Strategies to avoid biting flies by reindeer: field experiments with silhouette traps

Timo Helle, Jouni Aspi, Kyösti Lempa & Esa Taskinen

Helle, T., The Finnish Forest Research Institute, Rovaniemi Research Station, Eteläranta 55, SF-96300 Rovaniemi, Finland

Aspi, J., University of Oulu, Department of Genetics, Linnanmaa, SF-90570 Oulu, Finland

Lempa, K. & Taskinen, E., University of Oulu, Department of Zoology, Linnnanmaa, SF-90570 Oulu, Finland

Received 3 August 1991, accepted 27 September 1991

The effects of differences in grouping patterns (clumping vs. solitary) and habitat (open vs. forest) of reindeer on attack rates of blood-sucking flies were studied using CO₂ baited "reindeer-like" silhouette traps in Finnish Lapland near the Arctic Circle.

Within the grouped traps (24 traps/group) in an open habitat, flies attacked peripheral traps more frequently than middle and central ones. In an open habitat, black flies, biting midges and *Hybomitra* sp. preferred isolated to grouped traps. Isolated traps placed in the forest were attacked by flies less frequently than grouped ones in an adjacent open area.

The results suggest that gregarious females and calves of open-country reindeer are less subject to insect attack than more solitary males. For females and calves, herd formation may be the best strategy since severe insect harassment weakens the condition of calves and reduces their moving capacity. Forest reindeer use the forest as a refuge from insects, and although clumping would be beneficial, especially when feeding on open bogs, it is avoided because gregariousness may result in increased predation.

1. Introduction

Reindeer and caribou (*Rangifer tarandus* Linnaeus) commonly respond to various kinds of disturbances by herd formation (Baskin 1970, Bergerud 1974a, Skogland 1989). Clumping occurs most strikingly in open-country populations during the post-calving season. Gregariousness

has been proposed as an adaptation to predation (Bergerud 1974a) or to insect harassment (Baskin 1970, Roby 1978, Calef & Heard 1980, Downes et al. 1986). The association between herd formation and insect harassment is known also in some primates (Freeland 1977) and feral horses (Duncan & Vigne 1979, Keiper & Berger 1982, Rutberg 1987).

A closer examination reveals that social organization of Rangifer is highly variable in summer. Females of Scandinavian mountain reindeer (Rangifer tarandus tarandus Linnaeus) form herds of some thousands of individuals, but less than 20% of males join the female herds (Skogland 1974). The size of the purely male bands seldom exceeds 30 individuals (Skogland 1989). In forest areas in northern Finland, semidomesticated female reindeer (of mountain origin. see Siivonen 1975) are also gregarious in midsummer, whilst males tend to be solitary (Helle 1981). Forest reindeer (Rangifer tarandus fennicus Lönnberg) or woodland caribou (Rangifer tarandus caribou Gmelin), by contrast, do not form large herds at all (Banfield 1961), and males, in particular, are solitary (Helle 1981). Forest reindeer are known to seek relief from insects under the trees (Espmark 1967, Bergerud 1974a).

The objective of this study was to examine with silhouette traps the distribution of biting flies

- 1) within a group of traps,
- 2) between grouped and isolated traps, and
- 3) between open and forested habitats.

1.1. Study area

The study was carried out at two locations in northern Finland, close to the Arctic Circle during 1982 and 1984. The study area is a part of the north boreal section of the boreal coniferous forest zone (Ahti et al. 1968). Semi-domesticated reindeer of mountain origin (see Siivonen 1975) were introduced into the area about 250 years ago. The original wild forest reindeer (*Rangifer tarandus fennicus* Lönnberg) were exterminated by the end of the 19th century; the present population lives just south of a reindeer management area in an environment similar to that in Central Lapland (Helle 1981).

The biting and parasitic insects in the study area include mosquitoes (Diptera: Culicidae), black flies (Diptera: Simuliidae), gad flies (Diptera: Tabanidae), and biting midges (Diptera: Ceratopogonidae). The nose bot *Cephenomyia trompe* Modeer (subfamily Oestrinae) and the warble *Hypoderma tarandi* Linnaeus (subfamily Hypodermatinae) are quite rare (Helle 1980).

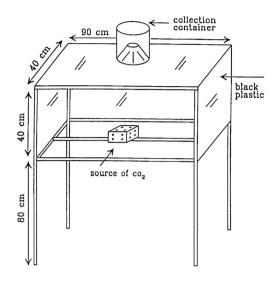


Fig. 1. The silhouette trap.

The insect season begins with the mass occurrence of mosquitoes around 15 June and lasts about two weeks. Black flies and gad flies are in flight from late June to early August, biting midges in July and August (Helle 1981).

1.2. Methods

We employed "reindeer-like" silhouette traps baited with CO₂ (Fig. 1). Silhouette traps have been used successfully in collecting females of gad flies, black flies and biting midges (Fredeen 1961, Morris 1963, Muirhead-Thomson 1982).

Trials with isolated and grouped traps in an open habitat were conducted in a field near Apukka, Finnish Central Lapland, on 30 July and 4 August 1982. Seven isolated traps, spaced 40 m apart, and a group of 24 traps were used. The distance between traps in a group was 0.25 m, simulating a reindeer herd being harassed by biting flies (Baskin 1970). Dry ice was added every 3 hours to a perforated container inside the trap. Average CO₂ release was calculated to be 0.3 l per min.

Grouped traps in an open habitat and isolated traps in a forest were compared in Kuusamo, northeastern Finland, on 26 June and 10 July 1984. The group of 24 traps was placed in a

meadow and the five isolated traps in an adjacent *Geranium-Myrtillus* type mixed spruce (*Picea abies* (Linnaeus)) and birch (*Betula pubescens* Ehrhardt) forest 40 m from each other; the height of the dominant trees was 16 m and the density about 700 trees per ha. CO₂ was released from underneath each trap from a pressure chamber at a rate of 1.0 l per min.

All four trials lasted from 12:00 h to 21:00 h and included the peak activity of flies involved in harassment. Collections were made on warm (temperature range 16–24°C at 3 pm.) and windless or almost windless days, most suitable for flying.

As a control, flies were collected around a domesticated (castrated) male reindeer using sweep nets. Due to the differences in escape responses of various insect families, the sweep net samples were obviously not quantitatively representative (see Muirhead-Thomson 1982). Therefore the sweep net samples were used only to determine if the most numerous flies in the traps were the same species as the ones frequently attacking the reindeer.

Because we were interested primarily in how trap density and habitat influence the number of insects, catches of each trap on the two collection dates at the same location were pooled for further analysis. The Chi-square test was used to test whether the observed frequencies of each fly family within grouped traps (peripheral, middle and central) and between grouped and isolated traps differed from the expected even distribution. When only two groups were compared (grouped vs. isolated) or when the expected frequency was less than 5, Yates correction for continuity was used (Sokal & Rohlf 1981).

2. Results

A total of 38 600 and 4 500 insects were collected in the traps at Kuusamo and Apukka, respectively. At both locations, black flies and biting midges comprised 99% of the total catch.

The most numerous black flies collected in the traps at Kuusamo were *Simulium (Simulium)* truncatum Lundström, *S. rostratum* Lundström and *Eusimulium (Schönbaueria) pusillum* Fries and at Apukka *S. truncatum*. These species were similarly abundant in the sweep net samples. The most common biting midge species both in the traps and in sweep samples around the reindeer was *Culicoides pulicaris* Linnaeus.

The most common gad fly in the traps at Kuusamo was *Haematopota pluvialis* Linnaeus (48 of 60) and at Apukka *Chrysops relictus* Meigen (19 of 42). These two species also occurred most frequently in the samples from the reindeer. The other species collected in the traps (Kuusamo: *Hybomitra arpadi* Szilady, *H. lundbecki* Lyneborg, *H. lurida* Fallen, and *H. tarandina* Linnaeus; Apukka: *H. arpadi*, *H. bimaculata* Macquart) were also found in samples from the reindeer.

Within grouped traps, all fly families at Kuusamo and black flies and biting midges at Apukka attacked the peripheral traps more frequently than the middle and central ones (Fig. 2). In an open habitat at Apukka, black flies and biting midges preferred isolated to grouped traps (Fig. 2). A similar but non-significant trend was also found in gad flies. For Hybomitra sp. the difference was significant (the observed frequencies for isolated and grouped traps were 11/ 7 and 1/24 respectively) $\chi^2 = 29.1$, df = 1, P < 0.001). At Kuusamo, all three fly families occurred less frequently in isolated traps in the forest than in grouped traps on the adjacent open area; catches in the forest were of the same magnitude as in the centre of the group (Fig. 2).

3. Discussion

3.1. Benefits of herd formation

The present experiment applied to the season after the mosquito peak, when reindeer are harassed mainly by black flies, gad flies and biting midges. The large post-calving herds of semi-domesticated reindeer split up into smaller bands which comprise some dozens of individuals, corresponding to the group size used in this study (Helle 1981). In open-country populations, however, herd size remains large throughout the whole insect season (Bergerud 1974a, Downes et al. 1986, Skogland 1989).

The results for black flies, gad flies and biting midges support the hypotheses that herd for-

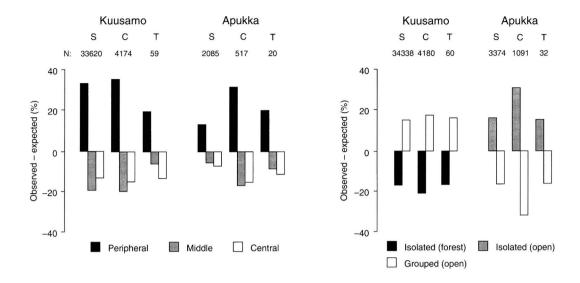


Fig. 2. The deviations from the expected frequences for black flies (S), biting midges (C) and gad flies (T) in a group of traps in an open habitat (left), and between isolated and grouped traps (right), at Kuusamo and Apukka. All deviations, except for gad flies in Apukka, are statistically significant (chi-square test).

mation reduces the attack by these flies and that the benefit of clumping depends on the individual's place in the herd. An inverse relationship between the group size and the number of attacking gad flies was also reported in feral horses (Duncan & Vigne 1979, Rutberg 1987). Baskin (1970) found that reindeer confining themselves to the periphery of the herd were also most prone to mosquitoes. Thus, in the mixed summer herds, dominant males and females with calves benefit most because they occupy places in the centre of the herd during insect attack, whilst low-ranking animals are commonly on the periphery (Gomoyunova 1976, White et al. 1981, Skogland 1989).

Two factors may explain why the clumping of hosts reduces harassment. Hargrove & Vale (1978) found that for several blood-sucking and parasitic fly species, catches increased proportionally with the bait mass up to a certain limit but not beyond. They proposed (Vale & Hargrove 1975) that catches may be limited by the capacity of insects to fly up the long odour trails produced by large bait masses. For gad flies, the bait mass limit corresponded to a livestock biomass with a CO₂ production rate of 2–5 l per min. In our trials the total release of CO₂ of grouped traps

was 7 l per min (Apukka) and 12 l per min (Kuusamo). This suggests that the bait mass limit was reached in our study resulting in a dilution of the number of attacking flies per trap.

Many black fly and gad fly species concentrate their attacks on the legs and belly of a large-sized mammalian host (Breev 1950, Skjenneberg 1965, Hollander & Wright 1980). If these sites are not available due to clumping, isolated or peripheral hosts provide the only access to preferential feeding sites.

3.2. The forest as insect relief

Flies attacked isolated traps in the forest much less frequently than grouped ones on the adjacent open area, but despite that semi-domesticated reindeer in the study area seldom use the forest as a relief from insects; more preferred are microhabitats such as open sands, sandy road-sides, empty hay sheds, and sheds built as insect shelters for the reindeer (Helle 1981). Convectional air currents over hot sand may interfere with the fly's ability to detect CO₂ cues (Helle & Aspi 1984), and most gad fly species tend to avoid dark places (Chvala et al. 1972). Thus, locations

in these micro-habitats may result in harassment levels lower than those found in the forest.

By contrast, forest reindeer habitats either lack man-made insect refuges, or the animals avoid them. After the mosquito season, both sexes have habitual resting places in the forest (Helle 1981). If a resting animal is irritated by biting flies, it jumps up and runs for a while in the forest before returning. Similar behavior is described in red deer *Cervus elaphus* Linnaeus during the fly season (Espmark & Langvatn 1979).

Within their original range in eastern Finland wild forest reindeer do not clump (Helle 1981, Heikura et al. 1983), although herd formation would reduce insect harassment when feeding on open bogs. Dispersed social organization combined with concealed living habits is thought to be an adaptation to avoid predation in conditions with restricted visibility where most predators use surprise as an attack technique (Eisenberg & McKay 1974, Hirth 1977, Helle 1981). However, clumping behavior shows plasticity, because wild forest reindeer reintroduced in Central Finland into a predator-free environment have been seen in bands of up to 30 females and calves during mass attack by black flies (Ilpo Kojola, pers. communication with T. Helle).

3.3. Male and female strategies

Gregarious females of open-country populations may be attacked by insects less than solitary males or males in small bands. We hypothesize that these strategies are related to individual fitness, i.e., to autumn body weight in males and calf survival in females (Bergerud 1974b), since insect harassment has an adverse effect on weight gain and survival on reindeer calves (Helle & Tarvainen 1984).

According to experienced reindeer herders, males are difficult to keep under close control during the insect season because of their energetic escape reactions to insects (Oinonen 1964, Jouni Labba and Juhani Valkeapää, pers. communication with T. Helle). Males can take advantage of locations which are free of insects at a given time, and thus effectively exploit separate foraging areas and insect refuges over long distances (Jouni Labba, pers. communication with T. Helle).

In contrast, movements of females with calves become slower during the insect season. In semi-domesticated populations tiring of the calves is clearly visible. Thus, herd formation is obviously the best strategy for females and their calves. It serves primarily to increase calf survival by reducing stress through protection against insects while ensuring at the same time a close relationship between the female and her calf. In testing the "calf anchor" hypothesis, females without calves are of particular interest, since male-like behavior is expected. In wild forest reindeer, females without calves escape from insects by running significantly more than females with calves (Kojola 1991).

Acknowledgements. We are grateful to Juha Hyvönen, Seppo Lohiniva, Aarno Niva and Eija Virtanen for technical assistance in preparing the manuscript. We would like to thank David Klein, Ilpo Kojola, Wendy Nixon, Margaret Penner, Hannu Saarenmaa and Nicholas Tyler for their valuable comments on an earlier draft of the manuscript.

References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5:169–211.
- Banfield, A. W. F. 1961: A revision of the reindeer and caribou, genus Rangifer. — Nat. Mus. Canada Bull. 177:1–37.
- Baskin, L. M. 1970: Reindeer ecology and behaviour. Moscow: Institute for Evaluation of Morphology and Ecology of Animals, USSR Academy of Science (in Russian, Unpubl. English translation by Foreign Language Division, Department of State, Ottawa).
- Bergerud, A. T. 1974a: The role of the environment in the aggregation, movement and disturbance behaviour of caribou. In: Geist, V. & Walther, F. (eds.), The behaviour of ungulates and its relation to management. IUCN Publ. New Ser. 24(2):552–584.
- 1974b: Rutting behaviour of Newfoundland caribou.
 In: Geist, V. & Walther, F. (eds.), The behaviour of ungulates and its relation to management. IUCN Publ. New Ser. 24(2):395–435.
- Breev, K. A. (Бреев, K. A.) 1950: [The behavior of blood-sucking Diptera and warble flies during their attack on reindeer.] (In Russian) Parazitol. Sb. 12:167–189.
- Calef, G. & Heard, D. C. 1980: The status of three tundra wintering caribou herds in northeastern Mainland Northwest Territories. — In: Reimers, E., Gaare, E. & Skjenneberg, S. (eds.), Proceedings of the 2nd International Reindeer/Caribou Symposium. Röros. Norway. 1979. Direktoratet för vilt og ferskvannfisk, Trondheim. pp. 582–594.

- Chvala, M., Lyneborg, L. & Moucha, J. 1972: The horse flies of Europe. Copenhagen. 498 pp.
- Downes, C. M., Theberge, J. B. & Smith, S. M. 1986: The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. — Can. J. Zool. 64:622–629.
- Duncan, P. & Vigne, N. 1979: The effects of group size in horses on the rates of attacks by blood-sucking insects.— Anim. Behav. 27:623–625.
- Eisenberg, J. F. & McKay, G. M. 1974: Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rainforests of Central America. In: Geist, V. & Walther, F. (eds.), The behaviour of ungulates and its relation to management. IUCN Publ. New Ser. 24(2):585–602.
- Espmark, Y. 1967: Observations of defense reactions to oestrid flies by semi-domestic forest reindeer (Rangifer tarandus L.) in Swedish Lapland. Zool. Beitr. 14(1–2):155–167.
- Espmark, Y. & Langvatn, R. 1979: Lying down as a mean of reducing fly harassment in red deer (Cervus elaphus).

 Behav. Ecol. Sociobiol. 5:51–54.
- Fredeen, F. J. 1961: A trap for studying the attacking behaviour of black flies, Simulium arcticum Mall. Can. Entomol. 92:73–78.
- Freeland, W. J. 1977: Bloock-sucking flies and primate polyspecific associations. Nature 267:801–802.
- Gomoyunova, N. P. (Гомоюнова, Н. П.) 1976: [On biology of warble flies.] (In Russian) Novosibirsk "Nauka". 112 pp.
- Hargrove, J. W. & Vale, G. A. 1978: The effect of host odour concentration on catches of tsetse flies (Glossinidea) and other Diptera in the field. — Bull. Ent. Res. 68:607–612.
- Heikura, K., Lindgren, E., Pulliainen, E., Sulkava, S. & Erkinaro, E. 1983: Grouping behavior of the forest reindeer in Kuhmo in 1978–81. — In: Pulliainen, E. (ed.), Proc 3rd Int. Reindeer/Caribou Symp. pp. 25–28.
- Helle, T. 1980: Abundance of warble fly (Oedomagena tarandi) larvae in semi-domestic reindeer (Rangifer tarandus) in Finland. Rep. Kevo Subarctic Res. Stat. 16:1-6.
- 1981: Studies on wild forest reindeer (Rangifer tarandus fennicus Lönnberg) and semi-domestic reindeer in Finland. — Acta Universitatis Ouluensis, Series A, Biologica 12:1–34.
- Helle, T. & Aspi, J. 1984: Do sandy patches help reindeer against insects? — Rep. Kevo Subarctic Res. Stat. 19:57–62.
- Helle, T. & Tarvainen, L. 1984: Effects of insect harassment and weight gain and survival in reindeer calves. Rangifer 4(1):24–27.
- Hirth, D. H. 1977: Social behaviour of white-tailed deer in relation to habitat. — Wildl. Monogr. 53:1–55.

- Hollander, A. L. & Wright, R. E. 1980: Impact of Tabanids on cattle: Blood meal size and preferred feeding sites.

 J. Econ. Entomol. 73:431–433.
- Keiper, R. & Berger, J. 1982: Refuge-seeking and pest avoidance by feral horses in desert and island environments. — Appl. Anim. Ethol. 9:111–120.
- Kelsall, J. P. 1968: The migratory barrenground caribou of Canada. Ottawa. 334 pp.
- Kojola, I. 1991: Reproductive status and behavioral responses to attacking insects by female reindeer. Appl. Anim. Behav. Sci. 32:91–93.
- Kojola, I., Nieminen, M. & Helminen, M. 1985: Successful reintroduction of wild forest reindeer in Finland.
 In: Trand. 17th Int. Cong. Game Biol., Brussels, Belgium 1985. pp. 125–132.
- Morris, K. R. S. 1963: A study of African tabanids made by trapping. Acta Tropica 2(1):16–34.
- Muirhead-Thomson, E. C. 1982: Behaviour patterns of blood-sucking flies. Pergamon Press. 224 pp.
- Oinonen, V. 1964: Lapin yliperällä. WSOY, Porvoo-Helsinki. 174 pp. (in Finnish).
- Roby, D. D. 1978: Behavioral patterns of barren-ground caribou of the central Arctic herd adjacent to the Trans-Alaskan Oil Pipeline. — M.Sc.thesis, University of Alaska, Fairbanks, AK.
- Rutberg, A. T. 1987: Horse fly harassment and the social behavior of feral ponies. Ethology 75:145–154.
- Siivonen, I. 1975: New results on the history and taxonomy of the mountain, forest and domestic reindeer in Northern Europe. In: Luick, J. R., Lent, P. C., Klein, D. R. & White, R. G. (eds.), Proc. 1st Int. Reindeer/Caribou Symp. pp. 33–40.
- Skjenneberg, S. 1965: Rein og reindrift. Lesjaskog. 326 pp.
- Skogland, T. 1974: Villreinens habitatferd. Hardangervidda 1970–73. NorskIBP, Direktoriatet for vilt og ferskvannfisk, Trondheim. 144 pp. (In Norwegian with English summary).
- 1989: Comparative social organization of wild reindeer in relation to food, predator avoidance and mates. — Advances in Ethology 29:1–71.
- Skoog, R. O. 1968: Ecology of the caribou (Rangifer tarandus granti) in Alaska. — Ph.D.thesis, University of California, Berkeley, CA.
- Sokal, R. R. & Rohlf, F. J. 1981: Biometry. Freeman, San Francisco. 2nd ed.
- Vale, G. A. & Hargrove, J. W. 1975: Field attraction of tsetse flies (Diptera; Glossinidae) to ox odour, the effects of dose. Trans. Rhod. Scient. Ass. 56:46–50.
- White, R. G., Bunnell, F. L., Gaare, E., Skogland, T. & Hubert, B. 1981: Ungulates on arctic ranges. — In: Bliss, L., Heal, O. & Moore, J. (eds.), Tundra ecosystems: a comparative analysis: 397–483. Cambridge Univ. Press, Cambridge.