

Collections of fleas (Siphonaptera) from Pacific marten, *Martes caurina* (Carnivora: Mustelidae), reveal unique host–parasite relationships in the Haida Gwaii archipelago

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ABSTRACT

Fleas and their host–parasite relationships are understudied in many parts of Canada, yet such relationships may contribute to our knowledge of ecosystems in ways we have yet to understand. A collection of 57 fleas from Pacific marten (*Martes caurina* (Merriam)) in Haida Gwaii, off the coast of British Columbia, Canada, led to the collection of five taxa of fleas: the European rat flea, *Nosopsyllus fasciatus* (Bosc), a squirrel flea, *Ceratophyllus (Amonopsyllus) ciliatus protinus* (Jordan), a mustelid flea, *Chaetopsylla floridensis* (I. Fox), *Hystrichopsylla (Hystriceras) dippiei*, likely ssp. *spinata* Holland, a parasite of mustelids and mephitids, and a generalist bird flea, *Dasypsyllus gallinulae perpinnatus* (Baker). All five species are first records for Haida Gwaii, and *C. floridensis* is recorded from Canada for the first time. Two new host–parasite relationships support a previous dietary study of marten in Haida Gwaii. This provides further evidence that fleas infesting predators may indicate prey composition within their home ranges.

INTRODUCTION

Of 154 species of fleas (Siphonaptera) reported in Canada (Galloway 2019), eight species are known to infest mammals and birds living in the remote archipelago of Haida Gwaii, off the coast of British Columbia, Canada (Holland 1985). Among the first western scientific collections are those of *Opisodasys keeni* (Baker) from Keen’s Mouse (*Peromyscus keeni* (Rhoads)) made by Reverend John Henry Keen in 1895 (Sealy 2018).

In addition to hosting their own characteristic species of fleas, carnivores are commonly infested with fleas from moribund prey and their nests (Rust *et al.* 1971). This makes predators useful targets for surveillance of flea-borne pathogens such as plague (*Yersinia pestis* (Lehmann & Neumann)) (Gage *et al.* 1994; Salkeld and Stapp 2006; Brown *et al.* 2011), which is an effective monitoring strategy in addition to sampling prey alone, because predators may be exposed to many individual prey animals of multiple species over time. For example, predators are known to be accidental hosts for at least 40 of 50 flea species that carry plague (Gage *et al.* 1994). Thus, while many species of fleas have evolved close associations with certain hosts, they may also be found commonly on predators of those host species. Because these fleas would not normally infest their predators as hosts, their presence on predators is incidental. This can allow researchers to infer predator–prey interactions from the species of fleas found on predators (Zielinski 1984).

At least 25 species of fleas have been found on martens (American marten, *Martes americana* (Turton), and Pacific marten, *Martes caurina* (Merriam)) in North America, most of which were likely acquired from their prey. In addition to the 19 species/subspecies reported by Holland (based on current nomenclature, 21 species/subspecies in Holland (1985)), six others have been identified more recently in the United States by Zielinski (1984) and Scharf (2017). Numbers of fleas collected from individual marten are often small, averaging about 3–4 fleas per host individual (DeVos 1957; Zielinski 1984). Of all the species of fleas documented from marten, none are monoxenous parasites of marten, though several have mustelids as their primary hosts (Holland 1985).

Two each of *Monopsyllus vison* (Baker) and *Kuichenliuopsylla atrox* (Jordan) were collected from American marten (DeVos 1957) in Ontario. Holland (1949) also documented *Nearctopsylla grahami* Holland on a marten in Ontario. *Nearctopsylla hyrtaci* (Rothschild) was found on marten in Montana (Senger 1966), and *Chaetopsylla floridensis* (I. Fox) was first documented on marten in Alaska (Hopla 1965). In what is perhaps the largest study of marten ectoparasites, seven species were found among 70

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fleas collected from 13 captures and recaptures of *M. americana* on 20 occasions in California (Zielinski 1984). These included *Ceratophyllus (Amonopsyllus) ciliatus* Jordan, *C. floridensis*, *Aetheca wagneri* (Baker), *Megarhroglossus* spp., *Orchopeas nepos* (Rothschild), *Eumolpianus eumolpi* (Rothschild), and *Oropsylla idahoensis* (Baker). *Orchopeas caedens* (Jordan) was found on marten in the Yukon (Haas and Johnson 1981; Haas *et al.* 1989), and both *C. ciliatus* and *Hystrichopsylla dippiei spinata* (Holland) have been found on marten in southeastern Alaska (Haas *et al.* 1989, 2005). *Chaetopsylla lotoris* (Stewart), *Nearctopsylla genalis* (Baker), and *Orchopeas howardi* (Baker) infested marten in Michigan (Scharf 2017).

Understanding host–flea relationships gives insight into predator diets, may complement traditional diet studies by enlightening our understanding of predator diets when such studies are scant or incomplete, and may provide important links in epidemiological studies. In Haida Gwaii (known for a time as the Queen Charlotte Islands), located off the north coast of British Columbia, only one study of marten diet has been undertaken (Nagorsen *et al.* 1991), and samples were limited to areas of industrial forest harvest where access was provided by logging roads. Here, we document new records for species of fleas for Haida Gwaii and for Canada, as well as two new host–parasite associations for marten.

MATERIALS AND METHODS

A female Pacific marten, accidentally struck and killed by a vehicle on the morning of 5 February 2018 on the outskirts of the Village of Queen Charlotte (53.2487°, –132.0286°), provided a large collection of fleas. Prior to necropsy performed the same day, the animal had been placed in a freezer for approximately six hours. Upon removal from the freezer, the carcass was placed on a white surface, and live fleas were collected by hand from the fur as they appeared at the surface during warming. On 17 January 2019, a male Pacific marten was found dead on the only paved road on northern Moresby Island, a 15-km stretch connecting the community of Sandspit with the Alliford Bay ferry terminal (53.2240°, –131.9440°). The cold carcass was sealed in a bag, and fleas were collected that evening using the method described above.

Fleas were also collected from two black rats (*Rattus rattus* (Linnaeus)) on the Swan Islands (52.3321°, –131.3063°), 28 March 2018, and another from the Village of Queen Charlotte (53.2554°, –132.0757°), 31 January 2019.

Fleas were first frozen, then preserved in 95% ethanol. Fleas were mounted in Canada balsam using the method described by Richards (1964). Voucher specimens were deposited in the Royal BC Museum (Victoria, British Columbia), Haida Gwaii Museum at Kay Lnagaay (Skidegate, Haida Gwaii, British Columbia) and the J.B. Wallis/R.E. Roughley Museum of Entomology (Department of Entomology, University of Manitoba, Winnipeg, Manitoba).

RESULTS

Fifty-four fleas were collected from the female marten. Gross physical examination of the marten indicated the animal was older, as evidenced by significant tooth wear and poor body condition. Forty-one (37 females, 4 males) of the fleas collected were northern rat fleas, *Nosopsyllus fasciatus* (Bosc), 11 (3 males; 8 females) were squirrel fleas, *Ceratophyllus (Amonopsyllus) ciliatus protinus* (Jordan), one (female) was a mustelid flea, *Chaetopsylla floridensis*, and one female was *Hystrichopsylla (Hystroceras) dippiei*, likely ssp. *spinata* Holland (males are needed for positive identification (Holland 1985; Lewis and Lewis 1994)), a parasite of mustelids and mephitids. Three fleas were collected from the male marten. Two of these were squirrel fleas, *C. ciliatus protinus* (1 male, 1 female), and the third was a generalist bird flea, *Dasyopsyllus gallinulae perpinnatus* (Baker) (1 female). All fleas collected from rats were northern rat fleas, *N. fasciatus*. Rats from the Swan Islands were infested with one male and three females, and the one from Queen Charlotte with one male and seven females.

DISCUSSION

Chaetopsylla floridensis is a new flea record for Canada. This flea is a known parasite of mustelids in Alaska and has been recorded from islands in the nearby southern end of the Alaskan panhandle (Alexander Archipelago). Although the one we found is a first record for Canada, its late detection is

probably a result of a general lack of study. The species has an odd history: it was originally described in 1939 from specimens gathered from leaf mold in Gainesville, Florida (Ewing and Fox 1943). Specimens collected since then have come from Alaska (Hopla 1965; Haas *et al.* 1978) and Colorado (Eads *et al.* 1979). Zielinski (1984) found that 31% of all fleas collected from 13 American marten (*M. americana*) in California were this species, although *C. floridensis* was previously unreported in that state. *Chaetopsylla floridensis* is of particular biogeographic interest because of its close relationship with marten. The extreme isolation of *M. caurina* in the Haida Gwaii archipelago (Dawson *et al.* 2017) suggests future research on the genetic uniqueness of *C. floridensis* in Haida Gwaii would be of interest. In contrast to marten populations on some islands in the Alexander Archipelago (SE Alaska), where introduced *M. americana* have likely interbred with native *M. caurina*, no introductions of *M. americana* are known to have occurred in Haida Gwaii.

On a smaller spatial scale, our collections from two marten increase the known flea fauna of the Haida Gwaii archipelago by 63%. Two of the five species found on the marten, *C. floridensis* and *H. dippiei spinata*, have mustelids as usual hosts, whereas *D. gallinulae*, *C. ciliatus protinus*, and *N. fasciatus* are likely secondary infestations from marten prey species. Their usual hosts, birds, red squirrel and rats, respectively, have all been documented as prey items for marten in Haida Gwaii (Nagorsen *et al.* 1991). Unlike squirrels and birds, rats were rare in marten diet in this study. None of these five flea species has been documented in Haida Gwaii previously and, although lack of sampling may contribute to a historical paucity of data, at least some of these species may be relatively recent arrivals to the Haida Gwaii archipelago, given the introduction mostly during the past century of several species of mammals (Golumbia *et al.* 2002). *Ceratophyllus ciliatus protinus* likely arrived with the red squirrel (*Tamiasciurus hudsonicus* (Erxleben)) in 1950 (Golumbia *et al.* 2002; Sealy 2012), whereas the introduction of *N. fasciatus* with rats (both *R. rattus* and *R. norvegicus* (Berkenhout)) probably occurred much earlier, perhaps in the 18th century. It is thus possible that the introduction of several mammal species to Haida Gwaii has increased flea loads on some native mammals and has perhaps contributed to a decline in fitness as a result. In contrast, *D. gallinulae* is a bird flea presumed to be native to the islands.

Ceratophyllus ciliatus protinus is a Pacific coast flea species that infests red squirrels, but is often recorded from predators of squirrels, including marten (Zielinski 1984; Haas *et al.* 1989). Red squirrels are now common on Graham and Moresby Islands and also on numerous smaller islands in the archipelago. Another species of squirrel flea, *O. caedens*, which is common on red squirrels throughout most of their range (Holland 1985) and is also documented in other mainland marten populations (Haas and Johnson 1981; Haas *et al.* 1989; TD Galloway, unpublished data), was not found on our two marten specimens. Neither are there documented records of *O. caedens* from Vancouver Island (Holland 1985). Vancouver Island was the source for Haida Gwaii red squirrels, and the absence of this flea species on Vancouver Island would explain its absence in Haida Gwaii.

Because the prey volume in the Haida Gwaii marten diet comprises twice the red squirrels compared to rats (Nagorsen *et al.* 1991), one would predict *C. ciliatus protinus* to occur on marten in higher numbers than rat fleas. Although this prediction holds true for the collection made from the male marten (67% squirrel fleas; 0% rat fleas), the opposite pattern was observed for the female marten (76% rat fleas; 20% squirrel fleas). Even though these patterns are inconsistent, they can be explained by the prey composition in the martens' home ranges. Rats are not present at the location where the male marten was collected, but they are abundant in the area where the female marten was collected (Gwaii Haanas 2019). As an avenue of future investigation, we suggest that marten living in sympatry with rats might prefer rats over squirrels as prey. The same may be true of other North American mesocarnivores that also include red squirrels in their diet. If so, this food preference might modify small mammal community composition and also may help explain why rats (*Rattus* spp.) are absent from certain areas of the North American landscape. Unlike red squirrels, rats did not co-evolve with marten and may be ill-adapted to avoid marten predation. This could mean they may be selected preferentially by marten in areas where both prey species occur. Similarly, in the United Kingdom, the newly re-introduced European pine marten (*Martes martes* (Linnaeus)) prefers the non-native grey squirrel (*Sciurus carolinensis* Gmelin) to the native red squirrel (*S. vulgaris* Linnaeus), and their differential predation is affecting community structure to the extent that the introduced grey squirrel may eventually be extirpated (Sheehy *et al.* 2018).

Hystrichopsylla dippiei spinata occurs on Vancouver Island, in the British Columbia Lower Mainland and at Williams Lake, British Columbia (Holland 1957, 1985), and has been recorded in Oregon (Lewis *et*

al. 1988). There are also records from southern Alaska (Haas *et al.* 2005). It is a parasite mainly of mustelids (Haas *et al.* 1978), with a number of records from marten (Haas *et al.* 2005); Haas *et al.* (2005) suggested that marten are the true hosts, but additional study is needed to confirm this relationship. We are fairly certain our specimen is this subspecies, based on location and host, but male specimens are needed as they have the diagnostic features for the subspecies. Because *H. dippiei spinata* is a winter flea, and our sampling effort was limited, it is likely this species has been present in Haida Gwaii for some time without being detected. Further sampling will no doubt provide new information about the occurrence of this flea.

There are no published records for two of the five flea species new for Haida Gwaii, *N. fasciatus* or *D. gallinulae*, infesting marten in Canada (Holland 1985, p. 480). These host–parasite relationships may be unique to the Haida Gwaii archipelago, where birds comprise a much higher proportion of marten diet compared to what has been observed in marten populations elsewhere (Nagorsen *et al.* 1991), and where rats are present only on small, off-shore islands where marten do not occur and in association with human settlements on the two largest islands. Specimens of marten on which Nagorsen *et al.* (1991) based their diet study were collected from traplines radiating from towns and accessed by logging roads. While historic studies of rat distribution in Haida Gwaii show rats present on many islands in the archipelago (Bertram and Nagorsen 1995; Golumbia *et al.* 2002), a more recent, finer-scale study of rat distribution demonstrates that rats are functionally absent from habitats where marten occur and human disturbance is low—that is, the majority of the land area of the archipelago’s two largest islands, Graham and Moresby (Gwaii Haanas 2019). Thus, rats occur on small Haida Gwaii islands where marten are absent, and on islands where marten are present but only in near proximity to areas of high human disturbance, including all towns in the archipelago (Gwaii Haanas 2019). As a result, there is little overlap between populations of marten and rats in Haida Gwaii, except at the margins of areas populated by humans. This would explain the low occurrence of rats in Nagorsen’s marten diet study, and yet the prevalence of rat fleas on our female marten which, given its location of death, apparently inhabited a rat-infested home range due to its proximity to human habitation. Less than a month after collection of this specimen, another marten was observed along the same stretch of road carrying a rat in its mouth and, as with the individual hit by a car, was travelling across the road from shore to forest in the early dawn hours.

Nosopsyllus fasciatus, the northern rat flea, is an immigrant to North America and is widely distributed with its hosts, including along coastal British Columbia (Holland 1940, 1985) and Alaska, USA. Rat fleas predominated in our sample, which may suggest rats are a large component of the diet of marten in this location. Moreover, this was the only flea species found on the black rat specimens collected as part of this study. Although not commonly documented as prey items for marten, rats are included in the diet of marten on both on Vancouver Island (Nagorsen *et al.* 1989) and in Haida Gwaii (Nagorsen *et al.* 1991).

The large number (54) of fleas collected from the one female marten appears atypical, given the much smaller numbers collected from individual hosts in other studies. The only other similarly documented large collection from an individual mustelid was described by Holland (1985): Martha Fern Munroe and her husband (Frank Banfield) collected 38 fleas from a mink, stating that “there were about 200 other fleas” on the mink. Holland goes on to state that this was remarkable, and that he “supplied most of the flea museums of the world with this species from this collection (*Megabothris atrox* (now in the genus *Kuichenliupsylla*))...” There is one record of 88 fleas infesting a female American marten in Manitoba (TD Galloway, unpublished data), consisting predominantly of the tree squirrel flea, *O. caedens* (n=84), plus *Chaetopsylla lotoris*, *Nearctopsylla hygini*, and *K. atrox*. *Kuichenliupsylla atrox* is considered to parasitize mustelids as its true hosts. It is possible that such large flea collections from a single host are not actually unusual, but rather related to the length of time after death until the host and its fleas are contained or frozen. Future studies should consider this factor if it is desirable to maximize the numbers of fleas collected from each individual host.

While ecologists often attempt to explain the presence of species, rarely is work done to explain a species’ absence. Rats are troublesome vermin in cities and agricultural landscapes across North America, yet they have not invaded many extensive tracks of northern forest where mesocarnivores such as marten are present. Why is this the case? On a continental scale, mesopredators such as marten may be responsible for preventing the spread of rats into such habitats. Our discovery of a new host–parasite relationship may indicate this valuable ecosystem service that mesocarnivores provide—one that has not

yet been recognized or valued and may be threatened by overharvesting through commercial trapping of mustelids.

ACKNOWLEDGEMENTS

We thank Gwaii Haanas for access to their archives and unpublished information on rat distribution in Haida Gwaii. TDG thanks the Department of Entomology and the Faculty of Agricultural and Food Sciences, University of Manitoba, for their continued support. Ralph Eckerlin (Natural Sciences Division, Northern Virginia Community College, Annandale, Virginia, USA) provided supplemental information on fleas in the United States.

REFERENCES

- Bertram, D.F. and Nagorsen, D.W. 1995. Introduced rats, *Rattus* spp., on the Queen Charlotte Islands: implications for seabird conservation. *Canadian Field-Naturalist*, **109**: 6–10.
- Brown, H.E., Levy, C.E., Enscoe, R.E., Schriefer, M.E., DeLiberto, T.J., Gage, K.L., and Eisen, R.J. 2011. Annual seroprevalence of *Yersinia pestis* in coyotes as predictors of interannual variation in reports of human plague cases in Arizona, United States. *Vector-Borne and Zoonotic Diseases*, **11**: 1439–1446.
- Dawson, N. G., Colella, J.P., Small, M.P., Stone, K.D., Talbot, S.L., and Cook, J.A. 2017. Historical biogeography sets the foundation for contemporary conservation of marten (genus *Martes*) in northwestern North America. *Journal of Mammalogy*, **98**: 715–730.
- DeVos, A. 1957. Pregnancy and parasites of marten. *Journal of Mammalogy*, **38**: 412.
- Eads, R.B., Campos, E.G., and Barnes, A.M. 1979. New records for several flea (Siphonaptera) species in the United States, with observations on species parasitizing carnivores in the Rocky Mountains. *Proceedings of the Entomological Society of Washington*, **81**: 38–42.
- Ewing, H.E. and Fox, I. 1943. *The Fleas of North America: Classification, Identification, and Geographic Distribution of These Injurious and Disease-Spreading Insects*. U. S. Department of Agriculture.
- Gage, K.L., Montenieri, J.A., and Thomas, R.E. 1994. The role of predators in the ecology, epidemiology and surveillance of plague in the United States. *Proceedings of the Sixteenth Vertebrate Pest Conference*, February, 1994. Pp. 200–206.
- Galloway, T.D. 2019. Siphonaptera of Canada. *In: Biota of Canada – A biodiversity assessment*. Part 1: The terrestrial arthropods. D.W. Langor and C.S. Sheffield (Eds). *ZooKeys*, **819**: 455–462. doi.org/10.3897/zookeys.819.25458
- Golumbia, T.E., Bland, L., Moore, K., and Bartier, P. 2002. History and current status of introduced vertebrates on Haida Gwaii. *In* A.J. Gaston, T.E. Golumbia, J.-L. Martin, and S.T. Sharpe (eds.), *Proceedings from the Research Group on Introduced Species 2002 Symposium: Lessons from the Islands, 2002*. Queen Charlotte, BC: Canadian Wildlife Service Special Publication. Pp. 8–31. http://publications.gc.ca/collections/collection_2019/eccc/CW69-20-1-2007-eng.pdf.
- Gwaii Haanas. 2019. *Rats On Board* (pamphlet). Gwaii Haanas archives, Gwaii Haanas National Park Reserve and Haida Heritage Site, Skidegate, BC.
- Haas, G.E. and Johnson, L. 1981. A Siphonaptera collection from small mammals by the Canol Road, Yukon Territory. *The Canadian Entomologist*, **113**: 567.
- Haas, G.E., Kucera, J.R., Runck, A.M.Y.M., MacDonald, S.O., and Cook, J.A. 2005. Mammal fleas (Siphonaptera: Ceratophyllidae) new for Alaska and the southeastern mainland collected during seven years of a field survey of small mammals. *Journal of the Entomological Society of British Columbia*, **102**: 65–76. <http://journal.entsofbc.ca/index.php/journal/article/view/58>.
- Haas, G.E., Barrett, R.E., and Wilson, N. 1978. Siphonaptera from mammals in Alaska. *Canadian Journal of Zoology*, **56**: 333–338. <https://doi.org/10.1139/z78-045>.
- Haas, G.E., Wilson, N., Zarnke, R.L., and Johnson, L. 1989. Mammal fleas (Siphonaptera) of Alaska and Yukon Territory. *Canadian Journal of Zoology*, **67**: 394–405.
- Holland, G.P. 1940. A survey of the rat fleas of the southern British Columbia Coast with relation to plague studies. *Journal of the Entomological Society of British Columbia*, **37**: 1–5. <https://www.cabdirect.org/cabdirect/abstract/19422900519>.
- Holland, G.P. 1949. *The Siphonaptera of Canada*. Dominion of Canada, Department of Agriculture, Publication 817, Technical Bulletin 70.
- Holland, G.P. 1957. Notes on the genus *Hystrichopsylla* Rothschild in the New World, with descriptions of one new species and two new subspecies (Siphonaptera: Hystrichipsyllidae) *The Canadian Entomologist*, **89**:

309–324.

- Holland, G.P. 1985. The fleas of Canada, Alaska and Greenland (Siphonaptera). *Memoirs of the Entomological Society of Canada*, No. 130.
- Hopla, C. 1965. Alaskan hematophagous insects, their feeding habits and potential as vectors of pathogenic organisms. I: The Siphonaptera of Alaska. Fort Wainwright Aeromedical Laboratory, AAL-TR-64-12, Volume I, xiii + 267 pp. <https://apps.dtic.mil/dtic/tr/fulltext/u2/469666.pdf>.
- Lewis, R.E. and Lewis, J.H. 1994. Siphonaptera of North America north of Mexico: Hystrichipsyllidae sens. str. *Journal of Medical Entomology*, **31**: 795–812.
- Lewis, R.E., Lewis, J.H., and Maser, C. 1988. The fleas of the Pacific Northwest. Oregon State University Press.
- Nagorsen, D.W., Campbell, R.W., and Giannico, G.R. 1991. Winter food habits of marten, (*Martes americana*), on the Queen Charlotte Islands. *Canadian Field-Naturalist*, **105**: 55–59.
- Nagorsen, D.W., Morrison, K.F., and Forsberg, J.E. 1989. Winter diet of Vancouver Island marten (*Martes americana*). *Canadian Journal of Zoology*, **67**: 1394–1400. <https://doi.org/10.1139/z89-198>.
- Richards, W.R. 1964. A short method for making balsam mounts of aphids and scale insects. *The Canadian Entomologist*, **96**: 963–966.
- Rust, J.H., Cavanaugh, D.C., O’Shita, R., and Marshall, J.D. 1971. The role of domestic animals in the epidemiology of plague. I. Experimental infection of dogs and cats. *Journal of Infectious Diseases*, **124**: 522–526. <https://doi.org/10.1093/infdis/124.5.522>.
- Salkeld, D.J. and Stapp, P. 2006. Seroprevalence rates and transmission of plague (*Yersinia pestis*) in mammalian carnivores. *Vector-Borne and Zoonotic Diseases*, **6**: 231–239.
- Scharf, W. 2017. Recent Siphonaptera host and distribution records from northern Michigan. *The Great Lakes Entomologist*, **50**: 31–34. <http://scholar.valpo.edu/tglehttp://scholar.valpo.edu/tgle/vol50/iss1/6>.
- Sealy, S.G. 2012. Voucher specimens of red squirrels introduced to Haida Gwaii (Queen Charlotte Islands), British Columbia. *Wildlife Afield*, **9**: 59–65. http://www.wildlifebc.org/pdfs/9_1_Red_Squirrel_Sealy_R.pdf.
- Sealy, S.G. 2018. Insect taxa named for the Rev. John H. Keen, early naturalist on the Queen Charlotte Islands and at Metlakatla, British Columbia. *Journal of the Entomological Society of British Columbia*, **114**: 15–21. <https://journal.entsofbc.ca/index.php/journal/article/view/972>.
- Senger, C.M. 1966. Notes of fleas (Siphonaptera) from Montana. *Journal of the Kansas Entomological Society*, **39**: 105–109. <https://doi.org/10.2307/25083495>.
- Sheehy, E., Sutherland, C., O’Reilly, C., and Lambin, X. 2018. The enemy of my enemy is my friend: native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. *Proceedings of the Royal Society B: Biological Sciences*, **285** (20172603). <https://doi.org/10.1098/rspb.2017.2603>.
- Zielinski, W.J. 1984. Plague in pine martens and fleas associated with its occurrence. *Great Basin Naturalist*, **44**: 170–175.