a highly variable diet, with small mammals, birds and rodents as its main food items (Elmeros et.al., 2018). Though they also scavenge (Needham, Odden, Lundstadveen & Wegge, 2014, Kronenberg, 2018) and forage on fruits and insects, they are regarded as carnivores (Macdonald, 1983). While group living might occur, red foxes are considered solitary foragers (Pouille et.al., 1994). Apart from resource availability (Macdonald & Bacon, 1982), social hierarchy and kinship have shown to play a major role in habitat and resource exploitation (Vincent, 1958, Von Schantz, 1981) and dispersal of juveniles (Whiteside, Dawson, Soulsbury & Harris, 2011).

In red foxes, non-dispersing females can gain fitness advantages by remaining philopatric, either directly by inheriting a territory (Baker et.al., 1998) or indirectly through alloparental care (Whiteside et.al., 2011). These related females are subdominant to their mother and can ‘help out’ with new young while not reproducing themselves (Macdonald, 1979). Even though dominant and subordinate females might have an overlap in space use, their difference in hierarchy would suggest variations in the use of resources, with dominant individuals having primary access to, for example, high quality resource areas. This has been shown by Von Schantz (1981), who found that subordinate non-breeding foxes used poorer habitats and smaller home ranges than dominant individuals, interpreting this as subordinates avoiding dominants. This resource partitioning was also observed by Pouille et.al. (1992), where foxes had overlapping home ranges but always foraged alone in exclusive foraging areas. However, much remains unknown about how red foxes in general, and female foxes in particular, interact on a daily basis. According to Pouille et.al. (1994), little is known about the intensity of contacts outside the breeding period, and there is only few data relating to the dynamics of group-living individuals (Baker et.al., 1889), where it is assumed that subordinates are philopatric offspring without genetic verification (Pouille et.al., 1994, Cavallini, 1996, Dorning & Harris, 2016).

Advances in both GPS- and DNA-data analyses provide novel opportunities to examine these issues in greater detail. With the use of GPS technology, researchers are able to track animals at a much higher frequency than with manual VHF-tracking, making it possible

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to look at individual interactions at a very fine scale. This is especially helpful when studying animals moving in difficult habitats or with an elusive nature. Further, genetic analysis tools such as the use of Single Nucleotide Polymorphisms (SNPs) allow for cost effective individual recognition and kinship assignment (Flanagan & Jones, 2019).

Kinship is predicted to influence how animals respond to and interact with each other. The term interaction applies to the shared space use (i.e. static interaction) or to events mutual in space, as well as time (i.e. dynamic interaction) (Benhamou, Valeix, Chamaillé-Jammes & Macdonald, 2014). Including time as a variable enables one to measure interdependency in the movement of two individuals, such as attraction or avoidance (Long, Nelson, Webb & Gee, 2014, Mattisson et.al., 2011).

The main aim of this study is to gain insight into shared space use among red foxes and the possible effect kinship has on their interactions. With this study, I seek to discover how individuals are related to each other and if their foraging behavior is modified by competitive interactions, for example through resource partitioning. Using five GPS radio collared female foxes, I analyzed their spatial behavior to calculate their shared space use, i.e. home range overlap (static interaction) and temporal overlap (dynamic interaction).

In accordance with the kinship theory, I hypothesize that related females have a high level of both spatial and temporal overlap, as related individuals should be more tolerant to each other than to non-related conspecifics (Hamilton, 1964, Elbroch et.al., 2016). Despite this spatial overlap, I expect resource partitioning to be present due to differences in hierarchy as subordinate juvenile females are expected to avoid dominant adults. Two individuals might therefore concentrate their activities in different parts of the shared area, with juveniles having access to only a proportion of the dominant's range (Doncaster, 1990, Von Schantz, 1981). Additionally, as red foxes are considered nocturnal species (Doncaster & Macdonald, 1997), I expect interactions to vary depending on time of day, with periods of activity coinciding with increased probability of interactions. For unrelated females, I expect spatial overlap to be much lower than for related females, with minimal temporal overlap.



## 2. Materials and methods

### 2.1 Study area

The study took place in Södermanland County in south central Sweden (58°40'N - 16°22'E, see Fig. 1). The area is characterized by a mixture of coniferous and deciduous forests, interspersed with agricultural land and human settlements. Average daily temperatures differ from 20°C in summer to -5°C in winter, with irregular snow cover from December to March.

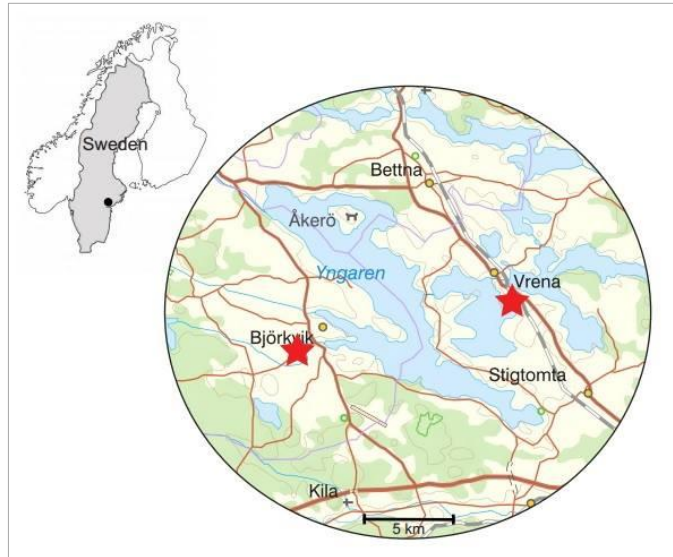


Figure 1. Overview (left) and detailed (right) map of the study area, located in Södermanland, Sweden. The red stars show where the female red foxes ( $N=5$ ) were captured and monitored.

### 2.2 Capture

As part of a larger study, red foxes were captured and fitted with GPS radio collars (Tellus Ultralight, 210 g, Televilt, Inc. Lindesberg, Sweden). Genetic material (tissue or blood samples) was collected during capturing and fitting of GPS collars. All capture and handling procedures were approved by and followed the ethical guidelines required by the Swedish Animal Ethics Committee. Collars were originally set to take positions every 4 hours, i.e. 6 positions per day. However, for the study of dynamic interactions, sampling interval was intensified to one position every ten minutes for periods of 2 – 5 weeks. Age was determined by looking at tooth wear and tooth coloration, and individuals were defined as subadult (< 1 year) or adult (> 1 year). For more details on capture and handling, see Walton et.al. (2017).

### 2.3 DNA-analysis

DNA extraction and genetic analyses for this project were performed at the Swedish University of Agricultural Sciences (SLU) in Umeå, using a 48 marker SNP chip specifically developed for red fox (H. Königsson and M. Hagenlund unpublished methodology). The SNP analysis allowed for individual recognition and genetic structure to be identified. To determine kinship among the studied individuals, relatedness values ( $r$ ) were determined using the

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program Relate (Kalinowski, Wagner & Taper, 2006) going back two generations. This program allows for us to determine the amount of genetic overlap between two individuals, indicating whether two individuals are related, and if so, the type of relationship they are most likely to have. A first-degree relative is defined as a close blood relative sharing approximately 50% genetic overlap (with relatedness value  $r \geq 0.50$ ). Such relationships include the individual's parents, full siblings, or offspring. A second degree relative is defined as a blood relative sharing approximately 25% genetic similarity ( $r = 0.25 - 0.50$ ), which includes the individual's grandparents, grandchildren, aunts, uncles, nephews, nieces or half-siblings. Third degree relatives are extended family members, sharing approximately 12.5% genetic overlap ( $r \leq 0.25$ ), and include first cousins, great-grandparents and great grandchildren.

## 2.4 Statistical analysis

I performed all statistical analysis in the program RStudio version 3.5.2 (R Development Core Team, 2018) in combination with Microsoft Excel 2013 for data preparation.

### 2.4.1 Static interaction

In order to look at interactions, I only analyzed resident female foxes that were overlapping in space and time. To examine the degree of space use shared between individuals, I used GPS positions collected from the entire period individuals were monitored. Positions obtained with less than three satellites and a degree of precision (DOP)  $> 10$  m (N = 49) were excluded from analysis due to their inaccuracy.

One female was captured in June 2017, while four females were captured in October that same year. I examined static interaction between individuals by estimating their total space use, i.e. their home ranges, and then examined the static interaction index (SI index), which is calculated as the proportion of overlap between individual ranges (Long, 2014). The SI index was calculated as 
$$\frac{HR_{\alpha} \cap HR_{\beta}}{HR_{\alpha} \cup HR_{\beta}}$$

where the area of home range overlap is divided by the total home range area of both individuals.

For comparison reasons, I chose to estimate home ranges using both Minimum Convex Polygon (MCP, Mohr, 1947) as well as kernel utilization distributions, using the package adehabitatHR (Calenge, 2006), as both methods are widely used in the literature. The MCP-

method functions as a measure of total space use by calculating the smallest convex polygon around all the included relocations, while the kernel method gives a utilization distribution. This utilization distribution is described by a bivariate probability density function; it gives the probability density to relocate the animal at a given place according to the coordinates of this place (Calenge, 2006), and thereby provides information on how shared areas are used (Doncaster, 1990). For this method, I chose the reference bandwidth as the smoothing parameter, and subset the data to one randomly selected position per day to avoid autocorrelation (Gehtz et.al., 2007).

As a home range is defined as the area used by an animal during its normal activities such as foraging and caring for young, it is common practice to exclude uncommon explorations (i.e. outliers) that are not to be considered ‘normal’ activities (Burt, 1943). Often, this results in excluding 5% of the outermost positions. However, I aim to distinguish between dominant and subordinate individuals, and subordinates are known to increase exploration to discover new foraging areas (Dorning & Harris, 2017). I therefore saw it fit to only exclude the most extreme positions by using 99% (instead of 95%) of the data. With both home range estimation methods, I distinguished between an animal’s complete home range and its core area (i.e. area of most intense use, Bertrand et.al. 1996), using 99%, 50% and 25% of the data, respectively.

## 2.4.2 Dynamic interaction

To examine temporal interactions between individual red foxes with overlapping space use, I restricted the data to only the intensive monitoring periods where positions were collected at ten-minute intervals. The terminology and notations used to describe dynamic interaction are shown in Table 1. As dynamic interaction takes into account both temporal and spatial components, most dynamic interaction indices need defined thresholds for time ( $t_c$ ) and distance ( $d_c$ ). For relocations, hereafter *fixes*, of two individuals to be simultaneous, a threshold

Table 1. The terminology and notations used to describe dynamic interaction (from Long et.al., 2014).

| Term                | Explanation   |
|---------------------|---|
| $\alpha$ or $\beta$ | Individual of a dyad (telemetry data)   |
| Dyad                | Pair of individuals ( $\alpha$ and $\beta$ )                                  |
| Fix                 | A telemetry record (spatial location and time stamp)                          |
| $t_c$               | Time threshold  |
| $d_c$               | Distance threshold  |
| $T_{\alpha\beta}$   | Temporally simultaneous fixes base on $t_c$                                   |
| $S_{\alpha\beta}$   | Spatially proximal fixes based on $d_c$                                       |
| $ST_{\alpha\beta}$  | Spatially proximal and temporally simultaneous fixes based on $d_c$ and $t_c$ |

of half the sampling interval is recommended (Long, 2014). I therefore calculated the number of temporally simultaneous fixes ( $\leq 5$  minutes apart) for each overlapping pair, using tools provided by the wildlifeDI-package (version 0.2, Long, 2014).

Further, a distance threshold  $d_c$  needs to be set in order to determine the maximum distance at which fixes are seen as proximal and thereby considered as interactions. Often, the distance threshold is chosen subjectively (Long et.al., 2014), as it is challenging to quantify when individuals are aware of each other (Gehrt & Fritzell, 1998). For small carnivores, 50 m or 100 m has previously been used in the literature (Lührs & Kappeler, 2013, Gehrt & Fritzell, 1998, Doncaster & Macdonald, 1997), without giving adequate information on the reason why. For red foxes, the furthest distance at which they can sense each other's presence was determined to be 50 m in cities (Doncaster, 1990), while Poulle et.al. (1994) argued that distances up to 100 m are close enough to be considered contact for rural red foxes. Because the choice of a threshold will influence the result, I chose to calculate dynamic interaction indices for multiple distances rather than just one, using 50, 100 and 250 meters. Additionally, because foxes mostly forage during the night and are therefore considered nocturnal species (Doncaster & Macdonald, 1997, Cavallini & Lovari, 1994), I separated between day (07:30 – 17:15) and night (17:16 – 07:29). I chose these times by averaging time of sunrise and sunset during my study period (Astronomical Applications Department, 2016).

### *Proximity analysis*

To understand the frequency at which a pair, or dyad, of foxes, is close to each other, I calculated the proximity rate: the proportion of simultaneous fixes that are defined as proximal fixes (i.e. under the distance threshold,  $d_c$ ). This is calculated as (Long, 2014):

$$Prox = \frac{T_{\alpha\beta}}{ST_{\alpha\beta}}$$

where  $T$  stands for the simultaneous fixes of individuals  $\alpha$  and  $\beta$ , and  $ST$  are fixes that are both simultaneous and proximal, based on the given thresholds. Results indicate how often a dyad is interacting, and therefore whether temporal resource partitioning is present.

### *Doncaster's (1990) non-parametric test of interaction*

To examine how tolerant individual foxes are towards each other, I used Doncaster's (1990) non-parametric test of interaction. This method compares the observed distances  $N$  ("paired" distances) with the expected probability of a pair being within a certain distance. The expected probability is generated by taking all possible combinations of fixes  $N^2$ , where for each fix on

one individual, distances are calculated to all fixes on the other animal (Fig. 2). A 2x2 contingency table is made of the paired distances under and above the distance threshold, as well as the  $N^2 - N$  (called “unpaired”) distances. Then, a  $\chi^2$  test is used to statistically examine the differences in paired and unpaired distances above and below the threshold, with a significant p-value ( $< 0.05$ ) indicating dynamic interaction. Additionally, graphs were examined to distinguish between positive interaction (attraction) and negative interaction (avoidance). Positive interactions mean a dyad is more likely to keep a certain distance from each other, whereas negative interaction indicates they are less likely (Doncaster, 1990).

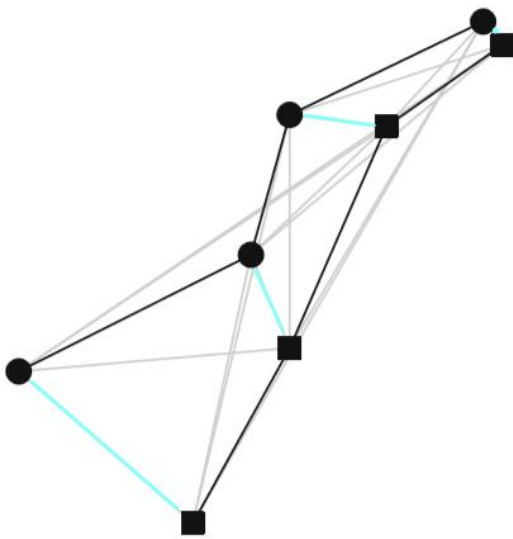


Figure 2. Visual explanation of the Doncaster non-parametric test of interaction. Circles and squares represent different individuals, and black lines show their movement paths. Distances between simultaneous fixes (blue lines) are compared to the expected probability. To estimate the probability density function, distances are measured between each fix of individual 1 (circle) to all unpaired fixes of individual 2 (square) (grey lines), and vice versa.

### ***Shirabe's (2006) correlation coefficient - Cr***

To further test the presence of attraction or avoidance, I calculated the correlation coefficient  $Cr$  (Shirabe, 2006). This method measures the degree of correlation in the movement of two individuals by looking at the data as a path, rather than just points as with the previous methods.  $Cr$  considers the movement data as time series with vectors connecting movement segments between consecutive fixes, and computes differences in those vectors with respect to overall path means; it essentially takes the form of multivariate Pearson product-moment correlation coefficient (Long et.al., 2014, Shirabe, 2006). Values range from -1 to 1, where 1 indicates highly correlated movement, such as travelling together, 0 random movement, and -

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1 negatively correlated movements such as avoidance or repulsion upon an encounter (Shirabe, 2006).

### *Interactions $\leq 50$ m*

Though it is hard to quantify at what distance red foxes are aware of each other (Gehrt & Fritzell, 1998), it is reasonable to assume they are able to detect each other when they are 50 m apart or less. I therefore saw it fit to analyse dyadic movement in greater detail within this distance threshold. I examined differences in each individual's displacement distance from a dyad's closest encounter point, using Net Squared Displacement (NSD). NSD is calculated by squaring the Euclidean distance (in order to remove directionality) between the closest point of interaction (i.e. the shortest distance between two individuals) and (until) the first observed distance  $> 50$  m. The individual with the lowest NSD remains closer to its initial interaction location, indicating dominance, while the individual moving further away indicates subordination within the interaction. I tested for normality with the Shapiro-Wilk normality test (Ghasemi & Zahediasl, 2012), which was not the case. I therefore used the Wilcoxon Signed Rank Test to assess significant differences in NSD values among interactions within dyads. Results of this test are given with the median (mdn) and interquartile range (IQR) for each individual.

### 3. Results

Two groups of female foxes had overlapping space use, resulting in four different dyads (Table 2). One overlapping group consisted of two individuals, Lisa, an adult, and Emelie, a subadult. The intensive monitoring period in which temporal interactions could be examined for this pair was 23 days. The other group consisted of two adults, Hildur and Piper, and one subadult, Madaline. The dyads Hildur & Piper and Piper & Madaline overlapped 13 days during their 10-min sampling period, while Hildur & Madaline overlapped 27 days.

*Table 2. Age, the total time period followed, the total number of fixes recorded, the total number of days, and the average number of locations per day per individual. Values in black represent the entire period foxes were monitored, values in grey represent the period when positions were taken every 10 minutes. The black line divides the two groups of individuals with overlapping home ranges.*

| FoxID           | Age | From       | To         | Fixes | Days | LocDay |
|-----------------|-----|------------|------------|-------|------|--------|
| <b>Emelie</b>   | SA  | 03.10.2017 | 01.12.2017 | 4010  | 59   | 68.0   |
|                 |     | 11.10.2017 | 11.11.2017 | 3878  | 32   | 119.9  |
| <b>Lisa</b>     | AD  | 25.06.2017 | 11.11.2017 | 3835  | 139  | 27.6   |
|                 |     | 19.10.2017 | 11.11.2017 | 3186  | 24   | 132.8  |
| <b>Hildur</b>   | AD  | 04.10.2017 | 05.12.2017 | 3268  | 62   | 52.7   |
|                 |     | 13.10.2017 | 14.11.2017 | 3178  | 34   | 93.6   |
| <b>Madaline</b> | SA  | 18.10.2017 | 14.11.2017 | 3166  | 27   | 117.3  |
|                 |     | 19.10.2017 | 14.11.2017 | 3155  | 27   | 116.8  |
| <b>Piper</b>    | AD  | 29.10.2017 | 05.02.2018 | 2176  | 99   | 22.0   |
|                 |     | 02.11.2017 | 14.11.2017 | 1523  | 13   | 117.2  |

#### 3.1 DNA-analysis

DNA-analysis showed that Lisa and Emelie are unrelated individuals (Table 3). Of the other overlapping groups, Hildur and Madaline are most likely mother and daughter ( $r = 0.50$ ), because they are first order relatives where Hildur is an adult and Madaline a subadult, making a full sibling relationship unlikely. Piper and Madaline can be considered third order relatives ( $r = 0.15$ ), as can Piper and Hildur ( $r = 0.10$ ).

| Dyad                         | r-value | Relationship |
|------------------------------|---------|--------------|
| <b>Lisa &amp; Emelie</b>     | 0.065   | U            |
| <b>Hildur &amp; Madaline</b> | 0.497   | FD           |
| <b>Hildur &amp; Piper</b>    | 0.098   | TD           |
| <b>Piper &amp; Madaline</b>  | 0.148   | TD           |

*Table 3. Relatedness ( $r$ ) values of the red foxes studied. Values  $\geq 0.5$  indicate individuals are first degree (FD) relatives. Values between 0.25 and 0.50 indicate individuals are second degree relatives, values  $\sim 12.5$  indicate third degree relatedness (TD), and values below this threshold indicate unrelatedness (Kalinowski, Wagner & Taper, 2006). With dyads containing an adult and a subadult, adult names are written first.*

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## 3.2 Static interaction

Individual red fox home ranges ranged from 2.41 km<sup>2</sup> to 12.67 km<sup>2</sup> using MCP estimation and from 4.89 km<sup>2</sup> to 33.65 km<sup>2</sup> when using kernel density estimates (Table 4). When only considering the core areas, these estimates decreased, ranging from 0.29 km<sup>2</sup> to 0.99 km<sup>2</sup> (50%) and from 0.01 km<sup>2</sup> to 0.78 km<sup>2</sup> (25%) for MCP estimates and 0.45 km<sup>2</sup> to 2.88 km<sup>2</sup> (50%) and 0.17 km<sup>2</sup> to 0.26 km<sup>2</sup> (25%) for kernel estimates.

The unrelated dyad Lisa & Emelie shared the greatest total amount of space use, with range estimates consistently overlapping to a higher degree than all other dyads (from 79% to 48%, Table 5, Fig. 3). However, this relationship changed when examining their utilization distribution within ranges, which showed that they consistently utilized different areas of their ranges (Table 5, Figure 4), indicating resource partitioning is present.

The third order, distant related dyad, Hildur & Piper, showed considerably less overlap in ranges (19%, 32%), with no overlap at the smallest core area (Table 5, Fig. 3). When examining their utilized areas, however, overlap was greater (from 34% to 21%, Table 5, Fig. 4), indicating intensive use of their shared area. Piper & Madaline, also distantly related, showed very little overlap in range estimates (21%, 20%) as well, with no overlap at all at the smallest core area (Table 5, Fig. 3) either. Their shared utilized area was considerably higher (from 45% to 29%), which indicates high usage of their shared area (Table 5, Fig. 4). Both Piper's and Madeline's utilization distribution showed used areas outside their core areas, indicating excursions.

Hildur & Madaline, mother and daughter, showed a high degree of range overlap (72 %, 49%), except with their smallest core areas, where overlap was very low (6%, Table 5, Fig. 3). Their utilization areas on the other hand overlapped extensively, indicating they shared and used about half of their ranges (Table 5, Fig. 4).



Table 4. Home range size estimates (km<sup>2</sup>) per individual, using 99%, 50% and 25% of the data. Values in black represent estimates from MCP, values in grey are estimated with kernel density estimates.

| FoxID    | Method | 99%   | 50%  | 25%  |
|----------|--------|-------|------|------|
| Emelie   | MCP    | 2.41  | 0.90 | 0.47 |
|          | Kernel | 33.65 | 2.88 | 1.16 |
| Lisa     | MCP    | 2.41  | 0.99 | 0.78 |
|          | Kernel | 4.90  | 1.09 | 0.40 |
| Hildur   | MCP    | 7.53  | 0.29 | 0.01 |
|          | Kernel | 4.89  | 0.45 | 0.17 |
| Madaline | MCP    | 8.02  | 0.50 | 0.11 |
|          | Kernel | 5.55  | 0.86 | 0.35 |
| Piper    | MCP    | 12.67 | 0.41 | 0.10 |
|          | Kernel | 9.19  | 0.90 | 0.36 |

Table 5. Static interaction index (SI) for each dyad, derived from MCP (black) and kernel (grey) home ranges using 99%, 50% and 25% of the data.

| Dyad              | Method | 99%  | 50%  | 25%  |
|-------------------|--------|------|------|------|
| Lisa & Emelie     | MCP    | 0.79 | 0.58 | 0.48 |
|                   | Kernel | 0.15 | 0.29 | 0.04 |
| Hildur & Madaline | MCP    | 0.72 | 0.49 | 0.06 |
|                   | Kernel | 0.50 | 0.49 | 0.46 |
| Hildur & Piper    | MCP    | 0.19 | 0.32 | -    |
|                   | Kernel | 0.34 | 0.34 | 0.21 |
| Piper & Madaline  | MCP    | 0.21 | 0.20 | -    |
|                   | Kernel | 0.45 | 0.47 | 0.29 |

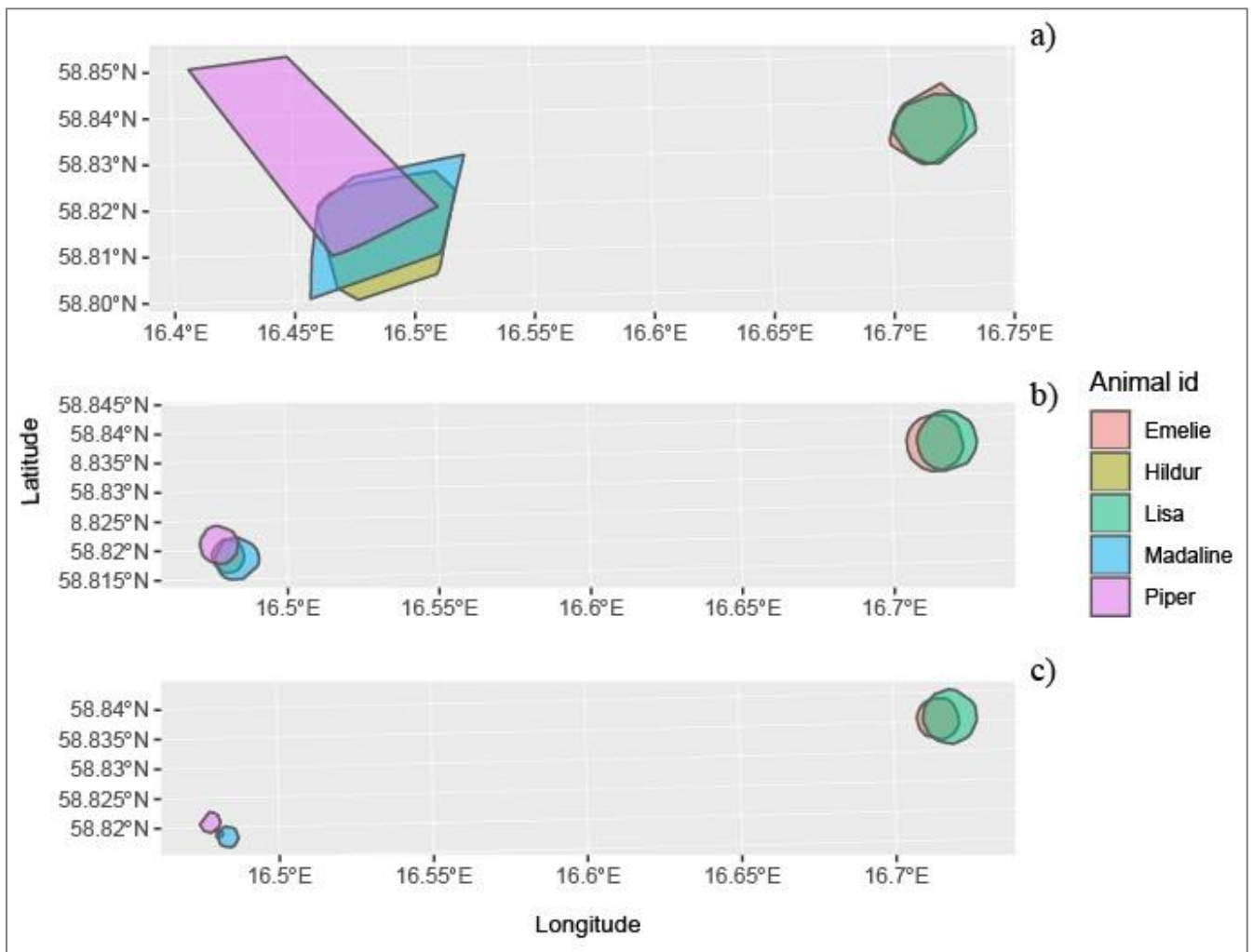


Figure 3. Individual home ranges of 5 female foxes estimated with Minimum Convex Polygon (MCP). (a) represents the entire home range estimated with 99% MCP, while (b) 50% MCP and (c) 25% MCP represent core areas.

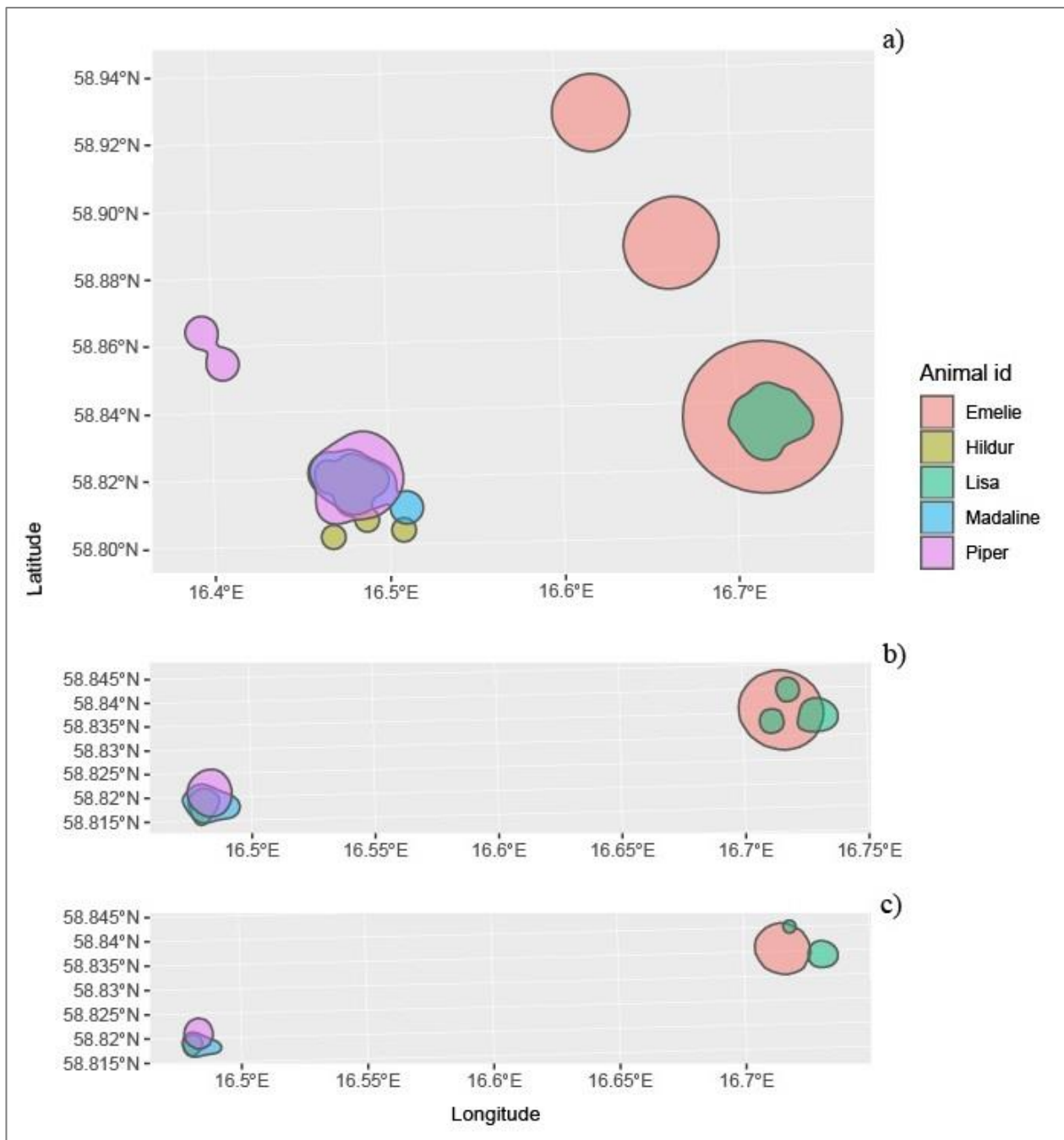


Figure 4. Individual home ranges of 5 female foxes estimated with kernel utilization distribution. (a) represents complete utilized ranges 99% kernel, while (b) 50% kernel and (c) 25% kernel represent core area utilization.

### 3.3 Dynamic interaction

#### 3.3.1 Proximity analysis

The number of simultaneous fixes per dyad ranged from 1217 to 2449 (Table 6). In general, the proportion of time spent in each other's proximity within each distance threshold increased with increasing distance (Table 6, Fig. 5). However, the two distantly related adults Hildur & Piper, were found less often within 100 m of each other than within the other distance thresholds. This might be due to them rarely encountering each other within 100 m during night, while this is higher during the day. Overall, they spent the lowest proportion of time in each other's proximity compared to the other dyads. The mother and daughter Hildur & Madaline, on the other hand, showed a considerably higher proportion of simultaneous fixes in close proximity compared to the other dyads, with 15.2% of the fixes within 50 m, and up to 26.8% within 250 m (Table 6). The proportions were fairly similar for daily and nightly positions, indicating they rested and foraged together. This was not the case for distant relatives Piper & Madaline, as they were considerably less often observed in each other's proximity. Though unrelated, Lisa & Emelie showed a slightly higher proportion of simultaneous fixes than Piper & Madaline, both during the day and night.

*Table 6. The proportion (%) of simultaneous fixes (N) within each distance threshold per dyad, for all observed fixes (All), all daily fixes only (Day) and all nightly fixes only (Night).*

| Dyad                         | Time  | N    | 50 m | 100 m | 250 m |
|------------------------------|-------|------|------|-------|-------|
| <b>Lisa &amp; Emelie</b>     | All   | 2449 | 0.8  | 4.6   | 14.5  |
|                              | Day   | 1088 | 0.0  | 5.1   | 16.8  |
|                              | Night | 1661 | 1.3  | 4.2   | 12.9  |
| <b>Hildur &amp; Madaline</b> | All   | 1966 | 15.2 | 18.2  | 26.8  |
|                              | Day   | 791  | 15.2 | 17.2  | 25.4  |
|                              | Night | 1175 | 15.2 | 18.9  | 27.8  |
| <b>Hildur &amp; Piper</b>    | All   | 1234 | 0.4  | 0.1   | 10.1  |
|                              | Day   | 542  | 0.2  | 0.7   | 10.7  |
|                              | Night | 692  | 0.1  | 0.0   | 9.7   |
| <b>Piper &amp; Madaline</b>  | All   | 1217 | 0.8  | 2.3   | 10.5  |
|                              | Day   | 524  | 0.0  | 1.0   | 9.4   |
|                              | Night | 793  | 1.4  | 3.2   | 11.2  |

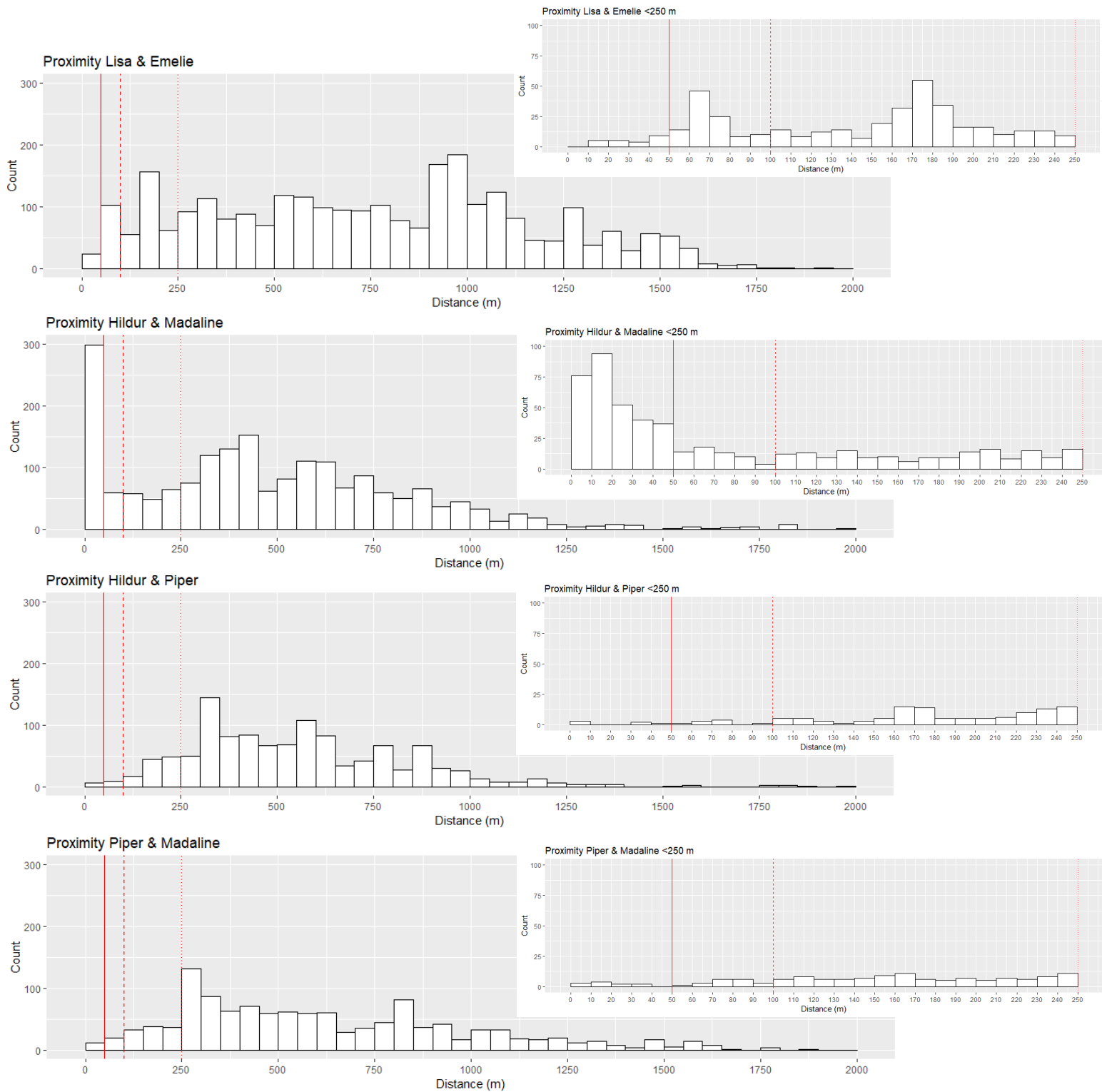


Figure 5. Histograms of observed distances between individuals in each dyad for all observed distances up to 2000 m (left figures) and  $\leq 250$  m (right figures). Red lines indicate distance thresholds (50 m, 100 m, 250 m).

### 3.3.2 Doncaster's (1990) non-parametric test of interaction

The related dyad Hildur & Madaline interacted significantly more than expected within all distance thresholds (Table 7), showing strong attraction both day and night (Fig. 6). The unrelated dyad Lisa & Emelie interacted significantly more than expected  $\leq 100$  and  $\leq 250$  m ( $p < 0.001$ ), though not within 50 m. This is probably due to them avoiding each other during the day while resting, whereas there is significant attraction during the night (Table 7, Fig. 6). Hildur & Piper, distant relatives, only showed avoidance during the night  $\leq 250$  m ( $p = 0.037$ ), indicating random movement. Piper & Madaline, also distantly related, showed attraction by interacting significantly more than expected during the night  $\leq 50$  m ( $p < 0.001$ ) and  $\leq 100$  m ( $p = 0.006$ , Table 7, Fig. 6). However, as they were observed very rarely together  $\leq 50$  m, these results should be taken with caution for Piper & Madaline and Hildur & Piper as the chi-square test assumes a sufficiently large sample size (Statistics Solutions, 2019). Conversely, few observations could also simply imply avoidance at this distance.

Table 7. Results of the  $\chi^2$  test on differences between observed and expected distances per dyad, based on Doncaster's (1990) non-parametric test of interaction. Significant  $p$ -values (in black) indicate dynamic interaction is present.

| Dyad              | Time    | 50 m    | 100 m   | 250 m   |
|-------------------|---------|---------|---------|---------|
| Lisa & Emelie     | Overall | 0.139   | < 0.001 | < 0.001 |
|                   | Day     | < 0.001 | 0.109   | 0.004   |
|                   | Night   | < 0.001 | < 0.001 | < 0.001 |
| Hildur & Madaline | Overall | < 0.001 | < 0.001 | < 0.001 |
|                   | Day     | < 0.001 | < 0.001 | 0.076   |
|                   | Night   | < 0.001 | < 0.001 | < 0.001 |
| Hildur & Piper    | Overall | 0.563   | 0.483   | 0.914   |
|                   | Day     | 0.739   | 0.398   | 0.331   |
|                   | Night   | 0.781   | 0.566   | 0.037   |
| Piper & Madaline  | Overall | 0.023   | 0.231   | 0.544   |
|                   | Day     | 0.234   | 0.226   | 0.776   |
|                   | Night   | < 0.001 | 0.006   | 0.454   |

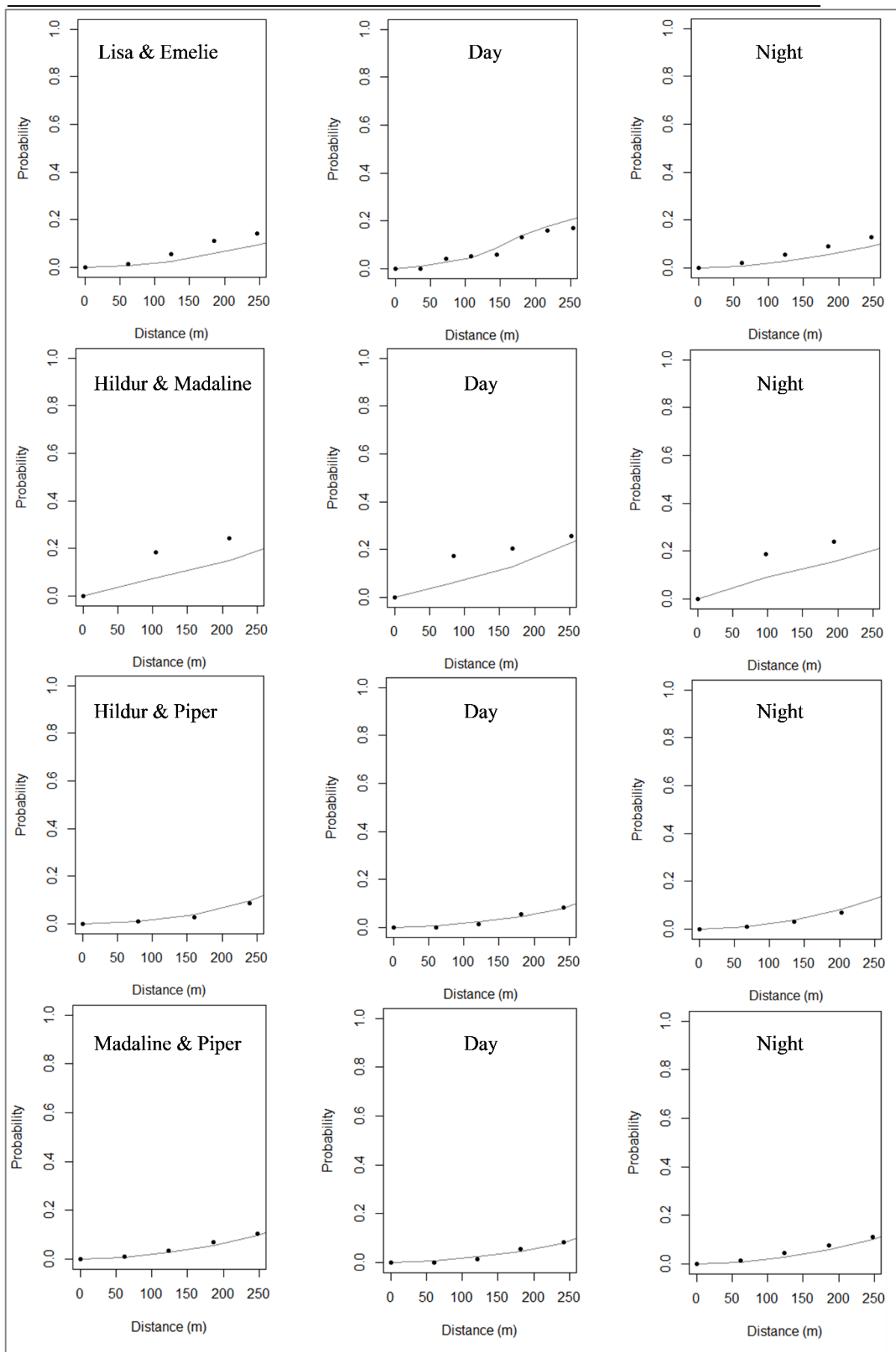


Figure 6. Cumulative distribution of observed (black dots) vs expected (grey line) fix distances estimated with Doncaster's nonparametric test for all dyads overall (left), during the day (middle) and night (right)  $\leq 250$  m. Values above the line indicate attraction, values under the line indicate avoidance, and values on the line indicate random movement. (For figures showing  $\geq 250$  m, see Appendix figures A1-A4.)

### 3.3.3 Shirabe's (2006) correlation coefficient - Cr

For most dyads, correlation coefficients are centred around zero, both during the day, the night and overall (Table 8), indicating independent movement by all the foxes. Highest correlation was found for Hildur & Madaline during the day (Cr 0.298) and can be considered medium positively correlated movement, indicating there is some attraction between them. Lisa & Emelie only have weakly negatively correlated movement during the day (Cr - 0.195), indicating avoidance.

*Table 8. Shirabe's correlation coefficient (Cr) for each dyad. A value of 1 indicates highly positively correlated movement, 0 random movement and -1 highly negatively correlated movement.*

| Dyad              | Cr     | Cr day | Cr night |
|-------------------|--------|--------|----------|
| Lisa & Emelie     | 0.052  | -0.195 | 0.030    |
| Hildur & Madaline | 0.043  | 0.298  | 0.045    |
| Hildur & Piper    | 0.042  | -0.036 | 0.027    |
| Piper & Madaline  | -0.005 | -0.007 | 0.055    |

### 3.3.4 Interactions $\leq 50$ m

The unrelated Lisa & Emelie were observed 24 times within 50 m of each other, spread over 10 days. Most interactions were short with only one position observed within the 50 m threshold, however, on two occasions they spent 30 minutes together. As all their interactions occurred during the night, it is plausible they met while foraging. For the net squared displacement (NSD) from the closest interaction point until the first position outside the 50 m interaction, the Wilcoxon Signed Rank Test showed no significant difference in net squared displacement between Lisa (mdn = 0.009, IQR = 0.018) and Emelie (mdn = 0.003, IQR = 0.006) ( $W = 160$ ,  $p = 0.132$ ), indicating that neither moved further away than the other.

Hildur & Madaline, mother and daughter, were observed 299 times within 50 m of each other, spread over 18 different days. As they were tracked for 27 days, this means they were together for over half the tracking period. Though most of the interactions occurred during night ( $N = 179$ ), a considerable proportion of fixes were during the day ( $N = 129$ ). Minimum distance observed was 1 m for both day and night, implying they both foraged and rested together. Average minimum distance between this dyad was 20 m and did not differ between day (21 m) and night (20 m). 21 interactions lasted shortly with just one observation  $\leq 50$  m; all other

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interactions lasted between 10 and 330 min (5,5 hours), with an average of 55 min. In other words, when within 50 m of each other, Hildur and Madaline usually spent a considerable amount of time together. No displacement was found, as the Wilcoxon Signed Rank Test showed no significant difference in net squared displacement between Hildur (mdn = 0.004, IQR = 0.003) and Madaline (mdn = 0.003, IQR = 0.002) ( $W = 15060.5$ ,  $p = 0.287$ ), indicating tolerance as neither moved further away than the other.

The two distantly related adults Hildur & Piper were only observed 6 times within 50 m, in a period of 13 days. They met mostly during the night and very briefly; only on one occasion were two consecutive fixes within the 50 m threshold, where they were 6-7 m apart. On another occasion the distance between them was just 3 m, which increased to 739 m ten minutes later where Hildur's displacement (NSD = 0.693) was considerably higher than Piper's (0.009), indicating a non-friendly encounter towards Hildur. The Wilcoxon Signed Rank Test showed no significant difference in overall net squared displacement between Hildur (mdn = 0.030, IQR = 0.059) and Piper (mdn = 0.017, IQR = 0.020) ( $W = 22$ ,  $p = 0.589$ ), however. Though the non-significance might be due to the small sample size, it is difficult to tell which fox remains closer to the initial interaction position and therefore can be considered dominant.

The distantly related Piper & Madaline were not observed often within 50 m of each other either, but they did spend more time together than Hildur & Piper. All interactions occurred while night, but of the 11 fixes total, 8 were during the same night. Here, interactions lasted half an hour on two occasions, where they stayed 4-22 m from each other. When within the 50 m threshold, they were on average 16 m apart, indicating overall close encounters. Surprisingly, the Wilcoxon Signed Rank Test showed that the subadult Madaline (mdn = 0.002, IQR = 0.004) had a significantly lower NSD than Piper (mdn = 0.018, IQR = 0.016;  $W = 7$ ,  $p = 0.005$ ), indicating Madaline retained positions closer to the closest interaction point, while the adult Piper moved away after the conspecific encounter.

As Hildur, Madaline and Piper all share space, it is possible the three of them encountered each other at the same. This was the case only twice. During the first encounter, which happened during the evening, Hildur & Piper were 3 m from each other, with Madaline 33 m from them (Fig. 7a). Piper & Madaline were within 50 m of each other 7 other times earlier that day, while Hildur & Madaline were already together for 20 min before this encounter. Hildur & Piper, on the other hand, only had this one encounter that day. Madaline retained her position (NSD < 0.001), while Piper (NSD = 0.009) and Hildur (NSD = 0.693) moved away.



During the second encounter, which happened early in the evening, all three individuals were in close proximity of each other (Fig. 7b). Before this encounter, Hildur & Madaline had been spending almost 4 consecutive hours together. Right after this interaction, Madaline again didn't move away far (NSD = 0.001), while Hildur (NSD = 0.026) & Piper (NSD = 0.027) stayed 10 more minutes together.

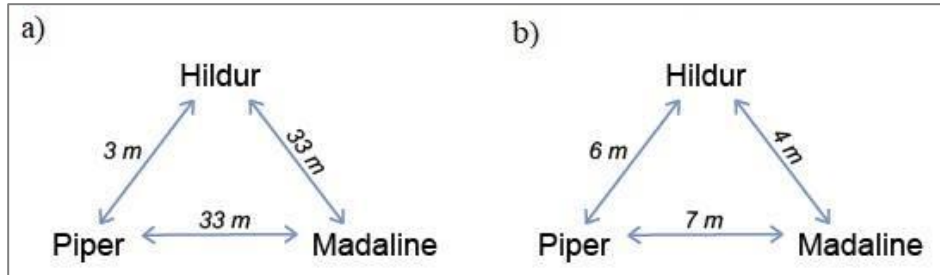


Figure 7. Interactions  $\leq 50$  m of the three overlapping female red foxes on occasion 1 (a) and occasion 2 (b).

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## 4. Discussion

My findings show that female red foxes share space to high degree but display variable tolerance towards each other, as shown by their differences in spatio-temporal overlap and resource partitioning, which is likely influenced by their kinship relationships.

As predicted, I found that the most closely related individuals, Hildur & Madaline, showed a considerably higher temporal and utilized range overlap compared to the other dyads. Their extensive overlap in utilization ranges combined with the large number of encounters, which sometimes lasted multiple hours, implies there was little resource partitioning between them and therefore a high degree of tolerance. The high number of times they were within each other's proximity also showed there was definite attraction between them, strengthened by the significant positive interaction. Even the Cr-statistic, which analyses the entire dyadic movement paths and is unable to show correlation when only few interactions occur, showed attraction between Hildur & Madaline. Interestingly, they spent quite some time together both during the day while resting, and during the night while foraging. While shared use of dens as a resource has been found in previous studies (Cavallini, 1996), red foxes are considered to be solitary foragers (Pouille et.al., 1994). In accordance with the kinship theory (Hamilton, 1964), it is reasonable to assume that their full parent-offspring relationship allows for higher tolerance from Hildur towards her daughter than to unrelated conspecifics, probably in combination with Madaline's young age. This dyad was monitored in October and November, and although juvenile dispersal primarily occurs in fall and winter (Gosselink, Piccolo, van Deelen, Warner & Mankin, 2010), I did not find evidence of Hildur behaving aggressively toward Madaline to drive her out. Madaline might very well stay in her natal area when reaching maturity, as red foxes are known to form spatially clumped social groups. These groups comprise of a dominant pair and subordinate adults/juveniles that are often related, when resource availability (Macdonald, Pouille et.al., 1994) and/or density (Dorning & Harris, 2017) is high enough. This is additionally affected by maternal social status, as daughters of dominant females are less likely to disperse, and consequently might gain inclusive fitness indirectly through alloparental care (Whiteside et.al., 2011), or directly by inheriting their mother's territory (Baker et.al., 1998). Whether Hildur is the dominant female is hard to tell, as no significant differences in NSD with the other overlapping adult female, Piper, were found. Interestingly, however, this was found for Madaline & Piper, where Madaline remained near their closest point of interaction while Piper moved away. It is possible Hildur is the

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dominant female, thereby giving Madaline higher social status than Piper, though findings in this study are not sufficient to conclude this. In red foxes, as well as many other group living carnivores, subordinate adults might suppress breeding, which is likely imposed socially by dominant adults (Macdonald, 1979, Creel & Macdonald, 1995, Henry, Poulle & Roeder, 2005). Future studies examining social hierarchy in red foxes might therefore assess breeding status to help evaluate which individuals are dominant and subordinate. Additionally, kinship could be determined in greater detail, as only speculations on the relationship between third degree relatives could be done here.

The distantly related dyad Piper & Madaline showed high overlap in utilization ranges. However, temporal overlap was minimal, indicating temporal partitioning of resources. To avoid conflict, individuals might visit feeding grounds at different times (Doncaster, 1990), where the dominant is most likely to be the first visitor (Dorning & Harris, 2017). Because of their age difference, the low number of encounters could have been explained as the juvenile avoiding the adult. Surprisingly, Madaline, the juvenile, stayed significantly closer to points of interaction while Piper moved away, indicating a certain tolerance of Madaline by Piper. Despite the relatively low number of close encounters between them, it is plausible they are familiar with each other, and tolerance could therefore be explained by the ‘dear-enemy’ effect, where responses to known neighbours are believed to be less defensive than to unknown intruders (Christensen & Radford, 2018).

All three foxes, Hildur, Madaline and Piper, interacted within 50 m of each other on two occasions. Hildur & Piper were within 50 m of each other only 6 times total, and so it is interesting that Madaline was involved on two occasions. After these interactions, Madaline stayed near the original interaction point, while Hildur and Piper moved away. While it is possible Hildur chased Piper away, as might be the case with the second encounter when Hildur & Piper are still together after the initial interaction, this isn’t the case during the first encounter. Here, Hildur moves away the furthest. It is possible that agonistic behaviour, which can be costly in terms of time and energy (Christensen & Radford, 2018), is not worth it here, as it is still early in the evening and Hildur has the possibility to forage somewhere else.

As unrelated individuals are expected to overlap much less than related individuals (Elbroch et.al., 2016), the high overlap of home ranges for Lisa & Emelie was surprising. High home range overlap with little or no territoriality has previously been reported by Harris (1980) in urban red foxes in Britain. Here, food availability was spatially and temporally unpredictable

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and therefore difficult to defend. When examining temporal overlap between Lisa & Emelie, however, resource partitioning became apparent, especially during the day. They were never observed  $\leq 50$  m and tended to avoid each other during the day. This was strengthened by their negatively correlated movement, which indicates opposing movement. During the night they would encounter each other slightly more often, though still only 1.3% of all nightly positions were within 50 m over the 24 day monitoring period. They appeared to avoid approaching each other within this distance, and it is therefore surprising that the Doncaster method showed significant attraction. One possible explanation is Lisa, the adult fox, exhibited agonistic behaviour by seeking out and chasing Emelie (Doncaster, 1990), though this was not supported by their differences in NSD. While the correlation coefficient by itself does not show evidence of such movements, it is possible to test for this kind of behaviour by implementing a time-lag, though this might prove challenging as following behaviour probably is not static (Shirabe, 2006, Joo, Etienne, Bez & Mahévas, 2018). Alternatively, Lisa might not be a dominant adult and tries to avoid encounters with other foxes (Henry et.al., 2005). Nonetheless, while their high home range overlap suggests tolerance of shared space, strong resource partitioning seems to be present. These findings show that kinship alone is not sufficient in explaining shared space use in female red foxes.

The two distantly related adults Hildur & Piper had a slightly higher overlap in utilized range compared to Piper & Madaline, but their temporal overlap was lowest of all dyads. They were observed only 6 times  $\leq 50$  m, indicating avoidance. Significant negative interaction was however only found during the night  $\leq 250$  m. Finding negative interaction like this is not common, as repulsion between individuals usually results in non-overlapping ranges (Doncaster, 1990). Furthermore, red foxes use indirect communication such as scent marks and vocalizations to mediate encounters (White & Harris, 1994).

I did not find juveniles to have access to only a proportion of the dominant's range (Doncaster, 1990); rather the opposite, that the juveniles were mostly found utilizing large parts of the dominant's ranges. The juveniles did, however, use relatively large areas outside the dominant's ranges, which is typical behaviour for subordinates. To compensate for the competition with the dominant, they increase exploration, potentially to discover other resources (Dorning & Harris, 2017). Following this reasoning, Piper could, in relation to Hildur, be considered a subordinate as well. Though their NSD did not show any significant differences, Piper is using areas outside the shared range similarly to the juveniles. This, in addition to the large temporal partitioning, shows that all dyads, except Hildur & Madaline,

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largely concentrate activities in different parts of their ranges, supporting earlier conclusions on red foxes as solitary foragers.

To further quantify social hierarchy in relation to foraging, the type, quality and distribution of resources can be examined. Other studies have shown that dominants have primary access to high quality resources, while subordinates may target resources of lower quality (Dorning & Harris, 2017, Von Schantz, 1981). Though food resources were not examined in this study, it is likely they were rich enough to allow for spatial groups or ‘group living’, defined by Poulle et.al. (1994) as foxes whose home ranges overlap 30% or more. There seems to be general agreement in the literature that groups comprise of related individuals. However, Lisa & Emelie show a striking of example on how this is not always the case; they have the highest home range overlap while being unrelated. It therefore seems that resources were high enough to allow large spatial overlap and group formation, but that social hierarchy may play an important role in maintaining a certain degree of territoriality through temporal resource segregation.

An issue that arises with dynamic interaction analysis is the choice of a distance threshold for defining an interaction. As mentioned previously, this choice is generally made subjectively (Long, 2014), and often authors do not specify their reasoning. For red foxes, different thresholds were used previously dependent on the study area (i.e. urban vs rural, Doncaster, 1990, Poulle et.al., 1994), and my findings clearly show that results differ depending on the chosen distance. It is therefore advisable to choose multiple distance thresholds depending on the questions studied (e.g. habitat, type of resources, mating or weaning period), but also to increase the ability to compare with other papers (Joo et.al., 2018).

Additionally, results from Doncaster’s non-parametric test of dynamic interaction should be taken with caution. This method generates null distributions by permuting (i.e. rearranging) the observed data, while assuming these data are independent. This and many other methods were developed during the 1990’s, when this assumption was less likely to be violated, as high resolution tracking systems were not available (Long, 2015). When studying dynamic interaction, short temporal sampling intervals give better insight in an animal’s continuous movement (Fieberg, 2007), but it inherently creates challenges because of increased serial autocorrelation (Benhamou et.al., 2014). With recent advances in GPS-technology (Zimmermann, 2013), data with high sampling frequency has become more common, while development of new methods have been very few (Miller, 2015). Although spatiotemporal

correlations contain important biological information (Getz et.al., 2007), autocorrelation typically causes underestimation of standard errors and in the case of Doncaster's test, increased Type 1 error (i.e. rejection of a true null hypothesis) (Long et.al., 2014). It has additionally been argued that the null distribution is not ecologically meaningful, as it does not resemble a realistic movement path (Long, 2015, White & Harris, 1994). Descriptive analysis (e.g. Proximity analysis), though perhaps lacking scientific rigour (Long, 2015), produce more reliable results across a wide range of sampling scales and may therefore provide a better understanding of behavioural interactions (Long et.al., 2014).

## 4.1 Conclusion

My findings clearly show that not all red foxes who share large areas can be assumed to be closely related, and that there was tolerance amongst individuals, whether related or unrelated. Though this was likely due to resource availability being high enough to discourage territoriality, resource partitioning was present amongst all dyads. It was, however, considerably lower for the mother and daughter, strengthening the prediction by the kinship theory. It therefore seems that resource availability and kinship have a synergetic effect on red fox social structure. Though more data is undoubtedly needed, this study provides the first steps of filling the gap in knowledge of red fox interactions and social structure.

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## Appendix

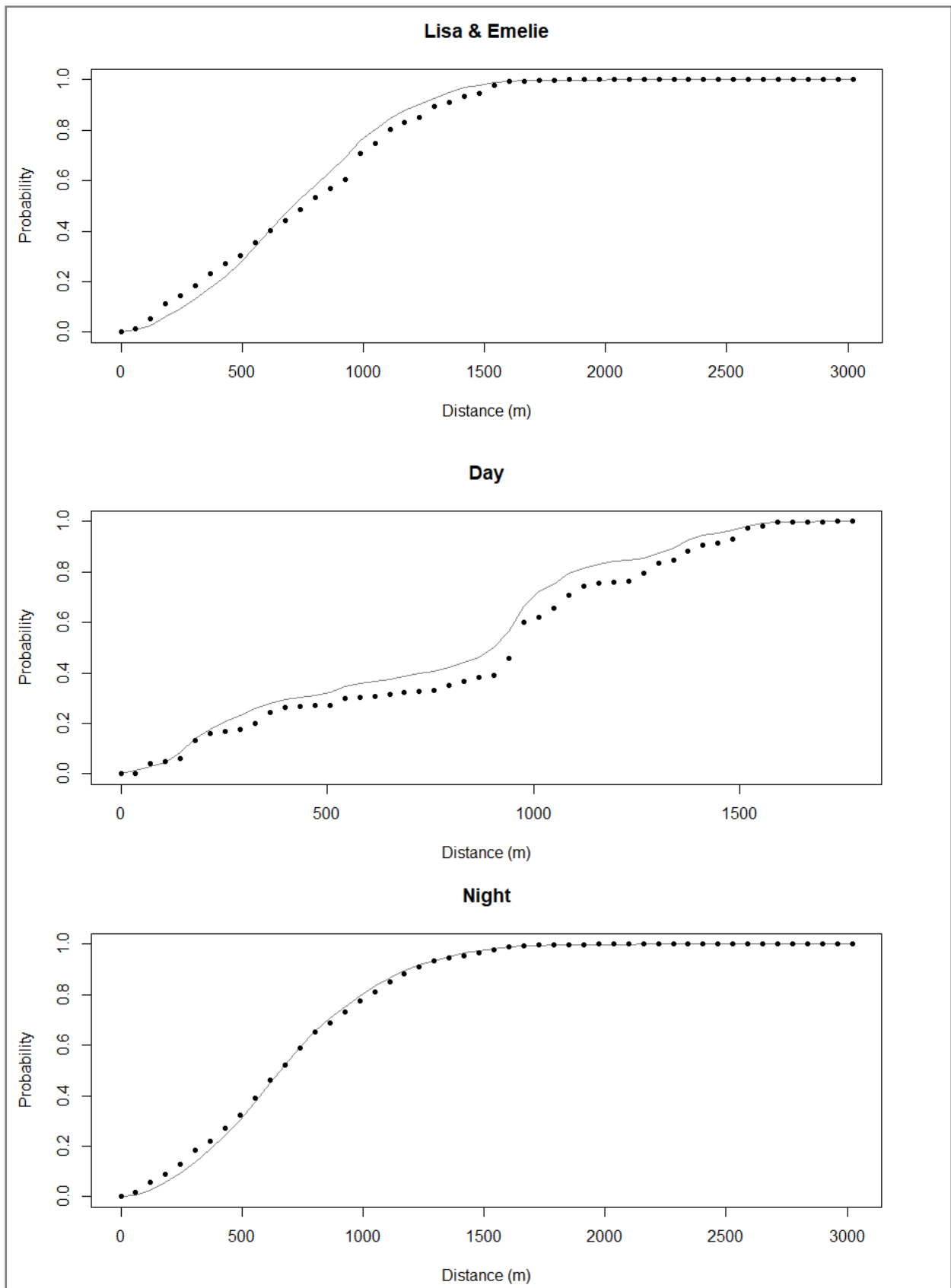


Figure A1. Cumulative distribution of observed (black dots) vs expected (grey line) fix distances estimated with Doncaster's nonparametric test for Lisa & Emelie overall (above), during the day (middle) and night (under).

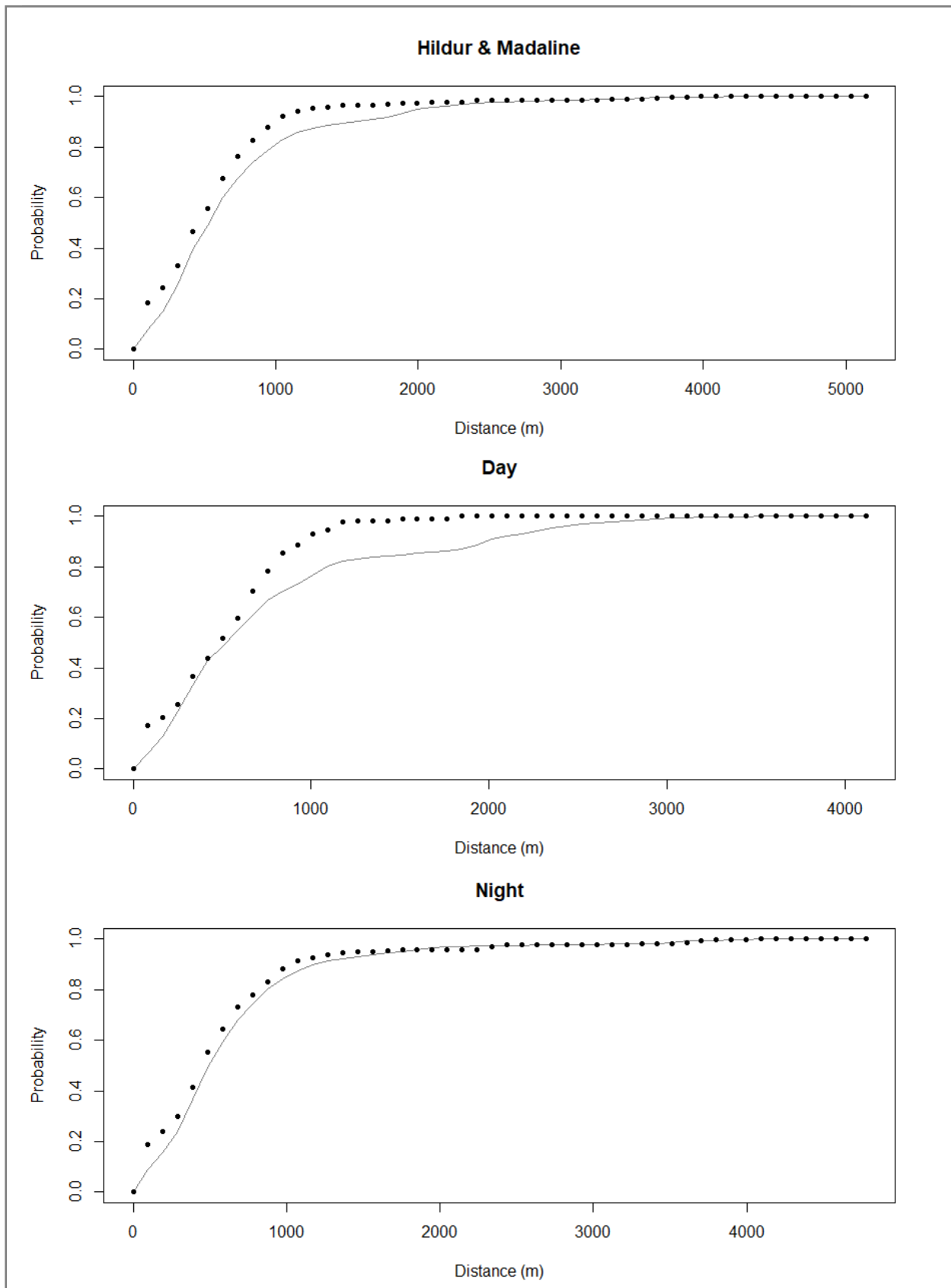


Figure A2. Cumulative distribution of observed (black dots) vs expected (grey line) fix distances estimated with Doncaster's nonparametric test for Hildur & Madaline overall (above), during the day (middle) and night (under).

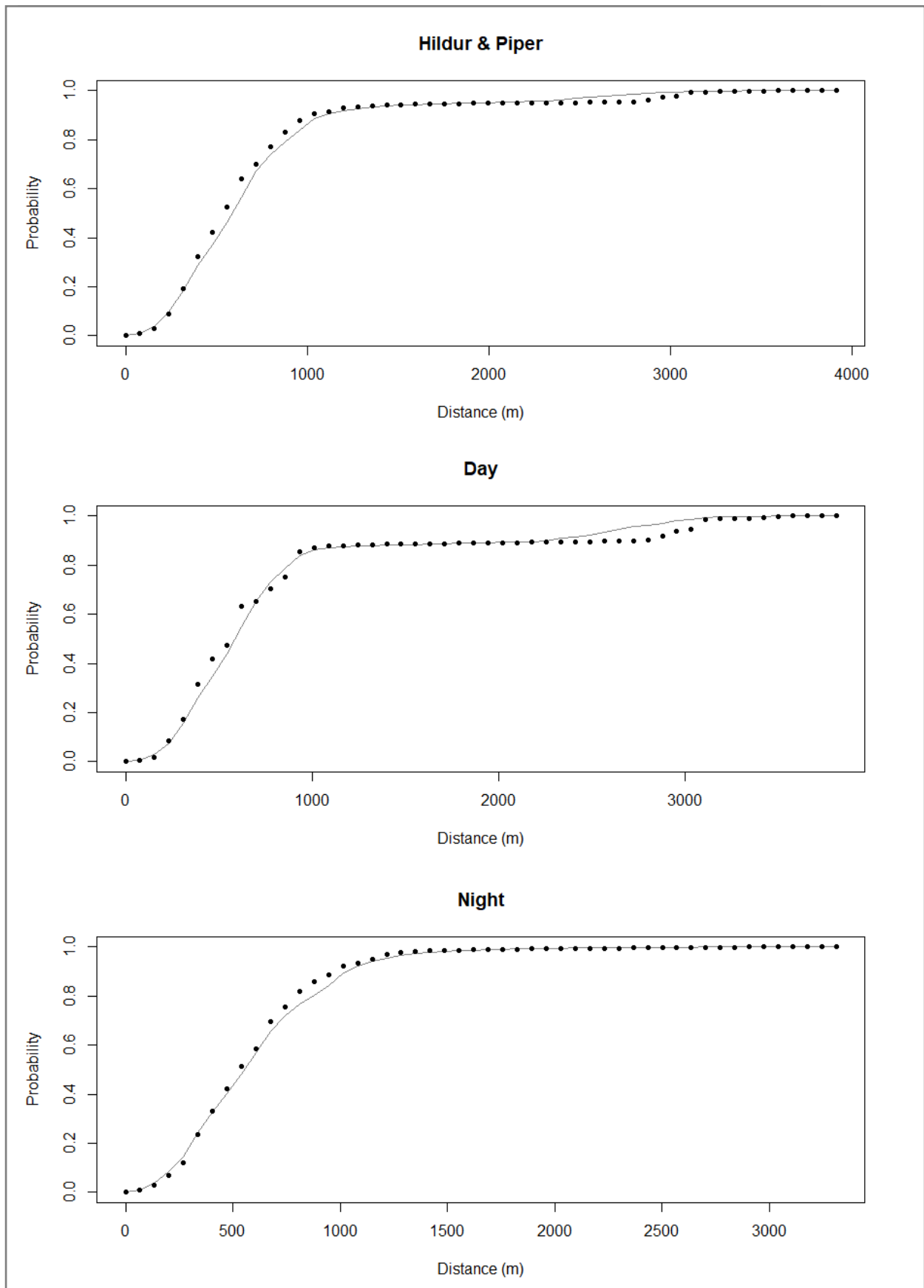


Figure A3. Cumulative distribution of observed (black dots) vs expected (grey line) fix distances estimated with Doncaster's nonparametric test for Hildur & Piper overall (above), during the day (middle) and night (under).

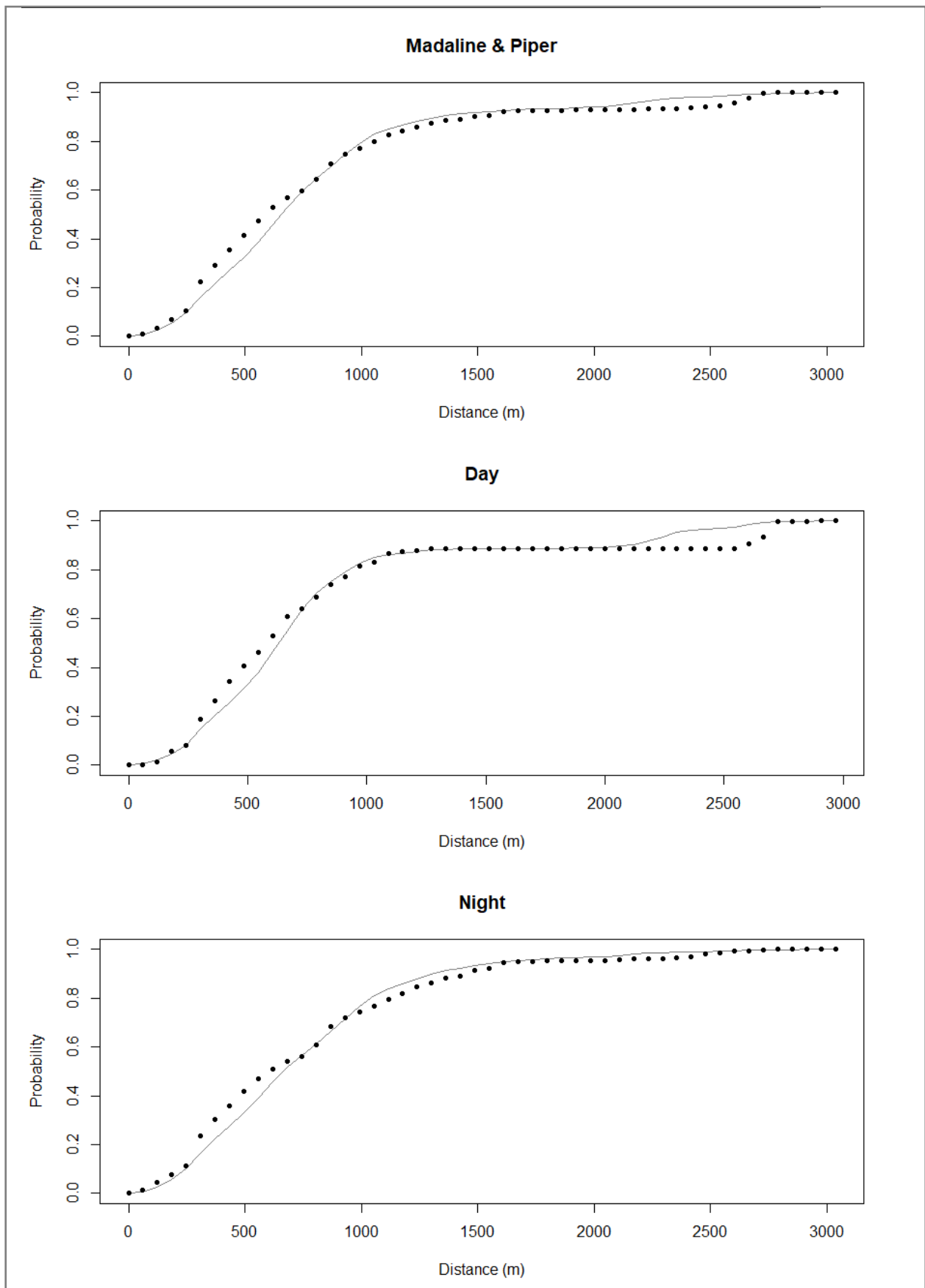


Figure A4. Cumulative distribution of observed (black dots) vs expected (grey line) fix distances estimated with Doncaster's nonparametric test for Piper & Madaline overall (above), during the day (middle) and night (under).