Predator evasion: the behavioral response of moose to a wolf-like predator

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Predation is a strong selective force favoring the individual with the most successful survival strategy. Predators affect prey through direct predation and through the costs of anti-predator behavioral. In Sweden moose (*Alces alces*) is an important game species annual harvest is ~100 000 animals. Wolves (*Canis lupus*) returned to Sweden in the 1980s. Wolves' main prey in Sweden is moose and can be as much as 95% of the consumed biomass. Because booth humans and wolves are important agents of mortality they are likely to affect the behavior of moose. I tested differences in moose flight response when hunted with loose dog, and if this was related to the amount their previous wolf exposure. I hypothesize that a high exposure to wolves would affect the flight behavior of moose. Disturbance trials were conducted with GPS collared dog and GPS collared moose. Wolf data was retrieved from GPS collared wolves. Several movement metrics such as speed, distance, duration and sinuosity were used to detect patterns of moose flight behavior. Results were also compared with a similar study conducted in Västerbotten where moose had no recent experience of exposure to wolves. I did not find support for my hypothesis that wolf exposure affect moose escape behavior when hunted with loose dog. Results from Grimsö and Västerbotten showed a similar response pattern in overall response by moose to disturbance. Differences between Grimsö and Västerbotten were found in net displacement and movement rate Differences are likely due to low sample size and environmental differences and not the presence of wolf at Grimsö. Moose flight behavior is likely shaped by a combination of both recent human hunting practices and previous predation by wolves and brown bears.

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”Dä här behöver du int å fôrsk på, dä ä så här”

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Introduction

Predation is defined as the event when one organism consumes another living organism, partly or completely (Sinclair et al., 2009). Predation generally takes place between two different trophic levels (Sinclair et al., 2009) and all animals are more or less potential prey (Lima and Dill, 1990). In a predator-prey environment, prey evolved different behavioral strategies to escape and avoid lethal encounters with predators (Lima and Dill, 1990). When escape fails, the animal most likely dies, hence success in escaping is crucial to prey, making predation a strong selective force favoring the individual with the most successful survival strategy (Ydenberg and Dill, 1986, Lima and Dill, 1990).

Anti-predation strategies

Predators affect prey demography through direct predation and through the costs of anti-predator behavioral responses, also called risk effects (Boonstra et al., 1998, Peckarsky et al., 1993). Prey behavioral responses may include escape tactics, vigilance, habitat selection, and activity patterns. These behavioral responses may ultimately affect the physiology of prey which in turn may result in lowered production of offspring (Creel et al., 2007). When prey encounters a predator, prey must balance the probability of capture while expending the minimum amount of energy (Ydenberg and Dill, 1986). There are several strategies prey can adopt in order to avoid predation. Ungulates, for instance, use different strategies to avoid predation such as group living (Hebblewhite and Pletscher, 2002), avoiding habitats with high predation risk (Edwards, 1983), migrating (Messier et al., 1988, Smuts, 1978), increased vigilance (Hunter and Skinner, 1998), grouping (Heard, 1992) and synchronized breeding (Sinclair et al., 2009). Prey focus their vigilance towards the most abundant predator in the system (Lima, 1992). It has been suggested that if a predator is removed from a system, a predator specific defense behavior may be lost due to high costs of maintaining a “useless” behavior (Blumstein, 2006). If the predator avoidance strategy fails and an attack is initiated, prey can utilize different defense strategies to escape (Barnard, 2004). Ungulates defense strategies can be divided into two main strategies, fight and flight (Mech and Peterson, 2003). When an animal chooses to fight, they are standing their ground and react aggressively against the threat (Lingle and Pellis, 2002, Mech, 1966). If an animal elects to flee, they are attempting to out run a perusing predator (Barnard, 2004, Mech, 1966) or running while rapidly changing direction (Stankowich and Coss, 2007, Barnard, 2004). Prey flight distance has been shown to be a good measurement of fear (Miller et al., 2006). Velocity can also be used as a measurement of fear but is shown to be related to the behavior of the predator (Ydenberg and Dill, 1986).

Moose

Moose (*Alces alces*) is the largest member of the deer family found in the northern parts of Europe, Asia and North America; inhibiting all of Sweden except the island of Gotland (Ekman et al., 1993). Moose are in general solitary, but can form groups during winter (Sweanor and Sandegren, 1985). They are not territorial and have overlapping home ranges (Cederlund and Sand, 1992) but aggression between individuals can occur, especially during mating season (Sweanor and Sandegren, 1985, Ekman et al., 1993). Moose, use two different strategies to avoid predation from wolves; being aggressive or flee (Mech and Peterson, 2003, Mech, 1966). In Sweden, most moose flee when attacked by wolves; as few as 6% take an immediate stand when attacked (Wikenros et al., 2009).

Moose in Sweden

Moose have been harvested for meat since the stone age in Sweden (Liberg et al., 2010, Karlsson, 2010). Because of intensive unregulated hunting and a perceived competition with livestock for food, moose populations declined drastically in Sweden, to the point of being extirpated in some parts of the country by the end of 19th century (Ekman et al., 1993, Karlsson, 2010). It was not until the 1950s and 1960s that the moose population started to recover. This increase was attributed to change in forest management practices, particularly due to the increase of clear cuts and young forest plantations (Lavsund et al., 2003, Karlsson, 2010). The moose population reached its peak in the early 1980s. In 1982, the harvest was 174 700 moose (Ekman et al., 1993). There are no good population data on moose in Sweden, but spring population was in 2005 estimated to 200 000 individuals (Liberg et al., 2010) and during the hunting season 2011/12, 99 492 moose was harvested in Sweden (Svenska jagareförbundet, 2012)

Moose Predators in south central Sweden

Humans

In Sweden, humans are the main predator of moose. Hunting harvest accounts for 81-91% of the moose mortality (Ericsson and Wallin, 2001). Approximately 4% of the adult Swedish population are active hunters, and four out of ten hunters own a hunting dog (*Canis lupus familiaris*), which is a relative high number compared to the rest of the world (Ericsson et al., 2010). Hunting moose with a dog is known to increase hunting success (Ruusila and Pesonen, 2004), and moose hunting with a loose dog is a very common form of hunting in Sweden (Thelander, 1992, Karlsson, 2010). When hunting with a baying dog, the dog will search for a moose and when found follow it or keep it at bay by barking until the hunter can approach and shoot (Thelander, 1992, Karlsson, 2010).

Wolf

Historically the gray wolf (*Canis lupus*) was found over most parts of the northern hemisphere (Mech, 1995). Worldwide, due to human persecution, gray wolf densities were reduced and regulated to remote areas with low human densities (Mech, 1995). Sweden was no exception to this pattern and wolves were persecuted for decades. By the time of legal protection, in 1966, the wolf was practically eradicated from Sweden, with the exception of a few individuals in the far north (Aronson and Sand, 2004) In 1978, the first documented reproduction since the legal protection occurred in Norrbotten in northern Sweden (Bjärvall and Nilsson, 1978). In 1983, the first reproduction in >100 years was documented in central Sweden, close to the Norwegian boarder (Aronson and Sand, 2004). Even though wolves had returned, it was not until the 1990s that the wolf population began to increase in numbers (Sand et al., 2007). From an initial estimate of 8 wolves and 1 confirmed reproduction in the winter of 1990/1991 (Sand et al., 2007), the wolf population increased to 260-330 individual wolves with 28 confirmed reproductions by the winter of 2011/2012 in Scandinavia (Sweden + Norway) (Svensson et al., 2012). The main prey of wolves are moose (Sand et al., 2005) comprising ≥95% of the consumed biomass and of that, calves are preferred compared to adult individuals (Sand et al., 2008). Compared to other wolf populations, the wolf in Scandinavia has a high hunting success rate (Sand et al., 2006).

Studies have shown that human hunting can affect prey behavior, such as habitat choice (Brøseth et al., 2005, Kufeld et al., 1988), causing longer flight distances (Behrend and Lubeck, 1968), changes in movement rate (Scillitani et al., 2010, Ciuti et al., 2012), increased home range size (Grignolio et al., 2011), causing animals to leave home ranges (Sweeney et al., 1971) or avoid particular habitats (Kilgo et al., 1998, Ciuti et al., 2012). Similar to human presence, wolf presence can effect prey behavior including causing prey to avoid habitats (Fortin et al., 2005, Creel et al., 2005), influence habitat selection (Stephens and Peterson, 1984), increase vigilance (Bøving and Post, 1997, Winnie Jr and Creel, 2007) and lower reproduction (Creel et al., 2007). Recent empirical research has shown that risk effects on prey dynamics can be as important as direct numerical effects of predation, or even larger (Schmitz et al., 1997, Nelson et al., 2004, Preisser et al., 2005).When risk effects are considered, many studies focus on effects that cascade from the prey to other trophic levels and species (Werner and Peacor, 2003, Bolker et al., 2003), rather than effects on the prey species itself (Boonstra et al., 1998).

Despite this knowledge, little research has been done on moose behavior during hunting (Baskin et al., 2004) and to my knowledge only Neumann (2009) has examined moose behavior in response to baying hunting dogs. Considering the economic and cultural value of moose (Boman et al., 2011), the widespread tradition of moose hunting with a dog (Thelander, 1992, Karlsson, 2010) and the effect wolves may have on their prey (Creel et al., 2007, Creel et al., 2005, Winnie Jr and Creel, 2007, Fortin et al., 2005, Stephens and Peterson, 1984) it is surprising that this activity has not received more attention from a research perspective on predator-prey behavior.

Objectives

My objective was to measure and test differences in moose flight response with regard to amount of previous wolf exposure, when hunted with a loose dog. Because dogs (*Canins familiaris*) are closely related to wolves and because the actual dog breeds used are externally relatively similar to wolves, albeit smaller, I assumed that the exposure of moose to a hunting dog would elicit a response similar to the one when exposed to a true wolf attack. In that sense, I therefore used moose hunting dogs as substitutes for wolves, or for a wolf-like predator, in this study. Several movement metrics such as speed, distance, duration and sinuosity to detect patterns of moose flight behavior were measured and I included other potential variables that may affect moose flight behavior such as snow depth, if a calf was present, duration of chase and which dog was used. Additionally, after being pursued, we assessed the time for the moose to resettle to pre-trial levels. We also determined if the immediate threat from the hunting dog was sufficient to cause moose to leave their home range. I tested the hypothesis that a high previous exposure to wolves would affect the flight behavior of moose. If risk effects were manifested in the moose population, I therefore, expected moose individuals to express different behaviors relative to their previous exposure to wolves. For instance, moose that have experienced a higher exposure to wolves were expected to have longer flight time, longer flight distance, higher flight speed and a longer time to resettle after disturbance, than moose with a lower previous exposure to wolves. Interestingly, there was a similar study conducted in Västerbotten in 2006 (see Neumann (2009)) on a moose population without wolf experience. This gave me an opportunity to compare moose responses in a population where humans have been the only top predator for an extended period of time with responses to a population that now has two potential top predators, wolves and humans.

Method

Study area

Grimsö Wildlife Research area was located in south-central Sweden (59˚5´N, 15˚5´E) (Figure 1). Elevation ranged between 100 – 150 m (Rönnegård et al., 2008). Grimsö consisted of 72% forest, 18% bogs, 7% lakes and streams and 3% meadows and farmland (Rönnegård et al., 2008). Norway spruce (*Picea abies*), scots pine (*Pinus silvestris*) and birch (*Betula pubescens* and *Betula pendula*) were the most common types of tree in the area (Rönnegård et al., 2008). Grimsö had Swedish inland climate with temperatures ranging > – 20˚C in winter and > 25˚C in summer (Rönnegård et al., 2008). Average yearly precipitation was 600-700 mm, of which 30% of precipitation was snow (Vedin, 1995). During trials the snow depth ranged between 0-26 cm ($\bar{x}$ = 5.69 cm). Snow depth for trial days was retrieved from Ställdalen metrological measuring station (SMHI, 2013).

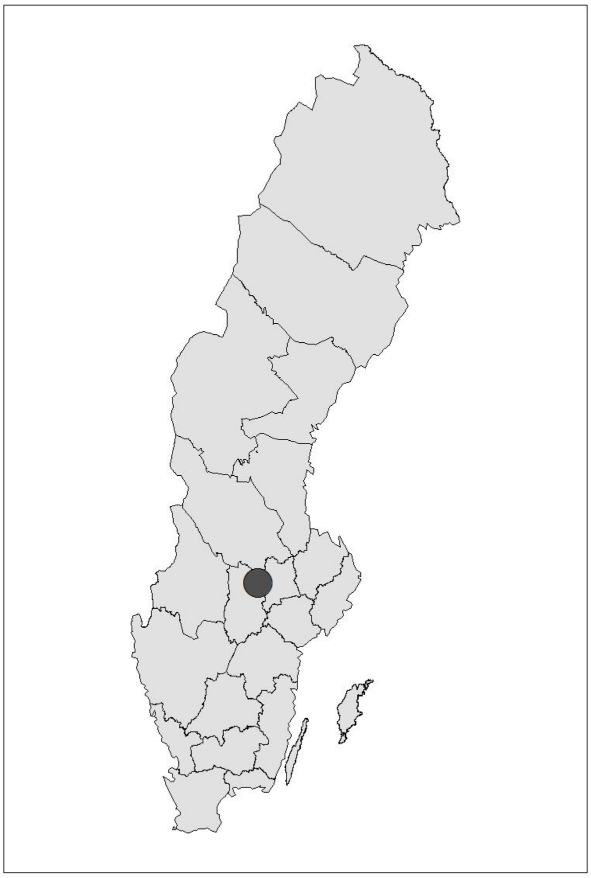

Figure 1 Location of Grimsö research area in Örebro County, south-central Sweden. Study area is marked with dark grey mark circle

Moose density within the Grimsö research area was estimated to 0.8 moose/km^2 in 2006 (Rönnegård et al., 2008). Hunting was allowed in the research area and was the main source of mortality for moose in the research area (Rönnegård et al., 2008). Wolves returned to the Grimsö area during the winter 2003-2004, and the first reproduction took place in 2004 establishing the Uttersberg pack (Wabakken et al., 2004). In the winter of 2009-2010 the Uttersberg pack was replaced by the Hedbyn pack (Wabakken et al., 2010) . During the years when trials were carried out (2010, 2011 and 2012) only the Hedbyn pack was present (Svensson et al., 2012).

Moose data

Moose were captured during either 2007 or 2010. Moose were immobilized from helicopter with a dart gun (Arnemo et al., 2003) and fitted with Global positioning system (GPS) /Global system for

Mobile communications (GSM) collars (GPS/GSM plus 4D; Vectronic Aerospace GmbH, Berlin, Germany). Moose collars were program to record position every 10 minutes on the days previous to and following the trial, whereas on trial day's collars acquired positions every 5 minutes. A re-discretization of moose positions to 600 second (10 min) intervals was performed, too insure equal time span between positions. We screened moose data for error positions following methods outlined in Bjørneraas et al. (2010). The data was screened in two steps. The first step removes positions that had a position distance $\bar{x} \geq 100$ km or position median ≥ 10 km. A window of ±10 positions was used to calculate the mean and median. The second step detects spikes in positions with high outgoing and returning speed, in combination with a turning angel. The speed limit was set to ≥ 1500 m/s and the turning angel to cosine (-0.97) (Bjørneraas et al., 2010). We calculated moose utilization distribution (UD) home ranges with GPS positions, with 2 h intervals, from 30 days before the trial day. We calculated home ranges for every individual moose and for each trial using 99% kernel density estimation with a smoothing parameter 60% of the href bandwidth and grid cell size set to 15x15 m. All calculations were performed in statistical software R 2.14.1 (R Development Core Team 2011) and with packages adehabitat (Calenge, 2006) and adehabitatLT (Calenge, 2006).

Wolf data

Wolves were captured through immobilization with a dart gun from a helicopter (Arnemo et al., 2007) and fitted with GPS/GSM collar (GPS/GSM plus 1D; Vectronic Aerospace GmbH, Berlin, Germany). Collars recorded one position every 12 h. During 2010 and 2011, at least one alpha animal in the pack was wearing a GPS collar but during 2012 there were no collared wolves. For this reason, the trials (n = 5) conducted during 2012 used information from wolf data collected in 2011.

We calculated a relative value of wolf exposure (previous exposure) for every moose trial. We calculated a UD for wolves using the same procedures as we did for moose. This resulted in a mean wolf UD for each moose home range. We used a linear transformation on the mean wolf UD value to minimize effects from outliers. We then used linear transformed mean wolf UD value to calculate a value of wolf exposure for each moose trial. To avoid overestimation of wolf exposure, we only used positions from one wolf collar every 12 hours. For further details see (Nicholson et al., In review)

Trials

Flight response trials took place between August and December in 2010, 2011 and 2012 (Appendix 1). We used three dog individuals during the trials. Ludde and Tanja were used for trials conducted during 2010 and 2011. Ida was used for trials during 2012. During the trials, moose were classified as either with or without a calf. Ludde, was a Swedish elk hound (male age 11 in 2010), Tanja and Ida were Norwegian elk hounds (Tanja age 6 in 2010) (Ida age 5 in 2012). The dogs were fitted with Garmin DC™ 30 radio collars (Garmin international, Inc., Olathe, Kansas USA) that obtained a location every 1 min. The dog and dog handler would approach the last known location of the collared moose downwind until ≤ 100 m before the dog was released and trial variables were measured. We did not actively retrieve the dog to abort trials.

To measure movement variables we divided the track of GPS locations and time segments from both the dog and the moose into several different phases (Figure 2). We considered the initiation of the close proximity chase (CPC) as when the dog handler released the dog. The end of CPC was considered over when the dog meet at least 2 of the following criteria: a) started back tracking on itself; b) the distance to moose was > 500 m; or c) the dog moved perpendicularly to the moose track and did not return to the moose track. The start of moose flight was set as the last recorded position before the start of the CPC (Figure 2). The CPC was followed by the post close proximity case (PCPC), and was measured from the closest moose position, in time, to the last dog position of the CPC and was considered to end when the moose was resettled (Figure 2). We defined resettled as four consecutive moose positions with < 100 m displacement between consecutive moose positions after the end of CPC (Figure 2). Using the various start and ending positions we measured cumulative flight distance [m], net displacement [m] (Equation 1) and time to resettle [min] from the start of moose flight to the point of resettlement (Figure 2).

Equation 1:

$$Net\ displacement = \sqrt{(x_{End} - x_{Start})^2 + (y_{End} - y_{start})^2}$$

Distance, duration and net displacement of the CPC was measured from the first position of the moose flight until the closest moose position, in time, to the last dog position of CPC. Distance, duration and net displacement of the PCPC were calculated as follows:

$$Distance_{PCPC} = Distance_{Total} - Distance_{CPC}$$

$$Duration_{PCPC} = Duration_{Total} - Duration_{CPC}$$

$$Net\ displacement_{PCPC} = Net\ displacement_{Total} - Net\ displacement_{CPC}$$

Velocity [m s^{-1}] for total trial, CPC and PCPC was calculated (Equation 2). Duration was multiplied with 60 to get [m s^{-1}] instead of [m min^{-1}].

Equation 2:

$$Velocity = \frac{Cumulative\ flight\ distance}{(Duration \times 60)}$$

We measured sinuosity as a ratio between 1 and 0; 1 being a straight line flight and <1 as a sinuous or windy escape. The ratio was given by dividing the net displacement and cumulative flight distance of the moose flight (Neumann, 2009). Distance to edge was defined as the Euclidean distance [m] of the moose at start of flight response trial to the closest edge of the moose home range. Distance to edge when resettled was the Euclidean distance [m] moose re-settled, from closest home range border. If moose did not resettled inside its previous 30-day home range, distance to edge = 0 m.

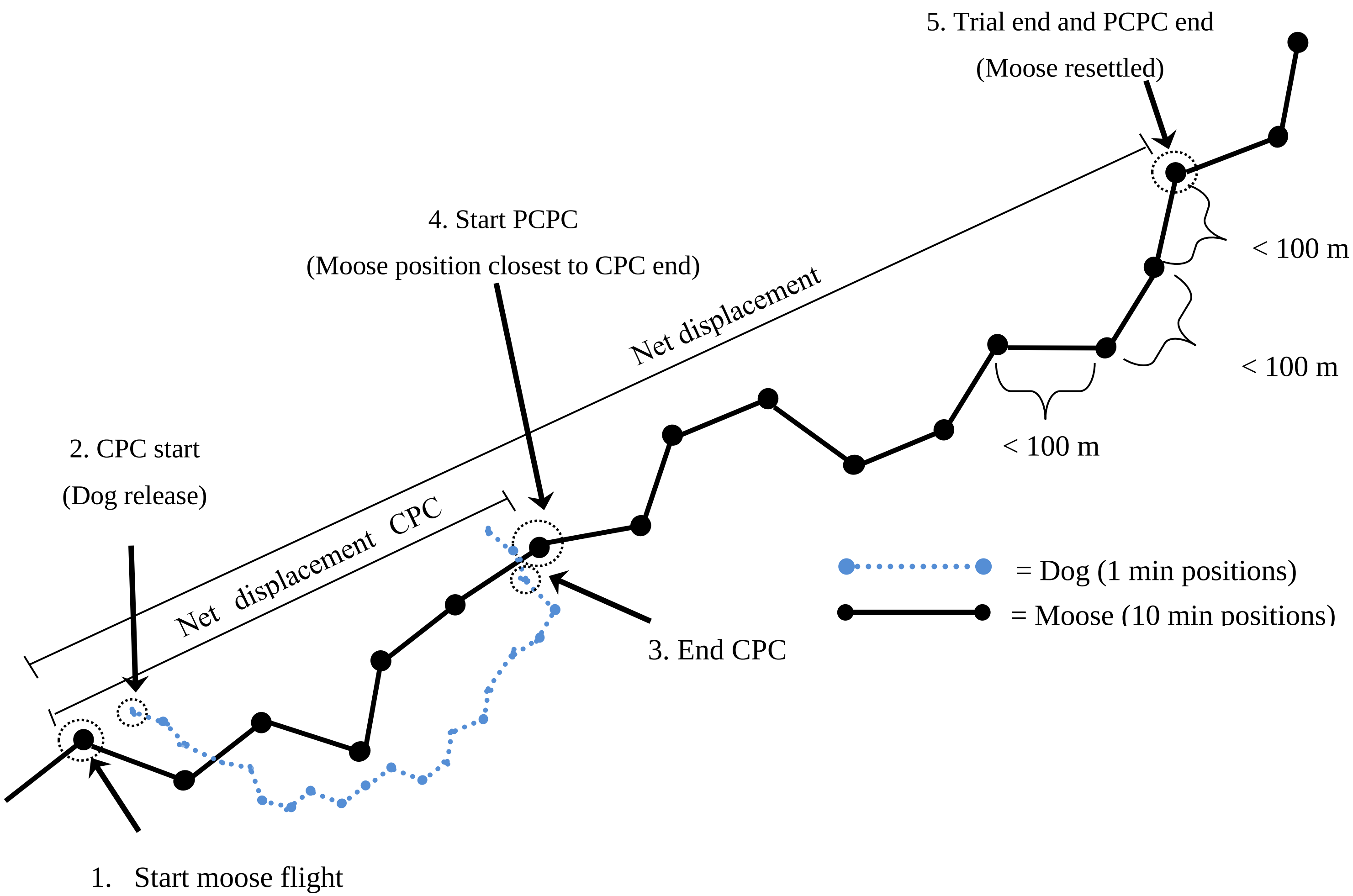

Figure 2 Schematic of variables measured during a moose flight response trial. 1. Start of moose flight: Last recorded moose position before release of dog. 2. Dog release: Position when dog is released from leash, start of the Close Proximity Chase (CPC). 3. End of CPC as determined by our 3 criteria. 4. Start of the Post-close Proximity Chase (PCPC): Moose position that is closest in time to the last dog position of CPC. 5. Moose resettled: End of PCPC and end of moose flight response trial. Moose resettled after four consecutive moose positions with < 100 m between after end of CPC. Net displacement: total Euclidean distance for trial. Net displacement CPC: Euclidean distance CPC.

Models

We used general linear models (GLM) to assess and model moose flight response. We focused on describing five flight response metrics including the mean velocity, duration, distance and net displacement of the PCPC. Additionally, we tested if a moose leaves their 99% home range as an escape tactic. Depending on the response variable of interest, we used a combination of explanatory variables such as wolf exposure, dog id, snow depth, presence of calf, distance to edge of home range, and duration CPC (Appendix 2).

Aikaike's information criterion (AIC), is a relative value, that describes how well the model fits the data, although, AIC values does not tell us how close the given model is to reality (Burnham and Anderson, 2002). We used AICc, instead of AIC, when ranking our models, because our sample size was relatively low (n =29) (Burnham and Anderson, 2002). The ΔAICc is a relative value to be used to compare and rank created models ($\Delta\text{AICc} = \text{AICc}_{\text{Best model}} - \text{AICc}_{\text{Model x}}$) with higher ΔAICc values indicating a poorer fit compared to the best model (Burnham and Anderson, 2002). We excluded all models with ΔAICc > 2 from final result (Burnham and Anderson (2002). If remaining models were nested, we performed a likelihood ratio test in order to test if the best model, given by AICc ranking, performed significantly better than the other remaining models (Huelsenbeck and Crandall, 1997). AICc-weight (ω) is the weight of evidence that favors the given model (Burnham and Anderson, 2002). That means that ω is the probability that the best model is the best model, with the given data as compared to other competing models (Link and Barker, 2006). Models were built with statistical software R 2.14.1 (R Development Core Team 2011), AICc ranking table created with package Multi-model interference (MuMIn) (Bartoń, 2013) and likelihood ratio test with package lmtest (Hothorn et al., 2013).

Result

Characteristics of moose flight response trials

We used 15 adult moose individuals in trials ($n_{male} = 2$; $n_{female} = 13$). Moose age ranged from 3 to 18 year ($\bar{x} = 8$ years). All moose was classified into categories; “Calf” ($n_{calf} = 20$) or “No calf” ($n_{no\ calf} = 9$) depending on if calf was present or not during moose flight response trial with males classified as “No calf”. Of the 15 moose individuals; 5 individuals were tested 3 times, 4 individuals were tested 2 times and 6 individuals were tested 1 time (Appendix 1). In total, thirty four trials were conducted including 29 successful and 5 failed (Appendix 2). Of the 29 successful trials, 2 ended after dog flushed moose but no CPC occurred (CPC = 0). In the 27 remaining trials CPC ended because the dog either abandoned the moose track (n = 7), or started backtracking on itself (n = 11), or the moose outran the dog (n = 9). Wolf exposure was 5.4 times higher for the moose individual with highest wolf exposure (0.003070) compared to the moose with lowest wolf exposure (0.000480) (Table 1). Average wolf exposure for moose trial was 0.00138.

Table 1 Descriptive variables measured from moose flight response trials using Swedish elk hounds at Grimsö, Sweden 2010-2012. Mean , standard error (SE) and number of trials (n). Total: Value measured during whole trial. CPC: Value measured during close proximity chase. PCPC: Value measured during post close proximity chase. * Used as variable in generalized linear models

Variable	**Mean**	**Range**	**SE**	**n**
*Wolf exposure	0,00138	0.000480 – 0.003070	0.00012	29
Duration (total) [min]	133	50 – 560	19	29
*Duration (CPC) [min]	58	0 – 497	18	29
*Duration (PCPC) [min]	72	32 -210	8	29
Distance (total) [m]	4121	349 -9584	497	29
*Distance (CPC) [m]	2551	0 – 7497	349	29
*Distance (PCPC) [m]	1570	20 – 6756	322	29
*Net displacement (total) [m]	2185	235 – 6039	282	29
Net displacement (CPC) [m]	1593	0 – 3908	199	29
Net displacement (PCPC) [m]	1124	6 – 5045	233	29
Sinuosity (total)	0.60	0.08 – 0.88	0.04	29
Sinuosity (CPC)	0.74	0.34 – 1.00	0.05	27
Sinuosity (PCPC)	0.66	0.18 – 0.97	0.04	29
*Velocity (total) [m s^{-1}]	0.53	0.10 – 1.16	0.05	29
Velocity (CPC) [m s^{-1}]	1.33	0.13 – 4.8	0.18	27
Velocity (PCPC) [m s^{-1}]	0.29	0.009 – 0.75	0.04	29
Distance to edge when resettled [m]	1170	5 – 5498	331	16

Table 2 Dog name, number of successful trials with (total number of trials) and duration of chase ± SE in minutes of moose in Sweden 2010-2012.

Dog	Successful (total)	Duration
Ludde	13 (14)	70 ± 36 min
Tanja	11 (15)	58 ± 19 min
Ida	5 (5)	24 ± 7 min
Total	**29 (34)**	**58 ± 18 min**

During our study, duration of dog pursuit of moose ranged from 0 min (moose was flushed by dog but no chase ensued) to 497 min ($\bar{x}$ =58 ± 18 min) (Table 2). Some of this variation was due to individual dogs used where Tanja and Ludde pursued moose for a longer time then Ida (Figure 3).

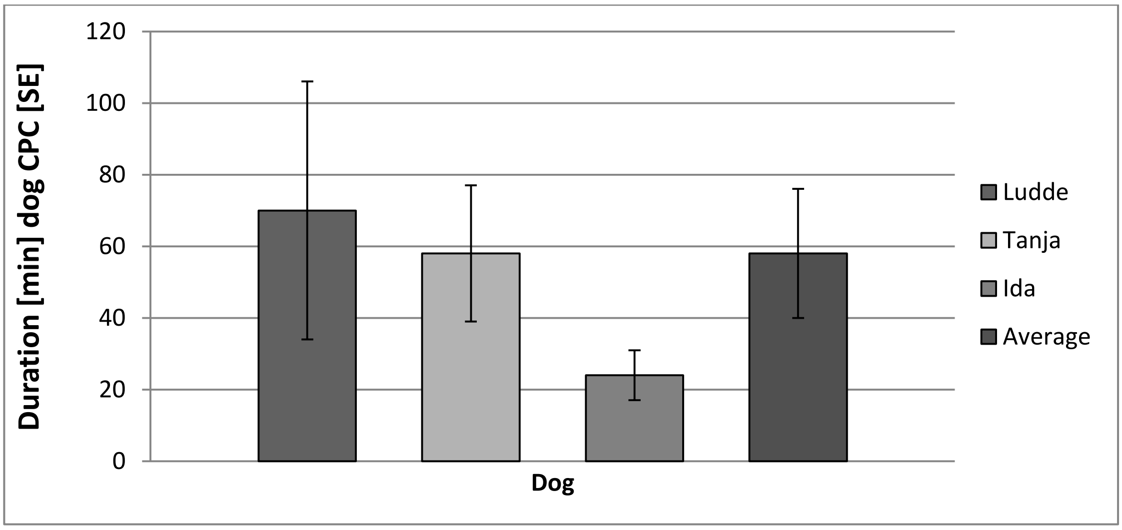

Figure 3 Individual dog and averaged duration [min] ± SE of the close proximity chase (CPC) during moose disturbance trials at Grimsö, Sweden 2010-2012.

The average total duration of all the flight response trials was 133 min, with the average total distance being 4121 m and with an average total net displacement of 2185 m. Average sinuosity were 0.60 and the average velocity 0.53 m s^{-1}. In 55% (16 of 29) of the trials, moose left their 30 day home range before resettling. Moose did not leave home range to re-settle as part of an escape tactic (Binomial test *P* = 0.71). For the 16 moose that re-settled outside their calculated 99 % 30 day home range, the average distance to edge of their home range was 1170 m (Table 1). The average CPC of a moose flight response trial lasted for 58 min, and during this time moose moved on average 2551 m. Net displacement from start to end of CPC were 1593 m, sinuosity 0.74 and velocity 1.33 m s^{-1}. On average it took 72 min from the end of CPC until moose was resettled. During PCPC moose moved on average 1570 m at a velocity of 0.29 m s^{-1} and with a sinuosity of 0.66. Moose net displacement, between last position of CPC and the first resettling position was 1124 m (Table 1).

Model selection

Velocity

As main effects, dog individual and the presence of a calf influenced moose escape velocity, whereas wolf exposure, snow depth and duration of CPC did not (Table 1). Our top ranked models (Table 3) were nested and although there was no significant difference found between them (Likelihood Ratio test *P*-value = 0.06), the more complex model (including calf presence) had a higher AIC weight than the less complex model only including dog individual. Moose velocity was on average 20% higher ($\bar{x}$ =0.58 ± 0.06 m s^{-1}) when moose was accompanied by calf, compared to when moose was not accompanied by calf ($\bar{x}$ =0.43 ± 0.08 m s^{-1}) (Figure 4). Depending on the dog used average velocity ranged from 0.68 ± 0.08 m s^{-1} to 0.41 ± 0.06 m s^{-1} (Figure 5).

Table 3 Beta estimates (β) and standard errors (SE) from an AICc ranking the general linear models testing total velocity [m s^{-1}] for moose during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. Models included with ΔAICc < 2. Prediction variables: Dog: dog individual. Calf: Calf present during trial. Intercept: = null model

Model	**Dog Tanja β ± SE**	**Dog Ludde β ± SE**	**Calf Yes β ± SE**	**Df**	**AICc**	**ΔAICc**	**ω**
6	0.17 ± 0.12	-0.11 ± 0.12	0.17 ± 0.09	5	4.539	0	0.328
3	0.14 ± 0.13	-0.13 ± 0.12		4	5.171	0.63	0.239

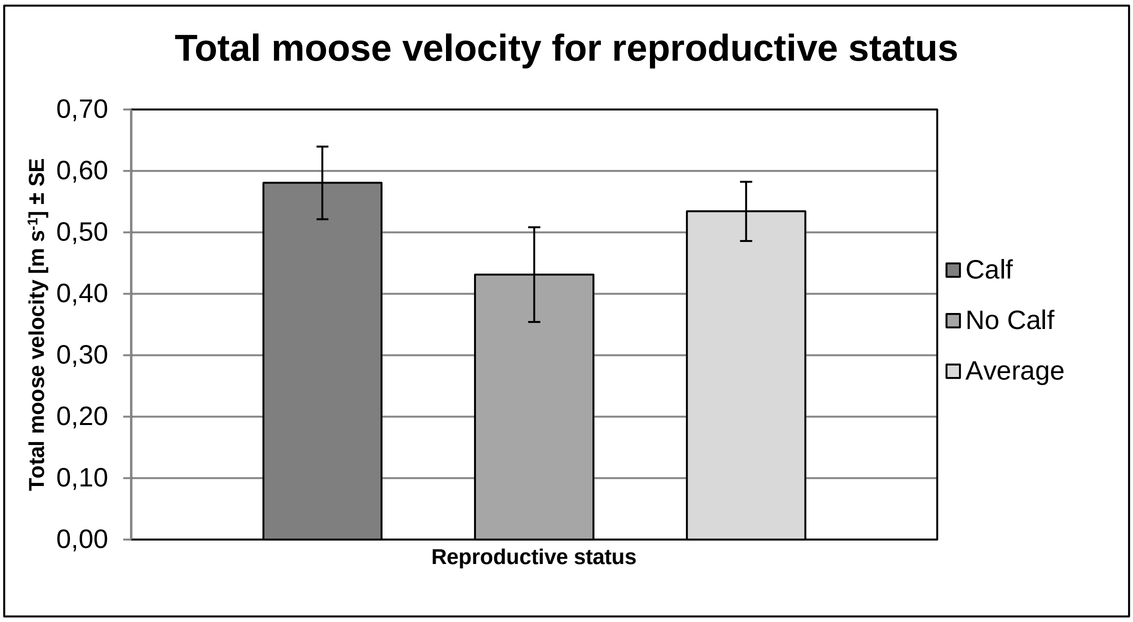

Figure 4 Moose reproductive status (Calf or No Calf) and average moose velocity ± SE for moose flight response trials (n = 29) conducted at Grimsö, Sweden 2010-2012

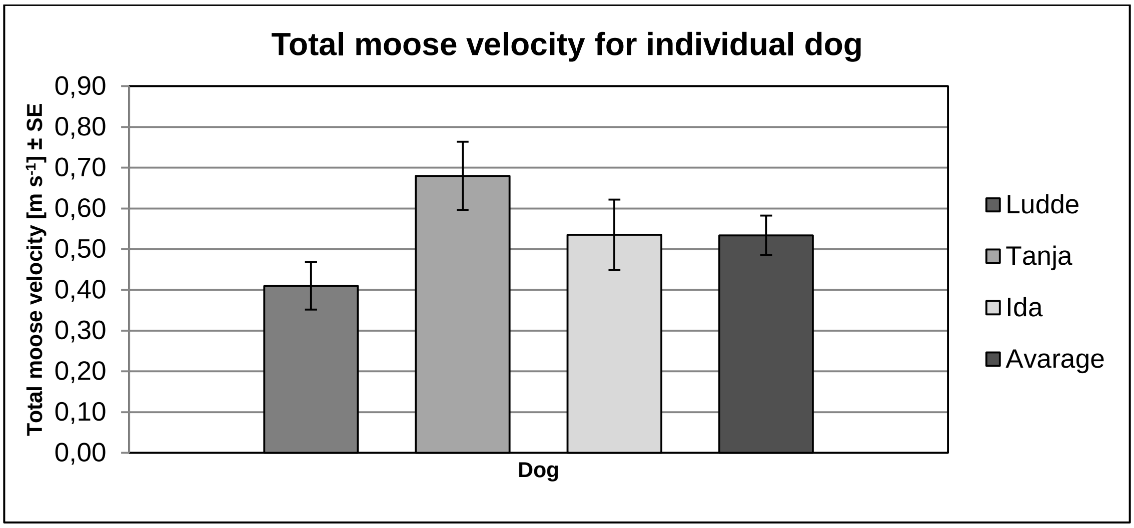

Figure 5 Individual dog and averaged velocity [m s^{-1}] ± SE of the close proximity chase (CPC) during moose disturbance trials (n =29) at Grimsö, Sweden 2010-2012.

Net Displacement

As with velocity total moose net displacement was affected by the dog used during trial and the presence of a calf during the trial (Table 4). Wolf exposure, snow depth and duration of CPC did not influence total net displacement. We were unable to distinguish between model 3 and model 6 (Likelihood Ratio test *P*-value = 0.12) but both model 3 (Likelihood Ratio test *P*-value = 0.03) and model 6 (Likelihood Ratio test *P*-value = 0.02) were significantly more likely to fit the data than model 1(Table 4). Thus, the null model was excluded from being the best model. Total net displacement was 38% longer when moose was accompanied by calf ($\bar{x}$ =2388 ± 358 m), compared to when moose was not accompanied by calf ($\bar{x}$ =1734 ± 431 m) (Figure 6). Depending on the dog used mean net displacement ranged from 3061 ± 585 m to 1406 ± 295 m (Figure 7).

Table 4 Beta estimates (β) and standard errors (SE) from an AICc ranking the general linear models testing total net displacement [m] during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. Models included with ΔAICc < 2. Prediction variables: Dog: dog individual. Calf: Calf present during trial. Intercept: = null model

Model	Intercept	Dog Tanja β ± SE	Dog Ludde β ± SE	Calf Yes β ± SE	Df	AICc	ΔAICc	ω
3		1655 ± 754	337 ± 735		4	508.9	0	0.285
6		1789 ± 742	426 ± 721	821 ± 553	5	509.4	0.49	0.223
1	Intercept				2	510.7	1.86	0.113

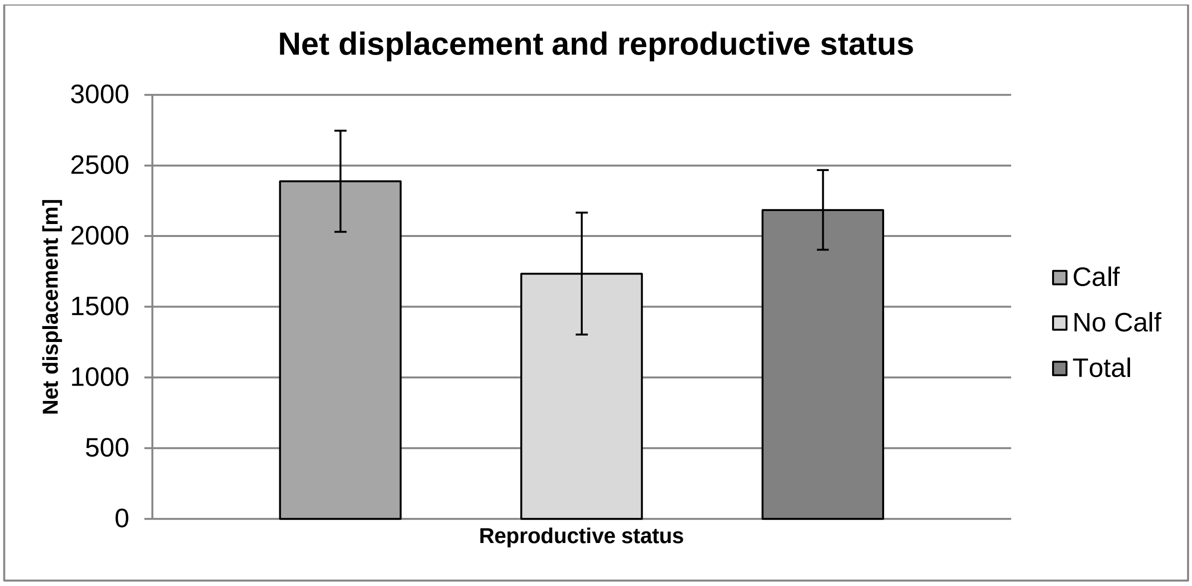

Figure 6 Moose reproductive status (Calf or no calf) and average total net displacement [m] ± SE for moose flight response trials (n = 29) conducted at Grimsö, Sweden 2010-2012.

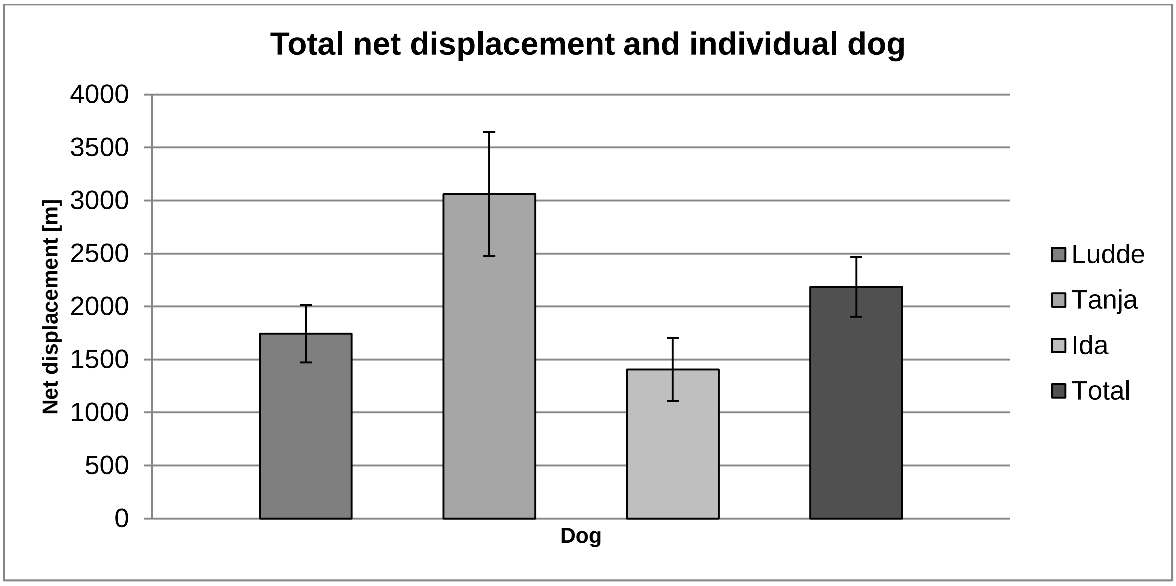

Figure 7 Individual dog and average total net displacement [m] ± SE for moose flight response trials (n = 29) conducted at Grimsö, Sweden 2010-2012.

Post Close Proximity Chase Variables

I tested if any predictor variables were able to explain the variation in distance PCPC (Table 5), duration PCPC (Table 6), and if moose resettled outside its 30 day home range (Table 7). For all the variables the null model had the lowest AICc value which is indicative of poorly fit models and that we were unable to identify factors important for variation in this variable.

Table 5 AICc ranking of general linear models testing total distance of post close proximity chase [m] during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. Models included with ΔAICc < 2. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Calf: Calf present during trial. Snow depth: Depth of snow [cm]. Duration CPC: Duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	ω
1	Intercept						2	518.3	0	0.208
7				Snow depth		Duration CPC	4	518.7	0.35	0.175
2		Wolf exposure					3	518.8	0.43	0.168
3			Dog				4	520.2	1.83	0.084

Table 6 AICc ranking of general linear models testing total duration of post close proximity chase [m] during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. Models included with ΔAICc < 2. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Calf: Calf present during trial. Snow depth: Depth of snow [cm]. Duration CPC: Duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	ω
1	Intercept						2	306	0	0.265
7				Snow depth		Duration CPC	4	306.5	0.56	0.200
2		Wolf exposure					3	307.1	1.14	0.150

Table 7 AICc ranking of general linear models testing; if moose leaves home range or not during moose flight response trial chase. 2010 – 2012 at Grimsö wildlife research area. Models included with ΔAICc < 2. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Calf: Calf present during trial. Distance to edge: Euclidean distance [m] moose re-settled, from closest home range border. If moose resettled in home range distance to edge = 0 m Duration CPC: Duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Calf	Distance to edge	Duration CPC	Df	AICc	ΔAICc	ω
1	Intercept						1	42.04	0	0.273
6						Duration CPC	2	43.73	1.7	0.116
4				Calf			2	43.75	1.71	0.116
5					Distance to edge		2	43.76	1.72	0.115

Grimsö vs. Västerbotten

We examined differences between our study, conducted at Grimsö 2010 – 2012, and a study conducted in Västerbotten 2006 (Neumann, 2009). Even though moose in our flight response trials showed the same overall pattern in their response of movement rate, as moose in Västerbotten (Figure 8), moose at Grimsö had significantly lower movement rate during the first two hours after the disturbance as compared to moose tested in Västerbotten (Figure 8). Next, we compared the linear distance between position of the moose initial to disturbance with the moose position after 1, 6, 12, 18 and 24 hours (Figure 9). Moose at Grimsö moved significantly shorter than moose in Västerbotten after hour 1, 12, 18 and 24 but not after 6 hours were there was no significant difference (Figure 9).

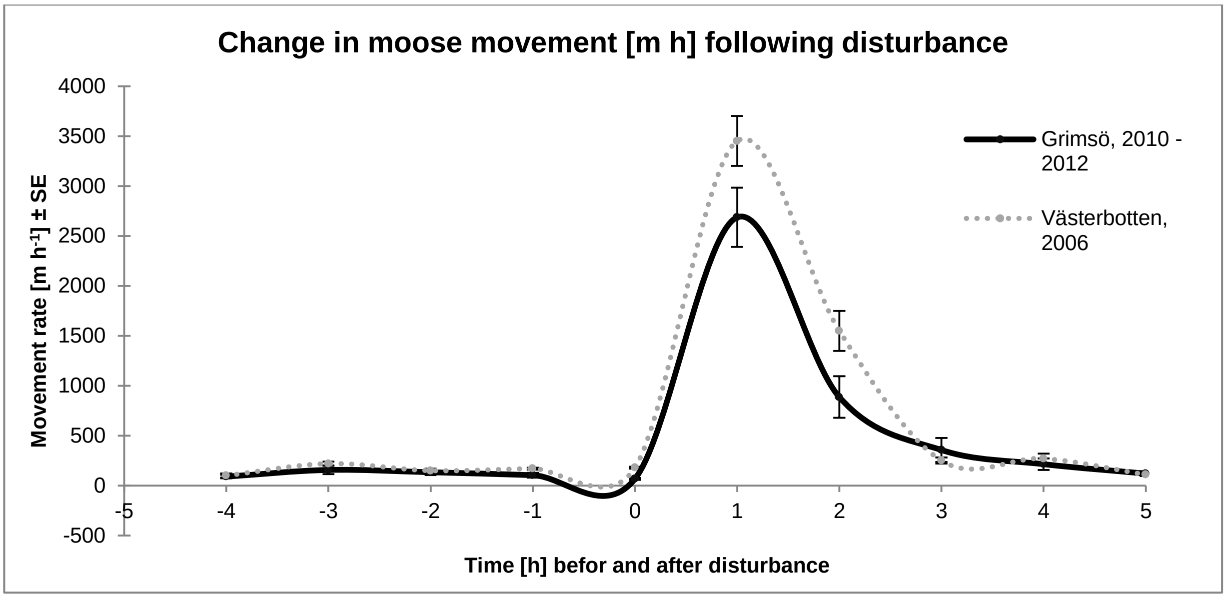

Figure 8 Comparative graph of change in moose movement rate [m h^{-1}] ± SE, before, during and after trial. Disturbance accurede = 0. Data collected during moose flight response trials at Grimsö, Sweden 2010-2012. Västerbotten data and SE visually retrieved from Neumann (2009).

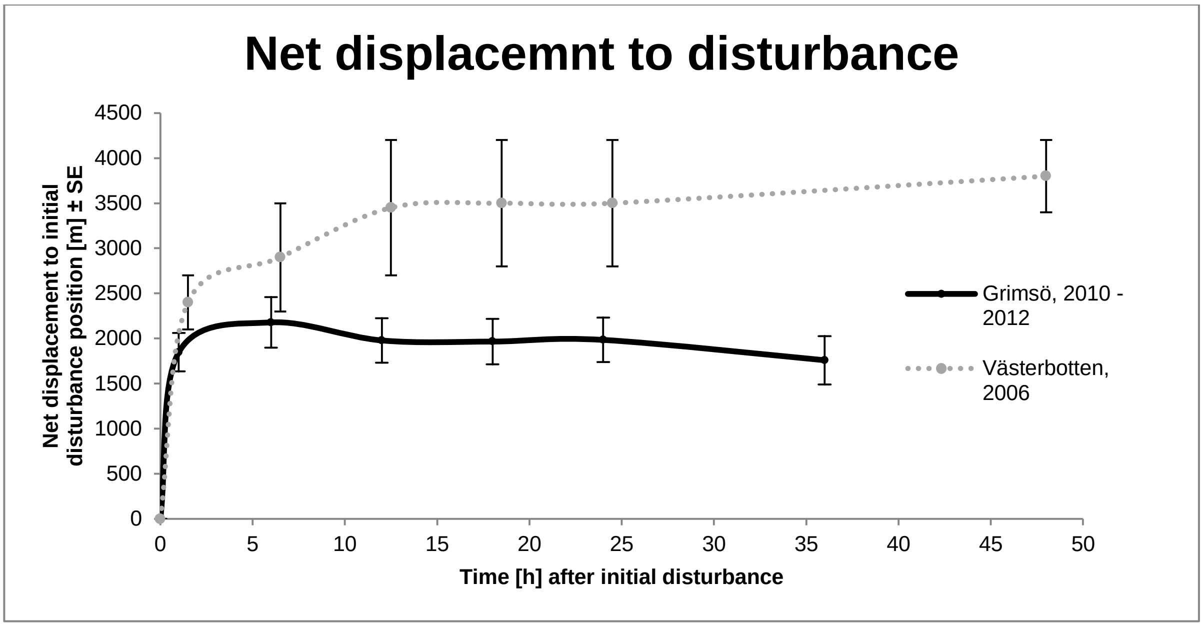

Figure 9 Linear distance [m] ± SE to initial disturbance. Distance measured at 1, 6, 12, 18, 24 and 36 h. Disturbance accrued = 0. Data collected during moose flight response trials at Grimsö, Sweden 2010-2012. Västerbotten data ± SE visually retrieved Neumann (2009)

Finally, we compared if there was a difference between Grimsö and Västerbotten with regard to the time it took for moose to resettle after the disturbance trial, and if the total net displacement or sinuosity of moose escape path differed (Table 8). However, we found no significant difference between Grimsö and Västerbotten for variables; time to re-settle and total net displacement. We were unable to compare total sinuosity because no SE was available for total sinuosity in Neumann (2009).

Table 8 Comparative data from Grimsö, 2010-2012 and Västerbotten (Neumann, 2009). Mean-values of time to re-settle [min] ± SE, net displacement [m] ± SE and sinuosity of moose escape path. All values measured from start moose flight response trial to end of moose flight response trial.

	Time to re-settle (min)	**Total net displacement (m)**	**Total sinuosity**
Grimsö, 2010 - 2012	133 ± 19	2185 ± 282	0.60 ± 0.04
Västerbotten, 2006	133 ± 16	2570 ± 507	0.55

Discussion

I hypothesized that a relatively higher previous exposure to wolves in the Grimsö moose population would affect the flight behavior of moose. In contrast, the results of my study suggest that moose flight behavior during hunting with baying dog, in our study area, was not related to amount of exposure to wolves. Hence, the results did not support my main hypothesis.

Wolves have recolonized south-central Sweden after being gone for ~100 years. When big predators like wolves return to an area prey may in a short period of time (i.e., a few years) regain their anti-predatory behavior (Berger, 1999, Laundré et al., 2001). Such a rapid change in behavior has not yet been identified in Sweden. I suggest that the moose flight behavior we see in my study is more a result of an adaptation to the combined effect of historical human harvest and the long-term evolutionary force of large carnivore predation rather than by the recent colonization by wolves. Important to this is the fact that humans have by far been the most important predator on moose in Sweden for ~150 years. With hunting being the main mortality factor for moose in Sweden (Ericsson and Wallin, 2001) and man being the most abundant predator in the system, we should expect to see a response by moose that is strongly shaped by human predation (Lima, 1992). Because of high turnover rate in the moose population due to high hunting pressure (Ericsson and Wallin, 2001, Wabakken et al., 2001), a change in moose escape behavior due to recent wolf colonization may not be likely in the nearby future. Additionally, the system has a high moose density and a relatively low wolf density (Eriksen et al., 2009) and the average out take of moose in wolf territories is estimated to be < 25-50% of the annual moose harvest (Solberg et al., 2003). This relatively low mortality by wolves, compared to human harvest, will limit the possibility to adapt to wolf predation and the advantage of doing so. So, even though fleeing may ,under some circumstances, be disadvantageous when confronted with a wolf (Peterson, 1977) it may still likely be the best strategy when confronted with wolf-like predator.

Moose showed a sinuous escape pattern in there flight with the cumulative flight distance almost being double the total net displacement. Moving in a sinuous pattern is probably a tactic evolved by prey to escape predators (Baskin et al., 2004). By fleeing in a sinuous pattern moose will increase the chance of losing a perusing dog by crossing another animal’s track and in that way make the dog switch to another animal (Cederlund and Kjellander, 1991, Ruusila and Pesonen, 2004). Moose in Västerbotten also showed a sinuous escape pattern (0.55) indicating that moose in Västerbotten and at Grimsö utilize the same pattern of escape tactic.

At Grimsö the size of moose hunting units commonly are 1.5 – 3 km^2 and a circle with an area of 3 km^2 has a radius of 1954 m. This means that with average total net displacement being 2185 m a moose would be able to leave most hunting units, regardless of the moose initial position in the hunting unit.

Variation in the approach and behavior of the predator is thought to affect the outcome of a predator-prey encounter (Stankowich and Coss, 2007). We used three different dogs of different sex, age, hunting experience and physical condition. We should therefore expect to see an effect of different dog individuals. Velocity can be a measurement of fear in a prey, but is also influenced by predator behavior (Ydenberg and Dill, 1986). In this study, dog id was included as variable in the two top models for velocity (Table 3) so the velocity of the chased moose was affected by what individual dog was used in trial. Velocity was also positively affected by the presence of a calf. Moose cows with a calf must take the physically weaker calf in to consideration when assessing the situation (Bouskila and Blumstein, 1996). A possible explanation is that the cows concern for the calf increases the amount of stress; therefore we see an increase in velocity when a calf is present during trial. By having a higher velocity during flight the moose cow attempts to out run the following predator and thereby lower the risk of being killed. Calves are physically weaker than adults and a preferred prey by wolves preying on moose (Peterson, 1977, Sand et al., 2005). The amount of energy a moose cow decides to invest in flight should therefore be more based on predation risk for the calf rather than her own risk.

For net displacement dog and calf came out as the two most important variables, followed by the null model. The presence of the null model indicates that even though dog and calf was included in the AICc selection, these variables was not very important as predictors of net displacement. When tested, calf or no calf had no significant effect on net displacement. However, the individual dog did have a significant effect. The trials with Tanja present had a significantly longer net displacement (3061 m) compared to Ludde (1744 m) and Ida (1406 m).

In Duration PCPC, Distance PCPC and whether or not moose left home range, the null model came out as the best model. This means that we were unable to identify any variables that were important for explaining the variation in duration of PCPC, Distance PCPC and whether or not moose left home range.

Overall, we found a similar response behavior of moose to hunting dogs in both this study and in the Västerbotten study. We found no difference between moose populations in Grimsö and Västerbotten with regard to time to re-settle, net displacement to initial disturbance when re-settled and sinuosity of flight (Table 8). In contrast, we had a significant difference in moose movement rate after disturbance and in net displacement after disturbance. A change in movement rate was clearly visible for as long as two hours after the initial disturbance (Figure 8). When comparing the two areas Västerbotten showed the same pattern as Grimsö with increased movement rate in hour one and two. However, Västerbotten showed a significantly higher movement rate hour one and two, compared to Grimsö. We also found that moose in Västerbotten had significantly higher net displacement to the initial disturbance position, when net displacement was measured after 1, 12, 18 and 24 h, but the difference after 6 hours was not significant (Figure 9). However, since we did not see a difference between Grimsö and Västerbotten when net displacement between initial disturbance point and resettling point was measured these results are hard to interpret. If moose have adapted their behavior to human harvest and the distance of net displacement (Figure 9) would be affected by the success of moose being able to leave the hunting unit, we should expect moose in Västerbotten to have a longer net displacement than at Grimsö. This is because hunting units in Västerbotten are generally larger than those at Grimsö, which means that moose have to move longer to exit the hunted area. One could also speculate that moose have a preferred habitat to resettle in. If this is the case, the landscape at Grimsö might be more fragmented compared to Västerbotten and have smaller landscape patches. Preferred habitat for moose to resettle in might therefore be in closer range at Grimsö then in Västerbotten.

To summarize, we tested how moose behavior, in terms of metrics associated with distance and time, was affected by previous exposure to wolves' presence as well as to other factors during trials with hunting dogs. We found no effect of wolf exposure on moose flight behavior of the variables measured. We were therefore unable to find support for our main hypothesis. Because harvest have been the main mortality factor for moose for a long time in south central Scandinavia (Sand et al., 2006, Milner et al., 2005) harvest will most likely still have an overriding effect shaping the behavior of moose. However, we cannot rule out the possibility that wolves affect moose in other ways than we have been able to measure their behavior during flight. It has been shown in other systems that when wolves and humans hunt the same prey, both wolves and humans affect the behavior of the prey, but that humans may have a stronger effect (Proffitt et al., 2009). It is also possible that the effects of wolf predation on moose behavior are too subtle to detect with our methods or that we failed to identify the right variables to detect the effects of the wolf exposure. Future studies should examine if moose have a preferred habitat to escape through and if exposure to wolves might affect that or what kind of habitat, moose prefer to resettle in after a disturbance. Interestingly, we also did observations during the disturbance trials were moose occasionally used water (streams, rivers and lakes) as a barrier to escape from the dog. If and how moose actively utilize water to escape should also be a subject of interest in future research. In particular, we do not know if moose have the same response when confronted by a dog as they do when confronted by a wolf, i.e. if they may identify the type of the wolf-like predator. Hence, a closer examination of moose flight behavior during an actual wolf attacks should be of interest. Excluding the potential effect of humans from predator-prey research might exclude an important shaping factor of the system. Therefore, including humans as an important factor in future research might gain valuable information for the understanding of predator-prey interactions.

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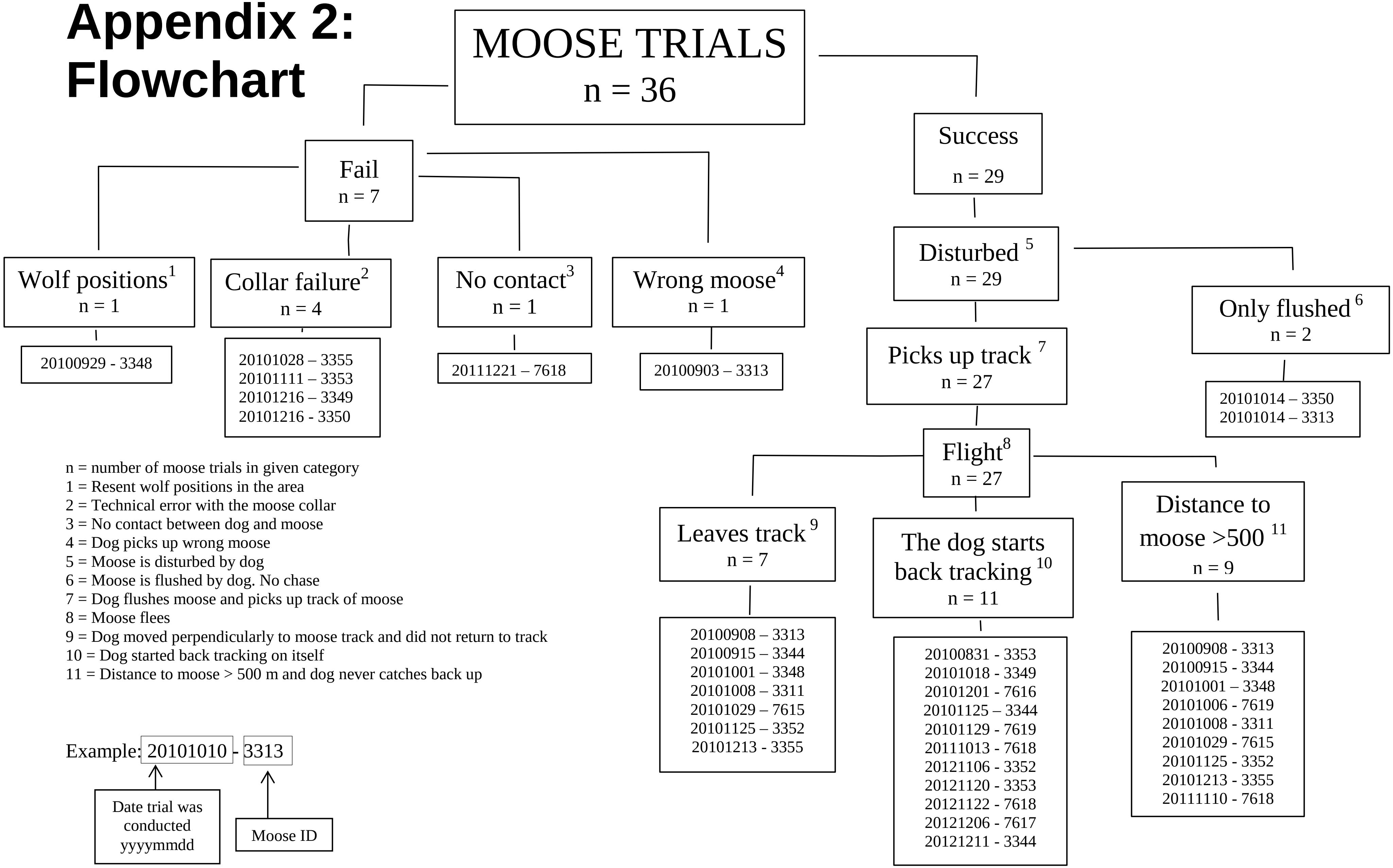
Appendix 1: Trial variables

Table 9 all trial variables extracted from moose disturbance trails conducted at Grimsö wildlife research area 2010 – 2012. Date: date of trail. Snow depth: Depth of snow [cm]. Individual: GPS-collar number. Moose-ID: moose identification number. Trial number: trials performed on moose. Age class: Age classification of moose (young, adult or old). Marked: year moose was equipped with GPS-collar. Dog: individual dog used in trial. Sex: sex of moose. Reproductive status: Calf present or no calf present during trail. Wolf exposure: linear transformed mean wolf UD value. Duration total: total duration of trial [min]. Duration CPC: Duration of close proximity chase [min]. Duration PCPC: Duration of post close proximity chase. Flight distance total: total flight distance [m]. Flight distance CPC: Flight distance close proximity chase [m]. Flight distance PCPC: Flight distance post close proximity chase [m]. Net displacement total: Total net displacement [m]. Net displacement CPC: net displacement close proximity chase [m]. Net displacement PCPC: net displacement post close proximity chase [m]. Sinuosity total: sinuosity of moose trial. Sinuosity PCP: Sinuosity of close proximity chase. Sinuosity PCPC: Sinuosity of post close proximity chase. Velocity: moose velocity during trial [m s^{-1}]. Velocity CPC: velocity of close proximity chase [m s^{-1}]. Velocity PCPC: velocity of post close proximity chase [m s^{-1}]. Leaves home range: If moose left home range (yes/no). Distance to edge start: distance to home range edge at start of trial [m]. Distance to edge re-settled: distance to home range edge when re-settled [m].

Date	Snow depth	individual	Moose-ID	Trial nr	Age class	Age	Marked	Dog	Sex	Reproductive status	Wolf exposure	Duration total	Duration CPC	Duration PCPC	Flight distance total	Flight distance CPC	Flight distance PCPC
2010-08-31	0	3353	F07002	1	adult	5	2007	Ludde	Female	calf	0.00080	110	42	67	3039	2444	595
2010-09-08	0	3352	F01001	1	old	11	2007	Ludde	Female	calf	0.00098	190	47	141	5199	2392	2807
2010-09-08	0	3313	F07006	1	adult	9	2007	Tanja	Female	calf	0.00135	120	37	73	8373	5081	3291
2010-09-15	0	3344	F07010	1	adult	7	2007	Tanja	Female	calf	0.00130	250	153	90	9584	7497	2087
2010-09-16	0	7616	F98015	1	old	11	2010	Ludde	Female	no	0.00120	90	8	80	2362	776	1587
2010-09-23	0	3602	F10004	1	young	3	2010	Ludde	Female	calf	0.00097	100	36	60	3907	2832	1075
2010-10-01	0	3348	F10008	1	old	10	2007	Tanja	Female	calf	0.00163	120	85	34	6308	6268	40
2010-10-01	0	7617	F07014a	1	adult	3	2010	Ludde	Female	calf	0.00183	150	83	66	7215	4600	2616
2010-10-06	0	7619	F10009	1	old	11	2010	Tanja	Female	calf	0.00208	100	14	80	5666	2065	3601
2010-10-08	0	3311	F07011	1	adult	4	2007	Ludde	Female	no	0.00104	80	37	40	1960	1841	118
2010-10-14	0	3313	F07006	2	adult	9	2007	Ludde	Female	calf	0.00267	99	0	99	2221	0	2221
2010-10-14	0	3350	F07020	1	old	18	2007	Tanja	Female	no	0.00248	90	0	90	1311	0	1311
2010-10-18	0	3349	F07021	1	adult	7	2007	Ludde	Female	calf	0.00100	110	70	38	1514	1394	120
2010-10-29	0	7615	M07012a	1	old	12	2010	Ludde	Male	no	0.00088	560	497	61	5269	3730	1539
2010-11-04	0	3355	F07005	1	old	10	2007	Tanja	Female	calf	0.00070	230	192	33	4325	4213	112
2010-11-18	3	3353	F07002	2	adult	5	2007	Tanja	Female	no	0.00091	80	34	44	2287	2102	185
2010-11-25	12	3352	F01001	2	old	11	2007	Tanja	Female	calf	0.00091	110	46	62	5925	4226	1699
2010-11-25	12	3344	F07010	2	adult	7	2007	Ludde	Female	calf	0.00125	120	62	52	4938	4405	533
2010-11-29	21	7619	F10009	2	adult	8	2010	Ludde	Female	calf	0.00108	50	9	35	600	580	20
2010-12-01	24	7616	F98015	2	old	11	2010	Tanja	Female	no	0.00048	190	5	184	8196	1440	6756
2010-12-08	21	7617	F07014a	2	adult	3	2010	Tanja	Female	calf	0.00173	250	36	210	8688	3871	4817
2010-12-13	20	3355	F07005	2	old	10	2007	Ludde	Female	calf	0.00263	70	8	54	1571	656	915
2011-10-13	0	7618	M10011	1	adult	5	2010	Ludde	Male	no	0.00121	60	15	38	349	275	74
2011-11-10	0	7618	M10011	2	adult	5	2010	Tanja	Male	no	0.00122	90	37	52	3406	2107	1299
2012-11-06	0	3352	F01001	3	old	13	2007	Ida	Female	calf	0.00111	80	31	43	3222	2777	445
2012-11-20	0	3353	F07002	3	adult	7	2007	Ida	Female	calf	0.00088	60	14	36	871	765	106
2012-11-22	0	7618	M10011	3	adult	6	2010	Ida	Male	no	0.00118	70	16	52	2994	2500	493
2012-12-06	26	7617	F07014a	3	adult	5	2010	Ida	Female	calf	0.00153	50	10	32	1347	1247	100
2012-12-11	26	3344	F07010	3	adult	9	2007	Ida	Female	calf	0.00307	190	48	132	6858	1888	4970

Date	individual	Moose-ID	Net displacement total	Net displacement CPC	Net displacement PCPC	Sinuosity total	Sinuosity CPC	Sinuosity PCPC	Velocity	Velocity CPC	Velocity PCPC	Leaves Home range	Distance to edge start	Distance to edge resettled
2010-08-31	3353	F07002	2365.418	2348.942	575.9253	0.778464	0.961112	0.9686127	0.46039	0.969835	0.147907	yes	361.54325	5.046661
2010-09-08	3352	F01001	2775.313	906.3598	2444-538	0.533791	0.378903	0.8708153	0.456074	0.84825	0.331818	yes	1254.5738	1512.2271
2010-09-08	3313	F07006	4394.147	2448.904	1961.772	0.524827	0.481946	0.5960517	1.162855	2.288864	0.751433	no	764.94743	1574.8877
2010-09-15	3344	F07010	2469.304	1090.206	1617.659	0.257653	0.14542	0.7751404	0.638923	0.816658	0.386467	yes	712.14787	201.2707
2010-09-16	7616	F98015	1498.741	775.6907	997.5081	0.634417	1.000001	0.6286676	0.43748	1.616021	0.330563	yes	519.41115	254.13174
2010-09-23	3602	F10004	3289.426	2737.941	582.7255	0.841944	0.96691	0.5419175	0.651157	1.310944	0.298695	no	298.95852	394.36432
2010-10-01	3348	F10008	3189.516	3169.985	21.91207	0.505605	0.50571	0.5487702	0.876155	1.229095	0.019573	yes	146.52571	1154.6508
2010-10-01	7617	F07014a	957.1851	1555.801	2261.243	0.13266	0.338238	0.8645257	0.801701	0.923639	0.660502	no	400.48487	469.03054
2010-10-06	7619	F10009	3735.212	2064.904	3089.93	0.659255	0.999897	0.8581494	0.944301	2.458471	0.750144	yes	502.19928	1186.7351
2010-10-08	3311	F07011	1491.727	1482.513	21.4916	0.761229	0.805194	0.1814502	0.408256	0.829363	0.049351	no	596.23937	1132.8218
2010-10-14	3313	F07006	1707.329	0	1707.329	0.768741	0	0.7687409	0.373896	0	0.373896	no	507.77567	1025.8815
2010-10-14	3350	F07020	545.35	0	545.35	0.415981	0	0.4159814	0.242777	0	0.242777	no	200.88635	212.95675
2010-10-18	3349	F07021	1205.221	1290.678	87.66413	0.79626	0.925885	0.7329176	0.229334	0.331903	0.05246	no	317.94788	634.65072
2010-10-29	7615	M07012a	2414.111	2039.342	1343.582	0.458199	0.546784	0.873029	0.156806	0.125074	0.420489	yes	493.22822	1166.7298
2010-11-04	3355	F07005	336.2142	343.1275	30.51492	0.077732	0.081447	0.2714945	0.313428	0.365704	0.056766	no	243.36358	356.87734
2010-11-18	3353	F07002	775.1811	871.9172	142.9812	0.339024	0.414805	0.7749075	0.476356	1.030389	0.069892	no	542.41959	464.54193
2010-11-25	3352	F01001	5228.853	3908.476	1336.402	0.882532	0.924835	0.7867204	0.897702	1.531208	0.45664	yes	513.24714	1377.1353
2010-11-25	3344	F07010	3077.046	3173.375	352.0813	0.623167	0.720458	0.6604487	0.6858	1.18405	0.170863	yes	667.61429	2031.4539
2010-11-29	7619	F10009	422.412	419.1098	5.890199	0.704041	0.722463	0.2964337	0.199994	1.074282	0.009462	no	806.07365	1167.5856
2010-12-01	7616	F98015	4517.385	1440.408	5045.005	0.551146	1	0.7467509	0.718978	4.80136	0.611951	yes	148.22333	1701.893
2010-12-08	7617	F07014a	6039.162	3612.067	3167.866	0.695134	0.933222	0.6576106	0.579185	1.791913	0.38232	yes	328.35085	5498.2529
2010-12-13	3355	F07005	1228.272	649.4096	601.7829	0.781877	0.990558	0.6574503	0.37403	1.365833	0.280689	yes	778.59113	83.15851
2011-10-13	7618	M10011	234.9605	221.9234	13.20757	0.67364	0.806311	0.1795497	0.096887	0.305815	0.032263	no	1171.3186	1161.3168
2011-11-10	7618	M10011	2440.163	1448.29	1034.782	0.716499	0.687521	0.7965137	0.630681	0.948891	0.416391	no	1703.0863	358.77824
2012-11-06	3352	F01001	2419.275	2580.359	219.1803	0.750864	0.929282	0.4922449	0.671248	1.492861	0.172584	yes	565.04242	1453.0392
2012-11-20	3353	F07002	765.115	760.3548	71.92218	0.878461	0.994359	0.6765721	0.241937	0.91032	0.049215	no	381.54214	173.23631
2012-11-22	7618	M10011	1687.787	1804.507	414.8361	0.563807	0.721737	0.8408886	0.712752	2.604403	0.158119	yes	496.9506	415.57835
2012-12-06	7617	F07014a	1149.379	1246.644	97.30493	0.853238	0.999885	0.9702259	0.449026	2.07798	0.052235	yes	190.15876	243.14048
2012-12-11	3344	F07010	1007.901	1818.354	2812.242	0.146958	0.96288	0.5658461	0.601617	0.655713	0.627522	yes	532.11616	441.97889

Appendix 2: Flowchart



n = number of moose trials in given category
1 = Resent wolf positions in the area
2 = Technical error with the moose collar
3 = No contact between dog and moose
4 = Dog picks up wrong moose
5 = Moose is disturbed by dog
6 = Moose is flushed by dog. No chase
7 = Dog flushes moose and picks up track of moose
8 = Moose flees
9 = Dog moved perpendicularly to moose track and did not return to track
10 = Dog started back tracking on itself
11 = Distance to moose > 500 m and dog never catches back up

Appendix 3: Full AICc-models

Total velocity

Table 10 AICc ranking of general linear models testing total velocity [m s^{-1}] for moose during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. All models included. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Snow depth: snow depth [cm] during trial. Calf: Calf present during trial. Duration CPC: duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	ω	Ranking
6			Dog		Calf		5	4.539	0	0.328	1
3			Dog				4	5.171	0.63	0.239	2
11			Dog			Duration CPC	5	6.951	2.41	0.098	3
1	Intercept						2	7.545	3.01	0.073	4
4					Calf		3	7.84	3.3	0.063	5
8		Wolf exposure	Dog				5	7.951	3.41	0.060	6
2		Wolf exposure									
5						Duration CPC					
7				Snow depth		Duration CPC					
9		Wolf exposure			Calf						
10		Wolf exposure				Duration CPC					
12		Wolf exposure	Dog			Duration CPC					
13		Wolf exposure	Dog	Snow depth		Duration CPC					
14		Wolf exposure	Dog		Calf	Duration CPC					

Distance PCPC

Table 11 AICc ranking of general linear models testing distance of close proximity chase during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. All models included. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Snow depth: snow depth [cm] during trial. Calf: Calf present during trial. Duration CPC: duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	Ω	Ranking
1	Intercept						2	518.3	0	0.208	1
7				Snow depth		Duration CPC	4	518.7	0.35	0.175	2
2		Wolf exposure					3	518.8	0.43	0.168	3
3			Dog				4	520.2	1.83	0.084	4
8		Wolf exposure	Dog				5	520.5	2.16	0.071	5
5						Duration CPC	3	520.7	2.4	0.063	6
4					Calf		3	520.8	2.47	0.061	7
6			Dog		Calf						
9		Wolf exposure			Calf						
10		Wolf exposure				Duration CPC					
11			Dog			Duration CPC					
12		Wolf exposure	Dog			Duration CPC					
13		Wolf exposure	Dog	Snow depth		Duration CPC					
14		Wolf exposure	Dog		Calf	Duration CPC					

Duration PCPC

Table 12 AICc ranking of general linear models testing duration of close proximity chase during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. All models included. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Snow depth: snow depth [cm] during trial. Calf: Calf present during trial. Duration CPC: duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	ω	Ranking
1	Intercept						2	306	0	0.265	1
7				Snow depth		Duration CPC	4	306.5	0.56	0.200	2
2		Wolf exposure					3	307.1	1.14	0.150	3
5						Duration CPC	3	308.1	2.19	0.089	4
4					Calf		3	308.4	2.5	0.076	5
3			Dog				4	309	3.03	0.058	6
6			Dog		Calf						
8		Wolf exposure	Dog								
9		Wolf exposure			Calf						
10		Wolf exposure				Duration CPC					
11			Dog			Duration CPC					
12		Wolf exposure	Dog			Duration CPC					
13		Wolf exposure	Dog	Snow depth		Duration CPC					
14		Wolf exposure	Dog		Calf	Duration CPC					

Net displacement total

Table 13 AICc ranking of general linear models testing total net displacement of moose during moose flight response trial 2010 – 2012 at Grimsö wildlife research area. All models included. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Snow depth: snow depth [cm] during trial. Calf: Calf present during trial. Duration CPC: duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Snow depth	Calf	Duration CPC	Df	AICc	ΔAICc	ω	Ranking
3			Dog				4	508.9	0	0.285	1
6			Dog		Calf		5	509.4	0.49	0.223	2
1	Intercept						2	510.7	1.86	0.113	3
8		Wolf exposure	Dog				5	511.3	2.42	0.085	4
11			Dog			Duration CPC	5	511.8	2.94	0.066	5
4					Calf		3	512	3.14	0.059	6
2		Wolf exposure									
5						Duration CPC					
7				Snow depth		Duration CPC					
9		Wolf exposure			Calf						
10		Wolf exposure				Duration CPC					
12		Wolf exposure	Dog			Duration CPC					
13		Wolf exposure	Dog	Snow depth		Duration CPC					
14		Wolf exposure	Dog		Calf	Duration CPC					

Leaving home range

Table 14 AICc ranking of general linear models testing; if moose leaves home range or not during moose flight response trial. 2010 – 2012 at Grimsö wildlife research area. All models included. Prediction variables: Wolf exposure: linear transformed mean wolf UD value. Dog: dog individual. Distance to edge: Euclidean distance [m] moose re-settled, from closest home range border. If moose resettled in home range distance to edge = 0 m. Calf: Calf present during trial. Duration CPC: duration of close proximity chase [min]. Intercept: = null model

Model	Intercept	Wolf exposure	Dog	Calf	Distance to edge	Duration CPC	Df	AICc	ΔAICc	ω	Ranking
1	Intercept						1	42.04	0	0.273	1
6						Duration CPC	2	43.73	1.7	0.116	2
4				Calf			2	43.75	1.71	0.116	3
5					Distance to edge		2	43.76	1.72	0.115	4
2		Wolf exposure					2	44.21	2.17	0.092	5
3			Dog				3	45.07	3.03	0.060	6
7		Wolf exposure		Calf							
8			Dog	Calf							
9				Calf	Distance to Edge						
10					Distance to edge	Duration CPC					
11		Wolf exposure	Dog								
12		Wolf exposure				Duration CPC					
13			Dog			Duration CPC					
14		Wolf exposure	Dog			Duration CPC					