*Encyclopedia of invasive introduced species*

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# Malaria vectors

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Invasion by insect vectors can significantly contribute to outbreaks of human and animal disease. Dispersion of insects can occur either naturally (by active flight or passive dispersal) or mediated by human activities (by land, air, or water transportation). Malaria is a mosquito-borne disease caused by blood parasites of the genus *Plasmodium* that infect a wide range of reptiles, birds, and mammals. Following successful introduction into a non-native area, establishment and spread of mosquito vectors of disease can profoundly alter the transmission dynamics of the pathogens they transmit.

## INVASIVE MALARIA VECTORS

With the exception of a single species infecting reptiles transmitted by phlebotomine sandflies, all known *Plasmodium* parasites are mosquito-borne. Over 170 *Plasmodium* species have been described in the classic literature, but several new species have been identified in the last few years and certainly more are yet to be discovered. Malaria parasites of mammals including humans are exclusively transmitted by mosquitoes of the genus *Anopheles* (subgenus *Anopheles*) of the sub-family *Anophelinae*. By contrast, *Plasmodium* species infecting other vertebrates can be transmitted by vectors belonging to different genera of the sub-family *Culicinae* (e.g., avian malaria is transmitted by *Culex*, *Aedes*, *Aedomyia*, and *Coquillettidia* mosquitoes). Distributions of *Anopheles* species range from highly local to sub-continental. For example, *An. ovengensis* is found only in forests of southwestern Cameroon and *An. bwambae* occurs exclusively within a 10 km radius of geothermal springs located in Bwamba County, Uganda. Conversely, *An. gambiae* and *An. funestus* occur in most of sub-Saharan Africa and *An. darlingi* is found across all of tropical South America east of the Andes.

This article reviews several documented cases of invasive malaria vectors that altered transmission cycles of native or non-native *Plasmodium* parasites. Although invasive malaria vectors may have other effects on resident species and ecosystems, the focus of this entry is their impact on human and animal health. The impact of malaria on non-immune host populations can be disastrous, as exemplified by the estimated 130,000 human deaths in Egypt in 1942 that followed the introduction of an efficient malaria vector species from Sudan. Introduced malaria vectors can affect human and animal health by (i) independent introductions of a novel vector and a novel *Plasmodium* species, (ii) acquisition of a native *Plasmodium* species by an introduced vector, and (iii) simultaneous introduction of a novel vector and a novel *Plasmodium* species.

### A- Invasion biology of malaria vectors

Introduction of a non-native species relies strongly on the frequency of successful transport from its native area to a new area (i.e., propagule pressure). Although over relatively short distances (up to a few hundred kilometers) adult mosquitoes can be transported by wind, most introductions of mosquitoes over long distances are thought to have occurred via human-aided transportation, especially by hitchhiking on ships and aircrafts. Introductions have therefore been considerably facilitated by the establishment of trans-continental steamer ship lines in the 19th century and international airlines in the 20th century. Extreme globalization of humans and goods transportation during the last half-century undoubtedly enhanced propagule pressure and has been incriminated in multiple events of mosquito introductions. Among factors that can influence the frequency of mosquito introductions, production of dessication-resistant eggs, preference for urban habitats, autogeny, use of man-made containers as larval habitats, and diapause favor human-aided transportation over large distances. In this regard, vectors of human malaria are much less likely to be transported and introduced into new areas than, for example, arbovirus vectors of the genus *Aedes* (especially, the invasive species

*Ae. aegypti* and *Ae. albopictus*). Indeed, *Anopheles* species that are efficient vectors of human malaria generally do not produce dessication-resistant eggs, are not autogenous, breed in natural habitats, and are not known to diapause. Because *Anopheles* species usually cannot breed on ships or aircrafts, their successful introduction requires that at least one inseminated adult female survive the entire duration of the trip. Reduction of long-distance travel duration to a few days or a few hours in the last two centuries allowed introduction of *Anopheles* mosquitoes to remote islands, distant parts of the same continent, and even new continents. Following successful introduction, factors that influence the subsequent steps of invasion – establishment and spread – include adaptation to the new environment and ability to overcome negative interactions with predators and competitors. International travel and trade generally connect major cities, making non-native species that are adapted to urban environments more likely to succeed in the early phase of establishment. Thus, adaptation of most *Anopheles* vectors of human malaria to rural environments does not particularly favor the first step of their establishment upon arrival in a very urban environment. However, no universal rule can be formulated on the general ability of malaria vectors to establish and spread in a new area because it depends on the specific location and circumstances of the introduction.

**B- Independent introductions of malaria vectors and *Plasmodium* species**

The opening of the steamer ship line between Tamatave, Madagascar and Port-Louis, Mauritius in 1864 coincided with a malaria outbreak in 1865. This outbreak was attributed to the introduction of mosquitoes of the *An. gambiae* species complex (*An. gambiae s.l.*) and *An. funestus*, the most important African malaria vectors. Malaria was almost certainly present among railway workers from India prior to the introduction of *An. gambiae s.l.* and *An. funestus*. It is believed that soon after, a cyclone was responsible for the introduction of *An. gambiae s.l.* from Mauritius into La Réunion Island (about 200 km away) where a malaria outbreak occurred in 1868. As in Mauritius, malaria parasites had probably been imported by human migration prior to the introduction of *An. gambiae s.l.* Thus, independent introductions of parasite and vectors resulted in the emergence of epidemic malaria on Mauritius and La Réunion Islands.

The Seychelles Archipelago had been free of *Anopheles* mosquitoes and therefore of endemic human malaria until 1908 when a malaria outbreak occurred on Aldabra Islands. No *Anopheles* specimens could be found that year, so that the mosquito species that vectored the outbreak remained a mystery. Following another malaria outbreak at Aldabra in 1930, larvae and adults of *An. gambiae s.l.* breeding on the islands were discovered. Malaria parasites had probably been present among workers from East Africa and Madagascar, so that subsequent introduction of the vector sufficed to trigger an outbreak. That 22 years elapsed between the two outbreaks suggests that *An. gambiae s.l.* may have been introduced a first time in 1908 but then disappeared before it was introduced a second time in 1930. If this hypothesis is true, it indicates that natural elimination of the invader mosquito does not preclude the occurrence of epidemic malaria.

*Culex quinquefasciatus* became established in the Hawaiian Islands in the early 19$^{th}$ century, several decades before the introduction of avian malaria with introduced birds from Asia in the early 20$^{th}$ century. It is believed that *Cx. quinquefasciatus* was initially introduced into Hawaii as early as 1826 by a ship from Mexico. Analysis of genetic markers indicates that current Hawaiian *Cx. quinquefasciatus* populations probably resulted from multiple introductions. Avian malaria has devastated many native Hawaiian bird populations, especially at lower elevations where *Cx. quinquefasciatus* occurs. The disease probably contributed greatly to the extinction of many Hawaiian bird species between 1910 and 1930 and subsequent range reduction of other species. As in Mauritius, La Réunion, and the Seychelles Islands, malaria emergence was due to independent introductions of the vector and the parasite.

**C- Introduced malaria vectors transmitting native *Plasmodium* species**

The African vector *An. gambiae s.l.* was introduced in Natal, Brazil in 1930, causing malaria outbreaks in the vicinity in 1930-1931. Larvae or adult mosquitoes are believed to have traveled by air of steamer ship from Dakar, Senegal. Although insecticide treatments allowed elimination of *An. gambiae s.l.* from the Natal area by 1932, some mosquitoes escaped out of the city limits. They subsequently spread to a vast portion of northeastern Brazil, especially along river courses, causing devastating malaria epidemics in 1938-1939. At the time *An. gambiae s.l.* was not recognized as a species complex, but molecular identification of museum specimens confirmed later that the invader was *An. arabiensis*, an arid-adapted species typical of the Sahel region of Africa. Human malaria was endemic in Brazil but local *Anopheles* species had much lower vectorial capacity than *An. arabiensis*. Therefore, although *An. arabiensis* had a long history with the same *Plasmodium* species in its native range, it caused malaria outbreaks by transmitting native parasites more efficiently than native vectors. A massive eradication campaign conducted by the Rockefeller Foundation mainly based on larval control rapidly led to complete elimination of the invader in 1941, immediately followed by a drop in malaria incidence. Successful elimination of invasive *An. arabiensis* in Brazil remains a strong argument for proponents of larval control of malaria vectors.

Among *Anopheles* species native to the New World, *An. darlingi* is the most efficient malaria vector and contributes to malaria transmission in the Central Amazon Region. Before the 1990s, it was totally absent from the Peruvian region of Iquitos, in the Upper Amazon Region. However, invasive populations of *An. darlingi* were implicated in a large malaria outbreak in Iquitos in 1997. The observation that artificial ponds used for tropical fish culture around Iquitos were used by *An. darlingi* as larval habitats suggested that *An. darlingi* larvae might have been transported by boat with tropical fish. Again, introduction of a malaria vector more efficient than native vector species resulted in epidemic transmission of native *Plasmodium* species.

**D- Simultaneous introduction of malaria vector and *Plasmodium* species**

In 1959, a malaria outbreak occurred along the Mediterranean Israeli coast, a region that had been considered malaria-free. It was hypothesized that the outbreak had been caused by introduction of infected *An. pharoensis* from the Nile delta region (about 280 km away) that would have been transported by a strong southwesterly wind. Massive migration of *An. pharoensis* in the direction of the prevailing wind had been previously reported at locations in the Egyptian desert, several tens of km away from the nearest breeding places. Wind-aided transportation of mosquitoes has been described as a form of long-distance migration resulting from "active" behavioral changes. If 89 confirmed malaria cases that occurred in 1959 in Israel were due to parasites introduced by *An. pharoensis*, a large number of mosquitoes (in the order of a million) must have been transported by wind.

Many long-distance flights connect malaria-ridden countries with malaria-free regions of the world. Among malaria vectors that hitchhike aboard aircraft and are released in malaria-free regions, some are infected with malaria parasites. Insect import by aircraft can be limited by treatments with insecticide either in-flight or on the ground, but this measure is not systematically applied or not totally efficient. Introductions of infected vectors are held responsible for cases of "airport malaria," when people with no recent history of travel to tropical countries but living or working near international airports become infected with malaria parasites. Diagnosis of these cases is often delayed because of their unexpected nature. Between 1969 and 1999, 89 confirmed or probable airport malaria cases were reported, mostly in Europe. Highest risk is at airports in Belgium, France, and the Netherlands, where numerous flights from sub-Saharan Africa arrive daily. To date, introduction of infected malaria vectors in malaria-free countries has never caused more than a few sporadic malaria cases. Airport malaria does not require establishment and spread of an invasive vector but provides direct evidence of frequent introductions of malaria vectors (the vast majority uninfected) into malaria-free regions. That multiple "silent" introductions of malaria vectors occur every year without successful invasion, even temporary, demonstrates the existence of efficient barriers to invasion. Global spread of African malaria vectors may have been limited so far by climatic constraints because most flights from Africa have a European destination.

**E- Conclusions**
Although they are frequently introduced into non-native areas, malaria vectors rarely establish populations. Historical records indicate that independent introductions of a novel vector and a novel malaria species and acquisition of a native *Plasmodium* species by an introduced vector occurred more often than simultaneous introduction of a novel vector and a novel parasite. Biological characteristics of *Anopheles* vectors of human malaria (eggs susceptible to desiccation, lack of autogeny, natural breeding sites, absence of diapause) make them relatively inefficient invaders. Most often, introduced malaria vectors fail to establish permanently or are quickly eliminated. The overall invasion success of *Anopheles* vectors of human malaria remains much lower than that of *Culex* vectors of avian malaria (and several other pathogens of humans and animals) or some *Aedes* vectors of numerous human and animal arboviruses. For example, *Cx. pipiens* and and *Ae. albopictus* have become nearly cosmopolitan in the last half-century, which is mainly attributed to their ecological plasticity and adaptation to urban environments. Despite their lower overall invasive potential, the considerable impact that invasive malaria vectors can have on human or animal health makes it essential to maintain prevention measures and surveillance programs to reduce the risk of their introduction and establishment.

**See also the following articles**
Disease Vectors, Human; Mosquitoes; Pathogens, Human

**GLOSSARY**

**Arbovirus**: arthropod-borne virus.
**Autogeny**: ability of a blood-sucking arthropod to produce eggs without a blood meal.
**Diapause**: physiological state of dormancy.
**Ecological plasticity**: ability of an organism to change its ecology in response to changes in the environment.
**Endemic disease**: a disease that does not need external inputs to persist in a population (as opposed to epidemic).
**Propagule pressure**: measure of the number of individuals of a species released in an area to which they are not native.
**Species complex**: group of species that satisfy the biological definition of species (i.e., that are reproductively isolated from each other) but are very similar (if not identical) morphologically.
**Vector-borne disease**: infectious disease caused by a pathogen transmitted from one host to another by another organism, most often a blood-sucking arthropod vector (insects or ticks).

Photo 1. *Anopheles gambiae s.s.* female, a major vector of human malaria parasites in tropical Africa. Copyright IRD/Nil Rahola.


Photo 2. *Culex pipiens* female, vector of avian malaria but incompetent to transmit human malaria parasites. Copyright IRD/Nil Rahola.

**Further Reading**


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