A Scenario for Invasion and Dispersal of *Aedes albopictus* (Diptera: Culicidae) in New Zealand

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ABSTRACT To date, there has been no confirmed, indigenously acquired case of arthropod-borne viral disease in New Zealand, but this may change in the near future due to the presence of exotic vectors and regular influx of infected humans. The risk of a disease outbreak may be aggravated if other exotic mosquito vectors become established, in particular *Aedes albopictus* (Skuse), a species that has already been intercepted several times in New Zealand. In this study, the possible means of invasion and dispersal of *Ae. albopictus* in northern New Zealand are discussed, along with the factors that should facilitate its establishment in the event it evades border controls.

KEY WORDS *Aedes albopictus*, invasion, dispersal, New Zealand

TO DATE, THERE HAS NOT BEEN a confirmed, indigenously acquired arboviral infection in humans within New Zealand (Derraik and Calisher 2004). This seems to be entirely fortuitous (Weinstein et al. 1997), because there are no particular characteristics that make the country intrinsically refractory to these viruses (Weinstein 1994). The rapid modern movement of people, the consequent routine arrival of infected humans (Weinstein et al. 1995, Kelly-Hope et al. 2002), and exotic arthropods already present in this country each is likely to terminate this blissful state, and it seems that it is just a matter of time before an arboviral outbreak occurs (Weinstein et al. 1995, Weinstein 1996, Derraik and Calisher 2004). Compounding this situation, apart from the four exotic mosquito species already established in New Zealand [*Culex* (*Culex*) *quinquefasciatus* Say, *Ochlerotatus* (*Finlaya*) *notoscriptus* (Skuse), *Ochlerotatus* (*Halaedes*) *australis* (Erichson), and *Ochlerotatus* (*Ochlerotatus*) *camptorhynchus* (Thomson)], at least 30 other exotic culicid species have been intercepted at national entry ports (Derraik 2004b; unpublished data; Table 1). The establishment of newly introduced vectors could greatly increase the likelihood of a disease outbreak.

The mosquito species that poses the greatest threat to New Zealand seems to be the Asian tiger mosquito, *Aedes* (*Stegomyia*) *albopictus* (Skuse) (Laird et al. 1994, de Wet et al. 2001, Derraik 2005a), and this study aims to discuss the most likely scenario regarding its introduction and consequent invasion of the North Island. To create a theoretical but credible scenario, information was gathered from the literature on the biology of the species and its methods of invasion and spread, and the patterns of dispersal previously observed for other exotic mosquito species already established in New Zealand.

The Potential Threat. A recent review of interception records has demonstrated that even though the main entrance pathway for invading mosquitoes in the past 75 yr has been aircraft, ships and their cargo accounted for 82% of 62 described interceptions of exotic mosquitoes in New Zealand borders since January 1990 (Derraik 2004b). Approximately 75% of mosquito interceptions aboard ships involved used machinery or used tires, which were the media for all 13 interceptions of *Ae. albopictus* in this country (Derraik 2004b). Used tires are this species' main mode of invasion worldwide (Reiter and Sprenger 1987, Craven et al. 1988, Hawley 1988, Cornel and Hunt 1991, Gratz 2004).

Climate is a key constraint to the establishment of exotic vectors in New Zealand, but the Auckland region has been identified as having favorable conditions for *Ae. albopictus* (de Wet et al. 2001). The latest work using the *Hotspots* computer model confirmed previous results, indicating that most areas of the Northland and Auckland regions do provide suitable climate, in terms of both temperature and rainfall requirements, for *Ae. albopictus* (Neil de Wet, personal communication). This species' cold hardiness also means that other North Island areas are likely to be suitable (Laird et al. 1994, Weinstein et al. 1995), and several studies in the United States have shown that *Ae. albopictus* is capable of overwintering in cold climates (Hawley et al. 1989, O'Meara et al. 1993, Swanson et al. 2000, Barker et al. 2003). The likely increase in

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Table 1. List of exotic mosquito species intercepted in New Zealand over the past 75 yr, adapted from Derraik (2004b) and Derraik (unpublished data)

Species	No. of interceptions	Main entrance pathway and location	Yr of last interception
Aedes (*Aedimorphus*) *nocturnus* (Theobald)	1	Aircraft–Aucklandx	1998
Aedes (*Aedimorphus*) *vexans* Meigen[a]	1	?–Russell	1929
Aedes (*Scutomyia*) *albolineatus* (Theobald)	1	Aircraft–Auckland	1950?
Aedes (*Stegomyia*) sp.	1	Used tires (ship)–Auckland	2003
Aedes (*Stegomyia*) *aegypti* (L.)	5	Used machinery (ship)–Auckland	2005
Aedes (*Stegomyia*) *albopictus* (Skuse)	13	Used tires (ship)–Auckland	2004
Aedes (*Stegomyia*) *polynesiensis* Marks	2	used tyres/machinery (ship)–Auckland	2004
Aedes (*Stegomyia*) *scutellaris* (Walker)	1	Aircraft–Auckland	1943–1944
Aedes (*Stegomyia*) *tongae Edwards*	1	Aircraft–Auckland	1946
Anopheles sp.	3	Aircraft–Auckland	2001
Anopheles (*Anopheles*) *maculipennis* Meigen[b]	2	Ship–Auckland	1929
Anopheles (*Anopheles*) *stigmaticus* Skuse	1	Cargo (aircraft)	2001
Coquillettidia (*Coquillettidia*) *crassipes* (Van der Wulp)	1	Aircraft–Auckland	1951
Coquillettidia (*Coquillettidia*) *xanthogaster* (Edwards)	1	Aircraft–Auckland	1943–1944
Culex (*Culex*) *annulirostris* Skuse	11	Aircraft–Auckland	1999
Culex (*Culex*) *?australicus* Dobrotworsky & Drummond	1	Cargo (ship)–Wellington	1998
Culex (*Culex*) *bitaeniorhynchus* Giles	4	Aircraft–?	1966–1972
Culex (*Culex*) *gelidus* Theobald	1	?–Auckland	2003
Culex (*Culex*) *pipiens pallens* Coquillett	1	Vessel refuse drum (ship)–Auckland	2001
Culex (*Culex*) *sitiens* Wiedemann	4	Aircraft–Auckland	2003
Culex (*Neoculex*) sp.	1	Aircraft–?	1955–1965
Lutzia (*Metalutzia*) *halifaxii* (Theobald)	1	Cargo (ship)–Tauranga	2002
Ochlerotatus sp.[c]	1	Used tires (ship)–Auckland	2002
Ochlerotatus (*Finlaya*) *japonicus* (Theobald)	10	Used tires (ship)–Auckland	2005
Ochlerotatus (*Muscidus*) *alternans* (Westwood)	1	Aircraft–Christchurch	2003
Ochlerotatus (*Ochlerotatus*) *vigilax* (Skuse)	4	Aircraft–Christchurch	2002
Ochlerotatus (*Ochlerotatus*) *vittiger* (Skuse)	1	Aircraft–?	?
Toxorhynchites sp.[d]	1	cargo (ship)–Auckland	2002
Tripteroides (*Polylepidomyia*) *tasmaniensis* (Strickland)	1	Used tires (ship)–Lyttleton	1993
Tripteroides (*Tripteroides*) *bambusa* (Yamada)	2	Used tires/machinery (ship)–Auckland	2005
Uranotaenia (*Pseudoficalbia*) *novobscura* Barraud	1	Used machinery (ship)–Auckland	2005
Verrallina (*Verrallina*) *lineata* (Taylor)	1	Aircraft–Auckland	1943–1944

The list excludes the interceptions of exotic species already established in the country. Note that where the year of interception is unknown, the period in which it was recorded is shown instead.

[a] Both Laird (1996) and Belkin (1962) agree that it is likely to have been a misidentification of *Aedes* (*Aedimorphus*) *nocturnus* (Theobald), which is not a disease vector.

[b] Laird (1996) and Belkin (1962) again believe it was a misidentification, but it was not possible to identify the likely species involved.

[c] The origin of this *Ochlerotatus* sp. shows it differs from the other species intercepted and those already established in the country.

[d] *Toxorhynchites* spp. do not blood feed.

temperature, rainfall, and humidity resulting from a climate change scenario should extend the availability of breeding sites and enhance mosquito survival (Weinstein et al. 1995, de Wet et al. 2001, Woodward et al. 2001). In addition, although climatic limitations may be an important constraint for the establishment of *Ae. albopictus,* overseas this species shows an evolution of locally adapted life history traits that can overcome such limiting factors (Juliano and Lounibos 2005).

Ae. albopictus has been listed as one of the world's worst invasive species by the World Conservation Union (Lowe et al. 2000), having already invaded many countries around the world (Savage et al. 1992, Pan American Health Organization 1993, Knudsen 1995, Lounibos 2002). Although *Ae. albopictus* has only been fully incriminated as an arbovirus vector of dengue viruses, this species is remarkably susceptible to oral infection with numerous arboviruses, most of which can be transmitted in laboratory conditions with varying degrees of efficiency (Mitchell 1995). *Ae. albopictus* has been found to be a very efficient laboratory vector of West Nile virus (Sardelis et al. 2002), and it may be implicated in the ecology of the disease due to the isolation of the virus from this species in nature (Turell et al. 2001). *Ae. albopictus* also has been found to be a competent laboratory vector of eastern equine encephalitis virus (Turell et al. 1994), and numerous strains of this virus have been isolated from various mosquito pools containing naturally infected *Ae. albopictus* in Florida (Niebylski et al. 1992). In Italy, this species also has been found to be a natural vector of *Dirofilaria immitis* (canine heartworm) (Cancrini et al. 2003). *Ae. albopictus* could potentially pose a public health risk also as a vector of yellow fever, Ross River virus (RR) (Knudsen 1995, Russell 2002), Chikungunya virus (Mangiafico 1971), La Crosse encephalitis virus (Gerhardt et al. 2001), and possibly Japanese encephalitis virus (Hawley 1988).

No human arbovirus of public health importance seems to be currently circulating endemically in New Zealand (Weinstein et al. 1995), but there is a regular influx of viremic travelers, particularly from Australia (Weinstein et al. 1995, Kelly-Hope et al. 2002, Derraik and Calisher 2004). According to Weinstein et al.

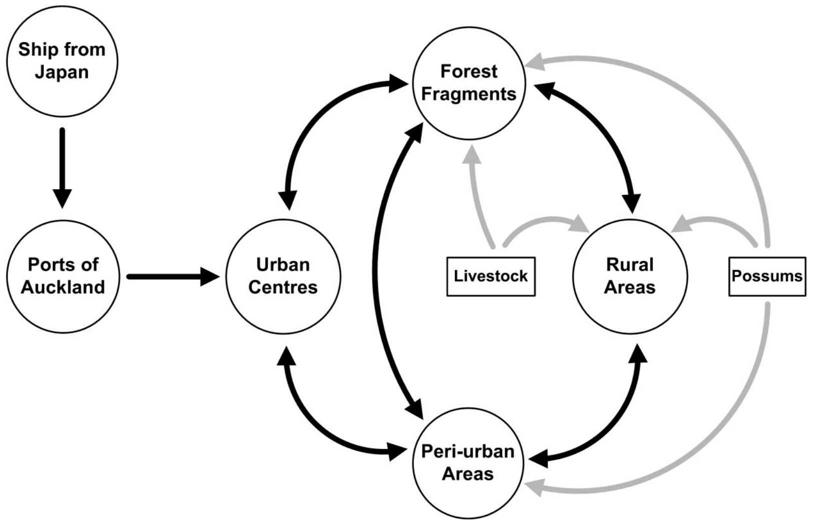

Fig. 1. Diagram of the likely scenario for *Ae. albopictus* invasion and dispersal in the Auckland region of New Zealand. Black arrows represent the species' movements, whereas gray arrows represent the availability of blood meals from livestock and possums that could facilitate *Ae. albopictus* establishment in certain areas.

(1995) people infected with both RR and dengue viruses "maintain an infective viremia for up to 7 days during the febrile period" (p. 667), and these travelers generally arrive in New Zealand within several hours of their departure. The authors also emphasize that the number of circulating virus particles in humans in Auckland is likely to initiate an outbreak if a competent mosquito vector is present.

Ross River virus is the most likely arbovirus to cause an outbreak in New Zealand because it is the most common etiologic agent of recognized arboviral disease in Australia, and two of the established exotic mosquitoes, *Oc. camptorhynchus* and *Oc. notoscriptus,* are competent vectors of this virus (Kelly-Hope et al. 2002, Russell 2002, Derraik and Calisher 2004, Derraik 2005b). In addition, as many as 70 million introduced brushtail possums, *Trichosurus vulpecula* Kerr, now occupy >97% of New Zealand's land area (Parliamentary Commissioner for the Environment 2000, Derraik 2005b). These animals are protected in Australia and information on possum serology is rare and difficult to obtain (Azuolas 1997), but these Australian marsupials are known competent hosts of RR (Boyd et al. 2001, Boyd and Kay 2001). According to Boyd and Kay (2001), 30% of brushtail possums exposed to RR may develop high-titer viremia after a bite by an infected mosquito; and although viremia lasted for up to 2 d, in the first 24 h approximately 53% of recipient *Ochlerotatus* (*Ochlerotatus*) *vigilax* (Skuse) became infected, which was therefore considered an efficient system. Serological survey data confirmed that possums in Australia are commonly exposed to RR in the field (Boyd and Kay 2001), where they are natural blood source for mosquitoes (Russell 2002). In New Zealand, at least *Oc. notoscriptus* has been shown to feed on possums (Bullians and Cowley 2001). *Ae. albopictus* is a competent vector of RR, known to transmit the virus experimentally (Mitchell and Gubler 1987, Mitchell et al. 1987, Russell 2002), and it could considerably aggravate the likelihood of a RR outbreak occurring and of the virus becoming established in this country. This is especially so as New Zealand's native mosquitoes are mostly bird feeders, in contrast to exotic species such as *Ae. albopictus* and *Oc. notoscriptus,* which not only feed primarily on mammals but are also anthropophilic.

In addition, *Ae. albopictus* is a particularly aggressive biter and could become a serious nuisance, especially because it often reaches high population densities in newly invaded areas (Gratz 2004). In Italy for instance, this species seems to have become the most serious pest mosquito through most of its range (Gratz 2004). *Ae. albopictus* bites are painful and provoke wheals that are particularly troublesome when victims are not used to its salivary secretions, occasionally leading to a hemorrhagic appearance (Rebora et al. 1993).

Arrival, Establishment, and Dispersal of *Ae. albopictus.* Incoming ships from Japan are likely to be the means of arrival for *Ae. albopictus,* and the Ports of Auckland (located in the city's central business district) would be the probable point of entry (Derraik 2004b). *Ae. albopictus* should initially become established in the immediate urban areas (Fig. 1) where it would be able to breed prolifically (Anon. 1986, Hawley 1988), even though it prefers less urbanized environments such as periurban (Adhami and Reiter 1998), rural, or forested areas (Hawley 1988, Easton 1994). *Ae. albopictus* would find in the Auckland urban surroundings many suitable hosts in the human population. This species is an opportunistic feeder (Marques and Gomes 1997) with a very wide range of hosts (Hawley 1988, Savage et al. 1993), but *Ae. albopictus* is anthropophilic throughout its range (Reid 1961, Tempelis et al. 1970, Sullivan et al. 1971, Gomes et al. 2003, Gratz 2004).

Ae. albopictus can breed in a wide range of natural and artificial containers (Hawley 1988, Forattini et al. 1998b), which also gives it a very efficient dispersal ability (Forattini et al. 1997). Although *Ae. albopictus* is considered a container breeder, it can use ground pools (Forattini et al. 1998a), underground storm water drains (Blackmore 1995), and other unusual habitats, such as water pools on cement floors 20 stories above the ground (Nathan and Knudsen 1994). One report from Japan described numerous larvae of this species from a catch basin accommodating telecommunication equipment, located in the basement floor of a modern concrete building (Ishii 1987).

An investigation carried out in Rio de Janeiro, Brazil, showed that blood-fed *Ae. albopictus* females were capable of dispersing >800 m in urban areas within a 6-d period (Honório et al. 2003). These results not only indicate that adults would be able to swiftly disperse through Auckland City but also that *Ae. albopictus* is probably capable of spreading pathogens over large areas relatively rapidly (Honório et al. 2003). It could therefore be expected that *Ae. albopictus* would move from Auckland City to the outskirts rather quickly, benefited by the widespread presence of vegetated areas, such as riparian strips, small forest fragments and other patches of native and exotic vegetation. The presence of vegetation is important, because once it is removed *Ae. albopictus* may become rare, even in rural areas (Nguyen et al. 1974). In contrast, the species is commonly found in large Asian cities such as Tokyo and Kuala Lumpur, where vegetation has not been entirely cleared (Hawley 1988).

Eradication of *Ae. albopictus* would likely be successful only if it is detected immediately. This was certainly the reason behind the elimination of this species in its 1993 incursion in New Zealand, when larvae were found in imported used tires that had been taken from ships into two Auckland suburbs (Laird et al. 1994). Once *Ae. albopictus* has a foothold in small forest fragments and starts to occupy natural containers, its detection and control would be very difficult. At this stage, even if wide-scale control operations were initiated, it would be somewhat complicated to target all larval microhabitats (e.g., broken bottles, beer cans, jars, tires, tree holes, and leaf axils of exotic and native plants), and all gravid females that might be resting on vegetation. Hawley (1988) pointed out that controlling *Ae. albopictus* may be very difficult due to its frequent presence in cryptic microhabitats. Laird and Mokry (1983), for example, suggested that past resurgences of *Aedes* (*Stegomyia*) *aegypti* (L.) in tropical American countries that were blamed upon accidental reimportation from neighboring countries, might in fact have been reconstituting populations based upon a minuscule percentage breeding in cryptic natural containers. After establishment in these habitats, *Ae. albopictus* would most likely evade control programs and start to invade the North Island.

Ae. albopictus dispersal would likely first occur in suburban districts and periurban areas (Fig. 1), where the presence of forests or scrublands provides greater habitat suitability for the species (Hawley 1988). Reaching rural areas would allow the species to thrive in one of its preferred habitats: used tires present in large numbers. Laird (1995) pointed out that the application of used tires in New Zealand to weigh down polythene sheeting covering farm silage piles and pits has greatly augmented the availability of artificial larval habitats and was probably one of the main facilitators of the southward dispersal of the exotic mosquitoes *Cx. quinquefasciatus* and *Oc. notoscriptus* on the North Island. *Oc. notoscriptus* seems to have used such used tires and other types of artificial containers to radiate into larval habitats more like its original ones in Australia, such as tree holes (Laird 1990). Laird (1990) also suggested that abundant artificial containers, such as beer cans, steel drums, and tires have opened the way for the establishment of *Oc. notoscriptus* into natural containers in Northland's Waipoua Forest. It is therefore possible that *Ae. albopictus* would follow a dispersal pathway similar to that of *Oc. notoscriptus*, aided by abundant discarded tires and stock drinking troughs. Moving into native forests fragments would be the next step, with the species having particular preference for forest fringes and areas of secondary growth (Hawley 1988, Easton 1994, Albuquerque et al. 2000). *Ae. albopictus* also may establish deeper into native forests, even though it is not a favored habitat (Hawley 1988).

Mammals are the preferred hosts of *Ae. albopictus* (Hawley 1988), but there are no indigenous terrestrial mammals in New Zealand apart from three species of bats, only two of which are extant (Diamond 1990, King 1990). Nonetheless, the establishment of *Ae. albopictus* in rural areas would be aided by the presence of abundant livestock (mainly cattle and sheep) in extensive areas of farmland, whereas the extremely abundant and widespread brushtail possums should be particularly important. These exotic animals could lead to an "invasional meltdown," a process by which a group of exotic species facilitate one another's invasion, increasing their likelihood of survival (Simberloff and Von Holle 1999). In northern New Zealand, livestock would provide abundant blood meals in rural areas where availability of other hosts, such as humans, is reduced, whereas possums are abundant throughout the region (Parliamentary Commissioner for the Environment 2000, Derraik 2005b).

It is likely that *Ae. albopictus* would become "so deeply entrenched in northern rural and forest country as to preclude eradication and render effective control very difficult and extremely expensive" (Laird 1990, p. 297). *Ae. albopictus* would be able to invade one habitat type from another, further complicating this situation. Even if eradication was successful in urban areas, this species could easily reinvade. This is a potential epidemiological problem, as the colonization and movement of *Ae. albopictus* between different environments overseas could potentially create a link between sylvatic and urban cycles of dengue (Gratz 2004) and yellow fever (Anon. 1986, Gomes et al. 1999).

It is also important to consider that *Ae. albopictus* could possibly hitchhike in containers being transported by road or railway and thereby have its invasion of the North Island facilitated by human activities. Graham (1939) mentioned that *Oc. notoscriptus* larvae were invariably found in fire buckets (for coal-fired steam locomotives) on railway stations in Auckland, particularly in suburban regions. Service (1997) believes that such breeding habitats facilitated the spread of *Oc. notoscriptus* to new localities in the North Island. Overseas, trains also have been shown to be a significant aid to mosquito dispersal, such as *Cx. quinquefasciatus* along the Texas–Mexico border (Campos et al. 1961). In the United States, Moore and Mitchell (1997) showed that during the earlier dispersal period of *Ae. albopictus* there was a strong relationship between its spread and the interstate highway system where most infested counties were found to be located. It is therefore plausible that similar human-aided pathways could facilitate the dispersal of *Ae. albopictus* in New Zealand.

It is not possible to provide a theoretical time-frame for the initial establishment and later spread of *Ae. albopictus* in New Zealand's North Island, because there are too many variables to allow for any reliable inferences. This is especially so, considering the observed patterns of spread for *Cx. quinquefasciatus* and *Oc. notoscriptus.* These two species were first recorded in New Zealand in 1848 (Laird et al. 1994) and 1920 (Laird and Easton 1994), respectively, but the most recent evidence indicated that the distribution of both species was still expanding (Laird 1990, 1995).

Possible Competitive Interactions. Three mosquito species are known to be dominant in the Auckland region and the North Island: the endemic *Culex* (*Culex*) *pervigilans* Bergroth and the exotic *Cx. quinquefasciatus* and *Oc. notoscriptus. Cx. pervigilans* is New Zealand's most abundant and widespread mosquito, capable of using a very wide range of larval habitats (Laird 1990, 1995; Hearnden et al. 1999), but this species is not a container breeder per se (Belkin 1968, Derraik and Slaney 2005). *Cx. quinquefasciatus* also rarely occupies container habitats in New Zealand, which now seem to be highly dominated by the Australian *Oc. notoscriptus,* particularly in anthropic habitats (Derraik 2004a, c; Derraik and Slaney 2005).

In addition, the underuse of larval mosquito habitats in New Zealand (Laird 1990, de Wet et al. 2001) means that *Ae. albopictus* would likely face limited competition for natural and artificial containers in most modified habitats (Derraik 2005c). There is mounting evidence that apart from *Cx. pervigilans* no other native culicids seem capable of inhabiting larval mosquito habitats within highly modified habitats, particularly urban areas. Native mosquitoes seem to have become restricted to areas within or adjacent to indigenous habitats.

The mosquito species in New Zealand that may compete with *Ae. albopictus* for container habitats is *Oc. notoscriptus.* The only laboratory study that seems to have been done on the latter species' competitive ability showed no clear advantage of *Oc. notoscriptus* over *Ae. aegypti* (Russell 1986). *Ae. albopictus* seems, by contrast, to be a very efficient biotic invader with a high competitive ability that can displace other species, including *Ae. aegypti* (Lowrie 1973, Juliano 1998, Lounibos et al. 2001). Lounibos et al. (2001) however, pointed out those biological traits which favor *Ae. albopictus* could be partly offset by the infrequency of this invasive mosquito in undisturbed woodlands, which in New Zealand could mitigate against displacement of native mosquitoes in such habitats. Nonetheless, superiority in competition is only necessary for invasion and spread if particular resources are limited (Juliano and Lounibos 2005), which is not likely to apply in New Zealand due to the apparent underuse of larval mosquito habitats.

In conclusion, although the invasion scenario was discussed in the context of New Zealand, it is likely to be applicable to some extent in other countries. The main lesson is that the most important biosecurity measure is to make border controls as tight as possible, particularly in regards to the sea-container pathway, which has been identified as a weak-link in New Zealand (Audit Office 2002a,b). All possible larval mosquito habitats (water-filled or not) must be treated, with particular care given to incoming ships loaded with used tires and/or used machinery. I also support the suggestion by Weinstein et al. (1995) that New Zealand should adopt WHO standards which recommend stringent elimination of all potential larval mosquito habitats within 400 m of the perimeter of ports and airports (World Health Organization 1983). Moreover, New Zealand should establish a rapid response team to act upon such biosecurity breaches as a postborder detection of an exotic mosquito (Derraik and Calisher 2004), while developing joint strategies with other countries to control possible mosquito invaders at a ship or aircraft's point of origin (Derraik 2004b).

Stopping exotic species from entering the country in the first place is the only way to be sure that a species such as *Ae. albopictus* will not become established and subsequently become a nuisance and pose a threat to public health. The New Zealand government for instance, plans to spend circa U.S.$21 million over 4 yr in an attempt to eradicate *Oc. camptorhynchus* (Ministry of Health 2003). It is much safer, easier, and cheaper to stop invading mosquitoes and other organisms at the border, rather than trying to eradicate them after their establishment (Mack et al. 2000).

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References Cited

Adhami, J., and P. Reiter. 1998. Introduction and establishment of *Aedes* (*Stegomyia*) *albopictus* Skuse (Diptera: Culicidae) in Albania. J. Am. Mosq. Control Assoc. 14: 340–343.

Albuquerque, C.M.R., M.A.V. Melo-Santos, M.A.S. Bezerra, R.M.R. Barbosa, D. F. Silva, and E. Silva. 2000. Primeiro registro de *Aedes albopictus* em área da Mata Atlântica, Recife, PE, Brasil. Rev. Saúde Pública 34: 314–315.

Anon. 1986. *Aedes albopictus* infestation - United States, Brazil. Morb. Mortal. Wkly. Rep. 35: 493–495.

Audit Office. 2002a. Management of biosecurity risks: case studies. Report of the Controller and Auditor-General. Office of the Auditor-General, Wellington, New Zealand.

Audit Office. 2002b. Ministry of Agriculture and Forestry: management of biosecurity risks. Report of the Controller and Auditor-General. Office of the Auditor-General, Wellington, New Zealand.

Azuolas, J. K. 1997. Arboviral diseases of horses and possums. Arbovirus Res. Aust 7: 5–7.

Barker, C. M., S. L. Paulson, S. Cantrell, and B. S. Davis. 2003. Habitat preferences and phenology of *Ochlerotatus triseriatus* and *Aedes albopictus* (Diptera: Culicidae) in southwestern Virginia. J. Med. Entomol. 40: 403–410.

Belkin, J. N. 1962. The mosquitoes of the South Pacific (Diptera, Culicidae), volume II. University of California, Berkeley.

Belkin, J. N. 1968. Mosquito Studies (Diptera: Culicidae) VII. The Culicidae of New Zealand. Contrib. Am. Entomol. Inst. 3: 1–182.

Blackmore, M. S. 1995. *Aedes albopictus* in Italy. Am. Mosq. Control Assoc. Newsl. 21: 9.

Boyd, A. M., and B. H. Kay. 2001. Solving the urban puzzle of Ross River and Barmah Forest viruses. Arbovirus Res. Aust. 8: 14–22.

Boyd, A. M., R. A. Hall, R. T. Gemmell, and B. H. Kay. 2001. Experimental infection of Australian brushtail possums, *Trichosurus vulpecula* (Phalangeridae: Marsupialia), with Ross River and Barmah Forest viruses by use of a natural mosquito vector system. Am. J. Trop. Med. Hyg. 65: 777–782.

Bullians, M. S., and D. R. Cowley. 2001. Blood feeding by *Aedes notoscriptus* (*Skuse*) (Diptera: Culicidae) on the brush-tailed possum, *Trichosurus vulpecula* (Kerr). N.Z. Entomol. 24: 87–88.

Campos, E. G., H. A. Trevino, and L. G. Strom. 1961. The dispersal of mosquitoes by railroad trains involved in international traffic. Mosq. News. 21: 190–192.

Cancrini, G., A. F. Frangipane di Regalbono, I. Ricci, C. Tessarin, S. Gabrielli, and M. Pietrobelli. 2003. *Aedes albopictus* is a natural vector of *Dirofilaria immitis* in Italy. Vet. Parasitol. 118:195–202.

Cornel, A. J., and R. H. Hunt. 1991. *Aedes albopictus* in Africa? First records of live specimens in imported tires in Cape Town. J. Am. Mosq. Control Assoc. 7: 107–108.

Craven, R. B., D. A. Eliason, D. B. Francy, P. Reiter, E. G. Campos, W. L. Jakob, G. C. Smith, C. J. Bozzi, C. G. Moore, G. O. Maupin, and T. P. Monath. 1988. Importation of *Aedes albopictus* and other exotic mosquito species into the United States in used tires from Asia. J. Am. Mosq. Control Assoc. 4: 138–142.

Derraik, J.G.B. 2004a. A survey of the mosquito (Diptera: Culicidae) fauna of the Auckland Zoological Park. N.Z. Entomol 27: 51–55.

Derraik, J.G.B. 2004b. Exotic mosquitoes in New Zealand: a review of species intercepted, their pathways and ports of entry. Aust. N.Z. J. Public Health 28: 433–444.

Derraik, J.G.B. 2004c. Mosquitoes (Diptera: Culicidae) breeding in artificial habitats at the Wellington Zoo. Weta 28: 28–31.

Derraik, J.G.B. 2005a. Aussie mozzies invade NZ. Australasian Sci. 26: 23–25.

Derraik, J.G.B. 2005b. Brushtail possums (*Trichosurus vulpecula*) may pose a threat to public health in New Zealand. Aust. N.Z. J. Public Health 29: 91.

Derraik, J.G.B. in 2005c. Mosquitoes breeding in phytotelmata in native forests in the Wellington region, New Zealand. N.Z. J. Ecol. 29: (in press).

Derraik, J.G.B., and C. H. Calisher. 2004. Is New Zealand prepared to deal with arboviral diseases? Aust. N.Z. J. Public Health 28: 27–30.

Derraik, J.G.B., and D. Slaney. 2005. Container aperture size and nutrient preferences of mosquitoes (Diptera: Culicidae) in the Auckland region, New Zealand. J. Vector Ecol. 30: (in press).

de Wet, N., W. Ye, S. Hales, R. Warrick, A. Woodward, and P. Weinstein. 2001. Use of a computer model to identify potential hotspots for dengue fever in New Zealand. N.Z. Med. J. 114: 420–422.

Diamond, J. M. 1990. New Zealand as an archipelago: an international perspective, pp. 3–8. *In* D. R. Towns, C. H. Daugherty, and I.A.E. Atkinson [eds.], Ecological restoration of New Zealand islands. Department of Conservation, Wellington, New Zealand.

Easton, E. R. 1994. Urbanization and its effects on the ecology of mosquitos in Macao, Southeast-Asia. J. Am. Mosq. Control Assoc. 10: 540–544.

Forattini, O. P., I. Kakitani, M.A.M. Sallum, and L. Rezende. 1997. Produtividade de criadouro de *Aedes albopictus* em ambiente urbano. Rev. Saúde Pública 31: 545–555.

Forattini, O. P., G.R.A.M. Marques, M. Brito, and M.A.M. Sallum. 1998a. An unusual ground larval habitat of *Aedes albopictus.* Rev. Inst. Med. Trop. São Paulo 40: 121–122.

Forattini, O. P., G.R.A. M. Marques, I. Kakitani, M. Brito, and M.A.M. Sallum. 1998b. Significado epidemiológico dos criadouros de *Aedes albopictus* em bromélias. Rev. Saúde Pública 32: 186–188.

Gerhardt, R. R., K. L. Gottfried, C. S. Apperson, B. S. Davis, P. C. Erwin, A. B. Smith, N. A. Panella, E. E. Powell, and R. S. Nasci. 2001. First isolation of La Crosse virus from naturally infected *Aedes albopictus.* Emerg. Infect. Dis. 7: 807–811.

Gomes, A. C., N. N. Silva, G. Marques, and M. Brito. 2003. Host-feeding patterns of potential human disease vectors in the Paraíba Valley Region, State of São Paulo, Brazil. J. Vector Ecol. 28: 74–78.

Gomes, A. C., M. D. Bitencourt, D. Natal, P.L.S. Pinto, L. F. Mucci, M. B. Paula, P. R. Urbinatti, and J.M.S. 1999. Barata. *Aedes albopictus* em área rural do Brasil e implicações na transmissão de febre amarela silvestre. Rev. Saúde Pública 33: 95–97.

Graham, D. H. 1939. Mosquito life in the Auckland District. Trans. Proc. R. Soc. N.Z. 69: 210–224.

Gratz, N. G. 2004. Critical review of the vector status of *Aedes albopictus.* Med. Vet. Entomol. 18: 215–227.

Hawley, W. A. 1988. The biology of *Aedes albopictus.* J. Am. Mosq. Control Assoc. 4: 1–39.

Hawley, W. A., C. B. Pumpuni, R. H. Brady, and G. B. Craig. 1989. Overwintering survival of *Aedes albopictus* (Diptera, Culicidae) eggs in Indiana. J. Med. Entomol. 26: 122–129.

Hearnden, M., C. Skelly, and P. Weinstein. 1999. Improving the surveillance of mosquitoes with disease-vector potential in New Zealand. N.Z. Public Health Rep. 6: 25–32.

Honório, N. A., W. C. Silva, P. J. Leite, J. M. Gonçalves, L. P. Lounibos, and R. Lourenço-de-Oliveira. 2003. Dispersal of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in an urban endemic area in the State of Rio de Janeiro, Brazil. Mem. Inst. Oswaldo Cruz 98: 191–198.

Ishii, T. 1987. An unusual indoor larval habitat of *Aedes albopictus* (Skuse) in Japan (Diptera: Culicidae). Jpn. J. Sanit. Zool. 38: 339–340.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? Ecology 79: 255–268.

Juliano, S. A., and L. P. Lounibos. 2005. Ecology of invasive mosquitoes: effects on resident species and on human health. Ecol. Lett. 8: 558–574.

Kelly-Hope, L. A., B. H. Kay, and D. M. Purdie. 2002. The risk of Ross River and Barmah Forest virus disease in Queensland: implications for New Zealand. Aust. N.Z. J. Public Health 26: 69–77.

King, C. M. 1990. The handbook of New Zealand mammals. Oxford University Press, Auckland, New Zealand.

Knudsen, B. 1995. Global distribution and continuing spread of *Aedes albopictus.* Parassitologia 37: 91–97.

Laird, M. 1990. New Zealand's northern mosquito survey, 1988–89. J. Am. Mosq. Control Assoc. 6: 287–299.

Laird, M. 1995. Background and findings of the 1993–94 New Zealand mosquito survey. N.Z. Entomol. 18: 77–90.

Laird, M. 1996. New Zealand's mosquito fauna in 1995: history and status. Ministry of Health, Wellington, New Zealand.

Laird M., and J. M. Easton. 1994. *Aedes notoscriptus* (Diptera: Culicidae) in Wellington Province. N.Z. Entomol. 17: 14–17.

Laird, M., and J. Mokry. 1983. Larval *Aedes aegypti* from Tuvalu papaya trees. Mosq. News. 43: 81–82.

Laird, M., L. Calder, R. C. Thornton, R. Syme, P. W. Holder, and M. Mogi. 1994. Japanese *Aedes albopictus* among four mosquito species reaching New Zealand in used tires. J. Am. Mosq. Control Assoc. 10: 14–23.

Lounibos, L. P. 2002. Invasions by insect vectors of human disease. Annu. Rev. Entomol. 47: 233–266.

Lounibos, L. P., G. F. O'Meara, R. L. Escher, N. Nishimura, M. Cutwa, T. Nelson, R. E. Campos, and S. A. Juliano. 2001. Testing predictions of displacement of native *Aedes* by the invasive Asian tiger Mosquito *Aedes albopictus* in Florida, USA. Biol. Invasions 3: 151–166.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species - a selection form the global invasive species database. Aliens 12.

Lowrie Jr., R. C. 1973. Displacement of *Aedes* (*S.*) *polynesiensis* Marks by *A.* (*S.*) *alpopictus* Skuse through competition in the larval stage under laboratory conditions. J. Med. Entomol. 10: 131–136.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10: 689–710.

Mangiafico, J. A. 1971. Chikungunya virus infection and transmission in five species of mosquito. Am. J. Trop. Med. Hyg. 20: 642–645.

Marques, G.R.A. M., and A. C. Gomes. 1997. Comportamento antropofílico de *Aedes albopictus* (Skuse) (Diptera: Culicidae) na região do Vale do Paraíba, Sudeste do Brasil. Rev. Saúde Pública 31: 125–130.

Ministry of Health. 2003. Saltmarsh mosquito eradication project gets permanent base at Parakai. Media release, 17 February 2003, Wellington, New Zealand.

Mitchell, C. J. 1995. The role of *Aedes albopictus* as an arbovirus vector. Parasitologia 37: 109–113.

Mitchell, C. J., and D. J. Gubler. 1987. Vector competence of geographic strains of *Aedes albopictus* and *Aedes polynesiensis* and certain other *Aedes* (*Stegomyia*) mosquitoes for Ross River virus. J. Am. Mosq. Control Assoc. 3: 142–147.

Mitchell, C. J., B. R. Miller, and D. J. Gubler. 1987. Vector competence of *Aedes albopictus* from Houston, Texas, for dengue serotypes 1 to 4, yellow fever and Ross River viruses. J. Am. Mosq. Control Assoc. 3: 460–465.

Moore, C. G., and C. J. Mitchell. 1997. *Aedes albopictus* in the United States: ten-year presence and public health implications. Emerg. Infect. Dis. 3: 329–334.

Nathan, M., and B. Knudsen. 1994. Global update on *Aedes albopictus.* Am. Mosq. Control Assoc. Newsl. 20: 8–9.

Nguyen, D. Q., D. V.R., and C. Y. Chow. 1974. *Aedes* mosquito surveillance in the republic of Vietnam. Asian J. Trop. Med. Public Health 5: 569–573.

Niebylski, M., J. Mutebi, G. C. Jr., J.A.J. Mulrennan, and R. S. Hopkins. 1992. Eastern equine encephalitis virus associated with *Aedes albopictus* - Florida, 1991. Morb. Mortal. Wkly. Rep. 41: 115–121.

O'Meara, G. F., A. D. Gettman, L. F. Evans, Jr., and G. A. Curtis. 1993. The spread of *Aedes albopictus* in Florida. Am. Entomol. 39: 163–172.

Pan American Health Organization. 1993. PAHO Advisory: *Aedes albopictus* in the Caribbean. PAHO Epidemiol. Bull. 14: 15–16.

Parliamentary Commissioner for the Environment. 2000. Caught in the Headlights: New Zealander's Reflections on Possums, Control Options and Genetic Engineering. Parliamentary Commissioner for the Environment, Wellington, New Zealand.

Rebora, A., F. Rongioletti, and V. Raineri. 1993. *Aedes albopictus* in Europe: a new challenge for dermatologists. Dermatology 187: 6–8.

Reid, J. A. 1961. The attraction of mosquitoes by human or animal baits in relation to the transmission of disease. Bull. Entomol. Res. 52: 43–62.

Reiter, P., and D. Sprenger. 1987. The used tire trade: a mechanism for the worldwide dispersal of container breeding mosquitoes. J. Am. Mosq. Control Assoc. 3: 494–501.

Russell, R. C. 1986. Larval competition between the introduced vector of dengue fever in Australia, *Aedes aegypti* (L.), and a native container-breeding mosquito, *Aedes notoscriptus* (Skuse) (Diptera: Culicidae). Aust. J. Zool. 34: 527–534.

Russell, R. C. 2002. Ross River virus: ecology and distribution. Annu. Rev. Entomol. 47: 1–31.

Sardelis, M. R., M. J. Turell, M. L. O'Guinn, R. G. Andre, and D. R. Roberts. 2002. Vector competence of three North American strains of *Aedes albopictus* for West Nile virus. J. Am. Mosq. Control Assoc. 18: 284–289.

Savage, H. M., V. I. Ezike, A.C.N. Nwankwo, R. Spiegel, and B. R. Miller. 1992. First record of breeding populations of *Aedes albopictus* in continental Africa - implications for arboviral transmission. J. Am. Mosq. Control Assoc. 8: 101–103.

Savage, H. M., M. L. Niebylski, G. C. Smith, C. J. Mitchell, and G. B. Craig. 1993. Host-feeding patterns of *Aedes albopictus* (Diptera, Culicidae) at a temperate North American site. J. Med. Entomol. 30: 27–34.

Service, M. W. 1997. Mosquito (Diptera: Culicidae) dispersal - the long and short of it. J. Med. Entomol. 34: 579–588.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1: 21–32.

Sullivan, M. F., D. J. Gould, and S. Maneechai. 1971. Observations on the host range and feeding preferences of *Aedes albopictus* (Skuse). J. Med. Entomol. 8: 713–716.

Swanson, J., M. Lancaster, J. Anderson, M. Crandell, L. Haramis, P. Grimstad, and U. Kitron. 2000. Overwintering and establishment of *Aedes albopictus* (Diptera: Culicidae) in an urban La Crosse virus enzootic site in Illinois. J. Med. Entomol. 37: 454–460.

Tempelis, C. H., R. O. Hayes, A. D. Hess, and W. C. Reeves. 1970. Blood-feeding habits of four species of mosquito found in Hawaii. Am. J. Trop. Med. Hyg. 19: 335–341.

Turell, M. J., J. R. Beaman, and G. W. Neely. 1994. Experimental transmission of eastern equine encephalitis virus by strains of *Aedes albopictus* and *Ae. taeniorhynchus* (Diptera: Culicidae). J. Med. Entomol. 31: 287–290.

Turell, M. J., M. L. O'Guinn, D. J. Dohm, and J. W. Jones. 2001. Vector competence of North American mosquitoes (Diptera: Culicidae) for West Nile virus. J. Med. Entomol. 38: 130–134.

Weinstein, P. 1994. The real and potential risks of human arboviral disease in New Zealand. Communicable Disease Centre, Institute of Environmental Science and Research Ltd., Porirua, New Zealand.

Weinstein, P. 1996. When will mosquitoes strike? N.Z. Sci. Mon. 7: 6–7.

Weinstein, P., M. Laird, and L. Calder. 1995. Australian arboviruses: at what risk New Zealand? Aust. N.Z. J. Med. 25: 666–669.

Weinstein, P., M. Laird, and G. Browne. 1997. Exotic and endemic mosquitoes in New Zealand as potential arbovirus vectors, Occasional paper. Ministry of Health, Wellington, New Zealand.

Woodward, A., S. Hales, and N. de Wet. 2001. Climate change: potential effects on human health in New Zealand. Ministry of Environment, Wellington, New Zealand.

World Health Organization. 1983. International Health Regulations, 3rd ed. World Health Organization, Geneva, Switzerland.

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