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THE ROLE OF NEOTROPICAL BLACKFLIES (DIPTERA: SIMULIIDAE) AS VECTORS OF THE ONCHOCERCIASIS: A SHORT OVERVIEW OF THE ECOLOGY BEHIND THE DISEASE

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ABSTRACT

The Blackflies (Diptera: Simuliidae) are a cosmopolitan dipteran family, comprising 2102 described species. Although insects of this family are widely distributed, their immatures are restricted to areas where suitable lotic conditions allow their development. While the Onchocerciasis has been largely studied over the years, it still lacks a more integrated approach with the vector ecology. In this paper, we examine the ecological factors that potentially play a role in the disease dynamics. Our aim is to identify the ecological factors that are potentially important in the vector dynamics and the gaps in the current knowledge of blackfly ecology that could lead to a better understanding of the underlying factors behind the disease dynamics.
Keywords: Blackflies; onchocerciasis; ecology.

RESUMO

O PAPEL DOS SIMULÍDEOS NEOTROPICAIS (DIPTERA: SIMULIIDADE) COMO VETORES DA ONCOCERCOSE: UMA BREVE REVISÃO SOBRE A ECOLOGIA POR TRÁS DA DOENÇA. Os simulídeos (Diptera: Simuliidae) são uma família cosmopolita dentro da ordem Diptera, compreendendo 2102 espécies descritas. Embora insetos desta família sejam amplamente distribuídos, seus imaturos estão restritos a áreas nas quais existam condições lóticas apropriadas para o seu desenvolvimento. Enquanto a Oncocercose foi extremamente estudada ao longo dos anos, ainda existe uma carência numa maior integração entre o conhecimento da ecologia dos vetores e o estudo da doença. Neste artigo, são examinados os fatores ecológicos que potencialmente desempenham um papel na dinâmica dos vetores da doença e as lacunas no atual conhecimento que poderiam eventualmente levar a uma melhor compreensão dos fatores por trás da dinâmica da doença.
Palavras-chave: Simulídeos; oncocercose; ecologia.

RESUMEN

EL PAPEL DE LOS SIMÚLIDOS NEOTROPICALES (DIPTERA : SIMULIIDAE) COMO VECTORES DE LA ONCOCERCOSIS: UNA BREVE VISIÓN DE LA ECOLOGÍA DETRÁS DE LA ENFERMEDAD. Los simúlidos (Diptera: Simuliidae) son una familia cosmopolita dentro del Orden Diptera que comprende 2102 especies descritas. A pesar de que los insectos de esta familia tienen distribuciones amplias, los estadios inmaduros están restringidos a áreas con condiciones lóticas apropiadas para su desarrollo.

Mientras la oncocercosis ha sido ampliamente estudiada a lo largo de los años, hace falta todavía una mayor integración con la ecología de los vectores causantes de la enfermedad. En el presente artículo examinamos los factores ecológicos que podrían desempeñar un papel importante en la dinámica de la enfermedad. Nuestro objetivo es identificar los factores ecológicos que son potencialmente importantes en la dinámica de los vectores y los vacíos en el conocimiento actual de la ecología de los simúlidos que podrían llevar a un mejor entendimiento de los factores detrás de la dinámica de la enfermedad.
Palabras clave: Simúlidos; oncocercosis; ecología.

INTRODUCTION

Vector-borne diseases are often approached as a three (parasite, vector and host) or four (parasite, vector, reservoir and host) compartmental model. Although such interpretation may prove itself useful for short term solutions, long term, sustained disease control should incorporate the ecosystem in the model (Ellis & Wilcox 2009). Another problem is that most of the current approaches on the dynamics of vector-borne diseases are simplistic approximations that deal mostly with the influence of abiotic factors in each of the compartments of the model, neglecting the influence of the biotic component of the ecosystem, such as density dependent factors leading to population regulation.

One form of interpreting disease dynamics is as the overlapping of the niches of the populations that are directly involved in the transmission (parasite, vector, human host and host reservoir). The ecological theory postulates that competitive pressures shape the realized niches of organisms, so, a more realistic approach to disease dynamics should incorporate, in the basic model, some additional compartments, such as the dynamics of the vector main predator, competitor or parasite. However, such approach demands a good knowledge of the ecological traits of the organisms involved in the model, which is not always the case.

The study of blackflies as disease vectors generally follows the previously described tendency, focusing on the Vectorial Capacity (Garret-Jones 1964), which is a concept originally developed for anopheline mosquitoes, defined as the average number of inoculations which arise from a single case of the disease in a unit of time, assuming that all flies biting that host become infected (Dye & Baker 1986). As some of the components of the Vectorial Capacity are difficult to measure, such as the amount of bites by infective flies that lead to an infection, in general what is measured is a composite index that varies proportionally to the Vectorial Capacity, which can be used to compare transmission between places and times (Dye & Baker 1986, Dye & Hasibeder 1986). This index is usually based on factors that are both potentially important and measurable, in the case of blackflies, these might be biting rates, latent period of parasite in the flies, survival rate per gonotrophic cycle and the amount of flies that release all infective larvae at a blood meal (Birley *et al.* 1983).

In this paper, the aim is to draw an overview of the relevant ecological factors involved in the disease dynamics, and identify gaps in the literature in order to build more realistic Onchocerciasis dynamics models.

THE ECOLOGY OF BLACKFLIES

Blackflies have a worldwide geographic range, being present in all continents, except Antarctica, as well as in most islands with streams capable of supporting their immatures, with the exception of Hawaii, the Falkland Islands and isolated desert islands (Currie & Adler 2008). The distribution of Simuliidae species can be locally restricted to areas where the appropriate lotic conditions for the breeding of their immature is present (Eymann 1993), hence, blackfly immatures are restricted to rivers and streams, due to their filter feeding habit. For immatures, appropriate current velocity can be considered a resource (Eymann 1993), a key dimension of the larval niche, because of its direct relation to feeding efficiency (Lacey & Mulla 1977, Kurtak 1978, Braimah 1987).

Blackfly larvae are usually present in almost every lotic habitat type (Burgherr *et al.* 2001), and they are often found at very high densities in lake outlets (Sheldon & Oswood 1977, Wotton 1987, Malmqvist 1994). This happens because of the great amount of organic matter exported from the lake which is a great source of food for Simuliidae larvae. On the other hand, literature shows that reservoirs from hydroelectrical schemes have an opposite effect on black fly populations below the dam (De Jalon *et al.* 1988, Céréghino & Lavandier 1997), because of the changes in their thermal and flow regimes.

The pest potential of blackflies is influenced by many factors, which include characteristics of their breeding site, seasonal abundance, flight range, mating and ovipositing behavior (Lake & Burger 1983). The major characteristics of the breeding site associated to blackfly larvae distribution and population dynamics are: distance from lake outlets, stream/river size, food supply, substratum, current velocity, depth, light and physico-chemical conditions (Ross & Merrit 1987). There are species adapted to different water current velocities (Palmer & Craig 2000, Roberts & Okafor 1987, Figueiró *et al.* 2008), different river sizes (Shelley *et al.* 2001, Hamada *et al.* 2002, Figueiró *et al.* 2006), etc.

Although the effect of abiotic factors on the occurrence and population dynamics of blackflies has been extensively studied in the Amazon forest, particularly in the works of Shelley *et al.* (2001), Hamada *et al.* (2002), Py-Daniel *et al.* (1999), Gorayeb (1981), there is little information on the effect of biotic factors such as competition and predation.

BLACKFLIES AND THE ONCHOCERCIASIS

The main disease transmitted by blackflies is the Onchocerciasis, which is caused by the nematode *Onchocerca volvulus* (Leuckart). This disease is most prevalent in Africa, but some endemic areas are also observed in the Latin America. Most of the literature has been historically concentrated in the the ecology of black flies from Nearctic (*e.g.*, Adler & Kim 1984, Shipp & Procunier 1986, Corkum & Currie 1987, Pistrang & Burger 1988, Ciborowski & Adler 1990, McCreadie & Colbo 1991, 1992, Eymann 1993, Adler & McCreadie 1997) and Palearctic (*e.g.*, Halgos *et al.* 2001, Wotton 1977, Malmqvist *et al.* 1999, 2004) regions. There are relatively few studies on the species from Neotropical (*e.g.*, Coscarón *et al.* 1996, Grillet & Barrera, 1997, Hamada 1993a, 1993b, 2002, Araújo-Coutinho *et al.* 1999, Strieder *et al.* 2002, Figueiró *et al.* 2006, 2008) and Afrotropical (*e.g.*, Roberts & Okafor 1987) regions.

This brings us to the first problem in applying the previously suggested approach to the study of Onchocerciasis dynamics: while some works on blackfly ecology of afrotropical and neotropical simuliids may be found in the literature, they are relatively scarce, thus, producing a fragmented knowledge of the ecological traits of this fauna.

In the Americas, The Onchocerciasis Elimination Program in the Americas (OEPA) has the overall goal to eliminate onchocerciasis as a public health problem, culminating in the elimination of the infection in the six disease-endemic countries of Latin America (Rodriguez-Perez *et al.* 2008). However, its approach is based in the epidemiology of the disease: the strategy applied by the OEPA is to encourage the endemic countries to provide sustained ivermectin treatment to at least 85% of the susceptible population, thus, it is a host-oriented strategy, rather than an integrative approach that encompasses the ecological factors behind the disease, such as the vector dynamics. By the end of 2007, all six endemic countries had established effective national programs.

One of the main obstacles to building better and more realistic models of the onchocerciasis transmission in the Neotropical region is the lack of integration between the ecological and epidemiological studies of the disease and their vectors. While there are extensive works on various aspects of the ecology of Amazonian blackflies, such as Hamada (1993a, 1993b), Grillet & Barreira (1997), Hamada & McCreadie (1999), Hamada & Adler (2001), Hamada *et al.* (2002), McCreadie *et al.* (2005), these studies do not approach the disease. On the other hand, the studies on the disease dynamics often focus on an epidemiological perspective (*e.g.*, Vivas-Martinez *et al.* 2000) or deal with ecological factors in a superficial way.

POPULATION REGULATION AND DENSITY-DEPENDENT PROCESSES INVOLVED IN BLACKFLY AND ONCHOCERCA DYNAMICS

Even though extensive lists of predators of black flies can be found in the literature (*e.g.*, Werner & Pont 2003), the quantitative importance of predators and how their life cycles match those of the prey is poorly known (Malmqvist 1994). In fact, population regulation of blackflies by predators is a topic that has rarely been approached in literature, which is mostly composed of reports on predation of Simuliidae by other organisms without further assessments on their effect on the blackfly population dynamics.

On the other hand, entomopathogenic infections are widely studied, due to the perspective of their potential use as biological control agents. The main blackfly parasites described n the literature are nematodes and microsporidians. Microsporidians are obligate intra-cellular parasites that can cause high mortality rates, along with reduced adult longevity and fecundity (Castello Branco Jr. 1999). Their species diversity and seasonal occurrence are poorly known in most localities, even though they are common pathogens of blackflies, and their mechanisms for transmission are unknown (Lacey & Undeen 1986). Araújo-Coutinho *et al.* (2004) studied the epizootics and enzootics of microsporidians in two populations of *Simulium pertinax* Kollar larvae in the Serra dos Órgãos region (Brazil), describing for the first time the seasonality of the infection rates in the Neotropical region. Nascimento *et al.* (2007) showed that there is a negative correlation between *Amblyospora* (Microsporida) occurrence in blackfly larvae and water temperature, in a natural population of *Simulium pertinax* in southeastern Brazil.

Other important agents in the natural population regulation of simuliids are the nematodes. Gaugler & Molloy (1981) showed in laboratory studies that nematode infections by *Mesomermis* Daday could lead to a 50% death rate among *Simulium vittatum* Zetterstedt larvae. Molloy (1987) reported that, when *Gastromermis* Micoletzky nematodes were introduced to watercourses where they did not occur previously, an important reduction in the number of blackfly larvae occurred after two years. In South America, *Mesomermis nortensis* Camino, *Mesomermis* sp. and *Gastromermis* sp. have been reported parasiting *Simulium lahillei* Paterson & Shannon larvae in watercourses in Argentina (Camino 1991). Basáñez *et al.* (1995) showed that *O. volvulus* larval development to the infective stage is also regulated by density-dependent mechanisms, acting at the early phase of microfilarial migration out of the blackfly's bloodmeal.

Some studies have suggested a comensal relationship between Trichomycete fungi and blackflies. Trichomycetes (Zygomycota) are cosmopolitan filamentous fungi that live in the guts of various arthropods such as larval blackflies (Lichtwardt 1986, 1996). In fact, McCreadie *et al.* (2005) showed that not only the larvae colonized by trichomycete did not show any negative effect to their fitness in relation to tricomycete-free larvae, but it also showed that stressed larvae with the fungi presented higher survival than trichomycete-free ones, thus, indicating a symbiotic rather than parasitic relationship.

ECOLOGICAL FACTORS AFFECTING VECTOR CAPACITY

In most female adult of Simuliidae the mouth parts are perfectly adapted for bloodsucking vertebrate host. The piercing structures consist of four different parts evolved by a proboscis: the labrum that stretch the host's skin; one pair of mandibles that incise the skin; one pair of maxilar lacinia that anchors the head in the skin; and the hypopharynx that pierces the wound and injects it with saliva (Sutcliffe & McIver 1984, Crosskey 1993). But, there are about 50 species, among the 2,102 Simuliidae species (Adler & Crosskey 2010, Hamada *et al*. 2010), wherein the proboscis is short and the piercing structures are weak, and therefore unable to bite. In the cibarium the area between the arms is usually unarmed, but some *Simulium* subgenera, such as *Psaroniocompsa*, *Psilopelmia*, *Psilozia* and *Hemicnetha*, have an elaborate cibarial armature with spines and spicules (Adler *et al*. 2004). Some authors suggested that this cibarial armature destroys part of the ingested microfilaria that could keep the fly alive and establish a parasitic infection (Sutcliffe & McIver 1984; Crosskey 1990), thus, simuliids with armed cibaria inflict damage to an important but variable proportion of ingested microfilariare, which reduces not only vector mortality but also vector competence (Basáñez & Ricárdez-Esquinca 2001).

In the Neotropical Region, 59 species were recorded biting humans at least once (Coscarón & Coscarón-Arias 2007). Among those 59 species, only two (*Lutzsimulium simplicicolor* (Lutz) and *Paraustrosimulium anthracinum* (Bigot)) do not belong to the genus *Simulium*. However, no blackfly species feeds exclusively on humans, and relatively few species include humans among their usual hosts

(Currie & Adler 2008). In the Neotropical Region, very few species are considered pests and their anthropophilic habits always vary geographically. For example, *Simulium* (*Chirostilbia*) *pertinax* is a vicious human biter in Southern and Southeastern regions of Brazil, but bites occasionally or does not bite humans in other regions. Only eight species are involved in the onchocerciasis transmission in the Neotropical Region: *Simulium* (*Aspathia*) *metallicum* Bellardi (Mexico, Guatemala and Venezuela); *Simulium* (*Notolepria*) *exiguum* Roubaud (Venezuela, Colombia and Ecuador); *Simulium.* (*Psaroniocompsa*) *oyapockense* Floch & Abonnenc (Brazil); *Simulium.* (*Psilopelmia*) *ochraceum* Walker (Mexico and Guatemala); *Simulium* (*Psilopelmia*) *quadrivittatum* Loew (Ecuador); *Simulium.* (*Trichodagmia*) *guianense* Wise (Brazil) (Crosskey 1993), *Simulium incrustatum* Lutz (Brazil) and *Simulium roraimense* Nunes de Melo (Brazil).

Lacey & Charlwood (1980) is probably the first, or one of the first efforts in Brazil to assess the biting activities of the Amazonian vector species and its association to environmental factors. Other relevant studies include Shelley *et al.* (1997), with focus on the Amazonian onchocerciasis , which reported *Simulium incrustatum* and *Simulium guianense* as the main vectors in the highlands, while *Simulium oyapockense* / *Simulium roraimense* are the main vectors in the lowlands, with *Simulium exiguum* being also an important vector in the wet season. The study also showed that even though *Simulium oyapockense* / *Simulium roraimense* is not an efficient vector, it occurs in high densities and have a bimodal biting activity pattern, which makes it effective as vector.

Andreaze *et al.* (2002) related that biting activity of *S.incrustatum* is influenced by temperature, humidity, luminosity and nebulosity. Medeiros *et al.* (2006) showed that the biting activity of *Simulium argentiscutum* Shelley & Luna Dias varied according to the precipitation (dry and rainy seasons), and that during the dry season, it was greater in the early morning, showing a positive association with humidity. However, during the rainy season, it was negatively associated with the same factor. The wind was also found to be an important factor, with biting activity reducing abruptly at wind speed higher than 10 km/h. Takaoka *et al.* (1984), studying the effect of temperature on the development of *Onchocerca volvulus* in *Simulium ochraceum*, suggested that the distribution of onchocerciasis in Guatemala may be related to ambient temperature and to day/night temperature cycles.

Py-Daniel *et al.* (2000) studied the association between seasonal changes in the breeding sites and the alternating dominance between the vector species *Simulium guianense,* which is more abundant in the dry season and at the end of the wet season, and *Simulium incrustatum* which is dominant during the wet season, showing that these alternating dominances is related to the substrate types available at the rivers.

Shelley (1988) reviewed studies on the Simulidae species in Latin America and reported their presence in the diversity of topographies, differently from what is observed in Africa. While in Guatemala/Mexico and northern Venezuela, endemic *foci* are located in the highlands, in Colombia and Ecuador, they are located in the lowlands. In the Brazil and Venezuela there are two *foci*, one in the highlands, and other in the lowlands. While the highlands are hyperendemic most of the times, lowlands are usually hipoendemic, even though there are exceptions.

The flight range of a vector is also an important component of its vector capacity. There are some efforts in the literature to establish the flight capacity of some black fly species, such as Bennett & Fallis (1971) and Baldwin *et al.* (1975). Most of the studies on black fly dispersal capacity are done through radioactive markers, a method that some authors pay some criticism, as it is suggested that the radiation may have deleterious effects on the individuals, thus, affecting its dispersal potential (Hunter & Jain 2000). Dalmat (1950) studied in Guatemala the dispersal of black fly adults with aniline markers, and later compared these results with the flight capacity of *Onchocerca* infected blackflies (Dalmat 1952).

CLIMATE CHANGE AND THE SIMULIIDAE

The current literature suggests that interannual and inter-decade climate variability have a direct influence on the epidemiology of vector-borne diseases. It is expected that by 2100 the average global temperatures will have risen by 1.0–3.5 °C, increasing the likelihood of many vector-borne diseases in new areas (Githeko *et al.* 2000). The effects of global climate change in blackflies have been poorly studied. Cilek & Schaediger (2004) related the severe infestation of *Simulium slossonae* Dyar & Shannon in Florida observed in 1998 in response to the increased precipitation in the winter of 1997/1998 caused by the El Niño phenomenon, while Kazanci (2006) assessed the relationship between Simuliidae species and some physical properties of their habitats and how climate change impacts species distribution using canonical correspondence analysis.

OVERVIEW AND PERSPECTIVES

The current literature is scarce relative to aspects of the ecology of neotropical blackflies, specially the effect of biotic factors. While abiotic factors have received attention, such as water velocity (Santos-Jr *et al.* 2007, Figueiró *et al.* 2008), pH and substrate type (Hamada *et al.* 1997, Pepinelli *et al.* 2005, Figueiró *et al.* 2006), the biotic factors seem to be widely neglected in the literature.

Most of the current literature on vector species focus on the biting activity of the adults, and correlate this with environmental data, however, most of the times these data are not crossed with the breeding sites, which are often unknown. There is a tendency towards studies on bionomic and population ecology of the vector species, however, their interactions with other species, which may prove itself very relevant to the population dynamics, and thus, with the disease dynamics, are ignored. We believe that a community ecology and complex interactions approach to blackfly vector species studies should be more common in the future.

For the moment, building more realistic models seems to be a distant reality, because of the lack of data on population regulation processes by natural competitors and predators. On the other hand, due to the biological control efforts, there is currently some knowledge on the natural pathogens of blackfly larvae that should be taken in account when building models for Onchocerciasis dynamics.

Another ecological interaction that could have an important impact on the population fluctuation of Simuliidae species is the symbiosis between trichomycete fungi and blackfly larvae. Since this interaction increases the survival rates under stress conditions (McCreadie *et al.* 2005), it acts directly in the rate of population growth (r), thus impacting the whole population dynamics.

The review of the current literature shows that studies on blackfly ecology and Onchocerciasis dynamics are separated efforts at the moment. We believe that in order to reach a better understanding of the disease, there should be more integration between ecological studies of the vector and the epidemiological studies of the disease in the form of interdisciplinary projects.

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