Inland Norway University of Applied Sciences

Faculty of Applied Ecology and Agricultural Sciences

Erik Versluijs

Master thesis

Wolf-human interaction: a method and pilot study for experimental human approaches on wild, GPS-collared wolves

Master in Applied Ecology

2020

1 June 2020	Evenstad	E.Versluijs
Date	Place	Signature

I agree that this thesis is for loan in the library   YES ☒ NO ☐

I agree that this thesis is open accessible in Brage   YES ☒ NO ☐

Abstract

Wolves are recolonising human-dominated landscapes, which increases conflicts as people express fear based on the perception that wolves are dangerous and unpredictable. Increasing knowledge about behavioural responses of wolves towards humans might improve appropriate management and decrease conflicts. Nowadays, behavioural responses can be monitored with high-resolution GPS data. I conducted trials in which wild, GPS-collared wolves were approached by humans. Based on these trials, I developed a standardised method for extracting variables such as flight initiation and resettling using statistical process control (SPC). Furthermore, I conducted a pilot study exploring the first results of experimental human approaches on wolves using GPS data. Experimental approach trials were conducted on six individual wolves over two years within three wolf territories along the border between Norway and Sweden.

In this thesis, I compared two statistical process control methods for determining the flight initiation distance (FID) during wolf approaches: the upper control limit (UCL) and the changepoint method. The FID is often used to describe the magnitude of an animal's response to a disturbance. Both methods performed similarly well for detecting the flight initiation. However, changepoint analyses increase reproducibility and comparability for this type of studies. Additionally, I used changepoint analyses to determine the moment of resettling. In the pilot study, I used changepoint analyses to extract both flight initiation and resettling.

Human-caused disturbance could result in anti-predator behaviour, even in apex predators. The intensity of the flight response may be a function of the wolf's perception of risk. Therefore, I measured flight distance, displacement, speed and straightness as measures of flight intensity. For 17 wolf-human interactions within this pilot study, I found a correlation between longer flight duration, distance, displacement and higher speed, indicating that these are associated with higher flight intensity. Two observers rather than one, wind blowing away from the wolf, and a higher noise level resulted in higher flight intensities, suggesting a combined effect of detectability and perceived risk. Additionally, I found that the perceived risk might be affected by horizontal cover, as wolves that were more concealed stayed longer at their initial site. Generally, the wolves' flight patterns diverted away from the observer and none of the wolves were seen or heard during approach trials. Future studies might inform conservation and management, as human-wildlife conflicts are increasing. Increasing knowledge of wolf behaviour towards humans might improve coexistence with carnivores.

Keywords: *Canis lupus,* animal behaviour, human-carnivore, wolf, spatio-temporal

Sammendrag

Rekoloniseringen av ulv i et menneskedominert landskap har resultert i økt konflikt mellom vilt og mennesker. Noen mennesker opplever frykt basert på en oppfatning av at ulven er farlig og uforutsigbar. Økt kunnskap om ulvens atferdsrespons når mennesker er i nærheten, kan bedre forvaltning av ulv og redusere konflikten. Ulvens atferdsrespons kan nå måles ved hjelp av GPS-data med høy romlig og temporær oppløsing. Jeg har gjennomført eksperimentelle tilnærmingsforsøk på ville, GPS-merkede ulver. Basert på disse forsøkene har jeg utviklet en standardisert metode for å hente ut variabler som når og hvor ulvens flukt startet og sluttet ved hjelp av statistisk prosesskontroll (SPC). Jeg gjennomførte også en pilotstudie som utforsker de første resultatene fra de eksperimentelle tilnærmingsforsøkene på ulver ved hjelp av GPS-data. Tilnærmingsforsøkene ble gjennomført på seks forskjellige ulver over to år i tre ulveflokker langs grensen mellom Norge og Sverige.

I denne studien har jeg sammenlignet to SPC-metoder for å definere de fluktinitierningsavstandene (FID) i løpet av tilnærmingsforsøkene, nemlig øvre krontrollgrense (UCL) og endringspunktanalyse. FID er ofte brukt for å beskrive intensiteten til et dyrs fluktrespons. Begge metodene ser ut til å fungere like godt for å oppdage fluktinitieringen, men endringspunktanalyser øker repeterbarheten og sammenlignbarheten med andre studier. Jeg brukte endringspunktanalyser for å definere når flukten sluttet. I pilotstudien brukte jeg endringspunktanalyser for å definere både når flukten startet (FID) og når den sluttet.

Menneskelig forstyrrelse kan forårsake antipredatoratferd, også hos toppredatorer. Intensiteten til fluktresponsen kan forventes å øke med økt opplevelse av fare. Jeg målte derfor strekning, forflytningsavstand, hastighet og retthet for hver flukt. For 17 interaksjoner mellom ulv og mennesker i denne studien fant jeg en positiv sammenheng mellom fluktvarighet, distanse, forflytning og hastighet, noe som tilsier at disse faktorene kan være assosiert med høy fluktintensitet. To observatører i stedet for én, vindretning bort fra ulvene og høyt støynivå var forbundet med høyere fluktintensitet. Jeg fant også indikasjoner på at ulvens opplevelse av fare ble påvirket av horisontal dekningsgrad da ulver som lå mer skjult ble liggende lenger før de flyktet. Generelt trakk ulvene seg vekk fra observatøren, og ingen ulver ble sett eller hørt under forsøkene. I fremtidige studier kan slik informasjon hjelpe til i avgjørelsesprosesser innenfor naturvern og naturforvaltning for å minke konfliktene mellom mennesker og vilt. I tillegg kan økt kunnskap om ulvens atferd når mennesker er i nærheten forbedre sameksistensen med rovdyr.

Stikkord: *Canis lupus,* dyrs atferd, menneske-rovdyr, ulv, romlig-temporær

Table of content

1. General introduction

As a result of European legislation, wolves (*Canis lupus*) are recolonising areas in Europe (Chapron et al., 2014). Increasing conflicts arise as wolves are entering human-dominated areas, although wolf attacks on humans are rare (Penteriani et al., 2016; Kuijper et al., 2019). Some people express fear based on a perception that wolves are dangerous and unpredictable (Johansson et al., 2012; Ordiz et al., 2013a), resulting in people experiencing a diminished quality of life and increasing conflicts in wolf management. Studies suggest segregation between human activities and wolves, both in space and time, might be the key for coexistence (Kuijper et al., 2019; Rio-Maior et al., 2019). However, other studies suggest that improving information about risk-enhancing human behaviour, and preventive measures might reduce conflicts (Røskaft et al., 2007; Penteriani et al., 2016). Negative attitudes towards wolves are not only related to fear, but also due to predation on livestock and pets, and the mistrust of managing authorities (Heberlein, 2012; Johansson et al., 2012). Regardless of the source of the conflict, increasing knowledge about wolf behavioural responses towards humans might improve management actions, as potential risk-enhancing human behaviours could be determined.

Nowadays, the use of telemetry for movement ecology studies is widespread. GPS movement data is used, e.g. for studies of predation (Zimmermann et al., 2015), species interaction and competition (Wikenros et al., 2010; Eriksen et al., 2011), distribution (Chapron et al., 2014), and human-animal interactions (Moen et al., 2012; Ordiz et al., 2019). This relatively new technology provides the opportunity to study behavioural reactions of wolves with high precision and spatio-temporal resolution when experimentally approached by humans. Modern GPS collars allow re-programming to one-minute positioning intervals, which results in spatial data with a high spatio-temporal resolution.

As recently shown in brown bears (*Ursus arctos*), experimental approaches increase knowledge about individual behavioural reactions when approached by humans. Such studies have already been conducted on brown bears (Moen et al., 2012; Ordiz et al., 2013b; Sahlén et al., 2015), moose (*Alces alces*) (Viljanen, 2019), lynx (*Lynx lynx*) (Sunde et al., 1998), red deer (*Cervus elaphus*) (Sunde et al., 2009b), buzzards (*Buteo buteo*) (Sunde et al., 2009a), and wolves (*Canis lupus*) (Karlsson et al., 2007; Wam et al., 2012, 2014). Experimental approaches provide information on initial reactions of animals (Moen et al., 2012; Sahlén et al., 2015), their behaviour across different

study areas (Moen et al., 2018), identifying long-term behavioural effects on animals (Ordiz et al., 2013b), and specific behavioural processes, such as the potential habituation to humans after repeated encounters (Ordiz et al., 2019).

Based on experience from previous studies on experimental human approaches on animals, I developed a standardised method to extract variables from positioning data of an approached animal, such as flight initiation distance and resettling. The development of a standardised method to extract basic variables increases the reproducibility and provides the opportunity for comparisons of wolf responses between populations and across different study areas. Based on this method, I conducted a pilot study to explore the first results of experimental approaches on wolves while collecting movement data at a high spatio-temporal resolution.

I divided my thesis into two chapters. In chapter I, I developed a standardised method to extract wolf flight initiation and resettling positions, as a contribution to the development of a new standardised protocol for approach studies (Eriksen et al., in prep). In chapter II, I described the initial flight response of wolves to experimental human approaches, and I explored the effects of different variables, such as the number of observers and wind direction, on the flight response. Both chapters share data collection methods. Therefore, I first introduce the general methods of conducting experimental approaches on wolves. The developed method and the pilot study in this thesis can be a useful tool to improve our knowledge about wolves' responses to human disturbances along anthropogenic gradients, which in turn should inform conservation and management.

2. General methods

I based both chapters on the same field data. The data collection followed the protocol as described in this method section.

2.1 Study area and animals

The study area is located along the border between Norway and Sweden. It includes two wolf territories (Varåa and Juvberget) south of Trysil (Norway) (61°02'N, 12°18'E), and one wolf territory (Magnor) near Charlottenberg (Sweden) (59°55'N, 12°11'E). The landscape is mainly dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with a lower abundance of birch (*Betula pubescens, B. pendula*) and aspen (*Populous tremula*). The intensively managed forests consist of a mosaic of stands with different age classes, with an extensive network of forest roads (Sand et al., 2008). The human population density around Magnor is higher (10 inhabitants per km^2) compared to the area around Varåa and Juvberget (2 inhabitants per km^2) (Statistisk sentralbyrå, 2020). In the area, moose is the most important prey for wolves and is found throughout the study area (Zimmermann et al., 2014; Sand et al., 2016).

Over two years, six wolves were captured and equipped with Vectronic VERTEX Plus GPS collars. The captures were part of the yearly wolf collaring conducted by the Scandinavian Wolf Research Project (SKANDULV) and the Interreg-funded border wildlife project (GRENSEVILT). The wolf captures took place in the winters of 2018 and 2019, and followed the ethically approved procedures as described by Arnemo & Evans (2017). In 2018, both scent-marking adults from Varåa and Juvberget were collared. In 2019, both adults from Varåa were recaptured and recollared, as well as the female from Juvberget. The Juvberget male was found dead in November 2018, and a new male was identified in December 2018 (Wabakken & Maartmann, 2019). The new scent-marking male in Juvberget was collared in 2019. The male in Magnor was collared as a pup in Norrsjö (Sweden) in early 2018, then dispersed (November 2018) and settled in Magnor (December 2018). In the winter of 2018-2019 the Varåa territory had a scent-marking pair and no pups. In the Juvberget territory, three pups were counted in May 2018. However, none of the pups were detected during the monitoring period from 1 October 2018 to 30 March 2019. (Svensson et al., 2019; Wabakken & Maartmann, 2019). In the winter of 2019-2020, both the Varåa and Magnor

pairs were accompanied by 3-5 pups each, whereas the Juvberget pair had no pups (Wabakken et al., 2020).

2.2 Field protocol

Experimental human approaches on the GPS-collared wolves (from hereafter approach trials) were conducted between August and December 2018, and between August 2019 and January 2020. The fieldwork was approved by the Norwegian Food Safety Authority (FOTS ID 15370) and the Animal Welfare Ethics Committee of Uppsala, Sweden (ref. 5.8.18-13246/2019). The approach trials followed the standardised field protocol, as developed by Eriksen et al., (in prep):

Days of the approach trials were divided into three periods. 1: The preparation period lasted from 08:00 to 12:00 local time (10:00 – 12:00 in 2018) and had 10-minute positioning intervals. 2: The approach period lasted from 12:00 to 14:00 local time and had one-minute positioning intervals. 3: The post-disturbance period lasted from 14:00 to 17:00 (14:00 – 15:00 in 2018) and had 10-minute positioning intervals. The 10-minute positioning intervals during the preparation period were used to determine the location of the wolf before the start of the approach trial. The one-minute intervals during approach trials gave the possibility for extracting the flight initiation with higher precision and provided fine-scale data for the initial flight response. The 10-minute positioning intervals during the post-disturbance period were used to capture the entire flight period and to identify resettling. The duration of the preparation period in 2019 was extended for logistical reasons to increase the likelihood of receiving updated wolf positions prior to the approach trial. Additionally, the duration of the post-disturbance period was extended to increase the likelihood of capturing the entire flight until resettling.

Figure 1 illustrates a spatial representation of an approach trial. The wolf starting position (WSP) was determined before the start of the approach trial using the last 10-minute GPS position, or if available, one of the first one-minute GPS positions. The observer starting position (OSP) was set at a minimum of 1000 metres from the WSP, the passing position (PP) was located 50 metres from the WSP, and the observer end position (OEP) was at least 500 metres after the PP.
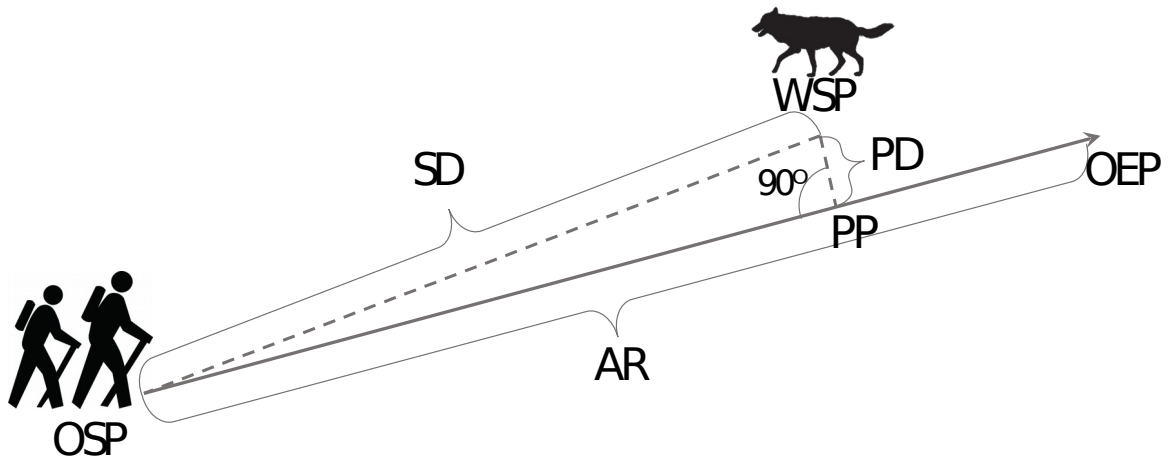
Figure 1: Illustration of a spatial representation of an approach trial. OSP = observer starting position, PP = Passing position, OEP = observer end position, WSP = wolf starting position, AR = approach route, PD = passing distance, SD = starting distance (Eriksen et al., in prep)

The observer used a handheld GPS and initiated the track-log with one-second positioning intervals at OSP. The observer walked towards the OEP, passing the PP at an average walking pace. When one observer was conducting the approach trial, this person was not talking but did not make an effort to be quiet. When two observers were conducting the approach trial, they talked to each other. While the observer continued walking, variables were noted at the OSP, PP and OEP, which included the time of passing, temperature, wind direction and strength, precipitation, humidity, horizontal vegetation cover (ground to waist, waist to head, and above head), vegetation noise and habitat type. From the OEP the observer circled back to the vehicle (or OSP) avoiding the WSP and saved the track-log. In order to collect flight data at a high temporal resolution, approaches were only conducted if the observer passed the passing position at least 10 minutes before the approach period ended.

3. Chapter I

Developing a standardised method to extract wolf flight initiation distances and resettling positions using statistical process control (SPC)

3.1 Introduction

Statistical process control (SPC) is a collection of different methods of quality control to achieve process stability and monitoring in order to improve quality (Montgomery, 2007). Even though SPC was originally developed for quality control in manufacture processes, it has adaptions in various fields of research, such as medicine and human health (Chen & Gupta, 2011; Je et al., 2018), economics (e.g. Lavielle & Teyssière, 2007), genetics (Chen & Gupta, 2011), climatology (e.g. Reeves et al., 2007), and oceanography (Killick et al., 2010). This also includes the field of ecology, where it is used to determine a change in a particular phase, e.g. animal movement (Gurarie et al., 2009; Moen et al., 2012; Patel et al., 2015; Evans et al., 2016a), physiological changes such as body temperature and heart rate (Mustonen et al., 2012; Evans et al., 2016b), or reproductive events (Nordli, 2018).

Most notable in the history of SPC is the Shewhart control chart, developed and described in detail by Walter A. Shewhart in the early 1920s (Shewhart & Deming, 1939; Montgomery, 2007). The basic principle behind the Shewhart control charts is that a stable process stays within a certain limit of variability, as variation is always present, however, when those limits are violated, the process is considered out-of-control. The limits are called upper control limit (UCL) and lower control limit (LCL).

Aside from the control chart method, another SPC method more commonly used nowadays is the changepoint model (Hawkins et al., 2003). This approach defines moments in time that the statistical properties of a process change compared to the previous state. Underlying algorithms are developed to calculate the changes and validate the likelihood of a change happening (Montgomery, 2007; Killick et al., 2016; Chen & Gupta, 2011; Truong et al., 2020).

When animals are exposed to a disturbance, their decision of leaving or staying depends on the perceived risk, balanced against the cost associated with leaving. Optimally, the animal's response

should maximise survival and the chance to reproduce. However, the response might be affected by previous experience and individual variation (Beale, 2007; Milleret et al., 2019). When the distance between a disturbance and an animal decreases, the risk of staying increases (Ydenberg & Dill, 1986; Lima & Dill, 1990; Cooper & Frederick, 2007). The distance between a disturbance and an animal at the moment that the animal leaves is often referred to as the flight initiation distance (FID) and is used as a parameter to describe the magnitude of the animal's response, e.g. to an approaching human (Moen et al., 2012; Ordiz et al., 2019). The moment of flight initiation also indicates the moment at which the animal's flight response started, and therefore forms the basis for extracting relevant variables, e.g. flight speed, distance, and straightness. For detecting the flight initiation, two methods of statistical process control can be used, i.e. Upper Control Limit (Moen et al., 2012; Sahlén et al., 2015; Ordiz et al., 2019) and changepoint analyses (Killick et al., 2012, 2016; Viljanen, 2019).

As GPS-collared animals move in the landscape, the movement can be described with speed, calculated from the distance and time between consecutive GPS locations. Whereas low speed indicates little or no actual movement (stationary state), higher speed indicates movement (non-stationary state). Low speeds recorded within the stationary state are due to the GPS measurement error or minor animal movement (Ordiz et al., 2019). The movement speed gives the possibility of using SPC to identify a change in the animal's current state from its movement in time and space (Moen et al., 2012; Ordiz et al., 2019). However, for reproducibility and the ability to make comparisons between studies, a standardised method for extracting FID and returning to a stationary state (resettling) in studies of animal responses to a source of disturbance, such as an approaching human, is needed.

In this chapter, I aimed to (1) develop a standardised method for extracting flight initiation and resettling using SPC, (2) compare two different SPC methods for extraction of flight initiation (UCL and changepoint analyses), and (3) describe the use of changepoint analyses to define the resettling position of the animal after the approach trial. I used approach trials on wild, GPS collared wolves to develop the standardised method. This method can be a useful tool to improve our knowledge about animal responses towards direct human disturbances and to compare the responses across different areas, e.g. with varying levels of anthropogenic impact. Therefore, the developed method was used in **chapter II** of this thesis for conducting a pilot study on the responses of wolves.

3.2 Methods

The data collection for this chapter followed the field protocol for conducting approach trials on GPS-collared wolves, as described in the **general methods**.

Data preparation

For all analyses, I used the software R (R Core Team, 2019) within the interface of R-Studio (RStudio Team, 2016). The data from wolves and observer were extracted and trimmed to a period from 12:00 to 17:00 with the *dplyr* package (Wickham et al., 2019). Time and date formats were handled with the *lubridate* package (Grolemund & Wickham, 2011). Time was corrected to time zone GMT+01:00, as approach trials during daylight saving time were in GMT+02:00. I visually assessed the data by plotting and animating individual approach trials with the *ggplot2* package (Wickham, 2016) and the *MoveVis* package (Schwalb Willmann et al., 2020). I calculated the Euclidean distance between consecutive wolf positions. The speed was calculated by dividing the distance by the difference in time (seconds) multiplied by 60, which resulted in speed in metres per minute (m/min).

Observer-wolf distance

I calculated the shortest distance between the observer and the wolf from the GPS data with one-minute resolution. I used the *rgeos* package (Bivand & Rundel, 2019) to transform the coordinates from the observer data to a projected coordinate system (WGS84/UTM zone 33N). I joined the observer data with the wolf data based on the date and time using the *dplyr* package (Wickham et al., 2019). If the observer data was lacking positions, in cases of when the observer track was not recorded with one-second intervals, I used the *data.table* package (Dowle & Srinivasan, 2019) to select the nearest observer position in time related to the wolf positions. After that, I calculated the Euclidean distance between simultaneous wolf and observer positions and selected for the shortest distance.

Flight initiation defined with Upper Control Limit

To define the distance at which the wolf moved away from the approaching/passing observer using the one-minute resolution GPS data, I used the wolf speed (m/min). Even a stationary wolf may show some movement in the GPS data and thus speed, due to the GPS measurement error.

Therefore, I calculated the variance of speed among stationary wolves to calculate the upper control limit following the process of SPC, as described by Montgomery (2007), Moen et al. (2012), and Ordiz et al. (2019). To create control data with stationary wolf movement speed, I extracted wolf GPS data out of successful approach trials when the wolves were not moving, based on visual inspection of the data. In addition, I used data from days when collars were programmed for an approach trial, but the approach trial was not carried out. I checked visually with QGIS (QGIS Development Team, 2019) if a wolf was stationary before I extracted the positions. I transformed speed by (log((speed+1)*100) to reach normality and fitted a linear model. I used speed+1 to avoid infinitive in the data caused by zeros. To calculate the UCL I used the intercept (β^0), standard error (*t*), degrees of freedom (*df*), residual variance (s^2), and the number of control days (*n*) (Montgomery, 2007; Moen et al., 2012; Ordiz et al., 2019), in:

$$UCL = \beta^0 + t\, 0.95\, df * \sqrt{\left(s^2\left(1+\frac{1}{n}\right)\right)}$$

Equation 1

In total, I extracted control data from the 26 interactions plus six days, where no approach trial was carried out when the collars were scheduled for an approach trial (total n = 32). I extracted the first 30 minutes of consecutive one-minute GPS data if visual inspection indicated no movement. In five cases, I used only 15 minutes due to observed movement. This resulted in a total of 998 data points reflecting speed from six individuals during a stationary, not moving, state.

The varying time it takes to acquire a GPS fix as well as occasional missing positions resulted in time intervals that varied from the scheduled one-minute intervals. This resulted in either higher (short intervals) or lower (long intervals) estimates for speed (appendix 1). Therefore, the variance of the speed data was biased and affected the linear model with a substantial increase in variation, which made it impossible to calculate the UCL. Therefore, I disregarded speed data in the control group when time intervals between consecutive positions were less than 30 seconds or more than 90 seconds. The control data resulted in a total of 802 data points. For detecting the flight initiation, I

used the unfiltered data for each approach trial. The flight initiation was defined as the time of the last wolf position before the speed exceeded the UCL for at least two consecutive positions. I calculated flight initiation distance (FID) as the wolf-observer distance at the time of flight initiation. The FID was not calculated if the observer has ended the trial (passed the OEP).

Flight initiation defined with changepoint analyses

For the changepoint analyses, I adjusted the one-minute wolf positioning data to a gamma distribution by changing speeds of 0 m/min to 0.01 m/min based on the assumption that exactly zero will be nearly impossible, due to GPS measurement error. Then I applied a pruned exact linear time (PELT) algorithm with a gamma distribution on both mean and variance with MBIC (Modified Bayes Information System) penalty on 95% CI using the function *cpt.meanvar* from the C*hangePoint* package (Killick et al., 2016). I used the MBIC penalty, as the AIC and BIC penalties are prone to overestimating changepoints (Lavielle, 2005). The flight initiation was defined as the first changepoint after the observer started the approach trial, and the FID was calculated as the wolf-observer distance at flight initiation.

Wolf resettlement defined with changepoint analyses

To detect the position where the wolf resettled, I down-sampled the data to 10-minute positioning intervals for the whole approach period (from 12:00 to 17:00). I used the *data.table* package (Dowle & Srinivasan, 2019) to create the 10-minute positioning intervals. I calculated the Euclidean distance between consecutive wolf positions. The speed was calculated by dividing the distance by 10 minutes, which resulted in speed in metres per minute (m/min). To adjust to a gamma distribution, I changed speeds of 0 m/min to 0.01 m/min. Then I applied a pruned exact linear time (PELT) algorithm with a gamma distribution on both mean and variance with MBIC penalty on 95% CI using the function *cpt.meanvar* from the C*hangePoint* package (Killick et al., 2016). Resettling is initiated during the first changepoint after the flight initiation at a 10-minute interval resolution. Therefore, I defined the position after this changepoint as the start of a stationary period (resettlement).

3.2 Results

Overview of approach trials

In total, 17 successful approach trials were conducted over two years, resulting in a total of 26 individual wolf-human interactions (hereafter written as interactions) on six different individuals. Out of 26 interactions, the wolf did not leave the initial site, i.e. remained stationary, five times.

Collar performance

Although the collars were programmed to one-minute positioning intervals, failure to record positions every minute regularly occurred. In total, two hours of one-minute positions should result in 120 positions, however regularly there were gaps of missing positions. This resulted in an average of 40±11 missing positions per approach trial. Gaps encompassed on average 3±1.3 missing positions.

UCL and changepoint analyses results

The obtained UCL for the speed between stationary and flight was 20.7 m/min (Figure 2A). Flight initiation with UCL could be detected for 21 out of the 26 interactions. In five cases, the wolves did not exceed the UCL of 20.7 m/min, and therefore no flight was detected (Table 1). With changepoint analyses, the flight initiation could be detected for 20 interactions (n= 26). For six interactions changepoint analyses did not detect changepoints within the time of the one-minute positioning intervals (during the trial period). Therefore, I could not define a moment of flight initiation (Table 1, Figure 2B).
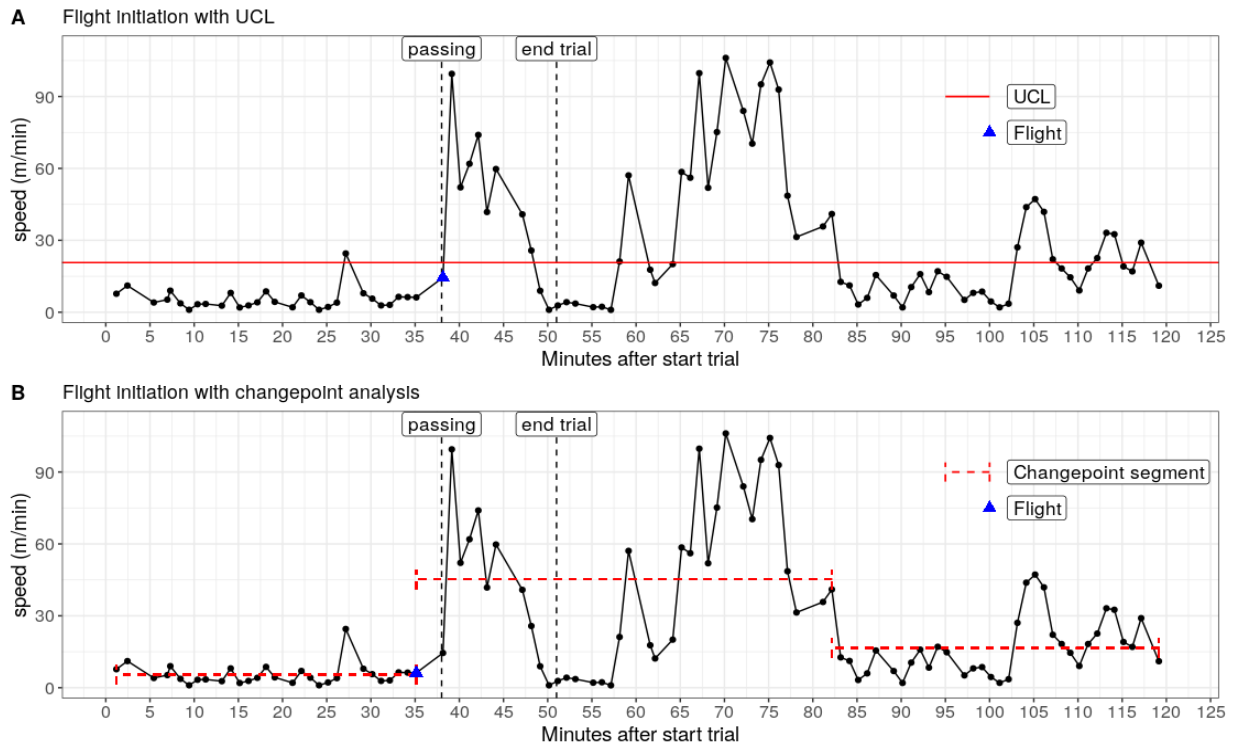
Figure 2: Visualisation of the detection of flight initiation of a wolf during an experimental approach trial. Flight initiation was detected based on wolf speed calculation from GPS positions using (A) UCL (Upper Control Limit) analyses and (B) changepoint analyses with change in mean and variance. The second changepoint in B shows a change in speed, however, this does not indicate the resettling.

Table 1: Descriptive statistics for the FIDs (flight initiation distances) detected with UCL (Upper Control Limit) analyses and changepoint analyses. FID is the distance in metres between the wolf and the observer at the flight initiation. Flight are the total number observer flights with UCL analyses, changepoint analyses and by visual inspection.

	UCL	Changepoint	Visual
Flights	21	20	21
Mean_FID	140	150	NA
SD_FID	97	111	NA
Median_FID	93	93	NA
Max_FID	381	381	NA
Min_FID	49	45	NA

Difference between UCL and changepoint analyses

The difference in FID between the changepoint analyses and UCL was not significant (Wilcoxon signed-rank test: V = 29, p = 0.48). On average, the FID calculated with changepoint analyses was 6.5 metres longer. For twelve interactions, the calculated FID was the same. For eight interactions there was a difference, where for six interactions the FID with changepoint analyses was longer (mean = 38 metres) and for two interactions the FID for changepoint analyses was shorter (mean = 49 metres) compared to UCL (Figure 3). In the 20 interactions, when the flights were identified with both SPC methods and visual inspection, no consistent bias in the two methods could be observed. Hence, both methods seem to reflect the flight initiation without consistently over- or underestimating the timing of the flight initiation.
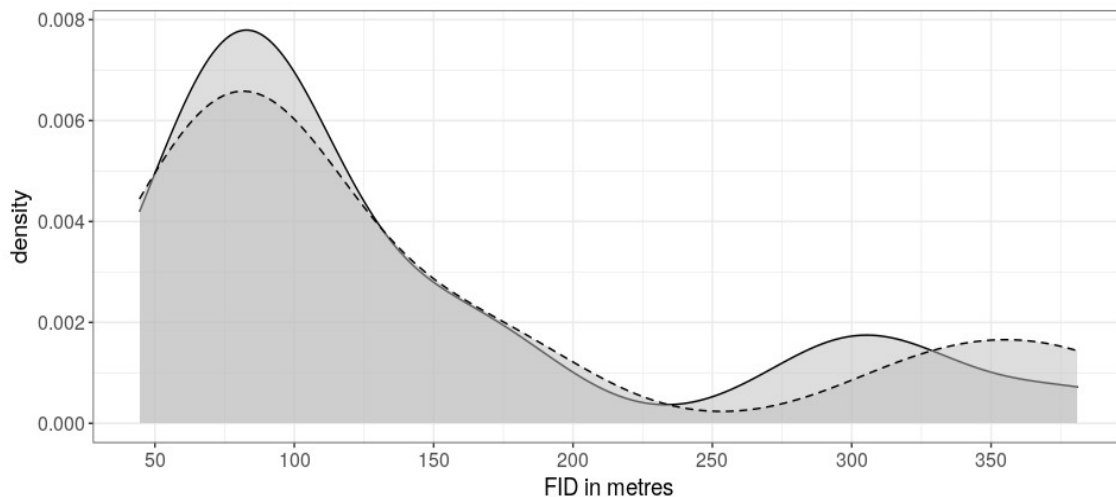

Figure 3: Density plot for the flight initiation distances (FIDs) of wolves during experimental approach trials identified using changepoint analyses (dashed line) and upper control limit analyses (UCL) (solid line).

Changepoint penalties

In one interaction, the changepoint analysis did not detect changepoints. However, both visual inspection and UCL analyses indicated that there was indeed a flight response. Therefore, I reran the changepoints analysis using the AIC penalty instead of the MBIC penalty to define changepoints for this interaction (Figure 4). This resulted in two changepoints, where the first

changepoint reflects the flight initiation. The FID was 58 metres, while for the UCL, the FID for the same interaction was calculated at 82 meters.
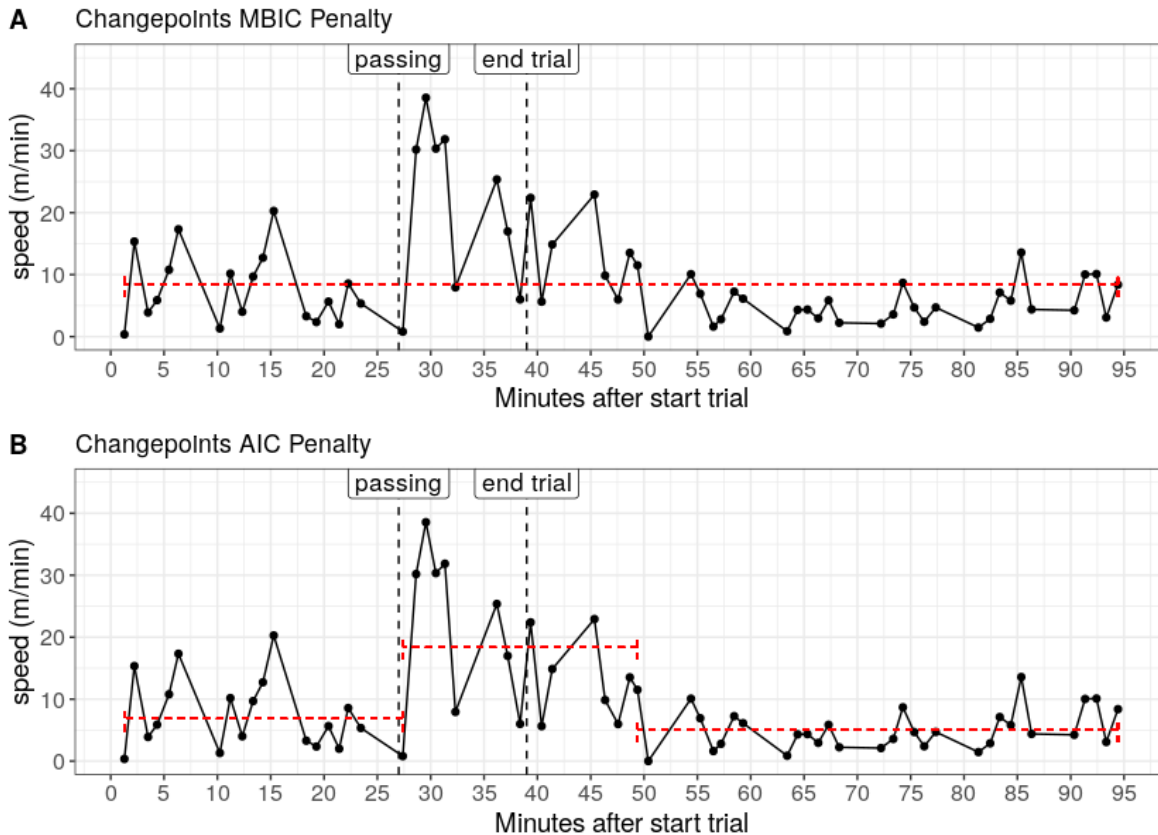

Figure 4: Results from changepoint analyses of a wolf's flight initiation during an experimental approach trial using (A) MBIC penalty and (B) AIC penalty. The moment that the observers passed the passing position (PP) and reached the observer end position (OEP) are indicated (see Figure 1).

To check if AIC might be preferable for all changepoint analyses, I reran the changepoint analyses with the AIC penalty for all interactions. This resulted in one or more changepoints for 25 interactions (n=26), where the first changepoint after the start of the trial did not match with the MBIC method and visual inspection. For 19 out of the 20 interactions, for which both AIC and MBIC detected changepoints, the changepoint locations detected as flight initiation with the MBIC penalty were also included when using the AIC penalty. However, AIC found 2.2±1.6 additional changepoints per interaction on average, which did not represent the flight initiation.

Resettling

The moment and location of resettling were found for 19 interactions (n = 26). For five interactions, there was no flight response. Therefore, there was no resettling location. In one interaction, only the flight initiation was detected, and the total flight, as observed visually, was shorter than 20 minutes. As the temporal resolution of the GPS positions used to identity resettling was at a 10-minute interval, a flight of 20 minutes was too short to be detected with the changepoint analyses. For another interaction, the wolf kept moving and did not stay stationary for a longer time period. Therefore, its resettlement was not recorded within the post-disturbance period of three hours.
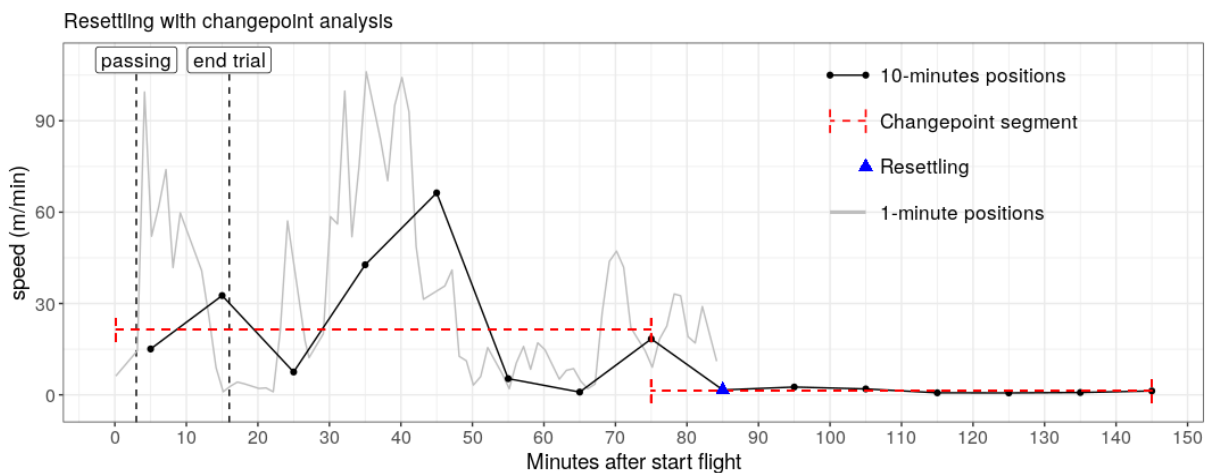

Figure 5: Resettling position of a wolf after an experimental approach trial detected with changepoint analysis based on speed calculated from GPS positions taken at 10-minute intervals. Resettling location is defined as the position after the changepoint. One-minute intervals in grey as reference to Figure 2, as the same approach trial was used for visualisation.

3.3 Discussion

In this chapter, I described and compared methods to detect wolf flight initiation and resettling positions during experimental approach trials from spatial data with a high spatio-temporal resolution. From 26 wolf-human interactions, UCL and changepoint analyses detected 21 and 20 flight responses respectively, and the two methods gave overall similar flight initiation distances. For the majority of the interactions, the flight initiation distance was equal, as for resettling, for most interactions a resettling location was found (19 out of 21 interactions with a flight). The flight and resettling locations also matched with visual inspections, therefore the methods seem appropriate.

Upper control limit

The obtained UCL of 20.7 m/min is comparable with the UCL found in brown bears approached by humans (15.1 m/min, Ordiz et al., 2019). With this UCL, the flight initiation could be identified for all interactions where a flight was confirmed by visual inspection. However, filtering the control data on one-minute time intervals (>30 and <90 seconds) was necessary to be able to calculate the UCL. As the UCL was used as a defined limit between stationary and non-stationary behaviour, a high UCL resulted in the inability to identify flight initiation. Therefore, omitting the deviating time intervals resulted in a better estimate for the UCL, as I was interested in the 'background' speed that is detected even when wolves are not moving due to GPS measurement error.

As described by Montgomery (2007), when a process exceeds the UCL, the process is out-of-control, which in this case means that the wolf exceeds the speed limit in which it is considered stationary. In the brown bear approach studies, the UCL was set and checked visually before defining the FID (Moen et al., 2012; Ordiz et al., 2019). Occasionally the UCL was exceeded with only one position, and visual inspection showed no spatial movement when this occurred. Therefore, I decided adding the condition that the flight is defined as the location before the UCL is exceeded, only if the UCL is exceeded for more than one position.

Changepoint analyses

Changepoint analyses depend on a certain length of data point segments to detect a change in mean and variance. This means that it is important to have enough data at the beginning and at the end of the time series (Killick et al., 2012). Specifically, this means that if the flight happens too early or too late within the two-hour timeslot of one-minute positions, there will be a chance that none or inaccurate changepoints are found. As the current protocol describes, the passing position (PP) needs to be reached minimum 10 minutes before the end of the approach period to ensure fine-resolution data for the first 10 minutes of the wolf's flight. However, since gaps in the data exist with an average length of 3±1.3 minutes per gap, I would recommend reaching the passing position (PP) at least 15 minutes before the approach period ends. Using 15 minutes as a buffer will likely create a minimum of 10 positions, which I expect will be enough to avoid problems with the changepoint analyses.

Changepoint analyses use a penalty structure to test the likelihood of a change happening. Different penalty methods are available, and in certain data specific cases it is known which penalty gives the most accurate results in changepoint location (Killick et al., 2012; Truong et al., 2020). However, in interactions when the wolf's flight duration is rather short, it might be expected that changepoint analyses with an MBIC penalty will not be able to detect changepoints. When visual inspection shows a flight that is not detected using MBIC penalty, it might be a possibility to use AIC as a penalty, as changepoint analyses ran independently for every individual interaction. The AIC is prone to overestimation as it increases the probability of detecting changepoints (Lavielle, 2005), and therefore, flight initiations identified with this method should always be checked visually.

Resettling

Overall, changepoint analyses detected the resettling position and moment with 10-minute positioning intervals. Exceptions were if the resettling did not take place within the post-disturbance period or when the flight was too short. Both exceptions can be detected by visual inspection of the data. In case of an interaction with a short flight, detecting the resettling with the one-minute positions might be considered. Additionally, using one-minute positioning intervals during the entire trial and post-disturbance period is a possibility. However, telemetry studies need a trade-off between the positioning frequency and the battery life of the GPS collar, as more

frequent sending of positions shortens the battery life. Therefore, the method should not lead to unnecessarily battery usage.

Comparing UCL and changepoint analyses

Overall, both methods perform similarly well for detecting flight initiation. As previous studies have shown, both UCL and changepoint can be used successfully to detect flight initiation (Moen et al., 2012, 2018; Ordiz et al., 2019; Viljanen, 2019). Additionally, visual inspection confirmed that the detected flight initiations were likely. Therefore, I would consider both methods as similarly appropriate for detecting flight initiation for experimental wolf approaches. However, both methods have limitations.

The collars were programmed to save six positions before sending the positions over the cellular network. This resulted in gaps in the data, corresponding with the time when the collars were transmitting the data. The gaps lead to a reduced temporal resolution, increasing the likelihood of finding an earlier flight initiation since the flight initiation will be the last position before the gap. The actual flight might have started within the gap. Therefore, to avoid a bias in the FID it is recommended to exclude the approach trials with lacking data around the time of the suspected flight initiation, which was done by Moen et al. (2012) in a comparable study conducting approach trials on brown bears (*Ursus arctos*). However, due to the small sample size, I decided to keep approach trials with gaps, as the frequency of the occurrence of gaps was too high to exclude those from the analyses. Imputation as an alternative method to account for the gap was inappropriate in this case as imputation is often based on the assumption that speed is relatively constant. Furthermore, different imputation techniques can differ in results (Moritz et al., 2015).

Since speed is based on the distance and difference in time between consecutive positions, assuming a straight-line movement between the positions, longer time intervals lead to a loss of spatial resolution, which will result in lower speeds. Conversely, occasional short intervals can lead to higher speeds since the distance moved relative to the time interval is large. Therefore, the speed in those deviating time intervals is not entirely comparable with the speed between one-minute intervals. To avoid additional variation, omitting deviating time intervals before running the analyses might be an option. However, this also results in losing the temporal and spatial aspects of those specific positions. Even though the speed has a bias compared with the rest of the data, omitting those positions resulted in less accurate flight initiation locations.

As for UCL, GPS measurement error can vary between collar type, location and environmental factors. Therefore, it might be necessary to calculate the UCL separately for different areas. Additionally, UCL calculations do rely on control data. Using control data from when the wolves were not moving, based on visual inspection, can result in interpretation errors. Although UCL is also used for moving animals (Moen et al., 2012; Ordiz et al., 2019), selecting control data requires a visual inspection, whereas changepoint analyses do not need control data. In the data used for this chapter, UCL detected all flights, which were also confirmed by visual inspection. However, Moen et al. (2012, 2018) reported cases in which visual inspection indicated a flight, but speed did not exceed the UCL.

Changepoint analyses do not require control data, and it requires less data preparation, as it can handle various data distributions. However, limitations like the bias towards the start and the end of the time series, and the probability that a short flight might not result in a changepoint, should be considered. Furthermore, changepoint analyses can be done in various ways, with a broad palette of possible requirements. Therefore, it is adjustable to many types of data (Killick et al., 2012, 2016; Truong et al., 2020). However, there is a risk of adjusting changepoint analyses to a desired result. Therefore, results of changepoint analyses should always be interpreted with caution.

<u>Recommendations</u>

Both methods are similarly suitable for defining flight initiation, and the use of changepoint analyses to determine the resettling position is appropriate. However, changepoint analyses increase reproducibility and comparability for this type of studies, as it is more straight forward in use, does not need control data, and can be used in a variety of situations. This is consistent with the objective of this chapter, which was to develop a standardised method which increases reproducibility and is applicable across different areas with varying levels of anthropogenic impact. For this reason, I will use changepoint analyses as the most appropriate method for the pilot study on the flight response of wolves during experimental human approaches in chapter II.

4. Chapter II

Flight responses of wolves during experimental approaches by humans:

A pilot study

4.1 Introduction

In predator-prey systems, the prey species can show anti-predator behaviour to avoid being preyed upon (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). Prey spend time, driven by fear (Laundré et al., 2001), being vigilant and adjusting foraging behaviour to lower the risk of predation (Beale, 2007; Laundre et al., 2010; Eisenberg et al., 2014). When a prey encounters a predator, it has three choices: flight, fight, or hide (Lima & Dill, 1990; Rupia et al., 2016; Roelofs, 2017). The response should increase an individual's fitness by helping individuals to stay alive in order to increase their chance of reproduction (Ydenberg & Dill, 1986; Lima & Dill, 1990). However, those responses come with an energetic cost, as the intensity of the response depends on the perceived severity of the risk. Optimally, when the potential risk of staying exceed the costs of fleeing, the animal should flee (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). However, the evaluation of the perceived risk and therefore, the animals' response varies between individuals (Beale, 2007).

It is not only prey species that show anti-predator behaviour. The same theory applies for predator species (Frid & Dill, 2002), which can show a similar set of behaviours to avoid intra-guild predation (Holt & Polis, 1997; Mech & Boitani, 2003; Wikenros et al., 2017) and as a response to human-induced disturbances (Gill et al., 1996; Frid & Dill, 2002; Moen et al., 2012). Similar to prey, a predator's response also depends on the perceived risk and therefore, should act on the risk in a cost-effective way (Ydenberg & Dill, 1986; Frid & Dill, 2002). As described by Ydenberg & Dill (1986), increased perceived risk leads to an increase in response, often measurable in the flight distance.

Predators, such as wolves, tend to avoid human activities (Lesmerises et al., 2012; Milleret et al., 2019; Carricondo-Sanchez et al., 2020). However, it is also known that wolves are using human-

made structures, such as roads and bridges, to move through the landscape (Zimmermann et al., 2014; Dickie et al., 2017; Bojarska et al., 2020). Due to protective legislation, wolves are recolonising into human-dominated landscapes (Chapron et al., 2014; Mech, 2017), resulting in an increased chance of direct human-wolf encounters (Penteriani et al., 2016; Kuijper et al., 2019). Encountering humans is not without risk for wolves, as legal hunting, poaching, and infrastructure increase wolf mortality (Colino-Rabanal et al., 2011; Liberg et al., 2012, 2020; Recio et al., 2018). Currently, human-related mortality limits the population growth of wolves (Liberg et al., 2012; Kuijper et al., 2019). Hence, human-caused disturbances are expected to result in anti-predator behaviour due to a potentially lethal risk for the wolf (Frid & Dill, 2002). However, it is not expected that the perceived risk is uniform across individuals and situations, as previous experience might affect animal responses (Beale, 2007; Milleret et al., 2019; Carricondo-Sanchez et al., 2020).

Responses of wolves to direct human encounters have been studied previously (Karlsson et al., 2007; Wam et al., 2014). However, previous studies based on VHF (very high frequency) collars have a lower spatio-temporal resolution compared to newer GPS technology (Karlsson et al., 2007; Moen et al., 2012, 2018). Therefore, studying wolf responses using a high-resolution GPS data gives the possibility to learn more about flight intensity and flight patterns, as a higher flight intensity might be associated with longer flight distance, duration, displacement, higher speed, and a straighter flight pattern. More intense flights come with a higher energetic cost, as the potential result of perceiving a higher risk by the individual (Ydenberg & Dill, 1986; Cooper & Frederick, 2007).

Within this chapter, I aimed to describe the flight response of wild GPS-collared wolves in Scandinavia by conducting experimental human approach trials. This is, by my knowledge, the first study assessing wolf flight responses towards humans with the use of high-frequency GPS data. The main objectives for this chapter are (I) to demonstrate which variables can be obtained by the method developed in Chapter I, and (II) to conduct a pilot study looking at effects of different explanatory variables (e.g. observer type, wind direction, noise) on different stages of the flight (initial and overall flight response). Together, this information will allow me to identify behavioural response patterns of wolves.

Based on the second aim of this study, I hypothesised and predicted the following:

H1: Wolves will show predominantly flight responses, to a lesser degree hide responses, and fight responses will not be observed.

> P1: Changepoint analyses, in combination with visual inspection, will detect flight responses for most approach trials, not detecting a flight (hiding) will be rare, and none of the wolves will approach the observer or show aggressive behaviour.

H2: The perceived risk might be highest just before the observer(s) passes the wolves initial location.

> P2: The flight initiation of the wolves will be before the observer(s) passes the passing position (PP).

H3: It is possible to identify flight intensities based on the flight variables.

> P3: There is a positive correlation between flight duration, distance, displacement, speed and straightness, along a gradient of low to high response intensity.

H4: Wolves will have a less intense flight due to a lower perceived risk when the observer is detected earlier (longer detection distance).

> P4: In approach trials with (a) two observers , (b) noisy vegetation, and (c) the wind blowing from the observer to the wolf, wolves will leave their initial site earlier (longer FID).

H5: Wolves in concealed resting sites will perceive risk as lower due to the wolf's perception of being less detectable by the observer(s).

> P5: Wolves with more concealed starting positions will be associated with a shorter FID and a higher occurrence of no flight.

H6: The wolf's flight is an evasive action based on a perception that human encounters are potentially lethal.

> P6: Wolves will move away from the observer and the observer's track, and therefore will not interact with the track (e.g. cross the track).

4.2 Methods

The data collection for this chapter followed the field protocol for conducting experimental approaches on GPS-collared wolves, as described in the **general methods**.

Additionally, during approach trials, the wind direction was measured at the observer starting position (OSP) using the observers' clock. The wind direction was measured relative to the observer when the observer was walking in a straight line towards the observer end position (OEP), where 12 o'clock referred to a straight wind direction from the OEP towards the observer. For the analyses, I converted the wind direction into a value between 0 and 1, where 0 was defined as the wind blowing from the OEP towards the observer, and 1 was defined as the wind blowing from the observer towards the OEP.

The horizontal vegetation cover of the wolf's resting site or at the last GPS location before the flight was measured using the method described by Ordiz et al. (2009). At the location, the observers placed a cylinder (brightly coloured with a length of 60 cm and diameter of 30 cm) and measured how far they could move before the cylinder was out of sight, in all four cardinal directions. The average of the four directions was used as a proxy for concealment of the wolf's location before the flight.

Noise by walking through the vegetation was assessed in three levels (silent, medium, and noisy) as the observer was passing the passing position (PP). The levels silent and medium occurred rarely (n = 2, n = 4, respectively). Therefore, I pooled them and used two levels (noisy and not noisy) for further analyses.

Data preparation

I used the software R (R Core Team, 2019) within the interface of R-Studio (RStudio Team, 2016) for all data handling and analyses. When two GPS collared wolves were approached in the same approach trial, only one was included in the analyses, because the response of two wolves in a pair cannot be considered to be independent of each other. If a flight was detected, I selected the wolf which was closest to the original wolf starting position (WSP), which was defined at the start of the trial. For stationary wolves, I chose the wolf which was passed closest by the observer.

The flight initiation and resettling were extracted by applying changepoint analyses for both mean and variance with an MBIC (Modified Bayes Information System) penalty (Killick et al., 2016). For 13 interactions changepoint analyses with an MBIC penalty detected changepoints indicating the flight initiation. Visual inspection, as well as UCL (Upper Control Limit) analyses suggested that the wolf fled in one additional interaction that was not identified with the MBIC penalty (see chapter I). The flight initiation for this interaction was identified by rerunning changepoint analysis with the AIC penalty.

Based on the obtained flight initiation and moment of resettling for every interaction separately, I extracted the following variables:

Direct flight variables:
- *Flight initiation distance*: The distance in metres between the observer and the wolf at the moment of flight initiation.

- *Minimum distance between observer and wolf*: The shortest distance in metres between the observer and the wolf during the approach trial.

- *Time difference between flight and observer passing PP*: The difference in time (in minutes) between the observer passing the PP and the flight initiation of the wolf. A negative difference defined the flight initiation before the observer passed the PP, and a positive difference defined a flight initiation after the observer passed the PP.

Initial flight variables using one-minute positioning intervals:

- *Initial speed*: the average speed for the first 10 minutes of the flight, calculated using one-minute positioning intervals and measured in metres per minute (m/min).

- *Initial flight straightness*: straightness index for the first 10 minutes after flight initiation. The straightness index is a value between 0 and 1, representing how straight an individual moved, where 1 represents a straight-line movement. The index was calculated by dividing the straight-line displacement by the accumulated distance moved over the same amount of time.

Overall flight variables using 10-minute positioning intervals:

- *Flight duration*: the difference in minutes between the flight initiation and resettling.

- *Flight distance*: the accumulated distance from flight initiation until resettling following the wolf's flight path based on 10-minute positioning intervals, the distance was measured in metres.

- *Flight displacement*: the linear distance between the flight initiation and resettling, distance measured in metres.

- *Overall speed*: the average speed for the total flight, calculated using 10-minute positioning intervals and measured in metres per minute (m/min).

- *Overall flight straightness*: straightness index for the total flight, calculated using 10-minute positioning intervals.

Analyses

I looked at relations between variables by using non-parametric Spearman's rank-order correlation tests (Dytham, 2011), visualised using the *ggplot2* package (Wickham, 2009) and the *GGally* package (Schloerke et al., 2018). To look at differences in the median of a continuous variable between categorical variables, I used the non-parametric Wilcoxon rank-sum test (Dytham, 2011). Flight patterns were inspected visually via the *MoveVis* package (Schwalb Willmann et al., 2020) and the *ggplot2* package (Wickham, 2009).

I did not include territory and year during further analyses due to the small sample size, as the Varåa territory had eight interactions, Juvberget had six interactions and Magnor had three interactions. None of the variables showed a clear difference between the territories (see appendix 2). In the year 2018, there were eight interactions, and in 2019 there were nine interactions, including one interaction in January 2020 (see appendix 3). However, there was only a significant difference in minimum observer-wolf distance between 2018 and 2019 (Wilcoxon rank-sum test: W = 6, p = 0.002). The FID did not show a difference between years (Wilcoxon rank-sum test: W = 12, p = 0.142).

4.3 Results

In total, 26 wolves were passed by humans during 17 approach trials. No wolves were seen or heard during the approach trials and therefore, no fight responses were observed. During an approach trial, one or two collared wolves were present, whereas the presence of uncollared pack members during trials was unknown. On average, an individual wolf was approached four times (range = 2-7), with either one observer (n = 16) or two observers (n = 10). For nine approach trials where two GPS-collared wolves were present, they either both fled or both stayed stationary. I selected one wolf for each trial as described in the methods.

Flight initiation and resettling

In total, I calculated the flight initiation distance (FID), initial speed, and initial straightness for 14 interactions (Table 2), while for three interactions no flight initiation was detected or seen by visual inspection. In 9 out of 14 interactions, the flight initiation of the wolf was before the observer passed the passing position (Figure 6). On average, wolves left 2.2 minutes before the observer passed the passing position (Table 2). For two interactions, the resettling location of the wolf was not found, either due to a short flight where changepoint analysis did not detect a changepoint or due to continuous movement until the 10-minutes positioning ended. For 12 interactions, I calculated the variables for the overall flight (Table 2).

Table 2: Overview of the descriptive statistics for all variables extracted based on the flight initiation and resettling positions detected by using changepoint analyses for 17 experimental human approach trials on wolves.

| Variable	Mean	SD	Median	Min	Max	N
Flight initiation distance (m)	133.17	102.32	91.38	44.56	376.90	14
Observer-Wolf distance (m)	94.43	63.31	73.36	35.51	309.11	17
Flight/passing time difference (min)	-2.22	3.50	-0.87	-7.98	2.05	14
Initial speed (m/min)	52.71	23.59	52.99	21.48	101.86	14
Initial straightness	0.81	0.19	0.90	0.33	0.99	14
Flight duration (min)	71.71	30.75	67.79	28.85	125.95	12
Flight distance (m)	2329.32	1630.50	1868.99	319.05	5789.82	12
Flight displacement (m)	2030.46	1431.90	1584.27	315.10	5172.16	12
Overall speed (m/min)	33.25	11.05	33.29	14.18	49.01	12
Overall straightness	0.89	0.10	0.92	0.67	0.99	12
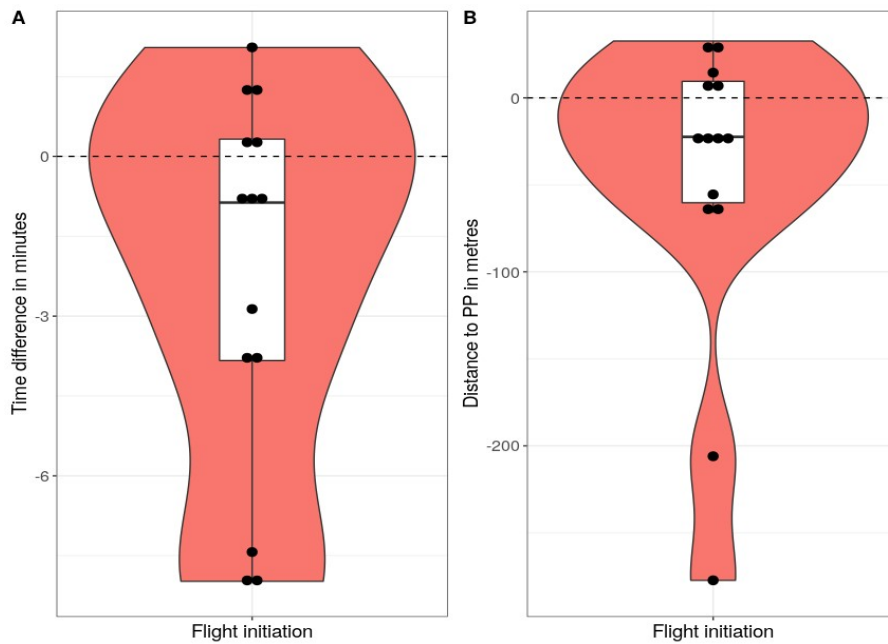
Figure 6: A) Time difference between the start of the wolf's flight and the observer passing the passing position (PP) of wolves during experimental approach trials by humans, where a negative time difference indicates a flight started before the observer passed the PP. B) The distance from the observer to the PP at flight initiation, where negative distance indicates a distance before passing and positive after the observer passed the PP.

Flight intensity

Flight distance, duration and displacement were all positively correlated (r_s > 0.90, Figure 7). Additionally, the overall flight speed had a strong correlation with flight distance (r_s > 0.70), and a modest positive correlation with flight displacement and duration (r_s > 0.50). Initial speed showed modest correlations with overall speed, flight distance and flight displacement (r_s > 0.40), while the initial straightness only showed weak or very weak correlations with the other variables (r_s < 0.30). The overall straightness showed a modest negative correlation with flight displacement, distance, duration and overall speed (r_s < -0.40, Figure 7).
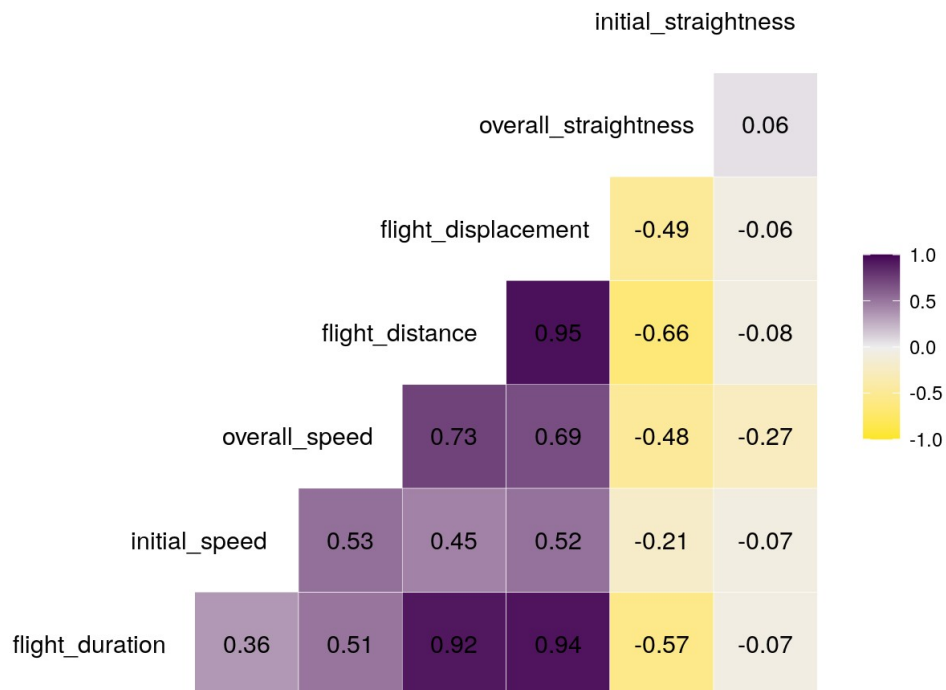

Figure 7: Correlation matrix with correlation coefficients showing relations between the variables, using nonparametric Spearman's rank-order correlation tests. The variables were extracted from experimental human approach trials on wolves.

Effects on FID and flight intensity

The FID did not differ significantly between one or two observers (Wilcoxon rank-sum test: W = 16, p = 0.32). However, the distribution of the FID for two observers had a wider range (Figure 8A). There was a difference in median flight displacement between observer types (Wilcoxon rank-sum test: W = 2, p = 0.01, Figure 8B) and a difference in flight duration between observer types (Wilcoxon rank-sum test: W = 5, p = 0.048), were flight displacement and flight duration was longer when two observer were present. The variables flight distance, initial speed, and initial and overall straightness, did not differ significantly.
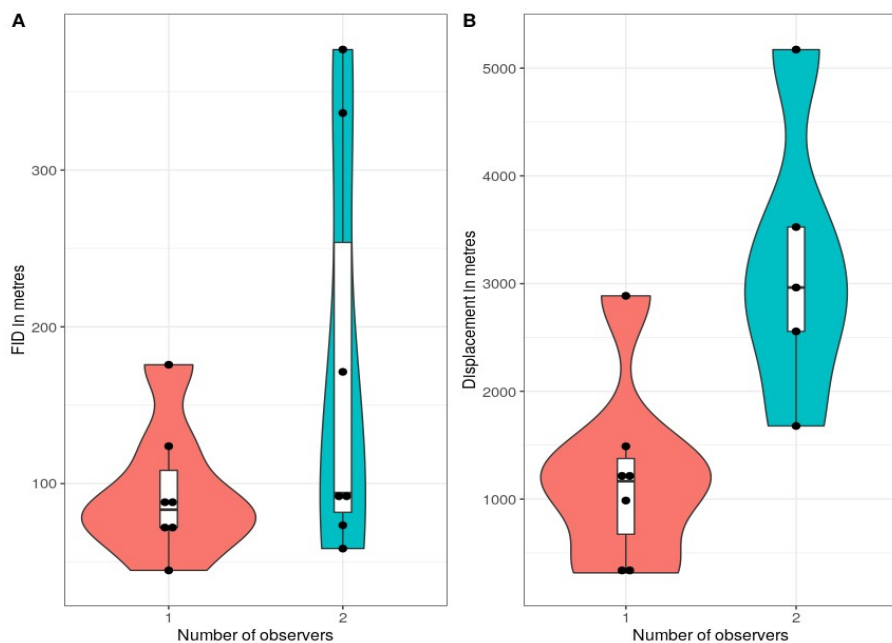

Figure 8: Data distributions for A) flight initiation distance (FID) and for B) flight displacement showing the difference between number of observers. The variables were extracted from experimental human approach trials on wolves.

The FID showed no difference in the median between the levels of noise (Wilcoxon rank-sum test: W = 27, p = 0.12). However, the distribution of the FID for noisy environments had a more extensive range (Figure 9A). There was a difference in median overall speed between the noise levels (Wilcoxon rank-sum test: W = 0, p = 0.004, Figure 9B), were the overall speed was higher with less noisy vegetation. The variables flight distance, displacement, duration, initial speed, and initial and overall straightness, did not showed a significant difference.
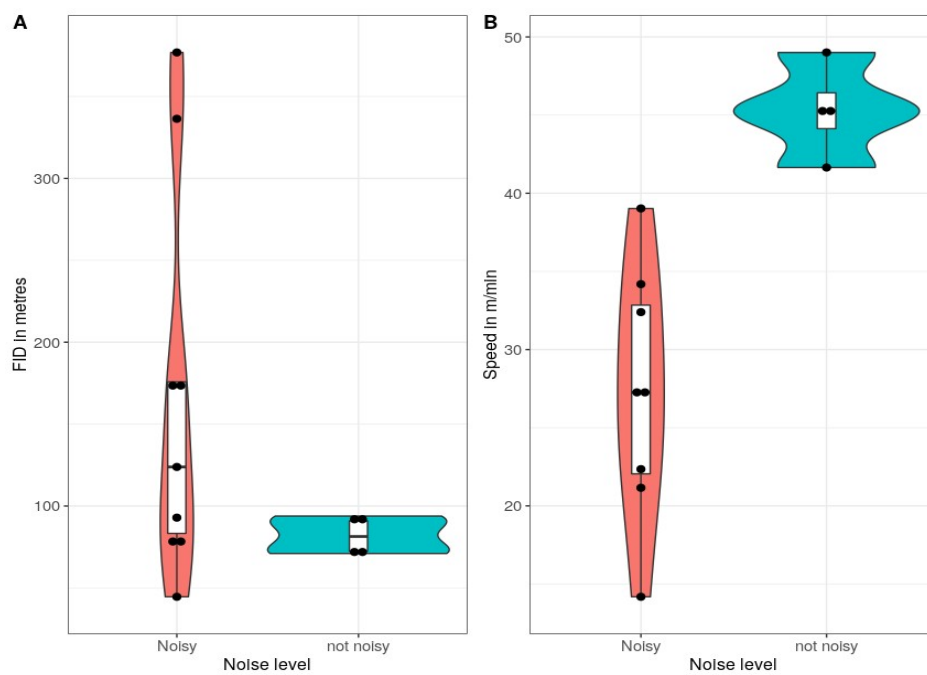

Figure 9: Data distributions for A) the flight initiation distance (FID) and for B) the overall speed showing the differences between the level of noise. The variables were extracted from experimental human approach trials on wolves.

The relative wind direction and FID showed a strong correlation (r_s = 0.72, n=8, Figure 10A), with longer FIDs at winds blowing towards the wolf starting position. The overall speed had a strong negative correlation with relative wind direction (r_s = -0.95, n=7, Figure 10B) and flight distance showed a strong negative correlation with relative wind direction (r_s = -0.73, n=7). Higher overall speed was found at winds blowing from the wolf starting position towards the observer. The variables flight displacement, initial speed, and initial and overall straightness, did not correlated with the relative wind direction.
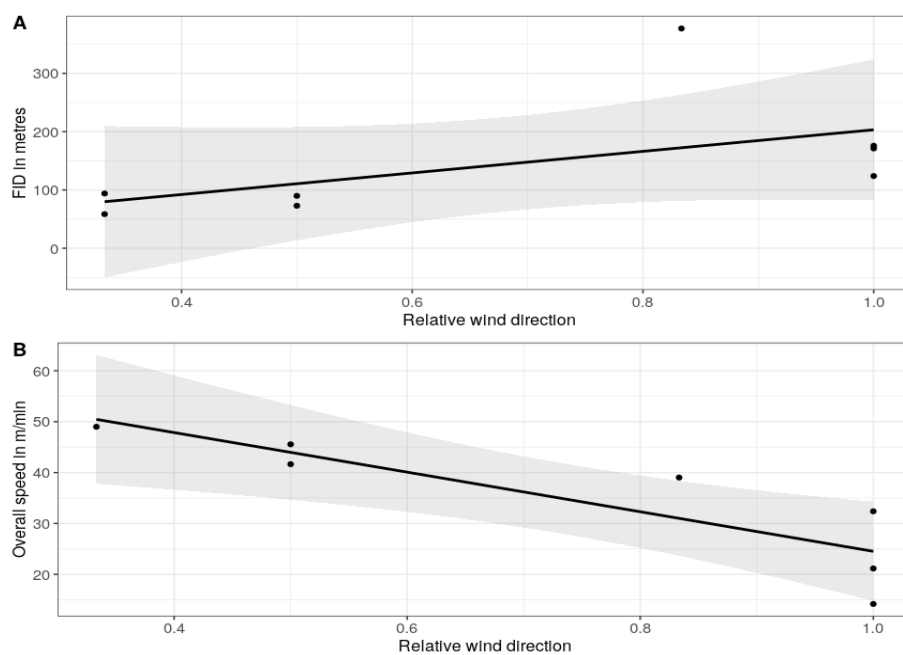

Figure 10: The relation between relative wind direction and, A) flight initiation distance (FID) and B) overall speed where a relative wind direction of 1 represents wind blowing from the observer towards the wolf's location. The variables were extracted from experimental human approach trials on wolves.

Concealment and FID

Concealment and FID showed a modest positive correlation (r_s = 0.61, n=8). Additionally, the concealment for two interactions where the wolf did not flee was four and six meters, respectively. Therefore, more concealed resting sites resulted in a shorter FID, compared to less concealed resting sites (Figure 11).
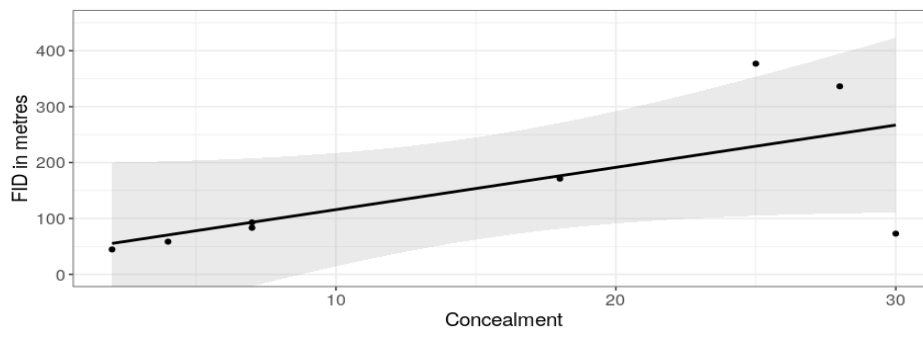

Figure 11: The relation between concealment and FID, based on the concealment of the wolves initial site and the flight initiation during experimental approach trials by human. Where concealment represents the distance of visibility, therefore lower values is a higher concealment.

Flight patterns

By visually assessing the approach trials, I found that during eight flights, the wolf did not cross or interact with the observer's track and diverted away from the observer(s). The flights did not look particularly straight (Figure 12C). During six flights, the wolf did interact with the observer's track by either crossing the track (n = 2) or circling back to the observer's track before moving away (n = 4) (Figure 12A). During three approach trials, the wolf did not initiate flight. During four approach trials, the minimum distance between wolf and observer decreased after flight initiation resulting in a shorter minimum wolf-observer distance compared to the FID. Visual inspection showed that for three approach trials, this was due to lower flight speeds or change of flight direction which resulted in a temporally decrease of distance between the observer and the wolf. In one approach trial, the wolf moved parallelly in the direction of the observer and circled to the observer's track after the observer passed, before moving away. The minimum wolf-observer distance was the moment when the wolf was perpendicular relative to the observer.

Figure 12 shows two approach trials, where A) and B) visualised a lower intensity flight, with an FID of 83 metres, a flight distance of 1006 metres, a duration of 49 minutes, and with an overall speed of 28 m/min (see appendix 4, Approach_ID: A2018-10-25_juv for all variables). The concealment of the resting site was 7 metres, the vegetation was noisy, and one observer was present. The approach trial in C) and D) visualise a higher intensity flight, with an FID of 309 metres, a flight distance of 3841 metres, a duration of 109 minutes, and with an overall speed of 39 m/min (see appendix 3, Approach_ID: A2019-12-30_juv for all variables). The concealment of the resting site was 25 metres, the vegetation was noisy, and two observers were present.
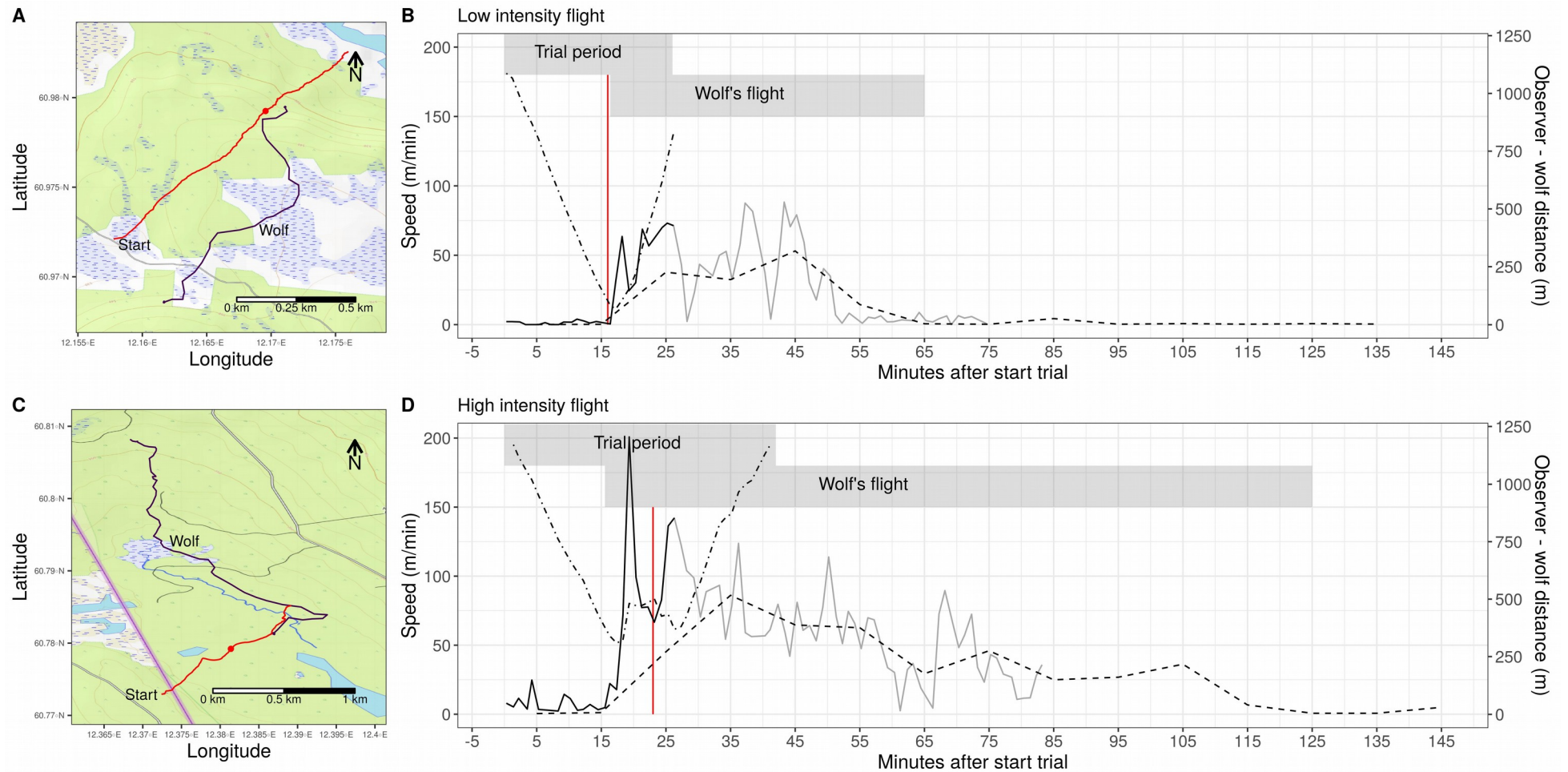
Figure 12: Two representations of an experimental approach trial on wolves, showing the spatial patterns for a lower intensity flight (A and B) and a higher intensity flight (C and D). The red dot at the observer tracks (A and C) indicates the location of the observer at the time of flight initiation. In C and D, the black line represents one-minute interval speed data until 10 minutes after flight initiation (grey line), the dashed line represents the 10-minute interval speed data, and the dotted-dashed line represents the distance in metres between observer and wolf. The red vertical line indicates the observer passing the passing position (PP).

4.3 Discussion

Flight initiation and observer passing

Wolves were not seen or heard during approach trials, even when the observer passed the wolf relatively close. Kuijper et al. (2019) described getting closer than 100 metres to wolves as 'risk-enhancing human behaviour'. However, during approach trials, no indications have been observed of any risks for the observers, i.e. no fight response. Other similar studies on wolves and brown bears reported similar experiences as the wolf/bear did not show any risk increasing behaviour (Karlsson et al., 2007; Moen et al., 2012; Ordiz et al., 2019). Consistent with prediction one, most wolves left their initial site resting site and showed no fight behaviour. Additionally, during some interactions, the wolf did not initiated flight or initiated flight after the observer passed. However, most wolf left before the observer passed the passing position, which was consistent with prediction two.

Flight intensity

Flight distance, duration and displacement were positively correlated, overall speed showed a strong positive correlation with flight displacement and duration. The other variables did not show strong correlations. Therefore, overall speed, flight duration, distance and displacement might reflect the intensity of the flight, which partially confirms prediction three. Longer distances and higher speeds can be seen as a higher intensity flight (Ydenberg & Dill, 1986). Straightness and initial speed seem not to reflect the flight intensity in my data.

Based on the strong correlations between flight displacement, distance, duration and overall speed, I consider those variables as a proxy for flight response intensity. More intense flights were characterised by longer flight duration and further flight distance with higher overall speeds, while lower intense flights were flights with shorter flight distances and lower speeds. However, it seems that a more intense flight does not result in a straighter flight pattern.

Effects on FID and flight intensity

The FIDs did not show a significant difference between observer types. However, the observer type with two observers had a more extensive range, including some longer FIDs

with two observers present, which was consistent with my prediction four(a). The flight distance and displacements did show a significant difference between the number of observers, where two observers resulted in longer flights. Therefore, in contrast with my prediction four(a), a longer flight with two observers might indicate a higher perceived risk by the wolf, resulting in a more intense flight.

Approach trials with noisier vegetation showed a more extensive range of FIDs, compared to not noisy vegetation for which all FIDs were quite short. This might indicate, as I expected in prediction four(b), that there is a longer detection distance with nosier vegetation. However, the difference in the FID between noise levels was not significant. The overall speed showed a significant difference between noisy and not noisy vegetation, where the overall speed was higher with not noisy vegetation This suggests that the flight had a lower flight intensity with noisy vegetation (early detection), which was consistent with my prediction four(b). Additionally, the sudden late detection of the observer with little vegetation noise resulted in an intense flight, I expect this was the result of the wolf's response perceiving suddenly a high risk.

A strong positive correlation between the relative wind direction and FID showed that the FID increased when the wind blew towards the wolf's starting position (WSP), which confirmed my prediction four(c). Overall speed and flight distance showed negative correlations with the relative wind direction, indicating longer distance and higher overall speeds when the wind blew from the wolf towards the observer. This might be an indication that when the wolf detected the observer earlier, it perceived a lower risk, and therefore resulted in a lower intense flight, which I expected with prediction four(c).

Concealment and FID

A modest correlation between the FID and concealment might indicate that wolves perceive lower risk when they are more concealed, which was partially consistent with prediction five. I expected that a shorter FID could be associated with more concealed wolf starting positions. Two interactions without a flight (hide response) had a concealed wolf starting position, which also gives the impression that the wolf perceived the risk as lower. However, other aspects, e.g. wind direction and noise, might have affected the detectability of the observer(s). I cannot conclude if the perceived risk by the wolf was lower due to the wolf's perception of being less detectable by the observer(s) or because the wolf did not detect the observer(s).

Flight patterns

The majority of flight patterns showed wolves diverting away from the observer and the observer's track, which I expected in prediction six, however during four interactions the wolf circled back to the track before leaving and in two interactions it crossed the observer's track. Circling back to the observer's track is also noted by Karlsson et al. (2007) as they hypothesised that the wolf might have tried to catch the scent of the observer before continuing the flight (Karlsson et al., 2007). However, I also found two interactions were the wolf crossed the observer's track and continued the flight. Therefore, I would suggest that there is also the possibility that a wolf might not knowingly circle back to the observer's track, but 'bumps' into the track during his flight, resulting in two possible choices the wolf can make, either crossing the track and continuing his flight as previously planned or diverting away from the observer's track and changing his intended flight plan. Future studies with more data and with the additional use of, e.g. accelerometry data (Bouet, 2019) might give the possibility to study this reaction.

Overall, the flight patterns seem to confirm the pattern of a more intense flight, with higher overall speed and longer flight distance and duration. Additionally, it showed that more intense flights did not result in straighter (more linear) flights. Occasionally in more intense flights, I observed the circling back to the observer's track pattern, this might suggest that the wolf changed his perceived risk during the flight and increased the overall flight intensity, after interacting with the observer's track.

Observer detection and perceived safety

The variables used in this pilot study reflect roughly two categories: the probability that the wolf detects the observers and the wolf's perception of safety at its location. Wolves rely mostly on olfactory and auditory signals to perceive their surroundings (Harrington & Asa, 2003). Therefore, detection of the observer would be affected by observer type, the noise of the environment and the wind direction. Other studies have shown similar patterns where animals fled earlier as the detection of the observer was higher (Moen et al., 2012; Wam et al., 2014). Additionally, wind speed might affect how the observer's scent is carried through the landscape. Karlsson et al. (2007) showed that with increasing wind speeds the FID decreased, regardless of the wind direction. For wolves it might be challenging to detect the moving observer by scent alone, as wolves use a criss-cross movement pattern in order to follow an

airborne scent (Harrington & Asa, 2003). In this pilot study, I showed that wolves might flee earlier when the wind was directed towards the wolves, with a higher noise level and with more observers present. However, I did not account for wind speeds, as the data was not sufficient enough to include.

The location where the wolf stayed at the start of the approach trial might affect the assessment of risk when the observer is detected. Wolves in very concealed resting sites might feel safer and do not leave until the threat is close. Additionally, as Wam et al. (2012) showed, wolves can adjust their strategy in choosing a rest site on a more concealed location after being disturbed. In this pilot study, I showed a modest correlation between FID and concealment, when the wolf's initial site was less concealed (longer visibility in metres), the FID increased. Moen et al. (2012) showed a similar pattern for Scandinavian brown bears, where the FID increased as the horizontal vegetation structure was less dense. However, spatial data does not show the moment when the wolf detects the observer, but rather shows the moment when the wolf responds spatially by dislocation. To find the initial physiological response to an approaching human, including accelerometry data from the wolf's GPS-collar might increase the level of understanding how wolves respond to human disturbances through fine-scale moment such as head movement (Bouet, 2019). This can lead to a better distinction between the factors affecting the detection of the disturbance and which factors affect the flight, as concealment of the resting site might affect the moment of flight, regardless of the detection. However, as I also showed in this pilot study, that flight intensity seems to be higher when the probability of detecting the observer is lower. This suggests a late detection of the observer results in a higher energetic cost for the flight, due to a higher perception of risk (Ydenberg & Dill, 1986; Frid & Dill, 2002).

Data limitation

The sample size in this pilot study was small and limited to only three territories, with a total of six wolves, which also partly changed between the two years. I could not account for individual differences between the wolves, as individual choices would be expected (Beale, 2007). Within this data, I did not find clear differences in response variables between the territories. However, between the years, I did find a difference in minimum observer-wolf distance. Therefore, this variable was not used in further analyses. Furthermore, I excluded year and territory from the analyses, as I assumed that the effect within this data would be

minimal as no differences were found. However, for future studies with larger sample size, I would advise considering the effects of individuals, territories and years.

Conclusion

In this chapter, I demonstrated which variables can be obtained by the method described in chapter I. I conducted a pilot study where I showed that:

1) Most wolves show a flight response, while some wolves showed a hide response. However, none of the wolves showed a fight response.

2) Wolves generally initiate their flight before the observer passed the passing position.

3) A longer flight duration, distance, displacement and higher overall speed (but not straightness) might be an indication of higher flight intensity.

4) More observers, the wind blowing from the wolf and lower noise level might increase the flight intensity.

5) The wolf's perception of risk might be affected by the horizontal vegetation cover surrounding the wolf's location.

6) Wolves' flights generally diverted away from the observer, with occasional interaction with the observer's track.

However, as the sample size was limited for the analyses, it would be advisable to continue studying wolves' responses to humans. With this pilot study, I showed the potential of studies with a high spatio-temporal resolution for experimental approaches on wolves. As human-wildlife conflicts are increasing, future studies might inform conservation and management. Increasing knowledge of wolf behaviour towards humans might improve coexistence with carnivores.

Acknowledgement

Two years ago I started this journey with a meeting about potential thesis topics, this resulted very soon in the idea to work with wolf-human interactions, a recently started project at the time. In this acknowledgement I would like to thank everyone who helped or supported me during this sometimes challenging journey.

First and foremost, I would like to thank **Ane Eriksen** for her guidance and advise, I am really grateful that I got this opportunity. I would like to thank **Barbara Zimmermann** for proposing this thesis topic and for feedback during the writing process.

I would like to thank everyone who helped and assisted during the fieldwork, specifically **Ane Eriksen** and **Boris Fuchs** for the 'remote' guidance during the approach trials. Additionally, I would like to thank **Henrike Hensel**, for her amazing flexibility for programming the wolf collars, even if we decided to do an approach trial in the weekend. Without everyone helping and assisting with the approach trials, I would not have been able collect the data.

Additionally, I would like to thank: **Kristoffer Nordli** for the discussions and explanations about changepoint analyses, **Andrés Ordiz** for helping me to understand the Upper Control Limit analyses, and **David Carrindo-Sanchez** for giving me advise and tips on how to improve my R-script.

Furthermore, I would like to thank everyone who read my thesis during the writing process and gave me valuable feedback and suggestions: **Cecilia Miltz**, **László Tonhauser**, **Jérémy Monsimet**, **Zea Walton**, **Léa Bouet**, and **Emma den Hartog**.

References

Arnemo, J. M., & Evans, A. L. (2017). Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx. *Inland Norway University of Applied Sciences.*, 16.

Beale, C. M. (2007). The Behavioral Ecology of Disturbance Responses. *International Journal of Comparative Psychology*, *20*(2). Retrieved from https://escholarship.org/uc/item/43m7b2d5

Bivand, R., & Rundel, C. (2019). *rgeos: Interface to Geometry Engine - Open Source ('GEOS')*. Retrieved from https://CRAN.R-project.org/package=rgeos

Bojarska, K., Sulich, J., Bachmann, S., Okarma, H., Theuerkauf, J., & Gula, R. (2020). Opportunity and peril: how wolves use a dense network of forest roads. *Mammalian Biology*. https://doi.org/10.1007/s42991-020-00014-0

Bouet, L. (2019). *Connecting acceleration data to specific behaviors in captive wolves (Canis lupus)* (p. 33 p.) [Master thesis]. Retrieved from Université Jean Monnet Saint-Étienne. website: https://www.slu.se/globalassets/ew/org/inst/ekol/forskning/projekt/skandulv/publikationer/rapporter/bouet-2019-connecting-acceleration-data-to-specific-behaviors-in-captive-wolves-canis-lupus.pdf

Carricondo-Sanchez, D., Zimmermann, B., Wabakken, P., Eriksen, A., Milleret, C., Ordiz, A., … Wikenros, C. (2020). Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. *Biological Conservation*, *244*, 108514. https://doi.org/10.1016/j.biocon.2020.108514

Chapron, G., Kaczensky, P., Linnell, J. D. C., Arx, M. von, Huber, D., Andrén, H., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517–1519. https://doi.org/10.1126/science.1257553

Chen, J., & Gupta, A. K. (2011). *Parametric Statistical Change Point Analysis: With Applications to Genetics, Medicine, and Finance*. Springer Science & Business Media.

Colino-Rabanal, V. J., Lizana, M., & Peris, S. J. (2011). Factors influencing wolf Canis lupus roadkills in Northwest Spain. *European Journal of Wildlife Research*, *57*(3), 399–409. https://doi.org/10.1007/s10344-010-0446-1

Cooper, W. E., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, *244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*(1), 253–263. https://doi.org/10.1111/1365-2664.12732

Dowle, M., & Srinivasan, A. (2019). *data.table: Extension of `data.frame`*. Retrieved from https://CRAN.R-project.org/package=data.table

Dytham, C. (2011). *Choosing and Using Statistics: A Biologist's Guide*. John Wiley & Sons.

Eisenberg, C., Hibbs, D. E., Ripple, W. J., & Salwasser, H. (2014). Context dependence of elk (Cervus elaphus) vigilance and wolf (Canis lupus) predation risk. *Canadian Journal of Zoology*, *92*(8), 727–736. https://doi.org/10.1139/cjz-2014-0049

Eriksen, A., Versluijs, E., Fuchs, B., Zimmermann, B., Wabakken, P., Ordiz, A., … Rieger, S. A. (in prep). *A standardized method for experimental human approaches on wolves.*

Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., … Pedersen, H. C. (2011). Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. *Animal Behaviour*, *81*(2), 423–431.

Evans, A. L., Singh, N. J., Friebe, A., Arnemo, J. M., Laske, T. G., Fröbert, O., … Blanc, S. (2016a). Drivers of hibernation in the brown bear. *Frontiers in Zoology*, *13*(1), 7. https://doi.org/10.1186/s12983-016-0140-6

Evans, A. L., Singh, N. J., Fuchs, B., Blanc, S., Friebe, A., Laske, T. G., … Arnemo, J. M. (2016b). Physiological reactions to capture in hibernating brown bears. *Conservation Physiology*, *4*(1). https://doi.org/10.1093/conphys/cow061

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1). Retrieved from https://www.jstor.org/stable/26271862

Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (1996). A Method to Quantify the Effects of Human Disturbance on Animal Populations. *Journal of Applied Ecology*, *33*(4), 786–792. https://doi.org/10.2307/2404948

Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, *40*(3), 1–25.

Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, *12*(5), 395–408. https://doi.org/10.1111/j.1461-0248.2009.01293.x

Harrington, F. H., & Asa, C. S. (2003). Wolf communication. In Mech, L. David & Luigi Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (Vol. 3, pp. 66–103). University of Chicago: Chicago, IL, USA.

Hawkins, D. M., Qiu, P., & Kang, C. W. (2003). The changepoint model for statistical process control. *Journal of Quality Technology*, *35*(4), 355–366.

Heberlein, T. A. (2012). *Navigating Environmental Attitudes*. Oxford University Press.

Holt, R. D., & Polis, G. A. (1997). A Theoretical Framework for Intraguild Predation. *The American Naturalist*, *149*(4), 745–764. https://doi.org/10.1086/286018

Je, K., Rb, G., Sm, H., & G, M.-T. (2018). When does cognitive decline begin? A systematic review of change point studies on accelerated decline in cognitive and neurological outcomes preceding mild cognitive impairment, dementia, and death. *Psychology and Aging*, *33*(2), 195–218. https://doi.org/10.1037/pag0000236

Johansson, M., Karlsson, J., Pedersen, E., & Flykt, A. (2012). Factors Governing Human Fear of Brown Bear and Wolf. *Human Dimensions of Wildlife*, *17*(1), 58–74. https://doi.org/10.1080/10871209.2012.619001

Karlsson, J., Eriksson, M., & Liberg, O. (2007). At what distance do wolves move away from an approaching human? *Canadian Journal of Zoology*, *85*(11), 1193–1197. https://doi.org/10.1139/Z07-099

Killick, R., Eckley, I. A., Ewans, K., & Jonathan, P. (2010). Detection of changes in variance of oceanographic time-series using changepoint analysis. *Ocean Engineering*, *37*(13), 1120–1126. https://doi.org/10.1016/j.oceaneng.2010.04.009

Killick, R., Fearnhead, P., & Eckley, I. A. (2012). Optimal Detection of Changepoints With a Linear Computational Cost. *Journal of the American Statistical Association*, *107*(500), 1590–1598. https://doi.org/10.1080/01621459.2012.737745

Killick, R., Haynes, K., & Eckley, I. A. (2016). *changepoint: An R package for changepoint analysis*. Retrieved from https://CRAN.R-project.org/package=changepoint

Kuijper, D. P. J., Churski, M., Trouwborst, A., Heurich, M., Smit, C., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes? *Biological Conservation*, *235*, 102–111. https://doi.org/10.1016/j.biocon.2019.04.004

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*(8), 1401–1409.

Laundre, J. W., Hernandez, L., & Ripple, W. J. (2010). The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! *The Open Ecology Journal*, *3*(3), 1–7. https://doi.org/10.2174/1874213001003030001

Lavielle, M. (2005). Using penalized contrasts for the change-point problem. *Signal Processing*, *85*(8), 1501–1510. https://doi.org/10.1016/j.sigpro.2005.01.012

Lavielle, M., & Teyssière, G. (2007). Adaptive detection of multiple change-points in asset price volatility. In *Long Memory in Economics* (pp. 129–156). https://doi.org/10.1007/978-3-540-34625-8_5

Lesmerises, F., Dussault, C., & St-Laurent, M.-H. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management*, *276*, 125–131.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Hobbs, N. T., & Sand, H. (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1730), 910–915. https://doi.org/10.1098/rspb.2011.1275

Liberg, O., Suutarinen, J., Åkesson, M., Andrén, H., Wabakken, P., Wikenros, C., & Sand, H. (2020). Poaching-related disappearance rate of wolves in Sweden was positively

related to population size and negatively to legal culling. *Biological Conservation*, *243*, 108456. https://doi.org/10.1016/j.biocon.2020.108456

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Mech, L. D. (2017). Where can wolves live and how can we live with them? *Biological Conservation*, *210*, 310–317. https://doi.org/10.1016/j.biocon.2017.04.029

Mech, L. D., & Boitani, L. (2003). Wolf social ecology. In Mech, L. David & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (Vol. 3, pp. 1–35). University of Chicago: Chicago, IL, USA.

Milleret, C., Ordiz, A., Sanz-Pérez, A., Uzal, A., Carricondo-Sanchez, D., Eriksen, A., … Zimmermann, B. (2019). Testing the influence of habitat experienced during the natal phase on habitat selection later in life in Scandinavian wolves. *Scientific Reports*, *9*(1), 1–11. https://doi.org/10.1038/s41598-019-42835-1

Moen, G. K., Ordiz, A., Kindberg, J., Swenson, J. E., Sundell, J., & Støen, O.-G. (2018). Behavioral reactions of brown bears to approaching humans in Fennoscandia. *Écoscience*, 1–11.

Moen, G. K., Støen, O.-G., Sahlén, V., & Swenson, J. E. (2012). Behaviour of Solitary Adult Scandinavian Brown Bears (Ursus arctos) when Approached by Humans on Foot. *PLoS ONE*, *7*(2), e31699. https://doi.org/10.1371/journal.pone.0031699

Montgomery, D. C. (2007). *Introduction to statistical quality control*. John Wiley & Sons.

Moritz, S., Sardá, Alexis, Bartz-Beielstein, Thomas, Zaefferer, Martin, & Stork, Jörg. (2015). *Comparison of different Methods for Univariate Time Series Imputation in R*. 20.

Mustonen, A.-M., Lempiäinen, T., Aspelund, M., Hellstedt, P., Ikonen, K., Itämies, J., … Nieminen, P. (2012). Application of change-point analysis to determine winter sleep patterns of the raccoon dog (Nyctereutes procyonoides) from body temperature recordings and a multi-faceted dietary and behavioral study of wintering. *BMC Ecology*, *12*(1), 27. https://doi.org/10.1186/1472-6785-12-27

Nordli, K. T. (2018). *On the way to independence : Ebbing cohesion in Scandinavian wolf family groups [MSc]*. Retrieved from https://brage.inn.no/inn-xmlui/handle/11250/2585250

Ordiz, A., Bischof, R., & Swenson, J. E. (2013a). Saving large carnivores, but losing the apex predator? *Biological Conservation*, *168*, 128–133. https://doi.org/10.1016/j.biocon.2013.09.024

Ordiz, A., Moen, G. K., Saebo, S., Stenset, N., Swenson, J. E., & Stoena, O.-G. (2019). Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. *Biological Conservation*, *232*, 228–237. https://doi.org/10.1016/j.biocon.2019.01.016

Ordiz, A., Støen, O.-G., Langebro, L. G., Brunberg, S., & Swenson, J. E. (2009). A practical method for measuring horizontal cover. *Ursus*, *20*(2), 109–113. https://doi.org/10.2192/08SC031.1

Ordiz, A., Støen, O.-G., Sæbø, S., Sahlén, V., Pedersen, B. E., Kindberg, J., & Swenson, J. (2013b). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*, *50*(2), 306–314.

Patel, S. H., Morreale, S. J., Panagopoulou, A., Bailey, H., Robinson, N. J., Paladino, F. V., … Spotila, J. R. (2015). Changepoint analysis: a new approach for revealing animal movements and behaviors from satellite telemetry data. *Ecosphere*, *6*(12), art291. https://doi.org/10.1890/ES15-00358.1

Penteriani, V., Delgado, M. del M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojola, I., … López-Bao, J. V. (2016). Human behaviour can trigger large carnivore attacks in developed countries. *Scientific Reports*, *6*(1), 20552. https://doi.org/10.1038/srep20552

QGIS Development Team. (2019). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Retrieved from http://qgis. osgeo. org

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Recio, M. R., Zimmermann, B., Wikenros, C., Zetterberg, A., Wabakken, P., & Sand, H. (2018). Integrated spatially-explicit models predict pervasive risks to recolonizing wolves in Scandinavia from human-driven mortality. *Biological Conservation, 226*, 111–119. https://doi.org/10.1016/j.biocon.2018.07.025

Reeves, J., Chen, J., Wang, X. L., Lund, R., & Lu, Q. Q. (2007). A Review and Comparison of Changepoint Detection Techniques for Climate Data. *Journal of Applied Meteorology and Climatology*, *46*(6), 900–915. https://doi.org/10.1175/JAM2493.1

Rio-Maior, H., Nakamura, M., Álvares, F., & Beja, P. (2019). Designing the landscape of coexistence: Integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. *Biological Conservation, 235,* 178–188. https://doi.org/10.1016/j.biocon.2019.04.021

Roelofs, K. (2017). Freeze for action: neurobiological mechanisms in animal and human freezing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1718), 20160206. https://doi.org/10.1098/rstb.2016.0206

Røskaft, E., Händel, B., Bjerke, T., & Kaltenborn, B. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, *13*(2), 172–185. https://doi.org/10.2981/0909-6396(2007)13[172:HATLCI]2.0.CO;2

RStudio Team. (2016). RStudio: Integrated Development Environment for R (Version 1.1.463). Retrieved from http://www.rstudio.com/

Rupia, E. J., Binning, S. A., Roche, D. G., & Lu, W. (2016). Fight flight or freeze hide? Personality and metabolic phenotype mediate physiological defence responses in flatfish. *Journal of Animal Ecology*, *4*(85), 927–937. https://doi.org/10.1111/1365-2656.12524

Sahlén, V., Ordiz, A., Swenson, J. E., & Støen, O. G. (2015). Behavioural Differences between Single Scandinavian Brown Bears (Ursus arctos) and Females with Dependent Young When Experimentally Approached by Humans. *PLOS ONE*, *10*(4), e0121576. https://doi.org/10.1371/journal.pone.0121576

Sand, H., Eklund, A., Zimmermann, B., Wikenros, C., & Wabakken, P. (2016). Prey Selection of Scandinavian Wolves: Single Large or Several Small? *PloS One, 11*(12), e0168062.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H. C., & Liberg, O. (2008). Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates? *Oecologia, 156*(1), 53–64. https://doi.org/10.1007/s00442-008-0969-2

Schloerke, B., Crowley, J., Cook, D., Briatte, F., Marbach, M., Thoen, E., … Larmarange, J. (2018). *GGally: Extension to 'ggplot2*.

Schwalb Willmann, J., Remelgado, R., Safi, K., & Wegmann, M. (2020). moveVis: Animating movement trajectories in synchronicity with static or temporally dynamic environmental data in r. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.13374

Shewhart, W. A. (Walter A., & Deming, W. E. (William E. (1939). *Statistical method from the viewpoint of quality control*. Retrieved from http://archive.org/details/CAT10502416

Statistisk sentralbyrå. (2020). Areal og befolkning, etter region, statistikk variabel og år. Statistikkbanken. Retrieved April 15, 2020, from https://www.ssb.no/statbank/table/11342/tableViewLayout1/

Sunde, P., Odderskær, P., & Storgaard, K. (2009a). Flight Distances of Incubating Common Buzzards Buteo buteo are Independent of Human Disturbance. *Ardea, 97*(3), 369–372. https://doi.org/10.5253/078.097.0313

Sunde, P., Olesen, C. R., Madsen, T. L., & Haugaard, L. (2009b). Behavioural Responses of GPS-Collared Female Red Deer Cervus elaphus to Driven Hunts. *Wildlife Biology, 15*(4), 454–460. https://doi.org/10.2981/09-012

Sunde, P., Stener, S. Ø., & Kvam, T. (1998). Tolerance to humans of resting lynxes Lynx lynx in a hunted population. *Wildlife Biology, 4*(2), 177–183. https://doi.org/10.2981/wlb.1998.020

Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., Flagstad, Ø., & Hedmark, E. (2019). *Inventering av varg vintern 2018-2019*. Retrieved from https://brage.nina.no/nina-xmlui/handle/11250/2599641

Truong, C., Oudre, L., & Vayatis, N. (2020). Selective review of offline change point detection methods. *Signal Processing, 167,* 107299. https://doi.org/10.1016/j.sigpro.2019.107299

Viljanen, A. S. (2019). *Moose (Alces alces) flight response when disturbed by off-track skiing*. Retrieved from https://brage.inn.no/inn-xmlui/handle/11250/2602722

Wabakken, P., & Maartmann, E. (2019). *ULV I NORGE PR. 30. APRIL 2019 FORELØPIGE KONKLUSJONER FOR VINTEREN 2018-2019 RAPPORT 4*. Retrieved from https://rovdata.no/Portals/Rovdata/Dokumenter/Rapporter/Forel%F8pige %20ulverapporter/uRapp4_190513_Status%20Norge_1819_pdf.pdf

Wabakken, P., Maartmann, E., & Nordli, K. T. (2020). *ULV I NORGE PR. 20. MARS 2020 FORELØPIGE KONKLUSJONER FOR VINTEREN 2019-2020 RAPPORT 3*. Retrieved from https://rovdata.no/Portals/Rovdata/Dokumenter/Rapporter/Forel %F8pige%20ulverapporter/Ulv_Forelop%20StatusRapp%203_20mar2020.pdf

Wam, H. K., Eldegard, K., & Hjeljord, O. (2012). From overlooking to concealed: predator avoidance in an apex carnivore. *European Journal of Wildlife Research*, *58*(6), 1001–1003. https://doi.org/10.1007/s10344-012-0670-y

Wam, H. K., Eldegard, K., & Hjeljord, O. (2014). Minor habituation to repeated experimental approaches in Scandinavian wolves. *European Journal of Wildlife Research*, *60*(5), 839–842. https://doi.org/10.1007/s10344-014-0841-0

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Retrieved from https://ggplot2.tidyverse.org

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wickham, H., François, R., Henry, L., & Müller, K. (2019). *dplyr: A Grammar of Data Manipulation*. Retrieved from https://CRAN.R-project.org/package=dplyr

Wikenros, C., Jarnemo, A., Frisén, M., Kuijper, D. P. J., & Schmidt, K. (2017). Mesopredator behavioral response to olfactory signals of an apex predator. *Journal of Ethology*, *35*(2), 161–168. https://doi.org/10.1007/s10164-016-0504-6

Wikenros, C., Liberg, O., Sand, H., & Andrén, H. (2010). Competition between recolonizing wolves and resident lynx in Sweden. *Canadian Journal of Zoology, 88*(3), 271–279. https://doi.org/10.1139/Z09-143

Ydenberg, R. C., & Dill, L. M. (1986). *The economics of fleeing from predators*. *16*, 229–249.

Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., & Liberg, O. (2014). Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behavioral Ecology*, *25*(6), 1353–1364. https://doi.org/10.1093/beheco/aru134

Zimmermann, B., Sand, H., Wabakken, P., Liberg, O., & Andreassen, H. P. (2015). Predator dependent functional response in wolves: from food limitation to surplus killing. *Journal of Animal Ecology, 84*(1), 102–112.

Appendices
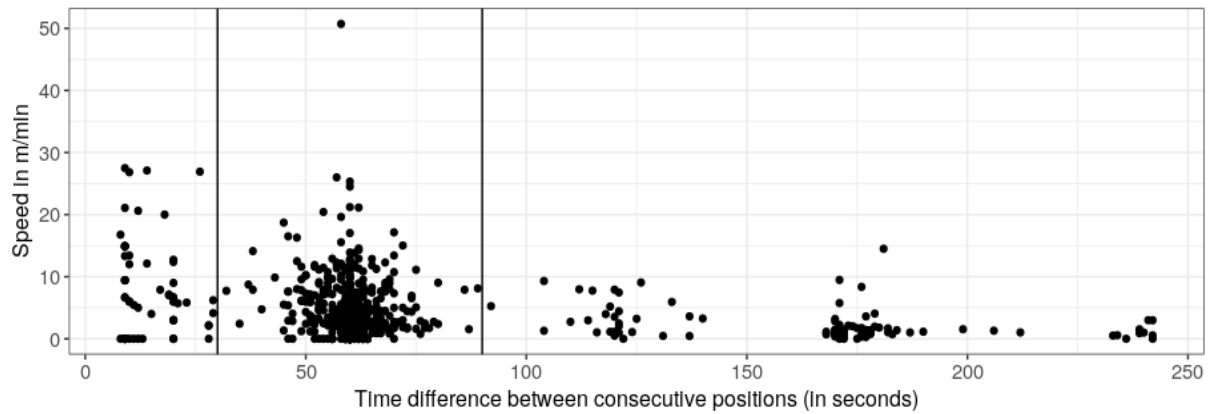
Appendix 1. Time difference in seconds between consecutive wolf GPS positions relative to the speed in m/min. The data consist of control data when wolves were not moving, based on visual inspection. The vertical black lines represent 30 and 90 seconds. 22 observations with more than 250 seconds time difference are omitted from the graph to increase readability (range = 8 - 532 seconds, n = 998).
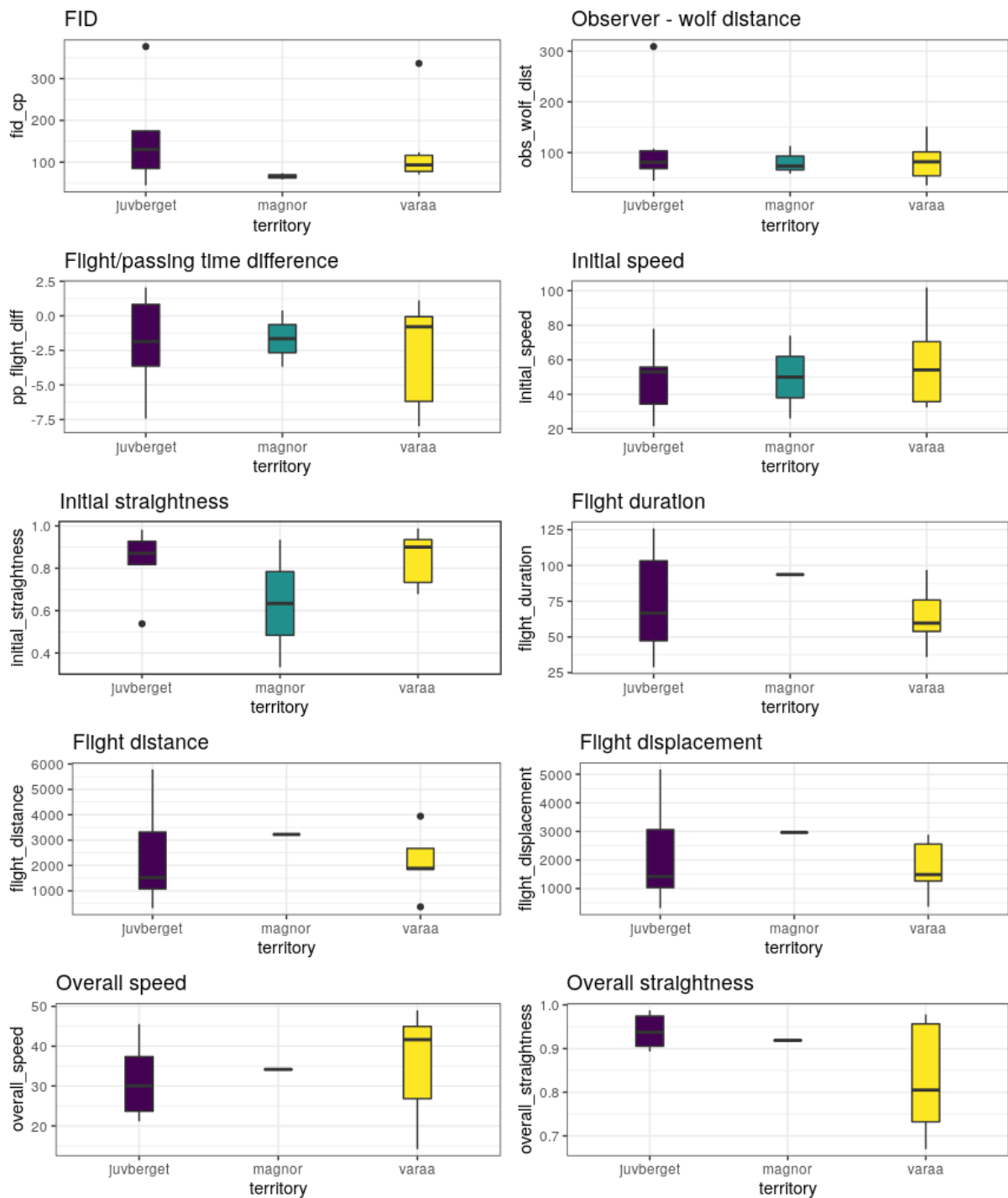
Appendix 2: Effect of territories on the different variables based on experimental human approach trials on wolves.
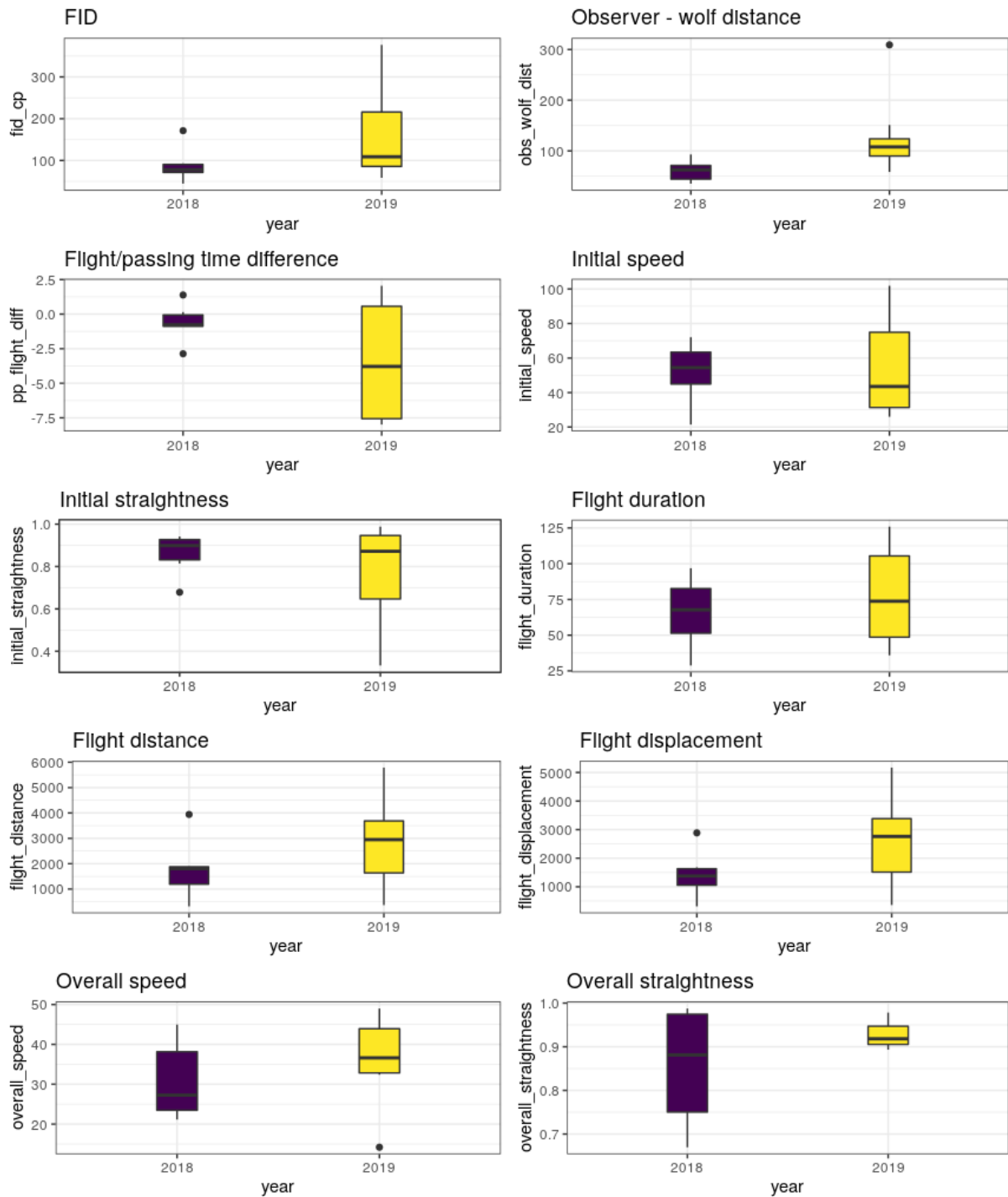
Appendix 3. Effect of year on the different variables based on experimental human approach trials on wolves.

Approach_ID	Territory	FID	Observer-Wolf distance	Flight/passing time diff	Initial speed	Initial straightness
A2018-09-13_juv	juvberget	171.25	72.15	-2.87	56.46	0.93
A2018-09-20_var	varaa	NA	35.51	NA	NA	NA
A2018-09-27_juv	juvberget	44.56	44.56	-0.85	21.48	0.91
A2018-10-04_var	varaa	72.86	43.42	0.15	65.73	0.68
A2018-10-25_juv	juvberget	83.29	67.27	1.38	52.42	0.81
A2018-11-01_var	varaa	92.88	92.88	-0.88	42.44	0.94
A2018-11-15_var	varaa	71.00	71.00	-0.70	72.03	0.88
A2018-11-29_var	varaa	NA	57.93	NA	NA	NA
A2019-08-27_var	varaa	93.90	93.90	1.12	101.86	0.92
A2019-09-01_mag	magnor	NA	113.16	NA	NA	NA
A2019-10-19_mag	magnor	73.36	73.36	-3.68	73.93	0.93
A2019-10-29_juv	juvberget	175.79	107.83	-3.88	53.56	0.83
A2019-11-21_var	varaa	336.39	151.04	-7.98	32.34	0.68
A2019-11-22_mag	magnor	58.49	58.49	0.38	25.98	0.33
A2019-12-13_var	varaa	123.83	123.83	-7.95	33.45	0.99
A2019-12-30_juv	juvberget	376.90	309.11	-7.43	77.94	0.54
A2020-01-30_juv	juvberget	89.89	89.89	2.05	28.32	0.98

approach_ID	Flight duration	Flight distance	Flight displacement	Overall speed	Overall straightness
A2018-09-13_juv	84.87	1753.51	1678.67	21.16	0.96
A2018-09-20_var	NA	NA	NA	NA	NA
A2018-09-27_juv	28.85	319.05	315.10	22.35	0.99
A2018-10-04_var	96.85	3942.18	2886.50	41.65	0.73
A2018-10-25_juv	48.62	1006.35	986.38	27.69	0.98
A2018-11-01_var	75.88	1887.33	1264.07	26.84	0.67
A2018-11-15_var	59.70	1850.66	1489.86	44.96	0.81
A2018-11-29_var	NA	NA	NA	NA	NA
A2019-08-27_var	53.88	2672.90	2556.44	49.01	0.96
A2019-09-01_mag	NA	NA	NA	NA	NA
A2019-10-19_mag	93.68	3225.65	2963.73	34.18	0.92
A2019-10-29_juv	46.88	1294.00	1166.16	32.39	0.90
A2019-11-21_var	NA	NA	NA	NA	NA
A2019-11-22_mag	NA	NA	NA	NA	NA
A2019-12-13_var	35.95	369.35	361.29	14.18	0.98
A2019-12-30_juv	109.43	3841.03	3525.14	39.03	0.92
A2020-01-30_juv	125.95	5789.82	5172.16	45.56	0.89

approach_ID	Nr. observers	Noise level	Relative wind direction	Concealment	Flight pattern
A2018-09-13_juv	2	Noisy	1.00	18	circling back
A2018-09-20_var	2	Medium	0.50	4	no flight
A2018-09-27_juv	1	Noisy	NA	2	diverts
A2018-10-04_var	1	Medium	0.50	30	circling back
A2018-10-25_juv	1	Noisy	NA	7	circling back
A2018-11-01_var	1	Noisy	NA	7	diverts
A2018-11-15_var	1	Silent	NA	NA	diverts
A2018-11-29_var	1	Silent	0.50	NA	no flight
A2019-08-27_var	2	Medium	0.33	NA	diverts
A2019-09-01_mag	1	Noisy	0.33	6	no flight
A2019-10-19_mag	2	Noisy	NA	NA	crossed
A2019-10-29_juv	1	Noisy	1.00	NA	diverts
A2019-11-21_var	2	Noisy	NA	28	diverts
A2019-11-22_mag	2	NA	0.33	4	circling back
A2019-12-13_var	1	Noisy	1.00	NA	diverts
A2019-12-30_juv	2	Noisy	0.83	25	diverts
A2020-01-30_juv	2	Medium	0.50	NA	crossed

Appendix 4. Table with variables for 17 interactions from the experimental human approach trials on wolves.