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REVIEW ARTICLE

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Transmission of pathogens by *Stomoxys* flies (Diptera, Muscidae): a review

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Abstract – *Stomoxys* flies are mechanical vectors of pathogens present in the blood and skin of their animal hosts, especially livestock, but occasionally humans. In livestock, their direct effects are disturbance, skin lesions, reduction of food intake, stress, blood loss, and a global immunosuppressive effect. They also induce the gathering of animals for mutual protection; meanwhile they favor development of pathogens in the hosts and their transmission. Their indirect effect is the mechanical transmission of pathogens. In case of interrupted feeding, *Stomoxys* can re-start their blood meal on another host. When injecting saliva prior to blood-sucking, they can inoculate some infected blood remaining on their mouthparts. Beside this immediate transmission, it was observed that *Stomoxys* may keep some blood in their crop, which offers a friendly environment for pathogens that could be regurgitated during the next blood meal; thus a delayed transmission by *Stomoxys* seems possible. Such a mechanism has a considerable epidemiological impact since it allows inter-herd transmission of pathogens. Equine infectious anemia, African swine fever, West Nile, and Rift Valley viruses are known to be transmitted by *Stomoxys*, while others are suspected. Rickettsia (*Anaplasma*, *Coxiella*), other bacteria and parasites (*Trypanosoma spp*., *Besnoitia spp.*) are also transmitted by *Stomoxys*. Finally, *Stomoxys* was also found to act as an intermediate host of the helminth *Habronema microstoma* and may be involved in the transmission of some *Onchocerca* and *Dirofilaria* species. Being cosmopolite, *Stomoxys calcitrans* might have a worldwide and greater impact than previously thought on animal and human pathogen transmission.

Key words: *Stomoxys* flies, Mechanical vectors, Pathogens, Vector-transmitted diseases.

Résumé – **Transmission de pathogènes par les Stomoxes (Diptera, Muscidae) : une synthèse.** Les stomoxes sont des vecteurs mécaniques de pathogènes présents dans le sang et les tissus cutanés de leurs hôtes, spécialement le bétail, mais aussi parfois les humains. Pour le bétail, leurs effets directs sont principalement la perturbation des animaux, les lésions de la peau, la réduction de l'alimentation, le stress, la spoliation sanguine et un effet immunosuppressif global. Ils entrainent aussi le regroupement des animaux pour une protection mutuelle ; tout cela favorise le développement des parasites chez les hôtes et leur transmission. Leur effet indirect est la transmission mécanique de pathogènes. En cas de repas interrompu, les stomoxes peuvent reprendre leur repas de sang sur un autre hôte. En injectant de la salive avant l'absorption de sang, ils peuvent inoculer du sang infecté qui restait sur leurs pièces buccales. En plus de cette transmission immédiate, il a été observé que les stomoxes pouvaient conserver du sang dans leur jabot, qui offre un meilleur environnement pour les pathogènes. Ces derniers peuvent être régurgités lors du prochain repas de sang. Ainsi, une transmission retardée semble possible par les stomoxes. Un tel mécanisme a une conséquence épidémiologique considérable, puisqu'il permet une transmission de pathogènes entre les troupeaux. Les virus de l'anémie infectieuse équine, de la fièvre porcine africaine, des fièvres à West Nile ou de la Vallée du Rift, sont connus pour être transmis par des stomoxes ; d'autres sont suspectés. Des rickettsies (*Anaplasma*, *Coxiella*), d'autres bactéries et des parasites (*Trypanosoma* spp., *Besnoitia* spp.) sont aussi transmis par les stomoxes. Enfin, les stomoxes sont aussi des hôtes intermédiaires de l'helminthe *Habronema microstoma* et pourraient être impliqués dans la transmission de certaines espèces d'*Onchocerca* et de *Dirofilaria*. En étant cosmopolite, *Stomoxys calcitrans* pourrait avoir un impact plus important qu'initialement imaginé sur la transmission de pathogènes aux animaux et aux humains.

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1. Introduction

The genus *Stomoxys* (Diptera: Muscidae) contains 18 described species [136]. They are obligate blood-sucking insects and some species are considered significant economic pests of livestock and other warm-blooded animals in many parts of the world [136]. *Stomoxys calcitrans* is a cosmopolitan species. In addition to *S. calcitrans*, several other stomoxyine flies also readily attack domestic animals, including *S. niger*, *S. sitiens*, and *S. indicus* [123]. Both male and female stable flies feed on blood and they are often aggressive and persistent feeders; they even can attack humans in the absence of preferred hosts. It has been recently shown that those flies (*S. calcitrans* and *S. niger*) also take sugars from flowers or ripe fruits [89]. Although they are most active and problematic around livestock farms, they can also be a nuisance insect on coastal beaches and in residential areas near agricultural production [91] (Figure 1).

Stable flies can cause severe problems in dairies and feedlots, where larval stages develop in moist soil and similar substrates [81, 88]. Severe biting activity can result in a reduction in animal weight and milk production. Reductions of 19% in weight gain and of 40–60% in milk yields have been reported [18, 19, 124]. *S. calcitrans* may also cause specific skin lesions like necrotic dermatitis at the tips of dog's ears, exsudative dermatitis on the legs of horses and in the "hair whirlpools" on the back of calves [131].

Stomoxys may also affect wild animals. A die-off of bongos (*Tragelaphus eurycerus* (Ogilby, 1837)) and other large ungulates occurred following a *Stomoxys* biting fly outbreak in the lowland forest of the northern Republic of Congo in April–May 1997 [37]. The direct effects of swarming biting flies and the resulting attempts to fight off the flies seem to have contributed to extreme fatigue, disruption of foraging patterns, modification of behavior, and increased exposure to predation and accidents. Observations of bongos and examination of carcasses suggested that the physical torment and disruption caused by the biting of *Stomoxys* contributed directly to the deterioration of their condition [37].

Independent from their direct nuisance (annoyance, toxic effects of saliva, blood loss, etc.), a high number of flies biting cattle and other affected animals may have a direct role in the epidemiology of transmissible diseases. Several *Stomoxys* species have been implicated as mechanical vectors of pathogens, including viruses, bacteria, protozoa, and helminths. This review discusses the direct and indirect effects of *Stomoxys* flies and provides an overview of existing literature on the pathogens they can transmit.

2. Direct nuisance and secondary effects

As partly described for tabanids [35] and stomoxes [11], the direct nuisance of *Stomoxys* flies and other biting flies can be summarized as follows:

2.1 Annoyances of animals

By flying around the eyes, landing on the skin, and attempting to bite, these insects disturb animals. This is especially important for livestock; they induce defensive movements of the head, ears, skin, legs, and tail, and escaping- or hiding-behaviors (hiding in a forest, or deep into the water; close gathering of animals to protect each other, etc.). Thus, their annoyance causes: (1) a loss of energy, (2) a reduction of the time spent feeding and the total feed intake, (3) stress due to flying and landing events.

Figure 1. *Stomoxys calcitrans.*

2.2 Pain and toxicity of skin puncture and saliva injection

The physical action of mouth parts and the chemical action of the saliva create a local pain at the biting site, which is a source of stress for the animals. It is also the origin of local cutaneous infections or secondary infections in case of myiasis. Additionally, the chemical and immunogenic actions of the saliva have a general toxicity and create a general immune response which contributes to stress and immunosuppression.

2.3 Blood loss

As blood feeders, *Stomoxys* flies can consume an average of 11–15 µL of blood per meal [106]. In addition to the direct loss of blood from feeding, more blood may pour out from the biting site when the mouthparts are removed from the skin, which may dry on the skin or be promptly absorbed by sucking flies. Often, *Stomoxys* will be disturbed by high abundances of sucking flies, which interrupts their blood meal, and creates more opportunities to lose blood by pouring from the biting site.

The primary consequences of loss of energy, reduction of food intake, stress, and blood losses are a reduction of meat, milk, manure production, and draught power, which is summarized by a consequent loss of productivity with significant economic impact. For example, Barré [4] estimated in La Réunion that a total of 0.5–1 L of milk/cow/day is lost due to stomoxes in highly infested farms. In their study of grazing yearling steers/calves, Campbell *et al.* [18] observed an average loss of 0.2 kg in the weight gains of untreated animals versus insecticide-treated ones.

As a consequence, these direct effects not only influence the rate of livestock production, but they also favor disease transmission. Indeed, the secondary consequences of the direct nuisance are (i) close gathering of animals (as a behavior to protect each other) which increases the probability for biting flies to move from one to another animal in case of interrupted feeding; (ii) immunosuppressive effects on the hosts (as a consequence of stress, energy losses, decrease in food-intake, and the toxic activity of the fly saliva [115]) have two important consequences: enhancing the pathogenesis of the infected animals (thus increasing the contaminative boost transmitted by the insects), and reducing the resistance of potential hosts (thus making the host more receptive and pathogen development easier). In summary, the direct effects of biting insects are notably favoring pathogen transmission and enhancing their development [33].

3. Mechanism of pathogens transmission by *Stomoxys* flies

Mechanical transmission is a simple mechanism of pathogen transmission which, in itself, is considered to be the most important "indirect effect" of blood-sucking insects. This mode of transmission appears to occur through either contamination of mouthparts or regurgitation of digestive tract contents. The chain of events leading to mechanical transmission is as follows: the initial blood feeding upon an infected animal is often interrupted because of the pain of the bite, leading to defensive movements of the host; the fly may then fly off and land on another animal, thus it is able to transfer blood pathogens remaining in its mouthparts to a susceptible animal. Pathogens are then transferred during the initiation of the second feeding through the saliva that hematophagous insects inject prior to blood-sucking. In addition to this "mouthpart" contamination, experimental evidence has shown that stable flies can regurgitate part of a previous blood meal before taking up another one [13]. Indeed, the regurgitation of a relatively high amount of the previously ingested blood meal could be an important way of transmitting high doses of disease agents. However, this phenomenon is limited by the short survival of pathogens which may be inhibited by digestive secretion. For example, *T. vivax* survival in a tabanid's guts was estimated to be around 5–7 h [38]. However, as observed by some authors in experimental conditions [23], some blood ingested can be directed to the insect's crop, where pathogens may survive longer since it is a more friendly environment devoid of digestive secretions. Blood can stay 24 h or more in the crop before being directed either to the gut or partially regurgitated during the early stage of a new blood meal. In such conditions, a partial regurgitation of blood from the crop would allow a delayed transmission, possibly up to 24 h or more. In tabanids, the interval between blood meals is quite long (5–7 days), above the maximum survival of most of the pathogens [43], regardless of whether they are kept in the crop or the gut. However, in stomoxe flies, which are frequent feeders [103], the interval between blood meals is variable, from 4 to 72 h [43, 74]. Thus, the crop regurgitation of infectious blood could easily establish in these flies.

As it was experimentally studied and mathematically modeled for tabanids and trypanosomes [35], the potential ability for transmission of pathogens mainly depends on the volume of blood left on the mouthparts after feeding (which is essentially governed by the size of the insect's mouth parts), the density of biting-insects flying around the animals, the level of parasitaemia in the host blood, and the relative proportion of infected and non-infected hosts which are close together. Specifically, it may also vary with the minimum infectious dose of a pathogen, the duration of the survival period of the pathogen in the insect, and the duration of the periods between repeated blood-sucking [42, 105].

Pathogens possibly transmitted by tabanids have been reviewed by several authors and proved to be as varied as bacteria, viruses, and parasites [41, 73]. Pathogens transmitted by stomoxes are thought to be the same; however, some more specific links may exist between stomoxes, pathogens, and their hosts, due to peculiar host species trophic affinity, type of bite or behaviour of stomoxes, and possible delayed transmission due to their higher frequency of blood meals. On top of the pathogens that are mechanically transmitted, stomoxes may also be a biological vector of a limited number of other pathogens.

4. Viruses

Numerous viruses can be transmitted mechanically by *Stomoxys* spp.

4.1 Equine infectious anemia virus (EIAV)

Equine infectious anemia is considered a worldwide disease caused by a *Lentivirus* (Retroviridae). EIAV is responsible for a persistent infection in horses that is characterized by recurring cycles of viremia and clinical episodes of fever, anemia, edema, thrombocytopenia, and various wasting symptoms [76]. Blood from persistently infected horses is the most important source of EIAV for transmission.

The mechanical transmission of EIAV by arthropods is generally accepted as a major factor in the transmission of this virus [64]. Large hematophagous insects, especially tabanids, which feed from extravascular sites (i.e., pool feeding) appear to be the most efficient vectors [63]. But stable flies have also been reported to be capable of mechanically transmitting EIAV [44, 52, 56, 110].

4.2 African swine fever virus (ASFV)

African swine fever, a disease of pigs, is caused by a virus of the genus *Asfivirus* (Asfarviridae). ASFV was first described from East Africa in 1921 [86], but subsequently identified in southern, central, and western Africa [97, 98]. The most recent outbreak of ASF outside Africa started in 2007 in Georgia and has spread to neighboring countries. Fever, skin lesion, convulsions, and usually death within 15 days (young animals) are the main symptoms. These signs are often indistinguishable from those of Classical Swine Fever.

ASFV persists in nature in a sylvatic cycle of transmission between wild suids (mainly the warthog, *Phacochoerus aethiopicus*) and *Ornithodoros moubata* ticks, which infest their burrows [129]. The transmission can also occur by per-oral route, through the ingestion of infected feed [24]. *S. calcitrans* has also been shown to be an experimentally competent mechanical vector. ASFV was transmitted to susceptible pigs by *S. calcitrans* infected one hour and 24 h previously and the virus survived in those flies for at least two days without apparent loss of titer [80]. The persistence of high titers of virus in stable flies for periods of up to two days strongly suggests that transmission should be possible for at least this length of time.

4.3 West Nile fever virus (WNFV)

West Nile Fever is caused by a *Flavivirus* (Flaviviridae). WNFV is a zoonotic pathogen that is primarily transmitted between birds by mosquitoes, but is also transmitted to mammals, including horses and humans [71]. Several species of *Culex* mosquitoes are particularly efficient vectors. This virus is currently the most widely distributed arbovirus in the world, occurring on all continents except Antarctica [72].

Johnson *et al.* [66] reported that stable flies were contaminated by WNFV through feeding upon American white pelicans. Fifty-four percent of abdomens from 67 blood-engorged flies tested positive for WNFV. Pelican viremia levels from the blood-engorged fly abdomens revealed that at least one of the ill pelicans circulated a viremia capable of infecting *Culex* mosquito vectors. Stable flies may also be involved in WNFV transmission within the pelican breeding colony by serving as either a mechanical vector or as a source for oral infection if ingested by predators [36].

4.4 Rift Valley fever virus (RVFV)

Rift Valley fever is a zoonotic disease of domestic ruminants and humans caused by an arbovirus belonging to the genus *Phlebovirus* (Bunyaviridae). It is widespread in Africa and has recently spread to Yemen and Saudi Arabia. RVF epidemics are becoming more and more frequent in Africa and the Middle East, probably in relation to climatic changes. Clinical manifestations vary depending on age and animal species. Animals usually experience fever with depression, hemorrhagic diarrhea, bloodstained muco-purulent nasal discharge, and icterus. Mortality rates may vary from 10% to 95% for newborn lambs. In pregnant animals, abortions are frequent, ranging from 5% to 100% [21].

Hoch *et al.* [59] conducted experimental studies to determine if hematophagous Diptera were capable of mechanical transmission of RVFV to laboratory animals. All species tested (*Glossina morsitans*, *Aedes aegypti*, *Aedes taeniorhynchus*, *Culex pipiens*, *Stomoxys calcitrans*, *Lutzomyia longipalpis*, and *Culicoides variipennis*) mechanically transmitted the virus to hamsters. *S. calcitrans* was able to mechanically transmit RVFV to susceptible hamsters (*Mesocricetus auratus*) after probing on infected hamsters with high viral titers. Therefore, *S. calcitrans* should be considered a possible mechanical vector of this virus and may contribute to the rapid spread of an RVF outbreak because of its close association with domestic animals that serve as amplifying hosts of RVFV. Other *Stomoxys* species present in Africa and elsewhere may also play similar roles [121].

4.5 Lumpy skin disease virus (LSDV)

Lumpy skin disease, caused by a *Capripoxvirus* (Poxviridae), is characterized in cattle by pyrexia, generalized skin lesions (nodules), internal pox lesions, and lymphadenopathy [69]. Lumpy skin disease was first recognized in Zambia in 1929 and is now endemic in most of sub-Saharan Africa, parts of North Africa and has also been reported in the Middle East [27].

S. calcitrans has been shown to mechanically transmit capripox virus (Yemeni strain) to susceptible hosts (sheep, goat) under experimental conditions [68, 80]. Lumpy skin disease virus was detected by isolation from *S. calcitrans* immediately post-feeding, and viral nucleic acid was detectable by PCR up to 24 h post-feeding [22]. Although epidemiological observations also suggest the role of stomoxe flies in the transmission of the LSDV [132], a formal demonstration has not yet been made.

4.6 Bovine herpes virus (BHV)

Bovid herpes virus-2 (BHV-2) (genus *Herpesvirus*, Herpesviridae) infection causes a bovine vesicular and ulcerative skin disease known as bovine herpes mammillitis (BHM). This is a localized, painful condition of the teats and udders, usually seen in first calving heifers. Both BHM and pseudo-lumpy skin disease (another manifestation of BHV-2 infection) have a seasonal prevalence, and both are thought to be initiated by biting insects. BHM can only be produced experimentally when the virus is introduced below the level of the stratum germinativum of the udder or teat skin, and *S. calcitrans* has been proposed as a mechanical vector [47, 48]. *S. calcitrans* fed on infected blood mechanically transmitted enough of the virus to infect cell monolayers in an experimental infection [49], and therefore stable flies are considered a potential mechanical vector of BHV-2.

4.7 Bovine leukosis virus (BLV)

The ability of tabanids to transmit enzootic BLV (genus *Lentivirus*, Retroviridae) has been experimentally demonstrated [45]. However, the role of stable flies has been investigated but not yet been demonstrated [14, 46, 126].

4.8 Vesicular stomatitis virus (VSV)

The mechanical transmission of VSV (genus *Vesiculovirus*, Rhabdoviridae) has been experimentally shown with stable flies [39]; but since 1955, no further studies have confirmed this result [19]. However, a recent study demonstrated the mechanical transmission of VSV to domestic swine by black flies [113].

4.9 Blue tongue virus (BTV)

BTV (genus *Orbivirus*, Reoviridae) causes an infectious, non-contagious disease of ruminants, and is transmitted between its vertebrate hosts by *Culicoides* (Diptera: Ceratopogonidae) acting as a biological vector. Until 2006, BTV existed around the world in a broad band covering much of the Americas, Africa, southern Asia, northern Australia and, occasionally, the southern fringe of Europe. Recently the virus causing this disease has extended northwards into areas of Europe. A BTV epizootic in South-Western France in the summer and autumn of 2008, with a high incidence of new cases, raised the question about the possibility of BTV transmission not only by biological *Culicoides* vectors but also by mechanical vectors. These mechanical vectors would amplify the epizootics observed, with biological consequences.

Other viruses are also suspected to be transmitted by *Stomoxys* such as Classical Swine Fever, African Horse Sickness, Yellow Fever, Foot and Mouth Disease, Myxomatosis, Bovine Viral Diarrhea, and a number of viral Encephalites (West Equine Encephalitis, East Equine Encephalitis, Central Equine Encephalitis, Venezuelan Equine Encephalitis, etc.); however no demonstrations were made so far [73].

5. Bacteria (with the exception of Rickettsia)

5.1 Anthrax

Anthrax is caused by a spore-forming bacterium, *Bacillus anthracis*, and is considered a serious zoonotic disease. The disease affects animals and humans, inducing pulmonary, gastro-intestinal, or cutaneous symptoms, including a boil-like skin lesion that eventually forms a typical ulcer with a black center (eschar). It is often lethal in the absence of treatment. Although *B. anthracis* can be found worldwide, anthrax cases usually only occur in a limited geographic region. Outbreaks are most common in areas characterized by alkaline, calcareous soil, and in warm environments with periodic episodes of flooding [62]. Anthrax is particularly common in parts of Africa, Asia, and the Middle East. Herbivores usually become infected when they ingest sufficient numbers of spores in soil or on plants in pastures. Carnivores usually become infected after eating contaminated meat.

However, *B. anthracis* infections can also be mechanically transmitted by stable flies. Schuberg and Kuhn [108] demonstrated with mice and guinea pigs that infections could be transmitted from sick animals to healthy ones via *S. calcitrans*. Schuberg and Boing [107] were able to infect sheep and goats using *S. calcitrans* [62]. Stable flies transmitted anthrax, even when they were held at room temperature for 4 h after exposure to the bacteremic guinea pig before being allowed to continue feeding on the susceptible animals. The potential for flies to mechanically transmit anthrax suggests that fly control should be considered as part of a program for control of epizootic anthrax [120].

5.2 Other bacteria

Mechanical transmission by stomoxes has been demonstrated for *Pasteurella multocida* (Hemorrhagic Septicemia in Buffalo), *Erysipelothrix rhusiopathiae* (an agent of erysipelas in animals and erysipeloid in humans), and *Francisella tularensis* (responsible for tularemia) [73]. For other bacteria, mechanical transmission by stomoxes is only suspected: *Clostridium perfringens*, *Pasteurella multilocida*, *Brucella abortus*, *Brucella suis*, *Brucella melitensis*, *Listeria monocytogenes*, *Leptospira* spp. [73].

Enterobacter sakazakii is an opportunistic food-borne pathogen causing meningitis, enterocolitis, and sepsis. Mramba *et al.* [87] reported that adult stable flies can carry *E. sakazakii* for several weeks and contaminate their food sources with this pathogen. *E. sakazakii* was supported during the development of immature stable flies in sterilized cattle manure and sterilized artificial medium. In addition, *E. sakazakii* survived during stable fly development and colonized the gut of emerging adult stable flies, which makes stomoxe flies biological vectors of this bacterium.

Dermatophilus congolensis is a Gram-positive coccobacillary actinomycete that causes an exsudative dermatitis in a variety of species, most notably in ruminants and horses, although rare infections occur in cats, dogs, and humans [1, 15]. It has a worldwide distribution but is more prevalent in the humid tropics and subtropics [133]. Domestic flies (*Musca domestica*), and biting insects such as *S. calcitrans*, *Glossina morsitans*, and mosquitoes have been reported to be involved in the transmission of the disease by breaking the skin barrier during feeding and releasing variable amounts of serum and blood which provide moisture, nutrition, and a suitable microclimate for the multiplication of *D. congolensis*. Richard and Pier [100] successfully infected rabbits through contaminated flies (*S. calcitrans* and *M. domestica*). Macadam [79] saw lesions of *D. congolensis* infection on sheep and horses in Sabah and noted that most lesions were not associated with ticks so he presumed that *S. calcitrans* was the main vector.

De Castro *et al.* [28] reported the existence of 33 distinct species of bacteria in stable flies. Bacterial species were isolated from three different segments (cuticle, mouthparts, and abdominal alimentary tract) of stable flies. A total of 161 colonies of 33 distinct species were isolated, such as *Escherichia coli*, *Staphylococcus aureus*, and *S. intermedius*. The cuticle was the segment from where most species were isolated, followed by the abdominal digestive tract and mouthparts.

6. Rickettsia

6.1 Bovine anaplasmosis

Bovine anaplasmosis caused by *Anaplasma marginale* occurs in tropical and subtropical areas throughout the world. The outstanding feature of clinical anaplasmosis is anemia associated with phagocytosis of parasitized erythrocytes.

A. marginale is poorly transmitted but surely amplified by ticks (*Rhipicephalus* (*Boophilus*) *microplus*, *Dermacentor andersoni*) and many hematophagous diptera are implicated as mechanical vectors, including *S. calcitrans*, *Haematobia irritans*, and *Tabanus* spp. [53, 70, 109, 122].

Anaplasma marginale multiplies in the lumen of the tick's gut (or Malpighi tubes) and migrates to the salivary glands of the ticks at adult stage. Thus *Anaplasma* can be re-injected into the host by adult ticks [20]. When there is a massive infestation of ticks, a large boost in re-injected *Anaplasma* may lead to immune failure and can explain why clinical cases of anaplasmosis are frequently observed during times of high tick infestations. However, this does not explain the transmission of *Anaplasma* by ticks. Although intrastasial transmission is possible during the adult stage, it requires the transfer of ticks from one to another host, which is numerically negligible for female ticks and occurs at low rate for males of *Rhipicephalus* (*Boophilus*) *microplus*. Thus ticks must be considered amplifiers of the parasitic burden rather than vectors [29]. On the contrary, Tabanids and stomoxes are responsible for the mechanical transmission of *Anaplasma* through blood-contaminated mouthparts of biting flies. Scoles *et al.* [109] provided evidence that the Florida strain of *A. marginale*, which is not transmissible by ticks, was more efficiently retained in stable fly mouthparts than was the St Maries strain, which is tick transmissible. The mechanical transmission is likely the major route of *A. marginale* in certain areas of the USA, Central and South America, and Africa, when tick vectors are absent.

A survey by Oliveira *et al.* [94] indicated that the exposure of cattle to *A. marginale* is common in dairy herds of Costa Rica and demonstrated the association between seroprevalence and presence of tabanids and stable flies. This endemic instability situation is probably due to inadequate vector control.

6.2 Other rickettsia

Q fever is a disease caused by *Coxiella burnetii* in cattle, goats, sheep, dogs and humans [26]. It can be transmitted directly by inhalation of dust contaminated by dried placental material or excreta of infected animals. It can also be transmitted by ticks, which are considered long-term carriers [111]. Livestock is commonly infected and can act as a reservoir. Clinical signs are fever, anorexia, respiratory signs, and abortion.

Flies that feed on the feces, milk, carcasses, or blood of domestic animals can be infected with *Coxiella burnetii* [61]. *S. calcitrans* collected from an elk and cattle ranch were positive for *C. burnetii* DNA [90] and should therefore be suspected as a mechanical vector of this bacterium.

7. Protozoa

7.1 Animal trypanosomes

Animal trypanosomes are major pathogens of livestock in Africa, they are mainly transmitted by tsetse flies, and can induce anemia, loss of milk and meat production as well as abortion and death. However, not only tsetse flies can transmit trypanosomes. Mechanical transmission of several *Trypanosoma* species has been demonstrated, notably for *T. vivax*, *T. congolense*, *T. brucei*, and *T. evansi* [31–33, 83, 101]. The relative impact of mechanical transmission is variable from one species to another. In the case of *T. evansi*, which is responsible for a worldwide disease called surra, and for *T. vivax* in Latin America, mechanical transmission is nearly the only route of transmission, and is thus very crucial [30, 93]. In their early series of experiments, Bouet and Roubaud [10] demonstrated that *T. evansi* might not only be immediately mechanically transmitted by stomoxes, but may also be transmitted with delays of 24, 48, and even 72 h. These experiments demonstrated a peculiar capacity of stomoxes for delayed transmission while compared to tabanids, such delayed transmission has never been observed.

The clinical signs of surra in most domesticated mammals and wild animals are characterized by fever and anemia, enlargement of the lymph nodes and spleen, followed by emaciation, edema, abortion, and cachexia [12]. Mihok *et al.* [83] demonstrated that *S. varipes* was capable of transmitting *T. evansi* mechanically to mice in the laboratory. Sumba *et al.* [114] studied the mechanical transmission of *T. evansi* (South American origin) and *T. congolense* of Kilifi DNA type (Kenyan origin) in laboratory mice using the African stable flies *S. niger niger* and *S. taeniatus*. *T. congolense*, one of the most important etiologic agents of African Animal Trypanosomosis, was also transmitted by *S. n. niger* at low rates and *T. evansi* was transmitted by both *Stomoxys* species at higher rates [114].

Two outbreaks of trypanosomosis caused by *T. evansi* in camels occurred in France in 2006 and in Spain in 2008. Both outbreaks were associated with the import of camels from the Canary Islands [55]. In France, trypanosomes were observed in the blood of five camels, three of them were indigenous to the farm and two had been imported. The parasite was probably transmitted by tabanids and *S. calcitrans*, which were abundant from July to September 2006. No parasites were observed in other animals on the farm or on neighboring farms, but some of the sheep on these farms were positive by PCR or serology [34].

Cuglovici *et al.* [25] assessed the epidemiological situation of bovine trypanosomosis caused by *T. vivax* in a dairy cattle herd in Minas Gerais state, Brazil. The highest incidence of the seroprevalence observed could be correlated with an increased population of *S. calcitrans* flies in that region.

7.2 *Besnoitia besnoiti*

Bovine besnoitiosis is a protozoal disease of cattle caused by the cyst-forming apicomplexan parasite *Besnoitia besnoiti*. This parasite has domestic and wild bovids as intermediate hosts. Bovine besnoitiosis is clinically characterized by the succession of three phases: (i) the initial febrile syndrome with photophobias, epiphora, ocular and nasal discharges, arrest of rumination, anorexia, increased heart and respiratory rates; (ii) the second phase with enlargement of lymph nodes, generalized edema, and hyperesthesia of the skin and; (iii) the third phase, i.e. the chronic form, with scleroderma, hyperkeratosis, hyperpigmentation, and extensive alopecia. Despite the recovery of appetite, weight loss becomes more marked, and death can occur in about 10% of cases [65, 77]. Bovine besnoitiosis had been previously described in Africa, the Middle East, and Europe, and was deemed to be an emergent disease in the 1990s in European countries such as Spain, Portugal, France, Italy, and Germany [104]. The life cycle of *B. besnoiti* remains a mystery: the definitive host is unknown and the transmission routes are poorly understood. *B. besnoiti* is thought to be transmitted mainly by hematophagous insects [65].

Mechanical transmission of *B. besnoiti* by *Stomoxys* has been demonstrated [8, 78] and the existence of blood-sucking flies could be a risk factor for the rapid spread of the disease.

A long-term investigation was performed in a dairy cattle farm localized in an enzootic area of besnoitiosis of South-western France between March 2008 and May 2009. The sero-prevalence determined by Western blot in a cohort of 57 animals continuously present during the whole survey increased from 30% in March 2008 to 89.5% in May 2009. New positive *B. besnoitia* seroconversions occurred throughout the year with the highest number in spring. In addition, many seroconversions were reported in the two months before turn-out and could be associated with a high indoor activity of *S. calcitrans* during this period [77].

7.3 Other protozoa

Berberian [6] successfully transmitted *Leishmania tropica* by the bites of *Stomoxys calcitrans*. But to our knowledge, this experiment has never been repeated, and there is no epidemiological evidence that this occurs in the nature.

8. Helminths

8.1 *Habronema microstoma*

Habronemosis caused by the nematode *H. microstoma* is considered to have a global distribution. *Musca domestica* and *S. calcitrans* were found to act as intermediate hosts for *H. microstoma* [130]. The competence of *S. calcitrans* as a vector of *H. microstoma* was demonstrated by the discovery of nematode DNA in different anatomic parts (heads, thoraces, and abdomens) of both field-collected and laboratory-reared flies [119]. The adults of *H. microstoma* occur on the horse stomach mucosa under a layer of mucus and can cause inflammation of the mucosa, followed by digestive disturbances or even chronic gastritis and ulceration. Ovoviviparous females of *Habronema* release embryonated eggs which pass into the feces. The embryonated eggs or the larvae that hatch in the fecal mass are ingested by maggots (*Musca* or *Stomoxys* larvae), within which they develop to the infective L3 stage. The infective stage is reached when the stable fly imago emerges from the puparium. The infective larvae are deposited on the nostrils, lips, eyes, or wounds of the host when the stable flies feed. Larvae deposited around nostrils and lips are swallowed and mature in the stomach of host. Gastric habronemosis is characterized by a chronic catarrhal gastritis with symptoms of varying degrees of severity, such as anorexia/dysorexia, digestive disorders, diarrhea, progressive weight loss, ulcers, and post-prandial colics [119]. Larvae deposited on mucous membranes (vulvae, prepuce, eye) or on injured tissues cannot complete their life cycle; however, they induce a local inflammatory reaction with strong eosinophilia causing cutaneous "summer sores" and/or ophthalmic habronemosis [118, 130].

8.2 Other helminths

Mechanical transmission by stable flies is also suspected for the nematodes *Dirofilaria repens* (which induces subcutaneous nodules in cats and dogs) [73], *Dirofilaria roemeri* (which induces subcutaneous nodules in wallabies and kangaroos), and *Onchocerca gibsoni* (subcutaneous filaria).

Associated with the dispersion of stable flies, the dissemination of pathogenic agents carried on their cuticle can also be important. Stable flies can disseminate microorganisms to many places and materials, including food for animals. They have the ability to be a mechanical vector for pathogens due to their feeding habits, as well as their great flying capacity, which may be up to 29 km in 24 h according to laboratory flight mill studies. However, field dispersal studies showed that the flies would travel at least 3 km after 6 days in search of a blood meal [2]. Adult stable flies in a given area are most likely to have originated from larval development sites within a 5 km radius of the subject cattle [117].

9. Control measures of *Stomoxys* flies

Many types of control methods have been tested for stable flies, including insecticides, biological controls, baits, and sterile insect technique [9, 16, 17, 40, 54, 67, 82, 84, 99, 116].

As no single control method is effective in controlling stable fly populations, the use of several vector management strategies for the control of the stable flies is highly recommended. Integrated vector management relies on three tactics for successful suppression of stable flies: sanitation, biological, and chemical controls [7, 75, 96, 128].

Sanitation is the most important method for reduction of stable fly populations in livestock farms. Most common larva sites are piles of decomposing vegetative material or manure, old manure under fences, and poorly drained areas. In confined animal facilities, the highest priority should be to eliminate stable fly breeding sites as much as possible.

Pupal parasitoids in the family Pteromalidae (Hymenoptera) such as *Spalangia* spp. have a high potential for the biological control of stable flies [112]. The parasitoid wasps lay their eggs in immature stable flies. The resulting wasp offspring feed on the stable fly maggot or pupa and eventually kill it. The immature parasitoid wasps will then develop into an adult, emerge from the fly pupa, and repeat its life cycle. Although parasitoid wasps offer some measure of control they do not produce immediate results. Therefore, biological control should not be used alone, but in concert with other methods, such as sanitation.

Many different traps have been used to both survey and control the fly population [57, 116]. Stable flies are attracted to certain olfactory stimuli such as carbon dioxide, ammonia, and phenylpropanoid compounds [50]. They are also attracted to visual stimuli such as fiberglass Alsynite which reflects near UV light [9], and the blue-colored fabrics used in insecticide impregnated screens [51] or in the Nzi and Vavoua traps [82].

Experiments are now performed to evaluate the association of the ATSB (Attractive Toxic Sugar Bait) method [5, 89] with attractive devices to control flies. The objective is to take advantage of the materials stable flies are attracted to (blue fabric or Alysnite) and sugar bait with insecticide to kill them.

Experiments are also performed to identify and evaluate the efficiency of potential repellents to protect domestic animals [3, 58, 134, 135].

Table 1. Disease agents associated with *Stomoxys* spp.

Disease agent	Geographic occurrence	Transmission	Association*	References
Viruses				
Equine infectious anemia virus (EIAV)	Worldwide	Mechanical	Experimental and natural transmission, isolation	[44, 56, 110]
African swine fever virus (ASFV)	Africa, Sardinia (Italy)	Mechanical	Experimental transmission	[80]
West Nile Fever virus (WNFV)	Worldwide	Mechanical	Experimental transmission, isolation	[36, 66]
Rift Valley Fever virus (RVFV)	Africa, Middle East	Mechanical	Experimental transmission	[59]
Lumpy Skin Disease virus (LSDV)	Africa, Middle East	Mechanical	Experimental transmission, isolation	[22, 68, 80]
Bovine Herpes Virus (BHV)	Worldwide	Mechanical	Experimental transmission	[49]
Bovine Leukosis Virus (BLV)	Worldwide	Mechanical	Experimental transmission	[14, 46, 126]
Vesicular Stomatitis Virus (VSV)	America	Mechanical	Experimental transmission	[39]
Bacteria				
Bacillus anthracis	Worldwide	Mechanical	Experimental and natural transmission	[107, 108]
Pasteurella multocida	Worldwide	Mechanical	Experimental transmission	[92]
Erysipelothrix rhusiopathiae	Worldwide	Mechanical	Experimental transmission	[127]
Francisella tularensis	North America, Europe, northern Africa, Middle East, Asia	Mechanical	Experimental transmission	[95, 125]
Enterobacter sakazakii	Worldwide	Biological and mechanical	Natural transmission, isolation, and development.	[87]
Dermatophilus congolensis	Worldwide	Mechanical	Experimental and natural transmission	[100]
Rickettsia				
Anaplasma marginale	Worldwide (Tropics and subtropics)	Mechanical	Experimental and natural transmission, isolation	[94, 109]
Protozoa				
Trypanosoma evansi	South America, North Africa, Asia, Europe	Mechanical	Experimental transmission	[10, 83, 114]
Trypanosoma vivax	South America, Africa	Mechanical	Experimental transmission	[83]
Trypanosoma brucei	Africa	Mechanical	Experimental transmission, isolation	[83, 85]
Trypanosoma congolense	Africa	Mechanical		[114]
Besnoitia besnoiti	South America, Europe, Africa, Middle East, Asia	Mechanical	Experimental and natural transmission	[8, 77, 78]
Leishmania tropica	North Africa, Middle East, Asia	Mechanical	Experimental transmission	[6]
Helminths				
Habronema microstoma	Worldwide	Biological	Experimental transmission, isolation, and development	[119, 130]

*Association between disease agents and stomoxes is described as follows: isolation (agent isolated from stomoxes), development (as if stomoxes were natural intermediate host), experimental transmission (transmission of agent by unnatural mode of infection or to unnatural host), and natural transmission (transmission of agent from one natural host to another by exposure to stomoxes) according to Krinsky (1976) [73].

If a stable fly problem persists, an insecticide can be used. Many compounds are available to suppress adult and larval stable fly populations. Insecticides applied as residual sprays, such as permethrin, have been applied to the sides of buildings where adult stable flies congregate. However, the persistence of residuals is not predictable over time. Sublethal exposure levels may be found less than one month after application [60] and some stable fly populations have already shown a high degree of resistance [102].

Regardless, integrated pest control should be adapted to the specific conditions of each farm, medium, area, and should be established with synergistic procedures, to get the maximum benefit, as was suggested in La Réunion [11].

10. Conclusion

Table 1 is a summary of the evidence available for incriminating stomoxes as mechanical or biological vectors of the disease agents discussed in this review. Few studies involving natural transmission or isolation of a pathogen from wild stomoxes have been done. That's why the evidence for considering stomoxes as natural vectors of some of these pathogens is meager. Nonetheless, because of their feeding habits, stomoxes are regarded as important potential mechanical vectors of various microorganisms. It is highly recommended that future research takes these questions into account. In vitro feeding of *Stomoxys* on membranes where they are allowed to pick up infectious disease agents, subsequent study whether the flies remain infected, where the infection retains through dissection and PCR of parts of the flies, are made possible thanks to breeding facilities. Due to its epidemiological importance, the mechanisms of regurgitation of blood by stable flies and its frequency should be further analyzed.

Recent studies carried out on trypanosomes in cattle have shown and quantified the role of tabanids in mechanical transmission. They allowed to develop mathematic model for risk assessment and to predict impact and evolution of prevalence under various circumstances [31–33]. Implementation of research projects on quantitative experimental studies on the capacity of stomoxes for transmission of parasites like *Trypanosoma evansi*, *Besnoitia besnoiti*, and the Blue Tongue Virus/BTV, including immediate/delayed transmission, artificially/naturally interrupted blood feedings, study of behavioral modifications and interactions host/insects, in contention/semi-liberty conditions, with a study of the behavioral modifications of hosts and vectors, in rodents, cattle, or sheep, should allow to develop a mathematical model of transmission of pathogens by stomoxes. The integration of diffusion models of pathogens by hosts (inter-herd transmission) with a synthetic model of transmission by biting insects (intra-herd transmission) will allow generating a global model of diffusion-transmission of pathogens aiming at evaluating risk and predicting disease spreading and prevalence evolution.

We hope that the information given in this review will stimulate more research on vector competence and capacity and on control of those Stomoxyine flies.

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