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Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis

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Increasing outdoor activities by humans could negatively influence reindeer and caribou *Rangifer tarandus* populations. We recorded the behaviour of feral reindeer *R. t. tarandus* when a person directly approached them on foot or on skis in Forolhogna, Norway, during March, July and September-October 1996. The farther away the person was when first sighted, the greater the distance the reindeer group fled. The distance the reindeer moved away in response to the approaching person was greatest in July and least in September-October during autumn rut and shortly after the hunting season closed. In September-October rutting activities affected reindeer behaviour more than the disturbance caused by the directly approaching human. Both the distance at which the reindeer group responded by flight and the distance they moved away decreased with increasing group size. Upon flight, when all escape options were available, reindeer more often escaped uphill and into the wind than along level ground, downhill, down wind or crossways to the wind. All reindeer in a group moved towards the approaching human before taking final flight during 50% of 82 disturbance events, the closest approach was within 43 m in March, 24 m in July, and 13 m in September-October. No reindeer group responded by flight when the approaching human was still > 310 m away in March, > 351 m in July, and > 180 m in September-October. In relation to the current level of human activity in the area, our observations indicate no serious negative consequences for the reindeer following disturbance from a directly approaching human, not even shortly after the hunting season.

Key words: feral reindeer, flight behaviour, human disturbance, *Rangifer tarandus tarandus*, recreation

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There are numerous activities in which people may negatively influence the behaviour of free-ranging reindeer and caribou *Rangifer tarandus* and their subsequent range use (Wolfe et al. 2000). Outdoor recreational tourism is an expanding and increasing activity (Helle & Sarkela 1993, Duchesne et al. 2000). In southern Norway, about 30,000 feral and wild mountain reindeer *R. t. tarandus* are distributed in 23 different and mostly isolated populations. Current population sizes of 600–8,000 animals occur in winter on ranges of 300–8,000 km². The 23 populations consist of 16 feral populations originating from semi-domesticated reindeer released mostly during the 1950–1960s and seven populations of wild origins. All populations are managed as 'wild' and hunted from 20 August until sometime in late September, depending upon area. In Forolhogna the hunting season closes on 14 September.

Recreational use of the reindeer's alpine habitat by hikers, skiers and hunters has been increasing and expanding into more remote areas during the last 35–40 years, and this trend is forecast to continue in the foreseeable future. Our knowledge concerning the potential disturbance of reindeer caused by recreational activities and hunting is largely restricted to the observation that flight is the usual overt behavioural response. At some point, flight causes reduced time for feeding and suboptimal resource utilisation as well as increased energy costs of locomotion, particularly when animals are moving relatively long distances, through deep snow or uphill, and especially when doing both (Fancy & White 1985). In extreme circumstances, recurring disturbances may also result in avoidance of some areas, leading to increased grazing pressure on remaining pastures, if available range is limited and animal density is high relative to the food supply.

In winter, when food availability and quality are more limited than during or shortly after the plant growing season, a large number of hikers or skiers may negatively influence animal condition either directly due to increased energy expenditure and decreased feeding time, or indirectly, due to avoidance of areas where disturbances occurred. Therefore, an understanding of what causes reindeer to respond by flight (avoidance or escape displacement) is needed to improve habitat management measures for free-ranging reindeer in areas where the amount of non-consumptive human recreation or hunting is increasing. Whether hunting has a negative effect on the behaviour of reindeer towards humans in general must be viewed in the context of the potentially confounding effects of increasing recreational use of the same areas.

In Forolhogna, one of the feral reindeer areas in southern Norway, flight responses were recorded upon disturbance by a person on foot or on skis approaching the animals directly at a constant speed. Our primary objective was to test whether season and the environmental factors changing with season (e.g. snow depth, icing and visibility) could cause variation in the reindeer's response to human-induced stimuli. We also tested the following predictions.

Several studies on wild ungulates have shown that vigilance rate per animal decreases with increasing group size (Berger 1978, FitzGibbon 1988, Frid 1997), at least for most of the animals in the group. de Vos (1960), Thomson (1977) and Klein (1991) found that reindeer in larger groups are more tolerant to negative or novel stimuli or, at least slower to respond to them, than are reindeer in smaller groups. We therefore predicted: 1) that the distances at which reindeer responded to a directly approaching person and 2) in turn, the proportion of groups (not individuals) that would approach the person before the reindeer made their final withdrawal are inversely related to group size.

The capacity of the *Rangifer* species to capture scent is well known by biologists, herders, hunters and hikers. We therefore predicted that reindeer would respond at greater distances to the directly approaching person when the wind carried the human scent to the animals than when the animals could not scent the human intruder.

Earlier studies by Skogland (1991), Baskin & Skogland (2001), and Colman et al. (2001a) indicate that reindeer favour an up-slope escape route over one on level ground or down slope. We therefore predicted that the same preference for up-slope escape routes would be exhibited in this study.

Measurements were made to determine effects on the response distances between the approaching observer and the animals in relation to topography, general weather conditions and group structure (Colman et al. 2001a). We also tested how flight patterns relate to wind direction and topographical position of the observer relative to the reindeer group (Colman et al. 2001a).

In the following we report the measurements that we made for five response distances and factors influencing the response distances. Our goal was to gain insight into variations and intensities of reindeer responses to a human's presence and to evaluate the possible influence of the disturbances on daily maintenance activities. This would advance our ability to predict the potential consequences of people*animal interactions during such encounters on the subsequent well-being of the reindeer population.

Study area

Forolhogna (62°45'N, 11°E; 1,822 km²) has a winter population of 1,700–1,800 feral reindeer, originating from semi-domesticated animals that escaped from neighbouring domestic groups during the 1950s. Low alpine regions with gently rolling hills above the tree line encompass about 1,662 km² (91%), with most of the area being situated at altitudes of 900–1,250 m a.s.l. Both winter and summer food quality and accessibility are excellent (Gaare & Eriksson 1981, Jordhøy 1995), and the reindeer are in prime condition with high body weights and recruitment rates (Skogland 1984, Jordhøy 1995, Meli 2001). The population has been hunted annually since 1956 (Meli 1997). During 1970–1984, annual harvest amounted to $\approx 35\%$ of the winter population (Reimers 1986) and has increased to a sustainable rate of $\approx 42\%$ since 1986 (Meli 1997, 2001). According to the hunting authorities, it is believed that the population size (barring extremely severe stochastic weather events) and the annual harvest rate will persist at the present level which has now lasted for more than a decade; Norway is one of the few countries where hunting is allowed in national parks. The road network in Forolhogna is well developed and only about 160 km² (9% of the area) are > 5 km away from the nearest road. This provides good access for hikers, skiers and hunters. However, since no professional outdoor recreational tourist organisations are active in the area and since there are no marked hiking trails in the area, recreational traffic is low compared to wild or other feral reindeer areas: Hardangervidda (8,000 km², 17 cabins, 775 beds and 30,000 overnight visits), Rondane (1,500 km², four cabins, 290 beds and 20,000 overnight visits), and Snøhetta (3,500 km², two cabins, 68 beds and 3,000 overnight visits; Torfinn Evensen, Den norske turistforening, pers. comm.). Forolhogna was only established as a national park in 2002; consequently, the level of tourism (primarily hikers and skiers) is forecast to increase.

Methods

In 1996, during the three sampling periods of March (winter), July (summer) and September–October (autumn hunting and rutting period), a single person on foot or on skis (hereafter referred to as the 'observer'), dressed in dark hiking clothing, disturbed reindeer during daylight hours by directly approaching them. The observer used Leica Geovid 7x42 BDA laser-binoculars (1 m accuracy at 1,000 m) to measure response distances between the reindeer and the observer and the resultant dis-

placement distance by the reindeer after taking flight. Upon location of a group (≥ 4 animals), 10 parameters were recorded: sample month(s), group size (continuous parameter), group composition (mixed, all ages and sexes; and males, yearlings and older), dominant activity of the group when first sighted (lying, foraging, moving-walking or trotting without foraging), wind direction relative to the observer (observer moving into, with or crossways to the wind), wind speed (The Beaufort Wind Scale: calm, $< 1 \text{ m} \cdot \text{sec}^{-1}$; light/gentle breeze, $1.6\text{--}5.4 \text{ m} \cdot \text{sec}^{-1}$; moderate/fresh breeze, $5.5\text{--}10.7 \text{ m} \cdot \text{sec}^{-1}$; or gale, $10.8\text{--}17.1 \text{ m} \cdot \text{sec}^{-1}$), topographic position of the observer relative to the group (above, level with or below); topography (terrain ruggedness) of the surrounding area (level or hilly), visibility/weather (sunny/partly sunny, cloudy, raining/snowing or foggy), and insect activity. In July, we recorded oestrid fly activity on a scale of 0–3 (Hagemoen & Reimers 2002). Mosquito (Culicidae) activity was not recorded, as mosquitoes rarely harass reindeer in the high mountain ranges of southern Norway (Hagemoen & Reimers 2002).

When a group of reindeer was first sighted, the observer measured the distance to the group, and used a 'direct approach' method that had an 'interrupted pattern': advancing directly towards the estimated centre of the group at a constant speed ($\approx 4 \text{ km} \cdot \text{h}^{-1}$) with ≤ 6 second stops to measure the four additional response distances defined below. The observer continued to approach the group on all occasions until the reindeer responded by flight. All measurements were made from the position of the directly approaching observer to the nearest animal in the group (Colman et al. 2001a). We used wildlife response distance terminology and methodology recommended by Taylor & Knight (2003) modified for our study in the following way:

- 1) Encounter distance (END): the distance used as the starting point of the disturbance.
- 2) 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.
- 3) Flight distance (FD): the distance from the directly approaching observer to the group when the reindeer initially took flight.
- 4) Escape distance (ED): the shortest straight-line distance from where the reindeer took flight in response to the directly approaching observer to where the reindeer resumed grazing or bedded down.
- 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.

After the reindeer returned to maintenance activities, the observer recorded the group's escape route, i.e. whether they retreated uphill, downhill ($\geq 10\%$ angle) or on the level, and if they ran into the wind, with the wind, or crossways to the wind. Some groups were disturbed by the directly approaching observer more than once on the same day. When this happened, the observer allowed a minimum of one hour between the first and the second disturbance, and a minimum of two hours between the second and the third disturbance. All disturbance events were treated as independent observations, but the number of previous disturbances on the same day was included as a variable. AD or FD was excluded when the animals became alerted or fled at the start of the observation. AD or FD was also excluded from the analysis when the observer went out of sight of the reindeer during a disturbance and the reindeer took flight immediately when the observer reappeared. If the observer remained undiscovered after returning in view of the animals, the disturbance was continued by the observer.

The response variables (i.e. END, FD and ED) were square-root transformed and group size transformed into natural logarithms (ln) to approximate the normal distribution. We used General Linear Models (GLM) to examine the relationship between response variables and several categorical and covariate independent variables. However, due to the limited number of observations compared to the large number of independent variables, only independent variables that had a suggestive P value of < 0.15 when analysed separately (ANOVA; analysis of variance) were used in the models for explaining variance in FD and ED. We used sample month(s) and group size as independent variables to explain variation in END. We also reported AD, which is synonymous with 'fright response' in this study, and CD between the observer and the group during a disturbance to provide two additional 'benchmarks' in our evaluation of disturbance responses.

Parameter estimates for the categorical variable in Table 2 (i.e. month) are given in relation to the month selected

as the reference level set to 0, using Simple Coding Contrast (SPLUS/R Library: Contrast Coding at WWW.ats.ucla.edu/stat/splus/library/contrast_coding.htm). Although there are different selection processes, we selected Simple Coding as a straightforward approach which compares each category of the variable with the reference category. The t-test is a test of whether the parameter estimate is different from the reference level.

We used Fisher's exact tests and binomial exact tests to test for differences in flight pattern in relation to the wind direction (into, crossways to or with the wind) and topography (uphill, on the level or downhill). We used a χ^2 -test to assess the relative seasonal frequency of occurrence among three group-size classes: small group-size class of 4-20 animals, medium of 22-90, and large of 125-700 animals. We used logistic regression with a backward procedure based on the likelihood ratio to test for the relationship between the number of groups that approached the observer after flight was initiated and the independent variables of group size, FD, month(s) when samples were obtained, and topographical position of the observer (above, level with or below the group). The statistical program 'S-plus' was used in all statistical analyses (Venables & Ripley 2002). Statistical significance was assessed at $\alpha = 0.05$, but P values of 0.05-0.1 were regarded as suggestive trends.

Results

During the three sample periods in 1996, 84 reindeer groups were encountered and used in our analysis of group size and for assessing whether the group would approach the observer. Although only 19 groups were encountered in March, these groups represented 44% of the groups in the large size class and 51% of all of the reindeer sampled in 1996 (Table 1). Reindeer groups were overrepresented in the large size class in March, in the medium size class in July, and in the small size class in September-October (see Table 1: $\chi^2 = 14.74$ df = 4; $P = 0.01$). Group size varied between 4 and 700 animals with a median value of 33 animals (25% quartile = 12 and 75% quartile = 146 animals). END increased with group size ($\beta =$

Table 1. Distribution of the reindeer group size classes small (4-20), medium (22-90) and large (125-700) according to sample period and the associated number of individuals involved in group samples from Forolhogna, Norway, in 1996.

Sample period	Distribution of groups			Number of individuals	Group size statistics		
	Small	Medium	Large		Mean	SE	Range
March	4	4	11	5439	286.3	61.6	10-700
July	8	15	8	3240	104.5	24.0	5-500
September-October	18	10	6	1911	56.2	15.8	4-340
Total	30	29	25	10590	126.1	20.0	4-700

Table 2. Relationship between response variables and independent variables measured during disturbance of feral reindeer groups caused by a directly approaching human on foot or on skis in Forolhogna, Norway, in 1996. Among the independent variables only variables with $P < 0.15$ when analysed separately entered the global model. $B \pm SE$ is the parameter estimate and the standard error of the parameter estimate.

Response variables	Independent variables	$B \pm SE$	t-value	P-value
$\sqrt{\text{Flight distance}}$	$\sqrt{\text{Encounter distance} + \text{season} + \ln \text{ group size} + \text{wind speed}, R^2 = 0.496}$			
	Intercept	12.79 ± 1.38	9.24	< 0.0001
	$\sqrt{\text{Encounter distance}}$	0.12 ± 0.05	2.50	0.001
	Sample month(s)	March	4.85 \pm 0.83	< 0.0001
		July	3.95 \pm 0.68	< 0.0001
		September-October ¹		
	Ln group size	-1.43 ± 0.22	6.56	< 0.0001
$\sqrt{\text{Escape distance}}$	Wind speed	-0.59 ± 0.33	1.76	0.082
	$\sqrt{\text{Flight distance} + \text{sample month(s)} + \ln \text{ group size}, R^2 = 0.459}$			
	Intercept	20.05 ± 4.90	4.09	0.0001
	$\sqrt{\text{Flight distance}}$	0.56 ± 0.25	2.24	0.028
	Sample month(s)	September-October	-8.58 ± 1.87	< 0.0001
		March	-5.94 ± 1.87	0.0022
		July ¹		
	Ln group size	-1.28 ± 0.61	2.10	0.039

¹ Month selected as reference level and set to 0, other month parameter estimates are in reference to zero using Simple Coding contrast. (For further details see SPLUS/R Library: Contrast Coding at www.ats.ucla.edu/stat/splus/library/contrast_coding.htm).

1.33 \pm 0.43, $t = 3.10$, $P = 0.003$), but did not differ between or among the sampling months ($F = 0.49$, $df = 2$, $P = 0.62$).

The distance (mean \pm SD) between AD and FD was 35 \pm 36 m in March, 24 \pm 33 m in July, and 20 \pm 22 m in September-October. With an encounter speed of $\approx 4 \text{ km} \cdot \text{h}^{-1}$, these distances suggest that there was a separation of 18-32 seconds, on average, from the reindeer group became alert until they took flight. The furthest distance (i.e. AD) at which the observer elicited a fright response (regardless of group size) was 338 m in March, 351 m in July, and 204 m in September-October. Correspondingly, the furthest distance for a flight response (regardless of group size) was 310 m in March, 351 m in July, and 180 m in September-October.

FD was shorter in September-October than in March and July (Table 2, Fig. 1). Our prediction that FD would be longer when the observer was seen against a high-contrast snow background than when against a low-contrast snow-free background or when strongly influenced by autumn rutting activities (even when the land was snow-covered) was not supported.

ED was longer in July than in March and September-October (see Table 2 and Fig. 1). Too few days without oestrid fly activity made it impossible to evaluate a possible relationship between insect stress in July and response distances.

Both FD and ED decreased with group size (see Table

2), supporting our prediction that response distances were inversely related to group size. ED increased with increasing FD whereas FD tended to decrease with wind

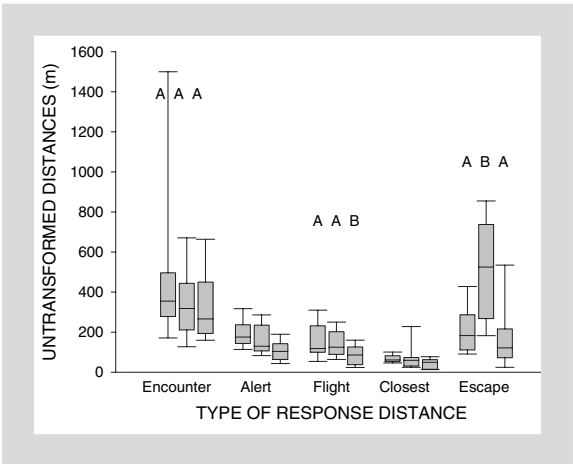


Figure 1. Temporal sampling effects on untransformed response distances of feral reindeer in groups disturbed by a directly approaching human on foot or on skis in Forolhogna, Norway, in 1996. The boxes represent 25th and 75th percentiles, the horizontal line through each box equals the median, and the whiskers extend to the 10th and 90th percentiles of the data set. The triplet bars in each type of response give from the left to the right distances in March, July and September-October, respectively, and bars with different letters are significantly different ($P < 0.05$). Only Encounter Distance (END), Flight Distance (FD) and Escape Distance (ED) are analysed statistically in this consideration. Sample sizes are: END, $N = 81$; Alert Distance (AD), $N = 78$; FD, $N = 80$; ED, $N = 79$; and Closest Distance (CD), $N = 41$.

speed (see Table 2). The position of the observer, whether upwind, downwind, or crossways to the wind, did not influence FD or ED ($F = 0.6$, $df = 3$, $P = 0.66$ and $F = 0.72$, $df = 3$, $P = 0.54$); thus lending no support to our prediction that reindeer scenting the observer earlier would respond earlier.

Sex and age composition of the group, animal activity when first sighted, position of the observer in relation to reindeer group (above, level with or below), weather conditions, terrain ruggedness, and number of encounters with the same group on the same day did not measurably influence FD or ED (all P -values ≥ 0.15). ED was also not measurably influenced by wind speed or the square root of the END (both P -values ≥ 0.51).

The probability that a group of reindeer would approach the observer immediately before initiating final withdrawal (CD) tended to increase with group size (Fig. 2: Wald = 9.831, $df = 1$, $P = 0.002$), supporting the other part of our prediction. All reindeer in 41 reindeer groups approached by the observer first moved towards the observer before they took final flight. Median group size of reindeer approaching the observer was 70 animals vs 19 animals in groups that took flight without approaching the observer first. The mean number \pm SE and range of group sizes for the groups that approached the observer was 176 ± 32 , 4-675 versus 71 ± 22 , and 4-700 for groups that did not approach the observer. Among the 41 groups, 13 (32%) approached the observer in March, 10 (24%) in July, and 18 (44%) in September-October. The closest approach by reindeer to the observer was 43 m by a group of 150 animals in March,

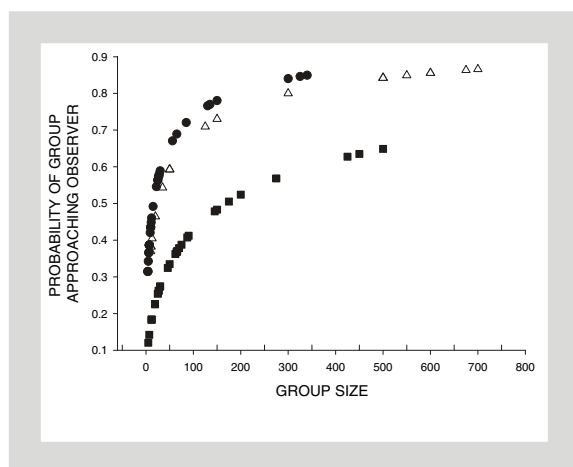


Figure 2. Probability that a feral reindeer group would approach the observer before final flight was initiated ($N = 41$) as a function of group size and the months (Δ March, $N = 19$; \blacksquare July, $N = 31$; \bullet September-October, $N = 34$) when samples were obtained in Forolhogna, Norway, in 1996. Symbols represent predicted values from a logistic regression model with group size and sample-month(s) as independent variables.

24 m by a group of 425 animals in July, and 13 m by three groups (of 130, 150 and 340 animals, respectively) in September-October. The likelihood of approach was lower in July than in March or September-October (see Fig. 2: Wald = 6.059, $P = 0.048$). Neither FD (Wald = 0.369, $P = 0.832$) nor topographic position of the observer relative to the reindeer (Wald = 1.019, $P = 0.313$) affected the probability that an entire group or some members of a group would approach the observer. In 27 mixed sex and age class groups that approached the observer after being disturbed, calves in 19 of these groups came closer to the observer than ≥ 1 -year old animals. Older animals came closer than did calves in the remaining eight groups ($\chi^2 = 16.9$, $df = 2$, $P < 0.001$).

Upon disturbance ($N = 75$), reindeer groups most often escaped against the wind ($N = 41$) rather than with the wind ($N = 15$, binomial exact test: $P = 0.0007$) or side wind ($N = 19$, binomial exact test: $P = 0.0062$; Fig. 3). With all topographical flight options available ($N = 68$),

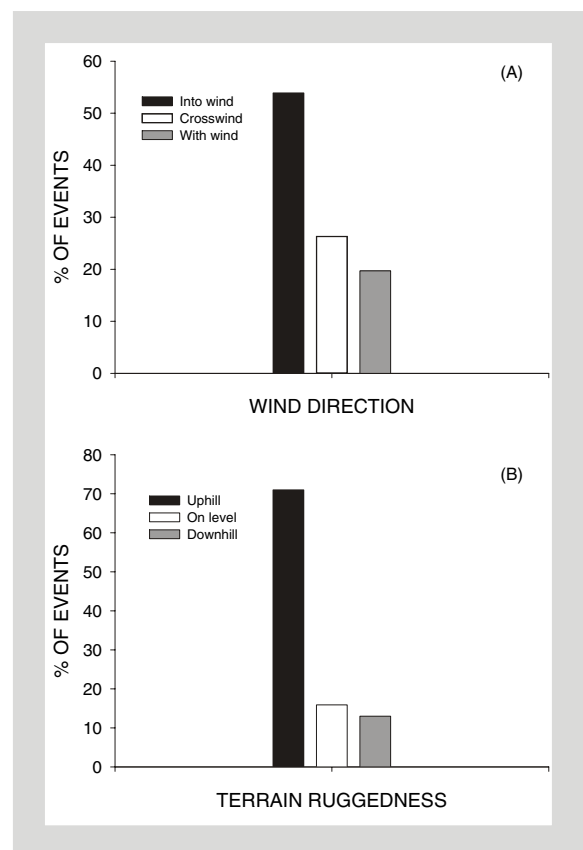


Figure 3. Flight pattern of feral reindeer groups in relation to wind direction relative to the group's course of flight (A; $N = 75$) and the topography (B; $N = 68$) expressed as terrain ruggedness along the escape route from the point where flight was initiated in Forolhogna, Norway, in 1996.

reindeer most often escaped uphill after being disturbed (N = 50) rather than on the level (N = 8) or downhill (N = 10; binomial exact test: $P = 0.0001$). This outcome supports our prediction that when disturbed, reindeer would exhibit a preference for an up-slope escape route (see Fig. 3). Escape direction in relation to wind and topography did not differ by sample months (Fisher's exact test: $P = 0.25$ and $P = 0.21$, respectively).

Discussion

Among the 10 independent variables, month(s) of sampling and group size had the strongest influence on response distances. Olfaction is generally considered a more dependable sense than vision in reindeer for earlier warnings and thus faster reactions at farther distances to negative or novel stimuli. However, reindeer did not respond differently during events when they were downwind of the observer compared to when they were upwind. This is contrary to the findings of de Boer et al. (2004) who showed that both roe deer *Capreolus capreolus* and fallow deer *Dama dama* fled at greater distances when approached by humans upwind of the animals (mean \pm SE values, 64.7 ± 5.8 m and 41.7 ± 3.3 m, respectively) than when approached by humans downwind of the animals. Vision might often be relatively more important than detection by scent or sound for reindeer in open mountain habitat compared to the relative importance of these senses for forest-dwelling ungulates. Nonetheless, reindeer that have visually detected a disturbance source will often approach or circle the source until they are able to confirm by scent the apparent need for flight.

ED was greater during July than during March and September-October. The median distance of 525 m moved in July exceeds the median ED in March by 342 m, or 187%, and the September-October median ED by 403 m, or 330%. The potential for greater energy costs at higher levels of disturbance would be markedly higher in July than in March (given the same level of response at a higher level of disturbance). This could be of particular importance to reindeer, as summertime recovery is essential for individuals to replenish their body reserves and attain the body condition necessary for successful reproduction in autumn (Thomas 1982, Reimers 1983, Cameron et al. 1993) and survival throughout the oncoming winter. Colman et al. (2003) found that continuous disturbances during summer for wild reindeer led to decreased autumn weights.

The effect of harassment by biting and bloodsucking insects on ED remains undetermined. This is an impor-

tant shortcoming, as harassment by biting and bloodsucking insects plays a central role in the reindeer's general daily behaviour and energetics in summer (Thomson 1977, Reimers 1980, Mörschel & Klein 1997, Colman et al. 2001b, Hagemoen & Reimers 2002, Colman et al. 2003). The longer ED exhibited by reindeer in July may reflect the added stress caused by insect harassment, when animals move constantly in search of relief areas (such as ridges, hilltops or snow beds). Another complicating factor influencing ED in July is that females with young calves are most intolerant of human-induced stimuli and may maintain longer distances between themselves and an intruder.

All response distances were shortest during September-October shortly after the autumn hunting season closed. Hence, reindeer exposed to stalking (hunting) movements during the hunting season did not exhibit increased levels of flight in response to a direct approach by a single human who paused only briefly. The rutting season in late September and early October undoubtedly influenced our observations. Rutting activities obviously affected reindeer behaviour more than the directly approaching observer during several September-October events. Apparently, neither the negative stimuli (the harassment level) caused by hunters between 20 August and 14 September nor the possible selection by hunters of less vigilant animals in 1996 or over the previous 50 years of hunting could override the effect of the rut.

The possible difference in the effect on FD caused by humans stalking animals during the hunting season and those caused by the direct approach of humans that are not hunting and not attempting to conceal themselves is not clear. Behrend & Lubeck (1968) concluded that properly controlled periodic autumn hunting of white-tailed deer *Odocoileus virginianus* in some New York parks may be compatible with summer viewing. In accordance with this, Colman et al. (2001a) concluded that present-day hunting practices did not strongly affect the summer FD of Svalbard reindeer *Rangifer t. platyrhynchus* or their habituation to humans on foot. Kufeld et al. (1988) concluded that hunting pressure did not cause a change in dispersal of female mule deer *O. hemionus* or cause them to leave their usual home ranges. In a recent paper, however, de Boer et al. (2004) suggested that roe deer FD was related to hunting regime. Differences in the number of outdoor recreationists, animal behaviour and habitat type and structure as well as small samples sizes may reduce the comparative usefulness of their findings in relation to our study.

Our finding that larger groups had a shorter FD and a shorter ED than did smaller groups is in general agreement with de Vos (1960), Thomson (1977) and Klein

(1991) who concluded that smaller groups of caribou and reindeer usually respond faster to moving negative or novel stimuli than do larger groups. Jarman (1974), LaGory (1986) and Mooring & Hart (1992) hypothesised that individuals in groups are thought to have a lower risk of attack by predators and parasitising insects than solitary individuals. Furthermore, several studies on wild ungulates have shown that the vigilance rate per animal decreases with increasing group size (Berger 1978, Fitz-Gibbon 1988, Skogland 1991, Baskin & Skogland 1997, Frid 1997, Colman et al. 2001a).

The finding that FD decreased with increasing wind speed might suggest that communication within the group is hampered in strong wind or that reindeer are more reluctant to flee in strong winds. However, given the forcefulness of the sights, sounds and scents (pheromones) of a large number of milling aroused reindeer or caribou, it is most likely that an explanation for these results must be sought elsewhere.

FD was also influenced by END, suggesting that both the time the observer was visible to the group and the distance to the observer might be important. Differences in mean END by sample month(s) suggest that the observer would have been in view in March for about two minutes longer than in July and three minutes longer than in September–October. This may imply that people moving parallel to a group or tangentially towards it might cause an aroused state similar to, but often less intense than, a direct approach. This possibility would probably be related mainly to the amount of time people are in sight. Reindeer groups exposed to a tangential approach by one person, and particularly by several people, are more likely to drift away from the perceived danger rather than to take rapid flight by trotting and especially by galloping away.

Animals most often retreated up-slope and into the wind when disturbed, independent of whether the observer proceeded uphill or downhill, or into or with the wind. The up-slope escape response is in accordance with results obtained on other reindeer (Skogland 1991, Baskin & Skogland 1997, Colman et al. 2001a) and caribou populations (Miller & Gunn 1979, Gunn & Miller 1980). A similar escape pattern has also been observed for big-horn sheep *Ovis canadensis* (Hicks & Elder 1979), elk *C. canadensis* (Kuck et al. 1985, Cassirer et al. 1992), and moose *Alces alces* (Andersen et al. 1996). The habitats of these species, and their relationship to their environment, are quite varied and, thus, it does not necessarily follow that the reason(s) for this up-slope flight pattern is/are universally the same, although it/they could be. By escaping uphill, animals usually gain a better visual perspective and a 'tactical advantage' in selecting a

route for continued escape from the perceived or real danger. How wind direction influences their flight direction is more uncertain. When retreating into the wind, caribou and reindeer are able to smell other possible predators ahead of them and avoid an ambush. The benefit of running into the wind is obvious for *Rangifer* species living with wolves *Canis lupus* and other large predators. Colman et al. (2001a) concluded that reindeer on the predator-free islands of Svalbard, usually retreated with the wind, and they suggested that this could be because the animals wanted to stay in olfactory contact with the alarming stimulus. Baskin & Skogland (1997) reported that even if moving into the wind was typical for the first flight reaction for wild reindeer, wind did not influence the direction of the final withdrawal after the animals calmed down. They found that reindeer kept moving in the direction that they were travelling prior to disturbance, and concluded that this probably reflected an overall movement tendency that was only temporarily suppressed by the escape response.

At some point in the disturbance, the position of the disturbance source relative to the fleeing animals may dictate which escape route must be taken, especially if the disturbance source is moving as fast as or faster than the animals and moving towards them. On occasion, the presence of physical barriers (e.g. cliffs, large boulder fields, deep soft snow, lakes and fast rivers) will govern the path the animals must take to successfully escape, regardless of other associated factors.

An energetic cost arises if avoiding a disturbance markedly reduces the time for food intake and thus the amount of food consumed. Repetitive intense disturbances over time, especially prolonged disturbances and those reinforced at varying frequencies, could result in an important loss of energy (Colman et al. 2003). Continued alterations in daily activity patterns could lead to markedly reduced food intake, resulting in energy loss and eventually serious weight loss that causes failure to breed or high calf mortality and increased susceptibility to predation or disease, and ultimately leads to population decline.

Direct encounters most likely represent a worst-case scenario (Tyler 1991). The fright and flight distances recorded in our study, therefore, should be regarded as potential maxima for reindeer in this area, at least, when approached by a single person.

It may be most important to know how close a person can approach animals without eliciting a fright response and more importantly a flight response. Such a 'threshold' measure would allow managers to suggest proximity distances for each season, particularly for the seasons that are energetically or reproductively crucial.

With this end in mind, although we are aware of the limitations of our data, we provide tentative 'threshold safe distances' by season based on the maximum (furthest) distance at which a group, regardless of group size, fled from the approaching observer in each of the three seasons. We suggest that 350 m in March and in July and 200 m in September-October would be good tentative approximations for reasonably safe distances to use in this area until further studies have been carried out. At the least, adherence to those thresholds should markedly reduce the possibility of reindeer being displaced from their preferred food patches. Future studies that measure both seasonal and annual repetitions of FD and ED would be necessary to determine the validity of these threshold values with biological confidence. Ideally, the same study design should be repeated several times on the same population and should be carried out on several different populations to get some measure of the general applicability of the threshold values.

Acceptance of these threshold values must be done with the realisation that animal responses to disturbance, and particularly harassment, are influenced by an array of biotic and abiotic factors together with the recent history of the exposed group and sometimes are simply the outcome of chance events. Also in our study, we measured only observed overt responses by the reindeer group to the observer, and we have no measure of physiological cost or any associated additive long-term effects.

Conclusions

In Forolhogna, single encounters between reindeer and a person on foot or on skis did not result in escape responses involving distances, intensities or durations of displacements that would entail substantial energy costs. With the current level of human traffic and similar reindeer reactions towards humans, reindeer and human encounters in Forolhogna would not cause serious negative consequences at the population level. This finding, however, is predicated on the untested assumption that reindeer would respond at similar levels to groups of people and their associated actions and activities (e.g. talking, shouting, whistling or individuals moving about in different directions) as they did to the direct, virtually steady, relatively silent approach of a single person.

We expect increased human use of the entire mountain range in Forolhogna. However, as there are no public tourist cabins available for overnight visits within the national park boundary, the increase in number of visitors is expected to be small in the near future. This expectation is in accordance with the finding that establishment of

national parks in areas with rather extensive tourist infrastructure has not resulted in more traffic (Torfinn Even- sen, Den norske turistforening, pers. comm.).

The effect of any future increase in human tourist activities on reindeer ranges ultimately depends on whether reindeer become habituated or sensitised to the presence of increasing numbers of people and the possible variety of their actions and activities in the areas. What factors will dictate the individual reindeer's response to increased human-induced novel stimuli in its environment remains unknown. It is possible that at some 'threshold' point reindeer will not adapt well to human encroachment, and a high level of human-reindeer interactions could negatively influence the long-term well-being of a reindeer population. The most important potential consequences from an ever-increasing number of encounters with humans are those associated with avoidance and displacement behaviours resulting in loss of access to otherwise optimal habitats, followed by overgrazing of the remaining areas where human-induced disturbances do not occur. Our long-term goal through proper management should be to prevent potential negative outcomes from multi-use by humans of reindeer range, and at the same time maximise the potential for present and future generations of people to enjoy the aesthetics and outdoor recreation opportunities afforded by these natural areas.

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References

- Andersen, R., Linnell, J.D.C. & Langvatn, R. 1996: Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. - *Biological Conservation* 77: 169-176.
- Baskin, L.M. & Skogland, T. 1997: Direction of escape in reindeer. - *Rangifer* 17: 37-40.
- Baskin, L.M. & Skogland, T. 2001: Vigilance and alertness of reindeer: Populations differences. - *Zhurnal Obshchei Biologii* 62: 78-84.
- Behrend, D.F. & Lubeck, R.A. 1968: Summer flight behavior of white-tailed deer in two Adirondack forests. - *Journal of Wildlife Management* 32: 615-618.
- Berger, J. 1978: Group size, foraging, and antipredator plays:

- An analysis of bighorn sheep decisions. - *Behavioral Ecology and Sociobiology* 4: 91-99.
- Cameron, R.D., Smith, W.T., Fancy, S.G., Gerhart, K.L. & White, R.G. 1993: Calving Success of Female Caribou in Relation to Body-Weight. - *Canadian Journal of Zoology* 71: 480-486.
- Cassirer, E.F., Freddy, D.J. & Ables, E.D. 1992: Elk responses to disturbance by cross-country skiers in Yellowstone National Park. - *Wildlife Society Bulletin* 20: 375-381.
- Colman, J.E., Jacobsen, B.W. & Reimers, E. 2001a: Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocations by humans on foot. - *Wildlife Biology* 7: 275-283.
- Colman, J.E., Pedersen, C., Hjermann, D.O., Holand, O., Moe, S.R. & Reimers, E. 2001b: Twenty-four-hour feeding and lying patterns of wild reindeer *Rangifer tarandus tarandus* in summer. - *Canadian Journal of Zoology* 79: 2168-2175.
- Colman, J.E., Pedersen, C., Hjermann, D.O., Holand, O., Moe, S.R. & Reimers, E. 2003: Do wild reindeer exhibit grazing compensation during insect harassment? - *Journal of Wildlife Management* 67: 11-19.
- de Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M. & van Wieren, S.E. 2004: Flight distance in roe deer *Capreolus capreolus* and fallow deer *Cervus dama* as related to hunting and other factors. - *Wildlife Biology* 10: 35-41.
- de Vos, A. 1960: Behavior of barren-ground caribou on their calving grounds. - *Journal of Wildlife Management* 24: 250-258.
- Duchesne, M., Cote, S.D. & Barrette, C. 2000: Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. - *Biological Conservation* 96: 311-317.
- Fancy, S.G. & White, R.G. 1985: Incremental cost of activity. - In: Hudson, R.J. & White, R.G. (Eds.); *Bioenergetics of wild herbivores*. CRC press, Inc., pp. 143-159.
- FitzGibbon, C.D. 1988: The antipredator behaviour of Thompson's gazelle. - PhD dissertation, University of Cambridge, 128 pp.
- Frid, A. 1997: Vigilance by female Dall's sheep: interactions between predation risk factors. - *Animal Behaviour* 53: 799-808.
- Gaare, E. & Eriksson, L. 1981: Lavforråd i vinterbeitet, Forelhogna villreinområde. - Direktoratet for vilt og ferskvannsfisk, Trondheim, 24 pp. (In Norwegian).
- Gunn, A. & Miller, F.L. 1980: Responses of Peary caribou cow-calf pairs to helicopter harassment in the Canadian High Arctic. - In: Reimers, E., Gaare, E. & Skjenneberg, S. (Eds.); *Second International Reindeer/Caribou Symposium*, Røros, Norway. Direktoratet for vilt og ferskvannsfisk, Trondheim, pp. 497-507.
- Hagemoen, R.I.M. & Reimers, E. 2002: Reindeer summer activity pattern in relation to weather and insect harassment. - *Journal of Animal Ecology* 71: 883-892.
- Helle, T. & Sarkela, M. 1993: The effects of outdoor recreation on range use by semi-domesticated reindeer. - *Scandinavian Journal of Forest Research* 8: 123-133.
- Hicks, L.L. & Elder, J.M. 1979: Human disturbance of Sierra Nevada bighorn sheep. - *Journal of Wildlife Management* 43: 909-915.
- Jarman, P.J. 1974: The social organisation of antelope in relation to their ecology. - *Behaviour* 48: 215-267.
- Jordhøy, P. 1995: Fokus på kjeveanalyser og kondisjon. - *Villreinen* 9: 64-66. (In Norwegian).
- Klein, D.R. 1991: Caribou in the changing north. - *Applied Animal Behaviour Science* 29: 279-291.
- Kuck, L.G.L., Hompland, L. & Merrill, E.H. 1985: Elk calf response to simulated mine disturbance in southeast Idaho. - *Journal of Wildlife Management* 49: 751-757.
- Kufeld, R.C., Bowden, D.C. & Schrupp, D.L. 1988: Influence of hunting on movements of female mule deer. - *Journal of Range Management* 41: 70-72.
- LaGory, K.E. 1986: Habitat, herd size, and the behaviour of white-tailed deer. - *Behaviour* 98: 168-179.
- Meli, J.J. 1997: Villreindistrikter og villreinområder i Norge. - *Villreinen* 11: 80-101. (In Norwegian).
- Meli, J.J. 2001: Tellinger i Forelhogna. - *Hognareinen* 10: 14-16. (In Norwegian).
- Miller, F.L. & Gunn, A. 1979: Responses of Peary caribou and muskoxen to helicopter harassment. - *Canadian Wildlife Service, Canadian Wildlife Service Occasional Paper* 40, 90 pp.
- Mooring, M.S. & Hart, B.L. 1992: Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. - *Behaviour* 123: 173-193.
- Mörschel, F.H. & Klein, D.R. 1997: Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta Herd, Alaska. - *Canadian Journal of Zoology* 75: 1659-1670.
- Reimers, E. 1980: Activity pattern; the major determinant for growth and fattening in Rangifer. - In: Reimers, E., Gaare, E. & Skjenneberg, S. (Eds.); *Second International Reindeer/Caribou Symposium*, Røros, Norway. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, pp. 466-474.
- Reimers, E. 1983: Reproduction in Wild Reindeer in Norway. - *Canadian Journal of Zoology* 61: 211-217.
- Reimers, E. 1986: Management of wild reindeer in Norway. - *Rangifer Special Issue* 1: 241-246.
- Skogland, T. 1984: The effects of food and maternal conditions on fetal growth and size in wild reindeer. - *Rangifer* 4: 39-46.
- Skogland, T. 1991: Bestandsfragmentering av villrein i Rondane pga. naturinngrep og turisme. - *Villreinen* 5: 66-73. (In Norwegian).
- Taylor, A.R. & Knight, R.L. 2003: Behavioral responses of wildlife to human activity: terminology and methods. - *Wildlife Society Bulletin* 31: 1263-1271.
- Thomas, D.C. 1982: The relationship between fertility and fat reserves in Peary caribou. - *Canadian Journal of Zoology* 60: 597-602.
- Thomson, B.R. 1977: The behaviour of wild reindeer in Norway. - PhD thesis, University of Edinburgh, 428 pp.
- Tyler, N.J.C. 1991: Short-term behavioral-responses of Sval-

- bard reindeer *Rangifer tarandus platyrhynchus* to direct provocations by a snowmobile. - *Biological Conservation* 56: 179-194.
- Venables, W.N. & Ripley, B.D. 2002: *Modern applied statistics with S*. - Springer Verlag, New York, 495 pp.
- Wolfe, S.A., Griffith, B. & Wolfe, C.A.G. 2000: Response of reindeer and caribou to human activities. - *Polar Research* 19: 63-73.