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Master thesis

Short term effects of capture on movements in free-ranging wolves (*Canis lupus*) in Scandinavia

Master in Applied Ecology

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Abstract

Remote monitoring of wild animals by radio-tags and bio-sensors is frequently applied in wildlife research, monitoring and management. These methods require capture and often anaesthesia of animals that in turn may affect post-capture behaviour. Assessment of post-capture effects is needed to avoid biases in the research data due to capture-related effect on behaviour, but also to measure unnecessary discomfort and suffering for the animals.

The Scandinavian wolf population has since its reappearance in the 1980´s been the subject to many studies, and the first wolves were radio collared in 1999. Between 1998 and 2015 several wolves have been captured in Scandinavia. For this study I used hourly GPS positions during the first 100 hours from 25 wolves chemically immobilized between 2001 and 2015. I examined how the cumulative post-capture movement was related to the intrinsic variables sex, body mass and social status, and to capture-related variables, number of captures, pursuit time and the type and dose of drugs used.

Sex was the most important factor explaining patterns of post-capture movement. Males had a higher movement rate than females between the release and 23 hours post capture. Body mass was correlated with sex and was positively related to sex-specific movement rates. Contrary to my initial predictions, medetomidine given as an additional tranquilizer during handling increased the movement rate after capture. I also found weak relationships between movement rate and the time the wolf was chased by helicopter prior the immobilisation, and between movement rate and drug doses. The small sample size however limits the inferences that can be drawn from these models.

I conclude that capture-related factors can induce differences in post-capture movements of wolves, and that sex is an important predictor of post-capture movement patterns.

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Introduction

Studying free-ranging animals in their natural habitats using GPS (Global Positioning System), telemetry devices, or bio-logging implants is a frequently used approach (Jedrzejewski et al. 2001; Sand et al. 2005) all over the world (Creel et al. 1997; Walton et al. 2001). Deployment of these devices usually requires invasive interventions, such as chemical or physical immobilization of the animal, surgical implantation of sensors, or attaching foreign objects such as collars (Seddon et al. 2005). Important factors to be considered when choosing a method are practicality, accuracy and the risk of biased results, as well as benefits, costs and the ethical perspectives (Haulton et al. 2001; Schemnitz et al. 2009). The benefits of invasive methods is that these devices can be an important tool to understand spatial information of individuals, populations or species, ecological functions, behaviour, interactions or population dynamics (Creel et al. 1997; Ropert-Coudert & Wilson 2005; Mattisson et al. 2013).

However, capture and attached devices may cause various degrees of stress and trauma and may alter behavior and physiology of the studied individual leading to biased results (Arnemo et al. 2006; Cattet et al. 2008; Omsjoe et al. 2009). According to the "Three R's", Replacement, Reduction and Refinement, the principle of ethical evaluation of animal use, all capture-events and secondary effects of capture and handling, should be evaluated to strive for improvement and a minimal negative impact on wild animals (Arnemo et al. 2006; Schemnitz et al. 2009; Lindsjö et al. 2016).

The effect of the capture depend both on the capture method and the anaesthetic protocol used. Reversible drugs have a short recovery period while non reversible drugs take longer to eliminate, hence results in a prolonged recovery (Arnemo et al. 2013). Negative effects such as

physical trauma from the impact of the dart used for immobilization, or from the chase or trapping have been shown in wildlife species (Arnemo et al. 2006).

Hyperthermia and hypothermia are physiological alterations that may potentially appear due to the capture-event (Fahlman et al. 2008; Kreeger & Arnemo, 2012). Hyperthermia (increase of body temperature above the normal range for the species) can be consequence of extreme physical exercise or stress when for example being chased by helicopter and increases metabolism and oxygen demands. Anaesthetic drugs tend to cause respiratory depression that might lead to hypoxemia (inadequate, decreased oxygen levels in the blood), causing a demand of supplemental oxygen (Fahlman et al. 2008; Kreeger & Arnemo, 2012). Increases in body temperature may further decrease oxygen levels of an already compromised animal (Fahlman et al. 2008; Kreeger & Arnemo, 2012). Hypothermia on the other hand is a decrease in body temperature that can be drug induced, due to low ambient temperatures, a lack of insulation due to wet fur, misplacing the animal on a cold surface or due to the animals body condition (Kreeger & Arnemo, 2012). These effects are physiologically challenging for the animal and can lead to multi organ failure, long term effects such as brain damage and death (Fahlman et al. 2008; Spraker, 1993),

Additional effects previously shown to be caused by capture or handling have been lower reproduction success, more frequently abandoned offspring (Côté et. al 1998), changes in body condition (Cattet et al. 2008), increased mortality (Arnemo et al. 2006) and altered movement (Cattet et al. 2008; Neumann et al. 2011). The movement pattern of an animal is depending on demographic traits (Walton et al. 2001), or environmental factors such as prey density or temporal variation (Mattisson et al. 2013), but can also be altered by a capture-event. Grizzly bears *(Ursus arctos)* and American black bears (*Ursus americanus*) showed a decreased movement

pattern up to 6 weeks after capture and a difference between sexes (Cattet et al. 2008). Studying moose (*Alces alces*), Neumann et al. (2011) concluded that during the first 5 days after capture data should be excluded from analysis due to spatial displacement. Dechen-Quinn et al. (2012) saw that white tailed deer (*Odocoileus virginianus*) needed up to 14 days after capture to recover to average movement.

The wolf (*Canis lupus*) population in Scandinavia is located in central Sweden and south-eastern Norway. The wolf was regarded as functionally extinct in Scandinavia until 1983 when the first reproduction by two wolves from the Finnish Russian population was confirmed (Vilà et al. 2003; Liberg et al. 2005; Wabakken et al. 2001). By 2015, the population has increased to an estimated size of 460 individuals (Svensson et al. 2015). Severe inbreeding depression has been documented due to only five Finnish-Russian wolves which genetically contributed to this population (Liberg et al. 2005). The increasing population has met human conflicts due to predation on domesticated and semi domesticated animals and competition for game (Sand et al. 2010; Sjölander-Lindqvist, 2008). Spatial information and movement of the Scandinavian wolf population has been useful in many studies exploring e.g. territory size, distribution and predatory behaviour (Mattisson et al. 2013; Zimmermann et al. 2014; Zimmermann et al. 2015).

In a long term joint Scandinavian research project these conflicts, inbreeding effects, and the ecological roles of the wolf in Scandinavia have been studied, with capture as an important tool to attach various types of collars to individuals (Rovdata, 2016).

Between 1998 and 2015, wolves were captured by darting from helicopter and equipped with VHF or GPS collars (Sand et al. 2010). Darting from a helicopter is a stressful way of capturing

free ranging animals (Omsjoe et al. 2009) and could cause both physical and behavioural short and long term effects. Recovery time and other potential effects of these capture-events have not been analysed. Tiletamine-zolazepam (TZ, Zoletil® 500 mg/vial, Virbac, Carros, France) is the drug combination used to immobilize wolves in Scandinavia. TZ produces a reliable anaesthesia in wolves, has a wide safety margin, and causes minimal depression of the cardiovascular and respiratory system. However, TZ cannot be antagonized leading to prolonged recoveries (Arnemo et al. 2013).

Due to previous studies of different capture effects on animal behavior, and to the extensive captures of Scandinavian wolves between 1998 and 2015, this study aims at analysing the movement pattern among a sample of captured free-ranging Scandinavian wolves.

Predictions and research questions

According to other studies biological factors could induce individual differences in post-capture movement patterns (Cattet et al. 2008). Hence the prediction would be that, 1) Intrinsic factors such as sex, social status and weight influence movement patterns after capture-events. Naïve animals, captured the first-time, are predicted to have less pursuit time (Arnemo et al. 2012). Longer pursuit time by itself or in combination with a higher initial body temperature (Cattet et al. 2003) as a sign of hyperthermia (Fahlman et al. 2008), leads to exhaust animals and could alter movements during recovery (Omsjoe et al. 2009). Thus, 2) Recaptured individuals differ in their post-capture movement pattern from first-time captured individuals, and pursuit time and increased body temperature inflict changes in cumulative distance post-capture.

All wolves are darted with a standard dose and a larger dose for equal body weight is assumed to cause a longer lasting effect, hence less distance travelled during the first 100 hours after capture. An additional tranquilizer (medetomidine) given during handling is assumed due to field observations to prolong recovery and decrease movement rate. The predictions are that, 3) Drug combination given in the dart and doses, as well as the effect of additional medetomidine causes different movement rates post-capture.

Material and methods

Study area

The reproducing Scandinavian wolf population is distributed throughout the south-central parts of Sweden and Norway (59°-62°N, 11°-19°E) (Figure 1). Human density within the wolf population range averages 16 per km^2, although large parts are below 1 inhabitant per km_2 (Wabakken et al. 2001). The area is covered by boreal forests, wet lands and alpine tundra. Agricultural areas are primarily found in the southern parts of the wolf distribution range (Wabakken et al. 2001). The boreal forest consists of Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*), birch (*Betula pubescens* and *B. pendula*), aspen (*Populous tremula*), alder (*Alnus incana* and *A. glutinosa*), blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*). Forest roads are numerous due to extensive forest management (Zimmermann et al. 2014).

The landscape varies from flat to mountainous, with a maximum height of 1800 meters above sea level. Winter temperatures span from -5 to -15 °C, and snow is covering the ground from December to March with an average maximum snow depth of 30 to 90 cm (Zimmerman et al. 2014).

Wolves in Scandinavia relay mostly on moose (*Alces alces*) and roe deer (*Capreolus capreolus*) as their most important prey species but they do also prey on beaver *(Castor fiber)*, red deer (*Cervhus elaphus*), wild reindeer (*Rangifer rangifer)* in Norway, and semi domesticated reindeer in the northern parts of both Sweden and Norway. Additionally they also prey on

mountain hare *(Lepus timidus)*, black grouse (*Tetrao tetrix)* and capercaillie (*Tetrao urogallus*) (Wabakken et al. 2001; Sand et al. 2005; Gervasi et al. 2012).

Individual wolf territory size in Scandinavia averages 1017 km^2 and spans from 259 km^2 to 1676 km2 (Mattisson et al. 2013).

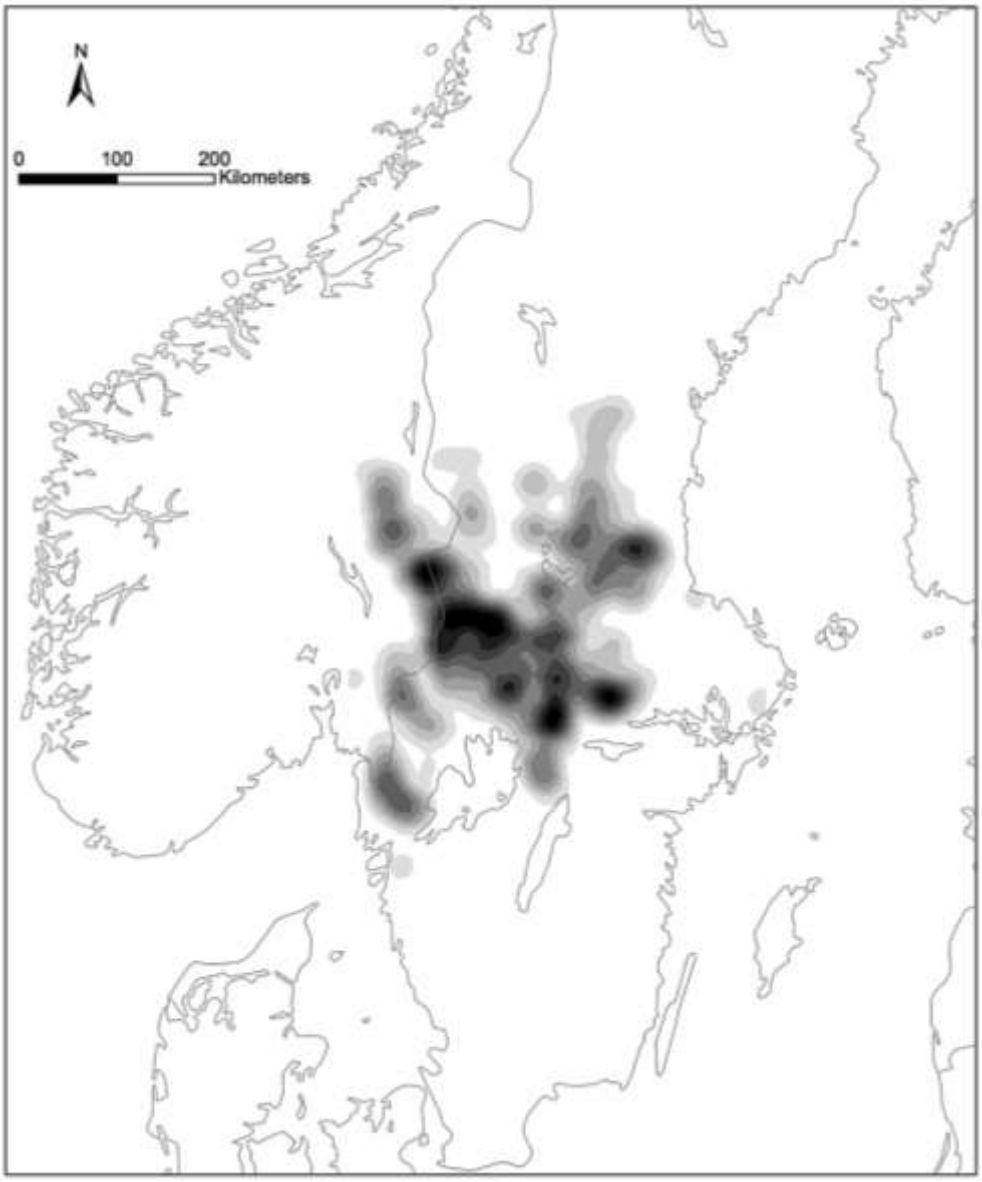

Figure 1. Spatial distribution of Scandinavian wolf territories detected during 2001-2015. A Kernel density estimation was computed on the centroid points of all spatial location available for each winter-territory. Colours from grey to black represent areas.

Intrinsic and capture related variables

For this study a total of 25 post-capture periods from 23 individual wolves from 16 different wolf territories have been analysed. Of the 25 individuals 12 were males and 13 females (Table 2).

The intrinsic information such as sex, weight, social status and initial rectal temperature were determined at capture-events. Captured wolves were grouped in to pups, yearlings or adults by tooth wear and by the growth zone on the radius and ulna (Gipson et al. 2000). In this study only adult animals (n=18) and pups (n=7) were included. All capture related information such as drug combination and doses, pursuit time, and first or second capture was retrieved from capture forms. The pursuit time was calculated in minutes, from the time the wolves have been first observed by the capture personal in the helicopter, to the time that the animal was laying down.

Capture-events

All wolves were darted using a CO_2 powered (Dan-Inject®) rifle from a helicopter in the winter months (December – March) between 2001 and 2015 as a part of a long-term joint Scandinavian research project following standard capture procedures (Arnemo et al. 2012). Deep soft snow is needed for tracking and for slowing the wolves down during the helicopter pursuit. The darts used in the study consisted of 3 ml syringes with 1.5x25mm barbed needles (Dan-Inject®). For three of the individuals a reversible drug combination (MKTZ), of 1.5 mg medetomidine (Zalopine® 10 mg/ml, Orion Pharma Animal Health, Turku, Finland), 100 mg ketamine (Narketan® 100 mg/ml, Chassot, Dublin, Ireland), and 50 mg tiletamine-zolazepam (Zoletil® 500 mg/vial, Virbac, Carros, France), was used. Today a combination of tiletamine-

zolazepam (TZ) is standard. Tiletamine is a dissociative anaesthetic, and zolazepam, a benzodiazepine. Dissociative anaesthetics cause's rough inductions, zolazepam which is a tranquilizer counteract the effect (Kreeger & Arnemo 2012; Arnemo et al. 2012). The doses for the captures ranged from 250 - 500 mg TZ per wolf (Arnemo et al. 2013), and 250 mg TZ is today a standard doses as it seems to be sufficient for most individuals. If this dose does not have an effect, a second dart with the same dose is distributed. The therapeutic index, i.e. the span between the agents causing an effect to overdose, is assumed to be large for TZ. Body weight cannot be assessed from the helicopter, thus the dose is the same for all body weights. Medetomidine (Domitor® 1 mg/ml, Orion), is a tranquilizer given additionally if the TZ effect is not sufficient, 0.5 mg if the anaesthesia is too light and 1 mg if the wolf was waking up. Medetomidine can be reversed with the antagonist atipamezole (Antisedan®, 5 mg/ml, Orion) (Kreeger & Arnemo, 2012).

The immobilized animals were positioned in lateral recumbency on an insulated blanket or on the snow if their rectal temperature was high. Eye gel was applied to the cornea to prevent them from drying, and the eyes were covered during the handling. All wolves were fitted with GPS collars and blood, hair and faecal sample were collected. During handling, temperature, heart rate and respiratory rate were monitored to prevent hypothermia, hyperthermia or insufficient ventilation (Arnemo et al. 2012). After wakening the wolves were monitored until they were considered stable, i.e. when walking relative steady. All the capture procedures were approved by the Swedish and Norwegian ethical committees (Swedish Animal Welfare Agency, Norwegian Experimental Animal Ethics committee).

GPS neck-collars

The GPS transmitters recorded positions at hourly intervals for 100 consecutive hours post capture. The schedule was then changed to suite other studies. The information was transmitted using SMS (Short Message System) through GSM (Global System for Mobile Communication). Transmitters were either Simplex® or Tellus® (Followit AB, Lindesberg, Sweden), or GPS-plus (Vectronic Aerospace, Berlin, Germany). The GPS data from each individual was retrieved as DBF or Excel files and sorted manually to initially three weeks after capture periods. Due to a lack of data the final dataset consisted of positions up to 100 hours after capture. The frequency of positions varied according to the initial study and was in this study set to hourly positions. The first position determined as the position at the time of "getting up" according to capture protocols. Post-capture movements were calculated as the Euclidean cumulated distance per hour after capture (Calenge et al. 2009). Data preparation and alignment were performed in Microsoft ® Excel 2010® and R 3.2.2 R Core Team (2016).

Statistical modeling

I used Analysis of variance (ANOVA) to compare body weights between sexes and social status (adult or pup). To compare pursuit time of first versus second capture, I used a t-test. To relate body temperature to pursuit time, I applied a linear regression model. With linear mixed effect regression models (nlme, Pinheiro et al. 2015), I determined if the intrinsic factors sex, body weight and the capture related factors drug and dose, additional drugs, pursuit time, rectal temperature and recapture had an effect on the cumulative distance moved post-capture (Table 1). Cumulative distance requires a gamma distribution and generalized linear mixed models. However the models did not converge applying a gamma distribution hence linear mixed models were used, assuming a normal distribution. Wolf Id was set as a random

factor to account for dependency within individuals (Zuur et al. 2010). Model selection was done by Akaike Information Criteria (AICc) for small sample size (Mazerolle et al. 2011). AICc delta was accordingly Mazerolle (2011), set to a cut off at 4.

Table 1. Summary of the explanatory variables used in the linear mixed models to determine the factors influencing the movement patterns post-capture for wolves in Scandinavia.

Variable name	***Variable type***	***Definition***
Hour post-capture	Continuous	Hour after capture, from 0 to 100
Sex	Categorical	Male (1) or Female (0)
Body weight	Continuous	26 – 51 kg
Social status	Categorical	Pup (0) or Adult (1)
Initial rectal temperature	Continuous	Numerical value (°C). The initial rectal temperature at capture
Pursuit time	Continuous	Numerical value (minutes)
Drug combination and doses	Categorical	250 mg TZ (1), 500 mg TZ (2) or 255 mg MKTZ (3).
Additional medetomidine	Categorical	Additional medetomidine administered during handling (1) or not (0)
Recapture	Categorical	First-time capture (0) or recapture (1)

The number of explanatory variables used in the model were limited due to the low sample size (Babyak, 2004). As cumulative distance is a function of time, the number of hours after capture was included in all models. Correlation and confounding effects were explored using variance inflation factor (VIF) (Zuur et al. 2009). Outliers were considered using Cook´s dis-

tance and the final models were optically examined with residual plots for distribution goodness of fit (Zuur et al. 2010). Considering effects of intrinsic covariates there was a strong support for models where cumulative distance varied by sex over time. Sex and hour were therefore included in all models as an interaction. The null model included hour and wolf id as random factor. I included a limited number of explanatory variables in the models due to low sample size.

I constructed models to test the following hypotheses:

Intrinsic factors: Post-capture movements can be explained by intrinsic factors such as sex, social status and body weight assuming a lower movement rate and a larger effect of the standard dose for lighter individuals. I assumed that movement after capture differed between males and females due to sexual dimorphism in body weight. It is also assumed that different social status is a cause of variation in post-capture movements.

Recapture and pursuit time: Recaptured animals have been observed by field personnel (Arnemo, personal communication), to be harder to capture, and thus have a longer pursuit time which is assumed to cause exhaustion and less rapid increase in movement post-capture. Different post-capture movement patterns can be explained by pursuit time. It is assumed that with longer pursuit time there is a risk of increased body temperature and hyperthermia, hence longer pursuit time is predicted to reduce movement after capture.

Drugs: Because all animals independent of body weight or sex get the same doses, I assumed that larger animals receive a smaller dose per kilogram and therefore a less effect on post-

capture movements. The combination of MKTZ is assumed to have less effect on movement leading to an increased activity due to a lower, hence shorter lasting, dose of TZ and the probability to reverse medetomidine.

I further assume that different post-capture movement can be explained by additional medetomidine.

Based on the predictions and the rule of parsimony I selected the models within the AICc cut off value to the top model.

Table 2. All wolf individuals included and the variables used to look at the effect of capture. Drug protocol consists of Zoletil® (TZ) or medetomidine-ketamine, tiletamine-zolazepam (MKTZ).

Wolf Id	Sex	Social status	Medetomidine	Pursuit time (min)	Recapture	Drug protocol	Initial rectal temp (°C)	Body weight (kg)
M0109	M	Adult	no	40	no	500 TZ	38.8	51
M0211	F	Adult	yes	5	yes	500 TZ	40.5	35
M0402	M	Adult	yes	17	no	500 TZ	41.6	47
M0404	M	Adult	yes	40	no	500 TZ	39.4	46.5
M0506	M	Adult	no	9	no	500 TZ	40.2	44.5
M0507	F	Adult	yes	42	yes	250 TZ	39.5	33
M0510	F	Adult	no	10	yes	500 TZ	40.2	36
M0510	F	Adult	yes	8	yes	250 TZ	39.4	35.5
M0611	M	Adult	no	14	yes	500 TZ	38.3	46
M0702	M	Adult	yes	84	no	500 TZ	40.6	40
M0902	F	Pup	no	5	no	250 TZ	39.8	26
M0906	F	Adult	yes	37	no	MKTZ	41.4	40
M0907	F	Pup	yes	35	no	250 TZ	40.3	34
M0908	F	Pup	no	9	no	MKTZ	42	33.5
M0909	F	pup	yes	6	no	MKTZ	41.4	32.5
M0909	F	Adult	no	16	yes	250 TZ	40.7	35.45
M0918	M	Adult	no	27	no	250 TZ	41.8	47
M1001	F	Adult	yes	40	no	250 TZ	38.7	32
M1108	M	Pup	yes	41	no	250 TZ	41.2	42.5
M1109	M	Adult	yes	7	no	250 TZ	39.8	47
M1111	F	Pup	no	12	no	250 TZ	40.1	30
M1112	M	Pup	yes	13	no	250 TZ	40.1	38
M1113	M	adult	yes	4	no	250 TZ	39.7	47.5
M1501	F	Adult	no	70	no	500 TZ	37.5	39
M1502	M	Adult	no	20	no	500 TZ	39	46
				*[1]27±5.14			*[1]40.2 ±0.26	
				[2]16±5.5			[2]39.8 ± 0.36	

*Mean values of pursuit time and initial rectal temperature for [1] first-time captures and, [2] recaptures.

Results

Intrinsic factors

The average body weight (± SE) of the captured wolves was 34 ±0.96 kg for females and 45 ±1.0 kg for males (Table 2). Weight varied with sex ($F_{1, 23} = 85.00$, $p < 0.001$) and social status ($F_{1, 23} = 21.13$, $p < 0.001$) (Figure 2). Males were on average 1.3 (adults) and 1.2 (pups) times heavier than females of the respective social class. Pups had reached on average 83% and 87% of adult weights of males and females, respectively.

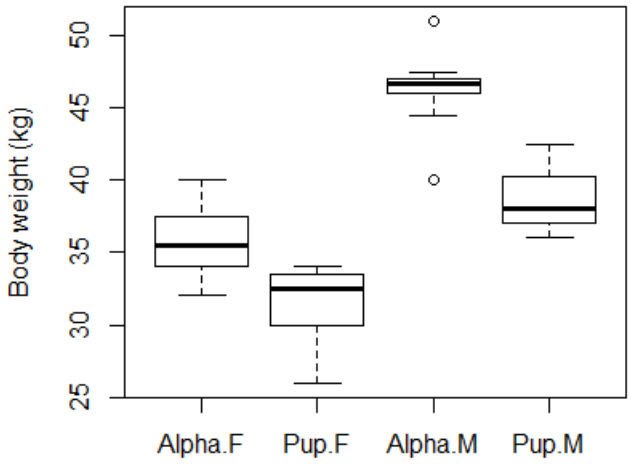

Figure 2. Body weight of captured wolves for adult females (n=8), female pups (n=5), adult males (n=10) and male pups (n=2). Boxplots represent medians (thick black line).

The most parsimonious model related cumulative distance moved after capture to the interaction of sex and hour (Table 3). This model had a 1.2 times higher evidence than the next-best model and performed better than the null model (Table 3).

The model Hour*Sex predicted a lower intercept and a steeper slope for females than for males (Table 4, Figure 3a). Shortly after capture males had a higher movement rate than females and 23 hours after capture female movement rates passed those of males. Males travelled 29 % more than females, 12 hours after capture. After 36 hours females had moved 10% more than males and 18 % more after 3 days (Figure 3a). According to the model including social status, adult animals showed a higher rate of cumulative distance post-capture than pups (Table 4; Figure 3b)

Table 3. Model comparison using linear mixed models including the final models within AICc cut off <4. Models explain the effect of sex, medetomidine (med), drug and dose in the dart (drug), recapture and pursuit time on the Euclidian cumulative distance per hour after capture on Scandinavian wolves (N = 25). Hour and sex are interacted due to an early detected difference. Wolf id is included as a random factor in all models.

Model	Variables	K	AICc	ΔAICc	ωi
*Sex	Hour * sex	6	42522.26	0.00	0.25
Medetomidine	Hour * sex + med	7	42522.65	0.38	0.21
Pursuit time	Hour * sex + pursuit time	7	42522.84	0.57	0.19
Drugs	Hour * sex + drug	8	42523.57	1.31	0.13
Recapture	Hour * sex + recapture	7	42523.58	1.32	0.13
Social status	Hour * sex + social status	6	42524.10	1.84	0.10
+ Sex	Hour + sex	5	42707.86	185.60	0.00
Weight	Hour + weight	5	42709.24	186.97	0.00
Null	Hour	3	42707.25	184.98	0.00

Table 4. Estimates of the models within the AICc cut off at <4. Including Model name, Factors, Beta and Standard Error (SE) for the models predicting cumulative post-capture movement with sex and social status.

Model	Factors	Beta	SE
Sex	Intercept	-1689.76	1156.87
	Hour	299.28	3.56
	Sex male	1751.60	1670.85
	Hour*sex male	-73.92	5.28
Social status	Intercept	-2090.94	1465.47
	Hour	299.28	3.56
	Sex male	1531.99	1684.67
	Social status adult	745.53	1781.81
	Hour*sex male	-73.93	5.29

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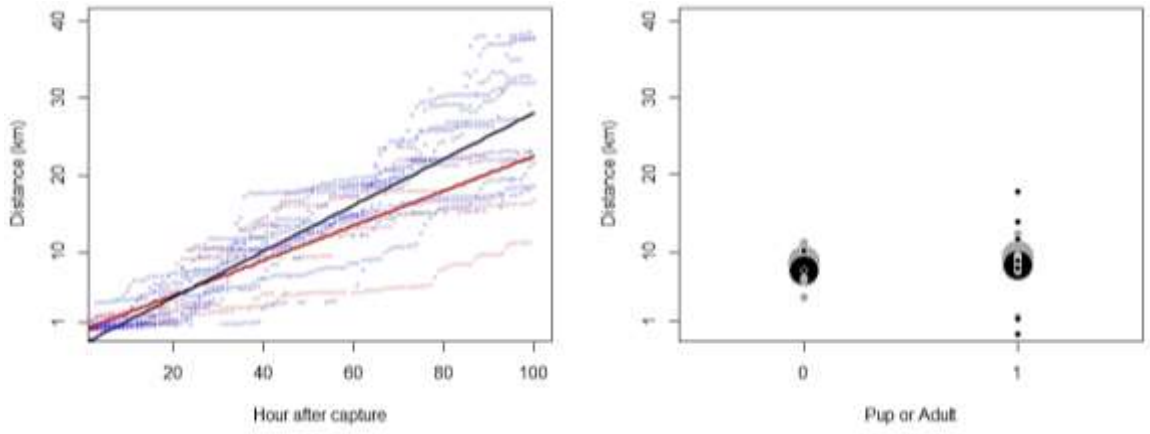

Figure 3. a) Increase in cumulative distance moved with time post-capture for females (blue) and male (red) wolves in Scandinavia. b) Cumulative distance moved after 36 hours as predicted for pups (0), and adult wolves (1) Grey dots represent females, black dots males.

Recaptures and Pursuit time

All models relating cumulative distance moved post-capture to the capture related variables and sex were within the AICc cut off (delta <4) relative to the Hour*Sex-model (Table 3). For two individuals (M0510 and M0909, Table 2), two capture-events were analysed. The model predicted that the cumulative distance moved post-capture was lower for recaptured individuals than for individuals captured for the first time (Table 5; Figure 4a). Three days after capture, recaptured individuals had travelled 20 % less than individuals captured for the first time. Initial rectal temperature was not depending on pursuit time (linear regression: $F = 1.42$, $df = 23$, $p = 0.25$). Pursuit time was similar between individuals that were captured for the first time compared to recaptured individuals (Table 2, t-test: $t = 1.51$, $df = 14.54$, $p = 0.15$).

The model including pursuit time suggested that the hourly distance travelled decreased with increasing pursuit time (Table 5; Figure 4b). Thirty six hours after capture, the model predicted that being pursued for 40 minutes gave a difference of 10 % less cumulative distance moved after capture, than if pursued for 20 minutes.

Mean of pursuit time and recapture is included in Table 2.

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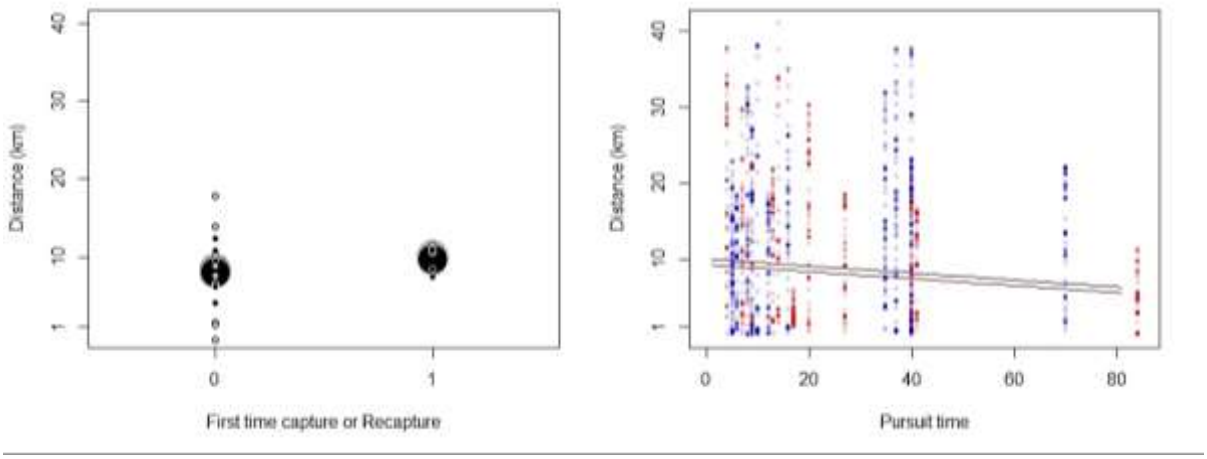

Figure 4 a) Cumulative distance effected by first-time captured (0), or recaptured (1), Scandinavian wolves. Grey dots represents females and black dots males, small dots represent the observed values and large the predicted values. b) Pursuit time affecting the cumulative distance 36 hours after capture. Red line symbolize males and blue line females. Blue and red dots are the observed values.

Table 5. Estimates of the models within the AICc cut off at <4. Including Model name, Factors, Beta and Standard Error (SE) for the models predicting cumulative post-capture movement with first-time capture or recapture and pursuit time.

	Factors	Beta	SE
Recapture	Intercept	-2320.57	1413.99
	Hour	299.28	3.56
	Sex male	2245.72	1797.08

	Recapture	1641.61	2080.63
	Hour * sex	-73.92	5.28
Pursuit time	Intercept	-654.61	1376.31
	Hour	299.28	3.56
	Sex male	1925.58	1568.35
	Pursuit time	-45.91	37.77
	Hour * sex	-73.92	5.29

Drugs

The drug combination of MKTZ was given to 12% of all the wolves (n = 3), both of them were females. 40 % were given 500 mg of TZ (n = 10), and 48%, 250 mg TZ (n = 12). Models including dose and drug were within the AICc cut of < 4 (Table 3). Results from the potential effect of MKTZ are not interpreted due to the low sample size.

Individuals given the combination 250 mg TZ had a higher level of post-capture movement than the ones given 500 mg TZ (Table 6). Thirty six hours after capture, wolves given 250 TZ had a 29% higher rate of cumulated distance than wolves given 500 mg TZ (Figure 5a).

The model including medetomidine predicted that wolves given medetomidine had a higher movement rate than the ones not given medetomidine (Table 6; Figure 5b). Thirty six hours after capture wolves that were given medetomidine had travelled 22% more than without.

a b

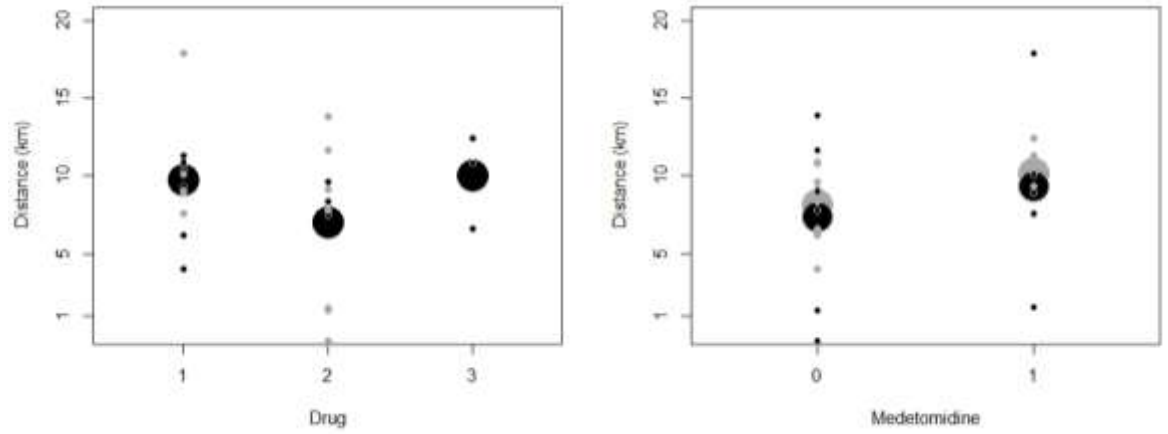

Figure 5.a) Drug and doses, 250 mg TZ (1), 500 mg TZ (2) and MKTZ (3), affecting the cumulative distance 36 hours after capture for Scandinavian wolves. b) Additional medetomidine (1), effecting the cumulative distance or no additional medetomidine given (0).

Table 6. Estimates of the models within the AICc cut off at <4, including Model name, Factors, Beta and Standard Error (SE) for the models predicting cumulative post-capture movement with drug dose and combination and medetomidine.

	Factors	Beta	SE
Drug	Intercept	-1125.22	1414.12
	Hour	299.27	3.56
	Sex male	2780.29	1843.08
	Drug 500 TZ	-2733.76	1824.85
	Drug MKTZ	282.47	2743.61
	Hour * sex	-73.91	5.28
Medetomidine	Intercept	-2613.91	1373.89
	Hour	299.28	3.56
	Sex male	1842.15	1655.33

	Medetomidine yes	2002.09	1645.13
	Hour * sex	-73.93	5.28

Body weight

Since body weight was correlated with sex and social status, I modelled the relation between cumulative distance and body weight separately for each sex. The addition of weight improved model parsimony with delta AIC = 20.4 for females and 12.5 for males compared to the associated null model including hour only. The models predicted an increase in cumulative distance moved with an increase in body weight for both females and males. Observing the beta estimate and standard error, weight was positively correlated with movement for females but was not supported for males (Table 7).

The smallest males (38 kg) had travelled 30% less than the largest males (51 kg) after 36 hours (Figure 6a). At 36 hours after capture females weighing 26 kg had travelled 62 % less than females weighing 40 kg (Figure 6b). Models divided between sexes including weight were not compared to the rest of the models.

a b

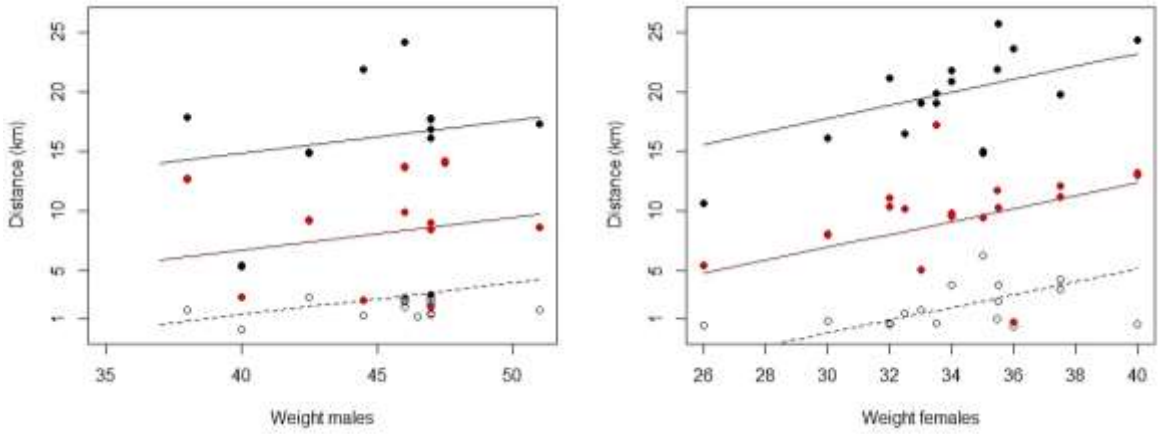

Figure 6. Separate models for each sex predicting cumulative distance moved with variation in weight for males (a) and females (b). The dotted line with open circles represents 12 hour after capture, red line and dots 36 hours, and black line and dots 72 hours.

Table 7. Estimates for the sex separated models predicting cumulative post-capture distance, including hour and weight. Presented are Model names, Factors, Beta and standard error (SE).

	Factors	Beta	SE
Female (n= 12)	Intercept	-20065.68	4581.06
	Hour	299.32	3.50
	Weight	542.54	134.48
Male (n = 13)	Intercept	-12181.75	21460.06
	Hour	225.36	3.98
	Weight	270.55	427.92

Discussion

Intrinsic factors

Among several intrinsic and extrinsic factors that could have affected post-capture movements of Scandinavian wolves, sex was the most important predictor. Males had a higher movement rate than females during the first 23 hours after capture. After that, females had higher movement rates than males. A study on post-capture movements of American black and grizzly bears also found sex differences (Cattet et al. 2008). They explain the increase in male movement rate compared to female movement rate with a natural sex-bias due to higher activity of male bears during breeding season in spring. Jedrzejewski et al. (2011), showed that male wolves in Poland move more than females during the mating season (January – February), and explains this with increased territorial behaviour during this period. However, according to Zimmermann et al. (2014; 2015), the adult pair is travelling together in Scandinavia, except for a short period during denning season. As all of our captures were carried out before this period, the observed sex-bias in post-capture movement of Scandinavian wolves may therefore not result from natural variation in sex-specific movement patterns.

Sexual dimorphism may be another plausible explanation. Male wolves are generally larger than females (Packard, 2003), and in my study, males were on average 1.2 – 1.3 times heavier than females. This may have implications for the metabolism of drugs. The liver, which is primarily responsible for metabolizing these drugs, has a size proportionate to body size, roughly ~ 3% of body weight in mammals (Tibbits, 2003). In this study all wolves were given the same absolute doses, resulting in a lower dose per kg body mass for heavier animals. However, sex difference by itself considering metabolism is rejected by Martignoni et al. (2006), concluding that no such difference exist in dogs. The drug TZ used for Scandinavian wolves cannot be reversed and recovery can take several hours (Arnemo et al. 2012).

This body mass effect may be due to the increased metabolism of drugs in larger animals, as described above. Additionally it may also relate to the social status as a function of adults and pups. The pups in this data set, captured from December to March were significantly smaller than the adults. The increased cumulative distance moved post-capture of adult animals compared to pups may be due to their physical advantage. In addition the captured wolves have often been transported by helicopter to a place suitable for handling. Adult individuals might have gained more experience in navigating, hence being faster at withdrawing from the handling location in order to reunite with the pack.

Recapture and pursuit time

Post-capture movement was lower for wolves that had been recaptured, than for wolves that had been captured the first time. This finding supports my initial expectation that wolves with previous capture experience could be more agitated pre-capture and hence more exhausted post-capture. This assumption was based on observations of field personnel who described that experienced animals were harder to capture and pursued over a longer time span. In contrast, pursuit time did not significantly differ during recaptures than during first-time captures in my study. A fear related behavior outlined by Misslin (2003), is to avoid an unexpected or naïve object in the natural environment of an animal. This could explain that pursuit time did not differ and that first-time captured individuals avoided the helicopter to the same extent as the wolves captured more than once. Experienced animals have been observed to avoid the helicopter and hide at an early stage of the pursuit resulting in unsuccessful captures. The individuals that were pursued but not successfully captured are not included in the data set but should be considered in future analysis. The definition of pursuit time is a relative concept, in

this study counted as the time from observing the wolf, until the dart was distributed. The actual time of pursuit, if defined as when the wolf truly noticed the presence of the helicopter, is difficult to evaluate.

The repeated negative experience and fear related to captures could cause a change in behavior and an increased level of stress. The assumption that recaptured individuals remember the event as negative can be supported if wolves can link the experience of being followed by helicopter with a negative experience (Fanselow, 1998). The drug tiletamine used as an anaesthetic is reported to cause memory loss in humans (Kreeger & Arnemo, 2012). It is not known however if memory loss also applies to animals, if it is reversible, and how long it may last.

Cattet et al. (2008), found that body condition decreased with number of capture-events for individual grizzly and American black bears. Long-term effects of repeated captures were not included in this study but for future studies physiological effects as well as reproduction success and survival rate should be considered.

Animals with longer pursuit time were predicted to have a higher rectal temperature caused by stress inflicted by the chase. Increased rectal temperature is a sign of hyperthermia which was assumed to alter post-capture movement due to exhaustion post-capture. Korhonen et al. (2000) observed an increase in rectal temperature in mink between the first-time captures and recaptures. In my study, however, initial rectal temperature was similar for first-time-and recaptured animals. Rectal temperature is only one of many ways of measuring the levels of stress. Future studies should aim at measuring e.g. cortisol levels in faecal samples pre-capture, compared with blood samples from capture-event and post-capture faecal samples (Reeder & Kramer, 2005).

As initially predicted, pursuit time was negatively correlated with post-capture movement rate. Wolves exposed to longer chase times probably were more exhausted post-capture resulting in less movement. In previous protocols concerning captures Arnemo et al. (2004), recommended a maximum pursuit time of 30 minutes. Longer pursuit time could accordingly lead to hyperthermia. Nine out of 25 captures was above 30 minutes. Very long pursuit times are usually related to delayed effects of the drug due to misplacement of the dart resulting in subcutaneous administration or incomplete dis-stress of the dart normally requiring a second dose. No support was found for increased rectal temperature due to increased pursuit time. However, the mean rectal temp was 40.1 ± 0.2 °C. Normal temperature for wolves range between 37- 40 °C (Kreeger & Arnemo, 2012), indicating relatively high rectal temperature. Fahlman et al. (2008) found an increased initial rectal temperature (40.1 ± 0.8 °C) in wolverines captured with helicopter compared to wolverines captured in the den (38.6 ± 0.8 °C). They defined wolverines with an initial temperature of ≥ 40 °C as hyperthermic. Fahlman et al. (2011) and Cattet et al. (2003) found frequent hyperthermia in bears captured by helicopter. Omsjoe et al. (2009) found a positive correlation between initial rectal temperature and pursuit time in Svalbard reindeer (*Rangifer tarandus platyrhynchus)*. However, comparing inter-guild species can be misleading according to Støen et al. (2010), who showed that moose and bears reacted differently to the approach of helicopters. Increased body temperature is likely to be closely linked to pursuit time which should be reduced as much as possible.

Drugs

Animals given the double dose of TZ had a lower post-capture movement rate than those given a single dose. The different drugs given in this study where TZ with two different doses (250 and 500 mg) and MKTZ. MKTZ was only given to three individuals, a sample size too small to allow model interpretations. The process of metabolizing drugs can depend on a number of

factors. Tibbits et al. (2003) conclude inter individual differences in dogs metabolizing drugs which makes it difficult to predict an effect. The total dosage per kg has a relatively large span when comparing a light female to the heaviest of males, which is likely to have an effect on the movements post-capture. Since determination of individual weight before darting is somehow difficult the implications for this finding needs further examination. Exploring the relationship using drug as a continuous variable, dosage per kg, could predict a more accurate result and should be further examines.

Direct observations of wolves after capture, revealed that they were apparently affected by the drugs for several hours; they walked in circles, staggered or went back and forth (Kreeger & Arnemo 2012; Arnemo et al. 2013). Tiletamine is the anaesthetic drug causing the abnormal movements during the induction and recovery, and Zolazepam is a sedative included in the combination to counteract side effects of tiletamine including muscle rigidity. Zolazepam is eliminated faster than tiletamine in dogs. Given at a relatively high doses compared to body weight results in an even longer elimination time of zolazepam while tiletamine is also causing deeper sedation (Ko, 2012). Arnemo et al. (2012), recommends not reversing e.g. medetomidine before 50-60 minutes after dart injection to minimize abnormal movements, excitation and vomiting. An additional suggestion would be to increase the amount of tranquilizer or to use a shorter acting anaesthetics to prevent abnormal movements. A third combination of medetomidin-ketamine (Domitor® 1 mg/ml, Orion and Narketan® 100 mg/ml, Chassot, Dublin Ireland) (MK), were evaluated by Arnemo et al. (2013), during the winters of 2002-2003 as a potential drug combination with a lower doses of the anaesthetic ketamine, to reduce side effects. However this resulted in an increase of hyperthermia as well as 2 cases of mortality, and are not recommended today.

The assumptions of additional medetomidine inducing a decrease in movement after capture was not supported in this study. Wolves given medetomidine during the handling had a higher movement rate post-capture compared to wolves that did not receive medetomidine. The initial assumption was based on empirical observations of animals during their recovery in the first couple of hours, and may not apply for longer periods. Additional medetomidine is given if the wolf is spontaneously recovering during handling or is not enough immobilized when captured, likely due to insufficient initial dosage of the immobilization drug. Since medetomidine is reversible, this would naturally lead to animals more active post-capture. My finding support the biomedical protocol of wolf captures (Arnemo et al. 2012), stating that additional medetomidine given during handling, will not prolong post-capture recovery, given that this drug is reversed during handling.

Weight

Because body mass was confounded with sex, I analysed potential effects of body mass for each sex separately. The two separate models predict that movement rates are positively correlated with body mass, independent of sex. Both models increase parsimony compared to the null models, however males had a higher standard error hence a much larger variation than the females. The prediction could be an effect of weight dependent metabolism as previously mentioned. Males weigh more than females, hence have a shorter elimination time of the received drug. The inability to compare these models with the rest of the prediction can only give us a trend of a possible relationship.

Statistical considerations

Building up models that are too complex related to the sample size will exceed the use of degrees of freedom, risk overfitting the models, and might give results that reflect the sample

size rather than representing the population (Babyak, 2004). Combining more variables would possibly increase the predictability in a more accurate way, but would demand a larger sample size. In addition, environmental and geographical variables should be considered, snow depth has been previously shown ta alter movement in wolves (Fuller, 1991), and the distance to forest roads can affect movement rates (Zimmermann et al. 2014).

The small ΔAICc-values of the highest ranked models suggests that separately adding different variables to the Hour*Sex model did not considerably improve nor reduce model fit considerably. Predicted effects of these additional variables should therefore be interpreted carefully. The low sample size of 25 individuals that e.g. is halved when compared between groups gives a rough estimate of a realistic pattern and a much larger sample size is recommended in future studies. The time frame in this study was limited because I focused on animals with hourly positions for at least 100 hours after capture. One way of increasing the time period for a wider insight could be using less frequent positioning over a longer time period. Cattet et al. (2008), however, found that an increase of the time interval between GPS positions decreased the accuracy of the result.

Considering that there is an increased variation in movement between sexes up to and possibly after 100 hours after capture, contradicting the findings on wolf movement not connected to capture, could be an indication that the spatial information given to us is not representative. A more exact evaluation of the spatial effect from capture demands another approach using e.g. a comparative period of "normal" movements. This would give a better overview of a recovery time frame. Using more data and longer period to explore a change point in time is another possibility that should be explored.

Conclusion

In conclusion post-capture movements in the Scandinavian wolf population is altered by the difference in sex and by the drug doses and additional drug given during the handling. When capturing, handling and studying wild animals, assessments of actions and consequences both prior and during capture is according to my findings of high necessity to ensure welfare and accuracy of the results.

My findings support adding more tranquilizer (medetomidine) if wolves are waking up during handling. To keep the wolf tranquilized for a longer period allowing TZ to be metabolized could be an option to reduce negative effects. Further use of my findings would be to calculate the drug dose for each individual to avoid decreased activity after capture. Lower doses for females and pups could be considered. However as previously mentioned, this is practically problematic due to the difficulties estimating the weight and determining the sex of the animals before capture.

Concerning the welfare of the wolves, pursuit time should be kept short if possible. The factors behind these findings remains unknown but should be considered in future studies due to a possible connection with the level of stress induced from the helicopter chase. To further asses long term effects concerning welfare, studies on reproductive success, body condition at repeated captures and survival should also be considered.

Cumulative distance as an assessment of capture has its limitations. Future evaluation using comparison to a normality period or statistical change point analysis to reveal potential recovery period should be considered for more accurate specification of how much information that should be omitted from spatial studies.

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