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Spatial Variation in Host Feeding Patterns of *Culex tarsalis* and the *Culex pipiens* complex (Diptera: Culicidae) in California

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Abstract

West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) is now endemic in California across a variety of ecological regions that support a wide diversity of potential avian and mammalian host species. Because different avian hosts have varying competence for WNV, determining the blood-feeding patterns of *Culex* (Diptera: Culicidae) vectors is a key component in understanding the maintenance and amplification of the virus as well as tangential transmission to humans and horses. We investigated the blood-feeding patterns of *Culex tarsalis* Coquillett and members of the *Culex pipiens* L. complex from southern to northern California. Nearly 100 different host species were identified from 1,487 bloodmeals, by using the mitochondrial gene cytochrome *c* oxidase I (*COI*). *Cx. tarsalis* fed on a higher diversity of hosts and more frequently on nonhuman mammals than did the *Cx. pipiens* complex. Several WNV-competent host species, including house finch and house sparrow, were common bloodmeal sources for both vector species across several biomes and could account for WNV maintenance and amplification in these areas. Highly competent American crow, western scrub-jay and yellow-billed magpie also were fed upon often when available and are likely important as amplifying hosts for WNV in some areas. Neither species fed frequently on humans (*Cx. pipiens* complex [0.4%], *Cx. tarsalis* [0.2%]), but with high abundance, both species could serve as both enzootic and bridge vectors for WNV.

Keywords

Culex tarsalis, *Culex pipiens*, bloodmeal; host identification; host diversity

Arthropod blood-feeding behavior is a crucial component in the transmission of vectorborne pathogens because it defines the frequency of host–vector contact. Understanding vector blood-feeding patterns can elucidate when and where particular vertebrate hosts are at risk of infection as well as what competent hosts contribute to maintenance and amplification transmission. Although important for all vectorborne diseases, blood-feeding patterns are especially of interest for a zoonosis such as West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV), where literally hundreds of vertebrate species have been found to be infected in the field (Kramer et al. 2008), but relatively few taxa develop sufficient viremias to infect blood-feeding mosquitoes (Komar et al. 2003, Kilpatrick et al. 2007). Because the

primary *Culex* vectors of WNV feed on a wide variety of avian and mammalian hosts with varying levels of WNV competence, insight into spatial variation in the blood-feeding patterns of these mosquitoes may be crucial in understanding why the transmission dynamics of WNV varies in different areas.

Culex tarsalis Coquillett and members of the *Culex pipiens* L. complex are the primary vectors of WNV (Goddard et al. 2002, Reisen et al. 2008a) and St. Louis encephalitis viruses (Reeves et al. 1990) in California. *Cx. tarsalis* also the primary vector of western equine encephalomyelitis virus (Reeves et al. 1990). *Cx. tarsalis* is historically a rural mosquito (Reisen and Reeves 1990), although recent housing foreclosures and associated neglected swimming pools have led to an increased abundance in urban areas (Reisen et al. 2008c, 2009). The *Cx. pipiens* complex, typically a more urban vector, is composed of at least two species in California. Traditionally, members of the complex found north of 39°N have been considered *Cx. pipiens* and those found south of 36°N have been called *Culex quinquefasciatus*, whereas members found between these latitudes have been identified as either species or as interspecific hybrids (Iltis 1966, Barr 1967, Tabachnick and Powell 1983). There is evidence, however, that hybridization of these two species is not limited to the area between these latitudes and may be extensive throughout California, especially in the Central Valley (Urbanelli et al. 1997, Cornel et al. 2003). With no reliable markers currently available for morphological or molecular identification, distinguishing these species and their hybrids can be difficult, if not impossible. For this study, members were simply referred to as the *Cx. pipiens* complex regardless of collection location.

The blood-feeding patterns of *Cx. tarsalis* and the *Cx. pipiens* complex have been assessed in several locations in the United States since the introduction of WNV and the advent of new molecular methods for host species identification (Kent 2009). These species seem to be generalist feeders, with host use patterns that have differed among species and collection locations (Kilpatrick et al. 2006a; Molaei et al. 2006, 2007; Savage et al. 2007; Hamer et al. 2009; Kent et al. 2009). In California, *Culex* feeding patterns were explored >40 yr ago in rural areas of the Central Valley by using serological methods (Tempelis and Reeves 1964; Tempelis et al. 1965, 1976; Tempelis and Washino 1967) and recently in more residential areas of southern California (Orange County and western portions of San Bernardino and Riverside counties) and rural Sacramento and Yolo counties by using molecular methods (Molaei et al. 2010, Montgomery et al. 2011, Thiemann et al. 2011). The current study explored the blood-feeding patterns of *Cx. tarsalis* and *Cx. pipiens* complex mosquitoes collected from five areas within four diverse ecological regions, all of which have supported WNV enzootic and epidemic transmission.

Materials and Methods

Study Areas

Blood-feeding patterns were determined for *Culex* mosquitoes collected in five areas throughout California, namely, the southeastern deserts of Coachella Valley, maritime coastal and highly urbanized Los Angeles, the southern San Joaquin Valley near Bakersfield, and the Davis and Yuba City areas of the Sacramento Valley (Fig. 1). These sampling sites span over 850 km from southern to northern California and offer a diversity of climates, ranges of urbanization, and a wide variety of potential host species.

Coachella Valley—Mosquitoes were collected within the Coachella Valley Mosquito and Vector Control District (MVCD) that is situated within the arid Colorado Desert, encompasses 6,200 km² of Riverside County, and has a human population of 332,000. Mosquitoes were collected at >50 sites throughout the valley, including wetlands near the Salton Sea, agricultural areas with citrus and date orchards, and in residential areas in the

upper valley near Palm Springs. Although WNV has been enzootically active each year in this area, few human cases have been reported (Reisen et al. 2008b).

Los Angeles—Blood-fed mosquitoes were collected within the Greater Los Angeles County Vector Control District (VCD) that encompasses a 3,400 km² area of Los Angeles County, with a human population of >6 million residents. Sampling was conducted at >100 sites distributed in both residential areas and embedded parklands. Two WNV outbreaks and intervening enzootic WNV transmission were documented previously (Kwan et al. 2010).

Kern County (Near Bakersfield)—Samples were collected in Kern County near Bakersfield within the boundaries of the Kern MVCD. The district covers 4,300 km² in the southern San Joaquin Valley and includes a population of >800,000 residents. Mosquitoes were collected from rural and urban sites, including residential, golf course, and agricultural and riparian habitats. West Nile virus transmission achieved epidemic levels during most years since its introduction, with the number of human cases peaking in 2007 (Reisen et al. 2009).

Yolo County (Within and Surrounding Davis)—Blood-fed *Culex* mosquitoes were collected in Yolo County from several residential neighborhoods and parks within the city of Davis (human population, 60,000). Additional samples were collected from the Yolo Bypass Wildlife Area, a 65-km² area consisting of rice (*Oryza sativa* L.) fields and managed wetlands. The wildlife area is home to >300 avian and mammalian species at various times of the year. A detailed investigation of *Cx. tarsalis* feeding patterns at a farmstead near Davis supporting a large nesting colony of herons and egrets was described separately (Thiemann et al. 2011). Enzootic WNV activity has been consistently detected in Davis, with a single outbreak documented during 2006 (Nielsen et al. 2008).

Sutter County (Near Yuba City)—Blood-fed mosquitoes were collected in Sutter County, around Yuba City, within the Sutter-Yuba MVCD that covers 1,800 km² and serves ≈ 160,000 people. This rural area of the northern Sacramento Valley is primarily agricultural habitat with extensive rice culture. WNV has been repeatedly active enzootically, but relatively few human cases have been reported (<http://westnile.ca.gov/reports.php>).

Mosquito Collection

Initially, walk-in red boxes (Meyer 1987) were deployed within urban, suburban, and rural locations in each of the study areas in an effort to collect fully blood-fed *Culex* mosquitoes. Red boxes were highly successful in Sutter County, where this method has been used for surveillance for >20 yr and productive collection sites have been located by trial and error. In contrast, few of the red boxes in other areas were sufficiently productive for our study. Although it was unclear why some red box locations were successful and others were not, it seemed that plentiful natural resting sites were detrimental to productive red box collections. In addition to red box collections, blood-fed mosquitoes were retained from traps used for WNV surveillance, including dry ice (CO₂)-baited CDC-style traps (Sudia and Chamberlain 1962, Newhouse et al. 1966) and up-draft gravid female traps baited with an alfalfa (*Medicago sativa* L.) infusion (Cummings 1992). Suction traps, operated without bait, were used in Los Angeles and the Coachella Valley. Because sampling methods may bias host selection (Thiemann and Reisen 2012), multiple trapping methods were used whenever feasible.

Culex mosquitoes were collected weekly or biweekly from April to October 2007–2009 from multiple sites (ranging from five to >100) in each study area. Mosquitoes were

anesthetized and enumerated by species. Blood-fed females were stored individually at -80°C pending host identification.

Bloodmeal Identification

Bloodmeals were identified using methods described previously (Thiemann et al. 2012). In brief, DNA was extracted from the blood-fed *Culex* abdomens by using the DNeasy 96 Blood & Tissue kit (QIAGEN, Valencia, CA). The 658-bp “barcoding” region of the mitochondrial gene cytochrome *c* oxidase I (*COI*) was amplified using a nested polymerase chain reaction (PCR). First, primers for the tRNA-coding regions flanking *COI* were used to amplify $\approx 1,900$ bp. Then, the barcoding region of *COI* was amplified using vertebrate-specific primers (Ivanova et al. 2006, Cooper et al. 2007). Host DNA was identified either using a microsphere assay for *COI* with species-specific probes (Thiemann et al. 2012) for common hosts in each study area or by sequencing the amplicon and using the Identify Specimen feature of the Barcode of Life Data Systems (BOLD; www.boldsystems.org) (Ratnasingham and Hebert 2007, Kent et al. 2009). Mixed bloodmeals were identified exclusively with the microsphere assay (Thiemann et al. 2012).

Statistical Analysis

To compare host species richness across study areas, rarefaction was used to generate the expected number of host species from a 50 bloodmeal subsample, by using the rarefy function in the vegan package version 1.17–8 of R (RDC 2011). Bloodmeal percentages within and between study areas were compared by pairwise chi-square analysis.

Bird Population Estimates

The weekly frequency of avian species from May to September 2007–2009 was downloaded from eBird (Sullivan et al. 2009), a project developed by Cornell Laboratory of Ornithology and the National Audubon Society to monitor avian prevalence from citizen-based reporting. The frequency of a particular species represents the proportion of citizen-submitted checklists reporting that species in a given area.

Results

Vertebrate host species were successfully identified from 515 (81%) blood-fed *Cx. tarsalis* and 972 (81%) blood-fed members of the *Cx. pipiens* complex across all study areas. In total, 99 host species (80 birds, 18 mammals, and one reptile) were identified from these 1,487 bloodmeals. Unidentified bloodmeals either did not produce a visible amplification product, probably due to small bloodmeal size or digestion of the blood-meal in half-gravid (Sella’s stage III–IV) and subgravid (Sella’s stage V) individuals (Sella 1920, WHO 1975), or could not be conclusively identified to host species.

Coachella Valley

In total, 399 blood-fed mosquitoes from the *Cx. pipiens* complex and 94 blood-fed *Cx. tarsalis* were collected from >50 sites in the Coachella Valley (Table 1). Overall, chickens comprised 47.6% of the *Cx. pipiens* complex bloodmeals and 16% of the bloodmeals from *Cx. tarsalis*. At collection sites ≥ 30 m from sentinel chicken flocks, $>70\%$ of the *Cx. pipiens* complex bloodmeals were from chickens. Because of this bias, collections within 50 m of sentinel chicken flocks were excluded from further analysis.

Away from sentinel chicken sites, house finch (13.3%), mourning dove (12.6%), domestic dog (11.5%), greater roadrunner (10.5%), house sparrow (7.0%), and northern mockingbird (7.0%) were the most frequent hosts of the *Cx. pipiens* complex. In total, 32 avian host species and three mammalian species were identified. For *Cx. tarsalis*, no host species

accounted for >8% of the total bloodmeals. Three mammalian species, domestic cow (7.2%), domestic horse (5.8%), and domestic dog (5.8%) were repeated hosts, and 10 mammalian species, including human, comprised >30% of the total bloodmeals. There was no significant difference in the bloodmeal percentage of any host (Table 1), and 36 host species in total were identified from 69 bloodmeals. Overall, host species richness was greater for *Cx. tarsalis* (30.5 host species/50 bloodmeals) than the *Cx. pipiens* complex (20.4 host species/50 bloodmeals) (Fig. 2).

Los Angeles

Walk-in red boxes were not productive, and most of the blood-fed *Culex* were collected in gravid and CO₂ traps from >100 sites dispersed throughout the Greater Los Angeles County VCD. Few *Cx. tarsalis* were collected over the 3-yr study period (10 females), so only bloodmeals from the 275 *Cx. pipiens* complex were identified and reported (Table 2). As in the Coachella Valley, chickens were the dominant host from mosquitoes collected near sentinel flocks, so bloodmeal host composition was presented with and without sentinel chicken sites. Contrary to Coachella, where no host species away from sentinel chicken flocks comprised >14% of the total bloodmeals (Table 1), members of the *Cx. pipiens* complex in Los Angeles County acquired >60% of their bloodmeals from two host species, house finch (39.4%) and house sparrow (21.6%) (Table 2). Mourning dove (6.9%), northern mockingbird (4.1%), and domestic dog (3.7%) were the next most frequent hosts. Mammalian bloodmeals comprised just 6% of the total, and only two human bloodmeals (0.9%) were identified, despite the dense human population in this area. With a majority of *Cx. pipiens* complex feeding on house finch and house sparrow, and 27 hosts in total identified away from sentinel chicken flocks, host species richness was 13.2 for 50 bloodmeals, significantly less than the more rural Coachella Valley (Fig. 2).

Underground Storm Drain System traps were operated without CO₂ or light as bait in the underground system of Los Angeles. Although few blood-fed mosquitoes were collected from these traps, it is interesting to note that these bloodmeals were derived from a variety of avian hosts, indicating that these mosquitoes fed above ground and then entered the underground to rest rather than remaining underground and feeding on small mammals such as rats that were abundant in the system.

Kern County (Near Bakersfield)

Blood-fed *Cx. pipiens* complex ($n = 162$) and *Cx. tarsalis* ($n = 101$) were collected from 15 sites, with the majority collected from a golf course, a riparian area, and various residential areas in and around Bakersfield (Table 3). European starling (19.1%), predominantly identified from an urban golf course, and chicken (12.3%) were the most frequently fed-upon host of the *Cx. pipiens* complex, whereas *Cx. tarsalis* most frequently fed on mourning dove (18.8%), western scrub-jay (11.9%), northern mockingbird (10.9%), and chicken (8.9%). Despite this difference in dominant host species, blood-feeding patterns were quite similar between the *Culex* species in this area. Eight host species, European starling, chicken, black-headed grosbeak, western scrub-jay, house finch, mourning dove, house sparrow, and northern mockingbird, were shared as the eight most fed-upon hosts by both mosquito species. It should be noted that although chickens were a frequent host for both mosquito species, these samples were not collected near sentinel chicken flocks, but rather from residential areas where chickens were kept in backyard coops. Domestic dog (5.6%) was the only nonavian host identified from the *Cx. pipiens* complex, whereas *Cx. tarsalis* took bloodmeals from domestic dog (2.0%), domestic cow (1.0%), and western fence lizard (1.0%). The host species richness for the *Cx. pipiens* complex near Bakersfield (14.6 host species/50 bloodmeals) was similar to that found in Greater Los Angeles (13.2 host species/

50 blood-meals). *Cx. tarsalis* host richness (17.0 host species/50 bloodmeals) in this region was slightly but not significantly higher than that of the *Cx. pipiens* complex (Fig. 2).

Yolo County (Within and Surrounding Davis)

Despite the use of CO₂ traps, gravid traps, walk-in red boxes, and backpack aspiration from backyard vegetation during over 3 yr of sampling, only 29 *Cx. pipiens* complex and 17 *Cx. tarsalis* engorged females were collected from residential areas in Davis, CA (Table 4). Although few definitive conclusions can be drawn from this small sample size, the host feeding patterns were generally similar to those in other areas of the Central Valley. Western scrub-jay was frequently fed upon host by both mosquito species, and house finch was used frequently by members of the *Cx. pipiens* complex. American robin, a species considered a preferred host in several previous *Culex* bloodmeal studies (Kilpatrick et al. 2006b, Hamer et al. 2009, Molaei et al. 2010, Montgomery et al. 2011), comprised >13% of the *Cx. pipiens* complex bloodmeals and nearly 30% of bloodmeals by *Cx. tarsalis*. Two unique galliform birds, helmeted guineafowl and wild turkey, were identified from bloodmeals collected at the Davis Cemetery, an area where these birds were frequently found in the wild. Only one mammalian bloodmeal from a black rat was identified from the residential samples. Because of the small sample size, host species richness was not calculated.

Engorged *Cx. tarsalis* collected at the Yolo Bypass Wildlife Area exhibited a remarkable diversity of bloodmeal hosts from a small collection area and relatively small number of engorged females. Thirty-three host species were identified from 72 bloodmeals (Table 5), resulting in a host richness of 27.2 host species/50 bloodmeals (Fig. 2) as calculated by rarefaction. Twenty-five avian species, including a variety of owls, hawks, and waterfowl, were identified, and the diverse mammalian bloodmeals included North American river otter, California vole, North American beaver, and common muskrat.

Sutter County (Near Yuba City)

Blood-fed *Culex* were collected resting in walk-in red boxes at five rural and semirural residential sites in Sutter County. Bloodmeals from 107 members of the *Cx. pipiens* complex and 231 *Cx. tarsalis* were identified (Table 6). *Cx. pipiens* complex mosquitoes fed almost exclusively on avian hosts, with American crow (26.2%), American robin (17.8%), and chicken (11.2%) most frequent. Yellow-billed magpie and western scrub-jay also were fed upon in this area, so corvid bloodmeals comprised >35% of the total. *Cx. tarsalis* fed predominantly on American robin (27.3%), domestic cow (20.3%), American crow (13.4%), and yellow-billed magpie (8.2%). Although both mosquito species were collected concurrently at the same red box sites, *Cx. tarsalis* fed on six mammalian species (27.3% of total), whereas human (1.9%) was the only mammalian bloodmeal identified from the *Cx. pipiens* complex. The *Cx. pipiens* complex did not feed on cattle or other domestic mammals, although these hosts were abundant. Despite differences in mammalian feeding, the host richness calculated by rarefaction of the two *Culex* species was similar in this area (13.8 host species/50 bloodmeals for *Cx. tarsalis* and 13.4 host species/50 bloodmeals for the *Cx. pipiens* complex) (Fig. 2).

Bird Population Estimates

The frequency of occurrence of some common avian hosts in each study area is shown in Fig. 3. Weekly frequencies from May to September were averaged over the 3 yr of the study (2007–2009) (eBird 2011). Some species, such as house finch, house sparrow, and mourning dove, were found in all study areas. Yellow-billed magpie and greater roadrunner had limited ranges, whereas American robin occurrence increased in frequency in northern areas. These data provide a general and qualitative look at the occurrence of avian species across the study areas, but they do not provide avian abundance at specific mosquito sampling

sites. These data helped explain why within mosquito species host use patterns varied spatially (Fig. 4).

Discussion

The blood-feeding patterns of the WNV vectors *Cx. tarsalis* and the *Cx. pipiens* complex were surveyed in five geographic regions of California spanning 850 km from the deserts of the southern Coachella Valley to the rice-growing regions of the northern Sacramento Valley. Both vector species fed on a wide variety of vertebrate hosts and exhibited significant spatial and interspecific differences in blood-feeding patterns. Nearly 100 different host species (avian, mammalian, and reptilian) were fed upon by these *Culex* mosquitoes across the state.

Both *Cx. tarsalis* and the *Cx. pipiens* complex were collected in nearly all study areas. As expected, few *Cx. tarsalis* were collected in highly urban Los Angeles where they remain a relatively rare species (Kwan et al. 2010), and no *Cx. pipiens* were collected in the Yolo Bypass Wildlife Area where most mosquitoes emerge from managed wetlands and rice fields. In general, when both species were collected from the same site, *Cx. tarsalis* fed on a greater diversity of hosts than did the *Cx. pipiens* complex (Fig. 2). Much of this diversity resulted from an increased feeding on mammals ($\chi^2 = 49.04$, $df = 1$, $P < 0.0001$), with *Cx. tarsalis* feeding on 17 mammalian species in total, whereas members of the *Cx. pipiens* complex fed on only four mammalian species. Even when the diversity of bloodmeals was similar between these vector species, such as near Yuba City, *Cx. tarsalis* fed more frequently on mammalian hosts than did the *Cx. pipiens* complex (27.3 vs 1.9%) ($\chi^2 = 28.77$, $df = 1$, $P < 0.001$). These findings were congruent with the idea that *Cx. pipiens* is primarily an avian feeder, whereas *Cx. tarsalis* is more of a generalist feeder (Reisen and Reeves 1990). There was no significant difference in the occurrence of human bloodmeals between these species ($\chi^2 = 0.048$, $df = 1$, $P = 0.83$), and only five (0.3% of total) human bloodmeals were identified throughout the study. Both *Cx. tarsalis* and the *Cx. pipiens* complex consistently have exhibited the highest WNV infection rates and presumably are responsible for transmitting virus to the human cases repeatedly reported from these areas. However, infrequent bloodmeals from humans, even in highly urbanized Los Angeles where several outbreaks have occurred, would indicate that these species are relatively inefficient bridge vectors.

Despite the long distances between study areas and the differences in climate and landscape, several vertebrate hosts were used repeatedly throughout the state. As in other areas around the United States (Molaei et al. 2007, Hamer et al. 2009, Kent et al. 2009, Molaei et al. 2010), house finch and house sparrow were ubiquitous (see avian frequency estimates in Fig. 3) and were fed upon by both *Culex* species (Fig. 4). These data agreed with previous studies at these same study areas that indicated both of these peridomestic passerine species were frequently infected with WNV (Table 7) and other arboviruses (Reeves et al. 1990, Reisen et al. 2000). House finches and house sparrows may be crucial for WNV transmission, especially in highly urban areas such as Los Angeles where these hosts account for >50% of the *Culex* bloodmeals (Table 2; Fig. 4; also see Molaei et al. 2010) and also in areas such as the Coachella Valley, where highly competent corvids were rare (Fig. 3) (Reisen et al. 2006a). Both house finch and house sparrow are competent experimental hosts (Komar et al. 2003, Langevin et al. 2005, Reisen et al. 2005) and have previously been implicated in virus maintenance transmission (Kwan et al. 2010). Western scrub-jay, a highly competent amplifying host in the laboratory (Reisen et al. 2005), was not previously identified as a frequent bloodmeal host, although this species frequently was WNV positive in dead bird (Wheeler et al. 2009) and seroprevalence surveys (Table 7). Our study revealed that Western scrub-jay may be an important contributor to WNV transmission in areas

where it was fed upon frequently, especially Bakersfield (10.2%) and other parts of the Central Valley. Some less competent species also were repeatedly fed upon and may have functioned to divert *Culex* from competent hosts, thereby diluting or decreasing transmission. For example, mourning doves frequently were used as bloodmeal hosts (Fig. 4), as described previously in Texas (Molaei et al. 2007), Colorado (Kent et al. 2009), and California (Molaei et al. 2010, Montgomery et al. 2011). Although frequently antibody positive (Table 7), adults generally were poorly competent hosts for WNV (Komar et al. 2003, Reisen et al. 2005) and other arboviruses (Reisen et al. 2003). Nestling mourning doves, however, develop elevated viremias to St. Louis encephalitis virus (Mahmood et al. 2004) and could play an important role in transmission. When available, chickens also were frequently fed upon. This was important to document, because they are used as sentinel birds in arbovirus surveillance programs. Chickens and other galliforms, such as quail and turkey, have low competence for flaviviruses (Langevin et al. 2001, Reisen et al. 2006b), so frequent feeding on this group would dampen transmission (Keesing et al. 2006, Swaddle and Calos 2008).

Variation in blood-feeding patterns across the state (Tables 1–6; Fig. 4) was due, in part, to the limited distributions of some host species (Fig. 3). For example, the greater roadrunner was a common host (10.5%) in the Coachella Valley but was not identified elsewhere where it is less abundant or absent. Likewise, yellow-billed magpie was only identified as a host within its restricted range in the Central Valley. Similarly blood-feeding on American robin, a frequent and preferred host in previous studies (Kilpatrick et al. 2006a, Savage et al. 2007, Kent et al. 2009), was more frequent in the northern part of California (also see Montgomery et al. 2011) where this species is abundant during summer (Fig. 3).

There has been much discussion about the role of American crows in WNV transmission. American crows originally were thought to be a key amplifying host in WNV transmission due to extremely elevated viremias and 100% mortality after experimental infection (Komar et al. 2003), high WNV infection prevalence in dead bird surveys (Reisen et al. 2006a, Wheeler et al. 2009), and significant population declines associated with outbreaks (Caffrey et al. 2003, LaDeau et al. 2007, Wheeler et al. 2009). In contrast, the near absence of crows in bloodmeal identification studies has led to speculation about their involvement in mosquito infection, and therefore bird–mosquito–bird transmission (Kramer et al. 2008, Hamer et al. 2009, Molaei et al. 2010). In our studies, American crow was identified as a host in two areas, a farmstead north of Davis (Thiemann et al. 2011) and the area in and around Yuba City, where the American crow was one of the most frequently fed upon hosts by the *Cx. pipiens* complex (26.2%) and accounted for 13.4% of the *Cx. tarsalis* bloodmeals (Table 6). These blood-meals were collected during spring and early summer, not near a large late season communal crow roost, and probably resulted from only a few nesting family groups. Interestingly, these crow bloodmeals were all detected in fully engorged *Culex* collected resting in red boxes. It may be that American crows are tolerant of mosquito feeding, so bloodmeals are less likely to be identified from CO₂ collections, which mostly collect females with partial interrupted meals. Given the complex staging and roosting behavior of crows, sampling in a manner to find crow bloodmeals may be difficult and require collections adjacent to nocturnal roosts, but from our study it seems that when available American crows are fed upon by *Culex* mosquitoes, even when house finches, American robins, and other avian hosts are present.

To summarize, *Cx. tarsalis* and the *Cx. pipiens* complex were generalist blood feeders and fed on a wide variety of avian and mammalian hosts throughout California. Both species fed predominantly on avian hosts, with *Cx. tarsalis* feeding more frequently on nonhuman mammals, including horses, than did the *Cx. pipiens* complex. Both vectors fed frequently on abundant and competent avian hosts, such as house finch and house sparrow, allowing

for the maintenance and amplification of WNV, even in the absence of highly competent amplifying hosts. Corvids, such as American crow, western scrub-jay and yellow-billed magpie, were fed upon by both *Culex* species when these hosts were available and probably contributed to WNV transmission particularly in the Central Valley. Similar to previous bloodmeal identification studies (Reisen and Reeves 1990, Montgomery et al. 2011, Molaie et al. 2010), few human bloodmeals were identified throughout the state in both *Cx. tarsalis* and the *Cx. pipiens* complex, even in highly urban Los Angeles. Similarly infrequent human bloodmeals were reported in studies designed specifically to detect human blood feeding at a park near Bakersfield (Tempelis et al. 1965) and at residential habitats in the Los Angeles basin (Reisen et al. 1990). This low frequency of human bloodmeals may explain the continued low incidence of human infection with encephalitis viruses detected historically (Reisen et al. 1996, Reisen and Chiles 1997) and during the current WNV epidemic (<http://westnile.ca.gov/reports.php>).

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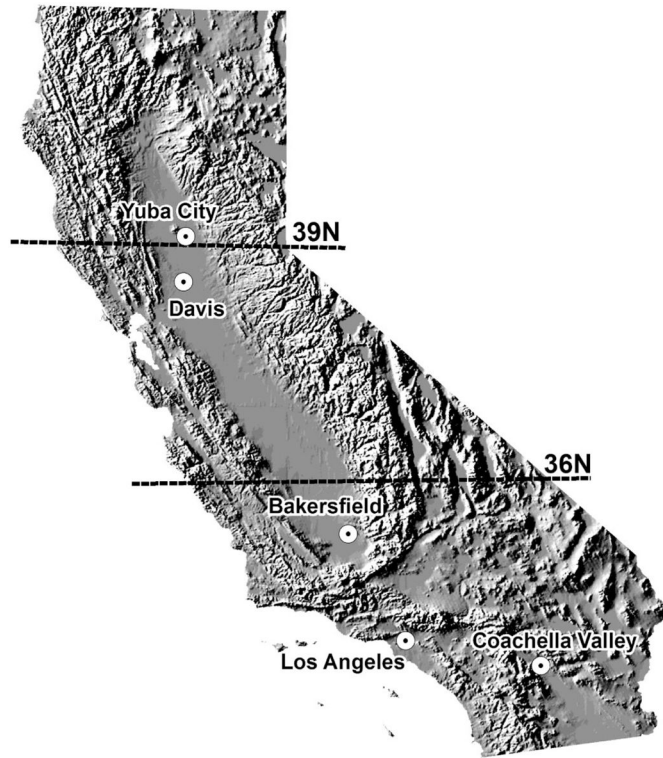


Fig. 1.
Map of California study areas.

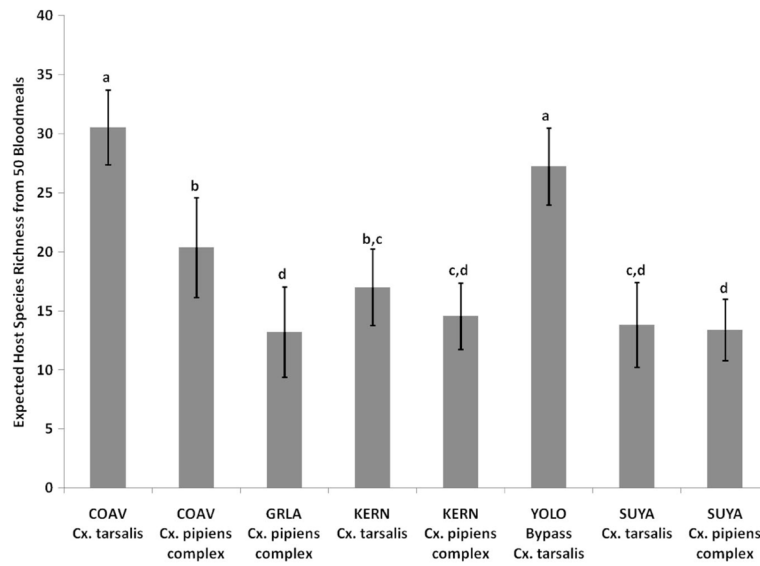


Fig. 2.

Expected host species richness (number of host species), as determined by rarefaction, in a random 50 bloodmeal subsample of *Cx. tarsalis* and the *Cx. pipiens* complex at each study site: Coachella Valley (COAV), Los Angeles (GRLA), Kern County (KERN), Yolo Bypass Wildlife Area (YOLO Bypass), and Sutter County (SUYA) Residential Yolo County was omitted because of small sample size. Error bars depict the 95% confidence intervals, and letters denote statistical similarity.

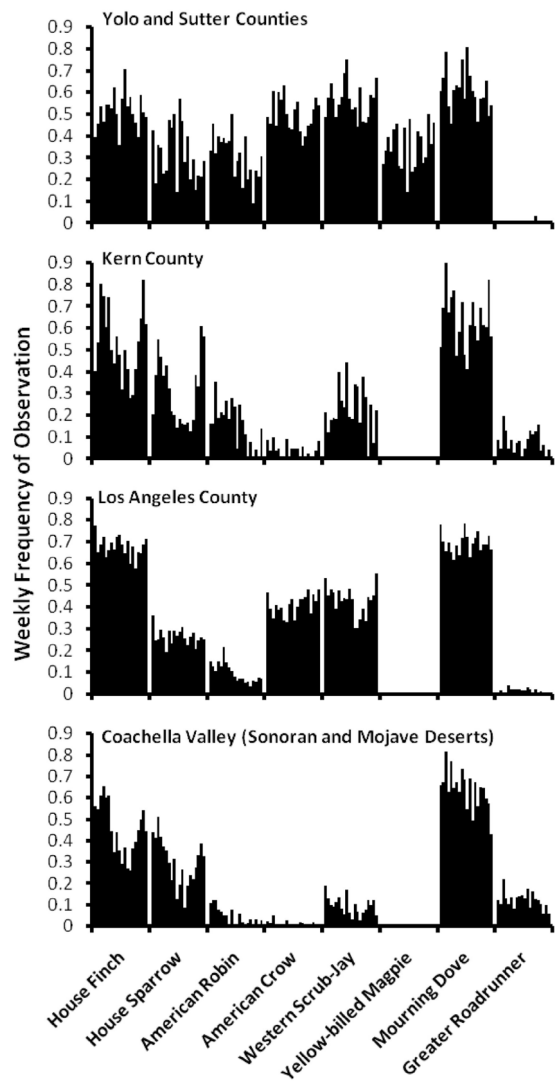


Fig. 3. Weekly frequency of some common avian host species, May–September 2007–2009, in California study areas. Frequency represents the proportion of citizen-submitted checklists reporting each species (eBird 2011).

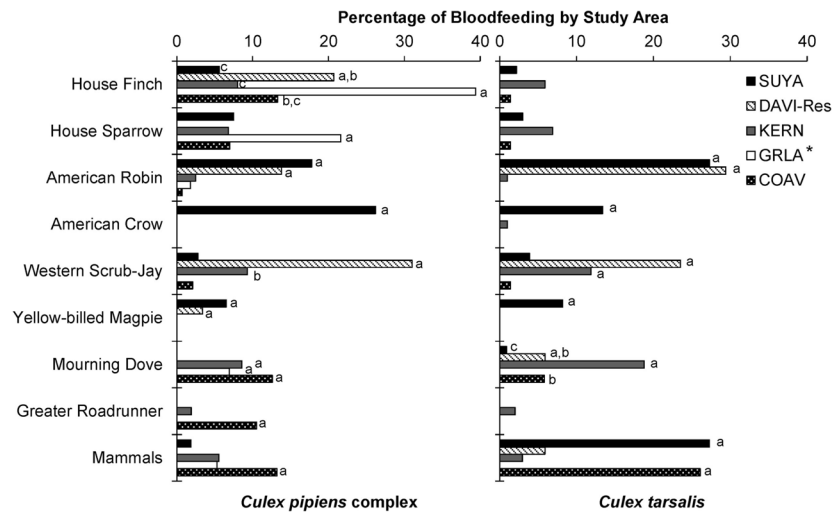


Fig. 4. Percentage of bloodmeals from some common vertebrate hosts by the *Cx. pipiens* complex (left) and *Cx. tarsalis* (right) compared between five study areas in California: Sutter County (SUYA), Residential Yolo County in Davis (DAVI-Res), Kern County (KERN), Los Angeles (GRLA), and the Coachella Valley (COAV). Asterisk (*) indicates no *Cx. tarsalis* bloodmeals were identified from Los Angeles. Percentages with different letters within host species groups for each mosquito species denote significance by chi-square analysis ($P < 0.05$).

Table 1

Number and percentage of avian- and mammalian-derived bloodmeals from the *Cx. pipiens* complex and *Cx. tarsalis* in the Coachella Valley, Riverside County, 2007–2009

Host	<i>Cx. pipiens</i> complex				<i>Cx. tarsalis</i>					
	CO2 ^a	GR ^b	Total	% chick ^{c,d}	CO2 ^a	GR ^b	Total	% total	% chick ^{c,d}	
Avian										
Chicken, <i>Gallus gallus</i>	167	23	190	47.6	4.2bcd	12	3	15	16.0	1.4a
House finch, <i>Carduelis mexicanus</i>	6	19	25	6.3	13.3a	1		1	1.1	1.4a
Mourning dove, <i>Zenaidura macroura</i>	8	16	24	6.0	12.6a	4		4	4.3	5.8a
House sparrow, <i>Passer domesticus</i>	13	7	20	5.0	7.0abc	3		3	3.2	1.4a
Greater roadrunner, <i>Geococcyx californianus</i>	1	18	19	4.8	10.5ab					
Northern mockingbird, <i>Mimus polyglottos</i>	2	11	13	3.3	7.0abc	2		2	2.1	2.9a
Common raven, <i>Corvus corax</i>		5	5	1.3	3.5cd					
Great-tailed grackle, <i>Quiscalus mexicanus</i>		5	5	1.3		2		2	2.1	2.9a
Verdin, <i>Auriparus flaviceps</i>	2	3	5	1.3	2.1cd					
Barn owl, <i>Tyto alba</i>	1	3	4	1.0	0.7d	2	1	4	4.3	4.3a
Gambel's quail, <i>Callipepla gambelii</i>	1	3	4	1.0	2.8cd	1	2	3	3.2	4.3a
Abert's towhee, <i>Pipilo aberti</i>		3	3	0.8	1.4d					
Brewer's blackbird, <i>Euphagus cyanocephalus</i>	3		3	0.8	1.4d	2		2	2.1	2.9a
Burrowing owl, <i>Athene cunicularia</i>		3	3	0.8	2.1cd					
Eurasian collared-dove, <i>Streptopelia decaocto</i>	2	1	3	0.8	2.1cd	1		1	1.1	1.4a
European starling, <i>Sturnus vulgaris</i>	1	2	3	0.8		1		1	1.1	
Great Horned owl, <i>Bubo virginianus</i>	1	2	3	0.8						
Western scrub-jay, <i>Aphelocoma californica</i>		3	3	0.8	2.1cd		1	1	1.1	1.4a
Wild turkey, <i>Meleagris gallopavo</i>		3	3	0.8		1		1	1.1	
Brown-headed cowbird, <i>Molothrus ater</i>	1	1	2	0.5	0.7d					
Cactus wren, <i>Campylorhynchus brunneicapillus</i>	1	1	2	0.5	1.4d					
Common ground-dove, <i>Columbina passerina</i>	1	1	2	0.5	0.7d	2	1	3	3.2	4.3a
Prairie falcon, <i>Falco mexicanus</i>		2	2	0.5	1.4d					
Western kingbird, <i>Tyrannus verticalis</i>	1	1	2	0.5	0.7d					
White-winged dove, <i>Zenaidura asiatica</i>	2		2	0.5	1.4d					

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Host	Cx. pipiens complex				Cx. tarsalis				
	CO2 ^a	GR ^b	Total	% chick ^{c,d}	CO2 ^a	GR ^b	ST ^e	Total	% chick ^{c,d}
American robin, <i>Turdus migratorius</i>		1	1	0.3					
Black-tailed gnatcatcher, <i>Poliophtila melanura</i>	1		1	0.3	1		1	1.1	1.4a
Brewer's sparrow, <i>Spizella breweri</i>		1	1	0.3					
Green heron, <i>Butorides virescens</i>		1	1	0.3	1		1	1.1	1.4a
Inca dove, <i>Columba inca</i>		1	1	0.3	2		2	2.1	2.9a
Indian peafowl, <i>Pavo cristatus</i>	1		1	0.3	1		1	1.1	1.4a
Peregrine falcon, <i>Falco peregrinus</i>		1	1	0.3					
Rock pigeon, <i>Columba livia</i>	1		1	0.3					
Ruddy duck, <i>Oxyura jamaicensis</i>	1		1	0.3					
Western bluebird, <i>Sialia mexicana</i>		1	1	0.3					
Western tanager, <i>Piranga ludoviciana</i>	1		1	0.3					
Yellow warbler, <i>Dendroica petechia</i>		1	1	0.3					
Yellow-rumped warbler, <i>Dendroica coronata</i>	1		1	0.3					
American kestrel, <i>Falco sparverius</i>					1	2	3	3.2	4.3a
American white pelican, <i>Pelecanus erythrorhynchos</i>					1		1	1.1	
Barn swallow, <i>Hirundo rustica</i>						1	1	1.1	1.4a
Black-crowned night-heron, <i>Nycticorax nycticorax</i>					1	1	2	2.1	2.9a
Caspian tern, <i>Sterna caspia</i>						1	1	1.1	
Cooper's hawk, <i>Accipiter cooperii</i>					2		2	2.1	2.9a
Great blue heron, <i>Ardea herodias</i>					2		2	2.1	2.9a
Least bittern, <i>Ixobrychus exilis</i>					1	2	3	3.2	4.3a
Marsh wren, <i>Cistothorus palustris</i>					1		1	1.1	
Pied-billed grebe, <i>Podilymbus podiceps</i>					2		2	2.1	2.9a
Ruby-crowned kinglet, <i>Regulus calendula</i>					1		1	1.1	1.4a
Song sparrow, <i>Melospiza melodia</i>					1		1	1.1	1.4a
Undetermined duck, <i>Anas</i> sp.						1	1	1.1	
Mammalian									
Domestic dog, <i>Canis familiaris</i>	13	9	22	5.5	4		4	4.3	5.8a
Black rat, <i>Rattus rattus</i> ^f	7		7	1.8	1		1	1.1	1.4a
Domestic cat, <i>Felis catus</i>	1	2	3	0.8					

Host	<i>Cx. pipiens</i> complex				<i>Cx. tarsalis</i>			
	CO2 ^a	GR ^b	Total	% chick ^{c,d}	CO2 ^a	GR ^b	Total	% chick ^{c,d}
Coyote, <i>Canis latrans</i>	1		1	0.3				
Desert cottontail, <i>Sylvilagus auduboni</i>		1	1	0.3	1		1	1.1
Black-tailed jackrabbit, <i>Lepus californicus</i>					2		2	2.1
Domestic cow, <i>Bos taurus</i>					5		5	5.3
Domestic horse, <i>Equus caballus</i>					7		7	7.4
House mouse, <i>Mus musculus</i>						1	1	1.1
Human, <i>Homo sapiens</i>					1		1	1.1
Raccoon, <i>Procyon lotor</i>					1		1	1.1
White-throated woodrat, <i>Neotoma albigula</i>					1		1	1.1
Mixed bloodmeals								
Chicken/common ground-dove	1		1	0.3	1		1	1.1
Chicken/house sparrow		1	1	0.3				
Total 63 species	243	156	399	<i>n</i> = 143	75	9	94	<i>n</i> = 69

^aDry ice-baited CDC trap.

^bGravid trap.

^cPercentages exclude sites with sentinel chicken flocks.

^dPercentages with different lowercase letters indicate that they are significantly different by chi-square test (*P* < 0.05).

^eSuction trap (no bait).

^fThese samples were identified in BOLD as *Rattus tanezumi*, but they are probably *Rattus rattus* Lineage II (Aplin et al. 2011) per personal communication with C. Conroy (Museum of Vertebrate Zoology, University of California–Berkeley).

Table 2

Number and percentage of avian- and mammalian-derived bloodmeals from the *Cx. pipiens* complex in Los Angeles County, 2007–2009

Host	<i>Cx. pipiens</i> complex					% total	% chick ^{e,f}
	CO2 ^a	GR ^b	RB ^c	USDS ^d	Total		
Avian							
House finch, <i>Carpodacus mexicanus</i>	15	69	8		92	33.5	39.4a
Chicken, <i>Gallus gallus</i>	22	30	1		53	19.3	3.2de
House sparrow, <i>Passer domesticus</i>	5	42	1		48	17.5	21.6b
Mourning dove, <i>Zenaidura macroura</i>	2	9	3	2	16	5.8	6.9c
Northern mockingbird, <i>Mimus polyglottos</i>	3	7			10	3.6	4.1cd
Western scrub-jay, <i>Aphelocoma californica</i>		4	1	2	7	2.5	
American robin, <i>Turdus migratorius</i>	1	4			5	1.8	1.8def
California towhee, <i>Pipilo crissalis</i>		5			5	1.8	2.3def
Bush-tit, <i>Psaltriparus minimus</i>	1	2			3	1.1	1.4def
Western bluebird, <i>Sialia mexicana</i>		3			3	1.1	1.4def
American kestrel, <i>Falco sparverius</i>		1		1	2	0.7	0.9ef
Brewer's blackbird, <i>Euphagus cyanocephalus</i>		2			2	0.7	0.9ef
Common raven, <i>Corvus corax</i>	1		1		2	0.7	0.9ef
European starling, <i>Sturnus vulgaris</i>		1		1	2	0.7	0.9ef
Oak titmouse, <i>Baeolophus inornatus</i>		2			2	0.7	0.9ef
Cedar waxwing, <i>Bombicilla cedrorum</i>	1				1	0.4	0.5f
Cooper's hawk, <i>Accipiter cooperii</i>		1			1	0.4	0.5f
Double-crested cormorant, <i>Phalacrocorax auritus</i>	1				1	0.4	0.5f
Green heron, <i>Butorides virescens</i>	1				1	0.4	0.5f
House wren, <i>Troglodytes aedon</i>		1			1	0.4	0.5f
Rock pigeon, <i>Columba livia</i>		1			1	0.4	0.5f
Swainson's thrush, <i>Catharus ustulatus</i>				1	1	0.4	0.5f
Yellow-rumped warbler, <i>Dendroica coronata</i>	1				1	0.4	
Mammalian							
Domestic dog, <i>Canis familiaris</i>	5	3			8	2.9	3.7cde
Human, <i>Homo sapiens</i>	1	1			2	0.7	0.9ef

Host	<i>Cx. pipiens</i> complex					
	CO ₂ ^a	GR ^b	RBC ^c	USDS ^d	Total	% total % chick ^{e,f}
Domestic cat, <i>Felis catus</i>		1			1	0.4 0.5f
Domestic horse, <i>Equus caballus</i>	1				1	0.4 0.5f
Raccoon, <i>Procyon lotor</i>	1				1	0.4 0.5f
Mixed bloodmeals						
House sparrow/house finch		2			2	0.7 0.5f
Total 29 species	62	191	15	7	275	

^aDry ice-baited CDC trap.

^bGravid trap.

^cWalk-in red box.

^dUnderground storm drain system trap (no bait).

^ePercentages exclude sites with sentinel chicken flocks.

^fPercentages with different lowercases letter(s) indicate that they are significantly different by chi-square test ($P < 0.05$).

Table 3

Number and percentage of avian-, reptilian-, and mammalian-derived bloodmeals from the *Cx. pipiens* complex and *Cx. tarsalis* in Kern County, near Bakersfield, 2007–2009

Host	<i>Cx. pipiens</i> complex				<i>Cx. tarsalis</i>			
	CO ₂ ^a	RB ^b	Total	% ^c	CO ₂ ^a	RB ^b	Total	% ^c
<i>Avian</i>								
European starling, <i>Sturnus vulgaris</i>	1	30	31	19.1a		6	6	5.9bcde
Chicken, <i>Gallus gallus</i>	2	18	20	12.3ab	3	6	9	8.9abcd
Black-headed grosbeak, <i>Pheucticus melanocephalus</i>		15	15	9.3b		6	6	5.9bcde
Western scrub-jay, <i>Aphelocoma californica</i>	1	14	15	9.3b		12	12	11.9ab
House finch, <i>Carduelis mexicanus</i>		13	13	8.0b		6	6	5.9bcde
Mourning dove, <i>Zenaidura macroura</i>		14	14	8.6b	1	18	19	18.8a
House sparrow, <i>Passer domesticus</i>		11	11	6.8bc	1	6	7	6.9bcde
Northern mockingbird, <i>Mimus polyglottos</i>		10	10	6.2bc		11	11	10.9abc
American robin, <i>Turdus migratorius</i>		4	4	2.5cd		1	1	1.0e
Cockatiel, <i>Nymphicus hollandicus</i>		3	3	1.9cd		1	1	1.0e
Greater roadrunner, <i>Geococcyx californianus</i>		3	3	1.9cd		2	2	2.0de
Western tanager, <i>Piranga ludoviciana</i>		3	3	1.9cd				
Mallard, <i>Anas platyrhynchos</i>		3	3	1.9cd				
American kestrel, <i>Falco sparverius</i>		2	2	1.2d		6	6	5.9cde
Bullock's oriole, <i>Icterus bullockii</i>		2	2	1.2d		1	1	1.0e
Swainson's thrush, <i>Catharus ustulatus</i>		2	2	1.2d				
Brewer's blackbird, <i>Euphagus cyanocephalus</i>		1	1	0.6d				
Cedar waxwing, <i>Bombycilla cedrorum</i>		1	1	0.6d		1	1	1.0e
American crow, <i>Corvus brachyrhynchos</i>						1	1	1.0e
Barn owl, <i>Tyto alba</i>					3		3	3.0cde
Black phoebe, <i>Sayornis nigricans</i>						2	2	2.0de
Black-crowned night-heron, <i>Nycticorax nycticorax</i>					1		1	1.0e
Bush-tit, <i>Psaltriparus minimus</i>						1	1	1.0e
Yellow warbler, <i>Dendroica petechia</i>					1		1	1.0e
<i>Reptilian</i>								
Western fence lizard, <i>Sceloporus occidentalis</i>						1	1	1.0e

Host	<i>Cx. pipiens</i> complex			<i>Cx. tarsalis</i>		
	CO2 ^a	RB ^b	% ^c	CO2 ^a	RB ^b	% ^c
Mammalian						
Domestic dog, <i>Canis familiaris</i>	1	8	5.6bc	2	2	2.0de
Domestic cow, <i>Bos taurus</i>				1	1	1.0e
Total 27 species	5	157	162	11	90	101

^aDry-ice baited CDC trap.

^bWalk-in red box.

^cPercentages with different lowercase letters indicate that they are significantly different by chi-square test ($P < 0.05$).

Table 4

Number and percentage of avian- and mammalian-derived bloodmeals from the *Cx. pipiens* complex and *Cx. tarsalis* in Davis, Yolo County, 2007–2009

Host	<i>Cx. pipiens</i> complex				<i>Cx. tarsalis</i>			
	BKPK ^a	CO2 ^b	RB ^c	% ^d	BKPK ^a	CO2 ^b	RB ^c	% ^d
Avian								
Western scrub-jay, <i>Aphelocoma californica</i>	2		7	9			4	23.5a
House finch, <i>Carduelis mexicanus</i>	1	1	4	6				20.7ab
American robin, <i>Turdus migratorius</i>	1		3	4	1		4	29.4a
Helmeted guineafowl, <i>Numida meleagris</i>			4	4				13.8ab
Northern mockingbird, <i>Mimus polyglottos</i>			4	4			3	17.6a
Chicken, <i>Gallus gallus</i>	1			1			1	5.9a
Yellow-billed magpie, <i>Pica nuttalli</i>	1			1				3.4b
Barn owl, <i>Tyto alba</i>							1	5.9a
Mourning dove, <i>Zenaidura macroura</i>							1	5.9a
Wild turkey, <i>Meleagris gallopavo</i>							1	5.9a
Mammalian								
Black rat, <i>Rattus rattus</i>							1	5.9a
Total 11 Species	6	1	22	29	1	3	13	17

^aBackpack aspirator.

^bDry ice-baited CDC trap.

^cWalk-in red box.

^dPercentages with different lowercase letters indicate that they are significantly different by chi-square test ($P < 0.05$).

Table 5

Number and percentage of avian- and mammalian-derived bloodmeals from *Cx. tarsalis* at the Yolo Bypass Wildlife Area, Yolo County, 2007–2009

Host	<i>Cx. tarsalis</i>			
	CO2 ^a	RB ^b	Total	% ^c
Avian				
House finch, <i>Carpodacus mexicanus</i>	1	9	10	13.9a
Red-winged blackbird, <i>Agelaius phoeniceus</i>	3	4	7	9.7ab
Black-crowned night-heron, <i>Nycticorax nycticorax</i>	2	2	4	5.6ab
Savannah sparrow, <i>Passerculus sandwichensis</i>	2	2	4	5.6ab
Ring-necked pheasant, <i>Phasianus colchicus</i>	1	2	3	4.2ab
Great egret, <i>Ardea alba</i>	1	2	3	4.2ab
Mallard, <i>Anas platyrhynchos</i>	2	1	3	4.2ab
Red-tailed hawk, <i>Buteo jamaicensis</i>		3	3	4.2ab
Brewer's blackbird, <i>Euphagus cyanocephalus</i>	1	1	2	2.8b
Brown-headed cowbird, <i>Molothrus ater</i>	1	1	2	2.8b
Mourning dove, <i>Zenaida macroura</i>	1	1	2	2.8b
White-faced ibis, <i>Plegadis chihi</i>		2	2	2.8b
Barn owl, <i>Tyto alba</i>	1		1	1.4b
Cooper's hawk, <i>Accipiter cooperii</i>		1	1	1.4b
European starling, <i>Sturnus vulgaris</i>		1	1	1.4b
Gadwall, <i>Anas strepera</i>		1	1	1.4b
Great horned owl, <i>Bubo virginianus</i>		1	1	1.4b
Marsh wren, <i>Cistothorus palustris</i>	1		1	1.4b
Northern pintail, <i>Anas acuta</i>	1		1	1.4b
Northern shoveler, <i>Anas clypeata</i>	1		1	1.4b
Pied-billed grebe, <i>Podilymbus podiceps</i>		1	1	1.4b
Swainson's hawk, <i>Buteo swainsoni</i>		1	1	1.4b
Undetermined goose, <i>Chen sp.</i>	1		1	1.4b
Western meadowlark, <i>Sturnella neglecta</i>		1	1	1.4b
Yellow warbler, <i>Dendroica petechia</i>	1		1	1.4b
Mammalian				
North American river otter, <i>Lontra canadensis</i>	3		3	4.2ab
California vole, <i>Microtus californicus</i>	2		2	2.8b
Mule deer, <i>Odocoileus hemionus</i>	2		2	2.8b
North American beaver, <i>Castor canadensis</i>	1	1	2	2.8b
Raccoon, <i>Procyon lotor</i>	2		2	2.8b
Black-tailed jackrabbit, <i>Lepus californicus</i>	1		1	1.4b
Common muskrat, <i>Ondatra zibethicus</i>	1		1	1.4b
Domestic cow, <i>Bos taurus</i>		1	1	1.4b
Total 33 species	33	39	72	

^aDry ice-baited CDC trap.

^bWalk-in red box.

^cPercentages with different lowercase letters indicate that they are significantly different by chi-square test ($P < 0.05$).

\$watermark-text

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Table 6

Number and percentage of avian- and mammalian-derived bloodmeals from the *Cx. pipiens* complex and *Cx. tarsalis* in Sutter County, near Yuba City, 2007–2009

Host	<i>Cx. pipiens</i> complex		<i>Cx. tarsalis</i>	
	RB ^a	% ^b	RB ^a	% ^b
Avian				
American robin, <i>Turdus migratorius</i>	19	17.8ab	63	27.3a
American crow, <i>Corvus brachyrhynchos</i>	28	26.2ab	31	13.4b
Yellow-billed magpie, <i>Pica nuttalli</i>	7	6.5cde	19	8.2bc
Chicken, <i>Gallus gallus</i>	12	11.2bc	13	5.6cd
Western scrub-jay, <i>Aphelocoma californica</i>	3	2.8de	9	3.9cde
House sparrow, <i>Passer domesticus</i>	8	7.5cd	7	3.0def
Brewer's blackbird, <i>Euphagus cyanocephalus</i>	5	4.7cde	6	2.6def
House finch, <i>Carpodacus mexicanus</i>	6	5.6cde	5	2.2def
Green heron, <i>Butorides virescens</i>	3	2.8de	3	1.3ef
European starling, <i>Sturnus vulgaris</i>	7	6.5cde	2	0.9ef
Mourning dove, <i>Zenaida macroura</i>			2	0.9ef
American kestrel, <i>Falco sparverius</i>	2	1.9e	1	0.4f
Brown-headed cowbird, <i>Molothrus ater</i>	1	0.9e	1	0.4f
Red-winged blackbird, <i>Agelaius phoeniceus</i>			1	0.4f
Ring-necked pheasant, <i>Phasianus colchicus</i>			1	0.4f
Rock pigeon, <i>Columba livia</i>			1	0.4f
Western kingbird, <i>Tyrannus verticalis</i>			1	0.4f
White-faced ibis, <i>Plegadis chihi</i>			1	0.4f
Wild turkey, <i>Meleagris gallopavo</i>			1	0.4f
American bittern, <i>Botaurus lentiginosus</i>	1	0.9e		
Northern mockingbird, <i>Mimus polyglottos</i>	1	0.9e		
Tree swallow, <i>Tachycineta bicolor</i>	1	0.9e		
Undetermined duck, <i>Anas</i> sp.	1	0.9e		
Mammalian				
Domestic cow, <i>Bos taurus</i>			47	20.3ab
Domestic horse, <i>Equus caballus</i>			5	2.2def
Black-tailed jackrabbit, <i>Lepus californicus</i>			3	1.3ef
Raccoon, <i>Procyon lotor</i>			3	1.3ef
Domestic sheep, <i>Ovis aries</i>			3	1.3ef
Domestic cat, <i>Felis catus</i>			2	0.9ef
Human, <i>Homo sapiens</i>	2	1.9e		
Total 30 Species	107		231	

^aWalk-in red box.

^bPercentages with different lowercase letters indicate that they are significantly different by chi-square test ($P < 0.05$).

Table 7

Percentage of sera collected from frequently selected avian bloodmeal hosts that tested positive for WNV antibodies by enzyme immunoassay

Avian species	COAY (2003–2005) ^a		GRLA (2003–2008) ^b		KERN (2003–2007) ^c		YOLO (2006–2009) ^d	
	%	N	%	N	%	N	%	N
House sparrow	2.3	656	2.3	5,476	5.1	972	1.9	270
House finch	4.7	615	11.3	8,249	16.8	1,381	5.9	187
Western scrub-jay					39.7	552	13.7	153
Mourning dove	4	1,761	24.1	137	30.8	1020	28.6	7

^aCoachella Valley MVCD (Reisen et al. 2008c).

^bGreater Los Angeles County VCD (Kwan et al. 2010).

^cKern MVCD (Reisen et al. 2009).

^dYolo County published in part (Wheeler et al. 2009).