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Review

Review

Detection and Establishment of *Aedes notoscriptus* (Diptera: Culicidae) Mosquitoes in Southern California, United States

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Abstract

Aedes notoscriptus (Skuse), the Australian backyard mosquito, is a pestiferous daytime-biting species native to Australia and the surrounding southwestern Pacific region. It is suspected to play a role in the transmission of several arboviruses and is considered a competent vector of dog heartworm, *Dirofilaria immitis* (Leidy). This highly adaptable mosquito thrives in natural and artificial water-holding containers in both forested and urbanized areas, from tropical to temperate climates, and has benefitted from a close association with humans, increasing in abundance within its native range. It invaded and successfully established in New Zealand as well as in previously unoccupied temperate and arid regions of Australia. *Ae. notoscriptus* was discovered in Los Angeles County, CA, in 2014, marking the first time this species had been found outside the southwestern Pacific region. By the end of 2019, immature and adult mosquitoes had been collected from 364 unique locations within 44 cities spanning three southern California counties. The discovery, establishment, and rapid spread of this species in urban areas may signal the global movement and advent of a new invasive container-inhabiting species. The biting nuisance, public health, and veterinary health implications associated with the invasion of southern California by this mosquito are discussed.

Key words: *Aedes notoscriptus*, Australian backyard mosquito, arbovirus, *Dirofilaria immitis*, California

Aedes notoscriptus (Skuse), the Australian backyard mosquito, is a highly adaptable species native to the southwestern Pacific region and widely distributed within Australia, Papua New Guinea, the Solomon Islands, the Philippines, New Caledonia, and Indonesia (Belkin 1968, Lee et al. 1982). This species is a primary vector of dog heartworm, *Dirofilaria immitis* (Leidy) (Spirurida: Onchocercidae), in Australia (Russell 1985, 1990; Russell and Geary 1992, 1996) and is suspected to play a role in the transmission of several arboviruses found within its range. Its preferred natural environments are temperate and tropical forests where it utilizes natural water-holding containers, such as tree holes, bamboo stumps, leaf axils, and rock pools, for larval development (Belkin 1968, Lee et al. 1982, Laird 1990, Fanning et al. 1997, Sunahara and Mogi 2004). However, this mosquito also thrives in urban areas using the multitudes of available artificial containers (Hamlyn-Harris 1928, Lee et al. 1982, Montgomery and Ritchie 2002, Derraik 2004, Kay et al. 2008, Lamichhane et al. 2017), and as a result, has become increasingly prevalent in domestic settings (Russell 1986). The close association with humans has facilitated the introduction and establishment of *Ae. notoscriptus*, presumably through trade and travel, to previously inaccessible and/or inhospitable temperate and arid regions of Australia, as well as to New Zealand where it is now present in both natural and urban environments (Belkin 1968, Foley et al. 2004, Whelan 2010, Endersby et al. 2013).

Ae. notoscriptus is an opportunistic and avid feeder and will take bloodmeals from a wide range of animals including mammals, birds, and humans (Lee et al. 1982, Kay et al. 2007). Females are both nocturnal and diurnal and can cause severe biting nuisance in urban areas (Foot 1970, Lee et al. 1982). The feeding habits of *Ae. notoscriptus* make it an ideal candidate for pathogen transmission within urban biomes where vectors, infected and uninfected susceptible vertebrates, and humans cooccur. Laboratory transmission studies, virus isolations from field-collected females, and epidemiological studies of arboviruses endemic to Australia have strongly implicated this mosquito in the urban transmission of Ross River virus (RRV) and Barmah Forest virus (BFV) (Doggett and Russell 1997, Ritchie et al. 1997, Watson and Kay 1998, 1999; Jacups et al. 2008). Together, these two arboviruses cause thousands of human infections annually in Australia, with RRV accounting for the majority of notifications (Australian Government Department of Health 2021). While laboratory transmission studies have demonstrated that this species is not a competent vector of Murray Valley Encephalitis virus (MVEV) (McLean 1953), its role in the transmission of Stratford virus remains unresolved (Toi et al. 2017). Additionally, Australian and New Zealand laboratory studies have attempted to elucidate the role of *Ae. notoscriptus* as a possible vector of arboviruses not endemic to the southwestern Pacific region that could be imported by viremic travelers or infected animals; various degrees of vector competency were demonstrated for Japanese encephalitis virus (JEV) (van den Hurk et al. 2003), Rift Valley fever virus (Turell and Kay 1998), West Nile virus (WNV) (Jansen et al. 2008), chikungunya virus (CHIKV) (van den Hurk 2010), and yellow fever virus (van den Hurk et al. 2011). *Ae. notoscriptus* successfully transmitted dengue virus (DENV) in a New Zealand study (Maguire 1994), but subsequent studies reported them as ineffective and unlikely vectors of all four DENV serotypes (Watson and Kay 1999, Kramer et al. 2011, Skelton et al. 2016). Females were susceptible to infection but failed to transmit Zika virus (Hall-Mendelin et al. 2016).

Ae. notoscriptus was discovered in Los Angeles County, CA, USA, in 2014, marking the first time this species had been found outside the southwestern Pacific region and only its second known invasion of a previously unoccupied landmass after New Zealand. This species spread rapidly, and by the end of 2019, immature and adult mosquitoes had been collected from 364 unique locations within 44 cities spanning three southern California counties. *Ae. notoscriptus* is the third species of container-inhabiting *Aedes* introduced and established in California since 2011 (Metzger et al. 2017), and together, this trio of invasive mosquitoes has created an unprecedented burden on local vector control agencies seeking to protect the public from mosquito-borne pathogens and biting nuisance. Herein, we report on the discovery, establishment, and rapid spread of *Ae. notoscriptus* in urban areas of southern California between 2014 and 2019, an event that may signal the beginning of a global movement and advent of a new invasive species. Observations and data elucidating larval habitat uses, adult seasonality, and adult trap preferences are presented along with a discussion regarding the possible origin of these mosquitoes and future geographical expansion. The potential public and veterinary health implications associated with this invasion are described, along with other studies providing pertinent background on the biology and ecology of this relatively understudied mosquito species.

Discovery, Confirmation, and Spread of *Ae. notoscriptus*

California has a network of over 65 local vector control agencies that operate under a cooperative agreement with the California Department of Public Health to serve approximately 80% of the state's population. The role of these local agencies is to protect the public from vector-borne pathogens as well as from biting nuisances, with a current focus on WNV, the state's most important mosquito-borne disease (Snyder et al. 2020). The discoveries of *Aedes albopictus* (Skuse) in 2011 and *Aedes aegypti* (L.) in 2013, hereafter referred to collectively as "invasive *Aedes*", created a disruption in established operations that required massive reorganization and reprioritization of staff and resources, public education and outreach, and surveillance strategies and tools. Mosquito surveillance was enhanced by implementing *Aedes*-specific traps, door-to-door residential property inspections, and community education and outreach programs to slow the dispersal of these exotic species and reduce disease transmission risk (Porse et al. 2015, 2018, Metzger et al. 2017). The initial discoveries and subsequent collections of *Ae. notoscriptus* were a result of enhanced invasive *Aedes* surveillance and conventional mosquito surveillance traps targeting endemic *Culex* mosquitoes (Ruedas et al. 2017).

In June 2014, a battered and unidentifiable female *Aedes* mosquito was collected in the city of Monterey Park (Los Angeles County, California) in a carbon dioxide-baited trap (CO_2 -baited trap) used for WNV surveillance (Ruedas et al. 2017). Two months later, in the adjacent city of Montebello, a residential service request for day-biting mosquitoes resulted in the collection of larvae and adults on the property; these specimens were tentatively identified as *Ae. notoscriptus* using taxonomic keys (Rueda 2004). The identification was verified through correspondence and photo sharing with mosquito experts in Australia. Nearly simultaneous with this finding, ovitraps previously placed in residential neighborhoods of Monterey Park collected eggs that were successfully reared in the laboratory and emerged as pristine *Ae. notoscriptus* adults, which solidified the discovery and identification of this species, and documented their presence and reproduction in more than one location. Almost exactly one year after the initial find, one male was collected in Monterey Park, followed by a small number of additional adult and larval collections between September and December 2015 in Montebello, Santa Monica, Los Angeles (i.e., Venice; Pacific Palisades), View-Park-Windsor Hills, and Ladera Heights. These detections not only confirmed that *Ae. notoscriptus* survived over the winter in Montebello and Monterey Park, but suggested a potentially vast distribution extending far into western Los Angeles County.

The geographical spread, number of positive locations, and the frequency of captures increased between 2015 and the end of 2019. The bulk of detections (72%; 536/744) were made by the Los Angeles County West Vector & Vector-Borne Disease Control District, which serves nearly five million people over an area of approximately 1,900 km^2, from downtown Los Angeles west to Malibu and south to the Palos Verdes Peninsula. Data from this agency best illustrate the annual increase in number of detection sites: 7, 57, 153, 164, and 155 from 2015 through 2019, respectively. The first discovery of *Ae. notoscriptus* in Orange County was made in September 2017, followed by San Diego County in May 2018. In total, 744 collections of *Ae. notoscriptus* were made from mid-2014 through 2019; 669 from Los Angeles County, 12 from Orange County, and 63 from San Diego County. Of these, 364 were unique locations. By the end of 2019, surveillance data indicated that *Ae. notoscriptus* was firmly established throughout the western portion of Los Angeles County. Although fewer collections were made east of downtown Los Angeles, the distribution of detections strongly suggested that this mosquito was widespread to the central part of the county (near the original detections) and southward into the northern half of Orange County. In San Diego County, surveillance documented widespread mosquito activity inland around the cities of El Cajon and La Mesa, with evidence of westward expansion. Fig. 1 illustrates the known geographical distribution of this mosquito by indicating the locations and relative density of the 744 individual detections. The chronology of first discovery within the 44 affected cities and census-designated places is listed in Table 1.

Mosquito Surveillance: Trap Performance and Larval Collections

Prior to the initial discovery of *Ae. notoscriptus*, southern California vector control agencies had already transitioned their mosquito surveillance programs to include invasive *Aedes* (Metzger et al. 2017). Standardized mosquito surveillance relied on CO_2-baited and gravid traps, but vector control agencies augmented surveillance with *Aedes*-specific traps including ovitraps, autocidal gravid ovitraps (CDC-AGO) developed and manufactured by the U.S. Centers for Disease Control and Prevention (Mackay et al. 2013), proprietary BG-Sentinel (BGS) and BG-Gravid *Aedes* Traps (BG-GAT) (Biogents AG, Regensburg, Germany), and CO_2-baited traps augmented with BG-Lure (Biogents AG, Regensburg, Germany). In addition, resident service requests for daytime-biting mosquitoes required meticulous property inspections to confirm the presence of invasive *Aedes* through examination of cryptic and ephemeral water sources (e.g., small containers, potted plant saucers, yard drains) for eggs, larvae, and pupae, and/or to collect host-seeking females attracted to technicians with nets or aspirators while on the property. These programmatic changes were not implemented uniformly among vector control agencies and evolved continuously and independently in response to growing infestations. As invasive *Aedes* became entrenched in cities and geographical expansion accelerated, agencies were forced to shift from individual property to neighborhood approaches, emphasizing through education and outreach that the public assist with mosquito control and bite prevention. Each agency adjusted its programs as necessary, based on surveillance data and resource availability, resulting in notable interagency differences in surveillance and control methodologies over time.

The vast majority of *Ae. notoscriptus* were collected serendipitously. Some specimens were collected in traps set as part of routine arbovirus surveillance, whereas others were collected in *Aedes*-specific traps and during property inspections for day-biting mosquito complaints expected to produce *Ae. aegypti* and/or *Ae. albopictus*. However, in some cases specific surveillance efforts targeting *Ae. notoscriptus* were conducted following initial detections. Some notable examples included: 1) surveillance around the Los Angeles International Airport to identify a potential point-of-entry into California from the southwestern Pacific region, 2) placement of multiple trap types at certain locations in Los Angeles County with a history of adult *Ae. notoscriptus* activity to evaluate trap preferences, 3) extensive neighborhood trapping and property inspections in and around the first detection sites in San Diego County, and 4) repeated trapping and inspections on the campus of California State University, Fullerton, Orange County.

The methods by which all 744 detections of *Ae. notoscriptus* were made between 2014 and 2019 are presented in Table 2. These data are not for comparison and only include traps and property inspections that produced *Ae. notoscriptus* (some property inspections produced adults in traps as well as larval collections). Columns reveal dissimilar numbers of traps, or lack thereof, giving some indication of the differences among agencies with regard to surveillance

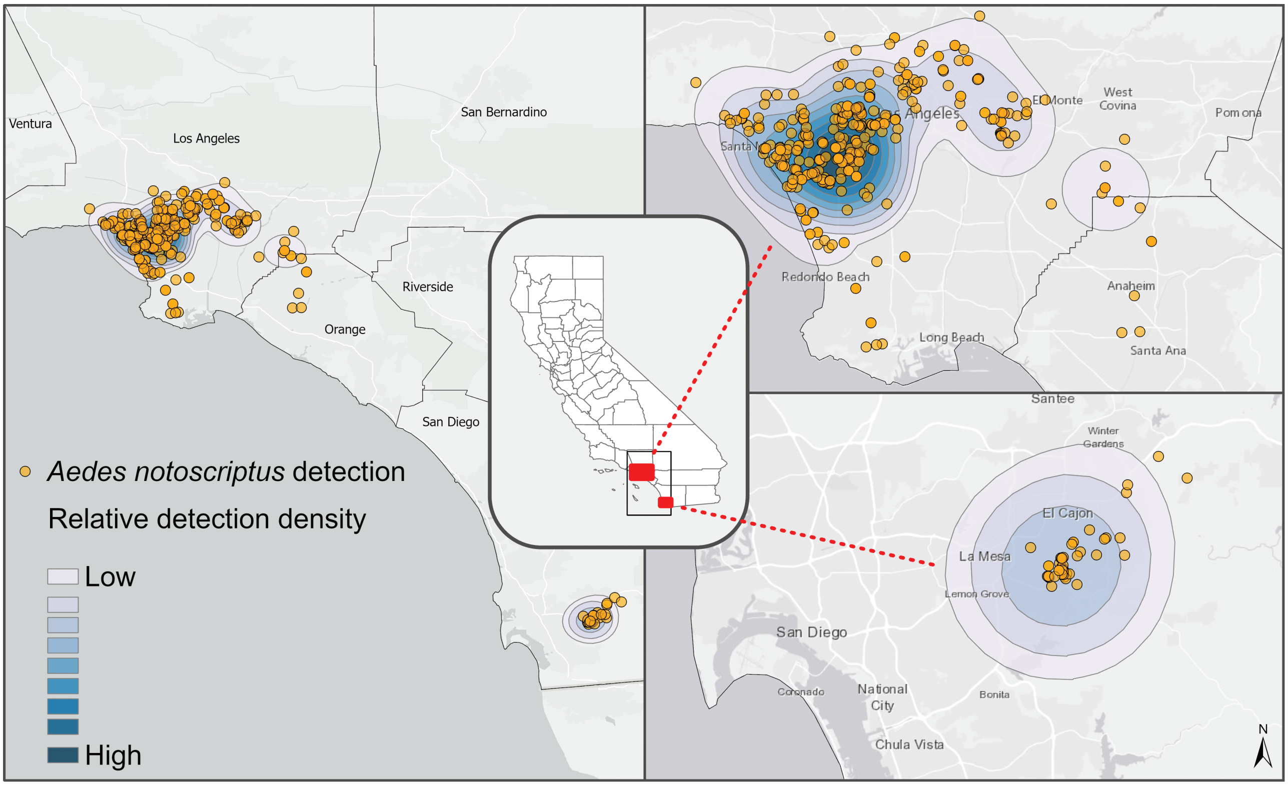

Fig. 1. Location and relative density of all southern California *Aedes notoscriptus* detections ($n = 744$), 2014–2019.

Table 1. First detections of *Aedes notoscriptus* (*n* = 44) by local vector control agencies in southern California cities and census-designated places (CDP), June 2014 to December 2019

Date	City/ CDP*	County	Agency	Method	Life Stages
5 June 2014	Monterey Park	Los Angeles	San Gabriel Valley MVCD	CO_2-baited trap	1F
14 Aug. 2014	Montebello	Los Angeles	Greater LACVCD	Property inspection	Larvae
6 Oct. 2015	Santa Monica	Los Angeles	Los Angeles County West VVBDCD	RSR	Larvae
27 Oct. 2015	Los Angeles	Los Angeles	Los Angeles County West VVBDCD	RSR	Larvae
28 Oct. 2015	View Park-Windsor Hills*	Los Angeles	Los Angeles County West VVBDCD	RSR	1F
2 Dec. 2015	Ladera Heights*	Los Angeles	Los Angeles County West VVBDCD	CO_2-baited trap	1F
26 May 2016	Alhambra	Los Angeles	San Gabriel Valley MVCD	Property inspection	1M, larvae
2 Aug. 2016	Inglewood	Los Angeles	Los Angeles County West VVBDCD	Gravid trap	1F
2 Aug. 2016	South San Gabriel*	Los Angeles	San Gabriel Valley MVCD	RSR	Larvae
5 Aug. 2016	Rosemead	Los Angeles	San Gabriel Valley MVCD	RSR	Larvae
3 Nov. 2016	Marina del Rey*	Los Angeles	Los Angeles County West VVBDCD	CO_2-baited trap	1F
8 Nov. 2016	Topanga*	Los Angeles	Los Angeles County West VVBDCD	BG-GAT	1F
15 Nov. 2016	El Segundo	Los Angeles	Los Angeles County West VVBDCD	BG-GAT	1F
17 Jan. 2017	Culver City	Los Angeles	Los Angeles County West VVBDCD	RSR	Larvae
4 May 2017	La Habra Heights	Los Angeles	Greater LACVCD	CO_2-baited trap	1F
12 July 2017	South Whittier*	Los Angeles	Greater LACVCD	Gravid trap	1F
12 July 2017	Rosemead	Los Angeles	Greater LACVCD	CO_2-baited trap	1F
9 Aug. 2017	Hacienda Heights*	Los Angeles	Greater LACVCD	Gravid trap	2F
27 Sept. 2017	Anaheim	Orange	Orange County MVCD	Property inspection	Larvae
14 Nov. 2017	West Hollywood	Los Angeles	Los Angeles County West VVBDCD	Property inspection	Larvae
14 Nov. 2017	Torrance	Los Angeles	Los Angeles County West VVBDCD	CO_2-baited trap	2F
25 April 2018	La Habra	Orange	Orange County MVCD	Gravid trap	1F
23 May 2018	Casa del Oro-Mount Helix*	San Diego	San Diego County VCP	CO_2-baited trap with BG Lure	3F
12 June 2018	Manhattan Beach	Los Angeles	Los Angeles County West VVBDCD	RSR	1F
16 July 2018	Garden Grove	Orange	Orange County MVCD	Property inspection	Larvae
14 Aug. 2018	Westmont*	Los Angeles	Los Angeles County West VVBDCD	RSR	larvae
7 Sept. 2018	Brea	Orange	Orange County MVCD	BGS	1F
22 Sept. 2018	El Cajon	San Diego	San Diego County VCP	BGS	1F
16 Oct. 2018	Lawndale	Los Angeles	Los Angeles County West VVBDCD	Gravid trap	1F
27 Oct. 2018	Lakeside*	San Diego	San Diego County VCP	Gravid trap	1F
20 June 2019	Glendale	Los Angeles	Greater LACVCD	CO_2-baited trap	1F
27 June 2019	City of Industry	Los Angeles	San Gabriel Valley MVCD	Gravid trap	1F
3 July 2019	Lomita	Los Angeles	Los Angeles County West VVBDCD	CO_2-baited trap	1F
16 July 2019	Fullerton	Orange	Orange County MVCD	BGS	15F
6 Aug. 2019	Pasadena	Los Angeles	San Gabriel Valley MVCD	Gravid trap	1F
8 Aug. 2019	Rancho San Diego*	San Diego	San Diego County VCP	CO_2-baited trap with BG Lure	1F
14 Aug. 2019	Rancho Palos Verdes	Los Angeles	Los Angeles County West VVBDCD	Property inspection	Larvae
22 Aug. 2019	San Gabriel	Los Angeles	San Gabriel Valley MVCD	Gravid trap	2F
25 Sept. 2019	Hawthorne	Los Angeles	Los Angeles County West VVBDCD	RSR	Larvae
4 Oct. 2019	Carson	Los Angeles	Greater LACVCD	CO_2-baited trap	2F
9 Oct. 2019	Redondo Beach	Los Angeles	Los Angeles County West VVBDCD	RSR	Larvae
14 Oct. 2019	East Los Angeles*	Los Angeles	Greater LACVCD	Gravid trap	1M
29 Oct. 2019	El Monte	Los Angeles	San Gabriel Valley MVCD	Gravid trap	1F
4 Dec. 2019	Crest*	San Diego	San Diego County VCP	CO_2-baited trap	2F

*Census-designated place.

RSR, Resident Service Request

methods and priorities. In total, 1,261 females and 30 males were collected in adult traps or during property inspections, eggs were collected in two ovitraps, and larvae were collected from 236 properties. Of 555 adult traps that collected *Ae. notoscriptus*, CO_2-baited (including those augmented with BG Lure) collected the greatest number (257/555), followed by gravid (168/555), BGS (47/555), CDC-AGO (44/555), and BG-GAT (39/555). Of note, the number of *Aedes*-specific traps (i.e., BGS, CDC-AGO, and BG-GAT) deployed by any one agency was far less than CO_2-baited and gravid traps. The least used traps were the CDC-AGO and BG-GAT (only used by one agency). The first detections of *Ae. notoscriptus* within the 44 cities were a result of a variety of surveillance elements; 10 tied to resident service requests, 11 from gravid traps, 10 from CO_2 -baited traps, 6 during residential property inspections, 3 from BGS traps, 2 from CO_2 -baited traps augmented with BG-Lure, and 2 from BG-GAT traps (Table 1). In contrast to first detections of *Ae. aegypti* and *Ae. albopictus* in California that were most often associated with resident service requests (Metzger et al. 2017), the initial discoveries of *Ae. notoscriptus* resulted from a broad array of different methods. Overall, larval and adult *Ae. notoscriptus* were collected during every month of the year with the smallest number in February and the largest in August (Fig. 2).

Discussion

The discovery and spread of *Ae. notoscriptus* in southern California was nearly simultaneous with the documented invasions of *Ae. albopictus* and *Ae. aegypti* (Metzger et al. 2017) and created an unprecedented burden on local vector control agencies seeking to protect the public from mosquito-borne pathogens and biting nuisance. Whereas *Ae. notoscriptus* was not anticipated to play a significant role in arbovirus transmission in California, the presence of *Ae. albopictus* and *Ae. aegypti* resulted in immediate concerns with their potential to initiate local transmission cycles of DENV, CHIKV (Porse et al. 2015), and Zika viruses (Porse et al. 2018) if fed on infected returned travelers. In addition, the severe biting nuisance of this trio of mosquitoes prompted a significant increase in resident service requests for local vector control agencies, particularly as these mosquitoes became more abundant in established areas and rapidly spread to new locations. *Ae. notoscriptus* was recognized to pose a lower public health threat in California relative to the invasive vectors *Ae. aegypti* and *Ae. albopictus*; however, there were still public and veterinary health concerns associated with this species.

Public and Veterinary Health Concerns

Ae. notoscriptus has a relatively low profile in the literature despite being an urban biting nuisance because its role as a potential vector

Table 2. *Aedes notoscriptus* eggs, larvae, and adults collected by local vector control agencies in traps and during property inspections, June 2014 to December 2019[a]

Agency	Adult traps[b]						Ovitraps[c]	Property inspections[d]	
	BG-sentinel	BG-GAT	CDC-AGO	CO_2-baited	CO_2-baited + BG lure	Gravid		# Adults	Larval collection
San Gabriel Valley MVCD	1M/1	--	--	4F/3	--	24F, 2M/17	28 eggs/2	4F, 1M/4	6
Greater LACVCD	70F, 4M/21	--	2F/ 2	75F/34	--	43F, 1M/32	--	2F/2	29
Los Angeles County West VVBDCD	10F/2	71F/39	97F/42	412F/191	--	261F/111	--	7F/7	184
Orange County MVCD	48F/7	--	--	--	--	2F/2	--	--	3
San Diego County VCP	24F, 2M/16	--	--	8F/2	65F, 1M/27	8F/6	--	24F, 18M/4	14

Number of adults collected by six different trap types, number of eggs collected in ovitraps, adults collected by hand during property inspections, and number of property inspections with larval collections.

[a] Local vector control agencies adjusted their surveillance programs as necessary, based on data, budgets, and preferences, resulting in notable interagency differences in trapping and property inspections over time. See text.

[b] Number of females (F) and males (M) collected/ total number of traps; only traps that collected *Ae. notoscriptus* are shown.

[c] Number of eggs collected/ total number of ovitraps.

[d] Number of females (F) and males (M) collected/ total number of property inspections; Number of property inspections where larvae were collected. Only property inspections where *Ae. notoscriptus* were collected are shown.

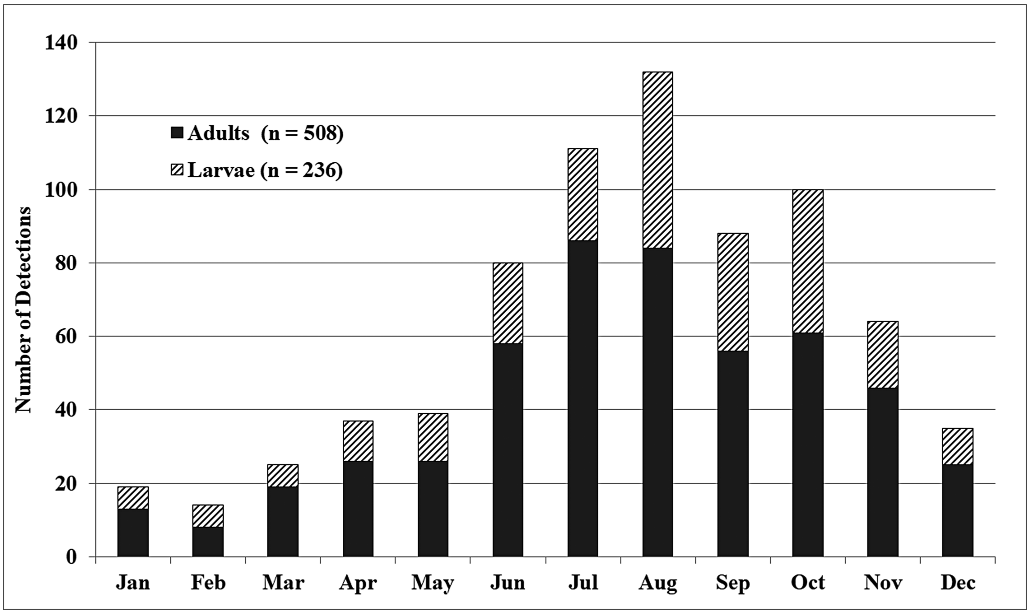

Fig. 2. All detections of *Aedes notoscriptus* ($n = 744$) in southern California cities and census-designated places, by month, June 2014 to December 2019.

of arboviruses and parasites was only recognized fairly recently. Public health interest in this species was triggered following multiple isolations of RRV from wild-caught females during the 1994 epidemic around Brisbane, Australia (Ritchie et al. 1997). Ross River virus circulates in an enzootic cycle in all mainland Australian states. It is the most common mosquito-borne pathogen in Australia with approximately 5,000 human infections reported per year (Russell 2002, Australian Government Department of Health 2021). Subsequent laboratory studies challenged *Ae. notoscriptus* originating in Brisbane and Sydney with RRV and confirmed that both populations were susceptible to infection and capable of transmission, while acknowledging the regional differences in vector competence among different strains of both virus and vector (Doggett and Russell 1997, Watson and Kay 1998). In fact, mosquitoes collected at Maroochy Shire, about 100 km north of Brisbane, were laboratory-susceptible to infection but unable to transmit virus (Ryan et al. 2000) as was a population from New Zealand (Maguire 1994). A retrospective analysis of 15 yr (1991–2006) of data collected in Darwin, Northern Territory found *Ae. notoscriptus* had a strong association with human RRV infections (Jacups et al. 2008).

The potential for arboviruses to migrate globally, whether via infected mosquitoes, reservoirs, or humans is of great concern because arboviruses can cause severe morbidity and mortality in humans, livestock, and wildlife, particularly when introduced into naïve environments. The fear of exotic arbovirus importation into New Zealand compelled Kramer et al. (2011) to test the vector competency of endemic and introduced mosquitoes for numerous arboviruses (i.e., BFV, CHIKV, DENV-2, JEV, MVEV, and WNV). A cooler incubation temperature more appropriate for New Zealand was used in these experiments, which may have been why vector competence of *Ae. notoscriptus* was only reported for BFV. Results of laboratory studies on vector capacity may not always predict field transmission outcomes in natural environments, nor does detection of virus isolates in field-collected mosquitoes conclusively confirm vector status. *Ae. notoscriptus* has been shown to have the capacity to transmit a multitude of arboviruses under laboratory conditions and given its close association with humans and relatively unrestricted feeding on mammals and birds, this mosquito could prove to be an effective vector under conducive circumstances. The studies on vector capacity suggest that the colonization of southern California by *Ae. notoscriptus* could facilitate the spread of existing and imported exotic arboviruses through human–mosquito–human cycles or those cycles that require a mammalian or avian reservoir. Evidence of field infection would be essential to implicate these mosquitoes as arbovirus vectors in California, and careful data analysis during any future arbovirus outbreaks in areas where this species is present would be necessary to elucidate the role of *Ae. notoscriptus* in virus transmission dynamics.

From a veterinary health perspective, Australian studies have incriminated *Ae. notoscriptus* as the most important domestic vector of dog heartworm because of its vector efficiency, urban population density (Bemrick and Moorhouse 1968, Russell 1985, 1990; Russell and Geary 1992, 1996), and extensive feeding on dogs (Lee et al. 1954, Bemrick and Moorhouse 1968, Lee et al. 1982, Kay et al. 2007). Southern California has a number of urban mosquito species with the capacity to acquire and transmit dog heartworm including introduced *Ae. albopictus*, *Ae. aegypti*, and *Culex quinquefasciatus* (Say), and native *Ae. sierrensis* (Ludlow) and *Culiseta incidens* (Thomson) (Theis et al. 2000, Ledesma and Harrington 2011). *Ae. notoscriptus* has demonstrated that it is a highly adaptable invader; it has been collected from ultra-urban downtown Los Angeles, within suburbs from the Pacific coast to over 35 km inland, from undeveloped urban peripheries, and from more rural foothill communities. Dog heartworm has had historically low rates of transmission in southern California (Companion Animal Parasite Council, Parasite Prevalence Maps 2021), but if this mosquito continues to increase in abundance and expand its range it could cause an upsurge in infections. Studies are needed to determine whether an increased risk of *D. immitis* infection exists in areas with established populations of *Ae. notoscriptus*.

Known Invasion Biology, Potential Point-of-Entry, and Origins

The establishment of *Ae. notoscriptus* in southern California is the first documented introduction of this species outside of the southwestern Pacific region. The potential for this species to invade and colonize new areas is based on a limited number of field surveys and observations, the most well-known from New Zealand. *Ae. notoscriptus* was first reported from the port city of Auckland in 1918 (Miller 1920). Live adults were collected on two different vessels arriving at the port of Auckland from Sydney during a survey in 1929, thereby documenting that conditions existed for repeated introduction. This evidence coupled with the only known detections of *Ae. notoscriptus* in and around the port cities of Auckland, Nelson, and Whangarei, was enough to declare it a recently introduced species (Graham 1939). This exotic species hypothesis was supported years later by genetic work conducted by Endersby et al. (2013) that demonstrated mosquitoes collected from both the northern and southern regions of New Zealand's North Island were indistinguishable from some specimens examined from Victoria and New South Wales, Australia. Subsequent mosquito surveys documented a gradual range expansion throughout the North Island and into isolated areas of the South Island as far south as Christchurch (Belkin 1968, Laird 1995, Kramer et al. 2011). Within mainland Australia, intracontinental movement of humans and goods by road and rail are suspected to have facilitated the translocation of this species from its native northern and eastern forests across vast dry land areas to establish in towns and cities on the west coast such as Perth, and in towns of the arid and semiarid inland regional areas such as Mount Isa, Tennant Creek, and Alice Springs (Foley et al. 2004, Whelan 2010, Endersby et al. 2013). This dispersal to new areas is most likely to have occurred by means of ground or sea transportation, but a series of meticulous studies demonstrated conclusively that adult *Ae. notoscriptus* were also capable of surviving domestic and international air travel (Laird 1948).

Local vector control agencies in California sought to determine the origin and modes of introduction of early discoveries. An intensive adult surveillance effort was conducted around the Los Angeles International Airport in late 2015. The airport was viewed as a logical port-of-entry from Australia and other countries within the southwestern Pacific region and was located within 8 km of five of the six collection locations in western Los Angeles County that year. Trapping was unsuccessful in collecting any specimens. All other efforts to elucidate origin were conducted through interviews with affected property owners. One of the first residential detections in the city of Montebello in 2014 led to a potential travel connection between California and New Zealand; however, the extensive and widespread collections of *Ae. notoscriptus* the following year did not support this location as a probable point-of-origin. Four years later, compelling evidence of in-state, human-mediated introduction was documented at a residential home within the neighborhood where the first discovery was made in San Diego County. The property belonged to a bromeliad collector, with more than 200 bromeliads on the property, who previously had traded with other enthusiasts in Los Angeles and Orange counties. Ultimately, no international pathway for introduction was identified through surveillance or communications with property owners.

The explosive growth of global trade and travel undoubtedly has facilitated the movement of invasive mosquitoes, allowed for repeated introductions into previously inaccessible habitats, and therefore provided opportunities for establishment (Tatem et al. 2006). California has experienced this first-hand with the ongoing invasions of *Ae. aegypti* and *Ae. albopictus*, which have flourished by utilizing the diverse habitats created within urban biomes (Metzger et al. 2017). The wide range of environments that *Ae. notoscriptus* occupies within the southwestern Pacific region indicates that this species is highly adaptable to habitat and climate, even more so when given an urban buffer, and with no apparent barriers that might impede the colonization of urban southern California. The widespread and increasing number of detections over a relatively short period of time, particularly between 2016 and 2019, suggest a recent invasion with multiple points of introduction, or a rapid succession of human-mediated dispersals. This mosquito has a relatively short adult flight range (Watson et al. 2000a, Trewin et al. 2020), and even with its documented year-round development, occupation of such a large geographical area from a single point source in only 5.5 yr was unlikely to have occurred without human assistance. Cars and light trucks are the primary mode of transportation in southern California and probably contributed to the inadvertent transport of eggs, larvae, and adults (Eritja et al. 2017). Regrettably, the origin of *Ae. notoscriptus* in California remains purely speculative. Genetic studies such as those conducted by Foley et al. (2004) and Endersby et al. (2013) are needed to elucidate a source population(s) within the southwestern Pacific region. To complicate matters, Endersby et al. (2013) provided compelling genetic evidence that *Ae. notoscriptus* may comprise at least three species in Australia, but there have been no efforts to formally describe them. If true, this might explain some of the differences in behavior, development, and vector capacity of different populations noted in past studies (discussed elsewhere in this review). Establishing a genetic link between the native range and California would clarify if invaders are of temperate or tropical origin, thus providing some insight on any potential preexisting adaptations that might serve to gauge the potential spread within California, and help to identify possible transportation pathways from the source area that could be mitigated to halt additional exportation of this emerging invasive species.

Biology and Ecology in the Native Range: Implications to Colonization of California

Like other container inhabiting *Aedes* mosquitoes, female *Ae. notoscriptus* glue individual desiccation-resistant eggs at or above the water line that are stimulated to hatch when inundated. Oviposition site preferences are water-holding containers in shaded places in or near trees and shrub cover, and in forested areas especially 4–7 m above ground level (Foot 1970). The eggs have structural characteristics on the lower surface that increase the contact area to a substrate and provide excellent adherence with cement, effectively protecting them from the flushing action of rain or removal by predators (Linley et al. 1991). Laboratory studies found eggs able to withstand desiccation for extended periods of time when exposed to several different combinations of temperature and relative humidity, with approximately 10% viability remaining after one year under all conditions (Faull et al. 2016). The authors speculated that these findings might partially explain the ability of this mosquito to inhabit such a wide range of environments within the southwestern Pacific region. Such hardy eggs improve the probability of survival during periods of drought and increase the likelihood of further introductions through unintentional transport by humans. Few eggs of *Ae. notoscriptus* have been collected in southern California, perhaps because the use of ovitraps by vector control agencies was limited after the first several years following the discoveries of *Ae. aegypti* and *Ae. albopictus*. Ovitraps were gradually replaced by adult traps as more efficient surveillance tools. Egg hardiness of *Ae. notoscriptus* is undoubtedly among the key factors driving the persistence and spread of this species in California.

In the absence of egg collection data, the presence of larvae and pupae in aquatic habitats provided evidence of where *Ae. notoscriptus* preferred to lay eggs. Nearly a third of all southern California detections were larval collections, the majority on residential private property. Larval surveys in urban areas of New South Wales, Western Australia, and Queensland, Australia, corroborate these observations. Productive habitats for larvae included a variety of small to medium backyard containers, garden bromeliads and broken bamboo stems, roof gutters, and cemetery vases (Hamlyn-Harris 1928, Fanning et al. 1997, Montgomery and Ritchie 2002, Kay et al. 2008, Lamichhane et al. 2017, Webb et al. 2021). In Brisbane (Queensland) cemeteries, Hamlyn-Harris (1928) noted a preference for wide-mouthed vessels with easy access to water and observed that vessels that protected larvae from direct sunlight were chosen over clear glass, except when glass containers had a considerable amount of decaying vegetation in the water that provided shade. Larvae were also abundant in subterranean habitats (i.e., wells, service manholes, and pits [catch basins]) of some north Queensland coastal towns, and in some surveyed areas produced a significant proportion of adults relative to surface containers. Oddly, *Ae. notoscriptus* was mostly absent from subterranean habitats of semiarid inland towns that provided critical refuge and larval habitat to other mosquito species during hot and dry periods (Kay et al. 2000, 2002). In New Zealand, larvae have been found in various types of large and small artificial containers, pools in drying stream beds, "gully traps" (i.e., stormwater catch basins), used tire casings, leaf axils of *Astelia* spp., banana, bromeliad, and nikau palms, rock holes, and tree holes, including those in mangroves just above high tide marks (Graham 1929, Belkin 1968, Laird 1990, 1995). Alkaline water is preferentially selected by females for oviposition and larvae can tolerate a fair degree of salinity (Hamlyn-Harris 1928, Belkin 1968, Foot 1970).

Larval collections of *Ae. notoscriptus* in southern California were consistent with the reported broad use of small water-holding sources within this species' native range. Larvae were collected from a wide variety of water-holding backyard containers, bird baths, children's wading pools, nonfunctioning fountains, stagnant ponds, the surface of impermeable tarps, trash cans, neglected swimming pools, and surface pools of irrigation runoff. Bromeliad leaf axils also were found to be productive sources of larvae as were subsurface yard drains. Despite their documented use of subterranean habitats in Australia and New Zealand (Laird 1990, 1995; Kay et al. 2000, Warchot et al. 2020), no evidence was collected to indicate *Ae. notoscriptus* used storm drains, catch basins, or utilities vaults in southern California. However, larval collections were made from roadside drainage channels in an undeveloped coastal area of Los Angeles County (Playa del Rey) and a suburban periphery of San Diego County (La Mesa), which suggests that this species may also be present or initiating spread outside the urban matrix.

In cool temperate climates, such as found in parts of New Zealand, *Ae. notoscriptus* passes the winter in both adult and larval stages (Graham 1939), while development is continuous throughout the year in warmer environments. Laboratory studies found ideal water temperatures for larval development and survival were between 18 and 29°C (Foot 1970, Russell 1986, Williams and Rau 2011), whereas a constant temperature of 35°C was fatal (Williams and Rau 2011). Larvae reared under summer (20.5–28.9°C) and winter (10.1–21.2°C) temperatures typical of Brisbane, Australia, indicated excellent survivorship and a potential for rapid generation turnover with average development times from egg hatch to adult emergence of 11 and 20 d, respectively. In addition, emerging adults were long-lived; males survived up to 45 d and females up to 49 d (Watson et al. 2000b). Field studies in Brisbane reported daytime water temperatures of containers with developing larvae ranged from 9 to 37°C, with the majority between 14 and 29°C. Adult collections in the study area indicated that development was completed even when average minimum ambient temperatures fell below 10°C (Kay et al. 2008). Water quality was found to affect larval development, with more rapid growth and increased adult size and fitness when in rainwater compared with aged tap water (Williams and Rau 2011).

Larvae are tolerant of crowding and can become very abundant in some containers (Derraik 2004, Kay et al. 2008). A survey of aquatic invertebrates occupying water in bamboo stumps in a mountainous area of West Timor, Indonesia found *Ae. notoscriptus* was the most common and abundant species (Sunahara and Mogi 2004), and a field study in northeast New South Wales, Australia, documented larval densities sometimes exceeding 200 in one liter of water (Jenkins et al. 1992). The warm, temperate climate of Los Angeles, Orange, and San Diego counties is seemingly ideal for *Ae. notoscriptus* as temperatures rarely exceed the high and low tolerances of larvae, especially considering their documented preference for shade. The multiple collections of larvae during all months of the year support this assumption. Urban habitats provide unique opportunities for invasive *Aedes* even in California's harsh deserts (Metzger et al. 2017), and thus this species conceivably could spread north into the Central Valley and eastward into the deserts.

Of key interest for southern California is how larval *Ae. notoscriptus* may compete for or share habitat with recently introduced *Ae. aegypti* and *Ae. albopictus*. *Ae. aegypti* has been in Australia possibly since the early 1800s and was once widespread nationally but for the past 50 yr or so it has been primarily confined to Queensland, despite numerous interceptions at various sea and airports around Australia (Beebe et al. 2009). While *Ae. aegypti* distribution was receding, that of *Ae. notoscriptus* was increasing, and laboratory experiments examining intra- and interspecific effects of larval crowding and competition for food were carried out to evaluate if *Ae. notoscriptus* may have out-competed *Ae. aegypti*. Results, however, indicated little competitive advantage of one species over the other, except when reared at cooler temperatures which favored *Ae. notoscriptus* survivorship (Russell 1986). A field-based study within residential suburbs of Queensland that searched for evidence of competitive displacement supported the laboratory studies and concluded that these two species had reached an equilibrium in the environment, often cohabitating within the same containers (Tun-Lin et al. 1999). Australia has also had repeated introductions of *Ae. albopictus*, which is now established in the Torres Strait Islands (van den Hurk et al. 2016) where it cohabitates with *Ae. notoscriptus*. Laboratory-based larval competition studies were carried out to determine whether cohabitation with temperate strains of *Ae. notoscriptus* from mainland Australia might prevent establishment of *Ae. albopictus* on the mainland. Findings indicated that larval *Ae. albopictus* had a slight advantage with consistently higher survivorship, especially at warmer temperatures, and thus presence of this species would likely not deter *Ae. notoscriptus* establishment (Nicholson et al. 2015). In southern California, all three *Aedes* species have been documented within the jurisdictional boundaries of several municipalities. Larvae of *Ae. notoscriptus* were collected from container habitats shared with *Ae. aegypti* or *Ae. albopictus* where they co-occur on several occasions. In time, evidence may emerge to indicate if one species has a competitive advantage over the other in southern California.

As documented with other container-inhabiting mosquitoes, adult *Ae. notoscriptus* dispersal distance is relatively short. Two mark–release–recapture studies examined the survivorship and dispersal ability of *Ae. notoscriptus* in urban environments of Queensland, Australia. Laboratory-reared females traveled an average of 105–180 m and a maximum of 238 m (Watson et al. 2000b). In contrast, adults emerging from rainwater storage containers (and marked) within urban environments indicated a highly dispersive species relative to other container-inhabiting species such as *Ae. aegypti*. Average daily distances traveled by females over a 13-day period was 78–91 m (Trewin et al. 2020). In both studies, dispersal appeared unrestricted by the presence of potential natural (e.g., trees, bushes) or artificial (e.g., roads, fences) barriers. Although mark–release–recapture studies have limitations because results are dependent on trap recaptures, they nonetheless provide valuable information on the potential movement of these mosquitoes. Collection data in southern California has documented a rapid geographical expansion over 5.5 yr, a portion of which is likely the result of their natural dispersal ability. In sum, and as exemplified in southern California, the known biology and ecology of *Ae. notoscriptus* defines a mosquito species with excellent invasive potential.

Feeding Preferences, Biting Nuisance, and Potential Control Measures

Studies on the bloodmeals of *Ae. notoscriptus* have revealed a preference for small marsupials, especially brush-tailed possums, *Trichosurus vulpecula* (Kerr) (Diprotodontia: Phalangeridae), that occupy both sylvatic and urban habitats in New Zealand and Australia (Bullians and Cowley 2001, Kay et al. 2007). However, they opportunistically feed on a wide range of ground and canopy-dwelling mammals and birds, humans, companion animals, and livestock (Graham 1929, Kay et al. 2007). Females are active near ground level and in the tree canopy where they forage for bloodmeals and search for oviposition sites (Foot 1970, Derraik et al. 2003). Some urbanized animals, such as brush-tailed possums and flying foxes, may serve as arbovirus reservoirs within domestic environments, thus creating a higher risk of virus transmission among animals and to humans residing in these areas. The peridomestic ecology and short flight range of *Ae. notoscriptus* raises the potential for this species to become a significant urban vector (Kay et al. 2007).

Ae. notoscriptus is typically referred to as a "day-biting" species, but studies have revealed a bimodal pattern of biting activity with distinct peaks at dusk and dawn. However, females are opportunistic and when hosts are present, they will bite both at night and during the day, preferably in the shade (Foot 1970). Like *Ae. aegypti* and *Ae. albopictus*, female *Ae. notoscriptus* prefer to attack humans low to the ground and settle on the legs rather than other parts of the body. They are attracted to dark surfaces and are persistent in their objective to feed (Graham 1929). Although early reports from Auckland, New Zealand alleged *Ae. notoscriptus* was a frequent intruder into houses (Graham 1939), no evidence exists in the literature to suggest that indoor activity is more than a transient occurrence, preferring instead to rest and feed outdoors. Resident service requests in southern California for day-biting mosquitoes, frequently caused by indoor and outdoor biting *Ae. aegypti*, did not detect *Ae. notoscriptus* indoors. Yet discussions with residents during vector control agency responses to mosquito complaints clearly indicated that *Ae. notoscriptus* were biting residents extensively in their backyards. This was most evident in western Los Angeles County where other invasive *Aedes* had not yet colonized. Controlling this species in urban southern California to alleviate biting pressure will require an approach similar to that employed against *Ae. aegypti* and *Ae. albopictus*, which at this time relies primarily on public action to remove potential larval habitats from their properties (Metzger et al 2017). Studies in Australia have documented susceptibility of *Ae. notoscriptus* to bacterial larvicides, residual pyrethroids (Russell et al. 2003, Pettit et al. 2010), and monomolecular surface films (Webb and Russell 2012), but area-wide application of any product against container-inhabiting species in California remains a complex problem with variable efficacy (Metzger et al. 2017).

Observations from Trapping and Property Inspections

The vast majority of *Ae. notoscriptus* collections in southern California resulted from mosquito surveillance activities associated with other species. Adult mosquitoes were captured from the spectrum of traps placed in the environment, including from traps that targeted *Culex* mosquitoes. Vector control agencies in Los Angeles County attempted to determine trap preferences by placing two or three different trap types at sites with a history of repeated captures of *Ae. notoscriptus*, but no clear trap preference was revealed; rather, some adults were captured by all available traps. Only about 2% of all adults captured were male. In general, studies conducted in the native range of this species report few or no males collected in traps. It was suggested that male mating behavior may not place them near host-seeking or oviposition-site-seeking females (Trewin et al. 2020). Most Australian studies referenced herein successfully utilized CO_2-baited traps (with or without the addition of octenol) to collect adult specimens. Octenol did not improve CO_2-baited trap performance for *Ae. notoscriptus*, but was found to broaden the attractiveness of traps towards other mosquito species (Ritchie and Kline 1995). At least one Australian study employed BGS and BG-GAT traps in order to sample both *Ae. aegypti* and *Ae. notoscriptus* (Trewin et al. 2020). With nearly half of all captured adults collected by CO_2-baited traps in southern California, there may not be a need to deploy *Aedes* specific traps like BGS, BG-GAT, and CDC-AGO to collect *Ae. notoscriptus*. San Diego County used CO_2-baited traps augmented with BG-Lure when targeting invasive *Aedes*, but it is uncertain if this increased attractiveness to *Ae. notoscriptus* over CO_2 alone. What is encouraging from published studies and from local collection data is that southern California vector control agencies should be able to conduct surveillance for this species using a variety of traps.

With less than 1,300 adult *Ae. notoscriptus* collected over a 5.5-year period, it is difficult to gauge the extent of the *Ae. notoscriptus* problem in southern California, despite the very large geographical area from which specimens were collected. More than half of the positive traps collected only one female, with only a few "hot spots" producing 20–30 adults overnight. The generally low trap counts throughout the range could be due to a population that is suppressed by yet unknown environmental factors. During the time period that these collections were made, most captures originated in western Los Angeles where *Ae. notoscriptus* existed in the absence of *Ae. aegypti* and *Ae. albopictus*, thus ruling out competition from these species. The wide range of habitats from which adults and larvae were collected, from ultra-urban downtown Los Angeles, to the Pacific Ocean, to mountain foothills does not indicate geographical limitations. A more likely explanation may be that populations are still becoming established. Trap captures of *Ae. aegypti* in southern California initially were widespread and very low in number, rising steadily over several years, indicating that some amount of time was needed for local populations to increase to a size where the probability of capturing adults increased. *Ae. notoscriptus* may be on a similar trajectory, but perhaps with a slower establishment time.

Conclusion

The invasion and establishment of *Ae. notoscriptus* in southern California underscores the potential of a new exotic species to spread globally. Evidence collected since 2014 has documented that this species is becoming well established in the urban environment and may be expanding beyond the urban matrix. *Ae. notoscriptus* appears to be competitive with *Ae. aegypti* and *Ae. albopictus* in southern California, with some potential advantages. For instance, *Ae. notoscriptus* has greater dispersal capacity, year-round larval development, broad use of larval habitat from subsurface to canopy, willing use of natural water-filled containers, and use of both sylvatic and urban habitats. In addition, *Ae. notoscriptus* possess many of the same traits and adaptations which have led to the global success of *Ae. aegypti* and *Ae. albopictus*; desiccation-resistant, long-lived eggs, tolerance to different climates especially when buffered by urban environments, and an intimate association with humans and their environment. It is possible that *Ae. notoscriptus* will carve out its own niche in southern California where it will become the dominant exotic *Aedes* mosquito. How these three species of invasive *Aedes* eventually settle into California's landscape, and whether they share habitat or become locally dominant, remains to be seen.

Ae. notoscriptus does not currently pose a known public health risk in southern California, but has the potential to transmit arboviruses under the right conditions given its peridomestic habits and broad host range. Its capacity to vector dog heartworm is a more immediate veterinary concern that will need to be explored. If the population continues to expand and increase in abundance, these issues will rise in importance. Control measures that specifically target this species have not been evaluated, but it is likely that the same physical and chemical controls used against *Ae. aegypti* and *Ae. albopictus* could also be used to reduce the abundance of *Ae. notoscriptus*. Establishing and maintaining laboratory colonies of *Ae. notoscriptus* (Watson et al. 2000b) may become necessary in the future to test for local insecticide resistance and vector capacity. No formal studies on the biology and ecology of *Ae. notoscriptus* have been conducted in California; therefore, anticipated life history and behavior is based primarily on Australian and New Zealand studies and from local observations by scientists and technicians working in infested areas. With year-round reproduction, seasonal control efforts may need to be replaced with ongoing routine treatments if population reduction is needed.

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