Response distances of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.) and semi-domestic reindeer (*R. t. tarandus* L.) to direct provocation by a human on foot/snowshoes

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Abstract: The objective of the study was to examine response distances of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.) and semi-domestic reindeer (*R. t. tarandus* L.) in Finland and Norway to direct provocation by a human on foot/snowshoes in 5 areas and in 15 reindeer herding cooperatives during different seasons in 2010-12. There were no significant differences in mean herd size or in sight, alert, flight and closest response distances of wild forest reindeer in the Kuhmo and Suomenselkä areas. The encounter distance in wild forest reindeer was significantly ($P< 0.005$) longer than in semi-domestic reindeer in Finland and in Finnmark, Norway, and it increased with the group size. The sight and the alert distances in wild forest reindeer were significantly ($P< 0.001$) longer than in semi-domestic reindeer. In addition, the flight distance for wild forest reindeer (mean 192 m) was significantly ($P< 0.001$) and almost three times longer than in semi-domestic reindeer in Finland (mean 68 m). The closest mean distance was in wild forest reindeer 191m (range 100-320 m) but only 44 m (range 2-110 m) in semi-domestic reindeer ($P< 0.001$). The sight, alert, flight and closest response distances were slightly longer in Norwegian than in Finnish semi-domestic reindeer. However, these distances were significantly ($P<0.005$) longer in Pohjois-Salla (no supplementary feeding) than in other Finnish reindeer herding cooperatives and at the Kaamanen experimental station. The mean flight distance of reindeer in Pohjois-Salla was 115 m but only 65 m in other cooperatives ($P< 0.001$). The closest distance of semi-domestic reindeer in Pohjois-Salla (mean 105 m) was more than 2.5 times longer than in other reindeer herding cooperatives (mean 40 m). The mean sight, alert and flight distances in wild forest reindeer in autumn and winter were significantly longer ($P<0.005$) than in semi-domestic reindeer in Finland. However, during summer these distances in wild forest reindeer herds with young calves were significantly longer ($P<0.005$). The mean herd size of Finnish semi-domestic reindeer was almost the same in different seasons, but in wild forest reindeer it was slightly bigger during winter and spring and smaller during summer and autumn, only 7-23 reindeer. The mean encounter and sight distances in semi-domestic reindeer were significantly longer ($P<0.005$) in winter, but the mean alert and flight distances were almost the same in winter and summer and slightly longer than during other seasons. The results suggest that the supplementary feeding practice during winter may likely cause a reduction in flight distances in semi-domestic reindeer.

Key words: human disturbance; response behaviour; flight distance; *Rangifer tarandus*; wild forest reindeer; semi-domestic reindeer; seasons; supplementary feeding

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Introduction

There are many activities in which people may negatively influence the behaviour of wild *Rangifer tarandus*, and also affect their movement and subsequent range use (Wolfe *et al.,* 2000). Human activities and infrastructure contribute with noise for example from power lines, generators, windmills, and also from moving objects like humans on foot, snowshoes and skis, snowmobiles, four-wheelers, cars, aircrafts and helicopters. While roads alone are not likely perceived as a threat to reindeer, increasing roads and traffic are. During the last 30-40 years outdoor ecotourism, hiking, skiing and hunting have been expanding and increasing activities in more remote areas, including mountain habitats of wild and semi-domestic reindeer (Helle & Särkelä, 1993; Colman *et al.,* 2001; Reimers *et al.,* 2006). There have also been many changes in reindeer herding and husbandry practices over the last years, especially in Finland (Nieminen, 2006).

According to Baskin & Skogland (2001) reindeer are at an early phase of domestication, but semi-domestic reindeer generally exhibit more relaxed fright and flight behaviour compared to wild reindeer (Reimers *et al.,* 2000; 2006). Therefore, when comparing behaviour between different reindeer herds, it is important to know the origin and history of the herds in question. While the caribou subspecies are wild, the Fennoscandian tundra reindeer population includes many domesticated herds (Reimers & Colman, 2006). The semi-domestic reindeer herds in Northern Finland, Sweden and Norway, as well as the wild reindeer herds (with a mix of wild and domesticated origin) in Southern Norway, are originally Eurasian wild tundra reindeer (*Rangifer tarandus tarandus* L.). DNA-analyses by Røed et al. (2008) support independent origin of semi-domestic reindeer in Fennoscandia and Russia. The domestic gene pools seem to meet only in eastern Finland, mainly in Halla reindeer herding cooperative. However, the wild forest reindeer (*R. t. fennicus* Lönnb.) population in eastern Finland and the wild reindeer populations in central Norway have contributed little or nothing to the domestic gene pool (Røed *et al.,* 2008). Domestication is the first step of selection, and it is argued that domestication has mostly resulted in quantitative rather than qualitative changes (Mignon-Grasteau *et al.,* 2005).

Human activities affect reindeer/caribou through the senses of hearing, sight and smell. According to Flydal et al. (2001) the hearing capacity of reindeer ranges from 70 Hz to 38 kHz at a sound pressure of 60 dB. It means that almost all noises and vocalizations are readily perceived by reindeer. Reindeer as other ungulates has apparently also very good day and night vision. Reindeer most likely perceive colours, but no particular colour appears to be dominant, and reindeer probably are unable to distinguish between red and green colour. It is mainly contrasts and movements that betray human presence. Because the eyes of reindeer are laterally positioned, the combined visual fields of both eyes cover virtually 360º (Nieminen, 1994). It means that reindeer can also spot predators and humans sneaking up from behind. Reindeer´s laterally positioned eyes limit, however, the binocular visual field. Although reindeer´s sense of smell is not well documented, the capacity to capture scents even under unfavourable wind conditions is well known by reindeer/caribou hunters, hikers and also reindeer herders. Sometimes smell alone can trigger flight of reindeer without input from other senses. Reimers & Colman (2006) predicted that reindeer would also respond at greater distances to the directly approaching person when the wind carried the human scent to the reindeer than when the reindeer could not smell the human intruder. The strongly elevated nasals of the wild forest reindeer living only in forested regions indicate the very keen sense of smell due to increased olfactory mucous membranes (Nieminen, 1980).

It has long been recognized that learning plays an important role in the manner and degree to which ungulates respond to humans (Geist, 1971), and there are usually three major learned responses which also are valid for reindeer: habituation, attraction and avoidance. Domestication, habituation and sensitisation are essential in shaping adaptability of reindeer and caribou (Reimers & Colman, 2006). Many impact studies focus on the behavioural responses of wildlife to humans, because these attributes are generally more amenable to study than other forms of response (Bejder *et al.,* 2009). The cases of presumed habituation or sensitisation may actually represent differences in the tolerance level of wildlife to anthropogenic activity. For example reindeer show decreased flight responses in areas with relative high amounts of human activities (Colman *et al.,* 2001; Reimers *et al.,* 2009), indicating the ability to habituate to human activities. Habituation to humans would occur more readily in caribou populations that were not hunted and lived in areas lacking natural predators (Klein, 1980; Aastrup, 2000). Habituation and also former experiences with predators significantly influence an ungulate´s perception of threat. The populations with few predators flushed at greater distance than those where predators are common. All predator studies reviewed by Stankowich & Blumstein (2005) classified humans as the predator and measured differences in flight initiation distance between ungulate populations that differed with regard to human exposure. Wild ungulate populations like Svalbard reindeer (*R. t. platyrhynchus* Vrolik) exposed to a relatively high level of human activities have become habituated to humans in a non-threatening context (Tyler, 1991). They are likely to perceive less risk when approached by humans than would animals in populations where encounter with humans are rare (Colman *et al.,* 2001; Lund, 2008). Even though semi-domestic reindeer are disturbed by human activities, they can increase their tolerance towards humans if insect harassment is severe during summer (Skarin *et al.,* 2004). Rutting activities during autumn obviously also affect reindeer behaviour more than the directly approaching human observer (Reimers *et al.,* 2006).

Flight initiation distance is the distance at which an animal begins to flee from an approaching predator or human. It is usually used in studies, because it is easy to measure and correlates with other key aspects of escape behaviour e.g. alert distance (Blumstein *et al.,* 2005). According to Vistnes & Nellemann (2008) accurate assessment of impacts from human activity requires, however, regional-scale and usually long-term studies. The objective of the present study was to examine response distances of wild forest reindeer and semi-domestic reindeer in Finland and Norway to direct provocation by humans on foot or on snowshoes. The observations were collected during different seasons in areas subjected to combinations of high or low human activity, supplementary winter feeding or freely-grazing in the forests or on the fields. The objective was also to determine if flight distances have changed over the last years in response to increased human activity and supplementary feeding of semi-domestic reindeer on natural pastures or in corrals.

Material and methods

Study areas and reindeer herds

In total, 55 different reindeer herds were included in the present study: 17 wild forest reindeer herds (*Rangifer tarandus fennicus* Lönnb.) in the Suomenselkä area (9 in Perho, 1 in Kyyjärvi and 7 in Alajärvi municipalities) and 3 in Kuhmo municipality in the Kainuu area, 32 semi-domestic reindeer herds (*R. t. tarandus* L.) in 15 reindeer herding cooperatives in Finland including a herd at Kaamanen experimental station (150 reindeer, fenced area, 44 km^2), and

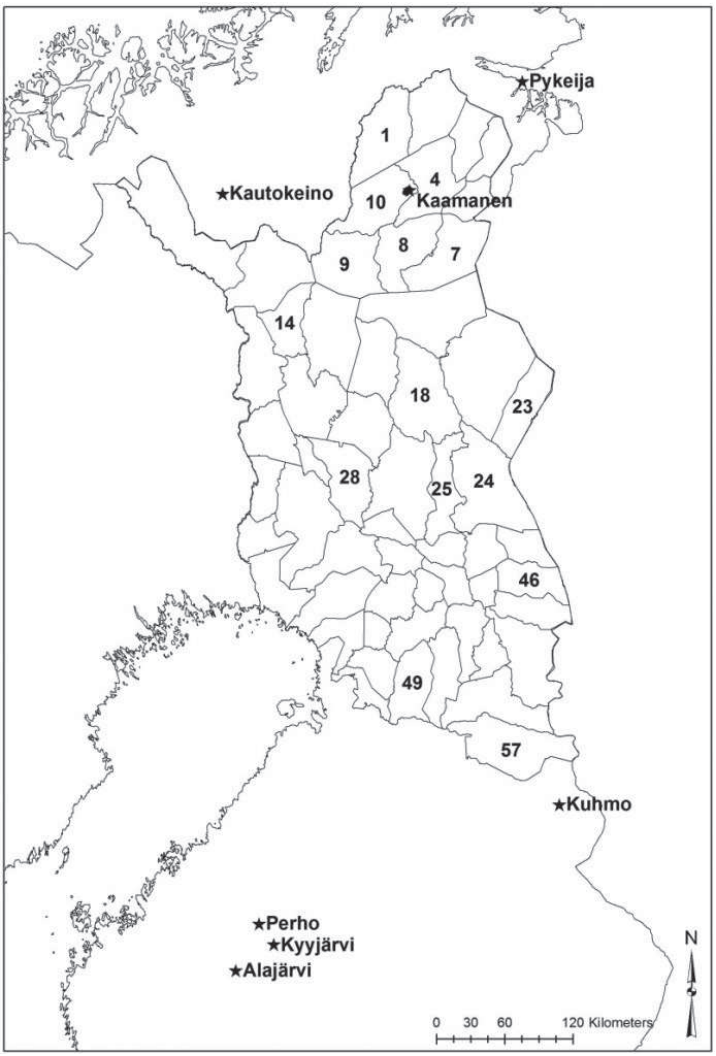

Fig.1. Study areas of wild forest reindeer in Kuhmo (64° 7′ N, 29° 31′ E) and Suomenselkä (Perho, Kyyjärvi and Alajärvi) (63°- 63° 13′ N, 24°-24° 25′ E) and of semi-domestic reindeer in reindeer herding cooperatives (1 = Paistunturi, 4 = Muddusjärvi, 7 = Ivalo, 8 = Hammastunturi, 9 = Sallivaara, 10 = Muotkatunturi, 14 = Kyrö, 18 = Oraniemi, 23 = Pohjois-Salla, 24 = Salla, 25 = Hirvasniemi, 28 = Poikajärvi, 46 = Oivanki, 49 = Pudasjärvi and 57 = Halla) (64°-70° N) and at the Kaamanen experimental station (69° 6′ N, 27° 11′ E) in Finland and in Kautokeino (69° N, 23° 2′ E) and Pykeija (69° 58′ N, 29° 38′ E) in Finnmark, Norway.

3 herds in Northern Norway (2 in Kautokeino, West-Finnmark and 1 in Pykeija, East-Finnmark) (Fig.1). Approximate herd size was 40 animals in wild forest reindeer and 115 animals in semi-domestic reindeer in Finland and Norway. The herds of wild forest reindeer were found with the help of GPS-collared females. In the studied reindeer herding cooperatives in Finland total numbers of counted reindeer varied between 2 200-8 300 animals. Reindeer herds were studied during different seasons in the central areas of the cooperatives. According to the reindeer herders these reindeer herds represent a mixture of animals owned by many herders (the animals have different earmarks), i.e. constitute of animals belonging to the main herd of the respective cooperative.

The wild forest reindeer disappeared from Finland for decades in the beginning of the 1900s. They came back to the Kuhmo area in the 1950s. During 1979-80 two forest reindeer males and eight females were transferred from Kuhmo to Salamajärvi National Park (Nieminen & Laitinen, 1983) and since then the population has increased in the Suomenselkä area to over 1 100 individuals. However, dur-

ing the last years the number of wild reindeer has decreased due to predation. In Kuhmo municipality, near the Russian border, the population of wild forest reindeer has also decreased, and the total number of reindeer is today about 900 (Kojola *et al.,* 2009). Northern Finland differs from the south mainly by the type of forest, but also by the elevated watershed areas in central and eastern Finland. Suomenselkä and Kainuu belong to the middle boreal vegetation zone (Ahti *et al.,* 1968). The landscapes are dominated by mires, and they are located on watersheds. Both areas are diverse in altitudes, mountains, hills and valleys, barren areas with forests, bogs and lakes. The landscapes are dominated by Norwegian spruce *(Picea abies)* and Scots pine *(Pinus sylvestris*) forests with ericaceous heather, lichen (*Cladonia, Cladina* spp.) and boggy areas. The northern reindeer herding cooperatives are situated in the north boreal vegetation zone (Ahti *et al.,* 1968). The terrain is dominated by rolling hills with different aged forest stands of mainly Scots pine. Mountain birch *(Betula pubescens czerepanowii)* grows in the slopes of the highest hills, and only the tops of the highest fells are barren. The cooperatives in the middle and southern parts of reindeer herding area belong, like Kainuu, to the middle boreal vegetation zone (Ahti *et al.,* 1968). Agriculture is common and there are many fields in the reindeer herding cooperatives and also in wild forest reindeer areas. Because the numbers of wild forest reindeer have decreased as described above, no reindeer was hunted during the study period in the Kuhmo and Suomenselkä areas.

In the reindeer husbandry area in Finland, and also in Finnmark, Norway, lichens pastures are generally strongly or very strongly worn (lichen biomass < 100-300 kg dry weight/ha) (Kumpula *et al.,* 2009; Mattila, 2006). As results of reindeer grazing, lichen ranges in mountain areas, large national parks, nature reserves and other wilderness areas are worn in Finland (Nieminen, 2010). In the northern cooperatives also the reindeer summer pastures are worn, and grazing has been the main reason to change vegetation and cause erosion in some places. The current condition of winter pastures in combination with a continuous state of change for the worse show that maintaining the current number of reindeer on their natural winter pasture is no longer possible. However, the body condition of reindeer in Finland has usually been good even during hard winters, due to the intensive supplementary feeding practised in the cooperatives. Totally over 40 million kg feed (calculated as dried hay) are used yearly during winters for feeding of semi-domestic reindeer, mainly on natural pastures or in corrals in the middle or southern reindeer herding cooperatives (Nieminen, 2006). Supplementary winter feeding of reindeer in Finnmark area, Norway, is not common, but in Finland only Pohjois-Salla reindeer herding cooperative has herded reindeer on the natural pastures without supplementary feeding during winters. The wild forest reindeer are freely-grazing in Suomenselkä and Kuhmo, and both winter and summer pastures are in rather good condition. In Kuhmo the amount of lichen biomass (dry weight) has over the last years been seven times higher than in the nearby Halla reindeer herding cooperative (Mattila, 2004). The road network in wild forest reindeer areas and also in reindeer husbandry areas are well developed, and every year some wild forest reindeer and over 4 000 semi-domestic reindeer die by traffic. Also, some adult wild forest reindeer and more than 4 000 semi-domestic reindeer are killed yearly by big predators in Finland (Nieminen, 2012).

Data collection

In 2010-12, during the four sampling periods of September-November (autumn and rutting period), February-March (winter), April (spring) and July (summer), a single and same

person (the observer) on foot or on snowshoes (used in deep snow), dressed in dark clothing, disturbed wild forest and semi-domestic reindeer during daylight hours by directly approaching them. The observer used binoculars and camera (Nikon D80) to document behaviour and places and measured later (using 1 m steps) response distances between the reindeer and the observer and the resultant distances by the reindeer after taking flight. Upon location of a group (≥ 4 reindeer), 10 parameters were recorded: 1) sample month, 2) group size (small: < 20 animals, medium: 20-49 animals, and large: >50 animals), 3) group composition (females and calves, males), 4) dominant activity of the group when first sighted (lying or grazing, rutting, moving), 5) wind direction relative to the observer (no wind, upwind or downwind), 6) vegetation type (open field, marsh, forest), 7) topography of the surrounding area (level, mountain, lake ice and feeding place), 8) visibility/weather (sunny, cloudy, raining/snowing), 9) snow depth and 10) temperature.

When a group of reindeer was first sighted, the observer took pictures, and used the so called direct approach method: advancing directly towards the centre of the group at a constant speed (about 4 km/hour) with < 10 second stops, to take pictures and later measured the four additional response distances defined below. When reindeer are first disturbed they show signs of awareness and fright by raising their heads and tails, urinating and sometimes jumping (deVos, 1960; Horejsi, 1981). The initial flight is often followed by curiosity behaviour: the disturbed reindeer circles around the intruder to catch the scent. All measurements were made from the position of the directly approaching observer to the nearest reindeer. The wildlife response distance terminology and methodology recommended by Taylor & Knight (2003) with the modifications following Reimers et al. (2003; 2009) were used in this study:

1) Encounter distance (END): the distance used as the starting point of the disturbance. The reindeer first discovers the provoker by sight or scent, indicated by looking, standing, turning their head or pausing from eating in a manner visible to the observer.
2) Sight distance (SD): the distance between the observer and closest reindeer when reindeer in the group displayed an alerted behaviour directed at the observer.
3) Alert distance (AD): the distance at which the reindeer group displayed an increased alert response by grouping together or by individuals urinating with one hind leg extended outward at an exaggerated angle, while staring at the directly approaching observer (Fig. 2).
4) Flight distance (FD): the distance from the directly approaching observer to the group when the reindeer initially took flight.
5) Closest distance (CD): the distance from the directly approaching observer to the nearest animal if a group approached the observer immediately before final withdrawal.
6) Escape distance (ED): the shortest straight-line distance from where the reindeer took flight in response to the observer to where the reindeer resumed grazing or bedded down.
7) Assessment time: the time elapsed from alert to flight initiation estimated from measured distances and assuming a constant observer speed of about 4 km/hour.

Statistical analyses

Initially, data of all areas and both wild forest reindeer and semi-domestic were pooled to analyse the effect of each factor on different distances separately. Correlation among dependent variables was tested with original (untransformed) data using Spearman rank correlation. The response variables (END, SD, AD, FD and CD) were first transformed into their natural logarithms prior to analysis. Sight, alert, flight and closest distances were analysed with Mixed Models Analysis. Marginal F-tests were

Fig. 2. The alert distance (AD) of a wild forest reindeer group in the Suomenselkä area, in February 2010. The reindeer group displayed an increased alert response by grouping together or by individuals urinating with one hind leg extended outward at an exaggerated angle, while staring at the directly approaching observer. Photo Mauri Nieminen.

used for the full models contained area, season, group size, wind direction relative to the observer, vegetation type and dominant activity of reindeer. To test for differences for provocation methods and to relate independent variables to reindeer responses, a mixed, stepwise analysis of ANOVA (analysis of variance) was used. χ^2 -test was used to assess the relative seasonal frequency in group-size classes. The statistical differences response distances in different groups were tested using *t*-test. Statistical tests were carried out by use of SPSS ver. 7.0 for Windows. The data were examined for statistical significance at $P<0.05$.

Results

During the four sampling periods in 2010-12 totally 55 independent reindeer groups were encountered and used in statistical analysis. A total of 2 216 reindeer were observed. Of these, 739 were wild forest reindeer and 1 477 semi-domestic reindeer.

Although 27 reindeer groups were encountered during autumn, these groups represented only 22 % of the groups in the large size class (> 50 animals) and 9.3 % of all of the reindeer sampled. During autumn, rutting season, most reindeer were in few large, mixed-sex groups. Totally 14 groups were encountered during winter, 50 % of the groups was in the large size class and represented 20 % of all studied reindeer. During spring and summer, 8 and 6 groups, respectively, were encountered, and only 1-2 groups were in the large size class. During summer, reindeer were distributed usually in small- and medium-sized female-calf

Table 1. Spearman rank correlation for the five dependent variables encounter (END), sight (SD), alert AD), flight (FD) and closest distance (CD).

	Encounter distance		Sight distance		Alert distance		Flight distance	
	r	*P*	r	*P*	r	*P*	r	*P*
Sight distance (SD)	0.843	0.001						
Alert distance (AD)	0.736	0.001	0.895	0.001				
Flight distance (FD)	0.699	0.001	0.867	0.001	0.960	0.001		
Closest distance (CD)	0.592	0.001	0.787	0.001	0.905	0.001	0.922	0.001

groups. Mean herd size of wild forest reindeer was 37, which was almost the same as for semi-domestic reindeer in Finland (mean 39). The groups observed in Norway (winter only) were bigger (mean 178 animals).

The encounter (END), sight (SD), alert (AD), flight (FD) and closest distance (CD) were positively correlated between areas, with a general decrease in the correlation coefficients from SD to CD (Table 1). FD increased with increasing encounter distance (END) (Table 2), as did also SD and AD, indicating that when the observer approached reindeer from farther away they responded at longer distances. No significant differences, depending on whether the approach was made on foot or on snowshoes in winter, were seen in any of the response distances. There were also no significant differences depending on area (Kuhmo and Suomenselkä) in mean herd size, END, SD, AD, FD or CD of wild forest reindeer. The Encounter distance (mean ± standard deviation) of wild forest reindeer (332 ± 24 m) was, however, significantly ($P< 0.005$) longer than that of semi-domestic reindeer in Finland and Norway (226 ± 13 and 250 ± 6 m, respectively) (Table 3). END increased with group size in both wild forest reindeer and semi-domestic reindeer. SD (253 ± 16 m) and AD (216 ± 13 m) in wild forest reindeer were significantly ($P< 0.001$) longer than in Finnish semi-domestic reindeer (144 ± 7 and 94 ± 6 m, respectively). The FD in

Table 2. Linear mixed-effects model for predicting flight-initiation distances (In transformed) of groups of wild forest reindeer and semi-domestic reindeer disturbed by anapproaching observer on foot/snowshoes in different areas in Finland and Norway in 2010-12.

Variable	Estimate	SE	df	t-value	*P*-value
Sight distance, Intercept	3.748	1.229	26	3.05	<0.005
Season (winter vs. autumn)	-0.555	0.463	26	-1.19	0.246
(winter vs spring)	-0.307	0.604	26	-0.51	0.612
(winter vs. summer)	-0.766	0.891	26	-0.96	0.348
Group size (large vs. small)	0.353	0.279	26	1.27	0.217
(large vs.medium)	0.157	0.205	26	0.77	0.451
Wind (no wind vs. upwind)	0.099	0.166	26	0.59	0.558
(no wind vs. downwind)	0.001	0.209	26	0.01	0.995
Vegetation type (open vs. forest)	-0.12	0.564	26	-0.21	0.833
(open vs. marsh)	-0.199	0.522	26	-0.38	0.706
Activity (rutting vs. feeding)	0.206	0.322	26	0.64	0.528
(rutting vs. lying)	0.008	0.231	26	0.03	0.974
(rutting vs. grazing)	0.003	0.205	26	0.02	0.987
Encounter distace (ln m)	0.327	0.089	26	4.11	<0.005

Table 3. Observed response distances of wild forest reindeer and semi-domestic reindeer in Finland and also of semi-domestic reindeer in Finnmark, Norway, when provoked by an observer on foot/snowshoes in 2010-12 (data pooled across years).

	Wild forest reindeer (Kuh, Suo)			Semi-domestic reindeer (Fin)			Semi-domestic reindeer (Nor)		
	mean	range	*n*	mean	range	*n*	mean	range	*n*
Herd size	37	4-152	20	39	11-121	32	116	72-220	3
Encounter (END)	332	120-600	20	226	100-400	32	250	232-255	3
Sight (SD)	253	100-450	20	144	80-250	32	200	198-205	3
Alert (AD)	216	100-320	20	94	50-160	32	150	145-156	3
Flight (FD)	192	100-320	20	68	30-120	32	135	120-150	3
Closest (CD)	191	100-320	15	44	2-110	26	120	100-140	2

wild forest reindeer (192 ± 14 m) was almost three times longer than in semi-domestic reindeer (68 ± 5 m) in Finland (P<0.001) (Fig. 3). The escape distance (ED) of reindeer was possible to measure only in the mountain areas, and the mean ED of semi-domestic reindeer in Muotkatunturi reindeer herding cooperative in Finland and also in Kautokeino, Norway was 360 m.

The mean distance between alert and flight was 24 m in wild forest reindeer and almost the same, 26 m in semi-domestic reindeer in Finland. With an encounter speed about 4 km/hour, these distances suggest that there was a separation of 22-24 seconds, on average, from when the reindeer groups became alert until they took flight. The mean closest distance was 191 m (range 100-320 m) in wild forest reindeer but only 44 m (range 2-110 m) in semi-domestic reindeer in Finland (P<0.001). The mean SD, AD, FD and CD in Norwegian semi-domestic reindeer herds were slightly, but not significantly longer than in Finnish semi-domestic reindeer. However, the mean SD, AD, FD and CD of the semi-domestic reindeer in Pohjois-Salla (no supplementary feeding) were significantly (P<0.005) longer than in the other Finnish semi-domestic herds (Table 4). The mean FD of the semi-domestic reindeer in Pohjois-Salla was 115 m, but only 65 m in the other herds. The mean CD of semi-domestic reindeer in Pohjois-Salla was 105 m, which was more than 2.5 times longer than in the other herds (mean 40 m) (Table 4).

The mean END, SD, AD and FD of wild forest reindeer were long in autumn and winter, and significantly longer (P<0.005) than in semi-domestic reindeer in Finland (Table 5, Fig. 4). However, during summer these distances of wild forest reindeer herds with young calves were significantly longer (P<0.005). The mean herd size of Finnish semi-domestic reindeer was almost the same during the four

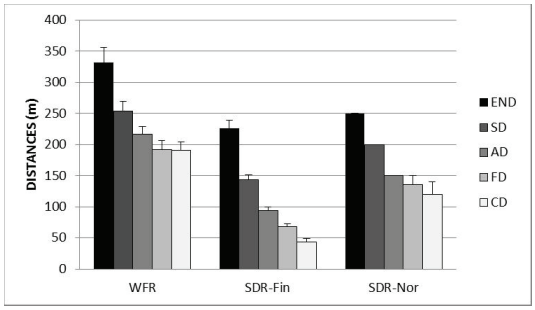

Fig. 3. Response distances (mean ± SD) of wild forest reindeer (WFR) and of semi-domestic reindeer in Finland (SDR-Fin) and in Norway (SDR-Nor) in groups disturbed by a directly approaching human on foot/snowshoes in 2010-12. Sample sizes are: END (encounter), SD (sight), AD (alert), and FD (flight distance), n = 20 for WFR, n = 32 for SDR-Fin and n = 3 for SDR-Nor, and CD (closest distance), n = 15 for WFR, n = 26 for SDR-Fin and n = 2 for SDR-Nor.

Table 4. Observed response distances of semi-domestic reindeer in different Finnish reindeer-herding cooperatives and areas (winter feeding common) and in Pohjois-Salla (no feeding), when provoked by an observer on foot/snowshoes in 2010-12 (data pooled across years).

	Semi-domestic reindeer (Fed)			Semi-domestic reindeer (P-S)		
	mean	range	*n*	mean	range	*n*
Herd size	36	11-121	30	30	28-31	3
Encounter (END)	223	100-400	30	260	250-270	3
Sight (SD)	142	80-250	30	170	160-180	3
Alert (AD)	91	50-160	30	138	125-150	3
Flight (FD)	65	30-120	30	115	110-120	3
Closest (CD)	40	2-100	26	105	100-110	2

seasons (37-43 reindeer) (Table 6). The mean herd size of wild forest reindeer was slightly larger during winter and spring (52-63 reindeer), and smaller during summer and autumn, only 7-23 reindeer. The mean END and SD of semi-domestic reindeer (285 m and 183 m, respectively) were significantly longer in winter (P<0.005), while mean AD and FD did not differ significantly depending on season.

Discussion

There were no significant differences depending on area (Kuhmo or Suomenselkä) in mean herd size, encounter, sight, alert, flight or closest distances of wild forest reindeer in Finland. Wild forest reindeer were transferred from Kuhmo to Suomenselkä more than 30 years ago (Nieminen & Laitinen, 1983). When approached by humans, reindeer are likely to respond as prey encountered by a predator (Frid & Dill, 2002). The behavioural responses of wild forest reindeer to human activity seem to be the same in both of the studied areas, where reindeer are today exposed to humans rather frequently. During autumn and winter wild forest reindeer are also grazing on the cultivated fields, quite close to human houses and other buildings. The encounter distance (END) of wild forest reindeer was, however, rather long (mean 332 m) and significantly longer than that of the studied semi-domestic reindeer. Differences in mean END suggest that the observer would have been in view with wild forest reindeer about two minutes longer than with semi-domestic reindeer. *Rangifer* with a wild origin appear to have longer response distances than reindeer with domesticated origin (Reimers & Colman, 2006), and females with calves are more easily alarmed and more likely to flee from a potential threat than are adult only groups (Lent, 1966; Bergerud, 1974; Stankowich, 2008). END increased with group size in wild forest reindeer as well as in semi-domestic reindeer. According to Reimers et al. (2006) the END of feral reindeer (wild reindeer with a semi-domestic origin) in mountain areas of south eastern Norway was longer than that of my observation of wild forest reindeer in the present study, and it also increased with group size. Klein (1979), Baskin (1986) and Baskin & Hjälten (2001) have also reported behavioural differences between forest living

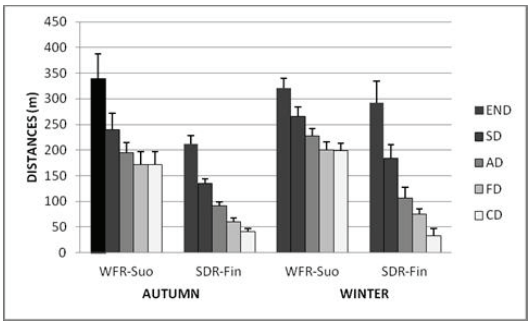

Fig. 4. Response distances (mean ± SD) of wild forest reindeer in Suomenselkä (WFR-Suo) and of semi-domestic reindeer in Finland (SDR-Fin) in groups disturbed by a directly approaching human on foot/snowshoes during autumn and winter 2010-12. Sample sizes are: END (encounter), SD (sight) AD (alert), and FD (flight distance), n = 10 for WFR in autumn and n = 7 in winter, n = 17 for SDR-Fin in autumn and n = 6 in in winter, and CD (closest distance), n = 7 for WFR in autumn and n = 5 in winter, n = 14 for SDR-Fin in autumn and n = 4 in winter.

Table 5. Observed response distances of wild forest reindeer during different seasons when provoked by an observer on foot/snowshoes in 2010-12 (data pooled across years).

	Winter			Spring			Summer			Autumn		
	mean	range	*n*	mean	range	*n*	mean	range	*n*	mean	range	*n*
Herd size	63	10-152	7	52	46-55	2	7	5-9	2	23	4-85	10
Encounter (END)	321	260-400	7	250	245-250	2	425	400-450	2	328	120-600	10
Sight (SD)	266	220-360	7	200	190-204	2	310	300-320	2	238	100-450	10
Alert (AD)	227	190-300	7	180	175-188	2	300	288-305	2	195	100-320	10
Flight (FD)	200	170-290	7	150	140-155	2	275	250-300	2	174	100-320	10
Closest (CD)	199	170-280	5	150	140-155	2	275	250-300	2	172	100-320	7

and tundra living reindeer. The forest reindeer/woodland caribou usually live in smaller herds and show less vigilant behaviour compared to tundra living reindeer. The flight distance (FD) was influenced by END, and it suggests that both the time the observer was visible to the reindeer group and the distance to the observer might be important. END of wild forest reindeer in the present study was longest in autumn and winter. It is explained by the observer being easier to detect against snow. END was also longest in feral reindeer in south eastern Norway in March, and this suggests that the observer would have been in view for about two minutes longer than during summer (Reimers *et al.,* 2006).

In reindeer, olfaction is generally considered a more dependable sense than vision for early warnings. Scent would thus result in faster reactions at farther distances to humans. However, feral reindeer did not respond differently during events when they were downwind of the observer compared to when they were upwind (Reimers *et al.,* 2006). Thus for reindeer in open or mountain areas vision might often be relatively more important than detection by scent or sound compared to the relative importance of these senses for ungulates in forest habitat. Usually both wild and semi-domestic reindeer that have visually detected a disturbance source, for example a human, will often approach or circle the source until they are able to confirm by scent the apparent need for flight. In the present study the mean closest distance (CD) was 191 m (range 100-320 m) in wild forest reindeer but only 44 m (range 2-110 m) in semi-domestic reindeer. According to Reimers et al. (2006) also Norwegian feral reindeer approached by the observer usually first moved towards the observer before they took final flight. The closest approach by feral reindeer in winter was the same as in Finland

Table 6. Observed response distances of semi-domestic reindeer in Finland during different seasons, when provoked by an observer on foot/snowshoes in 2010-12 (data pooled across years).

	Winter			Spring			Summer			Autumn		
	mean	range	*n*	mean	range	*n*	mean	range	*n*	mean	range	*n*
Herd size	37	12-72	6	43	22-80	6	42	18-85	3	38	11-121	17
Encounter (END)	285	140-400	6	195	100-350	6	223	200-250	3	216	120-350	17
Sight (SD)	183	100-250	6	123	80-170	6	147	120-160	3	137	90-200	17
Alert (AD)	113	50-160	6	67	50-120	6	110	90-120	3	94	50-150	17
Flight (FD)	83	50-120	6	62	50-100	6	77	60-90	3	63	30-120	17
Closest (CD)	45	30-100	4	45	30-100	4	33	30-35	2	45	20-120	14

with wild forest and semi-domestic reindeer.

The mean sight (SD) and the alert distances (AD) were significantly longer in wild forest reindeer than in semi-domestic reindeer, and the mean FD was almost three times longer in wild forest reindeer than in semi-domestic reindeer in Finland. Although reindeer are considered to be at an early phase of domestication (Baskin & Skogland, 2001), semi-domestic reindeer generally exhibit more relaxed fright and flight behaviour compared to wild reindeer (Reimers *et al.,* 2000; 2006). According to Tarlow & Blumstein (2007) an important interacting factor is frequency of interaction with humans, and reindeer – like other ungulates – show reduced flight responses in areas with frequent contact with humans compared to those in areas where human encounters are rare (Colman *et al.,* 2001; Stankowich, 2008).

In the present study the mean SD, AD, FD and CD in Norwegian semi-domestic reindeer herds were slightly longer than in Finnish semi-domestic reindeer. These distances were, however, significantly longer in reindeer in Pohjois-Salla reindeer-herding cooperatives than in other Finnish cooperatives. There was no supplementary feeding of reindeer in Pohjois-Salla. In other herding cooperatives almost all reindeer are fed 3-5 months every winter. The mean FD was 115 m in semi-domestic reindeer of Pohjois-Salla but only 65 m in other cooperatives in Finland. Also the mean CD of reindeer in Pohjois-Salla was 105 m and more than 2.5 times longer than in other cooperatives. The results suggest a strong taming effect due to the supplementary feeding practice, which in some areas have been going on for 40 years in Finland. Increased snowmobile use has also expanded the area where humans are daily in contact with reindeer during winter and spring. Several studies have also shown that people and dogs elicit usually greater flight responses than machines, e.g. skiers vs. snowmobiles (Freddy *et al.,* 1986).

The mean SD, AD and FD were longer in wild forest reindeer and also in semi-domestic reindeer in Finland during winter and autumn. It is in accordance with earlier results with wild mountain reindeer in southern Norway (Reimers *et al.,* 2009). Earlier studies (Dervo & Muniz, 1994; Kind, 1996; Eftestøl, 1998) on reactions of wild reindeer to humans on foot or skis have also revealed longer reaction distances during winter than in the other seasons, indicating that reindeer are especially vulnerable to disturbance during winter, usually a period of negative energy balance (Reimers *et al.,* 2003). The distance the feral reindeer in south eastern Norway moved away in response to the approaching human was greatest during summer (Reimers *et al.,* 2006). Farther alert and flight-initiation distance in winter may be explained by the observer being easier to detect against snow (Reimers *et al.,* 2009). Shorter alert and flight distances for larger than smaller groups are also in general agreement with previous studies (deVos, 1960; Baskin & Hjälten, 2001; Reimers *et al.,* 2006). The mean herd size of wild forest reindeer was slightly bigger during winter and spring, and smaller during summer and autumn. The mean END and SD of semi-domestic reindeer were also significantly longer in winter, but the mean AD and FD were almost the same in winter and summer and only slightly longer than during other seasons.

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