Ecology and Biting Activity of *Simulium damnosum* Complex in Nigeria: A Review

Ezugbo-Nwobi, I. K.* and Eneanya, C. I.
Department of Parasitology and Entomology, Nnamdi Azikiwe University, Awka, Nigeria.
*Corresponding author: ifeomaezugbonwobi@yahoo.com.

**ABSTRACT**
Dipterous insects of *Simulium damnosum* (Theobald) species complex transmit the parasite, *Onchocerca volvulus* which causes human onchocerciasis commonly called river blindness. *S. damnosum* breeds mainly in fast flowing, well-oxygenated water bodies. Its distribution is not even across Nigeria as there is correlation with basic geology. This is because the riverine conditions which create suitable breeding sites for the vector are most common where the African Precambrian basement rock is exposed to break the flow of water and create rapids. Ecological parameters such as water temperature, water pH, dissolved oxygen, ammonia content, rainfall, current velocity, relative humidity and conductivity influence the breeding of *S. damnosum* complex in Nigeria. Ecological factors which influence the adults include wind, humidity and light. Biting activity is highly seasonal in Nigeria. It ceases for several months in the long dry season of the northern savannas when rivers stop flowing, or are reduced to trickles and resumes only when rivers run again in the rains. On the other hand, where the climate is almost uniform throughout the year and rivers run continuously, biting activity occurs all-year round. Biting occurs outdoors at any daylight hour although each species may have its preferred time.

**Key words:** Ecology; Biting activity; *Simulium damnosum* s. l.

**INTRODUCTION**
Onchocerciasis which is a serious public health problem of considerable magnitude in many riverine areas of West Africa, is caused by a nematode parasite *Onchocerca volvulus*. The disease is prevalent in 35 countries of the world of which 28 are in Africa and Nigeria accounts for one quarter of the global infection (WHO, 2009). In West Africa, transmission is by members of the *Simulium damnosum* (Theobald) species complex (Boakye, 1999). The fly is widely distributed in Africa, ranging from Senegal in the West to Somalia in the East, from latitude 19°N to as far as 30°S in southern Africa. It occurs in savanna areas, rain forest, plateau areas and in the highlands. The species breed mainly in fast flowing, well-oxygenated streams and rivers. The distribution of *Simulium* breeding is not even across Nigeria (Adeleke et al., 2011) and biting activity can be highly seasonal.

*S. damnosum* is made up of a complex of sibling species described on the basis of cytotaxonomic identification which depends on variations of the larval polytene chromosomes (Vajime and Dunbar, 1975). Nine sibling species of *S. damnosum* complex have been taxonomically identified and documented in West Africa. The species include *S. sirbanum, S. damnosum sensu stricto, S. dieguerense, S. sanctipauli, S. soubrense, S. squamosum, S. yahense, S. leonense, S. konkorense* (Ibeh et al., 2006). The first three species are known as savanna flies while the rest belong to the forest group. Therefore, for any form of onchocerciasis control measure to be effective it is necessary that the ecology and behaviour of the *Simulium* vector species is properly understood.

**Ecology of Simulium Damnosum**
The Simuliidae have been the focus of extensive ecological investigations (Kim and Merritt, 1988; Crosskey, 1990; Adler et al., 2004). The ecology of the larvae is particularly well advanced, in great part because larvae can be identified to the species level using cytogenomic analysis. Macro- and microhabitat studies, species
interactions, community structure, and symbioses are all the foci of active study.

The members of the *Simulium damnosum* complex are classified into savanna and forest species according to their relative abundance in the respective climatic zones of West Africa and this largely depends on their preferred habitats (Boakye, 1999). Eco-climatic factors are known to affect onchocerciasis distribution in Nigeria (Okwa, 2004). Several species of blackfly vectors differ in their behaviour which causes differences in the disease transmission processes.

**Distribution**

*S. damnosum* is widespread over most parts of the country but the distribution is not even. There is a clear correlation with basic geology (Adeleke, 2010), as the riverine conditions which create suitable breeding sites for the vector are common mostly where the African Precambrian basement rock is exposed to break the flow of water and create rapids. Although parts of the country with sedimentary formations have been known to have mainly muddy or shallow sandy rivers that are unsuitable for *Simulium* breeding (except when man-made sites such as river drifts allow temporary opportunistic breeding) harder strata in the sand stones of such areas could also cause lodging of the river beds that breaks the flow thereby creating breeding sites. Confinement of breeding sites to Precambrian areas is therefore not absolute. Also, in parts of the mid-north and the northeast, volcanic intrusions occur that can also provide rapids suited to vector breeding similar to those of Precambrian areas (Okwa, 2004).

Savannah-dwelling group of *S. damnosum* s.l are usually found in savanna zone and the forest dwelling group are confined to the forest zone (WHO, 1995). In view of this, it is expected that only the forest-dwelling group of *S. damnosum* s.l will be found in the forest zone. The presence of the savannah-dwelling group of *S. damnosum* s.l in forest region could be due to the migration of the savannah-dwelling group of *S. damnosum* s.l flies into the forest zone from northern part of Nigeria which is savannah. This may be due to massive deforestation in the forest area, from farming, logging and other agricultural activities (Ecosystems and Human wellbeing, 2005). Some studies have reported the impact of deforestation on the abundance and distribution of vectors of diseases (Yasuoka and Levins, 2007; O’Sullivan et al., 2008). The implication of the presence of the savannah-dwelling group of *S. damnosum* s.l is the possible transmission of the blinding form of onchocerciasis which is associated with savannah-dwelling group (Nwoke et al., 1991). The establishment of savannah-dwelling group in the area will consequently result in changes in transmission, epidemiology and the pathology of the disease (Nwoke and Úwazie, 1991).

*S. damnosum* s.s and *S. sirbanum* are both widespread in the northern savanna. But the former apparently does not extend its range into south west, whereas the latter occurs in this area or at least near Lokoja (Bassey, 1998). *S. squamosum* is widespread in forest-savanna mosaic/forest areas of Nigeria including Jos Plateau periphery and is likely to be found widely in mid-central part of the country because of its above-average rainfall and associated heavy riparian vegetation in relation to latitude; it occurs in southern Adamawa and widely in south west and has been identified in Oji River (Manafa and Isama, 2002). *S. squamosum* has been known to be very widespread across Nigeria and has been identified from mountain, forest and Guinea savanna zones, but not yet the Sudan Savanna, being the dominant species throughout the year in the mountain areas but more abundant in the dry season samples in the Guinea savanna (Ibeh et al., 2006). *S. squamosum* is considered to be an efficient and important vector of *O. volvulus* in West Africa and has been known to have a patchy distribution in both West and Central Africa. This focal distribution might be expected to promote taxonomic variation and potential speciation. Nwoke et al. (1991) reported the subgrouping of six main vector species found in Nigeria on the basis of phytogeographical condition with *S. sirbanum* and *S. damnosum* s.s featuring as savanna forms, *S. sanctipauli* and *S. soubrense* as rainforest forms thriving in big rivers, *S. yahense* and *S. squamosum* are also rain forest forms but are breeding in small rivers, while some varieties of *S. squamosum* are found in pockets of rainforest rivers within the savanna zone. The sanctipauli subcomplex is widespread in the southwest, its *S. soubrense* constituent has been identified in the mid-north as well as south of...
River Niger, and the ‘Bessa’ form has been chromosomally identified from Ogun and Osun River (Meredith et al., 1983). The area north of Benue River towards northern Cameroon and Chad where the species complex is widespread and associated with severe ocular onchocerciasis, probably both sirbanum and damnosum s.s. occur here. The distribution of the different cytospecies of the S. damnosum complex found in Nigeria gives an insight into the distribution pattern in Nigeria. This is evidenced in the migratory movements of the adult flies over hundreds of kilometres, at least under some meteorological conditions makes it essential to consider the situation of any country where control is planned in relation to its neighbouring areas.

Physico-Chemical Characteristics of the Breeding Sites

The physico-chemical characteristics of the rivers are known to be correlated with the distribution of different species of blackflies (Crosskey, 1990). S. damnosum s.l. is traditionally considered to be a species of fast-flowing, broken ‘white-water’ in rapids of rivers, but also medium-sized streams, especially in upland areas (Crosskey, 1990). The breeding distribution of the S. damnosum complex is generally determined by changes in river volume and physical characteristics, especially when seasonal rainfalls determine the river volume (Adelke et al., 2011).

Among the chief ecological factors governing the existence of breeding places are adequate water velocity which is linked to food supply and the presence of suitable supports. The duration of larval development depends on adequate temperature. In West Africa, it usually takes 8-10 days. Other factors influencing productivity of breeding sites include hydrological variations, species competition, parasites, predators and man-made factors. There are indications that different species settle on different kinds of support (rocks or vegetation). Preliminary observations have shown that some hydrochemical factors (e.g., pH and conductivity) may have some influence on the development and distribution of the larval population of certain cytospecies.

Grunewald (1976, 1981) noted that members of the S. damnosum complex in West Africa have not been found in rivers with water velocities of <0.4 or >2.4 m/s, nor from rivers with water temperatures lower than 16.8°C or greater than 33°C (most being found in water at 18.3 – 31.8°C in West Africa; Ocran et al., 1982). Members of the complex have not been found breeding in rivers with high levels of ammonia (>0.5 mg NH₃-N/litre), a sign of organic pollution, although some other Simulium species such as S. hargreavesi and S. adersi, are found in such rivers (Grunwald, 1976, 1981). S. damnosum s.l. only breeds in water with relatively high oxygen saturations (75%>105%), whereas other species, such as S. alcocki and S. unicornatum, have been recorded in rivers with only 21.5% oxygen saturation (Grunewald, 1976, 1981). In Nigeria, members of the complex have been mostly found breeding in waters with velocities of 0.55-2.2 m/s, but Ibeh et al. (2007) reported a mean maximum of 2.8m/s, and Opara and Fagbemi (2005) reported a range of 0.1-5.6m/s. The latter observation is remarkable because it not only extends both the upper and lower limits for the velocities of water supporting breeding S. damnosum s.l., but also the upper limit of Simuliidae as a whole, which was previously recorded at 0.05-3.5m/s (Crosskey, 1990). Nigerian breeding sites have been found to have water temperatures of 18-33°C and pH values of 5.6-8.7, which are within the limits recorded elsewhere for S. damnosum s.l. (Grunewald, 1976, 1981). Opara and Fagbemi (2005) recorded S. damnosum breeding in rivers with unusually high levels of ammonia (but always <1mg/litre, except on one occasion when an unexplained measurement of approximately 6mg/litre was recorded).

With reference to the different sibling species within the S. damnosum complex, Mafuyai et al. (1996) concluded that the only physicochemical factor that separated the different cytospecies throughout the whole year was pH. Although Grunewald (1976, 1981) considered that conductivity was also important, dividing the West African members of the complex into Group I [S. yahense, S. santipauli and S. mengense, all supposedly found in acidic waters (pH 5.7-6.2) with low conductivity (<50 µS/m)] and Group II [S. squamosum, S. soubrense, S. damnosum s.s. and S. sirbanum, all supposedly found in nearly...
pH-neutral rivers with higher conductivity (50-150 µS/m), the results from Nigeria do not support this separation. Mafuyai et al. (1996), Bassey (1998) and Opara and Fagbemi (2005), for example, recorded low conductivity (0.5-20 µS/m) at all breeding sites used by members of the S. damnosum complex in Nigeria, including those used by sibling species in Grunewald’s Group II. Onyenwe et al. (2007) also recorded S. sirbanum (sudanese form) breeding throughout the entire year in fairly acidic water (pH 5.6-5.9), although Mafuyai et al., (1996) and Bassey (1998) recorded higher pH values (range 6.5-7.9) at all the breeding sites for the S. damnosum complex that they investigated in Nigeria. Ibeh et al., (2007) found S. yahense in neutral to alkaline rivers (pH 6.5-8.6) and S. squamosum in water showing an even wider range of pH values (6.4-8.7).

The differences seen in the physico-chemical characteristics of breeding sites used by a particular cytospecies, between the different Nigerian studies and between Nigeria and other parts of West Africa, could be related to cytoform differences. Onyenwe et al. (2007), for example, were dealing with the Sudanese form of S. sirbanum, and it is not known whether other related studies involved the Sirba form or Type IV. Similarly, it is not clear whether studies of S. damnosum s.s. in Nigeria refer to the Nile form, which is probably relatively uncommon to the west of the country (Boakye, 1993).

Factors Influencing the Adult Stage

Many factors influence adult S. damnosum s.l. Among these the following are considered to be particularly important:

Wind

All species are highly dependent on wind (Atting et al., 2005). Even a moderate breeze (a few metres per second) reduces the activity of blackflies rapidly and considerably. There seems to be some differences in this respect between the sexes, at least in some species. Sometimes, the wind causes the formation of dense swarms of both sexes which may spread widely, usually in open terrain or clearings (e.g. along rivers).

Temperature

Each species probably has a certain optimum temperature, which seems to be independent of such factors such as relative humidity, cloudiness, etc. Rapid changes in temperature, air pressure, and light seems to increase the activity of all species (Crosskey, 1990).

Light

As mentioned above, changes in light induce an increased activity (Crosskey, 1990). However, this is only true in natural surroundings. In rooms, cars, etc, the blackflies generally remain inactive, even in the case of flashes of varied intensities (Crosskey, 1990).

Precipitation

Light rain does not affect the activity of blackflies (Grunewald, 1981).

Intrinsic factors

Black flies are powerful fliers and to satisfy their physiological need for blood, the females migrate in search of an appropriate host. The males in swarms usually keep at a certain distance from the water course; they do not migrate to the same extent as the females, except when the wind causes both males and females to swarm and the swarms are blown far away by the wind (Crosskey, 1987).

Biting Activity of Simulium damnosum

Studies on biting behavior of insect vectors are prerequisites in understanding the epidemiology of the vector-borne diseases and planning effective control measures. Both males and females of S. damnosum feed on plant juices and naturally occurring sugary substances but only females are haematophagous (feed on blood). The blood meal is required for oogenesis. In West Africa, populations nearly always bite man (anthropophagic), although they also readily bite non-human mammals (zoophagic) and even birds (ornithophagic).

Feeding Habits

There are major differences between vector species in their feeding habits, for example, in the degree of preferences for human as opposed to animal hosts. To expatiate further, the intensity of microfilariae on the skin may play a critical role in determining infection of the vector, S. damnosum since each vector has a transmission threshold (WHO, 1995; Boakye, 1999).

Some survival strategies were observed in biting activities of blackflies. In addition to being cunning, swift and elusive, the blackflies first
perch on hairs on the body, which ensures that they are not noticed by their human host. They then crawl quietly to their choice site to bite. Until they start engorging blood, they remain agile and elusive. Another survival strategy is the short time lag of only 40 seconds from the time it chooses a biting site until the actual biting takes place. This minimizes the chances of being noticed by the human host. The biting itself lasts for about 18-120 seconds if undisturbed. However, blackflies become less active with increase in the amount of blood engorged, which diminishes their flying swiftness as well as their flight range. This is also the case with some other sucking insect vectors. The probing of human skin by the blackfly before actual blood feeding is facilitated by the use of her tarsal chemo and olfactory receptors (Sutchiffe et al., 1995).

People working close to the rivers are at the high risk of Simulium biting nuisance and onchocerciasis (Akogun and Onwuliri, 1991; Abdullahi and Oyeyi, 2003). Avoiding such high biting areas of Simulium is important in controlling onchocerciasis, as it will help to reduce man-fly contact. S. damnosum complex bites almost entirely on the legs. Researchers working in different parts of the world have observed that irrespective of the posture of the catchers, the legs and any exposed part of the body nearest to the ground are preferred biting sites (Adeleke et al., 2010). This preference appears to be correlated with differences in skin sites in which the heaviest microfilariae densities occur (Crosskey, 1959). Fly bites are mostly experienced outdoors. (Omolade et al., 2009).

Preferred Time of Bite

S. damnosum exhibit a bimodal peak of biting cycle. In Jos, Plateau State, Nwoke et al., (1992) reported a small peak in the morning and a more pronounced one in the evening. Also at the peak of the rainy season, a high level of biting activity was observed throughout the day with peak activity between 12:00 hours and 15:00 hours. In a study conducted along Osun River (Osun Budepo, Osun Ogbere and Osun Eleja) south west Nigeria (Adeleke et al., 2010), there was significant variation in daily biting activity of S. damnosum s.l. at the study area. The biting peaks of the flies were observed between 10:00 - 11:00 h and 15:00 - 16:00 h at Osun Budepo and between 07:00 - 08:00 h, 11:00 - 12:00 h and 15:00 - 16:00 h at Osun Ogbere and Osun Eleja. The three biting peaks could plausibly indicate the variation in biting period of different species of S. damnosum s.l at the study area or possibly be as result of differential variation in environmental conditions at different points within the same locality. However, the latter factor would have accounted for the variation since the same species of S. damnosum s.l exist at the three communities (Adeleke, 2010). This apparent biting pattern has epidemiological implications because the biting peaks correspond almost exactly to the working habit of the people in the study area, most importantly the farmers.

Opara et al. (2008) in a study conducted in Akwa-Ibom State also recorded that the biting activity of S. damnosum exhibited a bimodal pattern with an early morning peak (09:00 to 10:00 hrs) and more marked late afternoon peak (16:00 to 17:00 hrs). It is possible that the bimodal peak observed in this study might be due to decreased illumination and temperature during these peak periods, which is characteristic of climatic condition in southern Nigeria. Furthermore, the peak biting periods correspond with peak human outdoor activity, depending on the prevailing day length regime, the average Nigerian small-holder farmer spends an average of 6–8 h in the farm (Aisen et al., 2004). All these activities increase human-vector contact. In a study by Ikpeama et al. (2007) the circadian biting showed two peaks, the first between 7.00 hours and 11.00 hours and the second between 15.00 hours to 18.00 hours. Oluwole et al. (2009) in a study conducted in Ogun State, observed that biting rate of S. damnosum s.l. flies caught at the study area shows three peak of biting activity and not the usual two peaks reported by many authors This could possibly be due to climatic changes in the study area as a result deforestation, and possibly global warming.

The diurnal biting pattern of S. damnosum complex is usually different in different seasons of the year (Davies et al., 1981). Also at the peak of the rainy season, a high level of biting activity was
observed throughout the day with peak activity between 12:00 hours and 15:00 hours (Davies et al., 1981). Duke (1968) also observed that at the peak of rains, a high level of biting takes place throughout the day with the peak activity between 12:00 and 15:00 hours in the forest zone. During the beginning and end of the rainy season, biting pattern shows a bimodal peak activity, a smaller one in the morning and another in the evening, with the latter more pronounced (Nwoke, 1986).

Parous and nulliparous blackflies exhibit differences in their diurnal biting cycles. The time at which the nulliparous flies come for blood meal is dependent on the time of eclosion of the adults from their pupae. Nwoke et al. (1992) reported that the timing of emergence of S. damnosum complex is fairly controlled and that the peak of emergence is in the morning. He also observed that S. damnosum seek blood meal in the afternoon of the day following eclosion. Duke (1981) observed that most nulliparous flies biting in the evening period were made up of mostly newly hatched members of the population and newly hatched flies perform their mating fight in the morning and are first ready to bite in the afternoon. On the circadian activities of S. damnosum, parous flies are significantly abundant during the hot season in the savanna regions (Nwoke et al., 1992). This takes place in the morning hours while during the rainy season the parous flies are more abundant in the afternoon (nearly four times as high as parous caught before noon). Nulliparous flies are found to be more abundant in the afternoon than in the morning.

**Attractants**

Host-seeking behavior of many biting flies appears to be stimulated by visual stimuli originating from the host. Sutchiffe et al. (1995) reviewed this subject and suggested that host orientation by the flying blood feeder from long distance is directed by host odour while close range orientation and landing are directed by visual cues, probably acting in consent with host odour cues. However, the female blackflies may be attracted by carbondioxide expelled by the collectors. It is known that abundance, attractiveness and availability of the human hosts are influencing vector-biting behaviour. Since carbondioxide and host odour have been shown to be flight stimulants for blackflies (Bradbury, 1974; Sutchiffe et al., 1995), it appears logical that a higher density of people would attract more blackflies.

**CONCLUSION**

The clinical features of human onchocerciasis have been known to vary considerably from one geographical region to another and even between different bioclimatic zones within a single region. The sibling vector species composition and distribution have also been known to vary according to bioclimatic zones. For any of onchocerciasis control measure to be effective therefore, it is imperative that the taxonomy, ecology and behaviour of the Simulium vector species and their relationship to the parasites they transmit and the environment are properly understood.

**REFERENCES**


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