Impacts of mosquitoes and black flies on defensive behaviour and microhabitat use of the North American porcupine (*Erethizon dorsatum*) in southern Quebec

Annie Comtois and Dominique Berteaux

Abstract: Biting flies are known to influence the behaviour and microhabitat use of certain mammals. However, most studies were realized in open habitats. Our objective was to determine if mosquitoes (Culicidae) and black flies (Simuliidae) affect the behaviour and habitat use of a mammal typical of the boreal forest, the North American porcupine (*Erethizon dorsatum* (L., 1758)). The project was divided into three parts: (1) abundance of biting flies and their (2) direct effects (bites) and (3) indirect effects (repelling movements and microhabitat use) on porcupines. The abundance of insects was measured with CO_2-baited traps. Ten male porcupines were followed by telemetry. Mosquitoes were more abundant on the ground than in the tree canopy and the opposite was observed for black flies. The biting flies were less abundant inside dens than outside. The quantity of bites on porcupines was correlated with the abundance of black flies. We observed frequent repelling movements that were associated with the presence of insects. Some microhabitats offered excellent protection against biting insects, but porcupines did not use these refuges to a greater extent at the peak of insect abundance. We conclude that, although biting flies had measurable impacts on the wounding rate and behaviour of porcupines, this did not translate into important shifts in habitat use.

Résumé : Les insectes piqueurs influencent le comportement et le choix de micro-habitats de certains mammifères. Toutefois, la plupart des études ont été réalisées en milieu ouvert. Notre recherche vise à déterminer si les moustiques (Culicidae) et les mouches noires (Simuliidae) affectent le comportement et l'utilisation de l'habitat chez le porc-épic d'Amérique (*Erethizon dorsatum* (L., 1758)), un mammifère typique de la forêt boréale. Le projet comporte trois types de mesures : (1) l'abondance des insectes piqueurs et (2) les effets directs (piqûres) et (3) les effets indirects (inconfort et utilisation de micro-habitats) des insectes sur les porcs-épics. Les mesures d'abondance d'insectes ont été obtenues par des pièges à CO_2. Dix porcs-épics mâles ont été suivis par télémétrie. Les moustiques sont plus nombreux au niveau du sol que dans le feuillage des arbres et l'inverse s'observe chez les mouches noires. Les insectes piqueurs sont moins abondants dans les tanières qu'à l'extérieur. Les nombres de piqûres sur les porcs-épics sont corrélés avec l'abondance de mouches noires. Les comportements d'inconfort sont fréquents et associés à la présence d'insectes. Certains micro-habitats offrent une excellente protection contre les insectes, mais les porcs-épics n'utilisent pas plus fréquemment ces refuges potentiels lors du pic d'abondance des insectes. Nous concluons que les insectes piqueurs ont des effets mesurables (comportements d'inconfort et blessures) sur les porcs-épics, mais que ces effets ne semblent pas assez importants pour affecter de façon significative l'utilisation de l'habitat par leur hôte.

Introduction

Hematophagous insects, such as mosquitoes (Culicidae) and black flies (Simuliidae), can be extremely costly to their hosts because of the loss of blood and risk of transmission of pathogens (e.g., blood parasites, western and eastern equine encephalitis, St. Louis encephalitis, West Nile virus) associated with bites (Wood et al. 1979; Helson et al. 1980; Allan et al. 1982; Laird 1982; Mason and Shemanchuk 1990; Apperson et al. 2002). Investment of energy in defensive behaviours can thus represent to hosts an advantageous avenue to reduce the negative impacts of biting insects. Hart (1992, 1994) reviewed the defences used by hosts to repel biting flies. Defensive behaviours comprise grouping and selfish herding, which are limited to social animals, and fly-repelling behaviours and differential use of available microhabitats that can be performed by all potential hosts.

A variety of animals have been observed using repelling movements to keep biting flies away. Many studies have been done on the families Cervidae (Goldfuss, 1820) and

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A. Comtois and D. Berteaux.[1] Chaire de recherche du Canada en conservation des écosystèmes nordiques et Centre d'études nordiques, Département de biologie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

[1]Corresponding author (e-mail: dominique_berteaux@uqar.qc.ca).

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Bovidae (Gray, 1821), but horses (*Equus caballus* L., 1758), eastern chipmunks (*Tamia striatus* (L., 1758)), eastern gray squirrels (*Sciurus carolinensis* Gmelin, 1788), and asian elephants (*Elephas maximus* L., 1758) are other examples of hosts using discomfort behaviour in reaction to insect harassment (Duncan and Cowtan 1980; Walker and Edman 1986; Rubenstein and Hohmann 1989; Cully et al. 1991; Helle et al. 1992; Ralley et al. 1993; Toupin et al. 1996; Noel et al. 1998). The behaviours most commonly observed comprise head and body shaking, tail and ear flicking, and foot stamping. The level of defensiveness increases with the density of insects (Edman et al. 1972; Rubenstein and Hohmann 1989; Ralley et al. 1993; Noel et al. 1998; Mooring et al. 2003).

Microhabitat selection is also a largely widespread behaviour used by potential hosts to gain a refuge from biting flies. For example, large mammals use windy or high-altitude habitats, man-made constructions, water, or bare ground to escape the harassment from biting insects (Downes et al. 1986; Rubenstein and Hohmann 1989; Walsh et al. 1992; Pollard et al. 1996*a*, 1996*b*; Toupin et al. 1996; Noel et al. 1998; Mooring et al. 2003).

Most studies on the interactions between wild animals and biting flies have been performed in open habitats where animals are easy to observe. However, biting insects are widely distributed in forested areas and also represent a potentially important disturbance to animals living in closed habitats. Martin et al. (1994) showed that the average number of black fly attacks was greater in forested habitats than in open areas and indicated that hosts in forested sites should support more attacks. Behavioural studies in forested habitats are rare because hosts are more difficult to observe and microhabitats available to them are much more varied.

As a first step to quantify the costs incurred by forest mammals to hematophagous insects, we used the North American porcupine (*Erethizon dorsatum* (L., 1758)), a typical inhabitant of the North American forests, as our study model. We reasoned that using porcupines as a study model would present several advantages: (*i*) they are not very mobile and, once found through telemetry, their behaviour is easy to observe; (*ii*) they are partly arboricolous and thus use the full range of microhabitats available in the forest (i.e., both vertical and horizontal dimensions of the habitat); (*iii*) there are already indications in the literature that porcupines can be attacked by black flies and mosquitoes (Marshall et al. 1962; Roze 1989).

The objectives of our study were thus to determine if biting insects have a measurable impact on the behaviour and habitat use of porcupines.

Materials and methods

General approach

We compared behaviour of porcupines at different periods of the summer season, which differed markedly in insect abundance. We performed a preliminary field season (23 May – 26 July 2002) to explore variations in insect abundance across time and microhabitats, and to generate specific hypotheses that we tested in 2003 (6 May – 18 August).

Two confounding factors potentially limiting the efficiency of this design were the mid-May appearance of leaves, which could change the use of the tree canopy by porcupines, and the late May/early June birth season, which could change the behaviour of reproducing females. We circumvented these two difficulties by starting behavioural observations after trees were in leaf, and by studying only males. In May–August the spatial behaviour of males is stable and unaffected by reproductive activities, which occur during the October–November mating period (Roze 1989; Sweitzer 2003).

Study area

We worked in a ca. 2-km^2 area of Parc National du Bic (48°20′N, 68°46′W, elevation 0–150 m), Quebec, Canada. The study area is characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest dominated (in order of importance) by quaking aspen (*Populus tremuloides* Michx.), eastern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) P. Mill.). The area is fragmented by abandoned and cultivated fields (Morin and Berteaux 2003). Cold winters and mild summers characterize the climate. Precipitation is relatively abundant and is distributed uniformly throughout the year (mean total annual precipitation = 1005.3 mm) (Berteaux et al. 2005).

Insect abundance

We performed several measures of insect abundance to (*i*) describe seasonal variations in abundance of biting insects and identify study periods contrasted in terms of biting-insect abundance, (*ii*) identify taxonomic groups (genera) of biting insects present in the study area, and (*iii*) quantify differences in abundance of biting flies between microhabitats.

Biting flies considered in this study are mosquitoes (Diptera: Culicidae) and black flies (Diptera: Simuliidae). To evaluate the abundance of these two species, we used two models of CO_2-baited traps. CO_2-baited traps attract mostly blood-searching females (Bidlingmayer 1974; Service 1977), which were of interest to us since they are the only potentially important source of disturbance to hosts.

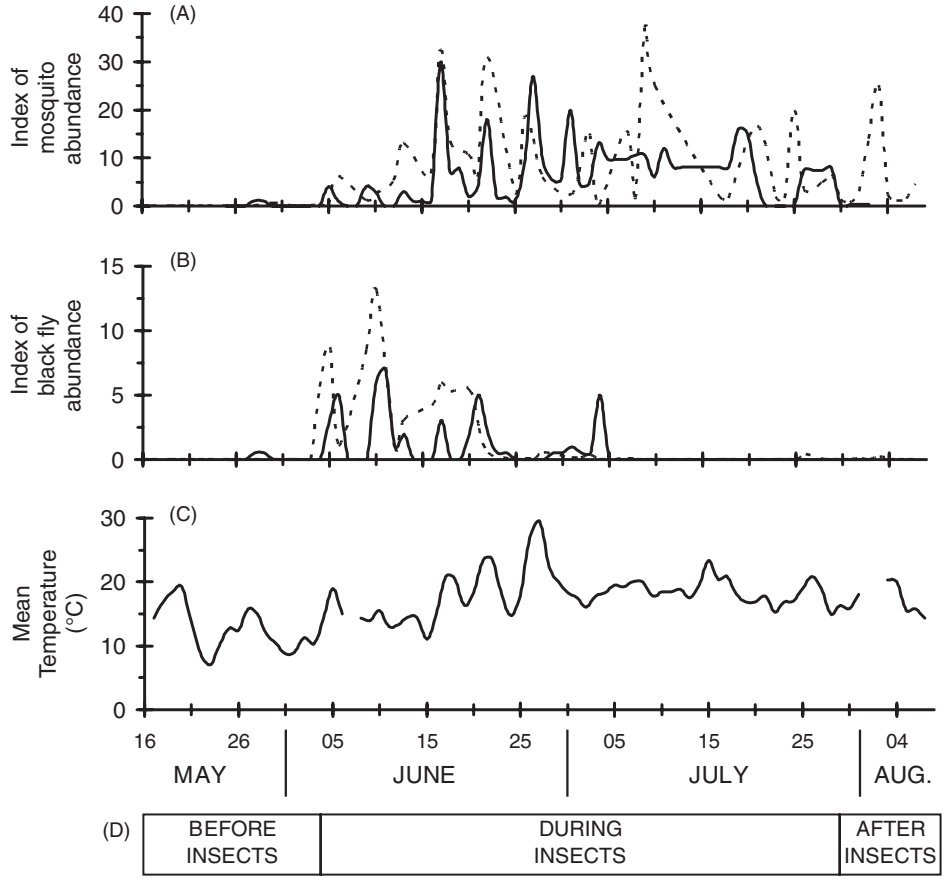
To describe the seasonal abundance of biting insects, we used 5-min landing counts on a blue cushion (30 cm × 33 cm), every day, at sunset, from 23 May to 26 July 2002. Based on these data, we used a Mosquito Magnet® garden edition trap (American Biophysics Corp., East Greenwich, Rhode Island; no octenol used in the trap) that was emptied approximately every day from 17 May to 8 August 2003. The insects captured in 2003 were kept frozen until counted, after which they were transferred to 70% ethanol for identification to genus using Wood (1984) for mosquitoes and McAlpine et al. (1987) for black flies.

Porcupines use both the horizontal (e.g., different tree species) and vertical (e.g., below-ground dens, herb layer, tree canopy) dimensions of the forest. We compared the abundance of biting flies among these sampling locations, which represent the full range of microhabitats available to porcupines in the forest. We used landing counts on a hemisphere (30 cm long × 21 cm wide × 30 cm high), which simulates a porcupine's silhouette, to estimate insect abundance. A plastic tube (200 cm long, diameter 0.79 cm) allowed the observer (the same for all the measures) to exhale in the

Table 1. Summary of data collection schedule for a study on the impacts of biting flies on the behaviour and microhabitat use of porcupines (*Erethizon dorsatum*), Parc National du Bic, Quebec, Canada, 2002–2003.

	2002			2003			
Sampling	Date	*n*	Number of replicates	Date	*n*	Number of replicates	Note
Seasonal abundance	23 May – 26 July	—	—	17 May – 8 Aug.	—	—	We used 5-min landing counts in 2002 and a CO_2-baited trap in 2003
Microhabitats							
Trees	27 June – 25 July	4 sites, 5 trees/site	3	29 June – 7 July	4 sites, 5 trees/site	2	The same sites and trees were used in 2002 and in 2003
Ground	27 June – 25 July	5 measures/tree site	3	29 June – 7 July	1 measure/tree site	2	Based on 2002 data, we made only one ground measure per site in 2003
Dens	28 June – 23 July	9 dens	2	23 June – 3 July	10 dens	3	We used the same 9 dens in 2003 as in 2002, plus a new one
Bites	—	—	—	4–13 June, 7–10 July, 4–7 Aug.	5 individuals, 6 individuals, 8 individuals	1, 1, 1	The number of bites on a given individual was never counted more than once in a given month
Telemetry	—	—	—	6 May – 7 Aug.	10 individuals		We localized each individual about twice per week

Fig. 1. Seasonal variation in insect abundance in 2003, as identified with the CO_2-baited trap (solid line) and the landing count during telemetry (broken line), for (A) mosquitoes (CO_2-baited trap: number of individuals captured; telemetry counts: number of landings) and (B) black flies (CO_2-baited trap: number of individuals captured; telemetry counts: number of landings/20 individuals). (C) Mean daily temperature in 2003. (D) Insect periods defined for our analyses of microhabitat use, Parc National du Bic, Quebec, Canada.



silhouette, which served as a source of CO_2. The silhouette was covered with a blue cloth, a colour known to attract mosquitoes and black flies (Brown 1951*a*, 1951*b*; Davies 1951; Service 1977; Allan et al. 1981). Most insects are attracted to a potential host 5 min after its arrival to a given location (Davies 1952) and black flies have an exploratory period before landing (Wolfe and Peterson 1960). We performed 5-min counts of all mosquitoes and black flies landing on the hemisphere.

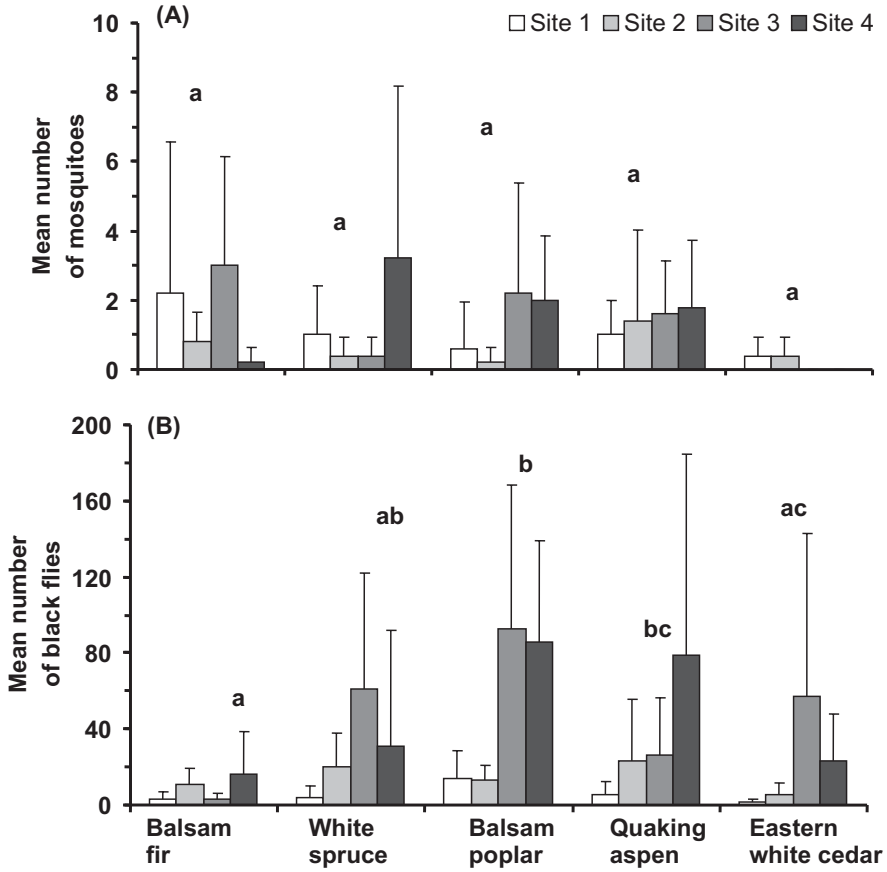
We performed 5-min landing counts inside (ca. 1 m from the entrance) and at the entrance of 10 rock dens known to be used by porcupines. In 2002, we used nine dens with two replicated measures each; in 2003, we used the same nine dens plus a new one with three replicated measures in each. As background information on den microclimate, we measured temperature (every 15 min; Smart buttons® Logger, QA supplies, Norfolk, Virginia) and light intensity (four replicates; Lunasix$_F$, Gossen Foto- und Lichtmeßtechnik, Nürnberg, Germany) inside and at the entrance of the 10 dens, from 22 June to 4 July 2004.

We selected five species of trees, common in the study area (balsam poplar (*Populus balsamifera* L.), quaking aspen, eastern white cedar, white spruce, and balsam fir) to evaluate if the abundance of insects differed across tree species. Four sites including an individual of approximately the same diameter (20.0 ± 4.2 cm) of each tree species were chosen in the study area. The observer, standing on a ladder, estimated insect abundance in the leaf area (ca. 5 m high) of each tree with the silhouette hanged on a branch. A measure was also taken on the ground at the foot of each tree in 2002; only one measure at the centre of each site was taken in 2003, as we did not observe a significant difference between ground measures in 2002. Three temporal replicates of each site were done in 2002, and two replicates in 2003. We summarize in Table 1 the various measures of insect abundance that we performed.

Repelling movements and microhabitat use

We quantified the repelling movements of and microhabitat use by porcupines using 10 male porcupines that were followed by telemetry (small mammal radio collar SMRC-5RB; Lotek Wireless Inc., Newmarket, Ontario) from 6 May to 7 August 2003. We located the porcupines at the beginning and end of the day, when insects were most abundant (Davies 1952; Wolfe and Peterson 1960; Bidlingmayer 1974; Allan et al. 1982; McCreadie et al. 1985; Anderson et al. 2001) and porcupines were thus potentially under the highest rates of attack (Day and Edman 1984; Sota et al. 1991; Canyon et al. 1998; Gibson and Torr 1999). We performed all behavioural observations during the 4 h following sunrise or during the 4 h preceding sunset. When a given animal was found, we noted the temperature

Fig. 2. Mean (+SD) abundance of (A) mosquitoes and (B) black flies among tree species in the summers of 2002–2003, Parc National du Bic, Quebec, Canada. Significant differences are represented by different letters.



and microhabitat (tree species, ground, or den) in which it was observed. A measure of abundance of mosquitoes and black flies was also taken through a 5-min count of insects landing on a blue cushion (30 cm × 33 cm) placed on the observer's legs, which sat within 30 m of the porcupine (these measures are later referred to as telemetry counts). When our presence did not disturb the porcupine, we performed a focal observation of 10 min (Martin and Bateson 1993) during which the frequency of five defensive movements was counted: head shaking, body shaking, leg shaking, scratching, and others (body movements apparently showing discomfort but not belonging to the previous categories).

Black fly bites

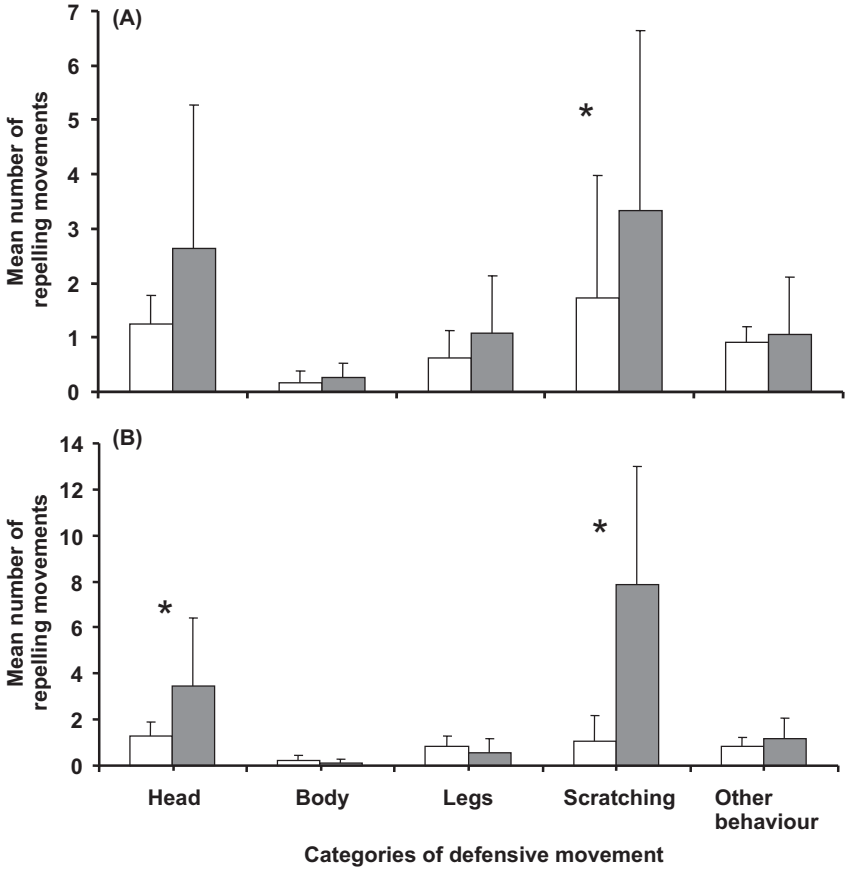
We measured the intensity of attacks by black flies by counting bites on a sample of porcupines. The saliva of black flies contains an anticoagulant and their bites are associated with more bleeding than that caused by other flies (Mead et al. 2000). The bites result in characteristic, small reddish or purplish hemorrhage in the centre of a variously raised area (Adler et al. 2004, p. 101). We could distinguish between mosquito and black fly bites because the few mosquito bites that we observed did not leave any obvious reddish or purplish hemorrhage as did black fly bites (D. Berteaux, unpublished data). Black fly bites can persist for many weeks (Coupland 1994). Some of the male porcupines followed by telemetry were immobilized (Morin and Berteaux 2003) and bites were counted inside circles drawn with a nontoxic pen on three sites on the abdomen: around the left teat (50.5 cm^2), at the centre of the abdomen (50.5 cm^2), and inside the right leg (23.0 cm^2). The number of bites was then compared with the abundance of black flies determined from telemetry counts, averaged for the week before the measure. Bite counts were performed in June, July, and August (Table 1). The number of bites on any given individual was never assessed more than once in a given month, and we considered these measures as independent.

In July, the number of bites was also determined on five young of the year through a measure on the centre of the abdomen (23.0 cm^2). The number of bites per square centimetre was then compared with figures obtained on adults in July to see if, as mentioned by Marshall et al. (1962), juveniles are less attractive than adults to biting flies. Capture techniques and immobilization procedures were approved by the Université du Québec à Rimouski Animal Care Committee (animal use protocol project No. CPA15-02-01) and the Société de la Faune et des Parcs, Gouvernement du Québec (permit No. 20030401-001-01-5-F).

Statistical analyses

Data on abundance of biting flies and from behavioural observations are usually not normally distributed (Mooring et al. 2003), so we used nonparametric statistical analyses when we could not normalize the data. We used Pearson's

Fig. 3. Mean (+SD) number of repelling movements observed per 10-min period for 10 male porcupines (*Erethizon dorsatum*) in the absence (open bars) and presence (shaded bars) of (A) mosquitoes and (B) black flies in the summer of 2003, Parc National du Bic, Quebec, Canada. Asterisks represent significant differences.



correlations (r) with 10 000 permutations (Legendre and Legendre 1998) and Spearman's correlations (r_S) to analyse continuous variables (insect abundance and black fly bites). We compared insect abundance, repelling movements, and black fly bites across periods or microhabitats using the Wilcoxon signed-rank tests and the Conover approach. Since the abundance of biting insects in trees and dens was evaluated in 2002 and repeated in 2003, we used a repeated-measures ANOVA obtained with the mixed procedure of SAS (SAS Institute Inc. 1992) to compare microhabitats. Finally, we used likelihood ratio tests to compare, at each time period considered, the observed distribution of habitat use by porcupines (habitats are balsam fir, white spruce, balsam poplar, quaking aspen, eastern white cedar, other trees, den, and ground) to an excepted distribution generated under the assumption that "habitat use by porcupines does not change according to the abundance of biting insects". The latter represents a proportional repartition of observations following the equation:

$$[1] \qquad E_{ph} = \frac{N_p N_h}{\Sigma N_p}$$

where E_{ph} is the expected number of observations for period p and habitat h, N_p is the total number of observations for period p, N_h is the total number of observations for habitat h, and ΣN_p is the total number of observations throughout all habitats and periods.

All results are expressed as means ± SD.

Results

Insect abundance

Mosquitoes were first observed on 28 May both in 2002 and in 2003, and remained active until the end of sampling on 25 July in 2002 and until 7 August in 2003. Black flies were first observed on 30 May in 2002 and on 28 May in 2003, and were not observed after 8 July in 2002 and 5 July in 2003. The detailed phenology of insect abundance for 2003 allowed us to define study periods contrasted in terms of biting-insect abundance (Fig. 1, and see below under Microhabitat use). We captured 385 mosquitoes from the following genera: *Ochlerotatus* Reinert, 2000 (75.3%); *Anopheles* Meigen, 1818 (8.8%); *Culex* L., 1758 (0.8%); and *Mansonia* Blanchard, 1901 (14.0%). Only 1.0% of the mosquitoes could not be identified to genus and males comprised only 0.5% of the mosquitoes. We captured 47 black flies from the genera *Prosimulium* Roubaud, 1906 (14.9%) and *Simulium* Latreille, 1802. Black flies from the genus *Simulium* belonged to the subgenera *Eusimulium* (17.0%) and *Simulium* (48.9%). We could not identify 19.1% of the black flies.

Table 2. Number of porcupine localizations in each microhabitat during the summer of 2003 at Parc National du Bic, Quebec, Canada, and comparison of the observed use of microhabitats between the insect periods with a theoretical distribution (proportional distribution of observations among the three periods) generated under the null hypothesis.

	Sample size (n)					
Microhabitat	Before insect	During insect	After insect	G_a*	df = $k - r$	p
Balsam fir	1 (1.5)	2 (2.8)	2 (0.6)	2.287	2	ns
White spruce	21 (11.6)	14 (21.6)	3 (4.9)	10.011	2	<0.05
Balsam poplar	1 (1.3)	1 (0.7)	—	0.190	1	ns
Quaking aspen	2 (4.9)	9 (9.1)	5 (2.1)	5.134	2	ns
Eastern white cedar	8 (7.6)	15 (14.2)	2 (3.2)	0.595	2	ns
Other tree	2 (2.1)	2 (4.0)	3 (0.9)	4.200	2	ns
Den	8 (9.4)	21 (17.6)	2 (4.0)	2.054	2	ns
Ground	9 (14.3)	33 (26.7)	5 (6.0)	3.828	2	ns

Note: Numbers in parentheses indicate the number of observations expected under the null hypothesis that habitat use by porcupines does not change according to the abundance of biting insects. k, number of classes (e.g., periods); ns, not siginificant.

*Likelihood ratio test calculates the adjusted value of the auxiliary variable G for low effective (e.g., when there are cells with low sample sizes) as $G_a = 6nG/(6n + r + 1)$, where n is the sample size and r is the number of parameters needed to define the theoretical frequency distribution.

Indices of abundance for mosquitoes and black flies, obtained through telemetry counts, varied the same way through the summer ($r_S = 0.390$, $p < 0.05$, $n = 222$), but we could not detect this relation with the results from the CO_2-baited trap since only a few black flies were captured ($r_S = 0.006$, $p > 0.05$, $n = 70$). The abundance of insects was positively correlated to temperature (mosquito: $r_S = 0.449$, $p < 0.05$, $n = 211$; black fly: $r_S = 0.259$, $p < 0.05$, $n = 211$).

In 2002, mosquitoes were captured in greater numbers on the ground than in the canopy (ground = 10.4 ± 10.8 landings, canopy = 1.5 ± 2.5 landings; $Z = 5.895$, $p < 0.001$, $n = 60$), but the opposite was true for black flies (ground = 12.9 ± 32.0 landings, canopy = 24.4 ± 47.3 landings; $Z = -2.880$, $p = 0.004$, $n = 60$).

We used the data from 2002 (three replicates) and 2003 (two replicates) to measure the difference in insect abundance between the five tree species. There was no significant difference in abundance of mosquitoes across tree species ($F_{[4,12]} = 2.25$, $p = 0.124$), but the abundance of black flies differed across tree species ($F_{[4,12]} = 3.80$, $p = 0.032$). Black flies were most abundant in balsam poplar, followed by quaking aspen, eastern white cedar, white spruce, and balsam fir (Fig. 2).

As far as dens are concerned, there were significantly fewer mosquitoes and black flies collected inside rock dens than at their entrance (mosquitoes: 2002–2003, 9 dens, inside = 1.04 ± 1.93 individuals, entrance = 9.96 ± 12.40 individuals, $F_{[1,8]} = 75.06$, $p < 0.001$; black flies: 2003, 10 dens, inside = 0.00 ± 0.00 individuals, entrance = 1.83 ± 4.03 individuals, $F_{[1,9]} = 7.04$, $p = 0.026$). We also observed that temperature was significantly lower inside dens than at the entrance (inside = 11.0 ± 1.4 °C, entrance = 12.5 ± 2.4 °C; $Z = 72.589$, $p < 0.001$, $n = 39$). Light intensity was much lower inside dens (inside = 13 ± 19 lx, entrance = 4105 ± 4549 lx; $Z = 5.443$, $p < 0.001$, $n = 39$).

Repelling movements

We localized each of our 10 focal individuals 13.8 ± 3.4 times. Most of our observations (70% ± 17%) were of porcupines resting, while 23% ± 16% and 7% ± 5% of observations were of porcupines travelling and feeding, respectively. No insect landed on the cushion during the 5-min count for almost half of our porcupine localizations. Therefore, we compare here the intensity of repelling movements according to the presence/absence of insects rather than to their abundance.

Porcupines generally performed more repelling movements when insects were present than when they were absent, but the effect of insect presence was only significant for a small portion of repelling-movement categories, that is scratching (mosquitoes: $F_{[9,123]} = 1.450$, $p = 0.016$; black flies: $F_{[9,123]} = 2.359$, $p < 0.001$) and head shaking (black flies: $F_{[9,123]} = 1.683$, $p = 0.044$) (Fig. 3).

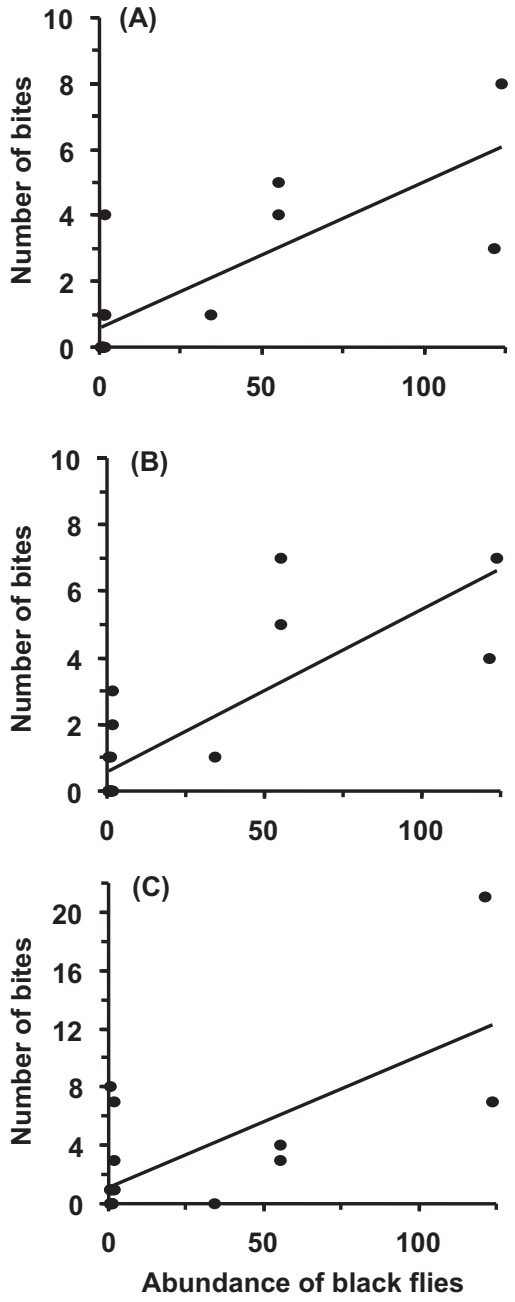
Microhabitat use

To test for differences in microhabitat use according to insect abundance, we divided the 2003 summer season into three periods differing in insect abundance: (1) before insects (17 May – 3 June) from the beginning of the field season to the first appearance of biting insects; (2) during insects (4 June – 29 July) when mosquitoes and (or) black flies were present; (3) after insects (30 July – 18 August) (see Fig. 1). We could not determine a priori which group of insects (mosquitoes or black flies) would have the greater influence on porcupines. To maximize the contrast between study periods, we decided to begin the after-insect period when both groups were completely or almost completely absent from collections. The only habitat type for which we observed a significant difference in use between insect periods is white spruce, with a use higher than expected in the before-insect period (Table 2).

Black fly bites

The number of bites observed on the teats, abdomen, and hind legs of porcupines increased with abundance of black flies as measured in the week prior to the counts of bites on porcupines (Fig. 4). We did not observe any difference in the number of bites incurred by adult and young porcupines in

Fig. 4. Relation between the number of black fly bites observed on different body parts of porcupines (A, teat; B, abdomen; C, leg) and the abundance of black flies, as measured in the week prior to the counts of bites on porcupines (A: $n = 19$, $r = 0.793$, $p < 0.001$; B: $n = 19$, $r = 0.809$, $p < 0.001$; C: $n = 19$, $r = 0.710$, $p < 0.001$), during the summer of 2003, Parc National du Bic, Quebec, Canada.



July (adults = 0.04 ± 0.03 bites/cm^2, young = 0.02 ± 0.01 bites/cm^2; $F_{[1,9]} = 0.818$, $p = 0.389$).

Discussion

We have studied porcupines in a forest ecosystem where biting-insect abundance varied through time (seasonal variation) and space (microhabitat variation). We have shown that porcupines used defensive movements when insects were abundant, although this did not prevent them from being bitten by black flies. Some microhabitats (e.g., dens) offered excellent protection against biting insects, but porcupines did not use these refuges to a greater extent at the peak of insect abundance. There was a measurable difference in biting-insect abundance between canopies of different tree species, but this did not affect use of tree species by porcupines.

Before discussing our results in the context of previous studies, we note that we do not have any absolute measure of insect abundance, but biting insects were abundant enough to disturb tourists seriously and to force all field workers to use insect repellents. We trapped few mosquitoes and black flies in comparison to results from other studies using the Mosquito Magnet® (Turell et al. 2003; Burkett et al. 2001; Kline 2002; Pucci et al. 2003; Dennett et al. 2004). The model of trap we used (Mosquito Magnet Garden®) has a coverage considerably smaller (1350 m^2) than that of the models used in the majority of studies: Mosquito Magnet Liberty® (4000 m^2) and Mosquito Magnet Pro® (5000 m^2) (American Biophysics Corp.). In addition, we did not use octenol as a short-range attractant.

Defensive behaviour

We observed porcupines mostly during their resting periods, at a time when hosts are especially vulnerable (Day and Edman 1984; Sota et al. 1991; Canyon et al. 1998; Gibson and Torr 1999) and discomfort owing to biting insects should have been easy to detect. Porcupines seem relatively tolerant to biting insects, as only a few defensive movements were significantly different between presence and absence of insects. Host size has an impact on the degree of defence shown by host species, with smaller hosts being generally more defensive than larger ones (Edman et al. 1974; Day and Edman 1984; Edman and Scott 1987). Because porcupines are among the largest rodents, species size could explain its tolerance. Wright and DeFoliart (1970), Edman et al. (1974), Washino and Tempelis (1983), Day and Edman (1984), and Walker and Edman (1985) have all mentioned the tolerance or the low attractiveness of rodents for biting insects. However, as seen in the laboratory for squirrels and chipmunks (Walker and Edman 1986; Cully et al. 1991) and in the field with our study, rodents still use defensive movements such as head shaking and scratching to reduce insect harassment. Biting insects prefer to bite in areas with less fur, as they have an easier access to the blood vessels (Walker and Edman 1985; Moore 2002). The face of porcupines is covered with much shorter hairs than other parts of their body, which could make it more attractive for mosquitoes and black flies. This could explain the use of head shaking as a defensive behaviour.

We observed a strong correlation between the number of bites and the black fly abundance averaged for the previous week. To our knowledge, no one has related the number of bites to insect density or abundance.

Microhabitat use

There was a strong contrast among microhabitats regarding the pressure exerted by biting flies on potential hosts. Yet porcupines did not change notably their use of microhabitats when insects were most abundant. We suggest

the following as a general hypothesis to explain this result. Throughout the study, porcupines were observed mostly while resting and, according to our results, resting sites were mainly in coniferous trees (white spruce and eastern white cedar) and dens. It is probable that the selection of resting sites minimized predation risk from mammalian predators, as fishers (*Martes pennanti* Erxleben, 1777) were the main cause of death in the study area (D. Berteaux, unpublished results). Given that dens and coniferous trees also offered good protection against biting insects, there was probably no major conflict between predation and parasitic avoidance so that microhabitat use did not change when insects became abundant in early June. In short, the strategy used by porcupines to avoid mammalian predators was probably also efficient against biting flies.

Below we detail some of the reasons why microhabitats differ in their degree of protection against biting insects. Roze (1989, p. 112) made anecdotal observations of tree den use by porcupines in response to high black fly harassment. Walker (1984) observed that even if mosquitoes seem attracted by a chipmunk in its burrow, the mosquitoes would fly above the entrance without entering the den. We suggest that lower temperature and light intensity could make dens unfavourable to biting flies. Temperature inside rock dens is usually lower than outside temperature during the summer, and temperature is an important factor regulating activities of insects (Davies 1952; Twinn 1952; Bidlingmayer 1974; McCreadie et al. 1986). Vision plays a major role in host location, especially in close-range orientation (Bidlingmayer and Hem 1979, 1980; Sutcliffe 1986, 1987; Allan et al. 1987; Sutcliffe et al. 1995; Gibson and Torr 1999), and the lower light intensity inside rock dens could prevent biting flies from getting the visual cues necessary for landing on hosts.

We were surprised to find the greatest abundance of black flies in deciduous rather than coniferous trees. Indeed, one could think that insects would be more abundant in conifers where the dense foliage offers protection against the wind, which limits the flight of insects (Fredeen and Mason 1991; Martin et al. 1994; Gibson and Torr 1999; Anderson et al. 2001). Perhaps the higher leaf density of conifers blocked the visual and olfactory cues necessary for the biting flies to locate their host (Fallis 1964; Bradbury and Bennett 1974; Allan et al. 1987; Gibson and Torr 1999). For example, the repelling action of eastern white cedars has been noted by several authors (MacNay 1939; Rutledge and Gupta 1996).

Marshall et al. (1962) have observed a smaller annoyance for young than adult porcupines. A difference of attacks according to the age class of host has also been noted for many birds and other mammals, but depending on the host species, young are not always the least disturbed (Sota et al. 1991; Smith et al. 1998; Heeb et al. 2000; Torr and Mangwiro 2000; Colman et al. 2003). In our study, we could not see a difference between juveniles and adults. This may be due to the low power of our test since we compared five young to six adults.

Biting flies can disturb the feeding patterns of large mammals and have a great impact on their energy budget (Colman et al. 2001, 2003; Hagemoen and Reimers 2002; Mooring et al. 2003). We could not test this with porcupines, as they were mostly resting during our observations. It would no doubt be interesting to investigate further in this direction.

In summary, we have shown that biting insects do have a measurable effect on the behaviour and wounding rate of a mammalian herbivore living in a forest ecosystem. Forest microhabitats are of varying quality regarding the protection they offer against biting insects. However, this did not impact in a major way the microhabitat use of the host species. We hypothesize that this is because there was no major conflict between the avoidance of insect harassment and the minimization of mammalian predation risk.

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References

Adler, P.H., Currie, D.C., and Wood, D.M. 2004. The black flies (Simuliidae) of North America. Comstock Publishing Associates, Ithaca, N.Y.

Allan, S.A., Surgeoner, G.A., Helson, B.V., and Pengelly, D.H. 1981. Seasonal activity of *Mansonia perturbans* adults in southwestern Ontario. Can. Entomol. **113**: 133–139.

Allan, S.A., Surgeoner, G.A., and Helson, B.V. 1982. Diel biting activity of *Mansonia perturbans* (Diptera: Culicidae) in southwestern Ontario. Proc. Entomol. Soc. Ont. **113**: 59–63.

Allan, S.A., Day, J.F., and Edman, J.D. 1987. Visual ecology of biting flies. Annu. Rev. Entomol. **32**: 297–316.

Anderson, J.R., Nielssen, A.C., and Hemmingsen, W. 2001. Use of host-mimicking trap catches to determine which parasitic flies attack reindeer, *Rangifer tarandus*, under different climatic conditions. Can. Field-Nat. **115**: 274–286.

Apperson, C.S., Harrison, B.A., Unnasch, T.R., Hassan, H.K., Irby, W.S., Savage, H.M., et al. 2002. Host-feeding habits of *Culex* and other mosquitoes (Diptera: Culicidae) in the Borough of Queens in New York City, with characters and techniques for identification of *Culex* mosquitoes. J. Med. Entomol. **39**: 777–785.

Berteaux, D., Klvana, I., and Trudeau, C. 2005. Spring to fall mass gain in a northern population of North American porcupines. J. Mamm. **86**(3): 514–519.

Bidlingmayer, W.L. 1974. The influence of environmental factors and physiological stage on flight patterns of mosquitoes taken in the vehicle aspirator and truck, suction, bait and New Jersey light traps. J. Med. Entomol. **11**: 119–146.

Bidlingmayer, W.L., and Hem, D.G. 1979. Mosquito (Diptera, Culicidae) flight behavior near conspicuous objects. Bull. Entomol. Res. **69**: 691–700.

Bidlingmayer, W.L., and Hem, D.G. 1980. The range of visual attraction and the effect of competitive visual attractants upon mosquito (Diptera, Culicidae) flight. Bull. Entomol. Res. **70**: 321–342.

Bradbury, W.C., and Bennett, G.F. 1974. Behavior of adult Simuliidae (Diptera). II. Vision and olfaction in near-orientation and landing. Can. J. Zool. **52**: 1355–1364.

Brown, A.W.A. 1951*a*. Studies of the responses of the female *Aedes* mosquito. Part IV. Field experiments on Canadian species. Bull. Entomol. Res. **42**: 575–582.

Brown, A.W.A. 1951*b*. Factors in the attractiveness of bodies for mosquitoes. Nature (Lond.), **167**: 202.

Burkett, D.A., Lee, W.J., Lee, K.W., Kim, H.C., Lee, H.I., Lee, J.S., et al. 2001. Light, carbon dioxide, and octenol-baited mosquito trap and host-seeking activity evaluations for mosquitoes in malarious area of the Republic of Korea. J. Am. Mosq. Control Assoc. **17**: 196–205.

Canyon, D.V., Hii, J.L.K., and Muller, R. 1998. Multiple host-feeding and biting persistence of *Aedes aegypti*. Ann. Trop. Med. Parasitol. **92**: 311–316.

Colman, J.E., Pedersen, C., Hjermann, D.Ø., Holand, Ø., Moe, S.R., and Reimers, E. 2001. Twenty-four-hour feeding and lying patterns of wild reindeer *Rangifer tarandus tarandus* in summer. Can. J. Zool. **79**: 2168–2175.

Colman, J.E., Pedersen, C., Hjermann, D.Ø., Holand, Ø., Moe, S.R., and Reimers, E. 2003. Do wild reindeer exhibit grazing compensation during insect harassment? J. Wildl. Manag. **67**: 11–19.

Coupland, J.B. 1994. Factors influencing nuisance black fly activity in the Scottish Highlands. Med. Vet. Entomol. **8**: 125–132.

Cully, J.F., Grieco, J.P., and Kissel, D. 1991. Defensive behavior of eastern chipmunks against *Aedes triseriatus* (Diptera, Culicidae). J. Med. Entomol. **28**: 410–416.

Davies, D.M. 1951. Some observations on the number of black flies (Diptera, Simuliidae) landing on colored cloths. Can. J. Zool. **29**: 65–70.

Davies, D.M. 1952. The population and activity of adult female black flies in the vicinity of a stream in Algonquin Park, Ontario. Can. J. Zool. **30**: 287–321.

Day, J.F., and Edman, J.D. 1984. Mosquito engorgement on normally defensive hosts depends on host activity patterns. J. Med. Entomol. **21**: 732–740.

Dennett, J.A., Vessey, N.Y., and Parson, R.E. 2004. A comparison of seven traps used for collection of Aedes albopictus and Aedes aegypti originating from a large tire repository in Harris County (Houston), Texas. J. Am. Mosq. Control Assoc. **20**: 342–349.

Downes, C.M., Theberge, J.B., and 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., and Cowtan, P. 1980. An unusual choice of habitat helps Camargue horses to avoid blood-sucking horse flies. Biol. Behav. **5**: 55–60.

Edman, J.D., and Scott, T.W. 1987. Host defensive behavior and the feeding success of mosquitoes. Insect Sci. Appl. **8**: 617–622.

Edman, J.D., Webber, L.A., and Kale, H.W., II. 1972. Effect of mosquito density on the interrelationship of host behavior and mosquito feeding success. Am. J. Trop. Med. Hyg. **21**: 487–491.

Edman, J.D., Webber, L.A., and Schmid, A.A. 1974. Effect of host defenses on the feeding pattern of *Culex nigripalpus* when offered a choice of blood sources. J. Parasitol. **60**: 874–883.

Fallis, A.M. 1964. Feeding and related behavior of female Simuliidae (Diptera). Exp. Parasitol. **15**: 439–470.

Fredeen, F.J.H., and Mason, P.G. 1991. Meteorological factors influencing host-seeking activity of female *Simulium luggeri* (Diptera, Simuliidae). J. Med. Entomol. **28**: 831–840.

Gibson, G., and Torr, S.J. 1999. Visual and olfactory responses of haematophagous Diptera to host stimuli. Med. Vet. Entomol. **13**: 2–23.

Hagemoen, R.I.M., and Reimers, E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. J. Anim. Ecol. **71**: 883–892.

Hart, B.L. 1992. Behavioral adaptations to parasites — an ethological approach. J. Parasitol. **78**: 256–265.

Hart, B.L. 1994. Behavioral defense against parasites — interaction with parasite invasiveness. Parasitology, **109**(Suppl.): S139–S151.

Heeb, P., Kölliker, M., and Richner, H. 2000. Bird–ectoparasite interactions, nest humidity and ectoparasite community structure. Ecology, **81**: 958–968.

Helle, T., Aspi, J., Lempa, K., and Taskinen, E. 1992. Strategies to avoid biting flies by reindeer: field experiments with silhouette traps. Ann. Zool. Fenn. **29**: 69–74.

Helson, B.V., Surgeoner, G.A., and Wright, R.E. 1980. The seasonal distribution and species composition of mosquitoes (Diptera, Culicidae) collected during a St-Louis encephalitis surveillance program from 1976 to 1978 in southwestern Ontario. Can. Entomol. **112**: 865–874.

Kline, D.L. 2002. Evaluation of various models of propane-powered mosquito traps. J. Vector Ecol. **27**: 1–7.

Laird, M. 1982. Biting flies in Canada: health effects and economic consequences. Publ. No 19248, Environmental Secretariat, National Research Council of Canada, Ottawa, Ont.

Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd English ed. Elsevier Science BV, Amsterdam, the Netherlands.

MacNay, C.G. 1939. Studies on repellents for biting flies. Can. Entomol. **71**: 38–44.

Marshall, W.H., Gullion, G.W., and Schwab, R.G. 1962. Early summer activities of porcupines as determined by radiopositioning techniques. J. Wildl. Manag. **26**: 75–79.

Martin, F.R., McCreadie, J.W., and Colbo, M.H. 1994. Effect of trap site, time of day, and meteorological factors on abundance of host-seeking mammalophilic black flies (Diptera, Simuliidae). Can. Entomol. **126**: 283–289.

Martin, P., and Bateson, P. 1993. Measuring behaviour: an introductory guide. 2nd ed. Cambridge University Press, Cambridge, UK.

Mason, P.G., and Shemanchuk, J.A. 1990. Les mouches noires. Publ. No. 1499, Agriculture Canada, Ottawa, Ont.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., and Wood, D.M. 1987. Manuel of nearctic Diptera. Vol. 2. Monogr. No. 28, Research Branch, Agriculture Canada, Ottawa, Ont.

McCreadie, J.W., Colbo, M.H., and Bennett, G.F. 1985. The seasonal activity of hematophagous Diptera attacking cattle in insular Newfoundland. Can. Entomol. **117**: 995–1006.

McCreadie, J.W., Colbo, M.H., and Bennett, G.F. 1986. The influence of weather on host seeking and blood feeding of *Prosimulium mixtum* and *Simulium venustum/verecundum* complex (Diptera: Simuliidae). J. Med. Entomol. **23**: 289–297.

Mead, D.G., Ramberg, F.B., and Besselsen D.G., and Mare, C.J. 2000. Transmission of vesicular stomatitis virus from infected to noninfected black flies co-feeding on nonviremic deer mice. Science (Wash., D.C.), **287**: 485–487.

Moore, J. 2002. Parasites and the behavior of animals. Oxford University Press, New York.

Mooring, M.S., Fitzpatrick, T.A., Fraser, I.C., Benjamin, J.E., Reisig, D.D., and Nishihira, T.T. 2003. Insect-defense behavior by desert bighorn sheep. Southwest. Nat. **48**: 635–643.

Morin, P., and Berteaux, D. 2003. Immobilization of North American porcupines (*Erethizon dorsatum*) using ketamine and xylazine. J. Wildl. Dis. **39**: 675–682.

Noel, L.E., Pollard, R.H., Ballard, W.B., and Cronin, M.A. 1998. Activity and use of active gravel pads and tundra by caribou, *Rangifer tarandus granti*, within the Prudhoe Bay oil field, Alaska. Can. Field-Nat. **112**: 400–409.

Pollard, R.H., Ballard, W.B., Noel, L.E., and Cronin, M.A. 1996*a*. Parasitic insect abundance and microclimate of gravel pads and tundra within the Prudhoe Bay oil field, Alaska, in relation to use by caribou, *Rangifer tarandus granti*. Can. Field-Nat. **110**: 649–658.

Pollard, R.H., Ballard, W.B., Noel, L.E., and Cronin, M.A. 1996*b*. Summer distribution of caribou, *Rangifer tarandus granti*, in the area of the Prudhoe Bay oil field, Alaska, 1990–1994. Can. Field-Nat. **110**: 659–674.

Pucci, T.M., Lynch, J., and Keiper, J.B. 2003. Insect composition of the Mosquito Magnet Pro registered mosquito trap in northeastern Ohio. Gt. Lakes Entomol. **36**: 25–30.

Ralley, W.E., Galloway, T.D., and Crow, G.H. 1993. Individual and group behaviour of pastured cattle in response to attack by biting flies. Can. J. Zool. **71**: 725–734.

Roze, U. 1989. The North American porcupine. Smithsonian Institution Press, Washington, D.C.

Rubenstein, D.I., and Hohmann, M.E. 1989. Parasites and social behavior of island feral horses. Oikos, **55**: 312–320.

Rutledge, L.C., and Gupta, R.K. 1996. Reanalysis of the C.G. MacNay mosquito repellent data. J. Vector Ecol. **21**: 132–135.

SAS Institute Inc. 1992. SAS®. Version 8.0 [computer program]. SAS Institute Inc., Cary, N.C.

Service, M.W. 1977. A critical review of procedures for sampling populations of adult mosquitoes. Bull. Entomol. Res. **67**: 343–382.

Smith, R.N., Cain, S.L., Anderson, S.H., Dunk, J.R., and Williams, E.S. 1998. Blackfly-induced mortality of nestling red-tailed hawks. Auk, **115**: 368–375.

Sota, T., Hayamizu, E., and Mogi, M. 1991. Distribution of biting *Culex tritaeniorhynchus* (Diptera, Culicidae) among pigs: effects of host size and behavior. J. Med. Entomol. **28**: 428–433.

Sutcliffe, J.F. 1986. Black fly host location: a review. Can. J. Zool. **64**: 1041–1053.

Sutcliffe, J.F. 1987. Distance orientation of biting flies to their hosts. Insect Sci. Appl. **8**: 611–616.

Sutcliffe, J.F., Steer, D.J., and Beardsall, D. 1995. Studies of host location behavior in the black fly *Simulium arcticum* (IIS-10.11) (Diptera, Simuliidae): aspects of close range trap orientation. Bull. Entomol. Res. **85**: 415–424.

Sweitzer, R.A. 2003. Breeding movements and reproductive activities of porcupines in the Great Basin Desert. West. N. Am. Nat. **63**: 1–10.

Torr, S.J., and Mangwiro, T.N.C. 2000. Interactions between cattle and biting flies: effects on the feeding rate of tsetse. Med. Vet. Entomol. **14**: 400–409.

Toupin, B., Huot, J., and Manseau, M. 1996. Effect of insect harassment on the behaviour of the Rivière George caribou. Arctic, **49**: 375–382.

Turell, M.J., O'guinn, M.L., Jr., Wasieloski, L.P., Dohm, D.J., Lee, W.J., Cho, H., et al. 2003. Isolation of Japanese encephalitis and Getah virus from mosquitoes (Diptera: Culicidae) collected near Camp Greaves, Gyonggi Province, Republic of Korea, 2000. J. Med. Entomol. **40**: 580–584.

Twinn, C.R. 1952. A review of studies of blood-sucking flies in northern Canada. Can. Entomol. **84**: 22–28.

Walker, E.D. 1984. Field evidence against rodent burrow entering by *Aedes triseriatus* (Diptera: Culicidae). Gt. Lakes Entomol. **17**: 185–186.

Walker, E.D., and Edman, J.D. 1985. Feeding site selection and blood-feeding behavior of *Aedes triseriatus* (Diptera: Culicidae) on rodent (Sciuridae) hosts. J. Med. Entomol. **22**: 287–294.

Walker, E.D., and Edman, J.D. 1986. Influence of defensive behavior of eastern chipmunks and gray squirrels (Rodentia: Sciuridae) on feeding success of *Aedes triseriatus* (Diptera: Culicidae). J. Med. Entomol. **23**: 1–10.

Walsh, N.E., Fancy, S.G., McCabe, T.R., and Pank, L.F. 1992. Habitat use by the Porcupine caribou herd during predicted insect harassment. J. Wildl. Manag. **56**: 465–473.

Washino, R.K., and Tempelis, C.H. 1983. Mosquito host bloodmeal identification — methodology and data analysis. Annu. Rev. Entomol. **28**: 179–201.

Wolfe, L.S., and Peterson, D.G. 1960. Diurnal behavior and biting habits of black flies (Diptera: Simuliidae) in the forests of Quebec. Can. J. Zool. **38**: 489–197.

Wood, D.M. 1984. Clés des genres et des espèces de moustiques du Canada. Research Branch, Agriculture Canada, Ottawa, Ont.

Wood, D.M., Dang, P.T., and Ellis, R.A. 1979. The mosquitoes of Canada. Part 6. The insects and arachnids of Canada. Publ. No. 1686, Research Branch, Agriculture Canada, Ottawa, Ont.

Wright, R.E., and DeFoliart, G.R. 1970. Associations of Wisconsin mosquitoes and woodland vertebrate hosts. Ann. Entomol. Soc. Am. **63**: 777–786.