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Behavioural responses of captive red fox (*Vulpes vulpes*) to telemetry collars

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Preface

This study was conducted at the Faculty of Environmental Sciences and Natural Resource Management at the Norwegian University of Life Sciences (NMBU). First of all, I would like to express my sincere gratitude to my supervisors Richard Bischof and Anne Lene Hovland for making this project happen and for all the work you did related to the experimental setup. I would like to thank the Department of Animal- and Aquacultural Sciences (IHA), and the staff at The Animal Production Experimental Centre (SHF) at NMBU for their maintenance of the foxes and help with this study, especially the help of Marianne Bratberg Skarra.

Richard Bischof deserves special thanks for all the help and guidance during this project. Thank you for always answering my numerous questions and for all the help with the statistical analysis as well as valuable comments on the manuscript. Many thanks to Anne Lene Hovland for valuable tips about silver fox behaviour and how to measure it, as well as helpful comments on the manuscript. I would also like to thank Mahdieh Tourani and Cyril Milleret for letting me occupy your office during my "fieldwork".

Last, but not least I would like to thank my family and friends for always supporting me.

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Abstract

Telemetry is one of the most important tools of wildlife research. It provides information about dispersal, home range, survival, movement and many other ecological and biological aspects. Although many animals are fitted with telemetry-collars, few studies show the behavioural effects these collars may cause on the individual. The collar may lead to a significant change in behaviour, and thus the study results may not be representative for the wild population. Additionally, collars may affect animal welfare by causing physical pain and discomfort. The objective of this research was to quantify possible short-time behavioural effects of red fox (*Vulpes vulpes)* to telemetry-collars. This were done by recording the behaviour of 16 captive foxes by around the clock video monitoring during a two-week experimental period. Proportion of day activity and behaviour linked to discomfort were scored at fixed time intervals post collar attachment, and body mass were measured. I fitted linear mixed effect models and general linear mixed effect models to analyse possible relationships between collars and activity, body mass and specific behaviours indicating discomfort. The results revealed distinct behavioural effects in red foxes as a result of wearing telemetry collars. The collars caused discomfort as collared foxes had a significant increase in performance of the behaviours “rubbing” and “shaking”. In addition, collared foxes lowered their weight gain compared to non-collared foxes. The behavioural effects caused by collars were found to diminish over time, indicating an acclimation to the collars. This thesis emphasizes the importance of understanding the possible effects related to collars on wildlife, both for animal welfare reasons and for good science. Scientists should always establish potential complications and consequences associated with telemetry before doing research in order to minimize collar impact.

Sammendrag

Telemetri er et av de viktigste hjelpemidlene i forskning på dyrelivet. Det gir informasjon om spredning, hjemmeområder, overlevelse, forflytning og mange andre økologiske og biologiske aspekter. Mange dyr blir i dag utstyrt med telemetrihalsbånd selv om det finnes få studier om hvordan disse halsbåndene påvirker dyrenes atferd. Halsbåndet kan føre til en betydelig atferdsendring, noe som fører til at resultatene fra studiet ikke representerer artens eller populasjonens atferd. I tillegg kan halsbåndet påvirke dyrevelferden ved å føre til skader eller ubehag på dyret. Målet med dette studiet var å kvantifisere mulige kortsiktige atferdsmessige effekter hos rødrev (*Vulpes vulpes)* forårsaket av telemetrihalsbånd. Dette ble gjort ved å registrere og observere atferden til 16 rever med og uten halsbånd ved hjelp av 24-timers videoovervåkning gjennom et to ukers langt forsøk. Andel dagaktivitet og atferd som tyder på ubehag ble samlet inn på bestemte tider etter påsettelse av halsbånd, og kroppsvekt ble målt. Jeg tilpasset lineære modeller for å analysere mulige sammenhenger mellom halsbånd og aktivitet, kroppsvekt og atferd som uttrykker ubehag. Resultatene viste at revene endret atferd som følge av å ha på halsbånd. Halsbåndene viste seg å forårsake ubehag ved at rever som bar halsbånd hadde en betydelig økning av atferdene «rubbing» og «shaking», i tillegg til at de opplevde en mindre vektøkning. De atferdsmessige effektene av halsbånd viste seg å avta med tiden, noe som kan tyde på at revene ble vant til halsbåndene. Denne oppgaven understreker viktigheten av å forstå de mulige påvirkningene halsbånd kan ha på dyrelivet, både med tanke på dyrevelferd og på god forskning. Før forskere gjør studier som inkluderer telemetri-halsbånd bør potensielle komplikasjoner og konsekvenser bli etablert slik at man kan forsøke å gjøre effektene av halsbåndene minst mulig.

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1 Introduction

Telemetry is one of the most important tools of wildlife research. Technological developments have over the last decades contributed to new ways of exploring ecology (Read & Clark, 2006), providing information that previously was hard or impossible to access (Rutz & Hays, 2009). Telemetry derives from the two Greek words “tele” meaning remote and “metron” meaning measurements (Ropert-Coudert & Wilson, 2005). Slater (1965) defines telemetry in biology as "the instrumental technique for gaining and transmitting information from a living organism and its environment to a remote observer”. This requires equipment that transmits and receives the data by radio waves or satellite systems (Boitani & Powell, 2012), where devices are attached on animals via backpacks, ear tags, collars, internally implanted devices etc.

Tracking animals with telemetry can help researchers investigate biological questions by letting the researches not only get records of *where* the animal have been, but also *when* it was there (Macdonald, 1978). Telemetry is used to study habitat use (Mauritzen et al., 2003; Riecken & Raths, 1996), home ranges (Coman et al., 1991), dispersal (Ables, 1969; Towerton et al., 2016), reproduction (Knopf & Rupert, 1996), interactions (Kortello et al., 2007) and survival (Gosselink et al., 2007). In recent years, telemetry have also been of great importance collecting information on the environmental influences, such as climate change and increased human activity, on wildlife (Kenward, 2001). For elusive, shy, small, rare or other species that are hard to observe, telemetry is often the only way to gather data systematically on behaviour and demography (Kenward, 2001).

The first wildlife tracking studies with telemetry took place in the mid 1960s (Cochran & Lord, 1963; Slater, 1965) and were based on VHF (very high frequency). The principle of VHF-technology is animal-attached transmitters which sends signals in the range of the electromagnetic spectrum 30-300 MHz to mobile or stationary receivers, providing the animals locations and movements (Millspaugh et al., 2012). VHF is a frequently used method due to relatively low costs (compared to other methods) and availability of transmitters for almost all kinds of species (Millspaugh et al., 2012). However, a major drawback on the VHF-system is the limited signal range and the considerable time investments for researches as they collect animal location information manually (Fancy et al., 1998; Hebblewhite & Haydon, 2010).

In the early 1980s, scientist started to use satellite systems to track wildlife after the development of accurate transmitters small enough to be mounted on animals (Fancy et al., 1998). The global positioning system (GPS) provides detailed location data by use of orbiting satellites transmitting signals to animal-borne GPS receivers (Hebblewhite & Haydon, 2010; Millspaugh et al., 2012). GPS data can be retrieved in multiple ways; directly via the transmitted signal from the receiver tag, by collecting the tag after use or via integration of a transmission network such as Argos Platform Transmitter Terminal (PTT) (Millspaugh et al., 2012). GPS-tracking is a modern system that provides highly precise global scaled data without requiring the researches to be present, which reduce the human resources needed and the human-caused collection bias compared with the VHF-technology (Hebblewhite & Haydon, 2010; Millspaugh et al., 2012). Although GPS-tools contributes with major advantages to wildlife research, the approach is not flawless as high cost, location-error and low battery capacity are some issues related to this tool (Brooks et al., 2008; Hebblewhite & Haydon, 2010; Millspaugh et al., 2012).

Neck-collars are commonly used to attach both VHF- transmitters and GPS-receivers on the animals, especially on terrestrial species (Boitani & Powell, 2012; Millspaugh et al., 2012). The shape, fit and mass are three main design criteria of the collar, where the collar should be pliable, and the shape should not cause skin irritation or ruin the animals silhouette (Brooks et al., 2008; Macdonald, 1978; Millspaugh et al., 2012). The fit should be individually adjusted, preventing the collar from falling off and allowing the animal to move and grow normally (Millspaugh et al., 2012). The mass depends on the size of the animal; for instance, small animals (<5kg) should not carry a collar that weigh >1% of their body mass (Brooks et al., 2008). However, a general rule is that the weight should

not exceed 3-5% of the animals' body mass, and preferably be as light as possible (Coughlin & van Heezik, 2014; Macdonald, 1978).
One of the most essential assumption when using telemetry-collars for wildlife research is that collared animals behave in the same manner as non-collared animals, indicating no impact of the collars or the attachment process (Millspaugh et al., 2012). If the telemetry-approach is causing marked animals to behave differently, bias in the research result may occur (Demers et al., 2003; Millspaugh et al., 2012). For example, if a study on ranging distance in a wild animal use telemetry-collars as the approach, the results would be biased if the presence of the collar alter the wild animal's behaviour, making it move significantly shorter or longer distances.

Attachment of the collar requires that the animal in some way has to be captured and handled. Dennis and Shah (2012) examined the immediate effects that trapping, handling and tagging had on the behaviour of the common brushtail possum (*Trichosurus vulpecula*), finding that stress, fear and physical damage are possible consequences of the collaring process.

The collar itself have also been shown to impact animals in terms of changes in activity (Brooks et al., 2008; Coughlin & van Heezik, 2014; Dennis & Shah, 2012), lower foraging efficiency (Godfrey et al., 2003), loss of body mass (Cypher, 1997; Legagneux et al., 2013; Tuyttens et al., 2002), reduced reproduction success (Demers et al., 2003) and lower survival rate (Cote et al., 1998; Cypher, 1997). Not only can this bias the research results (Millspaugh et al., 2012), it is posing concerns for animal welfare (Dawkins, 2006).

However, many studies report that collars do not have a significant impact on the animal. Bank et al. (2000) found no effect of collars on juvenile guanaco (*Lama guanicoe*) survival, Cote et al. (1998) discovered no long-term effects of radiocollars on reproduction success or foraging efficiency in mountain goat (*Oremnos americanus*), Durnin et al. (2004) observed no effects of radiocollars on behaviour related to stress in captive giant panda (*Ailuropoda melanoleuca*), and Horback et al. (2012) found no significant differences in behaviour due to collars on captive African elephant (*Loxodonta africana*). Furthermore, Laurenson and Caro (1994) monitored the long-term effects of collars in free-living cheetahs (*Acinonyx jubatus*), finding that collar did not affect hunting behaviour, food intake or reproduction success. Manning et al. (2017) examined the effects of collars on cattle (*Bos taurus*) behaviour, observing no significant behavioural differences between the collared and the non-collared cows, and Moll et al. (2009) found no physiological effects of video-collars on captive white-tailed deer (*Odocoileus virginianus),* as measured by faecal glucocorticoid metabolite (FGM).

Studies may fail to find an impact of collars because they lack sufficient controls (Cote et al., 1998; Durnin et al., 2004). This applies especially to research on wild animals, as most wild-ranging animals are hard to find and observe, making unmarked animals impossible to monitor and the collection of sufficient control-data difficult (Coughlin & van Heezik, 2014; Kenward, 2001). The challenge is that telemetry is the method that yields the data and at the same time it is the source of the impact. In Walker et al. (2012)'s review of the effects of marking and tagging methods on marine mammals, they call for more research under controlled conditions to examine the effects at a deeper level.

Despite the wide-spread use of collars, assessments of their impacts are rarely quantified. The mentioned studies above reporting no collar impact involved large animals (>50kg) where the telemetry collars constituted a small proportion of the body weight. Here I use an experimental setup to test for short-term behavioural effects of wearing telemetry collars on a medium-sized mammal, the red fox (*Vulpes vulpes*). To my knowledge there has been no previous published research on the red fox behavioural responses to telemetry collars, although telemetry collars have been used in many red fox studies. Because of the red foxes great presence and its influence on wildlife and ecosystems, many studies have used telemetry collars to track activity (Ables, 1969; Baker et al., 2007; Weber et al., 1994), movements (Towerton et al., 2016), survival (Gosselink et al., 2007), density and home range (Coman et al., 1991), interaction (Doncaster & Macdonald, 1997) and impacts and management (Saunders et al., 2010).

Red foxes are generalists and very adaptable to the environment which has allowed them to spread worldwide.
In order to be able to perform an experimental test of telemetry collar effects, we used captive silver foxes (*Vulpes vulpes*), which is a colour morph of the red fox. Using captive animals provides an opportunity for 24hour video surveillance, which make it possible to measure the foxes' circadian rhythm, behaviour and food intake. The most important advantage is the possibility to compare behaviour of collared and non-collared individuals, and thus provide available controls.

I hypothesized that wearing telemetry-collars will change red fox behaviour. Specifically, I test the following predictions:

◊ P1: Collared foxes exhibit a change in diel activity patterns compared with non-collared foxes by being less active during the usual active period (09-16).

◊ P2: Collared foxes will lower their weight gain compared with non-collared foxes.

◊ P3: Foxes wearing telemetry-collars will perform behaviour that indicates frustration and/or discomfort at a higher frequency than non-collared foxes.

2 Material and methods

The experiment was completed at the Norwegian University of Life Sciences (NMBU) research farm and lasted from 22th of November 2015 to 4th of February 2016. The experiment was approved by the Norwegian Animal Research Authority (ID 7803).

2.1 Study system

2.1.1 Animals and housing

A total of 16 silver foxes born and reared in the research farm participated in the experiment. The animals included 4 adult females (1-4 years old), 4 adult males (1-5 years old), 4 juvenile females (8-9 months old) and 4 juvenile males (8-9 months old) all originated from a standard commercial Norwegian line. Foxes were kept in individual standard plastic-coated wire mesh kennels (1.2 m × 0.76 m × 1.06 m). The kennels contained a wire mesh resting shelf, a wooden nest box and a chewable object (e.g. wooden block). They were also provided with a food tray and an automatic water system. The individual kennels were placed in a row of neighbouring kennels on both sides, and several rows with kennels facing each other (fig. 1). Kennels were located in a non-insulated barn which gave natural lighting and temperature. Foxes were inspected twice daily and were ad-lib fed once a day between 08.30 and 13.00 with standard food paste for fur animals.

Figure 1: The kennels where the foxes were kept, showing both neighbouring and facing kennels. Photo: Mona Kristiansen

2.2 Study design

2.2.1 The setup

The principle of the experimental setup followed a cross-over design, and thus each fox experienced treatment and control. Figure 2 provides an overview of the study design and shows how the 16 foxes were distributed over two bouts. Each bout lasted for two weeks and consisted of 8 foxes (4 females and 4 males). Bout 1 consisted of adult foxes (1-5 years old) and bout 2 of juvenile foxes (8-9 months old) to check if adult and juveniles were differently affected by wearing collars. Half of the foxes (n=4) were fitted with collars during the first week, and the other half during the second week. An example of a timeline for the experiment shown for one fox (id. 1) is given in figure 3.

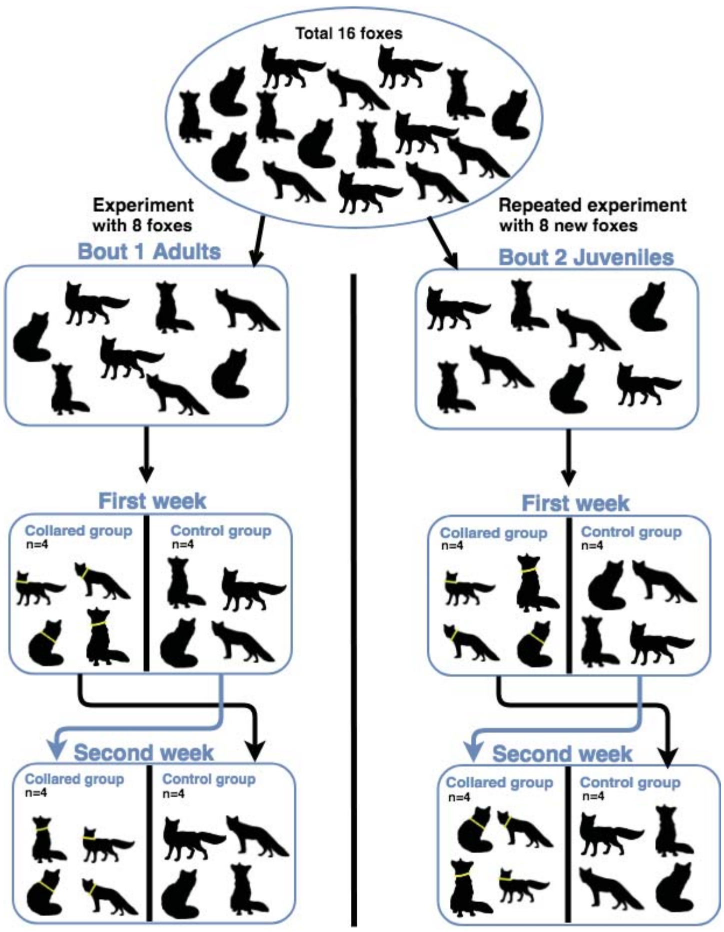

Figure 2: An illustration of the experimental setup and the distribution of the 16 foxes. Both bouts included 4 females and 4 males. Bout 1 consisted of adult foxes (1-5 years old) and bout 2 juvenile foxes (8-9 months old).

2.2.2 Handling and measurements

The foxes were handled in the beginning and at the end of each week (fig. 3). Handling refers to taking the foxes out of the kennels with a neck tong and gloves, attaching or removing the collar, measuring the weight and neck circumference and completion of a physical inspection which involves a check for potential injuries and the condition of the pelt.

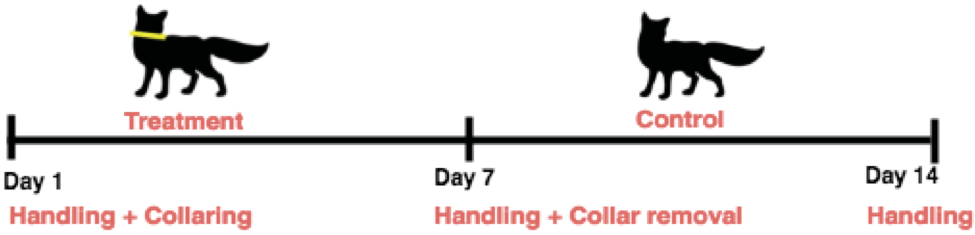

Figure 3: A timeline for the experiment with fox-id 1 as example. Handling refers to human handling and includes measures (weight, neck circumference) and collaring/collar removal. Fox 1 was part of bout 1 and collared during the first week.

2.3 Collar design

We fitted the foxes with dummy telemetry-collars consisting of the same dimensions and weight as commercial GPS-collars, but without functional GPS-system components. The dummy telemetry-collars were built with a BioThane® strap with an instrument case consisting of affixed epoxy moulded C battery attached (fig. 4). The collar was locked with a cable tie. All collars weighted between 130-140 g, constituting 1-2% of the foxes' body weight (the lightest fox weighted 6.5kg and the heaviest 11.1kg). The width of the strap was 2 cm, the length was 20 cm and the dimensions on the instrument case was 3cm x 5.5cm x 4cm (W x L x H).

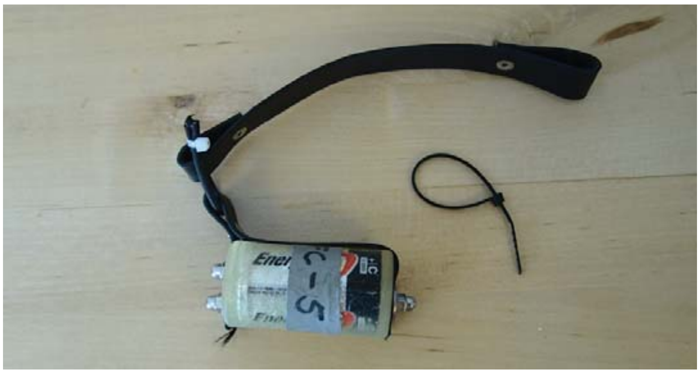

Figure 4: Example of a dummy telemetry-collar used in the study. The collars consisted of a BioThane® strap and affixed epoxy moulded C battery. The cable tie was used as a lock.

2.4 Data collection

The foxes were recorded throughout the experimental period by four H.R.R. CCD Cameras with arrays of infrared emitting diodes for recording during darkness. The cameras were set up to record two foxes simultaneously. Four weeks of video recordings were collected in total (672 hours), yielding over 330 hours of video for each fox. As I primarily focused on the days in the beginning and end of each week in both bouts when watching the videos, I extracted behaviour data from approximately 400 hours of videos in total. The videos were watched on a monitor showing all four cameras simultaneously, meaning that all 8 foxes were present in one screen.

Before measuring behaviour by watching the videos; the observation technique, recording rule and type of measure were established and defined by following the approach in Martin and Bateson (2007). The observation technique determines which individuals to watch and when, the recording rule specifies how the behaviour is recorded and the type of measure determines whether the behaviour should be recorded as frequencies, duration or both (Martin & Bateson, 2007). I used Solomon Coder version 17.03.22 (Péter, 2017), a programme that codes behaviour, to register the behaviours I observed.

2.4.1 Activity measures

Data regarding the foxes' circadian activity pattern (P1) were collected by recording if the foxes were active (standing, walking, running, jumping) or resting (sitting, laying). The recording rule was time sampling (observation at a fixed interval, every 10 minutes) and the observation technique was to observe all the 8 foxes simultaneously. That implies that every 10 minutes the behaviour (active/resting) of each individual at that moment was recorded (Martin & Bateson, 2007). I observed the foxes for 24-h the first and the fifth day of each week (fig. 5). This method measured the frequency of the behaviours, giving 145 sample points for each fox/24h. The observation started approximately 1 hour after handling on the first day to measure the acute responses to the collars and collar application. Ideally, one would make observations at the same time of day in all four weeks, but due to different handling times this was not always implemented.

Observations on the fifth day were made in order to investigate a potential acclimation to the collars. The reason why the observation was done on the fifth- and not on the sixth day, was because starting a 24-h observation on the sixth day meant that it would be finished on the seventh day (last day) and it was not always enough video material on that last day to complete a 24-h observation

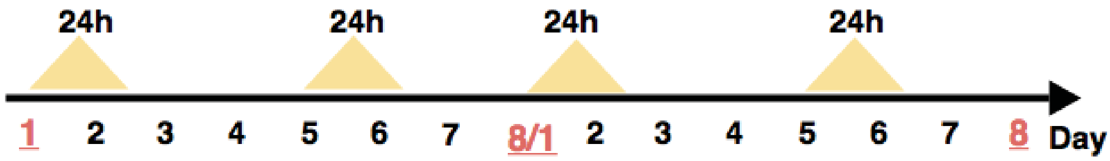

Figure 5: The observation periods regarding the foxes' activity. The days written in red refers to handling and includes measures (weight, neck circumference) and collaring/collar removal. The yellow triangles represent the observation periods.

2.4.2 Body mass measures

Weight measurements collected during handling provided the body mass data that was used to analyse a possible link between collars and weight (loss/gain) as predicted in P2.

2.4.3 Behaviour measures and considerations

To examine if the collars were causing the foxes to perform behaviour that indicates discomfort and/or frustration as predicted in P3, detailed behaviour were measured. Because the video resolution (quality) was low, especially during dark times (evening, night, early morning), I had to identify how detailed behaviour I was able to observe from the videos. I experienced that I was able to detect most behaviours despite the poor quality. However, some behaviours may be overlooked or mistaken. I excluded eating behaviour as I could not distinguish between if the foxes were eating, smelling, playing or just standing in front of the feeding tray. The grooming behaviours were also challenging to observe, and thus I recorded grooming behaviour as "assumed grooming" when the foxes performed head movements that appeared to be licking or pulling of the fur.

The behavioural events recorded are described in the ethogram (table 1). An ethogram is a description of behaviours that is typical for the species of interest (Martin & Bateson, 2007). It is a helpful tool when measuring behaviour because it defines the requirements for a behaviour to be measured as that specific event.
Since I wanted to examine behaviours that could indicate signs of discomfort or frustration, these behaviours had to be determined. Based on expert advice from A. L. Hovland (pers. comm.) and a literature review (see below), behaviours that could indicate discomfort or frustration in farmed foxes were set to be stereotypic behaviour, digging, rubbing, scratching, shaking and exaggerated grooming.

Stereotypic behaviour is traditionally defined as "repetitive and unvarying behaviour, with no obvious goal or function", and it is generally an indication of frustration as an animal struggles to perform its instinctive natural behaviour (Mason & Rushen, 2008). Digging may indicate frustration because it could be seen as an attempt of escaping not only from the kennel, but also from the situation. Increased rubbing, scratching and shaking behaviour could all indicate irritation, itching or attempts to get the collar off. Exaggerated grooming could indicate discomfort in terms of annoyance or increased awareness of something new interacting with the pelt.

To gather the behavioural data, the observation technique was to observe two foxes simultaneously, which meant that I had to watch the same video recordings four times to cover all the eight foxes. The reason for this was because it was difficult to observe detailed behaviour of eight foxes at the same time. The recording rule was continuous recording, meaning that foxes were observed continuously for a total of 60 minutes two times during the first and fifth day of the experiment (4h/fox totally). Whenever an interruption occurred (feeding, human presence etc.) a timeout was conducted, meaning that the observation stopped and did not start again until the interruption had passed.

Table 1: Ethogram of behaviours recorded during video observations regarding signs of discomfort. The recording type is specified for each behaviour.

Behaviour	**Description**	**Recording type**
Digging	Scratching or digging at any location in the kennel	Frequency
Stereotypic Pacing	Moving in a fixed, invariant pattern for more than three times in a row	Frequency
Rubbing	Rubbing or rolling the body against the wall or floor	Frequency
Scratching	Scratching in the head/neck region with hind or front legs	Frequency and duration
Shaking	Shaking the whole body or just the head	Frequency
Head twirls	Rolling the head backwards and up, often standing on two legs in one of the corners in the kennel	Frequency
Assumed grooming	Head movements looking like licking or pulling the fur	Frequency and duration

2.5 Statistical analysis

All analysis were done using the statistical software R version 3.4.3 (R Core Team, 2017).

2.5.1 Activity analysis

I prepared the activity data in Excel before analysing it in R. In the preparation, the proportion of day and night activity were extracted for each fox for each observation period (4*24h/bout). As the experiment was conducted during late fall/winter (November-February), “day” refers to the period between 09-16 (light hours), and “night” refers to the period between 16-09 (dark hours). The proportion of activity were extracted by adding together all sample points where the foxes were registered as active (standing, walking, running, jumping) between 09-16 (for day activity) and 16-09 (for night activity) and divide it on the total number of sample points (145). The data exploration (histogram and QQ-plots) and a Shapiro-Wilk test revealed that the day-activity-data could be normally distributed. Therefore, I fitted a linear mixed-effect model (LMM) to analyse a possible relationship between collars and day activity. I used the “nlme” package in R (Pinheiro et al., 2017) to fit the LMM, using proportion of day-activity as the response variable, treatment (collar/control), sex (male/female), day (first and fifth day since handling) and age (adult/juvenile) as fixed effects.

Fox-id was used as random effect to account for repeated measures. The function "stepAIC" from the R package "MASS" (Venables & Ripley, 2002) was used to run a backward model selection to determine the best model. This selection is based on the Akaike information criterion (AIC) values, selecting the model with the lowest AIC-value as the top model.

I used the "Overlap" package (Meredith & Ridout, 2017) in R to graphically explore the foxes activity patterns by fitting kernel density curves to the time when the foxes were registered as active (standing, walking, running, jumping). Before generating the graphic display, time-of-day was converted to radians by using the formula time*2*π, where time is a number between 0-1 and both 0 and 1 refers to midnight. The function "overlapPlot" fitted kernel density curves to the registered active times for both treatments (collared/control) for each fox in one plot, and shaded the area under the curves where the two distributions overlap (Meredith & Ridout, 2017). The Overlap package use a von Mises kernel density as it corresponds to a circular distribution (Meredith & Ridout, 2017). I followed Ridout and Linkie (2009) recommendations for small sample sizes ($n \leq 50$) and used a smoothing adjustment of 0.8 on the density plots.

2.5.2 Body mass analysis

The difference in body mass (in kg) were calculated by subtracting the foxes body weight (kg) at the end of the experimental week from the body weight (kg) in the beginning of the experimental week for both treatments (collar/control). To evaluate a possible relationship between collars and weight loss/gain I used the "nlme" package (Pinheiro et al., 2017) in R to fit a LMM. The weight difference (kg) were used as the response variable, treatment (collar/control), sex (male/female) and age (adult/juvenile) as fixed effects and fox-id as random effect. I conducted a Shapiro-Wilk test for normality on the residuals of this model. I used the function "stepAIC" from the R package "MASS" (Venables & Ripley, 2002) to run a backward model selection to determine the best model.

2.5.3 Behavioural analysis

The "glmmTMB" package in R (Brooks et al., 2017) were used to explore possible relationships between specific behaviours and treatments. The behavioural data consisted of many zeroes and followed a negative binomial distribution because of over-dispersion. The "glmmTMB" package allows fitting generalised linear mixed models (GLMM) for zero-inflated count data with negative binomial distributions (variance = $\varphi\mu$), using a log-link. All behaviours followed this distribution except duration of grooming which followed a different negative binomial distribution (variance = $\mu(1+\mu/k)$). I used specific behaviours described in table 1 (as counts or duration in sec) as the response variable, treatment (collar/control), sex (male/female) and day (first and fifth day since handling) as fixed effects and fox-id as random effect. The zero-inflation model use a logit-link, and the zero formula were set to ~1, indicating that all zero-counts have the same probability of belonging to the zero component (Brooks et al., 2017). The behaviours "pacing" and "head twirls" (table 1) were merged and analysed together as they both indicate stereotypic behaviour. I fitted and compared different candidate models for all the observed behaviours. AIC-values were used to select the best model. The most complex model included treatment, sex, day and their interactions as predictors.

3 Results

3.1 Activity

Following backward selection (based on AIC), the LMM with the variables treatment (collar/control) and day (first/fifth day since handling) appeared to be the best model predicting proportion of day activity. Day (fifth day since handling) had a significant negative effect on proportion of day-activity (β=-0.022, t=-3.107, $p<0.01$) indicating that the foxes were less active during daytime five days after handling than on the day they were handled. Treatment (collar) showed a negative relationship associated with proportion of day activity but was not statistically significant (β=-0.001, t=.0.171, p=0.865). Figure 6 graphically display the circadian activity patterns for all foxes (n=16) when they were collared and not-collared (control). The foxes activity was generally diurnal, with a peak around 12.00, and juveniles tended to be more active throughout the day than adults (fig. 6).

Table 2: Model coefficients for the top LMM on proportion of day activity. Treatment refers to collar/control and day refers to first/fifth day since handing. Random effect was fox-id to account for repeated measures.

LMM	Variable	β	SE	DF	t-value	p-value	
day.activity ~ treatment	(Intercept)	0.094	0.007	46	13.94	0.0000	***
+ day + (1|fox.id)	Treatment collared	-0.001	0.007	46	-0.171	0.8647	
	Day (fifth)	-0.022	0.007	46	-3.107	0.0032	**

Significance levels: * p<0.05, **p<0.01, ***P<0.001

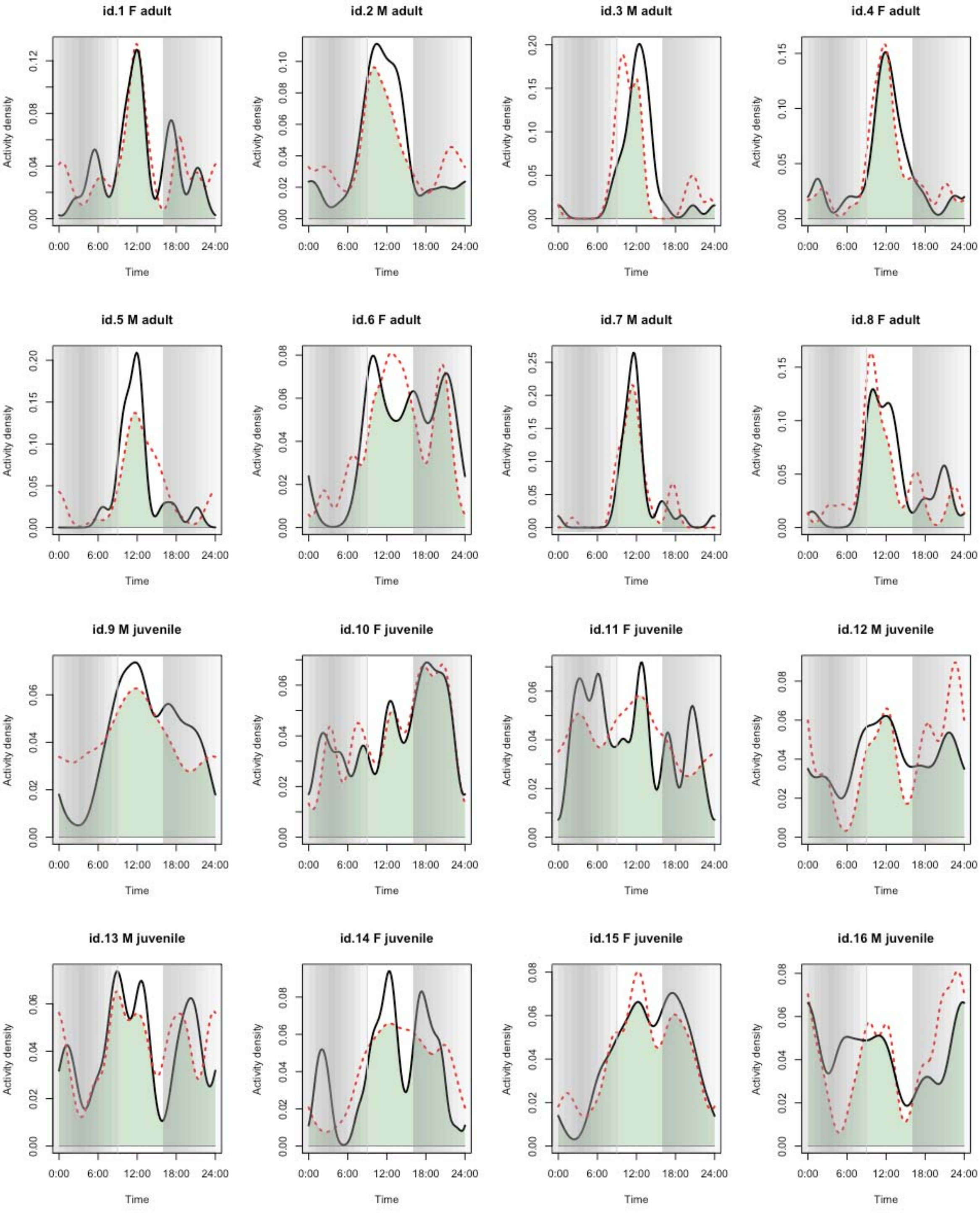

Figure 6: Overlap-plot of the circadian activity patterns for 16 captive foxes distributed over four sex-age categories (4 female (F) adults, 4 male (M) adults, 4 F juveniles, 4 M juveniles), when they were collared (dashed red line) and control (solid black line). The overlap in activity is displayed as the light green shaded area under the curves. The grey shaded area represents the time between sunset and sunrise (day: 09-16).

3.2 Body mass

The top LMM from the backward selection (based on AIC) for analysing difference in body mass included treatment (collar/control) and age (adult/juvenile) and the interaction term treatment*age as the predicted variables (table 2). Collars had a significant negative effect on difference in body mass (kg) (β=-0.868, t=-4.149, p=0.001). Age (juveniles) had also a significant negative effect on difference in body mass (kg) (β=-0.846, t=-4.047, p=0.001). The interaction between treatment (collar) and age (juvenile) had a positive effect on difference in body mass (kg) (β=1.005, t=3.399, p=0.004), indicating that the model predicts that an increase in age will enhance the effect of collars on body mass.

Table 2: Model coefficients for the top LMM on difference in weight. "Diff" refers to difference in weight (kg), treatment refers to collar/control and age adult/juvenile. Random effect was fox-id to account for repeated measures.

LMM	Variable	β	SE	DF	t-value	p-value	
diff ~ treatment*age	(Intercept)	0.702	0.148	14	4.752	0.0003	***
+ (1|fox.id)	Treatment collared	-0.868	0.209	14	-4.149	0.001	***
	Age juvenile	-0.846	0.209	14	-4.047	0.001	***
	Treatment *age	1.005	0.296	14	3.399	0.0043	**

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Adults experienced a higher increase in body mass when they were control (not-collared) compared to when they were collared, whereas juveniles experienced a stable weight for both treatments (collar/control) (fig. 7).

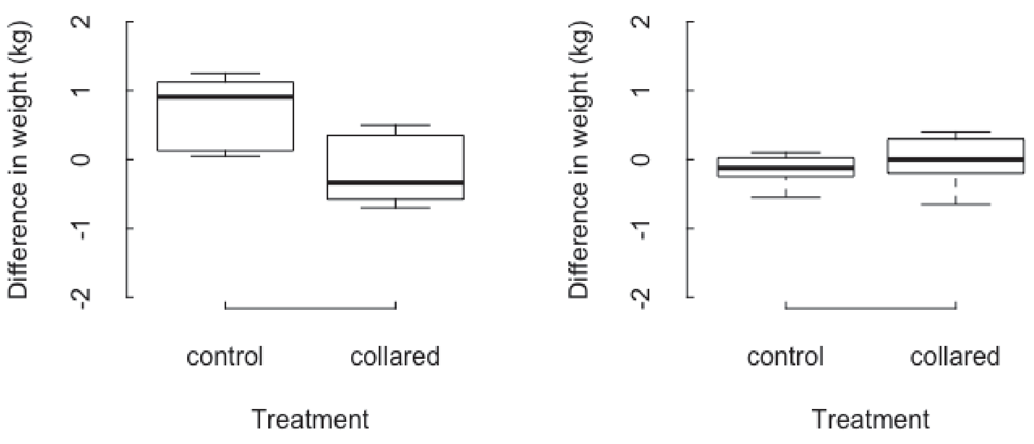

Figure 7: The change in weight (difference) in kg for 16 captive foxes distributed over four sex-age categories (4 F adults, 4 M adults, 4 F juvenile 4 M juveniles), when they were collared and control. Left plot displays adults and right plot displays juveniles. The data used in this plot is the real (observed) data.

3.3 Behaviour

The best GLMMs for specific behaviours were based on AIC, selecting the models with the lowest AIC-value (Bozdogan, 1987). If the AIC-values were less than 2 units apart, the model with the fewest explanatory variables were chosen as the best model (Bozdogan, 1987). The different candidate models with associated AIC-values for each specific behaviour is given in the appendix (table S1-S8).

Rubbing

For frequencies of rubbing behaviour, the top GLMM included the covariates treatment (collar/control) and day (first/fifth day since handling) (table S1). Collars had a significant positive effect (β=1.5682, z=-4.18, p<0.01) whereas day since handling had a significant negative effect (β=-1.2962, z=-3.71, p<0.01) on the frequency of rubbing behaviour (table 3). This indicates that the foxes performed more rubbing behaviour when they were collared vs. when they were not collared, and that rubbing behaviour decreased as time passed, indicating acclimation to the collar (table 3).

Table 3: Model coefficients for the top GLMM with negative binomial distribution on frequencies of rubbing behaviour: rubbing ~ treatment + day + (1|fox.id), ziformula~1. Treatment refers to collar/control and day refers to first/fifth day since handling. Random effect was fox.id to account for repeated measures.

	β	SE	z value	Pr(>|z|)	
Conditional model:					
(Intercept)	0.4858	0.4938	4.16	0.391810	
Treatment collared	1.5682	0.3752	-4.18	2.92e-05	***
Day	-1.2962	0.3498	-3.71	0.000211	***
Zero-inflated model:					
(Intercept)	-17.75	7106.5	-0.002	0.998	

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Shaking

For frequencies of shaking behaviour, the top GLMM included the covariates treatment (collar/control) and day (first/fifth day since handling) (table S2). Wearing a collar had a significant positive effect (β=0.6036, z=3.959, p<0.01) whereas day had a significant negative effect (β=-0.3527, z=-2.41, p=0.01596) (table 4). This indicates that the foxes performed more shaking behaviour when they wore a collar, and that shaking behaviour decreased over time, indicating acclimation to the collar (table 4).

Table 4: Model coefficients for the top GLMM with negative binomial distribution on frequencies of shaking behaviour: shaking ~ treatment + day + (1|fox.id), ziformula~1. Treatment refers to collar/control, day refers to first/fifth day since handling. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	1.0119	0.2739	3.695	2.20e-04	***
Treatment Collared	0.6035	0.1524	3.959	7.52e-05	***
Day	-0.3527	0.1463	-2.41	0.01596	*
Zero-inflated model:					
(Intercept)	-2.3097	0.5198	-4.443	8.86E-06	***

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Stereotypic behaviour

The best GLMM for frequencies of stereotypic behaviour (pacing and head twirls) included the covariates treatment (collar/control) and day (first/fifth day since handling) (table S3). Only day had a significant effect on stereotypic behaviour (β=-6.4404, z=-3.76, p<0.01), showing a negative effect indicating that foxes performed less stereotypic behaviour five days after handling compared to the first day of handling (table 5).

Table 5: Model coefficients for the top GLMM with negative binomial distribution on frequencies of stereotypic behaviour: stereotypic ~ treatment + day + (1|fox.id). Treatment refers to collar/control, day refers to first/fifth day since handling. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	2.40846	0.39116	6.157	7.40e-10	***
Treatment Collared	-0.01184	0.17156	-0.069	0.94496	
Day	-6.4404	0.17129	-3.76	1.70e-04	***
Zero-inflated model:					
(Intercept)	-3.476	1.004	-3.461	5.39e-04	***

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Scratching, grooming and digging

The top GLMMs for frequencies of scratching, grooming and digging included only the covariate treatment (collar/control) (table S4-S6). Treatment (collar) had a positive relationship associated with scratching behaviour, however this was not significant (β=0. 2979, z=0.967, p=0.334) (table 6). Treatment (collar) had a significant negative effect on grooming behaviour (β=-0.3036, z=-2.317, p=0.02) which indicate that the foxes groomed more when they were not wearing a collar (table 7). Treatment (collar) showed a positive relationship on digging behaviour, however, this was not statistically significant (β=0.407, z=1.017, p=0.309) (table 8).

Table 6: Model coefficients for the top GLMM with negative binomial distribution on frequencies of scratching behavior: scratching ~ treatment + (1|fox.id). Treatment refers to collar/control. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	-0.1011	0.3551	-0.285	0.776	
Treatment Collared	0.2979	0.3081	0.967	0.334	
Zero-inflated model:					
(Intercept)	-2.344	1.855	-1.264	0.206	

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Table 7: Model coefficients for the top GLMM with negative binomial distribution on frequencies of grooming behaviour: grooming ~ treatment + (1|fox.id), ziformula~1.Treatment refers to collar/control. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
Intercept	1.2069	0.1965	6.141	8.19e-10	***
Treatment Collared	-0.3036	0.1311	-2.317	2.05e-02	*
Zero-inflated model:					
Intercept	-2.3811	0.5233	-4.55	5.37e-06	***

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Table 8: Model coefficients for the top GLMM with negative binomial distribution for frequencies of digging behavior: digging ~ treatment + (1|fox.id). Treatment refers to collar/control. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	-1.222	0.6165	-1.982	0.0474	*
Treatment Collared	0.407	0.3997	1.017	0.3092	
Zero-inflated model:					
(Intercept)	-1.397	2.355	-0.593	0.553	

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Duration scratching and grooming

The top GLMMs for the duration of scratching and grooming behaviour (in sec.) included only the covariate treatment (table S7-S8). Treatment (collar) had a negative relationship associated with duration of scratching behaviour, but this was not statistically significant (β=-0.05, z=-0.263, p=0.793) (table 9). Treatment (collar) had a negative relationship associated with duration of grooming behaviour, however, this was not statistically significant (β=-0.18, z=-5.68, p=0.331) (table 10).

Table 9: Model coefficients for the top GLMM with negative binomial distribution on duration (in sec.) of scratching behavior: sec. scratching ~ treatment + (1|fox.id). Treatment refers to collar/control. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	4.0316	0.207	19.475	<2e-16	***
Treatment Collared	-0.0534	0.203	-0.263	0.793	
Zero-inflated model:					
(Intercept)	0.1307	0.1812	0.722	0.47	

Significance levels: * p<0.05, **p<0.01, ***P<0.001

Table 10: Model coefficients for the top GLMM with negative binomial distribution (variance=μ(1 + μ/k)) on duration (in sec.) of grooming behavior: sec. grooming ~ treatment + (1|fox.id). Treatment refers to collar/control. Random effect was fox.id to account for repeated measures.

	β	**SE**	**z value**	**Pr(>|z|)**	
Conditional model:					
(Intercept)	5.2249	0.1655	31.586	<2e-16	***
Treatment Collared	-0.1810	0.1862	-0.972	0.331	
Zero-inflated model:					
(Intercept)	-1.1937	0.2104	-5.675	1.39e-08	***

Significance levels: * p<0.05, **p<0.01, ***P<0.001

4 Discussion

As hypothesised, my experimental study revealed distinct behavioural effects in red foxes as a result of wearing telemetry collars. I found that collars caused discomfort as collared foxes had a significant increase in performance of the behaviours “rubbing” and “shaking”. In addition, collared foxes lowered their weight gain compared to non-collared foxes, and adults were found to be more affected by collars than juveniles. The behavioural effects caused by collars were found to diminish over time, indicating an acclimation to the collars.

4.1 Activity

I found no considerable change in proportion of day activity caused by collars. This is inconsistent with prediction P1. Wild-living red foxes are categorized as crepuscular animals, with a nocturnal tendency in human areas (Ables, 1969; Baker et al., 2007). I observed that the foxes in this study were mainly active during light hours (09-16). This observation is in accordance with previous findings on activity patterns for farmed foxes (Korhonen & Niemela, 1998). My result corresponds with what Durnin et al. (2004) found on the activity levels of giant panda, as they observed that collared and non-collared pandas were equally likely to be active, and their activity levels did not change post collaring.

Both this present study and Durnin et al. (2004) panda study included animals living in captivity, where the movement range was restricted, and human presence occurred daily. In addition, the movements or sounds made by neighbouring foxes could impact the other foxes activity. Hawkins (2003) highlights that wild animals may experience additional stress due to capture and human handling, and hence lead to a greater response to collars. Although the foxes in my study was habituated to humans, handling seemed to have an impact on the foxes as I observed a significant negative effect of “day”, indicating that the foxes were more active on the day they got handled than five days after handling. When I watched the videos, I observed that the foxes became more active, agitated and performed more stereotypic behaviours in presence of humans, regardless of whether they were wearing a collar or not (this behaviour was not included in the statistical analysis as I conducted a “timeout” whenever humans were present). Dennis and Shah (2012) observed that collared common brushtail possums were less active the first few days after handling and tagging. The authors explain this to be caused by a stress-response and mild myopathy (disorder of muscle tissue) not only from wearing a collar, but also from being trapped and handled (Dennis & Shah, 2012).

The restricted movement range may be one of the reasons why I did not observe a collar-effect on activity. Collars have previously shown to affect activity in other animals, including house cat (*Felis catus*) and common zebra (*Equus burchelli antiquorum*), where both cat and zebra reduced their travel rate when wearing collars (Brooks et al., 2008; Coughlin & van Heezik, 2014).

4.2 Body mass

My findings are consistent with prediction P2 as the foxes gained less weight when they were collared compared to when they were not-collared (control). Surprisingly, it was the adult foxes that experienced both the greatest loss (when collared) and the greatest gain (when control) in body mass (in kg) during the 2-weeks of experimental period, and not the growing juvenile foxes. The body mass of the juvenile foxes remained relatively stable during the experiment. My findings suggest that adult foxes experience a greater impact of collars than juvenile foxes. A reason for that could conceivably be that younger foxes are more adaptable to changes, and thus less affected by collars. However, Cypher (1997) observed that juvenile San Joaquin kit foxes (*Vulpes macrotis mutica*) experienced a decrease in body mass shortly after collaring, possibly due to the juveniles’ small size and inexperience (Cypher, 1997).

Other studies have revealed similar effects of collars on body mass. Legagneux et al. (2013) experienced that presence of neck collars had a negative effect on body condition of female Greater Snow Geese (*Chen caerulescens atlantica).* Godfrey et al. (2003) observed that wearing radio-telemetry increased the daily energy costs by 8.5% in Takahe (*Porphyrio mantelli)*, and Tuyttens et al. (2002) found that badgers (*Meles meles*) who had worn a collar for about three months had a higher probability to have a low body condition compared to non-collared badgers. Lower foraging efficiency, less appetite, higher energetic expense in terms of increased applied weight or chronic stress have been suggested to be possible impacts on body mass related to telemetry collars (Cypher, 1997; Godfrey et al., 2003; Legagneux et al., 2013). However, no impacts of collars were found on foraging efficiency in wild meerkats (*Suricata suricatta)* (Golabek et al., 2008), and collared cheetahs were found to have the same food intake and spending the same amount of time on feeding as non-collared cheetahs (Laurenson & Caro, 1994).

Since captive animals are being fed, telemetry collars will not affect foraging efficiency. However, less appetite or higher energetic expense as a response of extra weight or chronic stress may be a concern when using collars on captive animals (Cypher, 1997; Osborne et al., 1997). In a study on effects of radio-tags on captive Northern Bobwhite *(Colinus virginianus),* tagged birds were observed to have significantly lower body mass than the control birds, assumed to be caused by stress or higher energetic expense (Osborne et al., 1997). Although, these authors used telemetry-backpacks and not collars in that study, the result could be relevant for impacts of collars as the backpacks also adds extra weight and they were fastened with a line around the animals neck (Osborne et al., 1997).

4.3 Behaviour

I observed a significant effect of collars on the behaviours “rubbing”, “shaking” and “grooming”. Both rubbing and shaking are behaviours that are signs of discomfort as they may indicate irritation, itching and attempt of collar removal. Rubbing and shaking behaviour showed a significant decrease as time passed, indicating that the foxes experienced an acclimation to the collars. The significant effect on grooming behaviour showed that non-collared foxes performed a greater number of grooms (frequency) than collared foxes. However, no significant effect was found on the duration of grooming. This result was contrary to the findings by Rachlow et al. (2014) who observed that the frequency of grooming behaviour in collared pygmy rabbits (*Brachylagus idahoensis*) was more than three times higher compared to non-collared rabbits.

However, as previously mentioned, grooming was the behaviour that was most challenging to observe from the videos, and thus this result may not be reliable.

I found no significant effect of collars on scratching behaviour, either on frequency or duration. Nussberger and Ingold (2006) found that collared alpine chamois (*Rupicapra rupicapra rupicapra*) scratched twice as much as non-collared animals and explains this to be caused by irritation in terms of moisture or physical rubbing of the collar. However, their result was not significant as scratching represented a minor proportion of the time-budget. I found no significant effect of collars on stereotypic behaviour (pacing and head twirls). This results is consistent with what Durnin et al. (2004) experienced as they observed no significant effects of collars on stereotypic behaviour on giant panda. Horback et al. (2012) observed no differences in behaviour between collared and non-collared African Elephant at the San Diego Zoo Safari Park.

4.4 Implications for animal welfare and wildlife research

Animal welfare is a broad term including multiple different definitions. Dawkins (2006) describes good animal welfare as good physical health, and positive emotions, meaning that the animals are not experiencing fear and frustration. Broom (1991) considers signs of poor animal welfare to include lower survival or growth, failed or reduced reproduction, physical damage and disease. Although I found that collars caused discomfort and lower weight gain, the collar-effect diminished relatively fast after attachment. My findings on telemetry-collar-impacts could be caused by stress related to attachment and/or physical influence in terms of bad fit or skin irritation (Millspaugh et al., 2012; Morton et al., 2003). As good animal welfare is essential for good science (Morton et al., 2003), scientists should always establish potential complications and consequences associated with telemetry before doing research (Hawkins, 2003). Millspaugh et al. (2012) suggest creating a pilot project where researchers could measure the impact of their collars and attachment technique on their study animal, so that it could be adjusted to have a minimizing effect in the real study. Studies including telemetry tools should strive to minimize collar impact in terms of the shape, fit and mass of the collar, and follow the exciting guidelines (Macdonald, 1978). However, collar impacts were observed in this study although we used collars weighing 1-2% of the foxes body mass, which is within the general rule for collar weight (3-5%) (Macdonald, 1978).

4.5 Limitations of the study

This present study was limited by a short monitoring period (two weeks) and hence, possible long-term effects of telemetry-collars could not be investigated. In addition, the approach in this experiment, using captive-raised and not free-ranging foxes, did not provide data on how collars affect dispersal, habitat use, interaction and reproduction behaviour. It is therefore important to be aware of this when using telemetry-collars on wild red foxes. In my study system where all foxes were housed together, the foxes could influence each other's behaviour and thus cause inaccurate results of collar-impact. To avoid this, the foxes should have been tested in isolation. Some limitations regarding the study design, was that the foxes served as control immediately after collar removal and this could possibly bias the control behaviour as the foxes were experiencing a new state (non-collared). This could be avoided by adding an acclimation period between the two experimental weeks or treat all foxes as control the first week. Additionally, juveniles and adults should have been mixed in the two study sections to avoid confounding with time/season. The foxes body mass (weight in kg) could have been included as a variable in the behavioural GLMM to investigate if the collars had a greater impact on the lightest foxes compared to the heavier foxes.

4.6 Future research

Future research should explore wild foxes' behavioural responses to telemetry-collars in order to form a more thorough understanding of collar impact on red fox behaviour. The monitoring period should also be extended to consider possible long-term effects.
Lastly, I suggest that future wild-life studies in general, always consider possible effects of collars, and preferably test the impacts on their study species if that has not previously been done.

5 Conclusion

Telemetry-tools has become one of the most useful approach for wildlife research because it provides the opportunity to gather important biological information remotely and at a global scale (Millspaugh et al., 2012). This study of red fox behavioural responses to telemetry-collars revealed that lower weight gain and increased performance of behaviours indicating discomfort were consequences of wearing telemetry-collars. The behavioural effects of collars were found to decrease only four days after collar-attachment, suggesting a temporary, acute effect of collars. My results emphasize the importance of understanding the possible effects related to collars on wildlife, both for animal welfare reasons and for good science. I strongly recommend some precautions before attaching telemetry-collars on wild red foxes and wildlife in general. I suggest that researchers follow the guidance that Hawkins (2003) have provided on how to optimize the use of telemetry tools in the name of animal welfare and good science. Instead of assuming that telemetry-collars have no impact, the assumption should be that they do, and the goal should be to minimize that impact by optimising the collar design and the experimental setup. The lack of consensus of collar impact on wildlife calls for more research on this topic. Preferably, animal-specific collar guidelines in terms of shape, mass and fit should receive more attention.

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7 Appendix

Table S1: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **rubbing** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex * day	11	8.3	293.8
Treatment * day + sex	8	4	289.4
Treatment * day	7	2	287.5
Treatment + day + sex	7	2	287.4
Treatment + day	**6**	**0**	**285.5**
Treatment	5	13.4	298.9
Treatment * sex	7	16.9	302.3

Table S2: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **shaking** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex * day	11	7.6	518.2
Treatment * day + sex	8	2.8	513.4
Treatment * day	7	1.6	512.2
Treatment + day + sex	7	1.2	511.8
Treatment + day	**6**	**0**	**510.6**
Treatment	5	3.7	514.3
Treatment * sex	7	6.8	517.4
Treatment + sex	6	4.9	515.5

Table S3: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **stereotypic** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex * day	11	5.5	667.2
Treatment * day + sex	8	3.7	665.4
Treatment * day	7	2	663.7
Treatment + day + sex	7	1.7	663.4
Treatment + day	**6**	**0**	**661.7**
Treatment	5	11.7	673.4
Treatment * sex	7	12.8	674.4
Treatment + sex	6	13.4	675.1

Table S4: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **scratching** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex *day	11	7.9	390.2
Treatment * day + sex	8	3.9	386.1
Treatment * day	7	1.9	384.2
Treatment + day + sex	7	2	384.2
Treatment + day	6	0	382.2
Treatment	**5**	**1.5**	**383.8**
Treatment * sex	7	3.4	385.6
Treatment + sex	6	3.5	385.8

Table S5: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **grooming** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex * day	11	9	576.2
Treatment * day + sex	8	5.7	572.8
Treatment * day	7	3.9	571.1
Treatment + day + sex	7	3.7	570.9
Treatment + day	6	2	569.1
Treatment	**5**	**0**	**567.2**
Treatment * sex	7	2	569.2
Treatment + sex	6	1.8	568.9

Table S6: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for frequency of **digging** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	df	dAIC	AIC
Treatment * sex * day	11	8.1	212.5546
Treatment * day + sex	8	3.5	207.9651
Treatment * day	7	4.3	208.7476
Treatment + day + sex	7	1.5	205.9844
Treatment + day	6	2.3	206.7554
Treatment	**5**	**0.9**	**205.3629**
Treatment * sex	7	2.0	206.457
Treatment + sex	6	0	204.4635

Table S7: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for duration of **scratching** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	**df**	**dAIC**	**AIC**
Treatment * sex * day	11	7.1	792.3
Treatment * day + sex	8	1.8	787.0
Treatment * day	7	0.3	785.5
Treatment + day + sex	7	2.8	787.9
Treatment + day	6	1.5	786.7
Treatment	**5**	**0**	**785.2**
Treatment * sex	7	3.3	788.4

Table S8: Akaike's Information Criterion (AIC) model selection of GLMM with negative binomial distribution for duration of **grooming** behaviour. "Treatment" refers to collared/control, "day" refers to first or fifth day of the experiment. Delta AIC (dAIC) is the difference between the candidate model and the best model. The selected model is shown in bold.

Variables	**df**	**dAIC**	**AIC**
Treatment * sex * day	11	9.9	1373.6
Treatment * day + sex	8	4.5	1368.2
Treatment * day	7	2.9	1366.6
Treatment + day + sex	7	3.5	1367.1
Treatment + day	6	1.8	1365.5
Treatment	**5**	**0**	**1363.7**
Treatment * sex	7	3.5	1367.2
Treatment + sex	6	1.6	1365.3

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