

VIGILANCE BEHAVIOR IN WILD AND SEMI-DOMESTIC REINDEER IN NORWAY

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ABSTRACT: We recorded vigilance behavior of a wild reindeer (*Rangifer tarandus tarandus*) population in Rondane North and a population of semi-domesticated origin in Norefjell-Reinsjøfjell during 3 periods (April-May, June-July, and August) in 1997 in southern Norway. The 2 areas studied have different histories of hunting, domestication, predation, and human activity. A vigilance bout was defined as the act of interrupting feeding by lifting the head above the shoulders and briefly observing the surrounding area for < 10 seconds before returning to feeding. The Rondane North population of reindeer displayed a higher rate of vigilance during all periods compared with the Norefjell-Reinsjøfjell population ($P < 0.0001$). The Norefjell-Reinsjøfjell reindeer devoted more time to predator-vulnerable activities such as lying head down and lying head flat, than the population inhabiting Rondane North. Higher rates of vigilance behavior displayed by the Rondane reindeer most likely are related to differential elimination of animals during the evolutionary history of domestication, and by hunting in the 2 areas. Habituation to humans and the presence or absence of large mammalian predators may also contribute to the observed differences in vigilance behavior.

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Grouping and vigilance behavior in animals is a product of co-evolution with predators and parasitizing insects (Hamilton 1971, Mooring and Hart 1992), and selective pressure from hunting and domestication. Although food density, intra-group competition and other factors not directly related to predation may also affect vigilance, it is largely concerned with looking for predators (reviewed in Elgar 1989). Although availability of food, intra-group competition, and other factors not directly related to predation also may affect vigilance, animals are largely concerned with surveillance for predators (Elgar 1989). Because an animal must accomplish more in its lifetime than simply avoiding predation, its antipredator adaptations should be sensitive to the cur-

rent level of predation risk (Lima and Dill 1990, Frid 1997). Caribou and wild and semi-domestic reindeer (*Rangifer tarandus*), which live in comparable environments, are expected to have similar behavioral repertoires (Pruitt 1960, Kelsall 1968, Baskin 1970, Thomson 1975, Skogland 1989), although possibly different quantitative expression of behaviors (Skogland 1991) related primarily to the risk of predation (Lent 1974, Curatolo 1975, Skogland 1989).

Because vigilance behavior is a fitness-related behavioral trait, we expect natural selection to favor individuals that displayed the most suitable rate of vigilance. Reindeer in the Palearctic have co-existed for millennia with predators and man. Over time, this coexistence possibly has led to

selection for increased alertness and vigilance behavior of wild reindeer. Selection most likely works in the opposite direction in domestic reindeer husbandry. Vigilant animals are more difficult to handle, and control and herders tend to eliminate the shyest reindeer (Baskin 1970).

The purpose of our study was to compare vigilance behavior among semi-domestic reindeer released to the wild in Norefjell-Reinsjøfjell in 1968 with wild reindeer inhabiting Rondane North. We predicted that the semi-domesticated reindeer in Norefjell-Reinsjøfjell should exhibit lower vigilance overall compared with wild reindeer of Rondane North, because the domestication process should select for more docile, less-nervous and less-alert animals. We also discuss effects of proximate factors on vigilance including predator abundance, herd size, abundance of oestrid flies, reproductive status of females, time of year, hunting, and other human activities.

STUDY AREAS

Our study was conducted in 1997 in southern Norway with a population of semi-domestic reindeer in Norefjell-Reinsjøfjell (60°25'N; 9°15'E; 308 km²) and with a population of wild reindeer in Rondane North (62°N; 9°45'E; 1,441 km²). Both areas are alpine and are located within the continental part of Norway; precipitation ranges between 400-600 mm.

The domestic reindeer company in Norefjell started their activity in Norefjell-Reinsjøfjell in 1954; the population numbered 1,300 animals in 1968 when the company closed (Skjenneberg and Slagsvold 1968). Thirty animals left in the area in 1968 were bought from their owners and protection of this nucleus resulted in 734 animals before calving in 1992 (Reimers 1992). Hunting was initiated in 1992 and has maintained the population between 500 and 600 animals in winter. The animals are

in prime condition with carcass weights (\pm SD) in autumn of 40.3 ± 6.6 kg among ≥ 2 -year-old females. Young frequently become pregnant and give birth as yearlings in this area (E. Reimers, unpublished data).

The wild reindeer population in Rondane North has fluctuated between 1,200 and 2,400 animals during the last 20 years (Wegge 1997) and was estimated at 1,200 animals in 1997. The Rondane North population always has been hunted, except during 1902-1906, when wild reindeer were protected in Norway. Carcass weights (\pm SD) among females ≥ 2 years old average 36.1 ± 5.4 kg in autumn (Reimers et al. 1983) and were significantly lower than in Norefjell-Reinsjøfjell (ANOVA; $F_{59,305} = 28.8$, $P < 0.01$). Females reproduce for the first time as yearlings in Rondane North (Reimers 1983).

Golden eagles (*Aquila chrysaetos*) occur in both areas; Rondane North has a viable and stable population of wolverines (*Gulo gulo*), and there is a growing population of lynx (*Lynx lynx*) in the forests surrounding the Norefjell-Reinsjøfjell. These forests are frequented by reindeer during post-calving in early May.

Numerous cabins and several alpine centers are located within and in the outskirts of both areas. Both areas are easily accessible from all directions, and hiking and hunting traffic is extensive in most parts of both areas in summer, autumn (hunting), and winter (Easter and winter vacation in February). Reindeer in Rondane North are less influenced by human activities than the Norefjell-Reinsjøfjell population, because Rondane North is a bigger, more rugged area with a more distinctive wilderness character.

METHODS

The field study was conducted during 3 periods in 1997: Norefjell-Reinsjøfjell (14-22 April, 28 June -7 July, and 28 July-5

August) and Rondane North (28 April–3 May, 12–21 July, and 10–19 August). During summer, observation periods were scheduled relative to calving dates (7 May in Norefjell-Reinsjøfjell, and 22 May in Rondane North; Reimers 1997). We visited the 2 different areas so that the relative times after calving were equivalent.

Reindeer were located by sight and observed with spotting scopes from distances between 50 and 1,500 m. Observations were made from a concealed position so the reindeer were unaware of our presence. Focal-animal sampling (Altmann 1974) was employed to record the behavioral activities: feeding, searching, lying head up, lying head down, lying head flat, and other (including standing, walking, running, antler sparring, etc.). Activities were timed to the nearest second with a digital stopwatch with 100 lap times. Recording sessions lasted up to 10 min with an average duration of 8.9 min in the total sample of 737 recordings. An observation period was halted if any reindeer moved out of sight, or if an individual was clearly disturbed by some outside influence. If this happened, a new animal was chosen randomly.

Focal animals were selected among adult ≤ 1 -year-old females with or without young. Focal females were alternatively selected in the center or on the periphery of a group. As focal animals frequently shifted position from the periphery to the center (and vice versa) during recording sessions, we eliminated sampling for a comparison of vigilance relative to the animal position in the herd. When selecting between an animal lying or feeding, animals from the predominant behavior category of the herd were chosen. Because all focal observations in a group were made with different animals and at different times, we assumed them to be independent.

Feeding was defined as the act of ingesting forage with the muzzle down (Bøving

and Post 1997). Surveillance activities, like searching and lying-head up were considered to be vigilant forms of behavior. An animal was considered searching if it was standing alert, with head above the horizontal, clearly attentive and scanning the immediate area ≥ 10 sec (Langbein and Putman 1992). A vigilance bout was defined as the act of interrupting feeding to lift the head above the shoulders and observe the surrounding area for < 10 sec before returning to feeding (Bøving and Post 1997). Lying head up was defined as lying down with head raised above the level of shoulders, a position from which an individual can observe its surroundings while ruminating or resting (Bøving and Post 1997). Lying head down was defined as lying with the head resting on the ground, whereas lying flat was defined as lying head down on the side with the legs stretched.

Reindeer movements ranged from 2 to > 30 km per day, depending on wind conditions, hardness of snow, distance between food patches, the degree of insect harassment, and human disturbance. On days with high temperatures and insect harassment, reindeer frequently remained on snow patches from 0800 to 2000 h. Vigilance was not recorded on those days and because of extremely warm temperatures in 1997, vigilance was not measured frequently during June–July.

The response variable “vigilance bouts per 10 min” was ln transformed in all analyses. Data were examined for outliers applying Cook’s D regression diagnostic (Kleinbaum et al. 1988, Fry 1993). The 4 highest values for the response variable were considered to be outliers and were removed for each period in both areas. Because many animals displayed zero vigilance bouts per 10 min, it was difficult to separate the least vigilant animals from the remainder, thus these relaxed animals were excluded from calculations.



Student *t*-tests grouped for periods were used to examine differences in number of vigilance bouts between the 2 areas. Only data from feeding animals were used in the vigilance-bout analyses. ANOVAs were applied to determine if vigilance varied within an area during each season or between females with or without young. Proportions of time devoted to different activities in the 2 areas were not normally distributed. Hence, data on activity were analysed using the Mann-Whitney *U*-test (Siegel and Castellan 1988).

RESULTS

Number of vigilance bouts in female reindeer was significantly higher in Rondane North than in Norefjell-Reinsjøfjell for all 3 periods (*t*-test; $P < 0.0001$; Fig. 1). Vigilance decreased significantly in Norefjell-Reinsjøfjell from April-May to August (ANOVA; $P < 0.0001$), whereas it increased significantly during the same period in Rondane North (ANOVA; $P < 0.0004$).

Time devoted to lying activities decreased from April-May to August in both areas (Fig. 2). Females were lying with head down significantly more in Norefjell-

Reinsjøfjell than Rondane North (*U*-test, $P < 0.001$).

Time lying among females (\pm SE) decreased from $53 \pm 3\%$ in April-May to $28 \pm 3\%$ in June-July, and to $9 \pm 1\%$ in August in Norefjell-Reinsjøfjell. The corresponding values were $41 \pm 3\%$, $13 \pm 4\%$, and $13 \pm 2\%$ in Rondane North, respectively. Females changed their lying activities among areas during the same periods (Fig. 3). In April-May, females in Norefjell-Reinsjøfjell spent the same proportion of time lying head up and head down, whereas in Rondane North, females spent twice as much time in the head up posture. During June-July and August, Rondane North females had their head up while lying, whereas females in Norefjell-Reinsjøfjell spent 8 and 29% of the time lying with their head down, respectively.

We noted 2 proportional differences in activities for females with and without young calculated from total time of observation. Females with young in Norefjell-Reinsjøfjell displayed more vigilance bouts per 10 min in June-July than females without young (*U*-test; $P = 0.04$). In August, Rondane females with young spent more time lying with heads up, than did females without

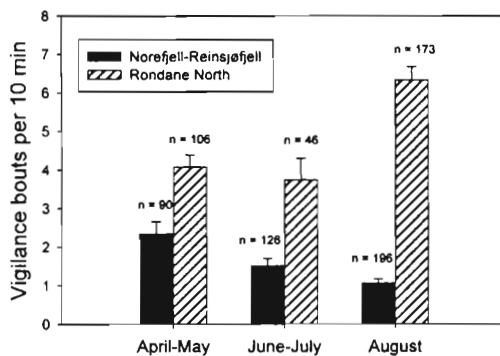


Fig. 1. Mean number of vigilance bouts per 10 min \pm SE of grazing ≥ 1 -year-old female reindeer for the 3 periods (April–May, June–July, and August) in Norefjell-Reinsjøfjell and Rondane North in 1997. Number of focal observations above bars.

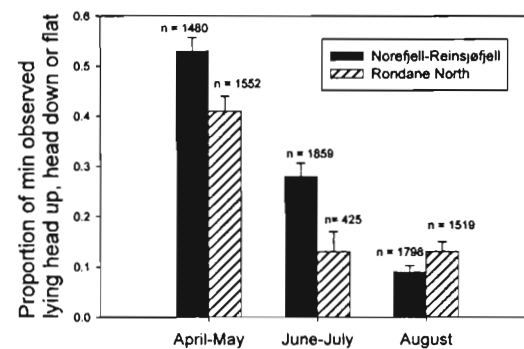


Fig. 2. Proportion of time spent on lying activities (head up, head down, and head flat) of ≥ 1 -year-old female reindeer for the 3 periods in Norefjell-Reinsjøfjell and Rondane North in 1997. Number of observation minutes above bars.

young (U -test; $P = 0.02$).

Mean herd size in all periods was significantly larger in Rondane North than in Norefjell-Reinsjøfjell (Fig. 4). Mean and minimum herd size was lowest in both areas in August. Smallest herd size was 18 animals in Rondane North and 5 animals in Norefjell-Reinsjøfjell. Vigilance recordings in small herds were few; 8% in herds < 10 animals in Norefjell-Reinsjøfjell, and 2% in the 18-animal herd in Rondane North. The number of vigilance bouts was unrelated to herd size in both areas (linear regression analyses; $P = 0.31$).

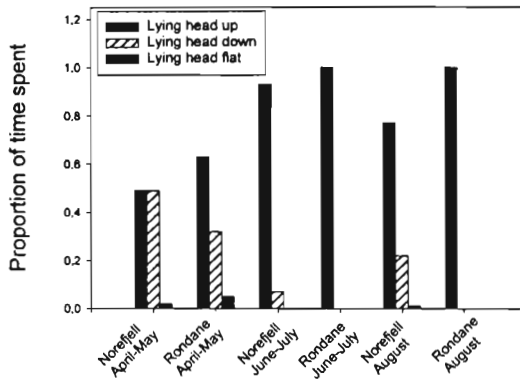


Fig. 3. Proportion of time spent on lying activities (head up, head down, and head flat) of ≥ 1 -year-old female reindeer for the 3 periods in Norefjell-Reinsjøfjell and Rondane North in 1997 calculated from the total time lying. Sample sizes are the same as in Fig. 2.

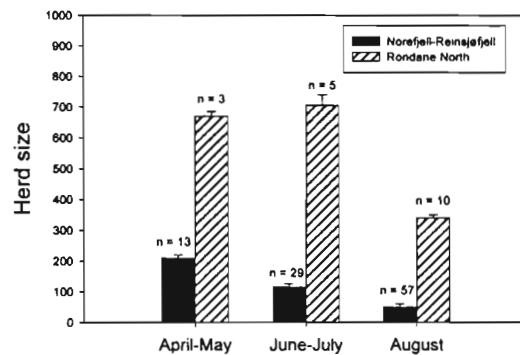


Fig. 4. Mean \pm SE wild reindeer herd size for the 3 periods in Norefjell-Reinsjøfjell and Rondane North in 1997.

In June-July, we observed in both areas a nonsignificant trend (ANOVA; $P = 0.12$) towards more vigilance bouts per 10 min with an increasing level of harassment from Oestridae; the warble fly (*Hypoderma tarandi*) and the nose bot fly (*Cephenemyia trompe*). Because of high temperatures and high insect activity in August, reindeer in both areas spent most of the day on snowfields. Thus, vigilance recordings during periods with high Oestridae activity are lacking in that month.

DISCUSSION

Behavioral patterns displayed in *Rangifer* result from co-evolution with man and other predators. *Rangifer* and wolves (*Canis lupus*) have co-evolved for approximately 500,000 years (Mech 1981, Leader-Williams 1988), during which time reindeer and caribou have become the primary prey of wolves where these 2 species co-exist. There also is evidence that reindeer co-evolved with wolverines (*Gulo gulo*) at least in prehistoric time. Wolves and wolverines have largely been absent from southern Norway since the 1800s until recently when protection (1972) and later establishment (1995) of core or nucleus areas for 20-40 wolverines in Rondane North-Dovre-fjell (Reimers, 2001). In Norefjell-Reinsjøfjell, the wolverine has, except for some stragglers, been absent for years, as have wolves in both areas. As discussed by Frid (1997), natural selection would favor interactive predator-prey relationships. Rather than making redundant investment in anti-predator behavior, animals that are already safe enough can make greater investment in foraging. We believe it unlikely that the differences in predation pressure at the time we made our recordings had an important effect on the observed changes in vigilance behavior in the 2 areas.

Other important population-environment



interactions that may have influenced our results include possible differences in habitat use, hunting pressure, grazing quality, insect harassment, and herd size. During fieldwork the habitats used by reindeer in both areas were open alpine terrain in which distance to concealment cover appeared to be unimportant. Differential effect of human hunting appeared unlikely, because the annual hunting pressure in terms of percentage of harvested animals was high in both areas in the 1990s (27-36% of the winter population; Wegge 1997, unpublished data). Although winter pastures of mostly lichens are well developed in both areas, lower altitudes in Norefjell-Reinsjøfjell result in a higher quantity of summer pastures in this area than in Rondane North (Reimers et al. 1983, unpublished data). As pointed out by Illius and Fitzgibbon (1994), food biomass relates negatively to foraging time, vigilance time, and vigilance cost, and varies positively with time for vigilance. In spite of a possible effect of lower food biomass in Rondane North during summer and hence less time for vigilance, we recorded a higher vigilance frequency at this time, as well as in April-May, when lichens were abundant and mean herd size in both areas were > 200 animals. Lower body size of reindeer in Rondane North than in Norefjell-Reinsjøfjell may reflect that vigilance scanning is incompatible with feeding, and thereby reduces rate of food intake.

Vigilance differences between study areas are likely related to history of domestication, hunting, and general human activity. Over time, man can influence behavioral changes of reindeer through selective slaughtering or hunting. In domestic reindeer husbandry, very alert and vigilant animals demand more effort and are eliminated to ease control of dispersal and group cohesion (Baskin 1970). Throughout the year, domestic reindeer have contact with herdsman during events such as gathering,

marking, slaughtering, castrating, supervision, and herding. In addition to selective elimination of shy animals, we expect that this regular contact has caused the animals to become more accustomed to humans.

Semi-domesticated reindeer in Norefjell-Reinsjøfjell have had 29 years (1968-1997) to turn from domestic to “wild.” Hunting of the population was initiated in 1992, and because the generation time in hunted populations of wild reindeer in Norway is < 10 years (E. Reimers, unpublished data), any major genetically based change in behavior is unlikely during that short period. Behavioral changes, hence, most likely have a learning base. We anticipate that forces favoring different behavioral directions influence learning in present-day reindeer. A free-roaming life with few encounters with humans and hunting most likely reinforces vigilance, whereas frequent encounters with humans relax vigilance (Eftestøl 1998, Reimers et al. 2000, Coleman et al. 2001). Because short-term effects of hunting on fright and flight responses in reindeer were not observed in Rondane North (Kind 1996) or in Norefjell-Reinsjøfjell (Dervo and Munitz 1994), we believe that hunting has only a long-term effect on vigilance behavior.

Wild reindeer in Rondane North have no previous influence of herding, and have been exposed to hunting by humans for thousands of years. In recent years, the Rondane North population was hunted annually at a sustainable rate (\pm SD) of 27% \pm 8 ($n = 7$) of the winter herd (Wegge 1997). Over time, selective killing of the least shy or least vigilant animals may have resulted in directional selection toward increased vigilance. Conceivably, prior to the advent of the rifle as the general hunting tool, close range hunting with pitfalls, spears, throw sticks (atlatls), and bow and arrows were stronger behavioral mediators, because animals were more frequently exposed to the

negative effects of human presence.

Several reports indicate that ungulates hunted by humans are less likely to habituate to human presence than those not subjected to hunting (Dorrance et al. 1975, Schultz and Bailey 1978, Klein 1980, McLaren and Green 1985, Jeppesen 1987). Those reports presented no supporting data, but rather cite earlier work that postulated a hypothesis (Behrend and Lubeck 1968, Geist 1971, Thomson 1977, Ferguson and Keith 1982). On Svalbard, reindeer (*R. t. platyrhynchus*) that were hunted did not consistently have the greatest fright and flight responses to direct provocation by humans on foot in summer (Colman et al., 2001). Increased non-negative interactions with humans may even facilitate habituation. Behrend and Lubeck (1968) noted that periodic hunting did not reduce summer viewing of white-tailed deer (*Odocoileus virginianus*) in some parks in New York, USA. Likewise, Grau and Grau (1980) and Kufeld et al. (1988) reported no increase in dispersal or home-range abandonment by white-tailed deer or mule deer (*O. hemionus*) as a consequence of hunting. Most likely, the accumulated effect of all human activities helps determine behavior of ungulates towards humans (Jeppesen 1987). Hunting, when added to other strong human stimuli like extensive tourism, does not necessarily increase vigilance.

Vigilance activities are supposed to reach a lower limit, the "predator-safe threshold" for which such activities will be maintained. Based on a cost-benefit account, evolution will not favor individuals that stop surveillance under dangerous circumstances. Costs of investing some energy in surveillance activities are small compared with the cost of being killed.

In Norefjell-Reinsjøfjell, the number of vigilance bouts decreased from April-May to August, whereas vigilance slightly decreased between April-May and June-July,

and significantly increased in August in Rondane North. Reindeer had longer sight, fright, flight, and running distances during winter than during summer and autumn in both areas (Dervo and Munitz 1994, Kind 1996). Distances were shortest in late summer or autumn. All distances were significantly longer in Rondane North than in Norefjell-Reinsjøfjell (Kind 1996). Except for the high rates of vigilance in Rondane North in August, our data fit the fright and flight pattern (Dervo and Munitz 1994, Kind 1996).

Our data indicate increasing vigilance with increasing level of Oestridae harassment, which may explain the high vigilance in Rondane North in August. Flying activity of the 2 oestrid species increases with increasing air temperature and the number of flies present (Folstad et al. 1991, Nilssen and Haugerud 1994, Hagemoen 1999). Average temperature for the last period (10-19 August) in Rondane North was 14.5°C and 5.5°C, respectively, above the long-term average, and higher than all other observation periods in both Norefjell-Reinsjøfjell and Rondane North (The Norwegian Meteorological Institute, personal communication).

Vigilance behavior is expected to vary with sex, age, dominance status, and parental status of individuals in the group. In an observation of red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in parks, females were more vigilant than males to increased levels of disturbance (Langbein and Putman 1992). Other studies have documented that females with young display a higher rate of vigilance behavior than females without them (Caro 1987, Sullivan 1988). Linnell (1994) showed that adult female roe deer (*Capreolus capreolus*) with young spent twice as much time on vigilance behavior as females without young. This tendency also occurred for pronghorn (*Antilocapra Americana*; Lipetz and

Bekoff 1982). Significant differences in lying activities and vigilance between females with and without young in Rondane North and Norefjell-Reinsjøfjell concur with these findings, and lend support to the prediction that females with young spend more time on vigilance behavior than females without them.

Unlike studies of other herbivores that indicate a negative correlation between herd size and vigilance (Siegfried and Underhill 1975, Lipetz and Bekoff 1982, Alados 1985) we observed no effect of herd size. Herd size remained high in our study and may have been above a threshold that may result in a change in vigilance. Although we randomly picked focal animals from the interior and the periphery of the various herds, we did not consider the “edge effect” (Elgar 1989). The confounding influence of the edge effect arises because the proportion of individuals at the edge of the group declines as the group gets larger, and hence the scanning rate for the group also declines (Lazarus 1978). Our findings correspond with work on caribou (Bøving and Post 1997), which reported that vigilance did not increase even when herd size was < 10 animals.

The more relaxed vigilance behavior displayed by the Norefjell-Reinsjøfjell reindeer compared with those in Rondane North likely relates to their domestic origin. High levels of tourist activities, low levels of predators, and a shorter period of exposure to hunting (from 1992), probably maintain the relatively relaxed behavior of the Norefjell-Reinsjøfjell reindeer. Vigilance appears to be influenced by insects and recording of vigilance for inter-population comparison should be limited to insect-free seasons.

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