Acute impacts of the deer ked (*Lipoptena cervi*) infestation on reindeer (*Rangifer tarandus tarandus*) behaviour

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Abstract

Blood-sucking ectoparasites have often a strong impact on the behaviour of their hosts. The annual insect harassment of reindeer (*Rangifer tarandus tarandus*) has increased in the southern part of the Finnish reindeer herding area because of the recent invasion of a blood-feeding ectoparasitic louse-fly, the deer ked (*Lipoptena cervi*). We studied the impact of the deer ked on the behaviour of reindeer. Twelve reindeer were infested with a total of 300 keds/reindeer on six occasions in a five-week period during the deer ked flight season in autumn, while six non-infested reindeer were used as controls. Behavioural patterns indicating potential stress were monitored by visual observation from August to December. The infested reindeer displayed more incidences of restless behaviour than the controls. Shaking and scratching were the most common forms of restless behaviour after infestation of deer keds. Increased grooming was also observed after the transplantation and also later, one month after the infestation. Based on the results, the deer ked infestation can cause acute behavioural disturbance in reindeer and, thus, could pose a potential threat to reindeer welfare. Antiparasitic treatment with, e.g., ivermectin, may increase the welfare of parasitized reindeer by reducing deer keds. If the deer ked infestation intensity on the reindeer herding area increases and restless behaviour of reindeer becomes more common, the present results can help in further evaluation of the duration and magnitude of behavioural changes.

Key words: host–parasite interaction, insect harassment, *Lipoptena cervi*, *Rangifer tarandus tarandus*, restless behaviour

Introduction

Blood-sucking insects usually have a negative influence on a wide range of vertebrates and they may directly affect the physiology and behaviour of their hosts (Boulinier et al. 2001). Such (ecto)parasites may also be harmful as they often act as vectors of pathogens, but they can also have direct fitness costs for their hosts (Fitze et al. 2004; Samuel 2007). Resisting and dispersing are the most common behavioural mechanisms of the host to face the risk of parasitism. Behavioural changes of parasitized animals can benefit the host or the parasite, or they can be side effects of this interaction and have no benefits (Poulin 1995; Moore 2002). Specialized parasite often use close related host species (Poulin 2007). As a result of parasite's range expansion, they may encounter to new potentially suitable host species. Behaviour of parasitized animals is quite well categorized but there is not much information about behavioural changes related to the novel host–ectoparasite interaction during experimental infestation (but see Samuel 1991). Studying the effects of a new ectoparasite on host behaviour is particularly important in determining possible threats of invasive parasites to new host animals.

Animals have three major strategies of defence against parasitism (Agnew et al. 2000). The host may *i*) avoid contact with parasites, *ii*) use defensive mechanisms to prevent or minimize infections and *iii*) the infection can be counteracted by the immune system. Behavioural changes of hosts depend on host and specific parasite species (Hart 1994). For example, insect harassment increases the mobility of reindeer (*Rangifer tarandus tarandus*) and reduces the time spent grazing (Reimers 1982; Hagemoen and Reimers 2002), which may lead to a lowered body weight (Toupin et al. 1996). Common avoiding behaviours are running (Agnew et al. 2000; Moore 2002), shifting a habitat and changing time of foraging (Moore 2002). For example, reindeer prefer open areas in warm weather when flying insects are abundant (Laaksonen et al. 2009) and gather into herds which is considered a seasonal change in social behaviour (Helle et al. 1992).

Defensive mechanisms of animals are behavioural fever, self-medication and physical removal of parasites (Poulin 1995). Sometimes potential host animals fight against ectoparasites by flicking ears, wagging tail, stamping foot, shaking the head and body, sneezing and biting the disturbing parasites (Bergman 1917; Hart 1994; Toupin et al. 1996; Moore 2002). Grooming may generally cover all the behavioural defences after a parasite has intruded upon the host animal (Moore 2002). Moreover, behaviours, such as scratching the body with hooves or antlers, grooming (biting or licking the body) and shaking the body, head or legs, are considered additional types of defensive behaviour of host animals against ectoparasites (Hart 1994; Toupin et al. 1996; Anderson and Nilssen 1998).

Recent invasion of a new blood-feeding ectoparasite of cervids, the deer ked (*Lipoptena cervi*, Diptera, Hippoboscidae), has been well-documented in Finland in the last half century (Välimäki et al. 2010, 2011). Despite the fact that the deer ked is a new species in Finland, there has been a long relationship between the deer ked and cervids in Europe as the oldest deer ked finding dates back more than 5000 years ago, observed from the mummified Late Neolithic man and his equipment in Italy (Gothe and Schöl 1994). The principal host of the deer ked in Finland is the moose (*Alces alces*), usually with 2000–10 000 parasites per individual with the highest intensity on bulls (Paakkonen et al. 2010). Deer ked infestation causes discolouration of moose bedding sites due to tissue fluids and deer ked faeces (Kaunisto et al. 2009). Some hair loss has also been observed on deer ked-infested moose (Madslien et al. 2011). Heavy parasitism on the moose has allowed the deer ked to widen its distribution area, as moose are known to migrate long distances (Cederlund and Liberg 1995). At present, the northern distribution limit of the deer ked is in the southern part of the Finnish reindeer herding area, at approximately 65ºN (Kaitala et al. 2009; Välimäki et al. 2010), but it may be able survive and go through metamorphosis even at 70ºN (Härkönen et al. 2010). Therefore, there is a concern whether the deer ked could invade the reindeer populations in Northern Europe. There are already several field observations (e.g., Ari Junttila, pers. comm.) of this novel parasite on reindeer. In the studies by Paakkonen et al. (2011, 2012), physiological, biochemical and clinical chemical responses to deer ked parasitism were examined both in moose and reindeer but they seemed to be minor with no significant health hazards during few months infestation. The deer ked may have effects on the behaviour of its host animals, and thus it is important to clarify the effects of harassment from the point of view of animal welfare.

The deer ked is likely to prolong the insect harassing period in the southern part of the reindeer herding area. In Finland, the deer ked has its flight season from July to October (Hackman et al. 1983; Härkönen et al. 2010). Adult deer keds are likely to attack any by passing large animal (Kortet et al. 2010). After finding a host, the deer ked sheds its wings and stay attached to the same host through their adult life-span (Bequaert 1953; Haarløv 1964). Thereby, and contrary to other flying insects, deer keds may remain on their hosts until the next spring (Härkönen et al. 2013). Mating of the deer ked takes place in the fur of the host and the viviparous female produces one fully grown pre-pupated larva at a time, which drops off the host after pupation. New-born pupae have been found on reindeer bedding sites even in March (Kynkäänniemi et al. unpubl. data). New adult deer keds emerge next autumn on the areas, where they were dropped as pupae (Haarløv 1964). The deer ked feed on host’s blood (Hackman *et al*. 1983) and it has been proposed to act as a potential vector for bacteria of the *Bartonella* genus (Dehio *et al*. 2004) and for haemoparasite *Trypanosoma* (*Megatyparum*) spp. (Böse and Petersen 1991).

The aim of this study was to examine, if deer ked infestation would alter reindeer behaviour and evaluate its effects on reindeer welfare (a potential host with a high economic importance in northern Finland). To reach this aim we conducted an experimental deer ked infestation on semi-domesticated reindeer. We hypothesized that deer ked infestation would cause general nuisance (e.g. by inducing skin irritation) and behavioural responses against deer ked parasitism. We also expected that routine antiparasitic treatment (Laaksonen et al. 2008) could be used to protect the reindeer against deer ked infestation.

Material and methods

Experimental animals

The present study was carried out at the Biological Research Facility of the University of Oulu, Finland (65ºN, 25ºE) between 29 May and 13 December 2007. The behavioural data were collected during three (I, II and III) periods between 16 August and 4 December. The experimental animals were 18 adult reindeer (11 females and 7 males; age 2.8 ± 0.6 years). The groups were kept at natural ambient temperature and photoperiod in their own enclosures (570 m^2) to prevent deer ked transfer between the groups. The reindeer were fed *ad libitum* with a commercial diet (Poron-Herkku, Rehuraisio, Espoo, Finland, energy content 11.7 MJ metabolizable energy/kg dry matter) supplemented with lichen (*Cladonia* spp.), hay as well as dried birch (*Betula* spp.) and willow (*Salix* spp.) leaves. For the detailed description of the experimental infection, see Kynkäänniemi et al. (2010).

On 29 May, the reindeer were assigned into three experimental groups (Infection group, Medication group and Control group) with an approximately equal sex ratio and average age. Each reindeer was fitted with a numbered ear tag and a collar with individual colouring for identification. Before the reindeer were infected, all animals were treated against possible pre-existing endo- and ectoparasites with subcutaneous (sc) ivermectin (0.2 mg/kg; Bimectin vet®, Vetcare Oy, Vantaa, Finland) and topical deltamethrin (75 mg/reindeer; pour-on lotion on dorsal skin; Coopersect spot on vet®, Schering Plough, Ballerup, Denmark) on 29 May. The ivermectin treatment was repeated on 13 June. The males were castrated to prevent rut in autumn, because it can be disturbing in corrals, result in injuries or cause stress to other reindeer. Moreover, rut alters the behaviour of the males and their handling can be difficult.

Experimental infection

The animals of Infection group and Medication group were infested on six occasions between 16 August and 27 September with an equal number of deer keds (35+35+35+45+35+115, *n* = 300/reindeer). The keds were applied on the anterior back of each animal. The control animals were immobilized similarly but they did not receive parasites. The number of deer keds was relatively low in order to mimic the situation in nature in the southern reindeer herding area (S. Kynkäänniemi, unpubl. observations) and to avoid exaggerated stress reactions. The intensity was low compared to moose in Finland (Paakkonen et al. 2010) but it is likely to be close to that of other cervids in Central Europe (Haarløv 1964). After the experiment in December, the numbers of alive and dead deer keds were counted from the pelts.

Behavioural data

The observations were conducted at 12:00–17:00 hrs and the time allocated per each animal was 30–60 min/observation day. The observation times between the three periods varied because the day length decreases rapidly from late summer towards early winter. Each group was monitored in its own enclosure. The observers (*n* = 3) performing the monitoring remained outside of the enclosures in small cabins to prevent anthropogenic disturbance.

The behavioural patterns were classified as follows: 1) scratching the body with hooves or antlers, 2) grooming (biting or licking the body), 3) shaking of the body, head or legs, 4) running and jumping, 5) aggressive kicking, goring or chasing. Behavioural patterns of classes 1–3 are good indicators of defensive behaviour of host animals against parasites (Hart 1994; Toupin et al. 1996;

Anderson and Nilssen 1998). In this study, classes 1–3 were pooled to calculate an index of restless behaviour. In previous studies, running has been classified as one form of defensive behaviour but only in the case of avoiding parasite attack and the subsequent infection (Agnew et al. 2000; Moore 2002). In contrast, defensive behaviour could not be determined during the attack on the host but only assessed at a later stage during the actual infection in the present study. For practical reasons, the incidence of each behavioural class lasting 10 s or less was reported as one item. If a continuous behaviour pattern lasted for more than 10 s, it was reported as two or more incidences (each 10 s) depending on the duration.

Period I; 16–21 August

During the first period only two groups, Infection and Control, were observed. Medication group was excluded from the first period because there were not enough observers available. The observation time was 60 min. The first period began on 16 August after the first deer keds had been transplanted on the reindeer and there were four observation days as follows: 16, 17, 19 and 21 August. During this period, a total of 35 deer keds were used to infest each reindeer in Infection group.

Period II; 23 August–2 October

During the second period, all three groups were observed on eight occasions and the observation time was 60 min as follows: 23, 25, 27 August, 4, 11, 20, 25 September and 2 October. On the 27 September all the 300 deer keds had been transferred on the reindeer. The two infected groups (Infection and Medication) were combined as a single Deer ked group (n = 12) because the mean values of restless behaviour of these groups did not differ (Welch Two Sample t-test; p = 0.66).

Period III; 5 November–4 December

On 6 November, Medication group was treated with sc ivermectin (0.2 mg/kg). Control and Infection groups were given equivolume 0.85% saline injections as a placebo treatment. During period III, all groups were observed on 5 and 15 November and on 4 December. The observation time during period III was 30 min. The number of experimental reindeer in Infection group was 5 on this period because the supervising veterinarian decided to euthanize one reindeer due to behavioural stress and observed hair loss on 24 October.

Statistical analyses

Statistical analyses were performed using the R program to compare the behavioural data between the groups (*v.* 3.0.1., R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). The statistical approaches differed for each observation period. Periods I–II were tested with Wilcoxon rank sum test to make results of the days between periods comparable. The model used for period II was inappropriate for periods I and III due to the low number of behavioural incidences in period I and the high amount of zero observations during period III. During period III, the lower number of experimental reindeer in Infection group and the medical treatment on 6 November also influenced the selection of the statistical approach.

The test used on period I was the Wilcoxon rank sum test for paired comparison. Each date was tested separately. On period II, comparison of mean values of restless behaviour between Infection and Medication groups was tested with Welch Two Sample t-test and the groups were pooled to form a single Deer ked group. For the statistical analyses on period II, incidences of each behavioural class (1–3) and index of restless behaviour were tested separately by comparing Control group and Deer ked group. A daily comparison was performed for behavioural classes with Wilcoxon rank sum test for paired comparison. The other test used for the whole period II was the linear mixed-effects model fitted by maximum likelihood. A logarithmic transformation was performed to attain normality. The model tested the effects of group, date and their interactions by using the data of repeated measures from individuals as a matrix. On period III, statistical analyses were performed using the Kruskal–Wallis test. *P* values were considered significant at $p < 0.05$ on all the periods.

Results

After each experimental transplantation, the deer keds entered the reindeer pelts and dropped their wings when passing through the top layer of hair (Fig. 1). During the later infestation dates, live deer keds could be observed in the reindeer hair. At the end of the experiment, Infection group had a few live deer keds, Medication group had only dead flies and no deer keds were found on Control group (details in Kynkäänniemi et al. 2010). No other ectoparasites were observed on the pelts of the animals. The average values of the index of restless behaviour are presented in Fig. 2. There were no differences between the groups in behavioural classes 4) and 5) (data not shown).

Period I; 16–21 August

The reindeer in Infection group scratched (class 1) themselves more than the reindeer in Control group on 19 August but not on the other dates (Table 1A). There were no differences in grooming (class 2), shaking (class 3) or in the index of restless behaviour on any of the observation dates. On 16 August, Infection group was shaking negligibly more often their pelts than Control group but this difference was not statistically significant ($p = 0.05$).

Period II; 23 August–2 October

The reindeer in Deer ked group displayed scratching (class 1) significantly more than those in Control group on 25 August, 20 September and 2 October (Table 1B). There was also higher rate of grooming (class 2) in Deer ked group on 2 October. Reindeer in Deer ked group shook (class 3) their pelts more on 27 August, 4, 11 and 20 September than in Control group. There was a difference between groups on index of restless behaviour on 25 August, 4 September and 20 September when reindeer in Deer ked group displayed restless behaviour. During period II, there were significant differences between groups in scratching (p = 0.01), shaking (p = 0.001) and index of restless behaviour (p = 0.001), but not in grooming (p = 0.06).

Period III; 5 November–4 December

Medication group had more incidences of grooming (class 2) than the other groups on 5 November but there were not differences in any other behaviour classes during period III (Table 1C). There was a significant difference between groups in the index of restless behaviour on 5 November, when Medication group had a higher rate of grooming. After medical treatment on 6 November, there were no differences between the groups on the last two observation dates. On the second date of Period III, the reindeer in Infection group had marginally higher rate (p = 0.06) of scratching but the restless behaviour reduced without antiparasitic treatment.

The reindeer infested with deer keds used their antlers and hoofs for scratching and damaged their pelts (Fig. 3).

Discussion

The main result of the present study was that the experimental deer ked infestation clearly induced defensive behavioural patterns of the reindeer. Restlessness in the deer ked-parasitized reindeer could be observed as increased incidences of restless behaviour, such as scratching the body with hooves and antlers, grooming (biting and licking the body) and shaking the body, head and legs, as the animals presumably tried to remove the deer keds or decrease the nuisance caused by them.

In our experiment, the number of infesting deer keds/reindeer was relatively low if compared to high numbers observed in wild moose (Paakkonen et al. 2010). However, previously even lower numbers, i.e. 5–10 keds/cow were observed to be sufficient to cause restlessness (Ivanov 1981). In the present study, shaking and scratching were the most commonly observed forms of restless behaviour and shaking seemed to be the first behavioural response against the deer keds. When the intensity of the infestation increased, the reindeer started to groom themselves more often. Grooming was the only form of restless behaviour which differed statistically between Medication group and Control group at the end of the experiment. Unfortunately, it was not logistically possible to observe groups before the deer ked infestation. Thus, the results regarding period I are preliminary and require further verification in the future. On period I, Medication group was not observed and, thus, some forms of restless behaviour could have stayed unnoticed. On period III, the observation time was 30 minutes shorter than on other periods, which may partly explain that biting was the only observed form of restless behaviour.

The occurrence of restless behaviour of reindeer was lower in period III than during period II. However, between these periods there was a month-long break in observations, and the numbers of live deer keds on all infested reindeer decreased dramatically during the experiment (recovery 4.7%; Kynkäänniemi et al. 2010). Behavioural changes of the host are affected by the intensity of parasitism (Hart 1990). The results suggest that behavioural responses or some other defence features of the reindeer could have been effective against this ectoparasite. A similar pattern was also noticed in sheep (*Ovis aries*) which were experimentally infested with the sheep ked (*Melophagus ovinus*), although their shared evolutionary history is longer (Nelson 1962). However, such behavioural changes are often adaptive for either the host or the parasite (Poulin 1995), but the relationship between reindeer and deer ked has emerged only recently (Kaitala et al. 2009; Kaunisto et al. 2009; Välimäki et al. 2010) and, thus, co-adaptation may have not occurred yet. The deer ked could have had a low viability on reindeer due to both of its morphology and physiology or the preservation of the deer keds before infestation. Despite the decreasing number of surviving deer keds as the experiment progressed, we cannot be sure how many of the deer keds had access to skin as the reindeer shook their pelts after infestation. For example, reindeer have a shorter and denser hair in their winter pelage compared to moose (Timisjärvi et al. 1984; Sokolov and Chernova 1987). Thus, reindeer may have a natural ability to resist deer keds, as their very dense hair could hypothetically prevent the deer keds from gaining sufficient access to skin for feeding or locating mating partners.

In the present experiment, the defensive behaviour seemed to damage the reindeer winter pelt (Kynkäänniemi et al. 2010). According to Madslien et al. (2011), there has been suspected deer ked infestation-related hair loss in several moose in Norway and Sweden contrary to the findings from deer ked-parasitized moose in eastern Finland of which only one moose of 23 had minor hair loss (Paakkonen et al. 2010). Usually ungulates display programmed grooming against ectoparasites driven by an internal timing mechanism, which is initiated periodically to decrease the ectoparasite load (Mooring and Samuel 1999). In previous studies, sheep were observed to bite and eat parasitizing sheep keds when they come to the surface of the fleece (Evans 1950). Skin irritation and the movements of ectoparasites may be triggering factors for the host to use its teeth and hooves (Hase 1940). However, grooming behaviour and biting the body can also be unbeneficial (Mooring and Samuel 1999); still, such behavioural responses are the most common mechanisms to remove ectoparasites and these types of behaviour (Moore 2002) as well as grooming-induced hair loss (McLaughlin & Addison 1986) may cause increased energy expenditure to the host. As the irritation caused by the deer ked induces grooming, scratching and shaking in reindeer, this may lead to stimulus-driven grooming. Similar responses have been earlier detected in the North American moose trying to get rid of winter ticks (*Dermacentor albipictus*; Mooring and Samuel

1999). The absence of programmed grooming in the moose–winter tick relationship is perhaps due to evolutionary history and a result of relaxed selection pressure for grooming.

According to our study, the deer keds seemed to decrease the welfare of the reindeer. In concert with this, Ivanov (1981) stated that the deer ked could induce scraping and associated skin changes to the host animals (cattle). Haarløv (1964) has suggested that the intensity of deer ked parasitism may be related to the host's health status and the persecution by the host. In contrast, physiological data of the same reindeer indicated no adverse health effects of deer ked infestation in autumn (Paakkonen et al. 2011). However, in the present experiment, the reindeer were in a good state of health, presumably because they had a good nutritional status, which may have lowered the negative effects of parasitism (Nelson 1984). It is well-known that summertime disturbance caused by insects increases the energy expenditure of reindeer (Weladji et al. 2003). According to Toupin et al. (1996), severe insect harassment can sometimes lead to poor physical condition in autumn. Furthermore, an important factor influencing the possible health effects of the deer ked on reindeer is the period, when host-seeking deer keds are the most abundant in nature. This occurs in Finland in August–September, immediately after the other harassing insects, e.g., *Culicidae*, *Simulidae* and *Tabanidae* decrease in numbers in the Finnish reindeer herding area (Laaksonen et al. 2009). One of the factors enhancing the deer ked's establishment in northern environments, in addition to the dense moose populations, may be the climate change, as observed for other ectothermic species (Parmesan et al. 1999; Beaumont and Hughes 2002; Vanhanen et al. 2007). As the global climate change affects especially the winter climate in Finland and, as a result, the ambient temperature increases (Lemke et al. 2007), the survival of parasites and their transmission may also increase (Weladji et al. 2002, Laaksonen et al. 2010). However, the shorter flight period in the North compared to the present range could be an obstacle for finding suitable hosts (Härkönen et al. 2010).

To conclude, our data indicate that deer ked infestation, even at a relatively low number of parasites, increases restless behaviour in the semi-domesticated reindeer. This may decrease the welfare of the animals and thus have indirect effects on *Rangifer* populations. A routinely used antiparasitic treatment for reindeer against other parasites could be effective in reducing the potentially deleterious effects of deer keds. More studies and observations among semi-domesticated and free-ranging reindeer are needed to investigate these novel host–pathogen interactions.

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Table 1 (A-C) The numbers and percentages of incidences/behavioural class/observation date and the index of restless behaviour, mean ± S.E. 1 = scratching the body with hooves or antlers, 2 = grooming (biting or licking the body), 3 = shaking of the body, head or legs, ∑ = index of restless behaviour.

A

Period I	Infection group (*n* = 6)		Control group (*n* = 6)		
16 Aug	%	mean (± S.E.)	%	mean (± S.E.)	*p*-value
1	5	2 ± 0.8	9	1 ± 0.6	0.93
2	27	8 ± 2.0	40	6 ± 2.4	0.47
3	68	19 ± 5.7	51	8 ± 2.1	0.05
∑	100	29 ± 8.0	100	15 ± 4.5	0.20
17 Aug					
1	41	5 ± 2.2	35	5 ± 3.4	0.26
2	20	3 ± 1.1	36	5 ± 2.5	0.62
3	39	5 ± 1.3	29	4 ± 1.3	0.37
∑	100	13 ± 2.1	100	13 ± 5.7	0.29
19 Aug					
1	24	5 ± 1.4	7	1 ± 0.6	0.03
2	31	6 ± 3.1	32	7 ± 2.0	0.57
3	45	9 ± 3.9	62	13 ± 7.0	0.94
∑	100	20 ± 6.7	100	20 ± 8.3	0.75

21 Aug					
1	18	2 ± 0.8	29	4 ± 1.5	0.33
2	36	4 ± 1.6	18	2 ± 0.6	0.56
3	46	5 ± 1.9	53	7 ± 2.1	0.19
∑	100	11 ± 3.5	100	13 ± 4.1	0.69

B

Period II	Deer ked group (n = 12)		Control group (n = 6)		*p*-value
23 Aug	%	mean (± S.E.)	%	mean (± S.E.)	
1	16	3 ± 0.9	14	2 ± 0.5	0.34
2	26	5 ± 0.9	45	5 ± 2.3	0.51
3	58	11 ± 2.9	42	5 ± 1.9	0.10
∑	100	19 ± 3.4	100	11 ± 2.9	0.12
25 Aug					
1	41	4 ± 1.1	37	1 ± 0.5	0.04
2	50	5 ± 2.6	26	1 ± 0.3	0.08
3	9	1 ± 0.4	37	1 ± 0.5	0.72
∑	100	10 ± 3.2	100	3 ± 1.2	0.02
27 Aug					
1	22	4 ± 1.5	34	4 ± 1.6	0.63
2	35	6 ± 1.8	41	5 ± 2.7	0.67
3	43	7 ± 1.6	24	3 ± 1.5	0.04
∑	100	17 ± 3.4	100	12 ± 3.4	0.35
4 Sep					
1	17	2 ± 0.8	28	1 ± 0.7	0.59
2	27	3 ± 0.9	32	1 ± 0.4	0.39
3	56	6 ± 1.3	40	1 ± 0.8	0.01
∑	100	11 ± 1.7	100	4 ± 1.2	0.03
11 Sep					
1	30	4 ± 1.3	45	5 ± 4.3	0.27
2	28	4 ± 1.1	34	4 ± 1.6	0.78
3	43	6 ± 1.3	21	2 ± 0.8	0.03
∑	100	15 ± 2.4	100	10 ± 4.9	0.17
20 Sep					

1	34	6 ± 1.9	8	0.3 ± 0.2	0.004
2	38	7 ± 2.3	50	2 ± 1.4	0.07
3	28	5 ± 1.1	42	2 ± 0.8	0.045
∑	100	18 ± 4.3	100	4 ± 1.6	0.008
25 Sep					
1	24	5 ± 1.6	13	2 ± 0.6	0.22
2	25	6 ± 1.7	46	6 ± 1.9	0.78
3	51	11 ± 2.5	41	5 ± 1.6	0.13
∑	100	23 ± 3.6	100	13 ± 3.3	0.05
2 Oct					
1	22	5 ± 2.7	4	0.2 ± 0.2	0.04
2	55	13 ± 4.0	48	2 ± 1.2	0.02
3	22	5 ± 1.6	59	3 ± 0.7	0.74
∑	100	24 ± 6.7	100	5 ± 1.6	0.07

C

Period III	Infection group (n = 5)		Medication group (n = 6)		Control group (n = 6)		
5 Nov	%	mean (± S.E.)	%	mean (± S.E.)	%	mean (± S.E.)	p-value
1	29	0.4 ± 0.2	3	0.3 ± 0.3	89	1 ± 1.1	0.79
2	14	0.2 ± 0.2	94	11 ± 4.9	11	0.2 ± 0.2	0.003
3	57	0.8 ± 0.4	3	0.3 ± 0.2	0	0	0.09
∑	100	1 ± 0.8	100	12 ± 4.6	100	3 ± 0.8	0.03
15 Nov							
1	15	0.8 ± 0.4	0	0	4	0.2 ± 0.2	0.06
2	70	4 ± 1.2	88	4 ± 2.5	92	4 ± 0.9	0.45
3	15	0.8 ± 0.4	12	0.5 ± 0.3	4	0.2 ± 0.2	0.33
∑	100	5 ± 1.6	100	4 ± 2.5	100	4 ± 0.8	0.35
4 Dec							
1	33	0.2 ± 0.2	33	0.2 ± 0.2	17	0.3 ± 0.2	0.79
2	33	0.2 ± 0.2	67	0.3 ± 0.3	75	2 ± 0.9	0.18
3	33	0.2 ± 0.2	0	0	8	0.2 ± 0.2	0.55
∑	100	0.6 ± 0.6	100	0.5 ± 0.5	100	0.6 ± 0.5	0.21

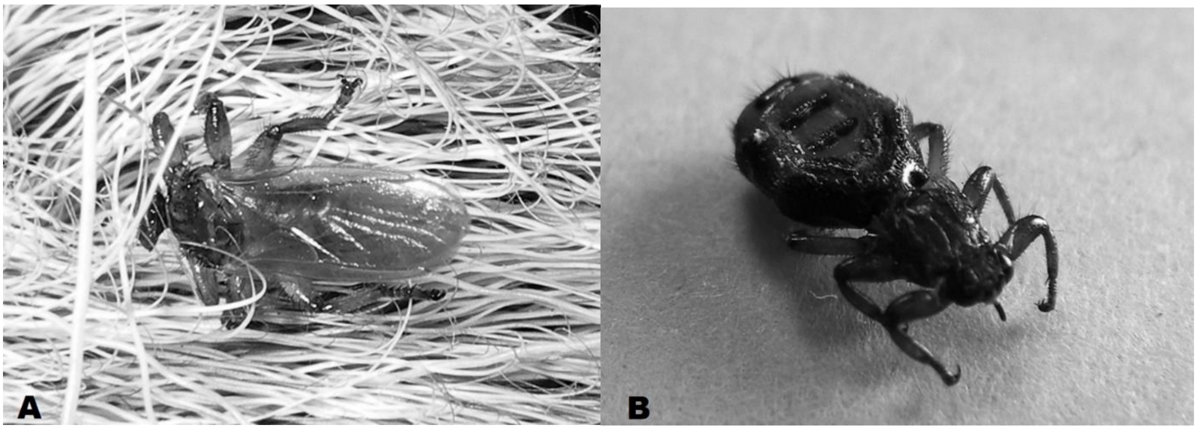

Fig. 1 A) The deer ked infiltrates through the reindeer hair. **B)** The deer ked sheds its wings after finding a host. After a blood meal distended abdomen can be observed. Photographs: Sauli Laaksonen

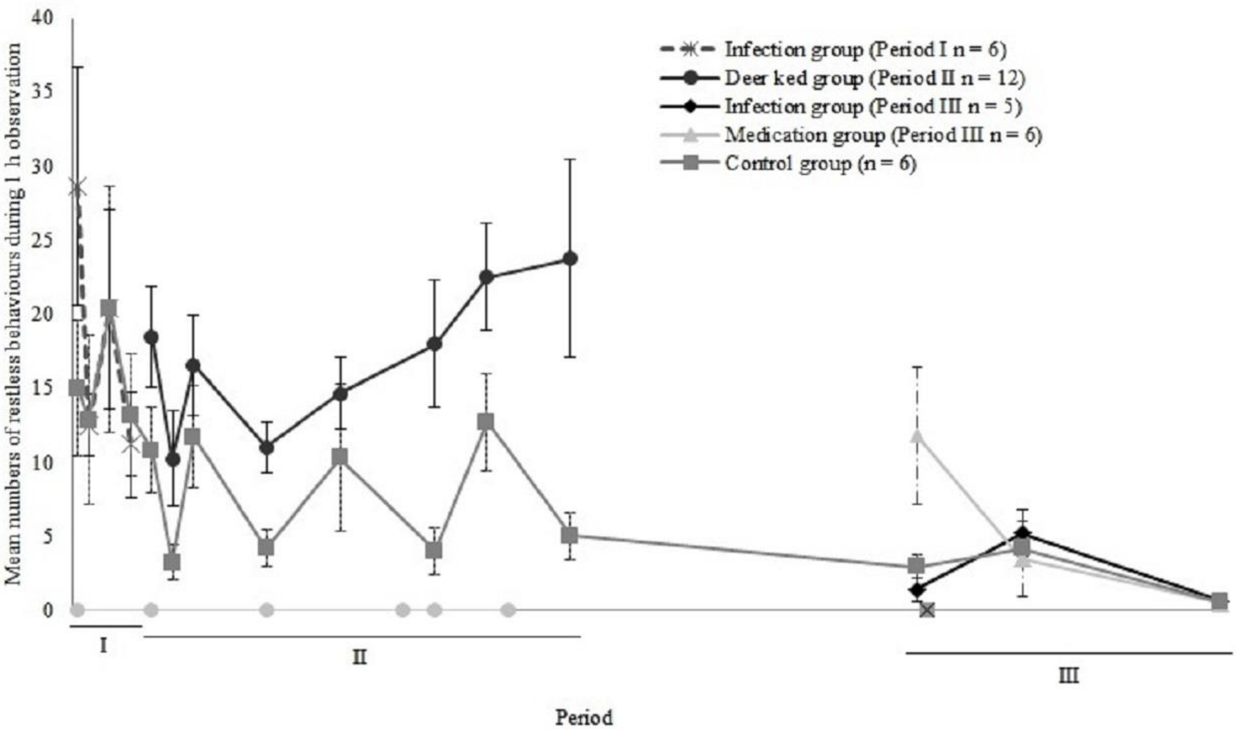

Fig. 2 The index of restless behaviour including scratching the body with hooves or antlers, grooming (biting or licking the body) and shaking of the body, head or legs, mean ± S.E. On the x-axis, the light gray dots indicate the infestation dates and the black symbol × on the grey

background indicates the treatment date of Medication group. During period II, Infection group and Medication group were pooled to form Deer ked group (see text for details)

Fig. 3 The reindeer infested with deer keds scratched themselves with antlers. This reindeer is from Medication group. Photograph: Sauli Laaksonen