



Vigilance in reindeer (*Rangifer tarandus*); evolutionary history, predation and human interference

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Received: 17 September 2020 / Revised: 24 March 2021 / Accepted: 26 March 2021 / Published online: 11 April 2021
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Abstract

To elucidate genetic variability in vigilance behaviour for reindeer with historical differences in their interactions with predators and humans, we measured vigilance frequency and duration for grazing reindeer in Southern Norway (Rondane and Norefjell-Reinsjøfjell), Svalbard (Edgeøya and Nordenskiöld Land) and Barf/Royal Bay and Busen in the southern Hemisphere (South Georgia). Averaged for all areas, frequency and duration of vigilance bouts were less than 0.5 and 2.5 s, respectively. Frequency was insignificantly 1.3 times higher in Rondane than Edgeøya, and significantly 2.0, 3.5, 5.2 and 12.4 times higher than Norefjell, Nordenskiöld Land, Barf/Royal Bay and Busen, respectively. Duration per vigilance bout was not different amongst the areas. Thus, while frequency varied considerably, duration remained constant, supporting a hard-wired adaptation to, among other suggestions, an open landscape. Plasticity in frequency allows for flexible behavioral responses to environmental factors with predation, domestication and hunting key drivers for reindeer. Other factors include (1) the open, treeless alpine/Arctic environment inhabited by *Rangifer* subspecies allowing warning time, (2) grouping behaviour, (3) relative low density of predators and (4) the anatomy and physiology of ungulate vision.

Keywords Watchfulness · Isolation on islands · Predation · Domestication · Ungulates · Reindeer · *Rangifer tarandus*

Introduction

Behavioural traits in animals certainly evolve, and the domestication of animals was essential for the development of modern human societies. Genetically based behavioural traits vary amongst animals. Early man utilized this variability to select species that served their needs for protection and hunting (dogs), as well as a wide variety of food and clothing purposes. Selection towards domestication supported tameness for improved handling and maintenance of livestock (Price 1984), while pre-modern hunting likely selected for traits increasing a species survival abilities through increased fright, flight and vigilance behaviours. Interestingly, knowledge about changes in behavioural traits related to wildness and tameness is lacking, often due to

extinction of the wild parent stock (Clutton-Brock 1987). There is limited experimental research on the evolution of different traits, including behaviour, during domestication. However, there is some evidence based on comparative studies of domestic stocks and their wild ancestors to identify a number of typical domestication changes, including the following aspects (Jensen 2006): external and internal morphology, physiology, body development and behaviour, which in this context includes reduced fear, increased sociability, and reduced anti-predator responses (Price 1997). Interestingly, this complex of changes may develop rapidly, in only a few generations, and in concert, even though only one of the traits is selected for (Jensen 2014). As with many traits, there can be variation in the amount of plasticity of expression in behavior traits involving the discovery and avoidance of predators.

While domestication tends to relax anti-predator behaviour, such as vigilance, predation tends to increase it (Reimers et al. 2012). Thus, in addition to domestication, local extinction of predators for prolonged periods should theoretically relax natural selection on predator recognition and other behavior responses, such as grouping. Over 100 s or 1000 s of years, prey may lose the ability to recognize

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locally extinct predators as dangerous (Coss 1999; Berger et al. 2001; Blumstein and Daniel 2005a; Blumstein 2006; Stankowich and Coss 2007; Lahti et al. 2009). Reindeer (*Rangifer tarandus*) present an interesting species because they inhabit areas with variable amounts of predation and hunting. Reindeer were only recently domesticated by humans, with extensive control of specific herds first evolving during the 16th and 17th centuries (Mirov 1945). Almost 50% of the approximate 3 million reindeer in the Old World are wild animals, and wild and domestic herds are managed in close coexistence (Reimers and Klein 1979; Baskin 2005). Reindeer in some areas exhibit variable amounts of grouping behavior and interactions with predators exemplified by Svalbard reindeer, as we present below.

The multi-predator hypothesis (Blumstein 2006) promotes that isolation from all predators may lead to a rapid loss of antipredator behaviour, including loss of the grouping behaviour and breakdown of predator recognition abilities. For example, both reindeer and caribou from regions without wolves (Svalbard and West Greenland) exhibited about a third of the vigilance towards playbacks of wolf howling at control sites (Denali National Park and Tetlin Wildlife Refuge) (Berger 2007).

Experience-dependent behavior, such as vigilance and fright and flight, may be moderated or lost after few generations in the absence of predators, while more “hard-wired” antipredator behavior, such as forming groups, may persist for 1000 s of years following isolation from predators (Byers 1997; Coss 1999). On the other hand, experience-dependent behaviour may be quickly restored the first time individuals encounter predators (Brown et al. 1997; Aastrup 2000; Berger et al. 2001), contrary to hard-wired behavior. In accordance with this, vigilance rates (frequency of “scans” per time interval) (Bøving and Post 1997; Frid 1997), displayed by Svalbard reindeer in Edgeøya, a location with a dense polar bear population, were 2.2 times higher than those for reindeer in Nordenskiöld Land that had fewer polar bears (Reimers et al. 2011). Furthermore, and in accordance with a hard-wired trait, reindeer in both areas remain alone or in small groups; i.e., they lack grouping behaviour in these two areas as well as in all other reindeer-inhabited areas on Svalbard.

Ungulates periodically scan their surroundings for potential threats that might be looming. This behaviour may be shared by members of a group, which would likely be more proficient at scanning than a solitary animal that must divide its time between scanning and other activities (e.g., foraging). Thus, there is likely an interaction between the experience-dependent vigilance rate and hard-wired grouping behaviours, with a decrease in vigilance rate with an increase in grouping. Grazing ungulates in groups or herds may also scan their surroundings in search of feeding hot spots or social cues relating to other intra and inter specific

interactions (Colman et al. 2012) that likely acts in synergy with predatory vigilance.

While vigilance rate seemingly varies (Reimers et al. 2012), we are less certain of whether the time an animal scans its surroundings per vigilance bout, vigilance duration, also varies. Grouping behaviour is widespread among mammals living in open landscapes, is most conspicuous among larger herbivores and primarily influenced by resource availability and distribution (Matthiopoulos 2003), parasites (biting flies, warble flies and parasitoids) (Mooring et al. 2004), and predator pressure (Hamilton 1971). Temporary or permanent aggregations commonly formed by mammals have a variety of potential benefits; enhanced vigilance through more scanning eyes, greater ability to find food or mates, group defense, confuse predators, and decreased probability to get killed during a predator attack (dilution effect). There are also potential costs; easier to locate by predators, potential for disease transmission, interference effects during foraging, and negative interaction with other animals. Declining individual vigilance rates with increasing group size has indeed been widely reported for both mammals and birds (Elgar 1989; Lima 1995), although other influential factors than predators and insects [e.g., nutrition and competitors (Colman et al. 2012)] may interfere. The duration of a vigilance bout in conjuncture with vigilant rate determines the extent of potential trade-offs. However, it remains unknown whether vigilance duration varies in a manner similar to rates. We aimed therefor to test and compare variation in both vigilance rate and duration for populations differing in other ways (grouping behaviour and interactions with humans and predators) as a starting point into whether these traits are hard-wired or experience based.

Wild reindeer in southern Norway conform to the grouping strategy in terms of vigilance and fright and flight behaviour (Reimers et al. 2012). Antipredator grouping behaviour should not persist on islands without predation if there is no net benefit (Blumstein and Daniel 2005a). Following this, the traditional grouping behaviour that characterizes *Rangifer* elsewhere (Reimers et al. 2011, 2012) is absent on Svalbard, where animals live individually or in small groups with limited predation for 1000s of years (Van der Knaap 1986).

In this study, we compare vigilance behavior for two reindeer herds in southern Norway, two herds in Svalbard and two herds, now exterminated, in South Georgia. All 6 areas are different in relation to predator presence and /or human influence through hunting and/or domestication. Based upon the presented extensive vigilance data, we hypothesize that in *Rangifer*, duration of individual vigilance bouts are genetically hard wired, while frequency of vigilance bouts and duration of vigilance per minute grazing are experience-based. We also relate the theorized experience-based vigilance rate behavior to the hard-wired grouping behavior, and include vigilance duration to test its variability.

Study areas

We collected data on vigilance between July and August 2006 for Edgeøya and Nordenskiöld Land, 5150 and 39,000 km², respectively (Svalbard, 74°–81° N), between June and July in the years 2004 to 2006 for Rondane and Norefjell-Reinsjøfjell, 1441 and 308 km², respectively (Southern

Norway, 60°–63° N) (Reimers et al. 2012), and between December and January (corresponding to June/July on the southern Hemisphere) in the year 2012 to 2013 for Barf/Royal Bay and Busen, 124 and 131 km², respectively (South Georgia, 53°–55° S) (Fig. 1 and Table 1). A detailed description of reindeer herds and ranges in southern Norway and Svalbard follows from Reimers et al. (2012), Reimers et al.

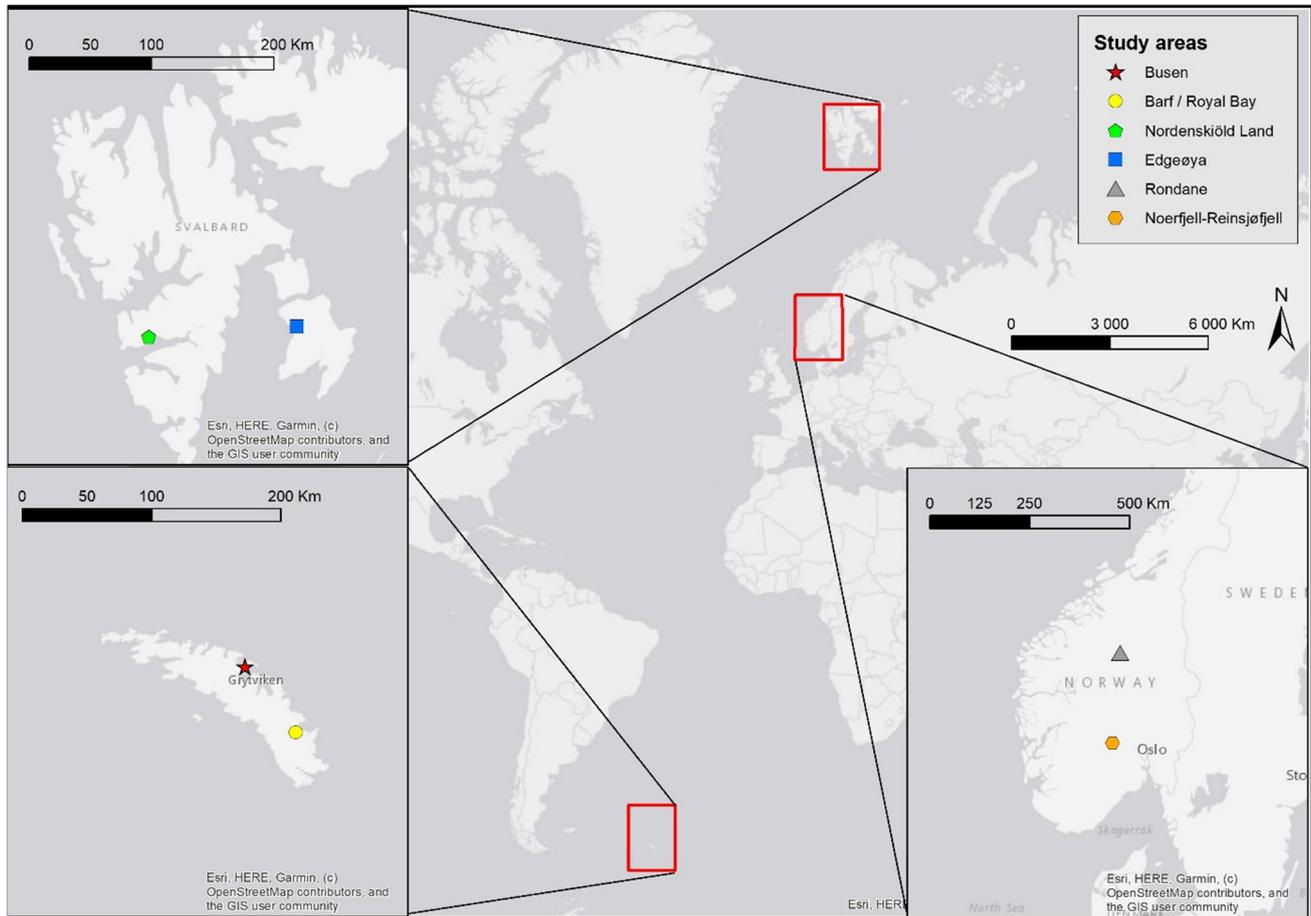


Fig. 1 Location of the various reindeer herds indicated by their latitudinal and longitudinal positions: Svalbard: 77°39'N, 22°29'E; Southern Norway: 62°15'N, 09°33'E and South Georgia: 54°16'S, 54°16'W

Table 1 Distribution of animal's video recorded in the areas, average scan duration, area size inhabited by video-scanned reindeer, animal density and average group size of video recorded reindeer

| Area | Sub-area | No of video-recorded animals | Average scan duration (s) | Area size (km ²) | Animals/km ² | Average group size (± SE) |
|-----------------|----------------|------------------------------|---------------------------|------------------------------|-------------------------|---------------------------|
| Southern Norway | Rondane | 260 | 181 | 1441 | 1.0 | 555 ± 23.1 |
| | Norefjell | 333 | 223 | 308 | 1.5 | 92 ± 4.1 |
| Svalbard | N.Land | 216 | 540 | 798 | 3.2 | 2.4 ± 0.12 |
| | Edgeøya | 174 | 432 | 120 | 1.5 | 2.2 ± 0.12 |
| South Georgia | Barf/Royal Bay | 325 | 349 | 189 | 25.1 | 50 ± 2.8 |
| | Busen | 170 | 449 | 124 | 16.2 | 50 ± 3.9 |

(2011) and correspondingly for South Georgia, from Leader Williams (1988).

Areas in southern Norway are mainly alpine terrain at altitudes of 1000–1500 m. Hunting is allowed in all areas and is the only important mortality factor, as wolves (*Canis lupus* L.) are essentially absent from the areas and wolverine (*Gulo gulo* L.), golden eagle (*Aquila chrysaetos* L.) and lynx (*Lynx lynx* L.), although permanently present or present as stragglers, exert minor predatory influence. Rondane reindeer are considered to be mainly of wild origin due to their distinct genetic variation when compared with domestic reindeer (Røed 1985, 1987; Røed et al. 2008). The Norefjell-Reinsjøfjell herd originated from some 30 reindeer that escaped slaughter in 1968 when the reindeer herding company closed (Reimers et al. 2009). Norefjell-Reinsjøfjell reindeer are genetically distinctly different from neighboring wild reindeer herds (Andersen and Hustad 2004; Reimers et al. 2012).

Despite the high latitude, the climate in Svalbard is relatively mild due to the North-Atlantic Current. The landscape is mountainous with peaks up to 1700 m. Large areas are covered by glaciers, and summer pastures for reindeer are restricted to valleys, coastal plains and plateaus. Hunting of Svalbard reindeer was banned in 1925 when Norway was assigned sovereignty of Svalbard. Since then, reindeer densities have increased, which led to the reopening of limited hunting on Nordenskiöld Land in 1983. Comprising the northernmost populations of *Rangifer*, the insular Svalbard reindeer (*Rangifer tarandus platyrhynchus*) inhabit an environment without grazing competitors or parasitizing insects. Besides polar bears (*Ursus maritimus*), which occasionally prey on Svalbard reindeer (Derocher et al. 2000; Sandal 2008; Hovelsrud 2009), and Arctic fox (*Vulpes lagopus*), which kill a few newborn calves (Tyler 1986), there are no other predators that are part of the natural habitat of reindeer elsewhere. This situation has prevailed for at least 4000 years (Van der Knaap 1986; Tyler and Øritsland 1989). Contrary to *Rangifer* subspecies elsewhere, Svalbard reindeer live

individually or in small groups (Alendal and Byrkjedal 1976; Alendal et al. 1979), are seasonally sedentary (Tyler and Øritsland 1989) and are not nomadic.

Norwegian domestic reindeer were introduced by whalers to the Barf Peninsula on South Georgia in 1911 (10 animals; 3 males and 7 females) (Olstad 1930). A second group (7 animals; 3 males and 4 females) was introduced to the Busen area in 1926 (Olstad 1930; Leader Williams 1988) (Table 2). Both introductions used animals from Filefjell domestic reindeer company in southern Norway (Lovatt 2007; Kilander 2014). The reindeer have been free ranging since their introduction and were protected under the Falkland Island Dependencies Conservation Ordinance of 1975. Permits were issued to shoot reindeer for consumption by personnel at the scientific station at Grytviken, and for scientific programs. Derived from the Barf herd during 1961–1965, an unknown number of reindeer spread around a retreating glacier snout which had previously formed a restriction boundary making a new herd: The Royal Bay herd (Table 2) (Leader Williams and Payne 1980; Lindsey 1973). While the Busen area has a small permanent human settlement, the Barf/Royal Bay area is isolated and rarely visited by humans. Due to this, only the reindeer herd in Busen were exposed to poaching/hunting (until their protection in 1975). None of the reindeer herds in South Georgia are affected by predators (Leader Williams 1988).

Because of concerns over the impact on the native vegetation, including over-grazing, soil erosion, loss of biodiversity in the plant communities and increased distribution of introduced plant species and rodents, the phased eradication of reindeer from South Georgia became policy of the SGSSI in 2000 (McIntosh and Walton 2000). Extermination of the herds occurred during 2012–2014, resulting in 6749 animals killed; approximately twice the number of animals estimated to live on the island. Apparently, only a few animals survived the extermination and were left to the British authorities to remove.

Table 2 History of the reindeer herd introduced to South Georgia, harvest and herd development

| Reindeer Herd | Area size (km ²) | Year of Introduction | No reindeer introduced | Estimated no reindeer in 1976 | No reindeer culled ^a in 1972–1976 | No reindeer culled ^b in 2013–2015 |
|---------------|------------------------------|----------------------|------------------------|-------------------------------|--|--|
| Barf | 131 | 1911 | 10 | 1000 | 370 | 4740 |
| Royal Bay | 58 | 1961–1965 | ? | 550 | 100 | |
| Busen | 124 | 1926 | 7 | 450 | 120 | 2009 |
| Total | 313 | | 17 | 2000 | 590 | 6749 |

With the exception of 1972/1976 harvest have not exceeded 30 reindeer per year since closure of the whaling stations in 1964–1965 (Leader Williams and Payne 1980)

^aCulled in a research program

^bCulled in an extermination program

Material and methods

Field work in Rondane and Norefjell (southern Norway), Edgeøya and Nordenskiöld Land (Svalbard) was conducted in June/July during 2003–2006 and Barf/Royal Bay and Busen (South Georgia) December–January in 2012 and 2013. We video recorded grazing animals from a hidden position and defined grazing as the act of ingesting forage with the muzzle down. The hidden position was usually several 100 m from the closest reindeer and varied according to, for example, topography, wind direction, movements of the reindeer and visibility. If there was any suspicion of being discovered, the recordings were terminated. Animals were randomly selected for video recording from different groups in the six areas. We recorded a total of 1478 reindeer 1 year or older combined for the six areas (Table 1). Each individual was recorded preferably for 10 min (in some cases longer than 10 min) or until the reindeer lied down or moved out of sight. We defined a *vigilance bout* as the act of interrupting feeding to lift the head above the shoulders (Frid 1997) and observe the surroundings for ≤ 10 s before returning to feeding (Bøving and Post 1997). If this change of behavior lasted more than 10 s, frequently resulting in non-vigilance behaviour like scratching, urinating, and licking before returning to grazing or moving on to another grazing spot, it was disregarded as a vigilance bout. Individuals were scanned only once on the same day.

While filming, the team registered group size, group structure (males, females and yearlings, mixed sex and age of the video recorded animal: lactating female with calf at heel, barren female and male, wind speed following the Beaufort Wind Scale (calm, $< 1 \text{ m s}^{-1}$; light/gentle breeze, $1.6\text{--}5.4 \text{ m s}^{-1}$; moderate/fresh breeze, $5.5\text{--}10.7 \text{ m s}^{-1}$ or gale, $10.8\text{--}17.1 \text{ m s}^{-1}$), weather (sunny/partly sunny, cloudy, rain/snow or foggy) and topography of the surrounding area (i.e., level or rugged). Senior author played back the videotapes on a 27" plasma TV-monitor following individual reindeer grazing throughout the observation period and registered the number and duration of vigilance bouts. Slow walking between vegetation hot spots with head down was included in total grazing time. Slow walking with head up was excluded from total grazing time.

To assess variation in the frequencies of vigilance bouts, *vigilance rate*, among main areas and subareas, we fitted the observed vigilance rate data to a Poisson model (Reimers et al. 2011). Assuming that the expected number of vigilance bouts observed for an individual was proportional to the time it was observed, we included $\ln(\text{time observed})$ as a fixed offset in the log-linear model vigilance rate. As the areas and groups were not surveyed on the same days, we included the random variation among

days and individuals within groups and days as variance components in the model to account for weather effects and to facilitate robust inferences about the differences among the areas. Hence, we assumed number of vigilance bouts for an individual i observed over τ_i seconds during day $d(i)$ to be Poisson distributed with the log-linear expectation

$$\ln(\lambda_i) = x_i\beta + \ln(\tau_i) + \delta_{d(i)},$$

where $\delta_{d(i)}$ is normally distributed, $\delta_{d(i)} \sim N(0, \sigma^2)$, and $x_i\beta$ models the difference between the areas and log-linear effects of covariates (x_i). This model was fitted with the function 'lmer' in the 'lme4' package in R version 3.4.3 (<http://www.r-project.org/>).

Besides effects of area, we evaluated the effect of group size. Groups were smaller in Svalbard than in southern Norway and South Georgia. Hence, group size categories were small: < 5 animals, medium: 6–8 animals, and large: > 8 animals in Svalbard, small: < 20 animals, medium: 20–50 animals, and large: > 50 animals in southern Norway and in South Georgia. Furthermore, we evaluated the effect of group structure (mixed sex groups or single sex groups of either females or males), functional category of the observed animal (lactating female, barren female or male), weather, wind force and wind direction relative to observer.

To compare the mean duration of the vigilance bouts among areas and groups of individuals, a log-normal linear model (including all the fixed and random variables in the model above) was fitted to the duration of the first observed vigilance bout per individual (Fig. 3). Inspection of the residuals showed that the model fitted well to the data. To facilitate interpretation of time spent vigilant while grazing, *vigilance duration*, in the 6 areas, we multiplied vigilance duration of the first vigilance bout (Fig. 3) with the vigilance rates (Fig. 4a) for presentation in Fig. 4b.

Results

Observation periods per animal averaged from 181 to 540 s in the six areas, with the shortest time span in Rondane. Density (reindeer/km²) varied from 1 in Rondane to an all-time high of 25.1 in Barf/Royal Bay, South Georgia (Table 1; Fig. 1).

The vigilance rate among reindeer in South Georgia was, although very low in both areas, three times higher and lasted in total time three times longer among reindeer in Barf than in Busen (Table 3; Fig. 2a, b). Vigilance rate was not influenced by sex of animals, weather conditions, wind force, wind direction or group structure. Vigilance rate and duration decreased with increasing group size (Fig. 2a,

Table 3 Generalized Linear Model for predicting number of vigilance bouts per min (ln transformed) during grazing in reindeer in Barf/Royal Bay and Busen (South Georgia) during summer in the southern Hemisphere (December–January) in 2012 and 2013

| Variable | Estimate | SE | z-value | Pr(> z) |
|--------------------------------|----------|--------|---------|----------|
| (Intercept) | −3.3688 | 0.24 | −14.035 | <0.0001 |
| Area: Busen vs. Barf/Royal Bay | −1.1207 | 0.2442 | −4.589 | <0.0001 |
| Group size: medium vs. large | −0.5451 | 0.2842 | −1.918 | 0.055 |
| Group size: small vs. large | 0.9615 | 0.2391 | 4.021 | <0.0001 |

The standard deviation of ln(number of vigilance bouts per min) among individuals within groups (random intercepts) were estimated at 0.389 and 0.152, respectively. The full model included area, group size (small < 20 animals; medium 20–50 animals; large > 50 animals), group structure (mixed; females; males), sex of the video recorded animal, weather, wind force and topography. Reference levels for categorical variables are provided in the table (the level after “vs.”)

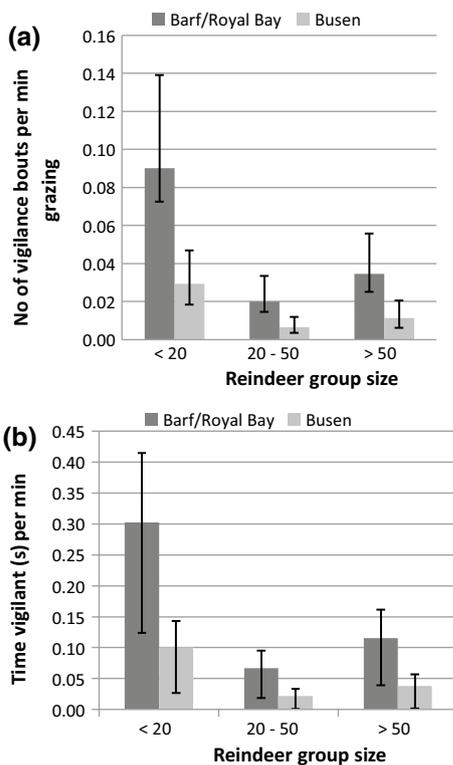


Fig. 2 **a** Predicted number of vigilance bouts (± 2 SE; approx. 95% CI) per min (vigilance rate) with head above shoulder height ≤ 10 s while grazing in groups of reindeer in Barf/Royal Bay and Busen, (South Georgia) during summer in the southern Hemisphere (December–January) in 2012 and 2013. **b** Calculated total time spent vigilant (s) per min grazing (± 2 SE; approx. 95% CI) in reindeer in Barf/Royal Bay and Busen, South Georgia during summer in the southern Hemisphere (December–January) in 2012 and 2013. Values are products of number of vigilance bouts per min grazing time \times mean duration of first observed vigilance bout in the respective herd size categories. Reference level for categorical variables are rugged area for vigilance duration and group size for vigilance frequency for product values

b). Animals in small groups (< 20 animals) were 2.6 times more vigilant than animals in large groups (> 50 animals).

We compared vigilance data from Barf/Royal Bay and Busen with data from southern Norway and Svalbard (Table 4; Fig. 4a). Vigilance rate was insignificantly 1.3 times higher in Rondane than in Edgeøya and significantly 2.0, 3.5, 5.2 and 12.4 times higher compared with Norefjell, Nordenskiöld Land, Barf/Royal Bay and Busen, respectively. Vigilance rate was not influenced by wind force, wind direction or group structure and decreased with increasing group size. Animals in small groups were 1.8 times more vigilant than animals in large groups and females were 1.3 times more vigilant than males. Finally, animals were 1.4 times more vigilant on sunny days than in overcast weather (Table 4).

Vigilance duration of first vigilance bout (among all individual reindeer observed) was similar, although Rondane reindeer tended to have somewhat shorter duration than animals in Norefjell and Nordenskiöld Land (Table 5; Fig. 3). Although low in all areas, vigilance frequency per minute grazing was 2.9, 1.2, 1.7, 4.7 and 10.7 times longer in Rondane vs. Norefjell, Edgeøya, Nordenskiöls Land, Barf/Royal Bay and Busen, respectively (Fig. 4a). Vigilance duration (duration of first bout multiplied with frequency rate) tended to be longer for female vs. males in small groups (Fig. 4b),

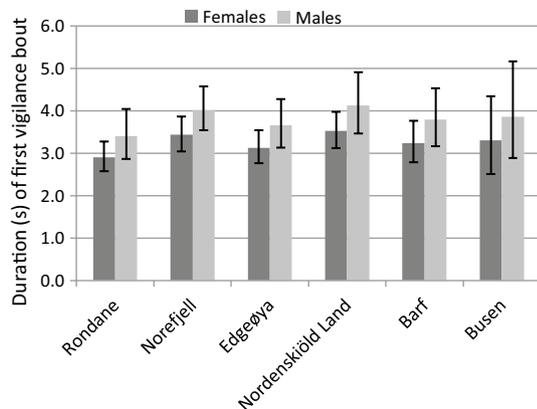
Table 4 Generalized Linear Model for predicting number of vigilance bouts per min (ln transformed) during grazing in reindeer in Rondane and Norefjell in southern Norway, Edgeøya and Nordenskiöld Land in Svalbard and in Barf/Royal Bay and Busen in South Georgia

| Variable | Estimate | SE | z-value | Pr(> z) |
|-------------------------------|----------|--------|---------|----------|
| (Intercept) | −1.5196 | 0.1045 | −14.540 | <0.0001 |
| Edgeøya vs. Rondane | −0.2255 | 0.1539 | −1.465 | 0.1429 |
| Norefjell vs. Rondane | −0.7022 | 0.1362 | −5.155 | <0.0001 |
| Nordenskiöld Land vs. Rondane | −1.2597 | 0.1544 | −8.158 | <0.0001 |
| South Georgia vs. Rondane | −1.9687 | 0.1410 | −13.963 | <0.0001 |
| Group size: Medium vs. Large | 0.3839 | 0.1480 | 2.594 | 0.0095 |
| Group size: Medium vs. Small | 0.5759 | 0.1236 | 4.661 | <0.0001 |
| Sex: Males vs. Females | −0.2824 | 0.0850 | −3.323 | 0.0009 |
| Weather: Sun vs. Overcast | −0.3258 | 0.0816 | −3.9910 | 0.0001 |

Vigilance was measured in June/July in 2004–2006 in southern Norway and Svalbard and during summer in the southern Hemisphere; December in 2012 and January and December in 2013. The standard deviation of ln (number of vigilance bouts per min) among individuals within groups (random intercepts) were estimated at 0.073 and 0.277, respectively. The full model included area, group size (small < 20 animals; medium 20–50 animals; large > 50 animals), group structure (mixed; females; males), sex of the video recorded animal, weather, wind force and topography. Reference levels for categorical variables are provided in the table (the level after “vs.”)

Table 5 Calculated duration of first vigilant bout (s) in grazing reindeer in small single sex groups in Rondane and Norefjell (southern Norway), Edgeøya and Nordenskiöld Land (Svalbard) and Barf/Royal Bay and Busen (South Georgia)

| Variable | Value | SE | df | t-value | p-value |
|-------------------------------|--------|--------|-----|---------|----------|
| Intercept | 1.0674 | 0.0599 | 399 | 17.809 | < 0.0001 |
| Edgeøya vs. Rondane | 0.0738 | 0.0846 | 399 | 0.873 | 0.3832 |
| Nordenskiöld Land vs. Rondane | 0.1922 | 0.0847 | 399 | 2.269 | 0.0238 |
| Norefjell vs. Rondane | 0.1662 | 0.0832 | 399 | 1.997 | 0.0465 |
| Barf/Royal Bay vs. Rondane | 0.1073 | 0.0955 | 399 | 1.124 | 0.2616 |
| Busen vs. Rondane | 0.1269 | 0.1486 | 399 | 0.853 | 0.3939 |
| Males vs. Females | 0.1574 | 0.0666 | 399 | 2.363 | 0.0186 |

**Fig. 3** Mean duration of first observed vigilance bout (s) (vigilance duration) in female and male reindeer in Rondane and Norefjell (southern Norway) and in Edgeøya and Nordenskiöld Land (Svalbard) in summer June to July in 2004 to 2006 and in Barf/Royal Bay and Busen (South Georgia) during summer in the southern Hemisphere (December to January) in 2012 and 2013

but decreased with increasing group size, as indicated in South Georgia (Fig. 2b).

Comparing 95% confidence intervals in Fig. 4a vs. b, vigilance rate apparently provides a more accurate measure of vigilance in reindeer than duration.

Discussion

The way in which antipredator behaviour is modified depends on both heritable predisposition (Riechert and Hedrick 1990) as well as experience (Berger et al. 2001; Blumstein 2004). Using an island as a model, terrestrial prey become naïve to predation risk when predators have been absent for long periods (Byers 1997; Blumstein and Daniel 2005b). In accordance with expectations, domestic reindeer introduced to the predator free South Georgia showed a low vigilance response. However, and although we found a generally low vigilance response on South Georgia compared to reindeer on Svalbard and southern Norway, the Barf/Royal Bay reindeer were 3 times more vigilant than the Busen reindeer. Even though the introduction of reindeer to

the two areas in South Georgia apparently originates from the same Norwegian domestic herd and hence same genetic stock during the 1920-ties (Lovatt 2007; Kilander 2014), only 10 and 7 animals, respectively, were transferred and the populations may have developed differently from “bottleneck” effects (Petersen et al. 2010). Animal density may also be an interacting factor, leaving the densely populated reindeer in Barf/Royal Bay more vigilant in search for food or space in competition with neighbouring animals (Kluever et al. 2008). A more likely explanation is adaptability to human presence (Colman et al. 2001; Reimers et al. 2010; Hansen and Aanes 2015). The Whaling station and associated human settlement (16–32 individuals during summer and winter) is located on Busen, and reindeer have over time adapted to the presence of human activities at Grytviken and of visiting scientists and tourist. The Barf/Royal Bay area are more remotely located and reindeer are rarely encountered by humans. During preparation prior to the extermination of the herds in 2012–2013, reindeer in both areas were exposed to extensive human activities that may have triggered a higher vigilance rate in the Barf/Royal Bay area than in Busen, where animals are more habituated to interacting humans. Such gradual habituation is widespread among animals and in this context, reported in Svalbard reindeer in Ny Ålesund (Hansen and Aanes 2015). As video recording of vigilance occurred in advance of extermination of the herds and from hidden positions in all areas, we find no support for vigilance differences being a result of recording activities.

“Predator free” Svalbard reindeer in Nordenskiöld Land exposed to frequent encounters with humans show relaxed vigilance behaviour with low vigilance rates and duration (Table 4; Fig. 4a, b). Surprisingly, Edgeøya displayed a higher vigilance rate comparable to wild reindeer in southern Norway subject to hunting and predation (Rondane). Polar bears are generally not regarded as predators on reindeer (Derocher et al. 2000). However, after the international harvest ban in 1973, the population of polar bears in the Svalbard archipelago has increased (Aars et al. 2009). In addition, the sea-ice cover in the arctic region during summer has decreased in recent years (Singarayer et al. 2006), resulting in more bears on land within several polar bear subpopulations (Schliebe et al. 2008; Rode et al. 2015) and

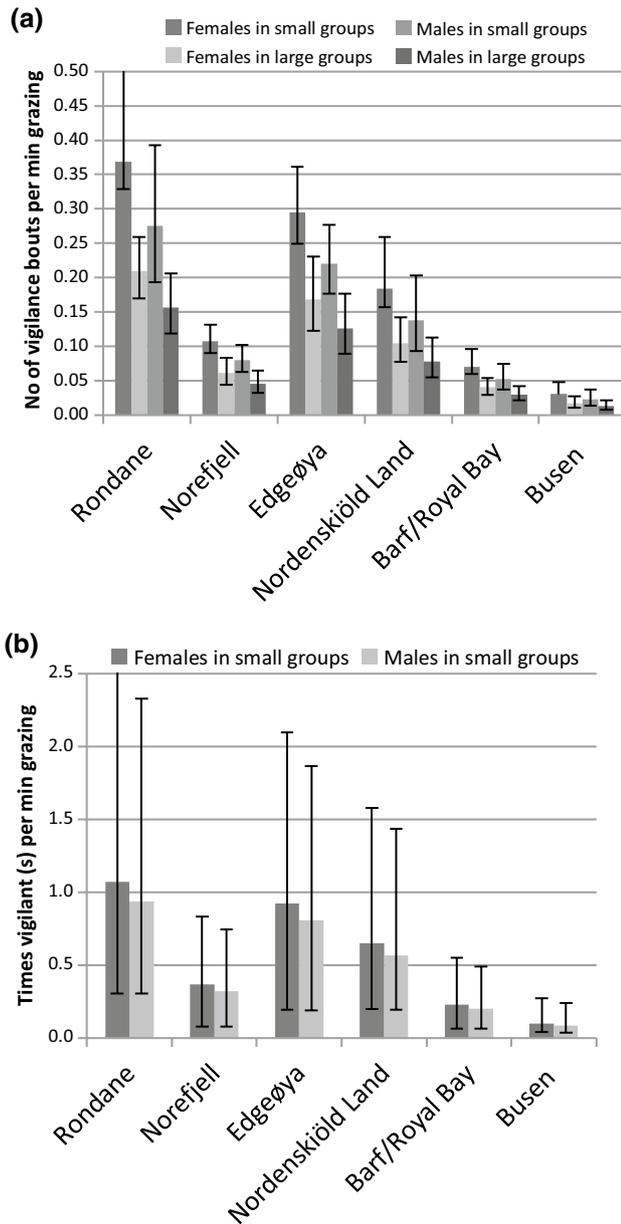


Fig. 4 **a** Predicted number of vigilance bouts (± 2 SE; approx. 95% CI) per min (vigilance rate) with head above shoulder height ≤ 10 s while grazing in groups of reindeer in Rondane and Norefjell (southern Norway), Edgeøya and Nordenskiöld Land (Svalbard) in June/July during 2003–2006 and Barf/Royal Bay and Busen (South Georgia) during summer in the southern Hemisphere (December–January) in 2012 and 2013. **b** Calculated total time spent vigilant (s) per min grazing (± 2 SE; approx. 95% CI) in reindeer while grazing in groups of reindeer in Rondane and Norefjell (southern Norway), Edgeøya and Nordenskiöld Land (Svalbard) in June/July during 2003–2006 and Barf/Royal Bay and Busen (South Georgia) December–January in 2012 and 2013. Values are products of number of vigilance bouts per min grazing time \times mean duration of first observed vigilance bout in the respective herd size and sex categories according to the equation below Reference level for categorical variables are in Tables 4 and 5. Vigilance duration (s) per min: grazing = $\exp(\ln(\text{predicted frequency} * (\text{predicted duration}) + c(0, -2) * \sqrt{(\text{SE frequency}^2 + \text{SE duration}^2)}))$

thus, more frequent encounters between reindeer and polar bears. Edgeøya, being an important polar bear denning area (Aars et al. 2005), has a high density of polar bears during summer, greatly exceeding the density in Nordenskiöld Land (Derocher et al. 2000; IUCN 2010), probably resulting in a predator prey relationship between the two species (Reimers and Eftestøl 2012). This may explain increased vigilance among reindeer in the more densely polar bear populated Edgeøya (Reimers et al. 2011; Reimers and Eftestøl 2012; Iversen et al. 2013; Stempniewicz et al. 2014) and support that experience-dependant behaviour may be restored quickly upon individuals encountering predators (Griffin et al. 2000; Berger 2001).

Vigilance rates in Rondane vs. Norefjell, Nordenskiöld Land, and South Georgia were 3.5, 2.0 and 7.2 times higher, respectively. As Rondane wild reindeer on mainland Norway coexist and share 1000s of years with predators and hunters, their higher vigilance rates presumably reflects a behavioural adaptation to these threats. Reindeer in Busen in South Georgia and Svalbard reindeer in Nordenskiöld Land presumably reflect baseline vigilance among wild reindeer in the absence of or reduced threats from predators.

Vigilance rates for wild reindeer herds on mainland Norway (Reimers et al. 2012), caribou in West Greenland and Alaska (Bøving and Post 1997) and introduced domestic reindeer in South Georgia are surprisingly low regardless of absence or presence of predators or hunting compared to other herbivores (Underwood 1982; Burger and Gochfeld 1994; Toigo 1999; Wolff and Van Horn 2003; Benhaïem et al. 2008; Periquet et al. 2010). An explanation most probably combines two factors; the generally open, treeless alpine/Arctic environment inhabited by these *Rangifer* subspecies that allow warning time and the anatomy and physiology of the ungulate vision (Sjaastad et al. 2016). The most important function of the external ocular muscles in most four-footed animals is to keep the eyes horizontal when the position of the head changes. When *Rangifer* or other deer species graze, the eyes move to a horizontal position in the orbits and the animal then has a combined visual field for both eyes of about 360° parallel to the ground, only limited by their legs. Therefore, grazing predominately in open habitats enables vigilance for *Rangifer* even when feeding, and hence, time used on “head lifting” vigilance can be reduced.

A commonly reported benefit of aggregation is seen when individuals reduce the time devoted to vigilance and increase time on foraging as group size increases (Lima and Dill 1990). Costly antipredator behaviour should not persist once there is no net benefit. And indeed, the traditional grouping behaviour that characterize *Rangifer* elsewhere is absent in Svalbard, where animals live individually or in small groups (Alendal and Byrkjedal 1976; Alendal et al. 1979). The lack of group behaviour in Svalbard reindeer as a response to the absence of predators and parasitizing

insects facilitates energetic optimization and enables these animals to cope with this harsh environment (Reimers 1980; Reimers et al. 1982). It is generally assumed that gregariousness increases safety (Turner and Pitcher 1986; Rieucou and Martin 2008) and that reproductive status influence how animals reduce predation risk and that some individuals take advantage of the vigilance effort provided by others (Rieucou and Martin 2008). Correspondingly, there was a group size effect in our study as vigilance generally decreased with increasing group size. High vigilance rates will in most cases compromise feeding time as suggested by (Laundre et al. 2001), although vigilance is not necessarily mutually exclusive with processing food (chewing and swallowing) (Fortin et al. 2004). Future studies should test whether the low scan frequency and total scan duration found for reindeer in this study compromise or increase feeding efficiency, along with the costs of head-bobbing within complete energy budgets.

Vigilance rates were higher among females with calf at foot than among males. This is consistent with results reported for other wild ungulates (Lipetz and Bekoff 1982; Burger and Gochfeld 1994; Toigo 1999; Childress and Lung 2003; Wolff and Van Horn 2003; Rieucou and Martin 2008) and also for domesticated ungulates (Kluever et al. 2008). In South Georgia, we found a close relationship between vigilance rate and duration: confidence intervals indicated a significant difference in both traits (Fig. 2a, b). There was a corresponding relationship between rate and duration in an area comparison (Fig. 4a, b); significant differences in vigilance rate, yet broad confidence intervals and non-significant differences in duration. This suggests that small differences in duration of first vigilance bout (Fig. 3), combined with large differences in rate (Fig. 4a) mask the area differences in duration, as reflected in Fig. 4b. Selection seemingly favours vigilance rate rather than duration in response to predators or neighboring animals competing for the same grazing resources. Feed intake and survival should both benefit from increased vigilance rates. This indicates flexibility in rate, but not in duration, that appear to be much less variable. Furthermore, a vigilance rate 2 times higher in Rondane than in Norefjell-Reinsjøfjell, 1.3 and 3.5 times higher than in Svalbard and Edgeøya and Nordenskiöld Land, and 7 times higher than in South Georgia indicates a variation in vigilance rates. This is probably caused by an interaction amongst factors including environment, genetics and human interference as suggested by Reimers et al. (2012).

Amongst our study areas, vigilance rate varied considerably, while duration remained constant, supporting a hard-wired adaptation for vigilance duration in *Rangifer* that appears even less variable than grouping behaviour. A minimum amount of time allowing for focusing, recognition and registration of stimuli will likely set a lower limit for duration. Additional investigations are necessary into mechanisms driving such adaptations and the evolution of

behavioural traits in wildlife. Reindeer provide the unique opportunity to study a species with both domestic and wild stock, along with differences in hunting, human interactions, predation and other key factors.

Acknowledgements We are indebted to personnel with the Office of the Commissioner Government House, Stanley, Falkland Islands for supplying data on reindeer vigilance from South Georgia prior to the extermination of the herds. In particular we thank J. Lee with the Office of the Commissioner Government House, Stanley, Falkland Islands, A. Black, A. Wolfardt and, A. Wilson for carrying out the field work. Financial support was provided from The Norwegian Science Foundation, Trygve Gotaas Fond, Direktoratet for Naturforvaltning, Stiftelsen Thomas Fearnley, Heddy og Nils Astrup. Sincere thanks to Roland Pape and two anonymous reviewers for most significant improvements to the manuscript.

Author contributions ER conceived and designed research. ER, SE and JEC conducted field work, analyzed the data and wrote the manuscript. All authors read and approved the manuscript.

Funding Open access funding provided by University of Oslo (incl Oslo University Hospital).

Declarations

Conflict of interest There are no conflict of interests related to our work.

Ethical approval We confirm that our work comply with the journal ethical standard.

Informed consent Informed consent was obtained from all individual participants included in the study.

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