Pathways of Entry and Spread of Exotic Mosquitoes, With Particular Reference to Southern Saltmarsh Mosquito, *Ochlerotatus camptorhynchus*

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Comprehensive review of the literature covering the spread of mosquitoes globally and any analysis of the pathways of entry and spread

Introduction

Among other insect vector invasions, Lounibos (21) has provided a recent review of mosquito (Diptera: Culicidae) invasions in one of the first compilations addressing such invasions in the context of invasion biology and medical entomology. Consequently, in the preparation of the following literature review, much of the relevant overview material contained herein draws upon the work of Lounibos (21). Lounibos's work also provides an effective starting point (having already covered significant works such as those of Laird[1] (1984) and Pillai and Ramalingam[2] (1984)) whence recent findings have been more thoroughly examined.

Two of the best known mosquito invasions globally involve the yellow fever mosquito *Aedes (Stegomyia) aegypti* (Linnaeus) and the African malaria mosquito *Anopheles (Cellia) gambiae* Giles. To quote Lounibos (21):

> "*Aedes aegypti*, the so-called yellow fever mosquito, is believed to have migrated from West Africa to the New World in the fifteenth through seventeenth centuries aboard slave ships. Alternatively or additionally, *Ae. aegypti* may have first invaded Portugal and Spain before reaching the Western Hemisphere on European ships. In either case, the evolution of domestic traits in an originally feral species was crucial for enabling *Ae. aegypti* to occupy and flourish in water storage jars in the holds of sailing vessels. . . . In tropical Asia, *Ae. aegypti* is presumed to have arrived and established later, . . . late in the nineteenth century. . . .
>
> The arrival from West Africa in 1930 and establishment and spread into north-eastern Brazil of the African malaria vector *Anopheles gambiae* s.l. rivals the introduction of *Ae. aegypti* into the New World for epidemiological impact. Larvae or adults of this anopheline are believed to have traveled by air or fast passenger ship from Dakar, Senegal to Natal, Brazil, where the first malaria epidemic attributable to *An. gambiae* s.l. occurred in March-May, 1930."

To examine the pathways of entry and subsequent spread of exotic mosquitoes globally, there are however many more cases of mosquitoes establishing in areas outside their native range that should be considered.

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[1] Laird, M. (ed.). 1984. Commerce and the Spread of Pests and Disease Vectors. New York: Praeger. 354 pp.
[2] Pillai, J.S. and Ramalingan, S. 1984. Recent introductions of some medically important Diptera in the Northwest, Central, and South Pacific (including New Zealand), p. 81-101. *In*: Laird, M. (ed.). 1984. Commerce and the Spread of Pests and Disease Vectors. New York: Praeger. 354 pp.

While there are documented records of long-distance dispersal of mosquito adults (unassisted by humans i.e., natural dispersal) far from their larval habitats, resulting in short-term colonizations that temporarily extend the range of a species, most recent successful invasions of mosquitoes have resulted from human transport of immature stages. This review specifically concentrates on those invasions arising from human-aided carriage.

Mosquitoes outside their native range in the United States

Lounibos (21) lists *Aedes (Stegomyia) albopictus* (Skuse), *Ochlerotatus (Ochlerotatus) atropalpus* (Coquillett), *Ochlerotatus (Howardina) bahamensis* (Berlin), *Ochlerotatus (Finlaya) japonicus* (Theobald), *Ochlerotatus (Finlaya) togoi* (Theobald), *Culex (Micraedes) biscaynensis* Zavortink and O, *Toxorhynchites (Toxorhynchites) brevipalpis* Theobald, *Toxorhynchites (Toxorhynchites) amboinensis* (Doleschall) and *Wyeomyia (Wyeomyia) mitchellii* (Theobald) as mosquito species establishing outside their native range in the United States. Two of the nine species listed are non-biting mosquitoes of the genus *Toxorhynchites* which were deliberately introduced into Hawaii in the 1950s as potential biocontrol agents. A recent review article (5) covers the biological control of pest and vector mosquitoes using *Toxorhynchites* species so the establishment of *T. amboinensis* and *T. brevipalpis* will not be further discussed here. Significantly, six of the remaining seven species are now categorized as natural and/or artificial container-breeders.

The establishment of the first four species listed above (*Ae. albopictus* in 1985, *Oc. atropalpus*, *Oc. bahamensis* in 1986 and *Oc. japonicus* in 1998) has been associated with the transport of vehicle tyres. *Ae. albopictus*, *Oc. bahamensis* and *Oc. japonicus* respectively originated from Japan (21, 51) or Taiwan (51), the Bahamas (21), and Japan (21). During the 1980s there was a large increase in the number of used tyres imported into the United States, most arriving in containerized shipments (51). Usually tyres are then sent to numerous locations where they may be stored outdoors enabling at least these three non-indigenous mosquito species to become well-established. Similarly, *Oc. atropalpus*, a native rock pool species has undergone a major range expansion attributable to its recent adaptation to water-holding tyres. Originally known only from the eastern United States, collections from discarded tyres in the late 1970s and 1980s extended the range into the midwestern states of Illinois, Indiana, Ohio and most recently, Nebraska (21).

Madon *et al.* (23) noted that the earliest published records of *Ae. albopictus* found [presumably meaning intercepted] in the continental United States were isolated introductions in used tyres shipped from Asian ports dating back to the 1940s. However, the first record of establishment in 1985 in Houston, Texas involved the discovery of a large population breeding in

used tyres shipped from Japan (8, 21, 23, 51, 62). By 1999, infestations of *Ae. albopictus* were reported from 26 states east of the Mississippi River (23). While there had been a couple of isolated occurrences of *Ae. albopictus* associated with recently imported tyres, prior to June 2001 California was free of any significant infestation of *Ae. albopictus*. However, at that time it was discovered that *Ae. albopictus* was being imported in maritime container shipments of "lucky bamboo" (*Dracaena* spp.) packaged in standing water (23).

According to Madon *et al.* (23), the ornamental plant commonly referred to as "lucky bamboo" had been imported into the United States for at least a decade from South China and other south east Asian ports. Until late 1999 the plants were packed dry (hydrogel or other material providing the moisture) and airfreighted. Around that time because of increased demand for these plants and the high costs of airfreight, containerized maritime shipments of large quantities of plants began. The cargo containers are refrigerated at 22° C during the voyage which takes between 12-15 days. Bundles of lucky bamboo are stored in various types of styrofoam boxes, plastic crates or corrugated cardboard cartons. The crates and cartons have snugly fitting plastic trays that hold 5-8 cm of water. Approximately 500 crates/cartons/boxes are stacked into each maritime container. After arriving at the Los Angeles/Long Beach Harbor, all maritime containers with plant material are trucked to a United States Department of Agriculture inspection site. The first indication of any problems with mosquitoes came in June 2001 when considerable numbers of adult mosquitoes escaped into the inspection facility when the doors of a maritime container of lucky bamboo were opened by inspectors. In a subsequent shipment arriving a week or so later, the observed mosquito breeding provided clear evidence that exotic mosquitoes were being imported into southern California, perhaps in large numbers in association with lucky bamboo.

A further incident involving dry, hydrogel-packaged air-freighted shipments highlighted the extent of the problem (52). Madon *et al.* (23) reported that upon inspection, immature mosquitoes (larvae and pupae that subsequently emerged, and were identified as *Ae. albopictus*) were found in the boxes/crates holding bundles of lucky bamboo that were immersed in 5 to 8 cm of standing water after the gel was removed. This observation confirmed that *Ae. albopictus* eggs attached to the individual cuttings were subsequently hatching when water was added.

As outlined by Lounibos (21), *Oc. togoi* is a maritime rock pool mosquito which has a tropical to subarctic distribution in the Oriental region and in the New World occurs along a 250-300 km stretch of the British Columbia and Washington state coastline. Furthermore, according to Lounibos (21), records of *Oc. togoi* larvae in tyre shipments, bilges, and an adult female on board a ship in Japan suggest that the North American founders may have

reached the Pacific Northwest via shipping from Asia sometime before the late 1960s when the first larvae were recovered from rock holes in Vancouver.

Wyeomyia mitchellii which occurs in Cuba, Dominican Republic, Haiti, Jamaica, Mexico and the United States (63) in Florida and whose larvae inhabit water-containing plant axils, was discovered in Hawaii in 1979 (21). Lounibos (21) states that the immature stages of this species probably reached the Hawaiian Islands in the axils of ornamental bromeliads transported from Florida or the West Indies, where *W. mitchellii* is native.

For completeness, but suffice to say, it is unclear whether the presence of the recently described and narrowly distributed species, *Cx. biscaynensis*, in southernmost Florida could be explained as a recent introduction from elsewhere in the Caribbean or is indigenous to south Florida but first detected only recently (21).

Establishment of exotic mosquitoes in New Zealand and Australia

The situation regarding the establishment of non-indigenous mosquitoes in New Zealand and Australia is summarized in Tables 1 and 2, respectively. The earliest establishments in New Zealand involve two container-breeding species (64), *Culex (Culex) quinquefasciatus* Say and *Ochlerotatus (Finlaya) notoscriptus* (Skuse). Another permanent immigrant to New Zealand, however, is *Ochlerotatus (Halaedes) australis* (Erichson), an Australian species that is common along coastal areas where it breeds in littoral rock pools above the high tide mark (22, 82). Notably, three of the four species of exotic mosquitoes that have established in New Zealand are native to Australia. The most recent Australian addition to New Zealand's otherwise depauperate native mosquito fauna, comprising just 12 species (18, 22, 64), is the southern saltmarsh mosquito, *Ochlerotatus (Ochlerotatus) camptorhynchus* (Thomson). As the common name suggests, this is a saltmarsh (sometimes referred to as a floodwater (Richard Russell *pers. comm.*)) species (22) and not, as might be expected from global trends of mosquito spread, a container-breeding species.

Oc. camptorhynchus was first detected in late 1998 near Napier in the North Island. Subsequent isolated areas of infestation in the North Island were found: in late 2000 around Gisborne, Mahia and Porangahau; and in 2001 around Kaipara Harbour and Mangawhai, in 2002 at Whitford and early 2004 at Whangaparaoa, near or north of Auckland. The only South Island infestation of *Oc. camptorhynchus* was located in May 2004 in the Wairau estuarine area (Plate 1)/Lake Grassmere near the northern South Island town of Blenheim. This discovery post-dated the eradication of the mosquito from Napier and Mahia (Maungawhio Lagoon), and a period of at least 18 months of no detections of adult or immature *Oc. camptorhynchus*

following treatment at Gisborne (including Wherowhero Lagoon and Sponge Bay), Porangahau, Mangawhai and Whitford. Furthermore, no adults or larvae have been caught in the Kaipara Harbour or Whangaparaoa since February 2004 and March 2004, respectively (Ministry of Health *pers. comm.*).

Plate 1: Part of the infested area in the Wairau Lagoons

Prior to the discovery of *Oc. camptorhynchus* in New Zealand, there had not been an exotic mosquito establishment since the early 1960s. The earliest establishment of an exotic culicid involved *Cx. quinquefasciatus*. It arrived in New Zealand (64) and Australia (21) during the early years of European settlement. *Cx. quinquefasciatus* comprises one of five exotic species (Table 2) to have joined Australia's rich native culicid fauna.

Setting aside the arrival in Australia of *Ae. aegypti*, *Cx. quinquefasciatus* (21, 64) and *Culex (Culex) molestus* Forskal (a synonym of *Culex pipiens* (63)[1]) (21) many decades ago, the establishment of *Aedes (Aedimorphus) nocturnus* (Theobald) (a synonym of *Aedes vexans vexans* (Richard Russell *pers. comm.*)[1]) and *Culex (Culex) gelidus* Theobald constitute very recent arrivals. Also, although *Ae. aegypti* had not been recorded in the Northern Territory since the 1950s, in February 2004 it was discovered during routine mosquito trapping in Tennant Creek (68). It has been suggested that it may have arrived as drought resistant eggs in a receptacle from Queensland (2, 53, 68). In recent times *Ae. aegypti* was only found in Queensland,

[1] Strictly, there is some doubt, even controversy, about the validity of this taxon (Richard Russell, *pers. comm.*).

although in the past (dating from the mid-late 19th century (Richard Russell *pers. comm.*)) it had been known from the states of New South Wales, Northern Territory and Western Australia (82) too. Incidentally, another comparatively frequent arrival to various Australian ports is *Ae. albopictus* (82). Unlike *Ae. aegypti* however, *Ae. albopictus* has never established in Australia. In light of particular media releases (1), the Walter Reed Biosystematics Unit (63) can perhaps be forgiven for including Australia erroneously in the growing list of countries in which *Ae. albopictus* is present.

In contrast to the international maritime movement of container-breeding species such as *Ae. aegypti* and *Ae. albopictus*, the introduction of *Cx. gelidus* to southeast Queensland, Australia was considered to be aircraft related (15, 50). *Cx. gelidus* was later discovered in the Northern Territory in February 2000 (66). Although specimens dating back to 1996 were located subsequently in Northern Territory collections (67), a specimen now identified as *Cx. gelidus* was collected in Queensland prior to the first record in the Northern Territory (67). Consequently, the prevailing view is that *Cx. gelidus* entered the Northern Territory from Queensland by road (67). Moreover a review of specimens from Katherine in the Northern Territory revealed *Cx. gelidus* larvae in a tyre at the Katherine dairy. The dairy and meatworks have commercial road transport links to Queensland providing a potential mode of transport between the two areas (66). In addition, adults could feasibly be moved inside the cabins with the road transport of cattle or people between Queensland and the Northern Territory (66).

The pathway by which *Ae. nocturnus* was introduced into the northeast Kimberley region of Western Australia is similarly speculative. Although the nearest international airport is about 500 km away (and therefore an unlikely point of entry (15)), Kununurra is occasionally used by light aircraft arriving from Timor and other close overseas islands. The arrival of *Ae. nocturnus* in northern Western Australia may thus have been effected via these aircraft. However another possibility is that *Ae. nocturnus* adults were carried to northeast Kimberley from islands of the Indonesian archipelago by cyclonic winds (15). Certainly wind-assisted dispersal into Northern Territory from southeast Asia is thought to have been the major immigration route for some species of *Culicoides* (Diptera: Ceratopogonidae), especially those of the *Avaritia* subgenus (9).

Regardless of the pathway of entry of the three most recent exotic species to arrive in Australia, it cannot go without mention that source populations of *Ae. aegypti*, *Ae. nocturnus* and *Cx. gelidus* exist in relatively close proximity to Australia in countries such as Indonesia, Papua New Guinea and the Solomon Islands. Similarly, it can be no coincidence that three of the four exotic mosquito species to have established in New Zealand are native to

Table 1: Exotic mosquito establishments in New Zealand

Scientific name	Year discovered	Area established in	Present in[1]	Reference to establishment
Culex (Culex) quinquefasciatus Say	Prior to 1848 (64)	Northern two thirds of the North Island (54)	Argentina, Australia, Bahamas, Bangladesh, Brazil, Cambodia, Chagos Archipelago (British Indian Ocean Territory), Chile, China, Comoros, Congo, Cook Islands, Cuba, Djibouti, Ethiopia, Federated States of Micronesia, India, Indonesia, Iran, Kiribati, Korea, Laos, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritius, Mexico, Myanmar [P], Nauru, Nepal, New Caledonia, New Zealand, Oman, Pakistan, Palau, Papua New Guinea, Peru, Philippines, Samoa, Saudi Arabia, Solomon Islands, South Africa, Sudan, Suriname, Tanzania, Tonga, Trinidad and Tobago, Tuvalu, United Kingdom, United States, Vanuatu, Zaire (63) Native to the warmer parts of	18, 37, 54, 61, 64

[1] Countries are listed in alphabetical order with the type country underlined in the Systematic Catalog of Culicidae (63). Occasionally the Systematic Catalog of Culicidae (63) refers to countries where the species is presumed to occur – these are indicated by [P] after the country name.

Scientific name	Year discovered	Area established in	Present in[1]	Reference to establishment
			the Americas (64) (southern United States and Mexico (54))	
Ochlerotatus (Finlaya) notoscriptus (Skuse)	1918 (18)	Auckland (initially), now most of the North Island (18)	Australia, Indonesia, New Caledonia, Papua New Guinea, New Zealand, Solomon Islands (63) All states in Australia (including Tasmania) (74)	18, 37, 54, 61, 64
Ochlerotatus (Halaedes) australis (Erichson)	1961 (64)	Stewart Island and the South Island provinces of Southland, Otago and Westland (64)	Australia, Lord Howe Island (Australia), New Zealand, Norfolk Island (Australia) (63) Australia: New South Wales, southern Queensland, South Australia, Tasmania, Victoria and Western Australia (76)	18, 22, 37, 61, 64
Ochlerotatus (Ochlerotatus) camptorhynchus (Thomson)	December 1998 October 2000 November 2000 November 2000 February 2001	Napier, Hawke's Bay (subsequently eradicated) Wherowhero Lagoon and Sponge Bay, Gisborne (subsequently eradicated) Porangahau, southern Hawke's Bay (subsequently eradicated) Maungawhio Lagoon, Mahia (subsequently eradicated) Kaipara Harbour	Australia (63) Australia: southern New South Wales, South Australia, southwest Western Australia, Victoria and Tasmania (70)	21, 22, 53, 61

Scientific name	Year discovered	Area established in	Present in[1]	Reference to establishment
		(eradication programme in progress)		
	April 2001	Mangawhai (subsequently eradicated)		
	March 2002	Whitford (subsequently eradicated)		
	January 2004	Whangaparaoa (eradication programme in progress)		
	May 2004	Wairau Lagoons near Blenheim/Lake Grassmere (eradication programme proceeding)		

Table 2: Exotic mosquito establishments in Australia

Scientific name	Year discovered	Area established in	Present in[1]	References to establishment
Aedes (Stegomyia) aegypti (Linnaeus)	Mid-late 19th century (Richard Russell *pers. comm.*) 2004 (2, 68)	Queensland (53, 82), but previously in New South Wales, Northern Territory and Western Australia (82) Northern Territory – Tennant Creek (eradication programme in progress (10, 68))	Albania, Bangladesh, Bosnia and Herzegovina, Cambodia, Comoros, Cook Islands, Djibouti, Egypt, Federated States of Micronesia, Fiji, Greece, India, Indonesia, Japan, Kenya, Kiribati, Laos, Macedonia, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritius, Myanmar (Burma), Nauru, New Caledonia, Papua New Guinea, Philippines, Samoa, Solomon Islands, Thailand, Tonga, Tuvalu, Vanuatu, Cosmotropical (within the 20°C isotherms) (63) Native to West Africa, but has been known in the New World for several centuries and tropical Asia since the late nineteenth century (21)	2, 10, 21, 53, 68
Aedes (Aedimorphus) nocturnus (Theobald) Synonym of *Aedes vexans vexans* (Richard Russell *pers. comm.*)	1996 (15)	Northern Western Australia (15)	Australia, Cook Islands, Fiji, Indonesia, Mariana Islands, Marshall Islands, New Caledonia, Palau, Papua New Guinea, Samoa, Timor, Tonga, Tuvalu, Vanuatu (63)	15, 53

[1] Countries are listed in alphabetical order with the type country underlined in the Systematic Catalog of Culicidae (63). Occasionally the Systematic Catalog of Culicidae (63) refers to countries where the species is presumed to occur – these are indicated by [P] after the country name.

Scientific name	Year discovered	Area established in	Present in[1]	References to establishment
Culex (Culex) gelidus Theobald	1999 (50, 66) 2000 (66) (but is likely to have established as early as 1996 (67))	Queensland (Brisbane, Mackay, Cairns and possibly Daintree) (66) Northern Territory (Katherine, Batchelor and Darwin and probably Alice Springs) (66, 67)	Bangladesh, Cambodia, China, India, Indonesia, Japan, Malaysia, Myanmar [P], Nepal, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam (63)	21, 50, 53, 66, 67
Culex (Culex) molestus Forskal Synonym of *Culex pipiens* (63)	After World War II (21)	Australia: New South Wales, Tasmania, Victoria (80, 82), South Australia, Western Australia (Richard Russell *pers. comm.*)		21, 78
Culex (Culex) quinquefasciatus Say	With or shortly after the colonial First Fleet (21)	New South Wales, Northern Territory, Queensland, South Australia, Victoria, Western Australia (73)	Argentina, Australia, Bahamas, Bangladesh, Brazil, Cambodia, Chagos Archipelago (British Indian Ocean Territory), Chile, China, Comoros, Congo, Cook Islands, Cuba, Djibouti, Ethiopia, Federated States of Micronesia, India, Indonesia, Iran, Kiribati, Korea, Laos, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritius, Mexico, Myanmar [P], Nauru, Nepal, New Caledonia, New Zealand, Oman, Pakistan, Palau,	21, 64

Scientific name	Year discovered	Area established in	Present in[1]	References to establishment
			Papua New Guinea, Peru, Philippines, Samoa, Saudi Arabia, Solomon Islands, South Africa, Sudan, Suriname, Tanzania, Tonga, Trinidad and Tobago, Tuvalu, United Kingdom, United States, Vanuatu, Zaire (63)	

Australia, New Zealand's close neighbour. Moreover, despite the possibility of a direct eastward arrival, it has been suggested (64) that even *Cx. quinquefasciatus* may have spread to New Zealand from Australia in the first third of the nineteenth century.

In order to get a complete picture of the movement of mosquitoes around the world it is important to examine potential mosquito establishments (i.e., those entering areas outside their native range without necessarily establishing) too. For the purposes of this review, it is therefore appropriate to introduce the terms 'interception' and 'establishment'. 'Establishment' has been defined by FAO, in the International Standards for Phytosanitary Measures No. 5: Glossary of Phytosanitary Terms (11), as "perpetuation, for the foreseeable future, of a pest within an area after entry". However, 'interception (of a pest)' means "the detection of a pest during inspection or testing of an imported consignment".

Tables 3 and 4 list the documented mosquito interceptions in New Zealand and Australia, respectively. Table 3 provides a complete list (as maintained by the Ministry of Health) of mosquito interception events at New Zealand ports and airports since 1998 as well as some additional well-documented one-off finds of species not otherwise intercepted in the last five years (i.e., *Tripteroides (Tripteroides) bambusa* (Yamada) and *Tripteroides (Polylepidomyia) tasmaniensis* (Strickland) (16)). The 35 interception events involved 18 different species of mosquitoes, two of which were identified to genus or subgenus level only. Of the remaining 33 interception events, there were three of *Ae. aegypti*, eight of *Ae. albopictus*, six of *Oc. japonicus*, two of *Ae. polynesiensis*, two of *Cx. quinquefasciatus*, two of Oc*. notoscriptus* and single interceptions of 10 other species. These interceptions highlight the need for New Zealand to continue to apply appropriate measures (inspection and/or treatment) to high risk pathways of entry such as tyre imports (containerized or not), used machinery, used cars, soft top containers – all or parts of which are potential water receptacles; similarly, to continue vessel inspections. Many mosquitoes of the genera *Aedes* and *Ochlerotatus* have a well known strategy for surviving long, unfavourable periods and for avoiding predators (59). Instead of laying eggs in established bodies of ground water, as is the tactic adopted by most mosquitoes, they oviposit in dried-out places prone to subsequent water inundation or flooding. Eggs are never laid directly onto water surfaces. The drought-resistant eggs remain dormant until soaked by rising water levels, often many months later (59).

Setting aside the 17 interception events involving *Ae. aegypti*, *Ae. albopictus* or *Oc. japonicus*, four of the remaining 16 events involved two exotic mosquito species (*Cx. quinquefasciatus* and *Oc. notoscriptus*) that have long been established in New Zealand. The twelve interception events (ten of which were single events) involving mosquito species unknown in New Zealand were, with possibly one exception, associated with airline flights or shipping vessels originating, if not directly arriving, from infested countries. Six of the ten singly intercepted mosquito species presently unknown in New Zealand are native to Australia; two (*Ochlerotatus (Mucidus) alternans* (Westwood) and *Ochlerotatus (Ochlerotatus) vigilax* (Skuse)) of which were intercepted at airports. Overall, only three of the 33 interception events listed in Table 3 involved air traffic. Notably, *Oc. camptorhynchus* has been intercepted only once; one dead male was found inside a sea container (Ministry of Health *pers. comm.*).

Table 4 is based on the published listing provided by Russell and Kay (53) but is by no means comprehensive (21). Interestingly, the Australian Quarantine and Inspection Service reported 41 interceptions of mosquitoes in association with various imported goods in 2000 (6). Of the 41 interception events, 22 involved species unknown to Australia, or of limited distribution, including 15 interceptions of *Ae. aegypti*, six of *Ae. albopictus* and one of *Culex (Culiciomyia) spathifurca* (Edwards). Clearly *Ae. aegypti* and *Ae. albopictus*, the two container breeding mosquitoes, have ongoing opportunities to enter and establish (albeit temporarily in some instances) in different locations in Australia. As with recent establishments, it is notable that the five other species that have been intercepted (i.e., *Aedes (Lorrainea) dasyorrhus* King and Hoogstraal, *Aedes (Stegomyia) scutellaris* (Walker) group, *Culex (Culiciomyia) fragilis* (Ludlow), *Cx. spathifurca* and *Ochlerotatus (Finlaya) papuensis* (Taylor) group) naturally occur in countries that are relatively close to Australia such as Indonesia, Papua New Guinea and the Solomon Islands (63). None of these five species have been intercepted by New Zealand inspectors. However, as with Australia, New Zealand has intercepted *Ae. aegypti* and *Ae. albopictus* more frequently than most other species (53). Unlike New Zealand and the United States (7, 12, 59) though, Australia has not intercepted *Oc. japonicus* (53). Similarly, *Tp. bambusa* (8) has not been intercepted.

Non-indigenous mosquitoes in other parts of the world

On a global scale, many insect vector invasions go unnoticed (21) for considerable periods of time because of a lack of adequate surveillance (e.g. the presence of *Ae. albopictus* in Nigeria determined as part of a post-yellow fever outbreak investigation (55)). The lack of a universal reporting system further complicates completion of an accurate and comprehensive review of

the pathways of entry and spread of mosquitoes globally and any analysis of the pathways of entry and spread. The entry and establishment of non-indigenous mosquitoes in Australia, New Zealand and the United States is better documented than most other countries. Many brief reports (e.g. the discovery of *Oc. japonicus* in Quebec, Canada in 2000 (56)), as well as published research findings (e.g., *Ae. albopictus* in Brazil where it was first detected in 1986 (3)) are available for other countries. Even though such information does not necessarily provide straightforward comparisons, recent data from France presented at the International Congress of Entomology in August 2004 (57) (Table 5) does show that, like New Zealand and the United States, France is concerned about the presence of the container-breeding mosquitoes, particularly *Ae. albopictus* and *Oc. japonicus*. As a result since 2001 the French Ministry of Health has supported surveillance and control operations to prevent the further spread of these species (57). In contrast, the Centers for Disease Control in the United States discontinued tyre inspections around 1997 because *Ae. albopictus* was already well established throughout much of the United States (52).

Implications of late twentieth century mosquito invasions

The global spread of the more cold-tolerant, container-breeding mosquito species, *Ae. albopictus* and *Oc. japonicus*, during the last two decades, as well as the ongoing threat of *Ae. aegypti* in tropical areas, suggests that few countries will ultimately be immune to the invasion of one or more of these species. Even those countries such as Australia, France and New Zealand with rigorous biosecurity systems in place targeting mosquito species are frequently challenged. As noted by Lounibos (21), regarding propagule pressure, it is noteworthy that most successful mosquito invaders have arrived by ship. Mosquito arrivals on aircraft are typically adults consisting of only a few individuals of any given species. In contrast, ships, especially modern container vessels, can themselves harbour, as well as transport cargo, which carries a large number of propagules, especially of the immature stages of mosquitoes. The transport of desiccation-resistant *Aedes* and *Ochlerotatus* eggs, for example in tyres, appears to account for the establishment of container-breeding species such as *Oc. atropalpus* in France (57) and Italy (21, 59), *Oc. japonicus* in France (57) and the United States (12, 21, 59) and *Ae. albopictus* almost worldwide (3, 21, 57, 59). Lounibos (21) further states that “the dominance of a few species among successful mosquito invaders suggests that previous success may be a potentially good predictor of vector invasiveness”. While one cannot fail to agree that such a statement applies to the aforementioned container-inhabiting species, the most recent and only new mosquito invader to New Zealand for over four decades has had no previous success.

Tracking interceptions, such as those listed for New Zealand and Australia in Tables 3 and 4, respectively, may be a further clue to possible future invaders. In addition, as mentioned previously, a substantial proportion of recent establishments seem to originate in countries that are near neighbours. Perhaps the interception of *Oc. camptorhynchus* and *Oc. vigilax* should be viewed as a sign indicating that Australian saltmarsh species can enter and establish. While the "journey" may be a rough one, the close proximity of Australia nevertheless enhances the probability of survival during the short trip, whatever the mode and propagule pressure.

In addition it is noteworthy that, while generally regarded as a saltmarsh breeder similar to *Oc. camptorhynchus* (e.g., 20, 77), *Oc. vigilax* is annually recovered from rock pools in the Northern Territory (Peter Whelan, *pers. comm.*). Recovery of such saltmarsh species from rock pools raises the possibility that breeding may occur, albeit very infrequently, in open structures where salt water has ponded. With this in mind, some previous invasion success is evident in the maritime rock pool mosquito, *Oc. togoi*, which colonized a 250-300 km stretch of the British Columbia and Washington state coastline sometime before the late 1960s (21). Similarly, the Australian coastal rock pool species, *Oc. australis* established in New Zealand in the early 1960s (64).

Table 3: Recent exotic mosquito interceptions in New Zealand

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
Aedes (Stegomyia) aegypti (Linnaeus)	November 1999: Auckland (38) April 2001: Auckland (38) January 2004: Auckland (47)	Albania, Australia (Queensland), Bangladesh, Bosnia and Herzegovina, Cambodia, Comoros, Cook Islands, Djibouti, Egypt, Federated States of Micronesia, Fiji, Greece, India, Indonesia, Japan, Kenya, Kiribati, Laos, Macedonia, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritius, Myanmar (Burma), Nauru, New Caledonia, Papua New Guinea, Philippines, Samoa, Solomon Islands, Thailand, Tonga, Tuvalu, Vanuatu, Cosmotropical (within the 20°C isotherms) (63, with Australia (Queensland) added (82)) Native to West Africa, but has been known in the New World for several centuries and tropical Asia since the late nineteenth century (21)	18, 38, 47, 53
Aedes (Stegomyia) albopictus	January 1998: Auckland (38)	Albania, Argentina, Bangladesh,	18, 53

[1] Unless specifically stated, intercepted at a seaport

[2] Countries are listed in alphabetical order with the type country underlined in the Systematic Catalog of Culicidae (63). Occasionally the Systematic Catalog of Culicidae (63) refers to countries where the species is presumed to occur – these are indicated by [P] after the country name.

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
(Skuse)	August 1998: Wellington (38) March 1999: Tauranga (38) March 2001: Auckland (38) October 2001: Auckland (38) November 2001: Auckland (38) March 2003: Auckland (41) May 2004: Auckland (48)	Cambodia, Chagos Archipelago (British Indian Ocean Territory), China, Djibouti, Greece, Guatemala, India, Indonesia, Italy, Japan, Korea, Laos, Madagascar, Malaysia, Maldives, Mauritius, Mexico, Myanmar (Burma), Nepal, Nigeria, Pakistan, Papua New Guinea, Philippines, Reunion (France), Seychelles, Solomon Islands, United States, Mariana Islands, Oriental Region (63, with Australia removed)	
Aedes (Stegomyia) sp. [First instar]	March 2003: Auckland (40)		40 (and 14 March 2003 SSM TAG Notification)
Aedes (Stegomyia) polynesiensis Marks	January 2004: Auckland (47) October 2004: Auckland (49)	Cook Islands, Fiji, Austral Islands (French Polynesia), Marquesas Islands (French Polynesia), Samoa Islands, Society Islands (French Polynesia), Tuamotu Archipelago (French Polynesia) (63, with Australia, New Zealand and United Kingdom removed)	47, 53
Culex (Culex) annulirostris Skuse	March 1999: Napier (38)	Australia, Cook Islands, Fiji, Indonesia, Kiribati, Nauru, New Caledonia, Palau, Papua New Guinea, Philippines, Solomon Islands, Tonga, Tuvalu, Vanuatu (63)	18, 38, 53

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
		Australia: New South Wales, Northern Territory, Queensland, South Australia (widespread, particularly Murray Valley), Victoria, Western Australia and one record from Tasmania (72, 82)	
Culex (Culex) gelidus Theobald	July 2003: Auckland International Airport (43)	Australia, Bangladesh, Cambodia, China, India, Indonesia, Japan, Malaysia, Myanmar [P], Nepal, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam (63, with Australia added (66, Peter Whelan *pers. comm.*)) Australia: Northern Territory (66, 67), Queensland (66) and Western Australia (67)	43
Culex (Culex) pipiens ssp. *pallens* Coquillett	September 2001: Auckland (38)	China, Japan, Korea, Mexico, United States (63)	38
Culex (Culex) quinquefasciatus Say	April 2003: Auckland (42) October 2004: Auckland (Ministry of Health *pers. comm.*)	Argentina, Australia, Bahamas, Bangladesh, Brazil, Cambodia, Chagos Archipelago (British Indian Ocean Territory), Chile, China, Comoros, Congo, Cook Islands, Cuba, Djibouti, Ethiopia, Federated States of Micronesia, India, Indonesia, Iran, Kiribati, Korea, Laos, Madagascar, Malaysia, Maldives, Marshall Islands,	42

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
		Mauritius, Mexico, Myanmar [P], Nauru, Nepal, New Caledonia, New Zealand, Oman, Pakistan, Palau, Papua New Guinea, Peru, Philippines, Samoa, Saudi Arabia, Solomon Islands, South Africa, Sudan, Suriname, Tanzania, Tonga, Trinidad and Tobago, Tuvalu, United Kingdom, United States, Vanuatu, Zaire (63)	
Culex (Culex) sitiens Wiedemann	March 2003: Auckland (40)	Australia, Bangladesh, Cameroon, China, Comoros, Djibouti, Fiji, India, Indonesia, Iran, Japan, Kenya, Korea, Madagascar, Malaysia, Maldives, Mozambique, Myanmar [P], Nauru, New Caledonia, Oman, Pakistan, Papua New Guinea, Philippines, Samoa, Saudi Arabia, Singapore, Solomon Islands, Sri Lanka, Sudan, Taiwan, Tanzania, Thailand, Tonga, Tuvalu, United Arab Emirates, Vanuatu, Yemen (63) Australia: New South Wales, Northern Territory, Queensland, northern Western Australia (82)	40 (and 14 March 2003 SSM TAG Notification)
Culex sp. [Head missing]	September 2003: Auckland (46)		46
Ochlerotatus (Mucidus) alternans (Westwood)	March 2003: Christchurch International Airport (Ministry of	Australia, New Caledonia, Papua New Guinea, Timor (63)	Ministry of Health *pers. comm.*

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
	Health *pers. comm.*)	Australia: New South Wales, Northern Territory, Queensland, South Australia, Victoria, Western Australia (79)	
Ochlerotatus (Ochlerotatus) camptorhynchus (Thomson)	September 2004: Christchurch (Ministry of Health *pers. comm.*)	Australia (63) Australia: southern New South Wales, South Australia, southwest Western Australia, Victoria and Tasmania (77)	Ministry of Health *pers. comm.*)
Ochlerotatus (Finlaya) japonicus (Theobald)	January 1998: Auckland (38) March 1999: Auckland (38) December 2001: Auckland (38) September 2002: Auckland (38) December 2002: Auckland (39) August 2003: Auckland (44)	China, Japan, Korea, Russia, Taiwan, United States (63)	16, 38, 39, 44, 53
Ochlerotatus (Finlaya) notoscriptus (Skuse)	September 2003: Auckland (45) November 2003: Auckland (Ministry of Health – SSM TAG Notification)	Australia, Indonesia, New Caledonia, Papua New Guinea, New Zealand, Solomon Islands (63) All states in Australia (74)	45, Ministry of Health – SSM TAG Notification
Ochlerotatus (Ochlerotatus) sierrensis (Ludlow)	December 2002, Auckland (Richard Russell *pers. comm.*)	Canada, United States (63)	53, Richard Russell *pers. comm.*
Ochlerotatus (Ochlerotatus) vigilax (Skuse)	January 2002: Christchurch International Airport (38)	Australia, Fiji, Indonesia, Japan, Malaysia, Papua New Guinea, New Caledonia, Seychelles, Solomon Islands, Taiwan, Thailand, Tonga, Vanuatu, Vietnam (63)	38

Scientific name	Recently intercepted[1]	Present in[2]	Reference to interception
		Australia: New South Wales, Northern Territory, Queensland, South Australia, Victoria, Western Australia (75)	
Tripteroides (Tripteroides) bambusa (Yamada)	January 1993: Christchurch (16)	China, Japan, Korea, Taiwan (63)	16, 53
Tripteroides (Polylepidomyia) tasmaniensis (Strickland)	March 1993: Christchurch (16)	Australia (63) Australia: New South Wales, southeast Queensland, South Australia, Tasmania and Victoria (81)	16, 18, 53

Table 4: Exotic mosquito interceptions in Australia

Scientific name	Intercepted in	Present in[1]	Reference to interception
Aedes (Stegomyia) aegypti (Linnaeus)	New South Wales (Richard Russell *pers. comm.*), Northern Territory (65, 67, 69, 70), Queensland and Western Australia (Richard Russell *pers. comm.*)	Albania, Australia (Queensland), Bangladesh, Bosnia and Herzegovina, Cambodia, Comoros, Cook Islands, Djibouti, Egypt, Federated States of Micronesia, Fiji, Greece, India, Indonesia, Japan, Kenya, Kiribati, Laos, Macedonia, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritius, Myanmar (Burma), Nauru, New Caledonia, Papua New Guinea, Philippines, Samoa, Solomon Islands, Thailand, Tonga, Tuvalu, Vanuatu, Cosmotropical (within the 20°C isotherms) (63, with Australia (Queensland) added (82)) Native to West Africa, but has been known in the New World for several centuries and tropical Asia since the late nineteenth century (21)	6, 53, 65, 67, 69, 70
Aedes (Stegomyia) albopictus (Skuse)	New South Wales (1, 82), Northern Territory (65, 67, 69, 70, 82), Queensland (1, 82), Victoria (Richard	Albania, Argentina, Bangladesh, Cambodia, Chagos Archipelago (British Indian Ocean Territory), China, Djibouti, Greece, Guatemala, India, Indonesia, Italy, Japan, Korea,	1, 6, 53, 65, 67, 69, 70

[1] Countries are listed in alphabetical order with the type country underlined in the Systematic Catalog of Culicidae (63). Occasionally the Systematic Catalog of Culicidae (63) refers to countries where the species is presumed to occur – these are indicated by [P] after the country name.

Scientific name	Intercepted in	Present in[1]	Reference to interception
	Russell *pers. comm.*) and Western Australia (82)	Laos, Madagascar, Malaysia, Maldives, Mauritius, Mexico, Myanmar (Burma), Nepal, Nigeria, Pakistan, Papua New Guinea, Philippines, Reunion (France), Seychelles, Solomon Islands, United States, Mariana Islands, Oriental Region (63, with Australia removed)	
Aedes (Lorrainea) dasyorrhus King and Hoogstraal		Indonesia, Santa Cruz Islands (Solomon Islands), Solomon Islands (63)	53
Aedes (Stegomyia) scutellaris (Walker) group	Northern Territory (69)	Australia (far northern Queensland), Indonesia, Papua New Guinea, Philippines (63, with Australia (far northern Queensland) added (82))	53, 69
Culex (Culiciomyia) fragilis Ludlow	Northern Territory (65, 70)	India, Indonesia, Malaysia, Philippines, Solomon Islands, Sri Lanka, Thailand (63)	53, 65, 70
Culex (Culiciomyia) spathifurca (Edwards)		India, Indonesia, Malaysia, Maldives, Philippines, Singapore, Sri Lanka, Thailand (63)	6, 53
Ochlerotatus (Finlaya) papuensis (Taylor) group		Indonesia, Papua New Guinea (63)	53

Table 5: Exotic mosquito establishments/interceptions in France

Scientific name	Year discovered	Area found in	Present in[1]	Reference to establishment/ interception
Aedes (Stegomyia) albopictus (Skuse)	1999 (57, 59) 1999 (57, 59) 2000 (57) 2002 (57) 2003 (57)	Normandie Poitou-Charentes Normandie Corse Poitou-Charentes	Albania, Argentina, Bangladesh, Cambodia, Chagos Archipelago (British Indian Ocean Territory), China, Djibouti, Greece, Guatemala, India, Indonesia, Italy, Japan, Korea, Laos, Madagascar, Malaysia, Maldives, Mauritius, Mexico, Myanmar (Burma), Nepal, Nigeria, Pakistan, Papua New Guinea, Philippines, Reunion (France), Seychelles, Solomon Islands, United States, Mariana Islands, Oriental Region (63, with Australia removed)	57, 59
Ochlerotatus (Finlaya) japonicus (Theobald)	2000 (57)	Northern France (59)	China, Japan, Korea, Russia, Taiwan, United States (63)	57, 59
Ochlerotatus (Ochlerotatus) atropalpus (Coquillett)	2003 (57)		Canada, Italy, United States (63)	57

[1] Countries are listed in alphabetical order with the type country underlined in the Systematic Catalog of Culicidae (63). Occasionally the Systematic Catalog of Culicidae (63) refers to countries where the species is presumed to occur – these are indicated by [P] after the country name.

An analysis of the historical spread of exotic mosquitoes in New Zealand

Prior to the detection of *Ochlerotatus (Ochlerotatus) camptorhynchus* (Thomson) near Napier in 1998 (21, 22, 53, 61), there were three species of exotic mosquitoes in New Zealand (37, 61, 64) namely, *Culex (Culex) quinquefasciatus* Say, *Ochlerotatus (Finlaya) notoscriptus* (Skuse) and *Ochlerotatus (Halaedes) australis* (Erichson). Table 1 indicates the year each was discovered in New Zealand as well as their current distribution according to Weinstein *et al.* (64). Weinstein *et al.* (64) drew largely on the data compiled by Laird (18) from the 1993-94 New Zealand mosquito survey which concentrated on the northern North Island and the hinterlands of container ports in Hawkes Bay, Wellington and Canterbury. Priority was given to artificial habitats which consequently provided detailed information for *Cx. quinquefasciatus* and *Oc. notoscriptus,* which both commonly oviposit in small artificial containers (18).

Prior to the survey, *Oc. notoscriptus* (known then as *Aedes notoscriptus*) was described as being absent from all parts of the North Island south of Gisborne. A notable extension to the previously documented distribution of *Oc. notoscriptus* became apparent early in the course of the survey so Marshall Laird and Jenny Easton formally reported the widespread establishment of this species in the Wellington region in 1994 (17). With the publication of the full results of the 1993-1994 survey (18), additional discoveries of *Oc. notoscriptus* extended its known distribution to include Napier, Hastings, Waipawa and Waipukurau. [Although not part of the survey, *Oc. notoscriptus* was similarly found to be present in Taranaki and Opotiki in the Bay of Plenty.] Consequently, *Oc. notoscriptus* was now known to occur throughout much of the North Island lowlands.

Notably, *Cx. quinquefasciatus* was also reported to be showing the beginnings of a move southwards from the northern North Island. Subsequent to the survey, the presence of *Cx. quinquefasciatus* was confirmed in the northern South Island areas of Nelson and Picton (64), as well as Taranaki and the Waikato.

Laird (18) implied that the southward dispersal of both *Cx. quinquefasciatus* and *Oc. notoscriptus* occurred naturally but emphasized that the move was “caused by the greatly enhanced augmented artificial larval habitat availability” due in no small way to the burgeoning trade in used tyres and the distinctive New Zealand use of

them – weighting down the polythene sheeting covering farm silage piles and pits (18).

The third exotic species, *Oc. australis* (formerly known as *Aedes australis*) uses brackish rock pools in the spray zone as larval habitats (18). In the late 1960s and early 1970s, its northward dispersal from Otago to Timaru was noted. However, during the 1993-1994 survey it was not found any further north. Suitable larval habitats were available as indicated by the detection of *Opifex fuscus* alone in spray-zone pools further north on Banks Peninsula and at Oaro. Apparently *Oc. australis* occupies the same larval habitat as the endemic *Opifex fuscus.* Notably, along the South Otago coastline, Laird (18) suggested that *Opifex fuscus* seems to have been replaced by *Oc. australis*.

It would seem that the observed dispersal of the three exotic mosquitoes from their foci of introduction into New Zealand has been relatively slow (at least compared with the dispersed findings of infestations of *Oc. camptorhynchus*). Significantly, *Oc. notoscriptus* has increased its rate of spread in recent years. Laird (18) quite reasonably suggests that the spread of *Oc. notoscriptus* may serve as a blueprint for the spread of cold hardy *Ae. albopictus* and *Oc. japonicus* were these container-breeding species to establish in New Zealand. Unfortunately, the relatively slow dispersal northwards from Stewart Island of *Oc. australis* offers no parallel to the observed spread (despite vigorous and timely containment and eradication efforts) of the newest arrival, *Oc. camptorhynchus*. However, the timely collection and regular reports of any mosquitoes obtained through the port surveillance and saltmarsh sampling surveillance (as directed by the Ministry of Health) will inevitably improve the comprehensiveness of any data sets. Potentially this will allow for more quantitative analyses of the data in the future.