



Insular black flies (Diptera: Simuliidae) of North America: tests of colonization hypotheses

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ABSTRACT

Aim To understand factors that facilitate insular colonization by black flies, we tested six hypotheses related to life-history traits, phylogeny, symbiotes, island area, and distance from source areas.

Location Four northern islands, all within 150 km of the North American mainland, were included in the study: Isle Royale, Magdalen Islands, Prince Edward Island, and Queen Charlotte Islands.

Methods Immature black flies and their symbiotes were surveyed in streams on the Magdalen Islands, and the results combined with data from similar surveys on Isle Royale, Prince Edward Island, and the Queen Charlotte Islands. Black flies were analysed chromosomally to ensure that all sibling species were revealed. Tests of independence were used to examine the frequency of life-history traits and generic representation of black flies on islands vs. source areas.

Results A total of 13–20 species was found on each of the islands, but no species was unique to any of the islands. The simuliid faunas of the islands reflected the composition of their source areas in aspects of voltinism (univoltine vs. multivoltine), blood feeding (ornithophily vs. mammalophily), and phylogeny (genus *Simulium* vs. other genera). Five symbiotic species were found on the most distant island group, the Magdalen Islands, supporting the hypothesis that obligate symbiotes are effectively transported to near-mainland islands. An inverse relationship existed between the number of species per island and distance from the source. The Queen Charlotte Islands did not conform to the species–area relationship.

Main conclusions The lack of precinctive insular species and an absence of life-history and phylogenetic characteristics related to the presence of black flies on these islands argue for gene flow and dispersal capabilities of black flies over open waters, possibly aided by winds. However, the high frequency of precinctive species on islands 500 km or more from the nearest mainland indicates that at some distance beyond 100 km, open water provides a significant barrier to colonization and gene exchange. An inverse relationship between number of species and distance from the source suggests that as long as suitable habitat is present, distance plays an important role in colonization. Failure of the Queen Charlotte Islands to conform to an area–richness trend suggests that not all resident species have been found.

Keywords

Aquatic insects, dispersal, island biogeography, islands, precinctive species, Simuliidae, *Simulium*, symbiotes.

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INTRODUCTION

Most of the world's islands, if they have flowing freshwater, are inhabited by black flies (Crosskey, 1990). All species of black flies breed in running water, where the larvae typically filter particulate matter from the current. The females of nearly all species are capable fliers, a necessity for locating avian and mammalian hosts from which they obtain blood to mature their eggs (Adler & McCreadie, 2002). More than 1787 species of black flies are found worldwide (Crosskey, 2002), with 255 of these in North America north of Mexico (Adler *et al.*, 2004).

Standing waters such as lakes and oceans are unsuitable for the development of black flies. The inhospitable waters surrounding islands, therefore, create filters that winnow the numbers of dispersing individuals. Most island colonizations probably have involved dispersal by inseminated females. However, the factors responsible for insular colonization – flight, human agency, phoresy (via birds and mammals), rafting, and wind – have not been tested. Dispersal by wind is the prevailing hypothesis (Crosskey, 1990, Craig *et al.*, 2001, Crosskey & Báez, 2004).

Successful colonization of islands involves two components, dispersal and establishment. Dispersal is influenced by factors such as wind direction and speed, size of the source population, and species behaviours, whereas establishment depends on factors such as habitat availability and immigration rate, which relate positively to island size (e.g. larger target, more suitable habitats) and negatively to distance (MacArthur & Wilson, 1967). Of the few studies involving black flies, the Society Islands conform to the MacArthur–Wilson predictions of area and distance (Spironello & Brooks, 2003), whereas the Canary Islands do not (Crosskey & Báez, 2004).

Precinctive species of black flies (i.e. those confined to the area under discussion, *sensu* Frank & McCoy, 1990) are found on many of the remote oceanic islands such as the Azores, Campbell Island, Crozet Islands, Juan Fernandez Islands, Norfolk Island, Saint Helena Island, Seychelles, and the Society Islands (Crosskey & Howard, 1997). Because the species of these far-oceanic islands are typically precinctive, speciation likely occurred on the islands after colonization. The simuliid faunas of distant islands generally are restricted to a few species (Crosskey, 1990), although the central-western Pacific islands are home to at least 48 precinctive species (Craig & Joy, 2000). The number of colonizations that produced these faunas and the directionality of dispersal events sometimes can be inferred from phylogenetic reconstructions in the context of geological history (Craig *et al.*, 2001).

The closer an island is to the mainland, the less likely that the species are unique to the island (MacArthur & Wilson, 1967). Each non-precinctive species on a near-mainland island thus represents at least one successful colonization event, assuming no past vicariant events (e.g. increased water levels where once existed a land bridge). The simuliid faunas of less remote islands, therefore, afford opportunities to examine aspects of black flies that might be important in

island colonization. In this study, we examined the black fly communities of four northern North American islands (or island groups), including three oceanic islands (or island groups) and one island in a large freshwater lake. One of these (the Magdalen Islands) had never been surveyed for black flies, so we also present simuliid data for this island group. Because our interpretations rely on taxonomic rigour, we used a combined morphological-cytological approach to identify the species. We tested the following hypotheses for their utility in providing insight into biological aspects that favour colonization of near-mainland islands by black flies:

(1) Ornithophilic species are more likely than mammalophilic species to be represented on islands. This hypothesis examines the possibility that bird-feeding black flies are more likely to be transported over open water by their hosts. The majority of black flies on remote oceanic islands have bifid claws, which are indicative of ornithophilic feeding habits (Crosskey, 1990), putatively because they are adapted for grasping the host's feather barbules.

(2) Multivoltine species are more likely to be represented on islands than are univoltine species. This hypothesis is based on the presence of adults of multivoltine species for more time during the year and, therefore, more opportunities to colonize islands. A corollary to the availability of more time for dispersal is the likelihood that dispersing flies would encounter more periods of weather suitable for dispersal.

(3) The genus *Simulium* is more likely to be represented on islands than are the more basal genera. This hypothesis is based on probable differences in flight capabilities between the prosimuliines and basal simuliines vs. the more derived simuliines (i.e. genus *Simulium*). These two major groups differ in wing attributes such as venational arrangement (more crowded anteriorly in *Simulium*), colour (more hyaline in *Simulium*), and the extent and density of setation (less in *Simulium*) (cf. Adler *et al.*, 2004). These differences are correlated with a broader habitat and geographic distribution of the genus *Simulium* compared with the prosimuliines and basal simuliines, which typically have not moved much beyond the mountainous regions of the world. Thicker, more spini-form setae on the wing veins of derived simuliids have been correlated anecdotally with stronger flight abilities (Crosskey, 1990).

(4) Species richness is related positively to island area.

(5) Species richness is related inversely to distance from the source area that supports the pool of potential colonists. Hypotheses 4 and 5 derive from the known effects of distance and area on dispersal and establishment of insular faunas (MacArthur & Wilson, 1967).

(6) Obligate, simuliid-specific symbiotes (e.g. parasites) occur on islands. We base this hypothesis on the ability of many simuliid symbiotes such as fungi, mermithid nematodes, and microsporidia to exist in the adult (i.e. dispersing) host, often in subclinical form (Adler *et al.*, 2004). We were particularly keen to test this hypothesis for the most distant of the four islands, the Magdalen Islands.

MATERIALS AND METHODS

Magdalen Islands survey

We surveyed black flies in streams on the Magdalen Islands (Îles de la Madeleine), a narrow group of islands roughly 100 km long in the middle of the Gulf of St Lawrence in the North Atlantic (Fig. 1). The three islands on which we found black flies are connected, or nearly so, by thin tracts of land and are here considered a single island. Sampling dates (4 and 5 May 2001, 16 June 2002 and 12 August 2001) were chosen to encompass the developmental periods of all resident species. Larval and pupal black flies were removed from all available substrate types and fixed in 2 or 3 changes of 1 : 3 acetic ethanol. Specimens were first identified morphologically. Larvae were then examined cytologically, using the Feulgen technique of Rothfels & Dunbar (1953), to ensure that all species were recognized and to determine if they were conspecific with morphologically similar populations on the mainland. Chromosomal banding patterns of larvae were compared with those of maps, representing mainland populations, available in the literature (e.g. Rothfels *et al.*, 1978) and in the laboratory of the senior author. All larval and pupal specimens are deposited in the Clemson University Arthropod Collection.

To examine the potential of symbiotic organisms to colonize the Magdalen Islands, we screened all fixed larvae, under a

dissecting microscope, for patent infections of parasites. In addition, the guts of selected larvae were dissected, cleared of the food bolus, slide mounted, and examined under a compound microscope for trichomycete fungi, which most authorities (e.g. Lichtwardt, 1986) claim to be non-pathogenic to larval black flies.

Tests of colonization hypotheses

In addition to the data from our survey of the Magdalen Islands, we used the faunistic data from the following three North American islands to examine factors that might be important in the colonization of northern islands: Isle Royale in Lake Superior, Prince Edward Island in the North Atlantic (Adler *et al.*, 2004), and the Queen Charlotte Islands (Haida Gwaii) off the coast of British Columbia (Currie & Adler, 1986) (Fig. 2). The three major islands of the Queen Charlottes are separated by no more than *c.* 1 km of water and are here considered a single island. The four study islands occur at comparable latitudes (46–54 N) and within 150 km of the mainland. We chose these islands because they (1) are the only ones in North America for which the simuliid faunas have been well surveyed and examined both morphologically and chromosomally, (2) have similar histories of glaciation, (3) accommodate no precinctive species, (4) provide numerous habitats for the immature stages, and (5) support

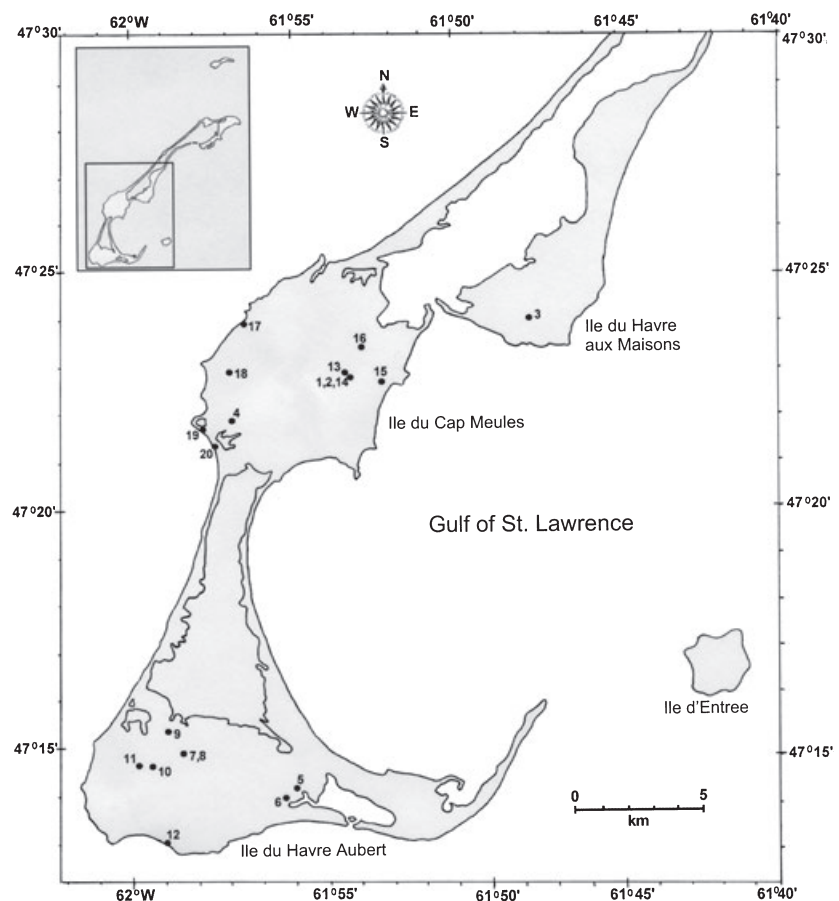


Figure 1 Magdalen Islands, Quebec, Canada, showing black fly sampling sites.

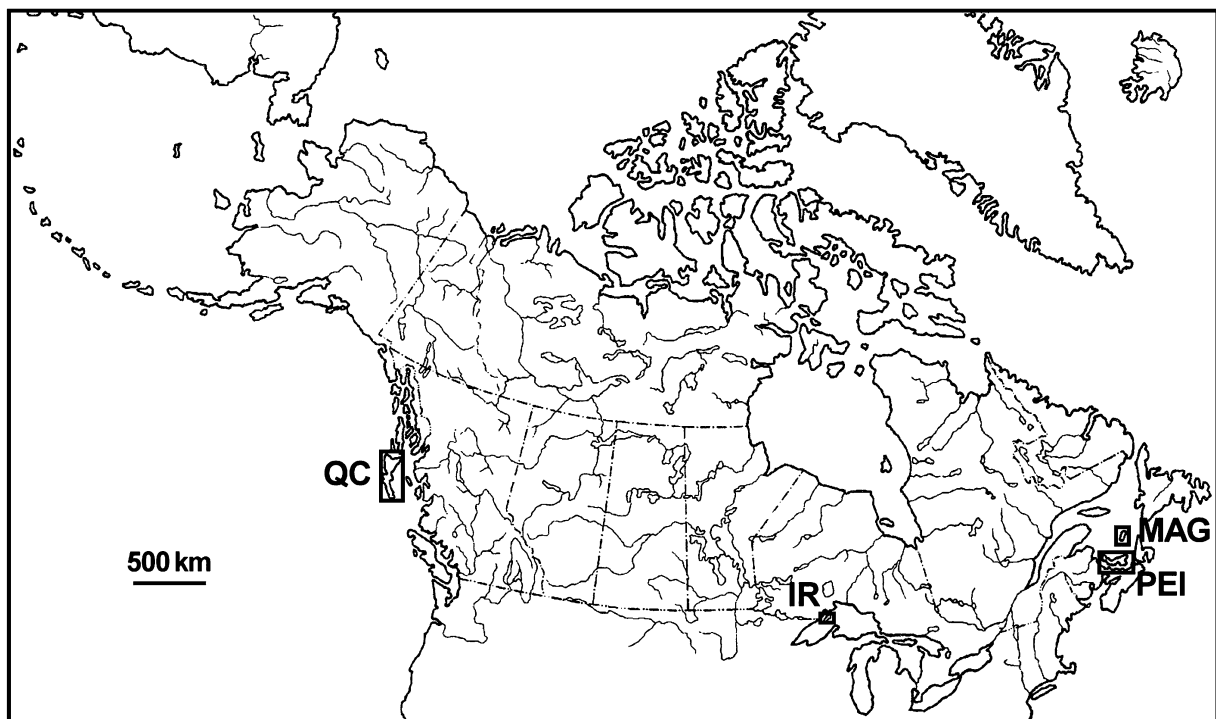


Figure 2 Map of northern North America, showing the location of islands evaluated for black fly colonization; IR, Isle Royale; MAG, Magdalen Islands; PEI, Prince Edward Island; QC, Queen Charlotte Islands.

populations of avian and mammalian hosts for blood meals. The weight of evidence indicates that the islands and their source areas were under ice during Wisconsinan times (Matthews, 1978, Dredge & Grant, 1987, Dubois, 1992, Byun *et al.*, 1999) and, therefore, must have been colonized by black flies since glacial retreat.

We examined two life-history traits and one phylogenetic component of black flies, possibly important for island colonization, by comparing their frequencies on the islands with those in the source areas. The life-history traits included host-feeding patterns (ornithophily vs. mammalophily) and voltinism (univoltine vs. multivoltine), while the phylogenetic component was the proportion of the derived genus *Simulium* vs. all other (i.e. more basal) genera on the islands. The source area was defined as an area circumscribed by a distance of 500 km outward from the periphery of each of the four islands. This area encompasses the upper limit of recorded dispersal capabilities for black flies over land (Fredeen, 1969, Garms & Walsh, 1988). Species within these source areas were determined from the distribution maps of Adler *et al.* (2004). All species found on the islands were also present within the respective source areas, with the exception of two species (*Prosimulium doveri* Sommerman and *P. travisi* Stone) on the Queen Charlotte Islands (Currie & Adler, 1986). These species are expected to occur within the source area and were included in our analyses. Tests of independence were made using the chi-square statistic. Island area and distance were determined from published atlases and topographical maps.

RESULTS

Magdalen Islands survey

Of the 20 sites sampled on the Magdalen Islands, 14 sites, representing 13 streams, had black flies during at least one sampling period (Table 1). Three genera and 13 species were present among the 2616 larvae and 315 pupae. Two species [*Simulium silvestre* (Rubtsov) and *S. rostratum* (Lundström)] represented only 0.1% of the total collected material, suggesting that a few additional rare species might be present on the Islands. Of the sites with black flies, 1–4 species (mean \pm SE = 2.6 ± 0.19) were collected per date per site.

Chromosomal differences between island and mainland populations were apparent in three species. *Stegopterna diplomutata* Currie and Hunter on the Magdalen Islands had a complex Y chromosome characterized by lack of nucleolar expression and as many as four inversions in chromosome I (cf. Basrur & Rothfels, 1959). In *S. pilosum* (Knowlton & Rowe), the diagnostic IS-3 inversion, which is fixed in all known mainland populations (Leonhardt, 1985), was polymorphic on the Magdalen Islands. In *S. hematophilum* Laboulbène, males on the Islands were heterozygous for the IIL-1 inversion and females were homozygous standard (cf. *S. venustum* CC2, Rothfels *et al.*, 1978). None of these chromosomal differences was sufficient, given current evidence, to recognize the insular populations as anything more than cytotypes (i.e. cytologically distinct but not reproductively isolated populations), particularly since the differences

Table 1 Black flies collected from the Magdalen Islands, Quebec, 2001–02

Species	Sites*	Number of larvae	Number of pupae	Symbiotes (%)†
<i>Prosimulium fuscum</i> Syme & Davies	6, 8, 15	42	0	<i>Harpella melusinae</i>
<i>Prosimulium mixtum</i> Syme & Davies	1, 8, 10, 11, 14–16	179	0	Mermithid nematode (0.6)
<i>Stegopterna diplomutata</i> Currie & Hunter	1, 6, 8–11, 14, 15	70	0	None
<i>Stegopterna mutata</i> (Malloch)	4, 5, 9, 12, 18	18	0	None
<i>Simulium pilosum</i> (Knowlton & Rowe)	6, 8, 17	203	2	<i>Coelomycidium simulii</i> (0.5)
<i>Simulium silvestre</i> (Rubtsov)	15	1	0	None
<i>Simulium moultoni</i> Adler, Currie & Wood	1, 14, 16	118	1	None
<i>Simulium vittatum</i> Zetterstedt X ₀ Y ₀ cytotype	1, 6, 8, 12, 16–18	529	41	<i>Coelomycidium simulii</i> (0.2), <i>Janacekia debaisieuxi</i> (1.9)
<i>Simulium rostratum</i> (Lundström)	6	2	0	None
<i>Simulium conundrum</i> Adler, Currie & Wood	1, 6, 8, 16	537	25	<i>Janacekia debaisieuxi</i> (0.4)
<i>Simulium vandalicum</i> Dyar & Shannon	1, 6, 8, 11, 15, 16	372	83	<i>Coelomycidium simulii</i> (0.3), <i>Janacekia debaisieuxi</i> (0.5)
<i>Simulium hematophilum</i> Laboulbène	1, 15–17	81	12	<i>Janacekia debaisieuxi</i> (1.2)
<i>Simulium molestum</i> Harris	6, 8, 11, 16	464	151	<i>Amblyospora fibrata?</i> (0.9)

*Sites are shown in Fig. 1; not all sites shown in Fig. 1 had black flies.

†*Harpella melusinae* = trichomycete fungus; prevalence of this symbiote was not calculated because only selected simuliid species and larvae were screened. *Coelomycidium simulii* = chytrid fungus. *Amblyospora fibrata* and *Janacekia debaisieuxi* = microsporidia. The prevalence of patently infected larvae is expressed as a percentage (%).

might not be unique if more mainland populations were to be examined.

Eight of the 13 species on the Magdalen Islands are univoltine. The females of three species are ornithophilic; those of the other 10 are mammalophilic. Eight species of black flies harboured at least one of the following five symbiotic taxa: one mermithid nematode, one chytrid fungus, one trichomycete fungus, and two microsporidia (Table 1). Prevalence in the larval populations did not exceed 2% for any of the symbiotes; prevalence, however, was not calculated for the trichomycete. All five of these symbiotes are specific to the family Simuliidae.

Tests of colonization hypotheses

The number of species on the islands ranged from 13 on the Magdalen Islands to 20 on Prince Edward Island (Table 2). The four islands had 56–75% fewer species than their respective source areas. All islands had smaller proportions of univoltine and ornithophilic species than did their source areas, although none of the differences was significant (Table 3). The proportions of the genus *Simulium* on the islands were not significantly different from those of the source areas (Table 3). A strong inverse relationship was evident between the number of species and distance from the source areas (Table 3). The relationship between species richness and island area was weak, particularly with respect to the Queen Charlotte Islands, which had fewer species than all but the Magdalen Islands despite their larger size.

DISCUSSION

Of the 255 species in North America (Adler *et al.*, 2004), 41 (16.1%) inhabit the four islands, with 13–20 species per island.

Two species, *S. rostratum* and *S. vittatum* Zetterstedt, were found on all four islands, while six species (*P. fuscum* Syme & Davies, *P. mixtum* Syme & Davies, *St. mutata* (Malloch), *S. silvestre*, *S. vandalicum* Dyar & Shannon, and *S. venustum* Say) occurred on three of the islands. These well-represented species are among the most common and widespread in North America. We recognize that some rare species might not have been detected on one or more of the islands.

Contrary to our hypotheses regarding factors affecting colonization, the simuliid faunas of the four islands reflected the composition of the respective source areas in the examined aspects of voltinism, blood feeding, and phylogeny. For North American islands within 100 km of their source areas, single-generation species are as likely to be represented as multi-generation species, and ornithophilic species show no greater likelihood of representation than mammalophilic species. The genus *Simulium* has no higher representation on these islands than in the source areas. The lack of a significant trend for any of the life-history or phylogenetic aspects in our study might reflect inconsequential distances (< 100 km) for the dispersal of black flies or the passage of sufficient geological time to mask the detection of any advantages that might have been manifested initially.

The absence of precinctive insular species in our study, despite observed chromosomal differences in a few species, argues for some degree of gene exchange between the islands and their source areas, although the short geological time available for colonization (since the late Wisconsinan for at least some of the islands) probably has played a role in curtailing speciation. Chromosomal divergence of island populations, relative to mainland populations, might provide some indication of the degree of gene flow. However, before the significance of chromosomal differences in the island

Species	Islands*	Voltinism†	Principal hosts‡
<i>Twinnia tibblesi</i> Stone & Jamnback	P	U	None
<i>Helodon decemarticulatus</i> (Twinn)	P	U	B
<i>Helodon onychodactylus</i> (Dyar & Shannon)	Q	U	B
<i>Prosimulium dicum</i> Dyar & Shannon	Q	U	Ma
<i>Prosimulium doveri</i> Sommerman	Q	U	Ma
<i>Prosimulium esselbaughi</i> Sommerman	Q	U	Ma
<i>Prosimulium formosum</i> Shewell	Q	U	Ma
<i>Prosimulium fuscum</i> Syme & Davies	I, M, P	U	Ma
<i>Prosimulium mixtum</i> Syme & Davies	I, M, P	U	Ma
<i>Prosimulium travisi</i> Stone	Q	U	Ma
<i>Stegopterna diplomutata</i> Currie & Hunter	M, P	U	Ma
<i>Stegopterna mutata</i> Malloch	I, M, P	U	Ma
<i>Stegopterna emergens</i> (Stone)	I	U	None
<i>Stegopterna permutata</i> (Dyar & Shannon)	Q	U	Ma
<i>Cnephia dacotensis</i> (Dyar & Shannon)	I	U	None
<i>Simulium neublosum</i> Currie & Adler	Q	U	B
<i>Simulium annulus</i> (Lundström)	I	U	B
<i>Simulium bracteatum</i> Coquillett	I, P	Mu	B
<i>Simulium pilosum</i> (Knowlton & Rowe)	M, Q	Mu	B
<i>Simulium violator</i> Adler, Currie & Wood	I	Mu	B
<i>Simulium aestivum</i> Davies, Peterson & Wood	P	U	B
<i>Simulium craigi</i> Adler & Currie	I, P	U	B
<i>Simulium silvestre</i> (Rubtsov)	I, M, P	U	B
<i>Simulium moultoni</i> Adler, Currie & Wood	M, P	Mu	B
<i>Simulium pugetense</i> (Dyar & Shannon)	Q	Mu	B
<i>Simulium hunteri</i> Malloch	Q	Mu	Ma
<i>Simulium vittatum</i> Zetterstedt	I, M, P, Q	Mu	Ma
<i>Simulium tribulatum</i> Lugger	I	Mu	Ma
<i>Simulium murmanum</i> Enderlein	I	U	Ma
<i>Simulium saxosum</i> Adler, Currie & Wood	Q	Mu	Ma
<i>Simulium decorum</i> Walker	I, P, Q	Mu	Ma
<i>Simulium rostratum</i> (Lundström)	I, M, P, Q	Mu	Ma
<i>Simulium tuberosum</i> (Lundström)	I, P	Mu	Ma
<i>Simulium conundrum</i> Adler, Currie & Wood	M, P	U	Ma
<i>Simulium vandalicum</i> Dyar & Shannon	I, M, P	Mu	Ma
<i>Simulium truncatum</i> (Lundström)	I	U	Ma
<i>Simulium venustum</i> Say	I, P, Q	U	Ma
<i>Simulium molestum</i> Harris	M, P	U	Ma
<i>Simulium hematophilum</i> Laboulbène	M	U	Ma
<i>Simulium verecundum</i> Stone & Jamnback	P	Mu	Ma

*I, Isle Royale; M, Magdalen Islands; P, Prince Edward Island; Q, Queen Charlotte Islands.

†Mu, multivoltine; U, univoltine.

‡B, birds, Ma, mammals.

Table 2 Black flies known from four North American islands, listed according to the classification of Adler *et al.* (2004)

populations can be evaluated, further prospecting in the source areas is necessary to exclude the possibility that the insular features are unique. Certain chromosomal rearrangements [e.g. in *Simulium pugetense* (Dyar & Shannon)] originally considered unique to the Queen Charlotte Islands (Hunter & Connolly 1986) are now known to be common on the adjacent mainland (Adler *et al.*, 2004).

Many of the world's near-mainland islands (i.e. those within c. 100 km of the mainland), such as the Balearic Islands, the Channel Islands, Cyprus, Isla de los Estados (Argentina), Malta, and Rhodes, have no species unique to them (Crosskey & Howard, 1997). Unfed females of some Nearctic species of

Simulium have a maximum flight range of 116 km in still air (Hocking, 1953), suggesting that females are capable of reaching these islands unassisted. Among the nearest mainland islands with precinctive species are the Canaries, where two or three of the six or seven species occur nowhere else but on these islands, the nearest being c. 115 km from the African mainland (Crosskey & Báez, 2004). The distant oceanic islands, however, are dominated by precinctive species, indicating that at some distance beyond 100 km, open water provides a significant barrier to colonization and gene exchange. Nearly all islands beyond 500 km from a continental landmass have at least some unique species of black flies

Table 3 Characteristics of simuliid faunas of selected North American islands

Island	Number of species (island/source*)	% Ornithophilic species (island/source)	% Univoltine species (island/source)	% <i>Simulium</i> (island/source)	Shortest distance to source area	Island area (km ²)
Isle Royale, MI, USA	19/56	26.3/42.0	57.9/66.0	73.7/69.6	24 km	541
Magdalen Islands, Quebec, Canada	13/52	23.1/40.4	61.5/69.2	69.2/71.2	95 km	202
Prince Edward Island, Canada	20/56	30.0/39.3	60.0/69.6	70.0/69.6	13 km	5660
Queen Charlotte Islands, British Columbia, Canada	16/36	25.0/38.9	56.2/58.3	56.2/58.3	60 km	9596

All chi-square values (not shown) for tests that blood-feeding habits (ornithophily vs. mammalophily), voltinism (univoltine vs. multivoltine), and generic representation (species in genus *Simulium* vs. species in other genera) are independent of location (island, source area) are non-significant ($P > 0.05$, d.f. = 1).

*Source is defined as the area within 500 km of the island's periphery.

(Crosskey & Howard, 1997); among the few exceptions are Reunion and Rodrigues, each with the widespread species *S. ruficorne* Macquart. These trends conform to the intuitive prediction that islands close to the source of colonizers will not show as much speciation as more distant islands (Heaney, 2000). Given the demonstrated colonization abilities of black flies on islands within *c.* 100 km of a continental landmass, we suggest, as a taxonomic corollary, that restraint be exercised in the naming of new species on near-mainland islands. Similarly, those species putatively unique to near-mainland islands should be carefully re-evaluated for conspecificity with mainland populations.

Birds, and in some cases mammals, regularly travel to the islands in our study, but if ornithophilic species do not have significantly greater representation on any of the four islands than expected, wind might be more important than hosts for transporting the flies. Although limited data exist on the ability of blood-fed black flies to be transported on hosts, several points argue against routine dispersal of black flies by birds. For instance, remote oceanic islands typically lie far off the regularly used bird-migration routes. A few reports mention that replete flies drop from their avian hosts (Garris *et al.*, 1975, Pinkovsky *et al.*, 1981), but these flies simply are more obvious than any that might remain beneath the feathers. Whether or not female black flies remain on their hosts for extended periods of time is a critical component of host-assisted dispersal that remains to be tested.

The role of human agency in the dispersal of black flies to islands is unknown, although various transports such as airplanes, ferry boats, and maritime vessels that routinely run from source areas to islands provide ample opportunity for contemporary dispersal. Nonetheless, recent introductions of non-native black flies to new geographic areas are rare. The scarcity of introduced black flies contrasts with the regularity with which many groups of insects, including numerous pest species, are introduced to new areas (Wheeler & Hoebeke, 2001). A notable exception is the putatively recent (1980s) introduction, possibly by airplane, of the mammalophilic pest *S. ochraceum* Walker (as *S. bipunctatum*) to the Galapagos Islands from the South American mainland (Abedraabo *et al.*, 1993).

Dispersal by wind remains an attractive explanation for colonization of islands by black flies. In our study, the prevailing wind direction across Canada is from west to east, although winds can blow from any direction during the black fly season and the remainders of Atlantic hurricanes can provide strong southerly winds in the North Atlantic. Airplane tow nets have captured female flies (rarely males) up to 1500 m above the ground (Glick, 1939, Choe *et al.*, 1984), well above the boundary layer, where they could be dispersed by wind. The lack of a biased phylogenetic component to insular black flies in our study, despite structural differences in wings (and possible correlated differences in flight abilities), suggests that wind rather than flight abilities might be more important in colonization. Crosskey & Báez (2004) speculated that colonization of black flies on the Canary Islands was brought about by chance dispersal on winds. Although wind might be a primary force driving dispersal of black flies to islands, we recognize that multiple means of transportation might best explain the many examples of insular black flies.

A strong negative relationship between the number of species and distance from the source, regardless of the size of the island, suggests that as long as suitable habitat is present, distance plays an important role in the colonization of near-mainland islands by black flies. Despite a weaker positive relationship between island area and species richness, island area still might play a role in colonization. The failure of the Queen Charlotte Islands to conform to an area-richness trend might be because not all of the resident species have been discovered or because certain aspects of these western islands (e.g. the species pool or the strong westerly winds) differ substantially from those of the eastern islands. Insular Newfoundland (112,790 km²) is too poorly surveyed to include in our analysis. Nonetheless, the total of 25 species, all non-precinctive, known from the island (Adler *et al.*, 2004) is greater than the total for any of the four islands in our study, conforming to the expected species–area relationship.

The availability of appropriate insular breeding habitats is important in the establishment of dispersing black flies. The stage of fluvial geomorphic development, for example, has played a major role in determining the simuliid species

composition of the Society Islands (Craig, 2003). Most of the islands in our study do not have large rivers; the widest flow on the Magdalen Islands, for example, is only *c.* 3–5 m at peak flow. The lack of larger flows could exclude big-river species such as *Helodon pleuralis* (Malloch), *Ectemnia invenusta* (Walker), and members of the *S. jenningsi* group from becoming established if they reached the islands. Dispersal distances up to 170 km have been reported for members of the *S. jenningsi* group on the mainland (Amrine, 1982, Fredeen, 1985), so the lack of any members of this group on the islands in our study, despite their occurrence in the source areas of the three eastern islands, is telling.

Parthenogenesis and obligate autogeny (i.e. egg production by species incapable of blood feeding) might be advantageous for island colonization. In our study, the only parthenogenetic species (*Stegopterna mutata*) in the source areas is also found on the three eastern islands. Of the seven obligately autogenous species in the source areas of our study, only three inhabit the islands: *Twinnia tibblesi* Stone & Jamnback on Prince Edward Island and *Cnephia dacotensis* (Dyar & Shannon) and *St. emergens* (Stone) on Isle Royale. Arctic islands are dominated by a few species with either or both traits, but whether this situation is related to a colonization advantage or to the preponderance of these species in the source areas of the Far North is unclear. *Prosimulium ursinum* (Edwards), a parthenogenetic, obligately autogenous species, is the only black fly on Bear Island (74°30' N), Norway (Davies, 1954). Victoria Island, Canada, which is north of the Arctic Circle, has four known species, all of which are obligately autogenous and two of which are parthenogenetic (Adler *et al.*, 2004).

Our study demonstrates that black flies on islands within 100 km of their source areas support a diversity of symbiotes. The simuliids on the Magdalen Islands, for example, have at least five species of symbiotes. The prevalence of patently parasitized larvae on the Magdalen Islands is comparable with the levels found in mainland populations (McCreadie & Adler, 1999). Transportation of the symbiotes by adult black flies is the most parsimonious explanation for their occurrence on islands, but does not rule out other means such as transportation of resistant stages (e.g. spores) by other organisms. Any symbiote requiring an alternate host, as suggested for microsporidia and chytrid fungi of black flies (Lacey & Undeen, 1988), would experience an additional barrier to colonization, being dependent on insular establishment by two taxonomically different hosts. Other than the presence of trichomycete fungi on many oceanic islands (e.g. Misra, 1998), the existence of symbiotes in simuliid species on remote islands is largely unknown. We predict that most are scarce and, like their hosts, precinctive.

Symbiotes could affect both the dispersal and establishment success of colonists. Trichomycete fungi, which can be beneficial under certain circumstances (Horn & Lichtwardt, 1981), could increase the fitness of colonists, whereas parasites such as mermithid nematodes could be detrimental. However, the role that symbiotes, most of which are parasites, play in

determining dispersal probability and ability, influencing the establishment of new colonists, regulating the population dynamics of insular species, and structuring insular communities is unknown.

In conclusion, we found no life-history or phylogenetic traits related to the presence of black flies on islands in northern North America. An examination of these traits for simuliids on islands in other zoogeographic regions of the world, as well as in springs (i.e. 'islands') in open deserts where similar colonization processes should apply, would be worthwhile. The lack of precinctive species of black flies on most of the world's islands within *c.* 100 km of their source areas argues for good colonization abilities and gene flow across open waters. At some point roughly between 100 and 500 km, however, island colonization becomes a far more formidable feat.

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