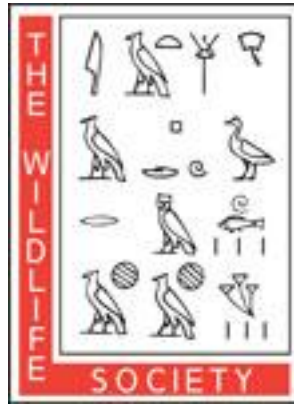


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Author(s): MARCO RAPONI, DAVID V. BERESFORD, JAMES A. SCHAEFER, IAN D. THOMPSON, PHILIP A. WIEBE, ARTHUR R. RODGERS and JOHN M. FRYXELL

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Research Article

Biting Flies and Activity of Caribou in the Boreal Forest

MARCO RAPONI, *Environmental and Life Sciences Graduate Program, Trent University, 1600 West Bank Drive, Peterborough, ON K9L 0G2, Canada*

DAVID V. BERESFORD,¹ *Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON K9L 0G2, Canada*

JAMES A. SCHAEFER, *Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON K9L 0G2, Canada*

IAN D. THOMPSON, *Canadian Forest Service, 1219 Queen St. East, Sault Ste. Marie, ON P6A 2E5, Canada*

PHILIP A. WIEBE, *Canadian Forest Service, 1219 Queen St. East, Sault Ste. Marie, ON P6A 2E5, Canada*

ARTHUR R. RODGERS, *Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, 103–421 James Street South, Thunder Bay, ON P7E 2V6, Canada*

JOHN M. FRYXELL, *Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, ON N1G 2W1, Canada*

ABSTRACT Habitat loss has been implicated in the decline of forest-dwelling caribou (*Rangifer tarandus caribou*), but it is unknown how biting insects, potentially important components of boreal forest habitat for caribou, influence the activity of this threatened species. During summers in 2011 and 2012 in northern Ontario, Canada, we quantified the relative abundance of black flies, mosquitoes, and tabanids in boreal forest stands of different ages and related their abundance to caribou activity. We counted insects in young (25–35 yrs since forest harvesting), intermediate (36–69 yrs), and old (≥ 70 yrs) stands using sweep nets and counts on human subjects. We related the daily variation in abundance of these insect families, along with daily maximum temperature, to the activity of female caribou, determined by accelerometers in global positioning system collars. We found higher insect abundance in young versus old stands. During the first 5 minutes in a forest stand, the rate of accumulation of mosquitoes and black flies on human subjects increased, but at a decelerating rate, whereas tabanid abundance declined over time. On days when tabanids were more numerous, female caribou were less active, possibly a response to reduce exposure and harassment. To a lesser extent, mosquitoes and black flies also tended to elicit lower activity of caribou. Our study reveals that biting flies can alter the behavior of female caribou in the boreal forest. Loss of old stands may accentuate the potential for insect harassment. © 2018 The Wildlife Society.

KEY WORDS boreal forest, Culicidae, habitat, insect harassment, logging, *Rangifer tarandus caribou*, Simuliidae, Tabanidae.

Habitat loss is the principal factor influencing the loss and endangerment of wildlife (Wilcove et al. 1998, Venter et al. 2006). Habitat includes the resources and conditions that govern the presence, survival, and reproduction of a population (Caughley and Gunn 1996). For wild ungulates, biting flies can be important elements of habitat. Insect harassment can have substantial effects on the behavior, habitat use, and demography of ungulates (Helle and Tarvainen 1984, Coleman et al. 2003, Vistnes et al. 2008). The stress from intense, prolonged exposure can reduce the time spent feeding and, consequently, the size and viability of offspring (e.g., wood bison [*Bison bison athabasca*], Morgan 1987; wild horse [*Equus caballus*], Duncan and Cowtan 1980; elk [*Cervus canadensis*], Collins and Urness 1982). Even

non-biting flies (head flies; family Muscidae) may evoke a behavioral response, as observed in red deer (*Cervus elaphus*; Epsmark and Langvatn 1979).

Such effects are established for barren-ground caribou (*Rangifer tarandus*). Insect harassment disrupts time and energy budgets, grouping behavior, and habitat selection (Russell et al. 1993, Pollard et al. 1996, Toupin et al. 1996, Witter et al. 2012a). To date, however, no studies have documented how biting flies affect the behavior of forest-dwelling caribou (*R. t. caribou*) of the continental taiga (Graham 1992). This species has declined across Canada in the past several decades (Festa-Bianchet et al. 2011). In the boreal forest, the decline of woodland caribou has often been traced to industrial disturbances—in particular, the shift to younger seral stages that can invite higher densities of other deer species, such as moose (*Alces alces*), which in turn support increased abundance of wolves (*Canis lupus*; Bergerud and Elliot 1986, Bergerud et al. 2008, Festa-Bianchet et al. 2011). The conversion of forests to earlier successional

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¹E-mail: davidberesford@trentu.ca

stages, however, might also lead to greater abundance and activity of ecto-parasites, such as black flies (Simuliidae), mosquitoes (Culicidae), and tabanids (Tabanidae; Deans et al. 2005, Lysyk 2011). Heightened insect harassment could represent an important component of habitat loss for this threatened species.

In response to biting fly harassment, barren-ground caribou typically spend more time spent walking, standing, trotting, and running at the expense of feeding and resting (Downes et al. 1986, Toupin et al. 1996, Morschel and Klein 1997, Witter et al. 2012a). These caribou also use shorelines, exposed ridges, and snow patches to escape insects (Ion and Kershaw 1989, Walsh et al. 1992, Anderson and Nilssen 1998, Hagemoen and Reimers 2002, Skarin et al. 2004). The consequences of this harassment can be demographic; fly avoidance may reduce opportunities for feeding and fattening during the summer (Downes et al. 1986, Toupin et al. 1996), which can translate into diminished fecundity (Helle and Tarvainen 1984, Coleman et al. 2003).

We anticipate, however, that the responses of barren-ground and forest-dwelling caribou may differ. Biting flies cue rapidly to host odors (Schofield and Brady 1997) and host movements (Phelps and Vale 1976, Allan et al. 1987, Mitzell et al. 2002), and flies often accumulate in large swarms (Twinn 1950, Lysyk 2011). Compared to their barren-ground counterparts, woodland caribou are less perceptible on the landscape, in part because they are typically dispersed during spring and summer. By limiting their movement, woodland caribou may limit their visibility and the size of their odor trail, reducing the size of these swarms. The dispersion of sedentary caribou during summer, the defining feature of the ecotype, also implies less scope for dilution, a tactic exhibited by the gregarious migratory ecotype during the fly season (Bergerud et al. 2008).

We tested these ideas by examining the relative abundance of biting insects and the activity of woodland caribou in the boreal forest of Ontario, Canada. Our objectives were to quantify the relative abundance of biting insects in harvested and unmanaged forest stands, determine the short-term accumulation of biting flies to potential hosts in these stands, and test whether caribou activity was related to variations in insect abundance. We hypothesized that woodland caribou would attempt to reduce encounters with biting flies by exhibiting less activity when fly activity was high.

STUDY AREA

Our study took place in north-central Ontario near the township of Nakina (50° 15'N, 87° 54'W). This study area was defined by a 18,200-km² section of boreal forest in the Lake Nipigon drainage basin, and represented a mosaic of heavily harvested and natural areas typical of the southern extent of woodland caribou range in Ontario. This area has thin sandy soil and glacial till covering precambrian bedrock, with a gently rolling topography ranging from 320 m to 390 m above sea level.

In the study area, mammal species important to caribou included moose, black bears (*Ursus americanus*), and wolves (McGreer et al. 2015). Oestrid flies (*Hypoderma tarandi*,

Cephenemyia trompe), common parasites of caribou in the arctic and subarctic, were absent (Bennett and Sabrosky 1962, Wood 1987). Forests were dominated by stands of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), scattered paper birch (*Betula papyrifera*), and aspen (*Populus* spp.), with numerous lowland bogs and fens and an extensive network of small lakes and rivers. Mean daily temperatures ranged from −18.6° C in winter to 17.2° C in summer, with 76.5 cm of mean annual precipitation (30-yr climate normals; Environment and Climate Change Canada 2017).

Access through the region was provided by a highway linking the communities of Nakina and Geraldton. The pulp and paper industry has been harvesting in this area since the 1940s, which produced a network of unpaved roads enabling access. We trapped insects to compare the relative abundance of biting flies in caribou habitats accessible by road. Sampling sites were distributed throughout the study area, 0.5–1 km from this road network, and chosen to represent a variety of the logged and unlogged habitats. We classified stands as young (harvested 20–35 yrs ago), intermediate (36–69 yrs), or old (≥70 yrs); the latter were unharvested stands.

METHODS

Temperature affects the activity of insects (Andrewartha and Birch 1954, Witter et al. 2012b) and potentially caribou, too (Hagemoen and Reimers 2002). After accounting for temperature, we focused on daily variations in insect abundance and tested its relationship to daily variation in activity of female caribou, monitored with GPS collars.

Relative Abundance of Insects

Our goal was to produce an index reflective of the daily abundance of biting flies in proximity to radio-collared caribou that was applicable across forest stand types in the study area. We sampled stand types identified from the Ontario Land Classification (OLC) and the Forest Resource Inventory (FRI). We stratified the sample sites by stand type using both classifications (Raponi 2014). We followed different routes each day that took us across the entire study area. Overall, we sampled 70 sites.

We collected insects, 31 May–18 August 2011 and 31 May–25 August 2012. At each site, we identified an area largely clear of obstructions, which would allow sweep netting. We visited sampling sites every 8–10 days. We sampled sites in proximity to each other (about 1 km apart), deliberately chosen to represent different types (OLC) and stand ages (FRI) on the same day. To capture the diurnal variation in fly activity, we sampled sites at a different time of the day at each revisit (0700–2000) and rotated systematically through the sites such that each year we sampled sites approximately equally at each time of day.

Two technicians sampled at each site; both wore dark clothing to maintain consistent visual stimuli. To reduce the chance of flies following field workers from 1 stand to another, we located the sites >1 km apart and travelled by vehicle. We assumed positive correlations between our measures of insect abundance and the harassment of caribou (Toupin et al. 1996, Hagemoen and Reimers 2002).

Landing counts.—To quantify the short-term accumulation of biting insects on a newly arrived host, we counted the number of lighted flies from each family (Tabanidae, Culicidae, Simuliidae) on each observer at 1, 2, 3, and 5 minutes after arrival at the central point of the sampling site. One person counted the number on the right arm, while the other person counted the number on the left leg. We combined counts from both technicians for each sample. We wanted to know how biting flies accumulate on a newly arrived host, when insects were numerous. To do this, we included counts with >4 landed flies per biting fly family (Tabanidae, Culicidae, Simuliidae) during the entire 5 minutes.

Sweep netting.—Immediately after the landing counts, the 2 technicians collected biting flies continuously for 5 minutes with aerial sweep nets 30 cm in diameter with a 1-m handle. Both technicians conducted sweep netting simultaneously in a figure-8 pattern while they walked around a marker in the center of the stand. After 5 minutes, technicians twisted the bag of each net to trap all specimens inside. We placed the section of net with trapped flies into a large jar containing a blotting paper charged with ethyl acetate ethanol for 3–5 minutes to kill or subdue the insects. We emptied the contents into labeled paper envelopes, then stored the specimens in bottles filled with 80% denatured ethanol. We combined the counts from each of the 2 individual sweeps at each site for the sample. Samples included only female flies.

Effect of stand age.—We tested for differences in relative fly abundance, separately for Tabanidae, Culicidae, and Simuliidae, across stand ages using a 1-way analysis of variance (ANOVA), followed by a Duncan's multiple range test with stand age (young, intermediate, old) as the independent variable and fly abundance, averaged across the whole season at each sample site (from sweep nets), as the response variable. We square-root transformed the sweep catch data to satisfy the assumption of homoscedastic standard deviations for ANOVA (Sokal and Rohlf 1997). We pooled the data across the whole season.

Daily insect abundance.—We normalized the sweep catch data from each sample session (daily) in each stand using a log-transformation ($\ln[n+1]$), then standardized them using the site mean and standard deviation. We used these data to obtain the daily mean across all sites to express the relative abundances of Tabanidae, Culicidae, and Simuliidae in the study area.

Caribou Activity

We used accelerometers housed in Lotek Argos and Lotek Iridium global positioning system (GPS) collars (Lotek, Newmarket, Ontario, Canada) deployed on female woodland caribou that frequented the study area (McGreer et al. 2015, Thompson et al. 2015). The Ontario Ministry of Natural Resources and Forestry provided accelerometer data, a subset of those used by Mosser et al. (2014). Accelerometers provided scores of movements on horizontal and vertical axes as the animal moved its head; these scores served as an index of animal activity (Mosser et al. 2014). This index included all vertical and horizontal movement of the head

sufficient to be registered by the collar. The index does not distinguish between eating and walking but would include other typical responses to insect harassment such as headshakes and nods.

Accelerometer recordings were made almost continuously, but we deemed only those readings associated with a valid GPS fix as suitable for analysis (Mosser et al. 2014). Because several accelerometer readings may be associated with each GPS fix, we calculated an average of all horizontal and all vertical accelerometer readings for every fix where ≥ 1 horizontal and ≥ 1 vertical measurements were available. In our analysis, we included the accelerometer data only where the date and time (i.e., 0700–1800) coincided with the insect sampling and only for caribou with a complete data set for June, July, and August in ≥ 1 year. In all, our analysis included 20 individual caribou in 2011 (31 May–18 Aug) and 10 individuals in 2012 (31 May–25 Aug). Six of these animals provided data in both years.

To express daily caribou activity, we summed the average horizontal accelerometer reading and the average vertical accelerometer reading for each observation. We computed the daily average of readings for each caribou with ≥ 2 readings/day, and then standardized these data by animal and year.

Insect Abundance and Caribou Activity

We tested the relationship between caribou activity and abundance of each family of fly using a multiple regression model for each individual caribou. The model applied daily maximum temperature from the nearby community of Geraldton (Environment and Climate Change Canada), black fly, mosquito, and tabanid indices as independent variables, and the mean daily activity of individual caribou as the response variable. Second, we tested our hypothesis. We retained the individual caribou as the experimental unit. For each family of fly and each year, we assembled the partial correlation coefficients for fly abundance from the multiple regressions. Using 1-sample *t*-tests, we tested these coefficients against an expected mean (under H_0) of 0. Given the uncertainty about the effects of biting flies on woodland caribou behavior, we applied 2-tailed tests.

RESULTS

Landing records at 1, 2, 3, and 5 minutes yielded differing rates of accumulation of black flies, mosquitoes, and tabanids (Fig. 1). For all families, the accumulation of flies was most rapid during the first 2–3 minutes after entering the stand. After 3 minutes, we observed a lower rate of accumulation for black flies and no apparent increase for mosquitoes, whereas tabanid numbers were significantly lower at 5 minutes than at 2 minutes (Wilcoxon sign-rank test, $n = 19$, $Z = 1.76$, $P = 0.039$ [1-tailed]; Fig. 1).

Black flies were the most plentiful of the biting flies in our sweep nets. They were roughly twice as numerous in young (25–35-yr-old) stands compared to intermediate (35–69-yr-old) and old (≥ 70 -yr-old) stands ($F_{2, 67} = 3.50$, $P = 0.036$; Table 1). Mosquito numbers did not differ across stand ages

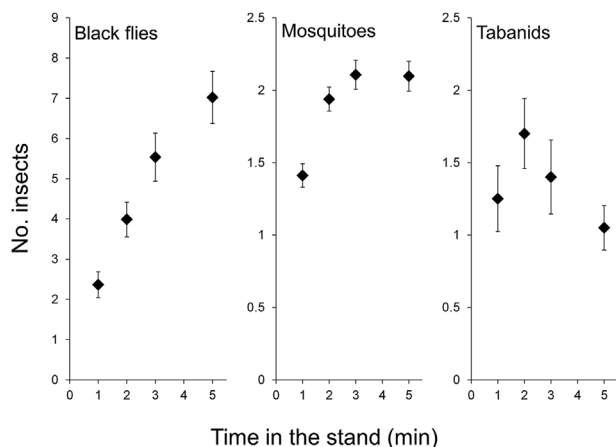


Figure 1. Mean relative abundance ($\pm$ SE) of 3 biting fly families, expressed as the number landed on the limbs of 2 observers after entering a forest stand, in the Nakina study area, Ontario, Canada, 2011 and 2012.

($F_{2, 67} = 1.24$, $P = 0.30$; Table 1). Tabanids, the least frequent of the flies, were approximately 45% more numerous in young and intermediate stands than in old stands ($F_{2, 67} = 4.28$, $P = 0.018$; Table 1).

Mosquito and black fly abundances peaked near the end of June, about 2 weeks earlier than peak tabanid abundance, which occurred near the second week of July. Mosquito abundance was the most constant over the season, whereas the tabanids had the most pronounced peaks, indicating a more restricted seasonal window relative to black flies or mosquitoes. There were weak correlations in abundance among families. On days when mosquitoes were most numerous, black flies and tabanids tended to be least numerous ($-0.413 \leq r \leq -0.117$; Table 2). These correlations were largely consistent across years.

Accelerometers indicated generally greater activity of female caribou at the beginning and end of the summer, with a mid-summer ebb. The high activity in early June was comparable to that in late August. Daily caribou activity was related to daily fly abundance, irrespective of temperature (Figs. S1 and S2, available online in Supporting Information). The set of partial correlation coefficients revealed that black flies and mosquitoes were associated with a decrease in caribou activity in 2011 but not in 2012 (Table 3). Tabanids had a stronger, more consistent effect. When these flies were most numerous, caribou were least active in both years (Table 3). Expressed as negative partial correlation

Table 2. Correlation coefficients in the daily relative abundance among biting fly families in the Nakina study area, Ontario, Canada, 2011 and 2012. Entries above the diagonal are from 2011; those below the diagonal are from 2012.

	Black flies	Mosquitoes	Tabanids
Black flies		−0.239	0.260
Mosquitoes	−0.117		−0.413
Tabanids	0.084	−0.299	

coefficients, 17 of 20 caribou (in 2011) and 9 of 10 caribou (in 2012) tended to be least active on days when tabanids were most numerous (Fig. 2). Caribou also tended to be least active when daily maximum temperatures were highest (Table 3).

DISCUSSION

Biting insects are an important element of the habitat of many wild ungulates (Collins and Urness 1982, Morgan 1987, Powell et al. 2006). For domestic cattle, individual and group behaviors can be altered when insect harassment is severe (Perich et al. 1986, Mooring and Hart 1992, Ralley et al. 1993, Mullens et al. 2006). For caribou, most studies of insect harassment have focused on tundra-dwelling populations (Downes et al. 1986, Toupin et al. 1996, Morschel and Klein 1997, Witter et al. 2012a), the caribou that aggregate in large, visible groups in summer. In contrast, woodland caribou during spring and summer occur singly or in small groups, scattered at low density across coniferous forests and peatlands (Darby and Duquette 1986, Cumming and Beange 1987, Ferguson and Elkie 2004). The features that define woodland caribou make them challenging to study by direct observation (Racey and Armstrong 2000). Not surprisingly, they have been the subject of little behavioral research, particularly during summer (Bergerud 1974; Thompson et al. 2012, 2015).

Our work revealed that female forest-dwelling caribou altered their activity when exposed to biting flies, but they showed different levels of response to mosquitoes and tabanids (Table 3). Moreover, because habitat loss is associated with decline of woodland caribou in the continental taiga (Festa-Bianchet et al. 2011), our study implies that the disturbance of the boreal forest (i.e., the conversion of old stands to earlier stages) could accentuate insect harassment for caribou (Table 1). Female caribou in our study area avoided young forest stands (Avgar et al. 2015,

Table 1. Average relative abundance of 3 biting fly families, determined from sweep netting in boreal forest stands of different ages, Nakina study area, Ontario, Canada, 2011 and 2012. The number of sites of each age class is represented by n . Means and 95% confidence intervals were back-transformed (from square root used in analysis of variance).

	Black flies			Mosquitoes			Tabanids			
Age (yrs)	$\bar{x}$	95% CI		$\bar{x}$	95% CI		$\bar{x}$	95% CI		n
Young (20–35)	351.5A ^a	233.8	493.1	14.0A	8.6	20.7	11.1A	7.4	15.5	17
Intermediate (36–69)	190.3B	102.3	305.5	14.7A	8.8	22.0	9.6AB	6.0	14.0	15
Old (≥ 70)	178.9B	122.4	246.1	10.0A	6.7	13.7	5.6B	3.8	7.6	38

^a Means within the same family with the same letter are not significantly different ($P > 0.05$).

Table 3. Mean partial correlation coefficients from multiple regressions of maximum daily temperature and the abundance of black flies, mosquitoes and tabanids versus the daily activity of female woodland caribou in 2011 (20 animals) and 2012 (10 animals) in the Nakina study area, Ontario, Canada. We used 1-sample *t*-tests to test the null expectation of 0.

	2011				2012			
	$\bar{x}$	Variance	<i>t</i> (19)	<i>P</i>	$\bar{x}$	Variance	<i>t</i> (9)	<i>P</i>
Temperature	−0.256	0.021	−7.93	<0.001	−0.158	0.021	−3.45	0.007
Black flies	−0.103	0.011	−4.48	<0.001	−0.014	0.025	−0.27	0.791
Mosquitoes	−0.068	0.016	−2.41	0.026	−0.034	0.009	−1.15	0.279
Tabanids	−0.149	0.022	−4.47	0.000	−0.166	0.032	−2.92	0.017

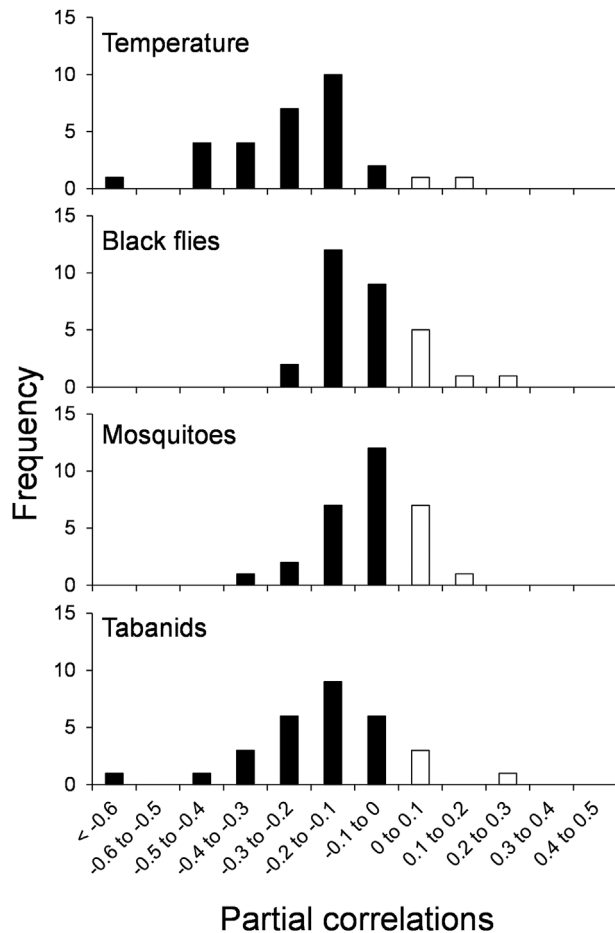


Figure 2. Frequency distribution of partial correlation coefficients, from the multiple regression model of the activity of 30 caribou, of maximum daily temperature, and the abundance of black flies, mosquitoes, and tabanids, in the Nakina study area, Ontario, Canada, 2011 and 2012 (combined). Black bars represent caribou that were less active when fly abundance was higher; white bars represent caribou that were more active. The lower value of each bin range is included in each bin.

McGreer et al. 2015, Thompson et al. 2015), a behavior widely documented for woodland caribou (Schaefer and Pruitt 1991).

Habitat cover appears to be key in governing the response of ungulates to biting flies. Under harassment, caribou on the barrens spend less time lying and more time standing and running (Downes et al. 1986, Toupin et al. 1996, Morschel and Klein 1997, Witter et al. 2012a). In forest cover, in

contrast, ungulate hosts might decrease their attractiveness by decreasing their activity. Indeed, when we sampled for biting insects in a restricted space, the accumulation of landed flies promptly slowed (≤ 5 min) after arrival in a forest stand; the number of tabanids even declined (Fig. 1). We conjecture that, on entering a stand, caribou experience an initial and rapid accumulation of biting flies in search of a blood meal (Allan et al. 1987), but by remaining in 1 spot, they may reduce visual cues and reduce the number of subsequent bites, especially by host-seeking tabanids (Fig. 1).

These observations and inferences align with our understanding of insect behavior. Black flies, mosquitoes, and tabanids rely on odors and visual stimuli to detect and pursue hosts (Gibson and Torr 1999). Unlike with mosquitoes and black flies, however, tabanids rely primarily on visual stimuli for long-range detection (McElligott and McIver 1987, Pellitteri 2004), and can detect hosts up to 80 m away using a combination of visual and olfactory cues, and up to 15 m away even in the absence of host odors (Phelps and Vale 1976). Black flies use visual cues ≤ 2 m away (Sutcliffe 1986); mosquitoes use visual cues 5–15 m away, once stimulated by host odors (van Breugel et al. 2015). We anticipated, therefore, that female caribou during peak fly abundance should limit their activity to limit insect harassment. Indeed, on days when tabanids were more abundant, caribou were less active (Table 3, Fig. 2). Movement can lead to exposure to unfed flies (Gibson and Torr 1999). In experimental trials, moving oxen attracted 37% more tabanids than stationary oxen (Phelps and Vale 1976).

Our inferences, nevertheless, are correlative. Indeed, the activity of parasitic flies tends to be correlated among insect families (Table 2; Witter et al. 2012a) and with temperature (Witter et al. 2012b). The diminished activity of caribou in our study could be an artefact of warmer weather. Although we cannot entirely discount this alternative explanation, our conclusion that woodland caribou respond directly to insect harassment is in keeping with the studies of barren-ground caribou (Witter et al. 2012a) and Norwegian reindeer (Anderson and Nilssen 1998) and is consistent with the high heat tolerance of caribou (Yousef and Luick 1975, Hagemoen and Reimers 2002). On the tundra, tabanids can induce caribou to seek refugia (Helle and Tarvainen 1984, Downes et al. 1986, Anderson and Nilssen 1998). In North America, studies have focused on the effects of mosquitoes, black flies, and oestrid flies on tundra-dwelling caribou. Our study is the first to report a link between biting flies and caribou behavior in the boreal forest.

Black flies and mosquitoes elicited more muted responses. Black flies often swarm in vast quantities. In our study, the number of black flies landing continued to rise during the first 5 minutes in a novel habitat (Fig. 1), which suggests that harassment from black flies may be constant and relentless. In response to mosquitoes, caribou showed a weak and inconsistent decrease in activity (Table 3). We surmise that this difference in response may stem from the difference in the relative importance of visual and olfactory stimuli in host-seeking behaviors among the fly families. Witter et al. (2012b), too, reported more numerous mosquitoes elicited a slight increase in walking by barren-ground caribou, presumably with an associated energetic cost.

MANAGEMENT IMPLICATIONS

For forest-dwelling caribou, our study implies that insect harassment may represent an additional element of habitat loss when the boreal forest is converted to early seral stages. To date, old stands have been regarded as refugia from predation. These stands may also serve as refugia from insect harassment. The loss of these stands may lead to altered summer activity of female caribou in response to biting insects. Our study underscores the importance of old boreal forest for woodland caribou.

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