

FRIGHT AND FLIGHT BEHAVIOR OF REINDEER

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ABSTRACT: Vigilance and avoidance behaviors of 8 reindeer (*Rangifer tarandus*) populations from different geographical areas were examined by measuring distances of detection and flight from a human approaching on foot. Differences in behavior among populations were mainly explained by differences in hunting pressure, genetic origin (wild, feral, and tame ancestors), and predation pressure. Populations subjected to intensive hunting were more vigilant than populations that experienced no hunting. A significant but less clear pattern occurred for predation. Domestic reindeer in large groups demonstrated the lowest levels of fright and flight behavior.

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Predation risk has been an important selective factor influencing the behavior of animals. As a result, animals exhibit specific antipredator behavior, for example vigilance (the capacity of animals to detect danger) that differ both among species and populations within a species (Elgar 1989, Bøving and Post 1997). Nevertheless, there is also a cost associated with vigilance behavior, because that behavior reduces time available for foraging and increases energy expenditure (Berger 1978, Elgar 1989). As a result, predator-avoidance behavior only should be realized in situations where the gain of such behavior is likely to be greater than its cost (Carl and Robbins 1988). This tradeoff is probably the reason why many animals, especially ungulates, show considerable plasticity in their vigilance behavior depending on the current risk of predation. Although vigilance behavior ultimately is determined by genetic factors, proximate factors such as hunting, predator density, group size, and presence of newborns are known to modify such behavior (Bergerud 1974, Semenov-

Tien-Shanskiy 1977, Bertram 1978, Skogland 1989a, Lima and Dill 1990).

Vigilance and avoidance behaviors have attracted much attention from researchers (Walther 1969, Baskin 1970, Lipetz and Bekoff 1982, Alados 1985, Lagory 1987, Fitzgibbon 1990, Tyler 1991). Factors affecting vigilance behavior include hunting (Skogland and Grøvan 1988, Colman 1995), predators (Lima and Dill 1990, Skogland 1991), frequency of contacts with humans (e.g., tourists; Tyler 1991, Colman 1995), occurrence of newborns (Lent 1966, Bergerud 1974), and domestication (Baskin 1970). Hunting, predation, and occurrence of young in groups usually lead to increased vigilance (Murie 1935, Pruitt 1960, Elgar 1989, Bøving and Post 1997).

Furthermore, many authors have investigated the influence of group size on vigilance. A decrease in scanning frequency with increasing group size has been reported for pronghorns (*Antilocapra americana*; Lipetz and Bekoff 1982), goats (*Capra pyrenaica*; Alados 1985), white-tailed deer (*Odocoileus virginianus*;

Lagory 1987), and gazelles (*Gazella thomsoni*, *G. granti*; Fitzgibbon 1990). Dehn (1990), however, demonstrated with a model that vigilance of groups of Rocky Mountain elk (*Cervus elaphus nelsoni*) increased only slightly above a group size of 10.

Groups of different size occur in reindeer populations. Groups of hundreds of animals are common, but gatherings of 80,000 animals have been observed (Crechmar 1966, Kelsall 1968, Pavlov et al. 1971, Baskin 1986). Nonetheless, in some populations, reindeer only occur in small groups (Bergerud 1974, Skogland 1989a). Lent (1966), Naumov and Baskin (1969), Bergerud (1974), and Skogland (1989b) considered gregariousness as an adaptation to predation. Those authors speculated that individuals in large groups would have a better chance to escape predators than solitary animals. Skogland (1989b) also suggested that reindeer gregariousness is an adaptation to the distribution of food. Thus, very sparse and scanty food in Svalbard resulted in small groups ($\bar{x} = 3.8$, range = 2-11 animals), but in the Dovrefjell and Forelhogna mountains in Norway (where food resources were plentiful) reindeer aggregated into large groups ($\bar{x} = 290$, range = 55-1,300 animals). Clearly, relationships between group size, vigilance, and escape behavior are important subjects for investigation, as are interrelationships of those behaviors with other features of reindeer ecology.

Furthermore, there are strong indications that the distance at which a predator or human can approach reindeer without causing them to flee differs for wild, feral, and domestic animals. The reason for this difference may be that predators and hunters try to kill prey with the least expenditure of effort and time. Consequently, less alert animals would be killed more often. The higher survival rate of alert animals via

natural selection may lead to changes in vigilance and escape behavior for the entire population.

By contrast, when a herder is managing reindeer, the whole group may run away when the most nervous animals start their flight, because the rest of the group may perceive those animals as leaders. As a result, the most nervous reindeer are systematically eliminated by herdsman to simplify their job (Baskin 1970). Such selective cropping might lead to genetic changes and generally lower alertness in such populations, and probably to changes in other features such as fearfulness of animals in a group. Thus, differences in selective cropping by pursuing predators or hunting by man for the least nervous wild reindeer and the cropping by herdsman of the most excitable individuals could change alertness of reindeer populations in opposite directions. In many areas, wild reindeer are subjected to strong hunting pressure. Hunting might select for more alert animals. Therefore, we would expect feral reindeer to be more alert than tame animals.

Frequent contact with humans may lead to habituation to human presence even in wild populations of reindeer, as demonstrated for wild reindeer on Svalbard, where sub-populations inhabit areas with different levels of human presence and activity (Tyler 1991, Colman 1995). In reindeer husbandry, herders keep animals in large groups by exerting nearly constant control on their behavior (referred to as close-keeping), or allow reindeer to run free to a large extent and only occasionally gather them in groups or move them into corrals (referred to as free-keeping). Those different levels of interactions between herders and reindeer also may alter reindeer behavior towards humans.

Many factors may influence the vigilance behavior of reindeer. Most studies on vigilance, however, have only considered

one of those factors we discussed, rather than simultaneously evaluating several factors. Furthermore, most studies have been conducted in areas inhabited by a single population of reindeer in which different groups have been compared (Bergerud 1974, Tyler 1991). To our knowledge, Bøving and Post (1997) conducted the only study of vigilance behavior in reindeer from different geographical areas (Alaska, USA, and Greenland).

The aim of our study was to compare vigilance behavior of reindeer populations in different geographical areas, which also varied with respect to group size, husbandry practices, and hunting or predator pressure. In addition, we wanted to determine if vigilance behavior was influenced by differences in the sex composition of groups or presence of neonates in groups. Based on the current knowledge of vigilance behavior, we tested the following predictions: (1) high hunting or predator pressure will increase vigilance; (2) vigilance will decrease with increasing group size; (3) feral reindeer will

be more vigilant than free-kept reindeer, and both will be more vigilant than close-kept reindeer; and (4) sex composition and presence of young in herds will influence fright and flight behavior.

STUDY AREAS

Reindeer Populations

We selected 8 populations of different origin (wild, feral, and domestic), that differed in the presence of predators or hunting. Furthermore, management differed among populations of domestic reindeer; some were managed with close herding, and others were kept free, but had some contact with humans (Table 1).

The Dovrefjell population in Norway is considered to be the last mountain reindeer herd in Europe (Skogland 1989a). This herd consists of several interacting subpopulations including those in the Snohetta and Rondane areas. Both subpopulations are hunted annually at a rate of about 25% of their population size in winter. The herd coexists with a population of about 20 wolverines

Table 1. Characteristics of the reindeer populations used in the analyses of vigilance behavior. The following factors were used (hunting pressure, no = 0, yes = 1; predation pressure, no = 0, yes = 1; group composition, females with yearlings = 1, male groups = 0 (domestic groups attributed to female groups); presence of newborns, female groups with newborns = +1, female groups without newborns (only yearlings) = -1, male groups in this context = 0).

Population	Genetic origin	Method of ranging	Hunting pressure	Predation pressure	Group composition	Presence of newborns
Dovrefjell	Wild	—	1	1	1,0	-1,0
Svalbard	Wild	—	0	0	1,0	-1,0
Wrangell	Feral	—	1	0	1,0	-1,0
Forelhogna	Feral	—	1	1	1,0	-1,0
Vaygach	Tame	Free	0	0	1	1,-1
Bol'shezemel'skaya Tundra	Tame	Close	0	0	1	1,-1
Chukotka	Tame	Close	0	1	1	1,-1
Lapland	Tame	Free	0	1	1	-1

(*Gulo gulo*) that hunt them regularly during winter.

On the high Arctic island of Svalbard, we studied a subpopulation in the Reindalen area of 600-1,000 individuals. Until 1925, this population was subject to heavy hunting. Hunting was later banned, and only since 1983 have hunters again killed 10-35 animals, or 2-6% of the population, annually (Colman 1995). Because of the low culling rate, the hunting factor was set as zero for this population.

The reindeer herd on Wrangell Island has been feral since 1974, when domestic herding practices were abandoned. Since that time, the herd has grown to 6,000-8,000 individuals in the late 1970s. In 1979, a program of population reduction began. Reindeer were herded annually by snowmobiles into a corral for slaughtering. Because 67% of the group usually escaped before reaching the coral, survivors have become wary of man. We therefore defined this population as hunted because of the response of reindeer to humans. In early summer 1991, when our experiments were conducted there, the herd consisted of about 3,000 animals. The Forelhogna herd in Norway east of Dovrefjell consisted of about 1,700 individuals. Those reindeer became feral in the mid 1950s. Since 1968, the Forelhogna herd has been hunted extensively, with an annual cropping rate of about 40% of the population in winter (T. Skogland, personal communication). Wolverines also were common in this area.

The domestic reindeer belonging to the indigenous Chukchi people on Chukotka and the Nentsi people on Vaygach and Bol'shezemel'skaya Tundra east of Arkhangle'sk in Russia are all part of the traditional reindeer husbandry in tundra areas of the north. The population of reindeer we studied consisted of 1,400-2,800 animals. An important difference between Vaygach and the other 2 domestic

populations is that Vaygach reindeer are mostly kept free to range, and are gathered by herdsman once or twice each week throughout the year to catch reindeer for pulling sledges. The Chukotka and Bol'shezemel'skaya Tundra reindeer are mostly kept by herdsman in dense groups.

To gather data on vigilance and avoidance behavior of domestic reindeer, their distances from a human during our provocation tests were measured in groups other than in the largest group, which was under the control of herders. Domestic reindeer in Swedish Lapland are free ranging most of the year, and gathered in corals only a few times per year. Predators (wolves, *Canis lupus*, and wolverines) occur in Chukotka and Swedish Lapland, but there are no predators of reindeer in Bol'shezemel'skaya Tundra and Vaygach.

METHODS

Vigilance Tests

As a measure of vigilance, we used the distance at which a group of reindeer reacted to a human approaching on foot. As a measure of avoidance behavior, we used the flight distance of the group from an approaching human. This method has been used by many authors (Walther 1969, Baskin 1970, Bergerud 1974, Lagory 1987, Fitzgibbon 1990, Tyler 1991). When a reindeer group had been located, an experimenter approached them on foot or skis. The experimenter always walked straight towards the animals and always in the upwind or cross wind direction, never downwind. As a result, our measurements concern only visual reactions of reindeer, not their reactions to human scent. Provocation tests were conducted mostly in late winter – early spring, although at Wrangell Island and Chukotka, we observed animals with neonates in June. We tried to keep other conditions (wind speed, snow conditions, our clothing, and other factors) similar

in all experiments.

When reindeer had discovered the experimenter, he continued approaching while recording details of their behavior on a tape recorder. The approach stopped when the disturbed group of reindeer took flight. The experimenter remained in the same place while the reindeer ran away, made a first stop to observe him, and then approached him or ran away again. The second approach started as soon as the reindeer group had stopped and begun feeding or laid down. We measured the second flight distance, and the second stopping distance.

During the provocation, the detection distance, distance of reindeer aggregation, first flight distance, first stop distance, second flight distance, the second stop, and the distance of pasture in view of the experimenter were measured by pacing. When we encountered animals suddenly, only the first stop distance, second flight distance, and the second stop distance were measured. The flight distance was calculated as the average of the following variables: the distance to animals gathering in compact groups; the distance of the first flight; the distance of the second flight; the distance of the first stop; the distance of the second stop; and the distances of lying or pasturing, when the animals kept visual contact with the experimenter.

Statistical Analyses

We used multiple-regression analyses to evaluate effects of independent variables, including predation, hunting, genetic origin (wild, feral, or tame), method of reindeer herding, group composition (sex), and presence of newborn on vigilance behavior. Original data did not fulfill requirements of normality and homoscedasticity. To satisfy those requirements, we excluded data on provocation of groups with >1,300 animals from analyses. This procedure excluded large groups of domestic reindeer and 1

observation in the Dovrefjell population. A total of 85 detection distances and 115 flight distances of the initial 116 detection distances and 207 flight distances remained in the analysis (Tables 2 and 3). Remaining data were transformed (\log_e+1) prior to analyses. After transformation, minor deviations from normality still remained but visual inspection of residuals showed that the distribution of data was acceptable. Analysis of variance (ANOVA) and regression analyses usually are robust against minor deviations from normality given a relatively large sample (Zar 1984). One remaining problem was collinearity between several independent variables (Table 1). Multicollinearity can result not only in regression coefficients being incorrectly estimated but also having the wrong sign (Hair et al. 1998). To avoid those potential problems and provide control over the regression variates, we used a 3-step process. First we obtained a simple correlation between each independent variable and the dependent variable to understand that relationship. Second we used a stepwise multiple regression (backward; criterion of probability of F -to-remove ≤ 0.1) to produce a model showing the best fit to data. Coding of independent variables was conducted following Cohen and Cohen (1983; Table 1). Thirdly, we used a confirmatory model (all independent variables included in the model) to judge the potential effect of multicollinearity on selection of independent variables and on overall fit of the model (a further description of this approach is provided by Fox 1991, Hair et al. 1998).

RESULTS

Disturbance experiments were repeated (on different days) in the Dovrefjell, Wrangell, and Forelhogna groups. Correlation analyses of detection distance in the first and second experiments revealed that those distances were highly correlated

Table 2. Detection and flight distance of reindeer in different populations (n = number of provocations).

Populations	Detection distance (m)			Flight distance (m)		
	n	Median	95% CI	n	Median	95% CI
Dovre fjell	16	471	358-512	24	409	347-450
Svalbard	15	270	233-352	21	150	113-195
Wrangell	15	256	220-318	16	216	188-265
Forelhogna	11	300	254-339	12	178	143-253
Vaygach	14	221	175-275	20	114	96-138
Bol'shezemel'skaya Tundra	10	201	135-285	61	49	49-64
Chukotka	22	106	93-152	33	60	51-93
Lapland	13	178	138-216	20	147	122-172

Table 3. Detection and flight distance¹ in reindeer from different populations.

Populations	Dovre fjell	Svalbard	Wrangell	Forelhogna	Vaygach + Lapland
Svalbard	DF				
Wrangell	DF				
Forelhogna	DF				
Vaygach + Lapland	DF	D	F	D	
Bol'shezemel'skaya Tundra + Chukotka	DF	D	F	DF	

¹D - significant differences of the detection distance, $P < 0.05$; F - significant differences in flight distance, $P < 0.05$; differences based on Tukey HSD test.

(Pearson $r = 0.92$, $n = 6$, $P < 0.0037$). That outcome indicated that the first provocation of a group provided a reliable estimate of the vigilance level for that group. There also was a significant correlation between the detection distance and flight distance (Pearson $r = 0.76$, $n = 83$, $P < 0.001$). The Dovrefjell population was much more vigilant and exhibited longer flight distances than other populations (Tables 2 and 3).

Detection distance did not differ significantly ($P < 0.05$) among Wrangell, Forelhogna, and Svalbard populations of

reindeer (Tables 2 and 3). Likewise, there were no significant differences among domestic populations (Lapland, Bol'shezemel'skaya Tundra, Vaygach, Chukotka; Table 3). Feral reindeer on Wrangell Island demonstrated a longer flight distance than all other populations except the Dovrefjell population (Table 2), and differed significantly from domestic populations (Table 3). No significant differences occurred between reindeer kept free or closely herded (Table 3).

Regression analyses indicated that al-

though several factors were collinear, that outcome did not have a severe effect on the selection of independent variables in stepwise-regression analyses (Table 4). Nonetheless, collinearity occurred in stepwise regressions of flight distance for the variables hunting, group size, and sex. One result of multicollinearity was that group size had a contrary sign of the correlation with the alert distance (+0.36) and the standardized β (-0.52). That result means that group size was a suppressor variable (i.e., the relationship of group size with hunting, and possibly with other independent variables, was hiding or suppressing their real relationship with flight distance; Cohen and Cohen 1983, Tabachnick and Fidell 1996). Overall, regression analyses indicated that those results still should be interpreted with considerable caution because of multicollinearity among our independent variables.

As hypothesized, heavy hunting and predation pressure increased vigilance (Table 4). Detection distance and flight in-

creased with increasing hunting pressure and flight increased with predation but detection distance did not (Fig. 1, Table 4).

As hypothesized, there was a negative relationship between group size and flight distance (Table 4). A correlation analysis revealed that this occurred for flight distance in Chukotka (Spearman $r = -0.589$, $P < 0.001$), Forelhogna (Spearman $r = -0.602$, $P = 0.038$), and there were indications of a similar pattern in most other populations (e.g., Bol'shezemel'skaya, Spearman $r = -0.242$, $P = 0.058$, and Dovrefjell, $r = -0.301$, $P = 0.153$). In contrast, we detected no significant relationship between group size and detection distance.

Sex composition of the group contributed significantly to the variability in flight but not detection distance (Table 4). The positive sign for β showed that groups of females had longer flight distances than groups of males. Domestication also was correlated with vigilance behavior (Table 5). Wild reindeer were more vigilant than feral, free-kept, and close-kept reindeer.

Table 4. Dependence of detection and flight distances of reindeer on different factors (backward regression, F -to-remove ≤ 0.1).

Independent Variables	Pearson correlation (r)		Detection ¹		Flight ²	
	Detection	Flight	β^3	Unique amount ⁴	β^3	Unique amount ⁴
Hunting	0.48	0.59	0.46***	0.22	0.95***	0.33
Wild or /nonwild	0.48	0.36	0.47***	0.22	0.31***	0.08
Group size	0.36	0.27	-0.02	-	-0.52***	0.10
Sex composition	-0.01	-0.05	0.07	-	0.22*	0.03
Predation	-0.03	0.14	-0.04	-	0.18**	0.03
Presence of calves	-0.23	-0.30	-0.09	-	0.3	-

¹Detection: $n = 85$; $R^2 = 0.45$.

²Flight: $n = 115$, $R^2 = 0.54$.

³ β - standardized regression coefficient; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

⁴Unique amount = partial correlation.

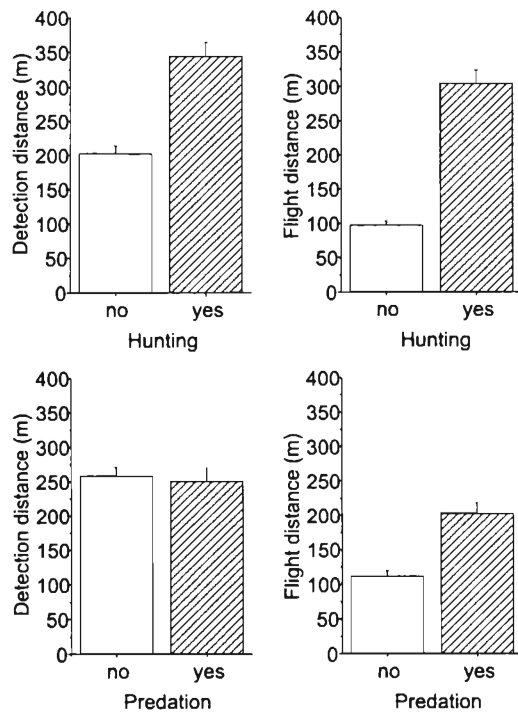


Fig. 1. Influence of hunting and predation on reindeer flight and fright. Both detection and flight distances were significantly higher in hunted populations ($P < 0.05$), whereas flight but not detection distance increased with predation.

DISCUSSION

We compared vigilance behavior of reindeer in different-sized groups belonging to 8 populations distributed over a large geographical area, allowing us to evaluate general patterns of reindeer behavior. Hunting and genetic origin (wild versus nonwild) were important factors affecting reindeer vigilance. Because of multicollinearity among independent variables, however, our interpretation should be viewed with some caution.

As hypothesized, increased hunting and, at least to some degree, predation pressure resulted in increased vigilance behavior in reindeer. Both distance for discovery and for flight increased with increasing hunting. Effects of predation were less clear, but there was an indication that occurrence of predators increased flight distance. Thus, we conclude that hunting was the main factor correlated with vigilance and avoidance behavior. Two of three Norwegian populations experienced heavy hunting pressure; not only were a high proportion of animals killed annually (up to 40%), but

Table 5. Dependence of detection and flight distances of reindeer on domestication factors (backward regression, F -to-remove ≤ 0.1). Detection and flight distances of wild reindeer were compared with reindeer with different degrees of domestication (feral, free-kept, and close-kept).

Independent Variables	Pearson correlation (r)		Detection ¹		Flight ²	
	Detection	Flight	β^3	Unique amount ⁴	β^3	Unique amount ⁴
Feral	0.17	0.27	-0.23***	.04	-0.13*	0.01
Free-keeping	-0.18	0.02	-0.50**	.17	-0.41**	0.11
Close-keeping	-0.50	-0.66	-0.75***	.38	-0.89**	0.48

¹Detection: $R^2 = 0.42$.

²Flight: $R^2 = 0.55$.

³ β - standardized regression coefficient; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

⁴Unique amount = partial correlation.

frequency of human disturbance during hunting also was high. During a day, reindeer can be disturbed 6-8 times (Skogland and Grøvan 1988). Bubenik (1975) observed that in western Alaska, USA, where hunting pressure was low, reindeer kept a distance to humans of approximately 150 m, with a maximum of 300 m. That distance corresponds well with those kept from wolves. Nevertheless, animals from the Nelchina population, which were heavily hunted, could not be approached closer than 400 m, and the usual flight distance was 600-800 m. Colman (1995) did not find a correlation between vigilance behavior and hunting in Svalbard reindeer, but in that population only 2-11% of the animals were shot annually.

Our results also support the hypothesis that increasing group size is associated with reduced flight distances. Larger groups had shorter flight distance than smaller bands. Hunters believe that large groups of reindeer will let a human approach more closely than animals in small groups (Naumov 1933). Our data, however, did not exhibit a significant pattern of detection distance with group size.

There is high variability in reindeer vigilance behavior. For example, among Svalbard reindeer in the Reindalen subpopulation, both very alert and very tame animals were observed. Minimum alert distance was 38 m (maximum = 585 m). Even a young animal could be approached to as close as 1 m. Lent (1966) reported that the flight distance for barren ground caribou varied from 1 to 740 m. De Vos (1960) estimated flight distance for caribou to be between 30 and 1,480 m (including occasions when animals were able to scent a human approach). Tyler (1991) estimated detection distance of Svalbard reindeer to a snowmobile (an average for 2 populations) to be between 50 and 1,280 m (median = 410 m), with the flight distance varying between

10 and 480 m (median = 80 m).

Although reindeer are not considered shy ungulates compared with other species, shy individuals occurred in all populations. Even in groups of domestic reindeer that have visual contact with herders regularly, the maximum alert distance was 350 m. These shy animals occurred in populations that had not encountered predators for many generations. Perhaps those alert animals would have a selective advantage in wild populations that experience severe predation and hunting and those individuals also can survive in the wild if they become separated from their herders. The longer the detection distances we observed, the longer were the flight distances. A similar result was observed by Colman (1995). The attention of reindeer may vary with their motivation. This could be why herders attract the attention of reindeer by shouting to chase them into a group (Baskin 1992).

As hypothesized, wild populations of reindeer were more vigilant than feral or domestic reindeer. Likely reasons for this finding could be that wild reindeer are less accustomed to human contact and that natural selection by predators or hunters favor vigilant individuals in wild populations more than in feral or domestic populations.

The sex ratio of groups (females with yearlings and male groups) had only a weak influence on flight distances of reindeer (only 3% of variation explained; Table 4). Thus, our results do not support Lent (1966) and Bergerud (1974), who concluded that female groups were much more alert than male groups. In addition, groups of females with newborns were not more alert in our study, which is also contrary to the suggestion of those authors. Bergerud (1974) studied caribou in forest-tundra habitat in Newfoundland where the average size of groups was 5.5 animals, and wolf predation was high. He reported that females without newborns detected a human at an average

distance of 350 m and ran for an average distance of 266 m, whereas females with newborns detected a human at 595 m and ran for 537 m.

Our results indicate that hunting is the main factor influencing vigilance behavior in reindeer. This outcome could result from an altered selective pressure and have evolutionary implications (Ericsson 1997). Our data also support the hypotheses that natural selection during domestication or in the opposite direction (feralization) may lead to significant changes in vigilance and avoidance behaviors. Furthermore, we noted a significant influence of group size on flight distance. Exploring the complex inter-relationships among flight behavior, group size, and other factors warrants further research.

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