

Original Contribution

Association Between Habitat Size, Brushtail Possum Density, and the Mosquito Fauna of Native Forests in the Auckland Region, New Zealand

José G. B. Derraik^{1,2}

¹Ecology and Health Laboratory, Wellington School of Medicine and Health Sciences, University of Otago, P.O. Box 7343, Wellington, New Zealand

²Disease and Vector Research Group, Institute of Natural Sciences, Massey University, Albany Campus, Private Bag 102-904, NSMC, Auckland, New Zealand

Abstract: Human activities have been causing dramatic and unprecedented changes to the Earth's ecosystems, and are a primary factor associated with biological invasions. Disturbed and fragmented habitats allow some vector mosquitoes to thrive. The New Zealand landscape has been extensively modified since the arrival of humans, and there is accumulating evidence that the distribution of mosquitoes is being altered as a result of anthropogenic environmental changes. This study aimed to assess whether forest habitat size affected the community composition of mosquitoes, and whether the density of the introduced brushtail possum would benefit exotic mosquito species that feed primarily on mammal hosts. Extensive sampling of the mosquito community was carried out using dry ice-baited light traps, oviposition traps, and larval surveys. The results provided the first experimental evidence in New Zealand that changes in forest habitat size affect the indigenous and introduced mosquito fauna differently. The proportion of native species making up the mosquito community appears to be steadily reduced as native forest habitats become smaller. In contrast, the opposite pattern appears to occur for the introduced vector *Aedes notoscriptus*. Although there was a trend indicating that possums may have a negative impact on a native species (*Culex pervigilans*), the impact of these animals on the mosquito fauna remains unclear. The evidence suggests that the conservation of large pristine forest ecosystems in New Zealand could have human health implications.

Keywords: habitat fragmentation, invasion, mosquito, forest, phytotelmata, brushtail possum

INTRODUCTION

Human activities have been causing dramatic and unprecedented changes to the Earth's ecosystems (Vitousek et al., 1997), and are a primary factor leading to the biological invasion of natural communities (Fox and Fox,

1986; Mack et al., 2000; Shea and Chesson, 2002). Derraik and Slaney (2007) recently discussed how anthropogenic environmental change may favor invasion by exotic mosquitoes (Diptera: Culicidae) and their subsequent establishment in native habitats in New Zealand.

Some vector mosquitoes thrive in disturbed and fragmented habitats (e.g., Frankie and Ehler, 1978; Forattini and Massad, 1998; Jones, 2003). The abundance of

anopheline vectors of malaria in human-disturbed areas in the Brazilian Amazon, for example, is on average five times that of undisturbed habitats (Tadei et al., 1998). Habitat fragmentation in particular can make ecosystems smaller and more susceptible to invasions than large contiguous ecosystems, and disturbed edge habitats may function as staging areas from which exotic species invade the surrounding landscape (Center et al., 1995). The physical and biological environments in fragmented habitats are considerably altered, particularly as a result of proportionally greater edge effects (Saunders et al. 1991; Laurance et al., 2007; Broadbent et al., 2008). Different mosquito species or, in the case of *Aedes aegypti*, different forms of the same species (Frankie and Ehler, 1978) have, for instance, varying tolerances to desiccation (e.g., Machado-Allison and Craig, 1972) and consequently have their distribution affected. A decrease in soil moisture, greater sunlight penetration, and increased wind disturbance as a result of edge effects may also lead to the elimination of ground pools that serve as larval habitats for certain species, tipping the balance in favor of invading container-breeders better able to exploit new habitats created by human activities.

Furthermore, mosquitoes may benefit from the deleterious effects of habitat fragmentation on predator populations, as other predatory insects and native insectivorous bats and birds can be negatively affected by forest size reduction (e.g., Sekercioglu et al., 2002). It is recognized that the loss of native biodiversity potentially favors exotic invaders (Peterson et al., 1998; Ostfeld and Keesing, 2000), and although the consequences of species loss may not be immediately noticeable, it appears to make ecosystems more vulnerable to disturbance and collapse (Peterson et al., 1998) and, therefore, generally more susceptible to invasive species. The decline in native biodiversity may consequently facilitate the establishment of exotic vectors, as well as lead to greater abundance of reservoir hosts or vectors of human pathogens through the disruption of ecosystem processes (Derraik and Slaney, 2007).

New Zealand has only 12 native and 4 introduced mosquito species (Derraik, 2004a). All the introduced mosquitoes are potential disease vectors, and at least 30 other exotic culicid species have been intercepted at national entry ports (Derraik, 2004a). Although, to date, there has not been a confirmed, indigenously acquired arboviral infection in humans in New Zealand (Derraik and Maguire, 2005), it is predicted that it is just a matter of time before an arboviral outbreak occurs (Weinstein, 1996; Derraik and Calisher, 2004).

The New Zealand landscape has suffered dramatic changes since the arrival of humans c. 800 years ago (McGillone and Wilmshurst, 1999), leading to extensive habitat destruction, extinction of native species, and the introduction of exotic ones (Cook et al., 2002). There is accumulating evidence that anthropogenic environmental change has been altering the distribution of mosquitoes in New Zealand. At least in the Auckland region, native species appear to be nearly absent from anthropic habitats where introduced mosquitoes thrive (especially in urban areas), in comparison to the opposite pattern occurring in relatively undisturbed indigenous ecosystems (Derraik and Slaney, 2007). Recent studies in a range of habitats in the Auckland region indicated that relatively pristine indigenous habitats harbored a mosquito fauna comprised almost entirely of native species (Derraik et al., 2005a, b), while the only introduced species recorded was *Aedes (Finlaya) notoscriptus* (Skuse), in very low numbers and at the forest edge. In contrast, sampling in urban and peridomestic habitats indicated that exotic mosquitoes were dominant (e.g., Derraik, 2004b, 2005a; Derraik and Slaney, 2005).

New Zealand's evolutionary history and its early separation from the rest of Gondwanaland led to an absence of indigenous terrestrial mammals, the dominant non-flying terrestrial animals in the rest of the world (Diamond, 1990), apart from three species of bats (King, 1990). As a result, native mosquitoes appear to be primarily ornithophilic (bird-feeders), although there is little experimental evidence on their feeding preferences (Derraik and Slaney, 2007). The presence of numerous introduced mammals provide a large supply of mammalian blood meals previously unavailable in New Zealand (Derraik and Slaney, 2007). Livestock provide abundant blood meals in rural areas where the availability of other hosts such as humans (and birds) is limited. Most importantly, however, may be the presence of the estimated 70 million Australian brushtail possums (*Trichosurus vulpecula* Kerr), which are well-established in over 97% of the New Zealand's land area (Cowan, 2000). Although brushtail possums thrive particularly well in modified habitats, especially at the forest/pasture interface (Cowan, 2000), these animals are abundant throughout the country, even in remote areas. Since *T. vulpecula* are primarily herbivores that also prey on a number of other food sources (Brown et al., 1993; Cowan, 1990; Montague, 2000), they should be largely unaffected by changes in forest habitat size. As a result, in New Zealand *T. vulpecula* would likely be the main source of mammalian blood meals within larger forest habitats where their populations are unchecked.

There are therefore, favorable conditions for the establishment of exotic mosquitoes such as *Aedes (Stegomyia) albopictus* (Skuse) (Derraik, 2006), which not only breeds in artificial and natural containers, but also prefer mammalian hosts (Hawley, 1988). The presence of exotic mammals can also boost vector populations so that these will seek additional hosts, consequently increasing the likelihood of pathogen transmission to humans (Patz and Wolfe, 2002). In addition, *T. vulpecula* directly preys on the bird fauna in New Zealand, on which it has significant impacts (Cowan, 1990; Montague, 2000). In high densities therefore, possums may displace the avian fauna on which most native mosquitoes would likely rely for blood meals, possibly displacing indigenous ornithophilic species in favor of more generalist feeders, especially those that are attracted to mammals.

This study aimed to test the hypothesis that forest habitat size has an effect on the community composition of mosquitoes, affecting indigenous and introduced mosquitoes differently. Furthermore, the density of brushtail possums was predicted to be positively associated with introduced mosquito species that feed primarily on mammalian hosts, in particular *Ae. notoscriptus*.

MATERIALS AND METHODS

Study Area

This study was carried out in the Auckland region (North Island, New Zealand), where eight different native forest sites of varying sizes were sampled (Table 1). All sites contained native kauri-podocarp-hardwood forests, which

varied in relation to levels of naturalness and protection status.

Mosquito Sampling

At each field site, a 1-km transect was established with a hip-chain. A walking track was present in most sites and used as the transect to minimize impact on conservation areas. In the two sites without tracks (Wainui and Tapu Bush), U-shaped transects were marked using a compass. Sampling was carried out from late austral spring until early autumn. Along each transect, all potential larval mosquito habitats within 5 m on each side were carefully surveyed during a one-off investigation. As a result, the total area closely studied was c.1 ha per site. Larval habitats examined included ground pools (both temporary and permanent), man-made drains, and phytotelmata (e.g., tree-holes, leaf axils, and fallen plant parts).

An aluminum ladder was carried through each site, so that the search height was extended to approximately 4 m in order to sample the native epiphyte *Collospermum hastatum* (Colenso) (Liliaceae), the main source of larval habitats for culicids in native forests further south in Wellington (Derraik, 2005b). Individual leaf axils and other phytotelmata were inspected for mosquito larvae, and all the water within each axil was extracted using a modified syringe (Derraik, 2009).

In addition, two sets of ovitraps were placed at each site to sample mosquito larvae. These were set in the shade at the base of trees, with their positions along (and away from) the transect selected using random numbers and coordinates. Each set consisted of four black plastic containers of two different aperture sizes (38.5 and 103.8 cm²), filled with two different solutions of 0.5 or 5.0 g of sheep

Table 1. Description of the Field Sites in the Auckland Region Where this Study was Carried Out^a

Site	Approximate coordinates	Area (ha)	Possum density (RTC)
Cascade-Kauri Park	36°54'S, 174°31'E	> 1,000	0.5
Goldies Bush	36°51'S, 174°28'E	192	12.0
McElroy Reserve	36°28'S, 174°42'E	145	30.0
Pohuehue Reserve	36°28'S, 174°39'E	75	3.5
Wenderholm Regional Park	36°32'S, 174°43'E	66	< 0.1
Tapu Bush	36°16'S, 174°38'E	50	50.0
Logues Bush	36°16'S, 174°35'E	41	10.0
Wainui farm	36°36'S, 174°37'E	3	5.0

^aNote that the area size has been estimated when the actual value was not available.

manure per liter of tap water (as per Derraik and Slaney, 2005). Ovitrap were set seven or eight times, and checked once every 3 weeks.

Dry ice-baited light traps (Bland Consultancy Trust, Napier, New Zealand) were employed to sample adult mosquitoes. These adult traps were set overnight in sheltered locations (in the forest understory) for approximately 15 hours, during relatively dry and windless conditions (as per Derraik et al., 2005a). Each trap was operated five times at each site during summer.

All specimens were taken to the laboratory and identified to species whenever possible. Voucher specimens of larvae were reared through to adulthood to confirm larval identifications, which were carried out using a key (Snell, 2005). Voucher specimens of adults and larvae were examined by a mosquito taxonomist (Amy Snell) to confirm identifications.

Possum Density Estimates

Possum density was assessed as a relative measure given by a residual trap-catch index (RTC), using a standard trap-catch method used for possum population monitoring (National Possum Control Agencies, 2002). The RTC expresses the number of traps in which possums are caught, and provides an index of the residual density (Fraser et al., 2004). RTC is used by regional authorities to estimate the density of possums within a particular area (in order to determine whether a control operation is necessary) and was therefore adopted in this study. At Goldies and Cascade-Kauri Park, 10 trap-lines were set by the Department of Conservation, while in all remaining sites 3 to 5 trap-lines were set by the Auckland Regional Council. Each trap-line consisted of 10 number one double-coil spring traps spaced at 20-m intervals. Three nights of trapping were carried out in all sites, and the data are shown in Table 1.

Data Analyses

Non-metric multi-dimensional scaling (NMDS) ordination (Clarke and Warwick, 2001; Quinn and Keough, 2003)—based on Bray-Curtis dissimilarity measures and run from 30 random restarts—was used to compare mosquito species assemblages between field sites. The NMDS was based on “relative abundance indices” (RAI) obtained by the sum of all specimens collected from ovitraps, adult traps and phytotelmata, therefore providing a single overall value for each species at each site. The RAI were used to account for

the uneven number of positive samples obtained at individual sites, and the fact that particular sampling methods were biased towards certain species. ANOSIM (analysis of similarities) (Clarke and Warwick, 2001; Quinn and Keough, 2003) was subsequently used to test whether mosquito species assemblages from different sites were statistically different from each other. These analyses were run in the computer program Primer-E (Plymouth Marine Laboratory, Plymouth, UK).

Parametric simple and multiple regressions were carried out in the statistical package Minitab (Pennsylvania State University, University Park, PA). The predictors were habitat size and possum density, and two response variables were used: RAI and relative proportion (RP). The latter was the percentage of the overall abundance made up by native or introduced species, in order to examine whether the community shifted in one way or another as a result of changes in habitat size or possum density. Relevant associations were plotted. Regression models were also run excluding data from Tapu Bush, which was considered an outlier.

In addition, G-tests of independence were performed to compare larva-positivity rates between sites, while Kolmogorov-Smirnov two-sample tests were carried out to assess the abundance distribution of individual mosquito species in the fallen leaves of nikau palms. Note that, where applicable, data were square-root transformed to stabilize the variance. Significance level for all analyses was set at $P < 0.05$.

As microclimate can affect the mosquito community (e.g., Haddow, 1945, 1947), the study sites selected were geographically close to prevent significant climatic variations. The longest distance between any two sites was approximately 75 km, and rainfall and temperature data were found to be similar among sites [Derraik, unpublished data].

RESULTS

Natural Larval Habitats

Relatively few permanent and temporary ground pools were observed. These were rarely larva-positive, from which the native species *Aedes (Ochlerotatus) antipodeus* Edwards and *Cx. pervigilans* were collected (only at Cascade and Goldies). Tree-holes were also rare, and only one (at Wainui) was found to be larva-positive for *Ae. notoscriptus*.

The leaf axils of *C. hastatum* were the most numerous phytotelm habitats observed, and 470 plants were surveyed totaling 3288 leaf axils. The culicid fauna in this plant species was found to be almost entirely monospecific, as all but three of the 1836 larvae recorded were the native *Culex (Culex) asteliae* Belkin, with the exception of three *Ae. notoscriptus* larvae recorded in two plants at Wenderholm. The overall larva-positive rate of *C. hastatum* plants was 50% (170/340), but rates varied significantly between sites as indicated by the G-test ($P = 0.005$; $G = 20.41$). Larva-positive rates at Wenderholm and McElroy were 88% and 75%, respectively, in contrast to Goldies where mosquito larvae were only recorded in 16%.

The other main phytotelm habitat observed were the numerous fallen leaves of the native nikau palm (*Rhopalostylis sapida* Wendl. and Drude; Palmae). A total of 146 water-filled nikau palm leaves were recorded in the survey, 28 of which (19%) were larva-positive for culicids, including the native *Cx. asteliae*, *Cx. pervigilans*, and *Maorigoeldia argyropus* (Walker), and the introduced *Ae. notoscriptus*. The largest occupancy rate of fallen nikau leaves was observed at the largest site, Cascade-Kauri Park, in which 7 of 16 leaves (44%) harbored mosquito larvae.

There were, however, no significant differences in larva-occupancy rates of nikau palms overall ($P = 0.127$; $G = 11.28$).

Adult Traps and Ovitrap

A total of 1152 adult mosquitoes were recorded in the survey of 40 adult traps (Table 2). Five native and two exotic mosquito species were recorded (Table 2). The introduced *Culex (Culex) quinquefasciatus* Say was the rarest and least abundant of all species, with just three adult specimens collected from all sampling (at Tapu Bush). The introduced *Ae. notoscriptus* was the only species collected at all sites, being also the most frequently recorded culicid and the second most abundant (Table 2). In regards to native species, *Ae. antipodeus* was the most abundant species followed by *Cx. pervigilans*, both of which were recorded in all but one site (Table 2). The only other native species with a substantial presence in adult traps was *Coquillettidia (Coquillettidia) iracunda* (Walker), which was absent only from traps at Wenderholm (Table 2). Other indigenous species recorded were *Cx. asteliae* and *Coquillettidia (Austromansonia) tenuipalpis* (Edwards), the latter being the rarest

Table 2. Collection Results from a Series of CO₂-baited Light Traps Set at the Eight Native Forest Sites Investigated in the Auckland Region^a

Field site	<i>Cq. iracunda</i>	<i>Cq. tenuipalpis</i>	<i>Cx. asteliae</i>	<i>Cx. pervigilans</i>	<i>Cx. quinquef.</i>	<i>Ae. antipodeus</i>	<i>Ae. notoscript.</i>	Total
Cascade	2–42	2–4	–	1–1	–	5–240	1–1	5–293
	8.4 (18.2)	0.8 (1.1)				48 (63.0)		58.6 (61.6)
Goldies	3–21	–	–	–	–	5–22	5–60	5–108
	4.2 (6.3)					4.4 (1.7)	12.0 (15.0)	21.6 (17.3)
Logues	1–1	–	2–6	5–199	–	5–226	5–47	5–495
			1.2 (2.2)	39.8 (46.0)		45.2 (54.4)	9.4 (14.4)	99.0 (101.0)
McElroy	3–6	–	1–1	3–4	–	1–3	3–3	5–17
	1.2 (1.6)			0.8 (0.8)			0.6 (0.5)	3.4 (1.1)
Pohuehue	1–1	–	–	3–5	–	–	4–13	5–19
				1.0 (1.2)			2.6 (2.3)	3.8 (1.9)
Tapu	1–4	–	–	3–13	1–3	1–2	1–2	3–24
				2.6 (4.7)				4.8 (6.9)
Wainui	1–4	–	1–1	4–8	–	2–35	4–20	4–71
				2.0 (1.4)		8.8 (15.6)	5.0 (5.7)	17.8 (13.3)
Wenderholm	–	–	–	1–2	–	1–4	5–118	5–125
							23.6 (15.2)	25 (14.9)
Total (N = 39)	12–79	2–4	4–8	20–232	1–3	20–532	28–264	37–1152

^aValues in each cell represent number of traps in which a species was recorded and total number of adults collected (top), and mean and standard deviation (bottom). The total value includes also the damaged, and therefore unidentifiable, specimens. Note that one trap at Wainui farm was lost due to trap malfunction, so mean is calculated over four overnight periods.

native mosquito with only four specimens collected at the largest site (Table 2). Note that the larvae of *Coquillettidia* spp. attach themselves to aquatic plants via a modified siphon to respire, and are therefore more difficult to sample. In fact, *Coquillettidia* larvae are yet to be collected in nature in New Zealand.

There were 480 ovitrap inspections, 26% (123) of which were larva-positive for culicids (Table 3). The only site with no larva-positive ovitraps was Tapu Bush, and there was strong evidence that larva-occupancy varied significantly between the sites ($P < 0.001$; $G = 143.89$; d.f. = 7). The 2797 larvae recorded comprised only two species, most of which (94%) were the introduced *Ae. notoscriptus*, with the remaining specimens being *Cx. pervigilans* (Table 3). Note that *Ae. notoscriptus* was particularly numerous and widespread at the smallest forest fragment (Wainui), where it was recorded in 77% of ovitraps (Table 3). In contrast, *Ae. notoscriptus* was rare at Cascade, the largest site, where only two larvae were recorded (Table 3). Significant differences in larva-occupancy of ovitraps were observed for both *Ae. notoscriptus* ($P < 0.001$; $G = 156.54$; d.f. = 7) and *Cx. pervigilans* ($P = 0.001$; $G = 14.70$; d.f. = 7).

Species Assemblages and Associations with Habitat Fragmentation and Possum Density

Although the NMDS ordination (not shown) failed to yield any clear results, the ANOSIM confirmed that the species assemblage at Cascade was significantly different from all other sites ($P < 0.05$). However, R -values were not high (ranging from 0.13 to 0.43), indicating that between-site

dissimilarities were relatively minor. Nonetheless, the mosquito community at Tapu Bush was not only significantly different from all others ($P < 0.01$), but R -values were high (varying from 0.45 and 0.83), a likely consequence of a rather poor culicid fauna and the presence of the introduced *Cx. quinquefasciatus*.

There were no significant associations between the native species relative abundance indices and either possum density or habitat size ($P = 0.270$). Since all but three exotic mosquito specimens recorded were *Ae. notoscriptus*, this species was examined in isolation. Similar results were obtained for *Ae. notoscriptus* RAI ($P = 0.156$), although there was indication of a negative association with habitat size ($P = 0.055$), for which the r^2 was relatively high (0.49). A closer examination of the scatter plots showed that Tapu Bush appeared to be skewing the data, due to its somewhat species-poor mosquito fauna (the only site with no larvae in ovitraps or in fallen nikau leaves) and extreme levels of possum-induced habitat disturbance. This particular site recorded what is likely to have been the largest possum density ever recorded in New Zealand, yielding 100% RTC [Dave Galloway, Auckland Regional Council, personal communication, 2003]. Therefore, in order to identify patterns that may have been obscured, further analyses were carried out excluding this data point, which appeared as a biological outlier as also illustrated by the NMDS/ANOSIM results. There was consequently a strong negative association between *Ae. notoscriptus* RAI and habitat size ($P = 0.003$; $r^2 = 0.86$; Figure 1), but not with possum density ($P = 0.767$).

Regression analyses were carried out also for the most common native species (*Cx. asteliae* and *Cx. pervigilans*).

Table 3. Results from the 3-Weekly Surveys of Ovitrap in Native Forest Sites in the Auckland Region^a

Field site	<i>Culex pervigilans</i>	<i>Aedes notoscriptus</i>	Total
Cascade-Kauri Park	1/64 (2%)–57	1/64 (2%)–2	2/64 (3%)–59
Goldies Bush	–	14/64 (22%)–220	14/64 (22%)–220
Logues Bush	1/64 (2%)–2	28/64 (44%)–557	29/64 (45%)–559
McElroy Reserve	2/56 (4%)–79	8/56 (14%)–73	10/56 (18%)–152
Pohuehue Reserve	–	17/56 (30%)–296	17/56 (30%)–296
Tapu Bush	–	–	–
Wainui farm	–	43/56 (77%)–1345	43/56 (77%)–1345
Wenderholm Regional Park	4/56 (7%)–29	5/56 (9%)–137	9/56 (16%)–166
Overall	8/480 (2%)–167	116/480 (24%)–2630	123/480 (26%)–2797

^aValues in each cell represent occupancy rate of ovitraps and total number of larvae collected.

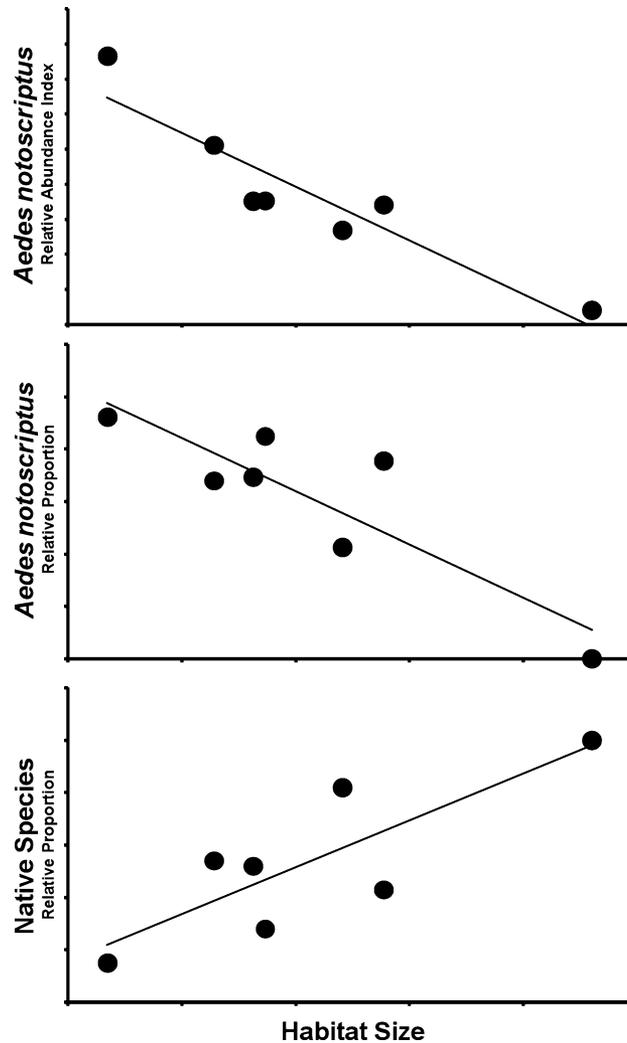


Figure 1. Scatter plots showing comparisons between: *Ae. notoscriptus* RAI \times habitat size ($P = 0.003$); *Ae. notoscriptus* RP \times habitat size ($P = 0.011$); and native species RP \times habitat size ($P = 0.024$). Data point from Tapu Bush was excluded. All variables have been square-root transformed and, therefore, values are not shown along the axes.

There was no significant association between *Cx. asteliae* RAI and habitat size ($P = 0.236$) or possum density ($P = 0.535$). Similar pattern was observed for *Cx. pervigilans* RAI and habitat size ($P = 0.675$). However, although not significant ($P = 0.072$), there was evidence of a negative association between *Cx. pervigilans* RAI and possum density ($r^2 = 0.51$).

The relative proportion of the exotic *Ae. notoscriptus* was also significantly and negatively associated with habitat size ($P = 0.011$; $r^2 = 0.76$; Figure 1), but not with possum density ($P = 0.907$). The native species RP was also significantly associated with habitat size ($P = 0.024$; $r^2 = 0.67$), but in contrast to the exotic species, the relationship was positive (Figure 1). No association was observed between native mosquitoes RP and possum density ($P = 0.977$).

DISCUSSION

This study provided the first experimental evidence in New Zealand that changes in forest habitat size affect the community composition of mosquitoes. More importantly, human-induced changes affect the indigenous and introduced culicid fauna differently. The proportion of native species making up the mosquito community appears to be reduced as native forest habitats become smaller. In contrast, the opposite pattern appears to occur for the introduced *Ae. notoscriptus*, which thrives in small habitats but seems yet to invade large pristine forest ecosystems.

Cascade-Kauri Park, the largest and most pristine native forest site studied, harbored the lowest RAI and RP of introduced mosquitoes recorded (only four *Ae. notoscriptus*

out of 913 culicid specimens; 0.4%), was the only field site where the native *Cq. tenuipalpis* was recorded, and it harbored the highest native species diversity. Furthermore, larvae of the native *Cx. asteliae* and *Mg. argyropus* were only present in fallen nikau leaves, there and at the second largest site (Goldies Bush). The latter species in particular was the most common and abundant species in those two largest sites, and Snell et al. (2005) recently discussed that fragmentation of native forests seems to have led to the displacement of *Mg. argyropus* to larger and more pristine sites, as previously proposed by Pillai (1965). In contrast, *Cx. asteliae* seems to be resilient to habitat size reduction, and able to maintain viable populations as long as healthy specimens of *C. hastatum* (its main host plant) remain, as observed for example at Tapu Bush and Wainui.

Particularly important was the dominance of the introduced *Ae. notoscriptus* in smaller forest habitats, and the evidence indicating that this species is favored by native forest reduction. This species is highly anthropophilic and it is a potential vector of arboviruses affecting humans such as Ross River virus and Barmah Forest virus (Doggett and Russell, 1997; Watson and Kay, 1998). Large native forest areas in New Zealand may not exclude *Ae. notoscriptus*, but rather that this species may prefer disturbed edge habitats. For instance, fallen nikau leaves inspected ad hoc near the forest edge at Cascade contained a higher frequency and numbers of *Ae. notoscriptus* larvae, and adults of the species were also biting in forest fringe, but were not recorded doing so deeper into the forest [personal observation]. In its native Australia, *Ae. notoscriptus* feeds primarily on mammals (Lee and Bugledish, 1999). No rodents have yet been identified among its hosts, and the only recorded non-mammal hosts for *Ae. notoscriptus* were poultry (Lee and Bugledish, 1999). In New Zealand, apart from feeding on humans and dogs (Derraik and Snell, 2004), *Ae. notoscriptus* has been shown to feed on possums (Bullians and Cowley, 2001; Derraik et al., 2007). Due to the near absence of mammals in native forest reserves such as Cascade-Kauri Park (where mammalian pest control is regularly carried out), the forest edge would likely provide a more suitable habitat, where the species could move onto adjacent areas to feed on livestock, rabbits, and possums.

The data suggested that possums may have a deleterious impact on certain native mosquito species. Although the relationship was not statistically significant, the analysis suggested that possum density was negatively associated with the native *Cx. pervigilans* RAI. Since *Cx. pervigilans* appears to rarely bite humans and its natural hosts are most

likely birds (Belkin, 1968; Derraik and Slaney, 2007), the extensive impact of *T. vulpecula* on the avian fauna may be displacing such indigenous ornithophilic mosquito species. Although the impact of brushtail possums on New Zealand mosquito communities is still unclear, their presence may be of significance in areas where they are the main mammalian hosts, particularly for introduced mosquitoes (Derraik and Slaney, 2007). However, the rather poor fauna observed at Tapu Bush (the most disturbed site) could be an indication that possums, at very high densities, may have such an extensive impact on native ecosystems, so as to displace not only most native species but also to make the habitat unfavorable to introduced species. The negative impact of the heavy infestation of possums on the forest was clear, as, for example, the forest understory was extremely bare, in contrast with all other sites studied.

It was not possible to survey all available mammalian hosts in this study. At Wenderholm, for instance, rabbits (*Oryctolagus cuniculus* (Linnaeus)) are common at the forest edge where they feed on regenerating seedlings (Auckland Regional Council, 1995). At that site, the number of adult *Ae. notoscriptus* recorded was high, and the species might have been taking blood meals from rabbits (the Wenderholm site was considered to be possum-free), on which they are known to feed in Australia (Lee and Bugledish, 1999). In addition, Watson et al. (2000) demonstrated that *Ae. notoscriptus* may travel over 200 m from the point of release, and although it is not clear how this would apply to a forest environment, *Ae. notoscriptus* may fly some distance to feed on livestock outside the forest itself. This was probably the case at Wainui farm, as although possum density within the forest fragment was relatively low, it was surrounded by pasture where livestock were regularly present.

Further studies are necessary to clarify the potential effects of possum density and forest habitat size on mosquito communities in New Zealand. However, the observed negative association between *Ae. notoscriptus* and forest habitat size is of particular relevance. In Australia, *Ae. notoscriptus* is the main peridomestic mosquito species (Foley et al., 2004), and this pattern is now seen in urban and suburban areas in the Auckland region (e.g., Derraik, 2005a). A similar pattern of invasion would likely apply to *Ae. albopictus*, which is closely associated with humans but prefers vegetated areas such as forest fragments (Derraik, 2006), and fragmentation of native forests would likely favor this and other exotic invasive species. *Aedes albopictus*, in particular, is of increasing importance as an

arbovirus vector worldwide, and regularly intercepted at New Zealand's ports of entry (Derraik, 2006). Therefore, the conservation of large pristine forest ecosystems in New Zealand could ultimately have human health implications.

ACKNOWLEDGMENTS

I thank Dave Galloway and Richard Gribble (Auckland Regional Council) for their invaluable logistical support that made this study possible, Gerry Quinn (Deakin University, Australia) for his goodwill in providing prompt and valuable statistical advice, Amy Snell for help with mosquito taxonomy, and Dave Slaney for support and input. Special thanks also to those people and organizations who provided me with free access to their land (and related information whenever necessary), in particular: Scott De Silva, Barry Green, and Pam Robinson (Auckland Regional Council); Rolin Elliot, Simon Mowbray, Thelma Wilson, Brendon Christensen, and Dale Williams (Department of Conservation); Peter Bilton, Ron Hewson, and Ian Murray (Rodney District Council); Richard Lloyd (Wainui farm); and Collin Lees (Tapu Bush). Thanks also to two anonymous reviewers for feedback on previous versions of this manuscript. The University of Otago provided funding support.

REFERENCES

- Auckland Regional Council (1995) *Wenderholm Regional Park—Management Plan (2nd Review)*, Auckland, New Zealand: Regional Parks Service, Auckland Regional Council
- Belkin JN (1968) Mosquito studies (Diptera: Culicidae) VII. The Culicidae of New Zealand. *Contributions of the American Entomological Institute* 3:1–182
- Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* 141:1745–1757
- Brown K, Innes J, Shorten R (1993) Evidence that possums prey on and scavenge birds' eggs, birds and mammals. *Notornis* 40:169–177
- Bullians MS, Cowley DR (2001) Blood feeding by *Aedes notoscriptus* (Skuse) (Diptera: Culicidae) on the brush-tailed possum, *Trichosurus vulpecula* (Kerr). *New Zealand Entomologist* 24:87–88
- Center TD, Frank JH, Dray FA (1995) Biological invasions—stemming the tide in Florida. *Florida Entomologist* 78:45–55
- Clarke KR, Warwick RM (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, Plymouth, UK: PRIMER-E Ltd
- Cook A, Weinstein P, Woodward A (2002) The impact of exotic insects in New Zealand. In: *Biological Invasions: Economic, Environmental Costs of Alien Plant, Animal, Microbe Species*, Pimentel D (editor), Boca Raton, FL: CRC Press, pp 217–239
- Cowan PE (1990) Brushtail possum. In: *The Handbook of New Zealand Mammals*, King CM (editor), Auckland, New Zealand: Oxford University Press, pp 68–98
- Cowan P (2000) *Factors Affecting Possum Re-infestation—Implications for Management*, Wellington, New Zealand: Department of Conservation
- Derraik JGB (2004a) Exotic mosquitoes in New Zealand: a review of species intercepted, their pathways and ports of entry. *Australian and New Zealand Journal of Public Health* 28:433–444
- Derraik JGB (2004b) A survey of the mosquito (Diptera: Culicidae) fauna of the Auckland Zoological Park. *New Zealand Entomologist* 27:51–55
- Derraik JGB (2005a) Mosquitoes breeding in container habitats in urban and peri-urban areas in the Auckland Region, New Zealand. *Entomotropica* 20:93–97
- Derraik JGB (2005b) Mosquitoes breeding in phytotelmata in native forests in the Wellington region, New Zealand. *New Zealand Journal of Ecology* 29:185–191
- Derraik JGB (2006) A scenario for invasion and dispersal of *Aedes albopictus* (Diptera: Culicidae) in New Zealand. *Journal of Medical Entomology* 43:1–8
- Derraik JGB (2009) A tool for sampling mosquito larvae from phytotelmata. *Journal of Vector Ecology* 34 (in press)
- Derraik JGB, Calisher CH (2004) Is New Zealand prepared to deal with arboviral diseases? *Australian and New Zealand Journal of Public Health* 28:27–30
- Derraik JGB, Ji W, Slaney D (2007) Mosquitoes feeding on brushtail possums (*Trichosurus vulpecula*) and humans in a native forest fragment in the Auckland region. *New Zealand Medical Journal* 120:U2830
- Derraik JGB, Maguire T (2005) Mosquito-borne diseases in New Zealand: Has there ever been an indigenously acquired infection? *New Zealand Medical Journal* 118:U1670
- Derraik JGB, Slaney D (2005) Container aperture size and nutrient preferences of mosquitoes (Diptera: Culicidae) in the Auckland region, New Zealand. *Journal of Vector Ecology* 30:73–82
- Derraik JGB, Slaney D (2007) Anthropogenic environmental change, mosquito-borne diseases and human health in New Zealand. *EcoHealth* 4:72–81
- Derraik JGB, Snell AE (2004) Notes on daytime biting catches of mosquitoes (Diptera: Culicidae) in native forest sites in the Auckland region. *The Weta* 28:14–19
- Derraik JGB, Snell AE, Slaney D (2005a) An investigation into the circadian response of adult mosquitoes (Diptera: Culicidae) to host-cues in West Auckland. *New Zealand Entomologist* 28:85–90
- Derraik JGB, Snell AE, Slaney D (2005b) Vertical distribution of mosquitoes in native forest in Auckland, New Zealand. *Journal of Vector Ecology* 30:334–336
- Diamond JM (1990) New Zealand as an archipelago: an international perspective. In: *Ecological Restoration of New Zealand Islands*, Towns DR, Daugherty CH, Atkinson IAE (editors), Wellington, New Zealand: Department of Conservation, pp 3–8
- Doggett SL, Russell RC (1997) *Aedes notoscriptus* can transmit inland and coastal isolates of Ross River and Barmah Forest

- viruses from New South Wales. *Arbovirus Research in Australia* 7:79–81
- Foley DH, Russell RC, Bryan JH (2004) Population structure of the peridomestic mosquito *Ochlerotatus notoscriptus* in Australia. *Medical and Veterinary Entomology* 18:180–190
- Forattini OP, Massad E (1998) Culicidae vectors and anthropic changes in a Southern Brazil natural ecosystem. *Ecosystem Health* 4:9–19
- Fox MD, Fox BJ (1986) The susceptibility of natural communities to invasion. In: *Ecology of Biological Invasions*, Groves RH, Burdon JJ (editors), Cambridge, UK: Cambridge University Press, pp 57–66
- Frankie GW, Ehler LE (1978) Ecology of insects in urban environments. *Annual Review of Entomology* 23:367–387
- Fraser KW, Overton JM, Warburton B, Rutledge DT (2004) *Predicting Spatial Patterns of Animal Pest Abundance: A Case Study of the Brushtail Possum (Trichosurus vulpecula)*, Wellington, New Zealand: Department of Conservation
- Haddow AJ (1945) The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate. *Bulletin of Entomological Research* 36:33–73
- Haddow AJ (1947) The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate. *Bulletin of Entomological Research* 37:301–330
- Hawley WA (1988) The biology of *Aedes albopictus*. *Journal of the American Mosquito Control Association* 4:1–39
- Jones N (2003) Diseases are running rife in forest remnants. *New Scientist* 2381:15
- King CM (1990) *The Handbook of New Zealand Mammals*, Auckland, New Zealand: Oxford University Press
- Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, Harms KE, et al. (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2:e1017
- Lee W, Bugledish E-MA (1999) Culicidae. In: *Diptera: Nematocera*, Bugledish E-MA (editor), Melbourne: CSIRO Publishing, pp 161–239
- Machado-Allison C, Craig GB Jr (1972) Geographic variation in resistance to desiccation in *Aedes aegypti* and *A. atropalpus* (Diptera: Culicidae). *Annals of the Entomological Society of America* 65:542–547
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710
- McGlone MS, Wilmshurst JM (1999) Dating initial Maori environmental impact in New Zealand. *Quaternary International* 59:5–16
- Montague TL (2000) *The Brushtail Possum—Biology, Impact and Management of an Introduced Marsupial*, Lincoln, New Zealand: Manaaki Whenua Press
- National Possum Control Agencies (2002) *Protocol for Possum Population Monitoring Using the Trap-catch Method*, Wellington, New Zealand: National Possum Control Agencies
- Ostfeld RS, Keesing F (2000) Biodiversity and disease risk: the case of Lyme disease. *Conservation Biology* 14:722–728
- Patz JA, Wolfe ND (2002) Global ecological change and human health. In: *Conservation Medicine: Ecological Health in Practice*, Aguirre AA, Ostfeld RS, Tabor GM, House CA, Pearl MC (editors), New York: Oxford University Press, pp 167–181
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18
- Pillai JS (1965) Notes on mosquitoes of New Zealand I. *Maorigoeldia argyropus* Walker (Diptera, Culicidae, Sabethini). *New Zealand Entomologist* 3:25–35
- Quinn GP, Keough MJ (2003) *Experimental Design and Data Analysis for Biologists*, Cambridge, UK: Cambridge University Press
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32
- Sekercioglu CH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sandí RF (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 99:263–267
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 14:170–176
- Snell AE (2005) Identification keys to larval and adult female mosquitoes (Diptera: Culicidae) of New Zealand. *New Zealand Journal of Zoology* 32:99–110
- Snell AE, Derraik JGB, McIntyre M (2005) *Maorigoeldia argyropus* Walker (Diptera: Culicidae): is this another threatened endemic species? *New Zealand Entomologist* 28:95–99
- Tadei WP, Thatcher BD, Santos JMM, Scarpassa VM, Rodrigues IB, Rafael MS (1998) Ecologic observations on anopheline vectors of malaria in the Brazilian Amazon. *American Journal of Tropical Medicine and Hygiene* 59:325–335
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277:494–499
- Watson TM, Kay BH (1998) Vector competence of *Aedes notoscriptus* (Diptera: Culicidae) for Ross River virus in Queensland, Australia. *Journal of Medical Entomology* 35:104–106
- Watson TM, Saul A, Kay BH (2000) *Aedes notoscriptus* (Diptera: Culicidae) survival and dispersal estimated by mark-release-recapture in Brisbane, Queensland, Australia. *Journal of Medical Entomology* 37:380–384
- Weinstein P (1996) When will mosquitoes strike? *New Zealand Science Monthly* 7:6–7