

Behavioral, Physiological, Demographic and Ecological Impacts of Hematophagous and Endoparasitic Insects on an Arctic Ungulate

Kyle Joly ^{1,*}, Ophélie Couriot ^{2,3}, Matthew D. Cameron ¹ and Eliezer Gurarie ³

¹ Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, National Park Service, Fairbanks, AK 99709, USA; matthew_cameron@nps.gov

² National Socio-Environmental Synthesis Center, SESYNC, 1 Park Place, Suite 300, Annapolis, MD 21401, USA; ocouriot@sesync.org

³ Department of Biology, University of Maryland, College Park, MD 20742, USA; egurarie@umd.edu

* Correspondence: kyle_joly@nps.gov

Received: 5 May 2020; Accepted: 15 May 2020; Published: 20 May 2020

Abstract: Animals that deliver a toxic secretion through a wound or to the body surface without a wound are considered venomous and toxungenous, respectively. Hematophagous insects, such as mosquitoes (*Aedes* spp.), meet the criteria for venomous, and some endoparasitic insects, such as warble flies (*Hypoderma tarandi*), satisfy the definition for toxungenous. The impacts of these insects on their hosts are wide ranging. In the Arctic, their primary host is the most abundant ungulate, the caribou (*Rangifer tarandus*). The most conspicuous impacts of these insects on caribou are behavioral. Caribou increase their movements during peak insect harassment, evading and running away from these parasites. These behavioral responses scale up to physiological effects as caribou move to less productive habitats to reduce harassment which increases energetic costs due to locomotion, reduces nutrient intake due to less time spent foraging, and can lead to poorer physiological condition. Reduced physiological condition can lead to lower reproductive output and even higher mortality rates, with the potential to ultimately affect caribou demographics. Caribou affect all trophic levels in the Arctic and the processes that connect them, thus altering caribou demographics could impact the ecology of the region. Broadening the definitions of venomous and toxungenous animals to include hematophagous and endoparasitic insects should not only generate productive collaborations among toxinologists and parasitologists, but will also lead to a deeper understanding of the ecology of toxic secretions and their widespread influence.

Keywords: *Aedes* spp.; behavior; caribou; demographics; energetics; *Hypoderma tarandi*; mosquito; movement; physiological; warble fly

Key Contribution: We review the wide-ranging effects of hematophagous and endoparasitic insects on the most abundant ungulate in the Arctic biome and highlight the causal connection of these insect-induced impacts on host demographics and ecology via behavioral and physiological responses.

“The buck, who had been standing motionless at the opposite end of the gravel bar all this time, suddenly exploded into action, showing all the typical reactions to an attack by a nose or warble fly. He threw up his head, stamped his feet, twitched his hide, and then began to gallop along the beach, bucking and tossing as he ran. He suddenly stopped and stood stock still. Then he wheeled, galloped back in his tracks, stopped again, shook his head, wheeled once more

and galloped full speed toward the band at the water's edge. He literally burrowed his way into their midst where I lost him and presumably the nose fly did likewise."

— W. O. Pruitt [1]

1. Introduction

Animals that produce a secretion used on another animal that disrupts physiological or biochemical processes in order to facilitate behaviors such as feeding or defense can be considered venomous if delivered through a wound, or toxungenous if delivered to the body surface absent a wound [2,3]. While sometimes overlooked in this regard, hematophagous insects such as the mosquito (*Aedes* spp.) and endoparasitic insects such as the warble fly (*Hypoderma tarandi*) have the requisite characteristics to be broadly characterized as venomous and toxungenous, respectively. Mosquitoes, like all hematophagous animals, secrete fluids to help them obtain blood [4,5]. After the mosquito's proboscis enters its target, it begins secreting saliva that has platelet aggregation inhibitors, like the enzyme apyrase, to prevent platelets from coming together to form blood clots as well as anticoagulant properties, which slow the formation of clots, help induce hematomas, and improve the chances of acquiring a blood meal [6,7]. Warble larvae secrete protease and other enzymes to create a wound in order to enter its host skin, which is an example of toxungen rather than a venom [3]. However, the larvae secrete enzymes while traveling through its host's body and the enzyme hypodermin C, which is used for the hydrolysis of the host's proteins that are then used as nutrients for the larvae while it is inside its host [8,9].

Arctic mosquitoes are in diapause over the winter. Snow and ice melt trigger the hatching of mosquito eggs, after which the larvae feed on vegetation [10]. From emergence (late May to mid-June) to cessation of activity (late July), adult females seek blood meals, which will allow them to reproduce. During this time period, mosquito numbers are remarkable, with an estimated 17 trillion individuals in Alaska alone [11,12]. Mosquito abundance is positively related to warmer summer temperatures, while their activity level is tied to low wind velocities because they are relatively poor fliers [10,13,14].

Warble flies are much less numerous than mosquitoes. However, almost every caribou and reindeer (both *Rangifer tarandus*; henceforth referred to as just caribou) is afflicted by them and exhibit stronger responses to them than from mosquitoes [10,15–17]. The presence of even a single warble fly can elicit strong responses by caribou [1,11]. While warble fly abundance and activity levels are also positively associated with warmer summer temperatures, they are strong fliers and thus less dependent on calm conditions [14,18]. Unlike mosquitoes, adult warble flies do not directly seek nutrients from its host. Rather, adults lay their eggs on the hair of caribou in July and August [19,20]. After 3–7 days, the larvae hatch, burrow into the skin of the caribou, migrate in its body and, eventually, the third instar forms nodules and overwinters in its host [8,9]. The mature larvae exit the host in May to June and then mature some weeks later to emerge as adult flies [21].

2. Impacts of Mosquitoes and Warble Flies on Caribou

It is hard to overstate the ecological and socio-economic importance of caribou for the Arctic. Caribou span the northern hemisphere and are the most numerous ungulate in the Arctic [22]. Herds of caribou can number into the hundreds of thousands of individuals [23]. Caribou are vital to the culture and economy of the Arctic [24]. Subsistence harvest of caribou remains high in northern regions, with caribou being the most utilized terrestrial resource in many regions. While Westerners have known of the impacts of insects on caribou for more than a century [25], aboriginal peoples must have known for millennia. The impacts of mosquitoes and warbles are obvious, wide ranging, and can be dramatic. The most immediate responses of caribou responses to mosquitoes and warble flies are behavioral, with direct and indirect physiological effects and, ultimately, potential demographic and ecological effects.

2.1. Behavioral Impacts

Behavioral responses to increasing insect harassment are numerous and wide ranging. First, insect harassment is thought to increase caribou movements [26–29]. For example, average movement rates of Western Arctic Herd caribou, found in northwest Alaska, range from 121 to 971 meters/hours (m/h) over the course of the year (Figure 1). Movement rates are lowest in winter (i.e., beginning of December through the beginning of April) but are elevated for both spring and fall migration. After spring migration, movement rates drop as female caribou give birth and the calves ready themselves to travel with the rest of the herd. Movement rates were consistently the greatest from June 19th to July 28th (also see [30–32]), when insect harassment was greatest. This was the only time of the year that movement rates exceeded 600 m/h (Figure 1). This pattern is striking and unexpected, as one might expect that movement rates would be highest during the iconic spring and fall migration periods but are actually greatest in the summer when caribou could be foraging in highly productive habitat to accumulate fat and protein to replenish stores depleted during the winter and aid in nursing their calves.

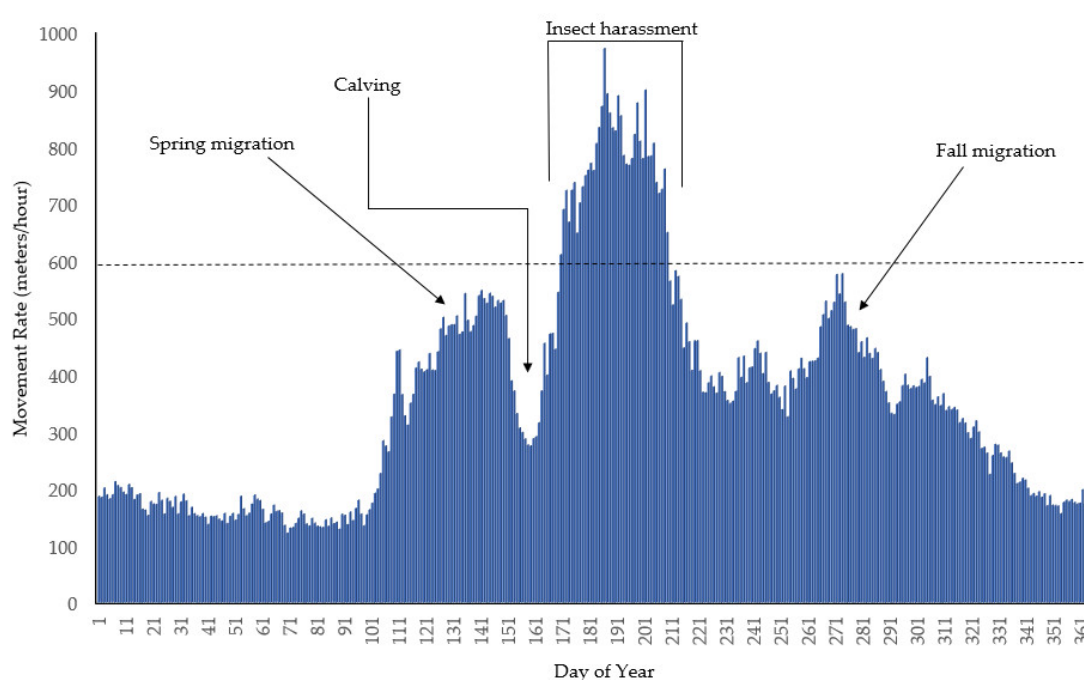


Figure 1. Average movement rates (meters/hour) of Western Arctic Herd female caribou by day of the year, northwest Alaska, 2009–2019.

The increased movement may be a direct response to evade insects [27]. Indeed, caribou are known to travel long distances in order to avoid warble flies [1,11]. This may include diverse strategies such as walking long distances into the wind or evasive actions such as erratic movements or swimming. However, this additional time spent moving has a cost, since it leaves less time for feeding, resting and ruminating [33].

Beside the tradeoff between insect avoidance and time spent on other essential activities, insect harassment can also impact the quality and the quantity of forage accessed by caribou. Often these insect-related movements will drive caribou to use insect relief habitats (Figure 2), such as windswept or snow-covered areas, or even gravel bars, lakes or ocean shallows [11,13,27,28,34–37]. Typically, these insect relief habitats have very low vegetative productivity. Moreover, the abundance of these habitats can be limiting. The result is that caribou can form extremely large (> 100,000 individuals) and tight aggregations in these habitats during peak insect harassment [38]. This increases competition for resources and diminishes the quantity of forage intake per capita. In addition, these large aggregations of caribou can have a direct impact on the parasitic load of some individuals, since social status can influence the spatial location of individuals in these aggregations and thus their

relative susceptibility to infestation [39]. Caribou found in the interior of an aggregation are exposed to relatively less insect harassment, as they are surrounded by and often physically touching other caribou, than caribou along its perimeter or off by themselves. Finally, as insect harassment impacts caribou habitat selection, avoiding areas with high parasites can also alter use of foraging areas and the distribution of caribou across the landscape [40]. It has also been hypothesized that caribou will move away from calving areas, where warbles drop out of caribou and hatch, in order to reduce harassment from the adult flies [39,41]. The impacts of these movements are not fully understood.



Figure 2. Caribou aggregating on gravel bars and in the river itself in an attempt to reduce insect harassment, northwest Alaska. Time spent in insect relief habitat reduces the amount of time spent foraging. Photo: K. Joly (NPS).

2.2. Physiological Impacts

All reported insect harassment-driven behaviors that caribou display can have direct or indirect physiological impacts. The greater movements increase energetic expenditures [42] and the reduced feeding time, in addition to lower forage quality and quantity due to altered habitat selection and large aggregations during the short arctic growing season, directly act to reduce body condition and/or growth rate. This is especially true for females that have the added demand of lactation, individuals already in poor condition, and on rapidly-developing calves [13,40,43]. Following summers with conditions that allow for high levels of insect harassment, females tend to reach their calving grounds later [44]. The indirect impacts of these late arrivals on calf survival and replenishing protein stores of parturient females represents a knowledge gap and a promising area of future research.

Male caribou tend to have greater warble larvae loads than females [15,17,45]. Poor growth during the first year of life of male calves can have long-term indirect impacts for entire cohorts born in a high insect harassment year, as body size helps determine competitive abilities during the rut [43]. However, some caribou calves have been known to exhibit compensatory growth during the winter [46].

Heavy warble infestations can also directly reduce weight gain [15,29,47,48] and limit the amount of stored fat caribou carry into the winter season [16,40]. These extra burdens add to the other direct and indirect costs associated with increased parasitic insect loads. Direct physiological impacts

of the parasites include costs associated with biochemical and inflammatory immune responses by the caribou and the siphoning off of nutrients and/or blood (blood loss has been estimated to reach up to 125 g/day), that can also lead to a lower body condition [8,9,18,40,49]. Host responses are designed to reduce the impacts of the parasites or even, in the case mosquitoes, kill them [6,7]. Thus, parasites have co-evolved by developing strategies to lower the amount of time required to breach their host [6,7,50].

2.3. Demographic Impacts

The behavioral and physiological responses of caribou to insect harassment can have demographic and population-level consequences. Females with lower body conditions are less likely to become pregnant [51,52] and heavy warble fly loads have been associated with lower pregnancy rates in caribou [40]. Therefore, particularly bad years of insect harassment can impact entire cohorts [43]. Moreover, extreme warble fly infestations can even lead to lower overwinter survival in calves and delay the timing of calving [16,43,44]. High pregnancy and recruitment rates are vital for population growth. Thus, physiological impacts can have a multiplier effects [53] that lead to demographic impacts in caribou [11,15,16,47,48,54]. In other words, small, sub-clinical changes in the amount of time spent foraging, energy expended for additional locomotion, and intake of high-quality forage accumulated over the course of the short Arctic growing season can make the difference in females becoming pregnant or not and calves surviving over the winter or not [16,55]. All these insect-related impacts would negatively influence caribou populations. Many caribou populations around the world are in decline and these negative influences of insects on caribou demographics are exacerbated during population declines [11].

2.4. Ecological Impacts

Caribou herds, which can number into the several hundreds of thousands of individuals, are an ecological force in the Arctic [23]. These herds can dramatically effect vegetation through grazing and/or trampling, reducing abundance of shrubs and lichens [56–58]. Caribou exhibit the longest terrestrial migrations on the planet, thus they transport nutrients over huge (>100,000 km²) areas which can affect soil nutrient concentrations [57,59,60]. These nutrients come from digestive waste products of caribou but also from their carcasses [59]. Caribou are the primary prey for wolves (*Canis lupus*) but are also sought after by brown bears (*Ursus arctos*), wolverine (*Gulo gulo*), golden eagles (*Aquila chrysaetos*), and other predators [61,62]. Remains of these carcasses are utilized by scavengers, like ravens (*Corvus corax*), and then eventually by decomposers. Thus, caribou affect all trophic levels in the Arctic and the ecological processes that connect them. Since hematophagous and endoparasitic insects have the capability to affect caribou demographics, as well as caribou habitat selection and density in insect relief habitats, they also have the potential to indirectly impact the ecology of the entire arctic ecosystem. Outside the sphere of caribou, mosquitoes have numerous direct impacts on arctic ecology including acting as decomposers (in their larvae stage), pollinators, and food sources for a variety of bird species [63].

3. Conclusions

By utilizing broad definitions of venomous and toxungenous that encompass hematophagous and endoparasitic insects, like mosquitoes and warble flies, biologists increase their ability to more fully understand the ecology of toxic secretions and their wide-ranging influence. Similar to other studies, we found that movement rates were greatest during the insect harassment period. We reviewed some, but not all, of the various impacts these insects can have on caribou—the dominant herbivore in northern climes. We suggest a causal mechanism, through behavioral changes (increased movements that lead to greater energy expenditures, reduced foraging time, and increased use of low productivity habitats), that link insect harassment to poorer physiological conditions in caribou which potentially culminate in detrimental demographic consequences. Changes in caribou population sizes can have profound ecological consequences in the Arctic. While pronounced in the

Arctic, hematophagous and endoparasitic insects can impact important ungulate species in other biomes [64] as well as arctic mammals other than caribou [38]. Indeed, these types of insects are widespread and impact a wide array of species across the globe including humans, birds, amphibians, and reptiles [65–67].

Temperatures have been rising twice as fast in the Arctic than other parts of the world [68]. These increased temperatures are predicted to lead to a numerical increase in hematophagous and endoparasitic insects [10,11]. Thus, warming associated with climate change may further increase the impacts of these insects in the future [11,47]. Warming may also allow the range expansion of other venomous parasites, like the winter tick (*Dermacentor albipictus*), into new areas that potentially could be highly damaging to native fauna [69,70]. The effects of hematophagous and endoparasitic insects may also interact with other disruptions like anthropogenic disturbances, other parasitic insects and predation pressure [11,13], potentially compounding the complexity and degree of impact. While extensive research has been conducted into the influence of hematophagous and endoparasitic insects on ungulates, there are still important knowledge gaps. One promising line of research is scaling up metrics of insect harassment, such as Witter et al. [71], to large geographic areas using remote sensing data and relating these to ungulate ecology. We encourage researchers to think broadly about venomous and toxungenous animals and their far-ranging consequences.

4. Materials and Methods

We instrumented over 250 female caribou from the Western Arctic Herd with GPS collars that were programmed to continuously collect relocations every 8 hours from 2009 to 2019 [72]. Animal handling protocols were approved by a State of Alaska Institutional Animal Care and Use Committee (IACUC 0040-2017-40, approval date: 10 August 2017). Movement rates (meters/hour) of caribou were determined by dividing the distance between successive GPS locations by the duration between them. To determine daily movement rates for each day of the year, movement rates for that day were averaged and the duration between relocations had to be between 7 and 9 hours as the amount of time between relocations affects the estimation of movement rates [73].

Author Contributions: Conceptualization, K.J., O.C., M.D.C., and E.G.; methodology, K.J.; formal analysis, K.J.; data curation, K.J.; writing—original draft preparation, K.J., O.C. M.D.C., and E.G.; writing—review and editing, K.J., O.C. M.D.C., and E.G.; visualization, K.J. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: We thank Matt Rowe, Bill Hayes, and Joel Berger for suggesting the idea of this manuscript. Caribou data come from a collaborative venture between the Alaska Department of Fish and Game and the National Park Service. We thank Matt Rowe, Bill Hayes, Alex Hansen, Eric Wald, and Jeff Rasic for reviewing previous versions of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Pruitt, W.O. Behavior of the barren-ground caribou. *Biological Papers of the University of Alaska*. **1960**, *3*, 1–44.
2. Casewell, N.R.; Wuester, W.; Vonk, F.J.; Harrison, R.A.; Fry, B.G. Complex cocktails: The evolutionary novelty of venoms. *Trends Ecol. Evolut.* **2013**, *28*, 219–229. doi:10.1016/j.tree.2012.10.020.
3. Nelsen, D.R.; Nisani, Z.; Cooper, A.M.; Fox, G.A.; Gren, E.C.K.; Corbit, A.G.; Hayes, W.K. Poisons, toxungens, and venoms: Redefining and classifying toxic biological secretions and the organisms that employ them. *Biol. Rev.* **2014**, *89*, 450–465. doi:10.1111/brv.12062.
4. Wilcox, C. 2016. *Venomous: How Earth's Deadliest Creatures Mastered Biochemistry*; Scientific American: New York, NY, USA, 2016.
5. Fry, B.G.; Roelants, K.; Champagne, D.E.; Scheib, H.; Tyndall, J.D.A.; King, G.F.; Nevalainen, T.J.; Norman, J.A.; Lewis, R.J.; Norton, R.S.; et al. The toxicogenomic multiverse: Convergent recruitment of proteins into

- animal venoms. *Annu. Rev. Genomics Hum. Genet.* **2009**, *10*, 483–511. doi:10.1146/annurev.genom.9.081307.164356.
6. Ribeiro, J.M.C. Role of saliva in blood-feeding by arthropods. *Ann. Rev. Entomol.* **1987**, *32*, 463–478.
7. Champagne, D.E. Antihemostatic molecules from saliva of blood-feeding arthropods. *Pathophysiol. Haemost. Thromb.* **2005**, *34*, 221–227. doi:10.1159/000092428.
8. Colwell, D.D. Life cycle strategies. In *The Oestrid Flies: Biology, Host-Parasite Relationships, Impact and Management*; Colwell, D.D., Hall, M.J.R., Scholl, P.J., Eds.; CABI Publishing: Oxforshire, UK, 2006; p. 376.
9. Åsbakk, K.; Kumpula, J.; Oksanen, A.; Laaksonen, S. Infestation by *Hypoderma tarandi* in reindeer calves from northern Finland—Prevalence and risk factors. *Vet. Parasitol.* **2014**, *200*, 172–178.
10. Culler, L.E.; Ayres, M.P.; Virginia, R.A. In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster. *Proc. R. Soc. B* **2015**, *282*, 20151549. doi:10.1098/rspb.2015.1549.
11. Witter, L.A.; Johnson, C.J.; Croft, B.; Gunn, A.; Gillingham, M.P. Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. *J. Anim. Ecol.* **2012**, *81*, 284–295. doi:10.1111/j.1365-2656.2011.01905.x.
12. Cameron, M.D.; Joly, K.; Weaver, L. Caribou: Did you know? National Park Service 2017. Fairbanks, AK, USA. Available online: https://www.nps.gov/gaar/learn/nature/upload/DidYouKnow_CaribouFinalMarch2017.pdf (accessed on 7 May 2020).
13. Walsh, N.E.; Fancy, S.G.; McCabe, T.R.; Pank, F. Habitat use by the Porcupine Caribou Herd during predicted insect harassment. *J. Wildl. Manage.* **1992**, *56*, 465–473.
14. Witter, L.A.; Johnson, C.J.; Croft, B.; Gunn, A.; Poirier, L.M. Gauging climate change effects at local scales: Weather-based indices to monitor insect harassment in caribou. *Ecol. Appl.* **2012**, *22*, 1838–1851.
15. Thomas, D.C.; Kiliaan, H.P. Warble infestations in some Canadian caribou and their significance. *Rangifer* **1990**, *3*, 409–417. doi:10.7557/2.10.3.889.
16. Cuyler, C.; White, R.R.; Lewis, K.; Soulliere, C.; Gunn, A.; Russell, D.E.; Daniel, C. Are warbles and bots related to reproductive status in West Greenland? *Rangifer* **2012**, *12*, 243–257.
17. Simard, A.; Kutz, S.; Ducrocq, J.; Beckmen, K.; Brodeur, V.; Croft, B.; Côté, S.D. Variation in the intensity and prevalence of macroparasites in migratory caribou: A quasi-circumpolar study. *Can. J. Zool.* **2016**, *94*, 607–617. doi:10.1139/cjz-2015-0190.
18. Nilssen, A.C.; Anderson, J.R. Flight capacity of the reindeer warble fly, *Hypoderma tarandi* (L.), and the reindeer nose bot fly, *Cephenemyia trompe* (Modeer) (Diptera:Oestridae). *Can. J. Zool.* **1995**, *73*, 1228–1238.
19. Helle, T. Abundance of warble fly (*Oedemagena tarandi*) larvae in semi-domestic reindeer (*Rangifer tarandus*) in Finland. *Report from the Kevo Subarctic Research Station* **1980**, *16*, 1–6.
20. Anderson, J.R.; Nilssen, A.C. Trapping oestrid parasites of reindeer: The response of *Cephenemyia trompe* and *Hypoderma tarandi* to baited traps. *Med. Vet. Entomol.* **1996**, *10*, 337–346.
21. Nilssen, A.C.; Haugerud, R.E. The timing and departure rate of larvae of the warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae) from reindeer. *Rangifer* **1994**, *14*, 113–122. doi:10.7557/2.14.3.1143.
22. Mallory, C.D.; Boyce, M.S. Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environ. Rev.* **2018**, *26*, 13–25. doi:10.1139/er-2017-0032.
23. Joly, K.; Klein, D.R.; Verbyla, D.L.; Rupp, T.S.; Chapin, F.S., III. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography* **2011**, *34*, 345–352. doi:10.1111/j.1600-0587.2010.06377.x.
24. Wolfe, R.J.; Walker, R.J. Subsistence economies in Alaska: Productivity, geography, and development impacts. *Arctic Anthropol.* **1987**, *24*, 56–81.
25. Schwatka, F. *A summer in Alaska*; J. W. Henry: St. Louis, MO, USA, 1894; p. 418.
26. White, R.G.; Thompson, B.R.; Skoogland, T.; Person, S.J.; Holleman, D.F.; Luick, J.R. Ecology of caribou at Prudhoe Bay, Alaska. In *Ecological investigations of the tundra biome in the Prudhoe Bay region, Alaska*; Biological papers of the University of Alaska; Special Report No. 2; University of Alaska: Fairbanks, AK, USA, 1975; pp. 150–201.
27. Russell, D.E.; Martell, A.M.; Nixon, W.A.C. Range ecology of the Porcupine Caribou Herd in Canada. *Rangifer* **1993**, *8*, 1–168.
28. Hagemoen, R.I.M.; Reimers, E. Reindeer summer activity pattern in relation to weather and insect harassment. *J. Anim. Ecol.* **2002**, *71*, 883–892. doi:10.1046/j.1365-2656.2002.00654.x.

29. Colman, J.E.; Pedersen, C.; Hjermann, D.Ø.; Holand, Ø.; Stein, R.; Moe, S.R.; Reimers, E. Do wild reindeer exhibit grazing compensation during insect harassment? *J. Wildl. Manage.* **2003**, *67*, 11–19. doi:10.2307/3803056.
30. Fancy, S.G.; Pank, L.F.; Whitten, K.R.; Regelin, W.L. Seasonal movements of caribou in Arctic Alaska as determined by satellite. *Can. J. Zool.* **1989**, *67*, 644–694. doi:10.1139/z89-093.
31. Person, B.T.; Prichard, A.K.; Carroll, G.M.; Yokel, D.A.; Suydam, R.S.; George, J.C. Distribution and movements of the Teshekpuk Caribou Herd, 1990–2005: Prior to oil and gas development. *Arctic* **2007**, *60*, 238–250.
32. Prichard, A.K.; Yokel, D.A.; Rea, C.L.; Person, B.T.; Parrett, L.S. The effect of telemetry locations on movement-rate calculations in arctic caribou. *Wildl. Soc. Bull.* **2014**, *38*, 78–88. doi:10.1002/wsb.357.
33. Murphy, S.M.; Curatolo, J.A. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. *Can. J. Zool.* **1987**, *65*, 2483–2490.
34. Skoog, R.O. *Ecology of the caribou (Rangifer tarandus granti) in Alaska*; University of California Berkeley: Berkeley, CA, USA, 1968.
35. Skogland, T. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. In *Life History Characteristics of Wild Reindeer (Rangifer tarandus L.) in Relation to their Food Resources; Ecological Effects and Behavioral Adaptations*; Skogland, T., Ed.; Meddelelser fra norsk viltforskning: 3. serie Nr., Berlin, Germany, 1985.
36. Downes, C.M.; Theberge, J.B.; Smith, S.M. The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. *Can. J. Zool.* **1986**, *64*, 622–629. doi:10.1139/z86-092.
37. Wilson, R.R.; Prichard, A.K.; Parrett, L.S.; Person, B.T.; Carroll, G.M.; Smith, M.A.; Rea, C.L.; Yokel, D.A. Summer resource selection and identification of important habitat prior to industrial development for the Teshekpuk caribou herd in Northern Alaska. *PLoS ONE* **2012**, *7*, e48697. doi:10.1371/journal.pone.0048697.
38. Kelsall, J.P. *The Migratory Barren-Ground Caribou of North America*; Queen's Printer: Ottawa, Ontario, Canada, 1968.
39. Fauchald, P.; Rødven, R.; Bårdsen, B.-J.; Langeland, K.; Tveraa, T.; Yoccoz, N.G.; Ims, R.A. Escaping parasitism in the selfish herd: Age, size and density dependent warble fly infestation in reindeer. *Oikos* **2007**, *116*, 491–499.
40. Hughes, J.; Albon, S.D.; Irvine, R.J.; Woodin, S. Is there a cost of parasites to caribou? *Parasitology* **2009**, *136*, 253–265. doi:10.1017/S0031182008005246.
41. Folstad, I.; Nilssen, A.C.; Halvorsen, O.; Andersen, J. Parasite avoidance—The cause of post-calving migrations in Rangifer. *Can. J. Zool.* **1991**, *69*, 2423–2429. doi:10.1139/z91-340.
42. Fancy, S.G.; White, R.G. Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* **1987**, *65*, 122–128. doi:10.1139/z87-018.
43. Helle, T.; Tarvainen, L. Effects of insect harassment on weight gain and survival in reindeer calves. *Rangifer* **1984**, *4*, 24–27.
44. Gurarie, E.; Hebblewhite, M.; Joly, K.; Kelly, A.P.; Adamczewski, J.; Davidson, S.C.; Davison, T.; Gunn, A.; Sutor, M.J.; Fagan, W.F.; et al. 2019. Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations. *Ecosphere* **2019**, *10*, e02971. doi:10.1002/ecs2.2971.
45. Folstad, I.; Nilssen, A.C.; Halvorsen, O.; Andersen, J. Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? *Oikos* **1989**, *55*, 87–92.
46. Dale, B.W.; Adams, L.G.; Collins, W.B.; Joly, K.; Valkenburg, P.; Tobey, R. Stochastic and compensatory effects limit persistence of variation in body mass of young caribou. *J. Mammal.* **2008**, *89*, 1130–1135. doi:10.1644/07-MAMM-A-137.1.
47. Weladji, R.B.; Holand, Ø.; Almøy, T. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. *J. Zool.* **2003**, *260*, 79–85. doi:10.1017/S0952836903003510.
48. Ballesteros, M.; Bårdsen, B.-J.; Langeland, K.; Fauchald, P.; Stien, A.T.; Tveraa, T. The effect of warble flies on reindeer fitness: A parasite removal experiment. *J. Zool.* **2012**, *287*, 34–40. doi:10.1111/j.1469-7998.2011.00883.x.
49. Zhigunov, P. *Reindeer husbandry*, 2nd ed.; Israel Program for Scientific Translations: Jerusalem, Israel, 2008; pp. 343.
50. Anderson, R.M.; May, R.M. Coevolution of hosts and parasites. *Parasitology* **1982**, *85*, 411–426.

51. Cameron, R.D.; Smith, W.T.; Fancy, S.G.; Gerhart, K.L.; White, R.G. Calving success of female caribou in relation to body weight. *Can. J. Zool.* **1993**, *71*, 480–486. doi:10.1139/z93-069.
52. Cameron, R.D.; Ver Hoef, J.M. Predicting parturition rate of caribou from autumn body mass. *J. Wildl. Manage.* **1994**, *58*, 674–679. doi:10.2307/3809681.
53. White, R.G. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* **1983**, *40*, 377–384. doi:10.2307/3544310.
54. Albon, S.D.; Stien, A.; Irvine, R.J.; Langvatn, R.; Ropstad, E.; Halvorsen, O. The role of parasites in the dynamics of a reindeer population. *Proc. R. Soc. Lond. B* **2002**, *269*, 1625–1632.
55. Pachkowski, M.; Cote, S.D.; Festa-Bianchet, M. Spring-loaded reproduction: Effects of body condition and population size on fertility in migratory caribou (*Rangifer tarandus*). *Can. J. Zool.* **2013**, *91*, 473–479. doi:10.1139/cjz-2012-0334.
56. Henry, G.H.R.; Gunn, A. Recovery of tundra vegetation after overgrazing by caribou in arctic Canada. *Arctic* **1991**, *44*, 38–42. doi:10.14430/arctic1516.
57. Joly, K.; Jandt, R.R.; Meyers, C.R.; Cole, M.J. Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005: Potential effects of grazing and climate change. *Rangifer* **2007**, *27*, 199–207. doi:10.7557/2.27.4.345.
58. te Beest, M.; Sitters, J.; Ménard, C.B.; Olofsson, J. Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environ. Res. Lett.* **2016**, *11*, 125013. doi:10.1088/1748-9326/aa5128.
59. McKendrick, J.D.; Batzli, G.O.; Everett, K.R.; Swanson, J.C. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct. Alp. Res.* **1980**, *12*, 565–578. doi:10.1080/00040851.1980.12004213.
60. Joly, K.; Gurarie, E.; Sorum, M.S.; Kaczensky, P.; Cameron, M.D.; Jakes, A.F.; Borg, B.L.; Nandintsetseg, D.; Hopcraft, J.G.C.; Buuveibaatar, B.; Jones, P.F.; Mueller, T.; Walzer, C.; Olson, K.A.; Payne, J.C.; Yadamsuren, A.; Hebblewhite, M. Longest terrestrial migrations and movements around the world. *Sci. Rep.* **2019**, *9*, 15333. doi:10.1038/s41598-019-51884-5.
61. Adams, L.G.; Singer, F.J.; Dale, B.W. Caribou calf mortality in Denali National Park, Alaska. *J. Wildl. Manage.* **1995**, *59*, 584–594. doi:10.2307/3802467.
62. Magoun, A.J.; Laird, C.R.; Keech, M.A.; Valkenburg, P.; Parrett, L.S.; Robards, M.D. Predation on caribou (*Rangifer tarandus*) by wolverines (*Gulo gulo*) after long pursuits. *Can. Field-Nat.* **2018**, *132*, 382–385. doi:10.22621/cfn.v132i4.2050.
63. Fang, J. A world without mosquitoes. *Nature* **2010**, *466*, 432–434. doi:10.1038/466432a.
64. Brazda, A.R. Elk migration patterns, and some of the factors affecting movements in the Gallatin River drainage, Montana. *J. Wildl. Manage.* **1953**, *17*, 9–23.
65. Tempelis, C.H. Host-feeding patterns of mosquitoes, with a review of advances in analysis of blood meals by serology. *J. Med. Entomol.* **1975**, *11*, 635–653. doi:10.1093/jmedent/11.6.635.
66. Kulasekera, V.L.; Kramer, L.; Nasci, R.S.; Mostashari, F.; Cherry, B.; Trock, S.C.; Glaser, C.; Miller, J.R. West Nile virus infection in mosquitoes, birds, horses, and humans, Staten Island, New York, 2000. *Emerg. Infect. Dis.* **2001**, *7*, 722–725. doi:10.3201/eid0704.010421.
67. Rätti, O.; Ojanen, U.; Helle, P. Increasing group size dilutes black fly attack rate in Black Grouse. *Ornis Fennica* **2006**, *83*, 86–90.
68. Cohen, J.; Screen, J.A.; Furtado, J.C.; Barlow, M.; Whittleston, D.; Coumou, D.; Francis, J.; Dethloff, K.; Entekhabi, D.; Overland, J.; Jones, J. Recent Arctic amplification and extreme mid-latitude weather. *Nature Geosci* **2014**, *7*, 627–637. doi:10.1038/ngeo2234.
69. Samuel, W.M. Grooming by moose (*Alces alces*) infested with the winter tick, *Dermacentor albipictus* (Acari): A mechanism for premature loss of winter hair. *Can. J. Zool.* **1991**, *69*, 1255–1260. doi:10.1139/z91-176.
70. Cabezas-Cruz, A.; Valdes, J.J. 2014. Are ticks venomous animals? *Front. Zool.* **2014**, *11*. doi:10.1186/1742-9994-11-47.
71. Witter, L.; Johnson, C.; Croft, B. *Weather-Based Indices of Parasitic Fly Activity and Abundance for the Bathurst Caribou Post-Calving and Summer Range: Users Guide. Manuscript Report 246.* University of North British Columbia, Prince George, British Columbia: Prince George, BC, Canada, 2014; p. 37.

72. Joly, K.; Cameron, M.D. *Caribou Vital Sign Annual Report for the Arctic Network Inventory and Monitoring Program: September 2018–August 2019*; Natural Resource Report NPS/ARC/NRR–2019/2041; National Park Service: Fort Collins, CO, USA, 2019; p. 29.
73. Joly, K. The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. *Rangifer* **2005**, *25*, 67–74. doi:10.7557/2.25.2.254.



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).