

The Roles of Predators, Competitors, and Secondary Salinization in Structuring Mosquito (Diptera: Culicidae) Assemblages in Ephemeral Water Bodies of the Wheatbelt of Western Australia

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ABSTRACT Studies that consider both biotic and abiotic determinants of organisms are rare, but critical to delineate underlying determinants of community richness (number of taxa) and abundance (number of larvae per water body). In this study, we consider the importance of disturbance (salinity) and predator and competitor variables on mosquitoes (Diptera: Culicidae) in small ephemeral water bodies across the Wheatbelt of Western Australia. Similar to mosquitoes, and contrary to general perceptions, nonculicid aquatic fauna (aquatic fauna) had a common occurrence (number or percentage of water bodies occupied) and were abundant (average density) in ephemeral water bodies, albeit with a simplified trophic structure. The occurrence and density (number per unit area) of aquatic fauna between water bodies were highly variable, but general relationships of aquatic fauna with rainfall, water body surface area, salinity, and mosquitoes were apparent. In contrast to mosquitoes, the density of aquatic fauna declined with recent rainfall, implying mosquitoes may colonize newly created water bodies more quickly than aquatic fauna. Assemblages (richness and density of taxa) of aquatic fauna changed along a salinity gradient, as did mosquitoes, and this was pronounced for predator groups. Densities of mosquitoes were not limited by any single taxonomic group, by a negative relationship. However, the density and richness of mosquitoes generally declined in association with increased richness of predators and density of all other taxa (taxa not specifically classified as predators or competitors of mosquitoes). These relationships may account for higher densities of mosquitoes in smaller water bodies, where richness of predators is reduced and the density of other taxa does not differ from larger water bodies. Our results also suggest salinity in the Western Australia Wheatbelt may facilitate greater abundance of halotolerant mosquitoes, *Aedes alboannulatus* Macquart and *Aedes camptorhynchus* Thomson (a vector of Ross River virus [Togoviridae: *Alphavirus*]), by releasing them from biotic regulation.

KEY WORDS Dryland salinity, temporary water, community, biotic interactions, environmental change

Biotic interactions, such as those with predators and competitors, may strongly limit mosquito (Diptera: Culicidae) abundance (average density) (Blaustein and Chase 2007, Bradshaw and Holzapfel 1992, Knight et al. 2004, Spencer et al. 2002). Numerous taxa influence the dynamics of mosquito populations (see reviews: Juliano 2007, Lounibos 2007, Mogi 2007), but few studies simultaneously investigate how biotic and abiotic factors, such as disturbance, affect mosquitoes

in nature (but see Yee and Yee 2007). Ephemeral water bodies serve as a significant source of mosquito production. This may be because of culicid fauna preferentially colonizing these water bodies to avoid interspecific interactions with predators and competitors, found in more permanent water sources, that have not encountered or entered these transitory water sources (Campos et al. 2004, Chase and Knight 2003, Juliano 2007, McDonald and Buchanan 1981, Munga et al. 2007, Williams 2006). As a result of the often simplified nature of ephemeral water bodies, theory and some evidence suggest they are less resistant to the effects of disturbance (Hart et al. 2003, Ives and Cardinale 2004). Consequently, the effect of disturbance on trophic interactions may be pronounced (Fleeger et al. 2003). Understanding which factors (biotic and abiotic) account for variation in mosquito abundance across the landscape is critical for mosquito control and vector-borne disease management.

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Ephemeral water bodies are a characteristic feature of the Wheatbelt of Western Australia (WA), and the environment in this region is disturbed by dryland salinity (a secondary salinization as a consequence of land clearing and rising groundwater tables bringing stored salt to the surface [Clarke et al. 2002, McKenzie et al. 2003]). Currently, more than one million hectares of the Wheatbelt region are affected by this secondary salinization, which is expected to expand 2- to 4-fold by 2050 (George et al. 2006, Jardine et al. 2007). Mosquitoes frequently colonize small ephemeral water bodies across the Wheatbelt, and their densities (number per unit area), within water bodies, increase rapidly after rainfall (Carver et al. 2009a, Jardine et al. 2008). It has been shown that the assemblage structure (richness and density of taxa) of mosquitoes changes with increasing water body salinity, leading to a reduction in halosensitive species and dominance of halotolerant species, such as *Aedes camptorhynchus* Thomson, a mosquito vector of Ross River virus (RRV; Togoviridae: *Alphavirus*) (Carver et al. 2009a, Jardine et al. 2008). Similarly, the assemblage structure of nonculicid aquatic fauna (potential predators and competitors of mosquitoes) in the Wheatbelt is also affected by secondary salinization (Carver et al. 2009b; Halse et al. 2003, 2004; Pinder et al. 2004, 2005). Relationships between salinity and mosquitoes may be a direct physiological effect on individual taxa and/or mediated by underlying trophic changes. In general, the trophic consequences of salinity are poorly understood.

Despite predators and competitors of mosquitoes being ubiquitous across the landscape and known to affect the abundance of mosquito larvae in individual water bodies (Brendonck et al. 2002, Kay et al. 2001, Williams 2006), their role in the regulation of mosquito populations at the landscape scale remains disputable (Srivastava 2005). A wide variety of taxa has been demonstrated to predate on mosquito larvae (reviewed by Mogi 2007). Coleoptera, Hemiptera, and Odonata are the most dominant and diverse predatory groups. Some predators are also known from Diptera, Araneae, Acarina, Crustacea, Annelida, Platyhelminthes, and Chordata (predominantly species of amphibian and fish). Taxa that act as competitors of mosquitoes are not as well defined, but generally include species in most of the above groups, as well as species of zooplankton and molluscs (Blaustein and Chase 2007, Bradshaw and Holzapfel 1992, Braks et al. 2004, Chase and Knight 2003, Greenway et al. 2003, Hagman and Shine 2006, Hart and Lovvorn 2005, Juliano 1998, Knight et al. 2004, Munga et al. 2006). Additionally, the occurrence (number or percentage of water bodies occupied) of predators, competitors, and their allelochemicals can affect oviposition by mosquitoes (Blaustein et al. 2004, Mokany and Shine 2003, Spencer et al. 2002).

The structure (assemblage structure) of aquatic fauna occurring in permanent and seasonal wetlands in the WA Wheatbelt and their relationships to salinity are well documented (Cale et al. 2004; Halse et al. 2003, 2004; Pinder et al. 2004, 2005). Little is known,

however, of the structure of aquatic fauna communities that occur in small ephemeral water bodies in the WA Wheatbelt. Biotic interactions between nonculicid aquatic taxa and larval of mosquito species in the WA Wheatbelt, and the effect of salinity on these, have not previously been considered, so broad relationships are examined in this study. We investigate the following: 1) the relationship of nonculicid aquatic fauna (predators and competitors of mosquitoes, as well as other taxa that may interact with mosquitoes) that occur in ephemeral water bodies to water body size and rainfall; 2) the relationship between the disturbance of secondary salinity and the structure of nonculicid aquatic fauna; 3) broad relationships of mosquitoes with potential predators, competitors, and other taxa across the landscape (while controlling for the interrelated effects of salinity on culicid and nonculicid aquatic fauna); and 4) implications of salinity to biotic interactions in ephemeral water bodies.

We define predators as taxonomic groups that are predominantly composed of known predatory species (primarily Coleoptera, Hemiptera, Odonata, and Araneae). Competitors are considered to be taxa within a similar functional feeding mode (filter feeders) to mosquitoes. Little is known of the extent to which other taxa compete with mosquitoes. Grazers, collectors, and bottom feeding aquatic fauna are treated as other taxa, which may be independent or indirectly interact with mosquitoes in unidentified ways (for example, molluscs; Knight et al. 2004). We predict the following: 1) smaller ephemeral water bodies have few predators and competitors, but the abundance of nonculicid aquatic fauna exhibits a similar response to rainfall as mosquitoes; 2) nonculicid aquatic fauna will change with increasing salinity. We hypothesize secondary salinity is too simplistic to account for the abundance of mosquitoes and, in addition to salinity, biotic relationships will be evident.

Materials and Methods

Study Area. This study was undertaken in the Great Southern meteorological district of the WA Wheatbelt (Fig. 1). The study area has a Mediterranean climate with hot dry summers and mild wet winters. Annual rainfall declines from ≈ 600 mm at the western boundary of our study area to 350 mm in the east (Australian Bureau of Meteorology). A large proportion (80–90%) of the region has been cleared for agriculture (Halse et al. 2004).

Surveys. A random stratified sampling design was used whereby samples of aquatic fauna were collected from rain-fed ephemeral water bodies (size range, 0.2–9700 m²) occurring within one hectare square quadrats, with quadrats stratified across the Great Southern meteorological district of the WA Wheatbelt (Fig. 1). Quadrats were located in patches of remnant native vegetation corresponding with locations previously used by the WA Department of Environment and Conservation to assess the impacts of secondary salinization (Keighery et al. 2004). For this study, individual pools within quadrats were used as repli-

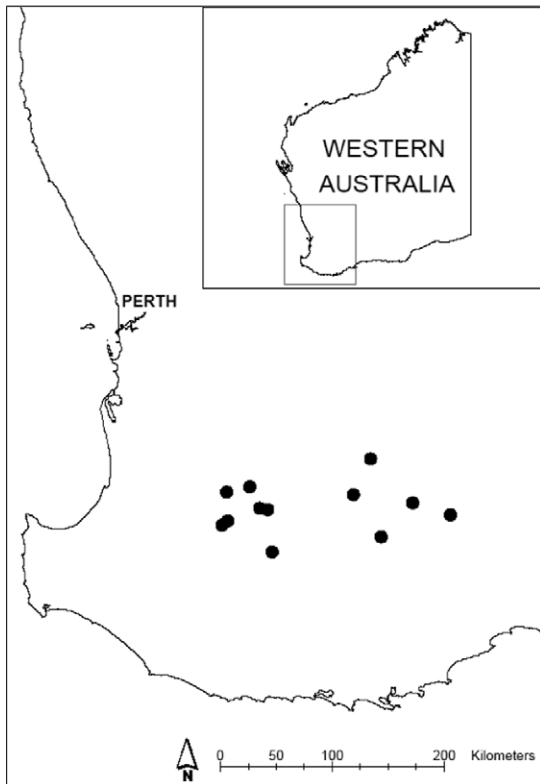


Fig. 1. Locations of quadrats from which water bodies were surveyed for aquatic fauna in the Wheatbelt of south-west WA. Site coordinates (latitude, longitude): $-33.35628, 116.62067$; $-33.31329, 116.80671$; $-33.48809, 116.88669$; $-33.49884, 116.95164$; $-33.59043, 116.63058$; $-33.62621, 116.58273$; $-33.84380, 116.98703$; $-33.08636, 117.77947$; $-33.37755, 117.64134$; $-33.71999, 117.86499$; $-33.44393, 118.11712$; $-33.54058, 118.42258$.

cates to assess changes across the Wheatbelt. Surveys were undertaken fortnightly from September to November 2005 (spring) and February to May 2006 (late summer and autumn), giving a total of 11 sampling occasions. These seasons were chosen to maximize the number of mosquitoes, water bodies, the range of water body sizes, and salinities observed in the field. Sampling was not conducted in winter because higher rainfall and subsequent dilution result in fewer saline water bodies. In summer, there are few water bodies because of low rainfall, high temperatures, and evaporation.

At each water body, sampling consisted of sweeping a standard D-frame 500-mm-diameter Freshwater Biological Association pond net (250 μm mesh size; Australian Entomological Supplies, Bangalow, New South Wales, Australia) through each water body. Every effort was made to sample all microhabitats evenly within a water body. Up to 10 m^2 surface area was swept per water body, with the total surface area of the water body recorded (calculated from measurement of water body dimensions [circular, oval, or oblong in most cases] using a tape measure). In water

bodies with a surface area $<10 \text{ m}^2$, the whole water body was sampled and the area was recorded. All samples were preserved in 70% ethanol and returned to the laboratory, where aquatic fauna were classified under a microscope. Large samples were homogenized, then split into half or quarters for subsampling. Abundance of each taxon was standardized to number per meter^2 of water body surface area (number of mosquitoes per surface area sampled).

For each water body, salinity was recorded using a YSI-63 m (YSI, Yellow Springs, OH). Rainfall for water bodies within each stratified quadrat was recorded as the cumulative amount of rain for 14 d preceding sampling (the time period between each sampling trip). Rainfall data were derived from the weather station of closest proximity to each quadrat (Australian Bureau of Meteorology; weather stations: Collie, Katanning, Lake Grace, Narrogin, and Wagin).

Classification of Taxa. Nonculicid aquatic fauna (referred to as aquatic fauna in this study) were broadly classified as predators (taxa predominantly composed of species known to predate on mosquitoes), competitors (taxa predominantly composed of species that were filter feeders, thus resource competitors with mosquito larvae), and other taxa (taxa that were neither filter feeders nor potential predators of mosquitoes) (Appendix 1). Taxa were identified into the following groups: Mollusca, Annelida, Cnidaria, Platyhelminthes, and Chordata were grouped by phylum; Odonata, Trichoptera, Araneae, and Crustacea were grouped by order; Notonectidae and nonculicid Diptera were identified to family; Dytiscidae, Hydrophilidae, and Corixidae were identified to genus; and Culicidae were identified to species (Liehne 1991). Multiple species were likely to occur within taxa that were not discriminated to species level.

Larval and adult Coleoptera were encountered during surveys and possibly have differential predatory relationships to mosquitoes. A preliminary analysis of relationships between densities of mosquitoes and densities of larval and adult coleopterans, however, found associations were consistent for both larvae and adults. Thus, within each coleopteran genus, larvae and adults were pooled for all further analyses. Additionally, interspecific interactions among mosquito species may occur, but we did not find negative relationships among the density of mosquito species or their richness in preliminary analyses.

Analyses. This study was undertaken over two sampling periods during a 9-mo time frame. Previously, we were unable to detect temporal changes in assemblage structure of mosquito larvae between sampling weeks and seasons (Carver et al. 2009a). This investigation focused on broad relationships as evidence of biotic regulation of mosquito larvae by aquatic fauna. Accordingly, investigation of temporal changes in relationships between aquatic fauna and mosquito larvae was beyond the scope of this study, and samples of aquatic fauna across all sampling occasions were combined for analyses.

To examine our predictions, nonparametric permutation based multivariate analysis of variance

(NPMANOVA) was used to relate aquatic faunal assemblage structure and linear regression analyses and to relate taxon richness (number of taxa) and density data, to regional rainfall, surface area, and salinity of ephemeral water bodies. Rainfall, water body surface area, and salinity were categorized for the analyses (0–9.9, 10–19.9, 20–29.9, 30–39.9, and 40+ mm; 0–0.9, 1–9.9, 10–99.9, 100–999.9, and 1,000–10,000 m²; and 0–4.9, 5–9.9, 10–14.9, 15–19.9, and 20+ gL⁻¹ total dissolved solids (TDS), respectively). Post hoc analyses of pairwise comparisons were used to determine significance between categories. Assemblage structure data were fourth root transformed, to reduce the dominance of abundant taxa on the analysis, and based on Bray–Curtis similarity matrices. NPMANOVA enabled multivariate comparison of uneven category sizes (NPMANOVA program; Anderson 2004). Linear regression analyses were used to examine relationships between individual taxa and groups of taxa to rainfall, surface area, and salinity variables. Before analyses, data used in linear regression were examined for normality using Shapiro–Wilk’s test of normality, and non-normal data were normalized by transformation. Analyses were undertaken using SPSS 15.0 (SPSS, Chicago, IL).

To examine our hypothesis, that in addition to salinity, biotic relationships between mosquito larvae and aquatic fauna would be evident, a stepwise multiple regression was used. Total density of mosquito larvae, species richness, and the density of each mosquito species were analyzed against the density and richness of aquatic faunal groups. In cases in which mosquito and aquatic faunal groups were significantly associated with salinity, we analyzed the residuals to control for interrelated effects of salinity on the multiple regression. Analyses were undertaken using SPSS 15.0 (SPSS, Chicago, IL). Three mosquito species, *Aedes bancroftianus* Edwards (Diptera: Culicidae), *Culiseta atra* Lee (Diptera: Culicidae), and *Coquillettidia nr linealis* Marks (Diptera: Culicidae), were seldom encountered (see Appendix 1) and excluded from analyses.

For all statistical tests, the significance level was set at 0.05. But to reduce the probability of committing type-I statistical errors, α was adjusted for multiple comparisons using the sequential Bonferroni method (Rice 1989), where k is the number of analyses testing the same hypothesis. The Bonferroni adjustment was applied individually to broad community descriptors (density and richness of total aquatic fauna, predators, competitors, and other taxa), predator groups, competitor groups, and other taxa, because the number of taxa and taxonomic groups was large ($n = 61$). Splitting up taxonomic groups reduced the probability of committing type-II statistical error (Nakagawa 2004).

Results

Aquatic Fauna in Ephemeral Water Bodies. Across 11 sampling occasions, 180 samples were collected. Predators, competitors, and other taxa were widespread and had a similar or more common occurrence (87.8, 94.4, and 95.6% occurrence, respectively) than

Culicidae (86.1% occurrence) (Appendix 1). Competitors were the most numerous, comprising 95.18% of total faunal abundance, whereas predators were the least abundant group at 0.35% of total faunal abundance (Appendix 1). The most common occurring predator groups were as follows: dytiscids (Coleoptera: Dytiscidae) *Necterosoma* sp., *Antiporus* sp., *Rhantus* sp., Bidessini, *Platynectes* sp., and *Paroster* sp.; the hydrophilids (Coleoptera: Hydrophilidae) *Paracymus* sp., *Limnoxenus* sp., and *Berosus* sp.; and the corixid (Hemiptera: Corixidae) *Micronecta* sp. and Odonata (Appendix 1). Of these groups, Dytiscidae were most widespread and abundant, with an occurrence of 82.2%, at average densities of 20/m² (Appendix 1). Ostracoda, Copepoda, and Cladocera had a common occurrence and were abundant competitors (Appendix 1). Other taxa were variable between water bodies (Appendix 1). Chironomidae were the most common (86.7% occurrence) and abundant (average density 262.4/m²) of other taxa, but Ephydriidae and larval anura (Chordata) also occurred in 17.8 and 15.6% of water bodies, respectively (Appendix 1).

Rainfall and Aquatic Fauna. Assemblage structure of all aquatic fauna, predators, competitors, and other taxa groups exhibited a significant relationship with increasing rainfall (NPMANOVA: $F_{4, 175} = 3.250, P < 0.001$; $F_{4, 175} = 4.078, P < 0.001$; $F_{4, 175} = 2.659, P < 0.001$; and $F_{4, 175} = 4.3643, P < 0.001$, respectively). These relationships between assemblage structure and rainfall were indicative of overall declines in the density of aquatic fauna, predators, and competitors with increasing rainfall (Fig. 2a; Table 1). Only *Platynectes* sp. and Chironomidae increased with rainfall (Table 1). Explained variation of significant relationships between rainfall and nonculicid aquatic fauna was low (Table 1). The general decline in density of aquatic fauna was contrary to densities of mosquitoes (Fig. 2a). Average richness of aquatic fauna, predators, competitors, and other taxa was unrelated to rainfall (linear regressions, $P > 0.05$ in all instances).

Surface Area and Aquatic Fauna. Similar to mosquitoes (Carver et al. 2009a), assemblages of aquatic fauna, predators, competitors, and other taxa were associated with increasing surface area of water bodies (NPMANOVA: $F_{4, 175} = 4.550, P < 0.001$; $F_{4, 175} = 2.791, P < 0.001$; $F_{4, 175} = 3.932, P < 0.001$; and $F_{4, 175} = 1.632, P < 0.05$, respectively). Densities of aquatic fauna, predators, and competitors were negatively related to water body surface area (Fig. 2b; Table 1), whereas richness of aquatic fauna, predators, and other taxa was positively related (Fig. 2b; Table 1). Again, the explained variation of significant relationships was low (Table 1).

Relationship of Aquatic Fauna to Salinity. Assemblage structure of aquatic fauna (nonculicid) exhibited a change associated with salinity, reflecting a gradient (NPMANOVA: $F_{4, 175} = 6.267, P < 0.001$; post hoc comparisons among salinity [gL⁻¹ TDS] categories 0–4.9a, 5–9.9b, 10–14.9c, 15–19.9cd, 20+ d). Overall, there was a negative relationship between the density and richness of aquatic fauna with increasing

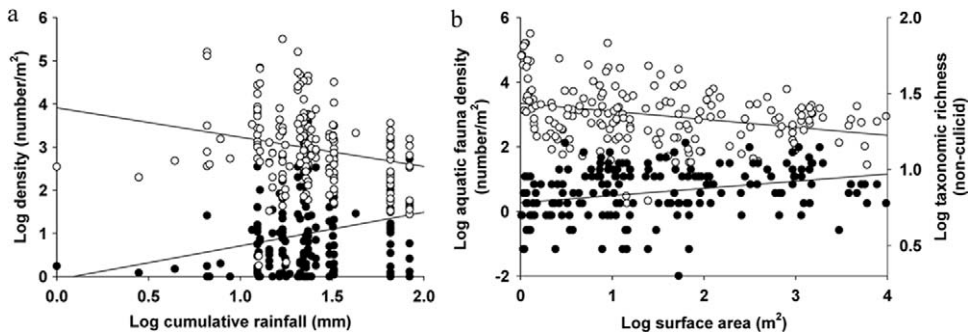


Fig. 2. Relationship between (a) the density of nonculcid aquatic fauna (○) and mosquitoes (●) in ephemeral water bodies ($n = 180$) to cumulative rainfall (14 d preceding aquatic sampling) (linear regressions: $r^2 = 0.049$, $F_{1, 178} = 9.264$, $P < 0.01$, and $r^2 = 0.064$, $F_{1, 178} = 12.148$, $P < 0.001$, respectively); and (b) the density (○) and richness (●) of nonculcid fauna with water body surface area (linear regressions: $r^2 = 0.088$, $F_{1, 178} = 17.169$, $P < 0.001$, and $r^2 = 0.087$, $F_{1, 178} = 16.971$, $P < 0.001$, respectively).

salinity (Table 1; Fig. 3). Of the 48 taxonomic groups of aquatic fauna, 25 were not detected above 10 gL^{-1} TDS (Fig. 3). The relationship of predator assemblage structure and richness to salinity was pronounced (NPMANOVA: $F_{4, 175} = 4.644$, $P < 0.001$; post hoc comparisons among salinity [gL^{-1} TDS] categories 0–4.9a, 5–9.9b, 10–14.9c, 15–19.9c, 20 + c; Figs. 3 and 4; Table 1). As salinity increased, the assemblage structure of predators changed and richness declined up to 10 gL^{-1} TDS (Figs. 3 and 4; Table 1). However, the overall density of predators was unrelated to salinity (linear regression, $P > 0.05$), reflecting increased oc-

currence and densities of *Necterosoma* sp. associated with increasing salinity (Table 1; Fig. 3). Assemblage structure of competitors was significantly associated with increasing salinity (NPMANOVA: $F_{4, 175} = 5.305$, $P < 0.001$), because of the density and richness of competitors, Copepoda and Cladocera, declining with increasing salinity (Table 1; Fig. 3), and Ostracoda also having a declining trend (Table 1 and $r^2 = 0.021$, $F_{1, 178} = 3.873$, $P = 0.051$). Assemblages of other taxa changed with increasing salinity (NPMANOVA: $F_{4, 175} = 3.348$, $P < 0.001$), reflecting an overall increase in the density of other taxa with increasing salinity

Table 1. Significant linear regressions of nonculcid aquatic fauna (no. per m^2 and taxonomic richness) with cumulative rainfall (mm, 14 d preceding aquatic sampling), water body surface area (m^2), and salinity (gL^{-1} total dissolved solids)

	r^2	$F_{1, 178}$	P	Critical α	Reg. coef. (\pm SE)	y-intercept (\pm SE)
Cumulative rainfall (mm)						
Density (nonculcid)	0.049	9.264	<0.010	0.010	-0.678 (0.222)	3.907 (0.311)
Predator density	0.057	10.717	<0.001	0.010	-0.525 (0.160)	1.563 (0.224)
Competitor density	0.063	11.869	<0.001	0.010	-1.041 (0.302)	4.047 (0.422)
<i>Platynectes</i> sp.	0.052	9.673	<0.002	0.002	0.175 (0.056)	-0.164 (0.079)
Chironomidae	0.046	8.500	<0.003	0.003	0.716 (0.246)	0.587 (0.343)
Surface area (m^2)						
Density (nonculcid)	0.088	17.169	<0.001	0.025	-0.247 (0.060)	3.344 (0.109)
Taxonomic richness (nonculcid)	0.087	16.971	<0.001	0.025	0.749 (0.182)	5.521 (0.331)
Predator density	0.036	6.653	<0.025	0.025	-0.114 (0.044)	1.014 (0.081)
Predator richness	0.093	18.193	<0.001	0.025	0.068 (0.016)	0.355 (0.029)
Competitor density	0.061	11.536	<0.001	0.025	-0.281 (0.083)	3.038 (0.151)
Other richness	0.081	15.681	<0.001	0.025	0.046 (0.012)	0.381 (0.021)
Salinity (gL^{-1} TDS)						
Density (nonculcid)	0.055	10.312	<0.025	0.025	-0.452 (0.141)	3.233 (0.102)
Taxonomic richness (nonculcid)	0.088	17.272	<0.001	0.025	-1.749 (0.421)	7.589 (0.305)
Predator richness	0.055	10.264	<0.025	0.025	-0.120 (0.037)	0.521 (0.027)
<i>Necterosoma</i> sp.	0.202	44.995	<0.001	0.002	0.476 (0.071)	-0.020 (0.052)
Competitor density	0.163	34.600	<0.001	0.025	-1.065 (0.181)	3.218 (0.131)
Competitor richness	0.221	50.422	<0.001	0.025	-0.164 (0.023)	0.580 (0.017)
Copepoda	0.164	34.904	<0.001	0.025	-1.195 (0.202)	2.205 (0.147)
Cladocera	0.084	16.234	<0.001	0.025	-0.864 (0.214)	1.899 (0.156)
Other taxa density	0.025	4.546	<0.025	0.025	0.292 (0.137)	1.605 (0.099)
Diptera (nonculcid)	0.048	8.96	<0.003	0.003	0.453 (0.151)	1.359 (0.110)
Stratiomyidae	0.098	19.321	<0.001	0.003	0.112 (0.026)	-0.031 (0.019)
Empididae	0.088	17.119	<0.001	0.003	0.141 (0.034)	-0.037 (0.025)
Amphipoda	0.155	32.544	<0.001	0.003	0.377 (0.066)	-0.049 (0.048)
Chordata	0.056	10.521	<0.003	0.003	-0.125 (0.039)	0.139 (0.028)
Mollusca	0.074	14.23	<0.001	0.003	-0.250 (0.066)	0.281 (0.048)

Predictors corrected for multiple comparisons using the sequential Bonferroni method, critical α -value displayed. Reg. coef., Regression coefficient.

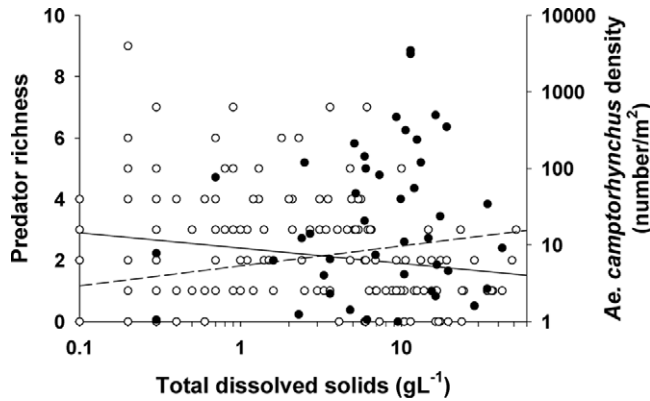


Fig. 4. Relationship of the richness of predators (○, solid line) and density of *Ae. camptorhynchus* (●, dashed line) to salinity (g L^{-1} total dissolved solids, linear regressions: $r^2 = 0.055$, $F_{1, 178} = 10.264$, $P < 0.01$, and $r^2 = 0.179$, $F_{1, 178} = 38.715$, $P < 0.001$, respectively).

Relationships Between Mosquitoes and Aquatic Fauna. No single taxonomic group was significantly linked to all species of mosquito (Table 2). The total density of mosquitoes and densities of *Aedes albopictus*, *Aedes camptorhynchus*, and *Culex australicus*, however, were negatively related to predator richness (Table 2; Fig. 4). The richness of mosquito species declined with increasing densities of other taxa (Table 2). Other relationships between mosquitoes and aquatic fauna were positive, many of which were with predatory groups, such as between *Ae. camptorhynchus* and *Necterosoma* sp. (Table 2; Fig. 4). The overall amount of variation in larval mosquito abundance and richness, and in the abundance of

individual species explained by aquatic fauna was low (Table 2).

Discussion

This study principally found that mosquitoes and aquatic fauna in the Wheatbelt are widespread and abundant in ephemeral water bodies. The occurrence and abundance of aquatic fauna between water bodies are highly variable, but some general relationships of noncyclic aquatic fauna with rainfall, water body surface area, salinity, and mosquitoes were apparent. Unlike mosquitoes, the density of most aquatic fauna in the Wheatbelt did not increase in the 14 d after

Table 2. Stepwise multiple regression of how mosquito density (no. per m^2), richness, and the density of each species changed with the density and richness of predators and competitors ($n = 180$)

	Predictors	r^2	Regression coefficient	SE	$t_{1, 178}$	P
Density	(Constant)	0.193	0.673	0.100	6.727	<0.001
	Predator richness		-1.729	0.281	6.158	<0.001
	Coleoptera		0.459	0.112	4.094	<0.001
Richness	(Constant)	0.128	2.832	0.356	7.964	<0.001
	Diptera		0.877	0.181	4.858	<0.001
	Other taxa density		-0.725	0.197	3.686	<0.001
<i>Ae. albopictus</i>	(Constant)	0.115	-0.063	0.055	1.133	0.259
	Predator richness		-0.861	0.227	3.787	<0.001
	<i>Platynectes</i> sp.		0.825	0.232	3.553	<0.001
<i>Ae. camptorhynchus</i>	(Constant)	0.135	0.001	0.046	0.001	0.999
	<i>Necterosoma</i> sp.		0.458	0.105	4.349	<0.001
	Predator richness		-0.710	0.199	3.561	<0.001
<i>Cx. australicus</i>	(Constant)	0.279	0.186	0.041	4.562	<0.001
	Arthropoda		0.164	0.044	3.683	<0.001
	<i>Sternoprisus</i> sp.		0.923	0.268	3.444	<0.001
	<i>Limbodessus</i> sp.		0.703	0.194	3.615	<0.001
	<i>Platynectes</i> sp.		0.623	0.169	3.693	<0.001
	Predator richness		-0.536	0.168	3.191	0.002
<i>Cx. globocoxitus</i>	(Constant)	0.123	1.197	0.034	5.781	<0.001
	Cladocera		1.128	0.026	4.995	<0.001
<i>An. annulipes</i>	(Constant)	0.187	-0.042	0.049	0.848	0.397
	Ostracoda		0.093	0.021	4.529	<0.001
	<i>Limbodessus</i> sp.		0.469	0.132	3.560	<0.001

Analysis controlled for the effect of salinity on aquatic fauna, where a significant salinity relationship occurred. Predictors are corrected for multiple comparisons with the sequential Bonferroni adjustment. Critical α -values after sequential Bonferroni correction: density, 0.002; richness, 0.003; *Ae. albopictus*, 0.002; *Ae. camptorhynchus*, 0.002; *Cx. australicus*, 0.003; *Cx. globocoxitus*, 0.01; *An. annulipes*, 0.002.

rainfall, which may suggest a slower numerical response than mosquitoes. Salinity influences the assemblage structure of aquatic fauna, generally resulting in reduced abundance and richness of taxa (Pinder et al. 2004, 2005), which potentially influences the density and richness of mosquitoes by modifying interspecific interactions. Nevertheless, negative relationships between groups of aquatic fauna and mosquitoes are apparent, suggesting some biotic regulation of mosquito populations occurs. In particular, densities of *Ae. alboannulatus*, *Cx. australicus*, and the RRV vector, *Ae. camptorhynchus*, were negatively related to richness of predators.

Predators and competitors can affect the survival, growth, and development of mosquitoes, which may be why mosquitoes chose habitat minimizing these interactions (Arav and Blaustein 2006, Knight et al. 2004). In support of our first prediction, the richness of aquatic fauna, predators, and other taxa was greater in larger water bodies. However, contrary to our initial predictions, aquatic fauna are common (as common, if not more so than mosquitoes) and abundant in ephemeral water bodies, with greater densities in smaller water bodies. Traditionally, mosquito predators and competitors have been perceived as less common in small ephemeral water bodies (Knight et al. 2004, Mottram and Kettle 1997, Roth and Jackson 1987, Spencer et al. 1999), but increasing evidence suggests this generalization may not be valid (Brendonck et al. 2002, Chase and Knight 2003, Eitam and Blaustein 2004, Lundkvist et al. 2003, McDonald and Buchanan 1981, Mogi et al. 1999). For example, Mogi et al. (1999) found coleopterans, odonates, and chironomids were common in small artificial ground pools (occurring in 52–100% of pools) in Indonesia. Likewise, Chase and Knight (2003) observed predators and competitors to be common, and competitors abundant, in temporary wetlands. Despite aquatic fauna being conspicuous in ephemeral water bodies, the richness of predators and competitors was in general reduced in smaller water bodies, which may suggest fewer interspecific interactions occur therein.

The density of mosquitoes, *Ae. alboannulatus*, *Ae. camptorhynchus*, and *Cx. australicus*, was negatively related to the richness of predators independent of salinity, supporting our initial hypothesis. Dytiscidae are the most frequently occurring predator group (82.2% of water bodies), and other studies have also found these insects to be widespread and capable of regulating mosquito larvae (Campos et al. 2004; Lundkvist et al. 2003; Mottram and Kettle 1997; Munga et al. 2007; Nilsson and Svensson 1994, 1995; Schafer et al. 2006; Stout 1982). However, we were unable to implicate dytiscids, or any other individual predator group, as widespread regulators of mosquito abundance, by a negative association, across the landscape. This may be because of the level of taxonomic discrimination, but most predators are polyphagous (Campos et al. 2004, Cisneros and Rosenheim 1997, Mogi 2007, Shaalan et al. 2007, Woodward and Hildrew 2002). It is possible we consistently missed some predators, through sampling error. However, we were me-

ticulous to sample all habitats, within water bodies, and our records of aquatic fauna are consistent with other studies in the same region (Cale et al. 2004; Halse 1981; Pinder et al. 2004, 2005). A more parsimonious explanation is that occurrence of individual predator groups in ephemeral water bodies is highly variable, and top-down control by a single predator group may not be widely limiting of mosquitoes. Instead, richness of predators appears to be a better determinant of mosquito densities. In several cases, mosquito densities were positively associated with the density of predator groups. It is possible these predators facilitated increased abundance of mosquitoes by having preferences for prey taxa, which are competitors of mosquitoes (Griswold and Lounibos 2005).

Much recent literature has focused on effects of odonates and hemipterans as predators and oviposition deterrents of mosquitoes (Arav and Blaustein 2006; Blaustein 1998; Blaustein et al. 2004; Bond et al. 2006; Quiroz-Martinez et al. 2005; Shaalan et al. 2007; Spencer et al. 2002; Stav et al. 1999, 2000; Yanoviak 1999, 2001). We found a negative, but nonsignificant, trend between the density of mosquitoes and densities of Odonata and Hemiptera (linear regressions: $r^2 = 0.022$, $F_{1, 178} = 4.001$, $P = 0.047$, and $r^2 = 0.041$, $F_{1, 178} = 7.581$, $P = 0.007$, respectively, critical $\alpha = 0.002$). These groups occupied a small proportion of water bodies (23.3 and 10.6%), however, and appear unlikely to have a widespread regulatory role on mosquito abundance across the landscape.

The general negative relationship between rainfall and abundance of aquatic fauna may suggest rain, at least initially, dilutes densities of aquatic fauna, which potentially compete with or predate upon mosquitoes. Nondipteran aquatic fauna probably respond to rainfall over a longer temporal period than mosquitoes. For example, Chase and Knight (2003) observed predators and competitors of mosquitoes were slow to reinvade semipermanent wetlands after a drought, because these species had slower generation times than mosquitoes. Mosquitoes are opportunistic invaders, able to use available habitat rapidly, potentially avoiding density-dependent population regulation. McDonald and Buchanan (1981), for example, created artificial water bodies and observed *Culex annulirostris* Skuse and *Cx. australicus* larvae within 48 h. Colonization of predators (Coleoptera, Hemiptera, and eventually Odonata) was also rapid, but it took longer for predators to become abundant and influence mosquito densities (McDonald and Buchanan 1981). Chironomids also increased rapidly with rainfall, which may be because of similar life history traits as mosquitoes (larval occurrence as a result of oviposition directly on water bodies or surrounding substrate by aerial adults). Additionally, mosquitoes may have an advantage over competitor groups in colonization of newly created water bodies, because adult mosquitoes actively seek out water bodies. Some groups we identified as competitors, however, are reliant on other taxa or suitable environmental conditions for dispersal (Gooderham and Tsyrlin 2003).

We predicted assemblages of aquatic fauna would be associated with secondary salinity, an environmental disturbance. Changes in assemblage structure of aquatic fauna were consistent with a salinity gradient. This gradient was particularly pronounced for predators, with numerous predatory groups replaced by *Necterosoma* sp., which became more abundant in saline water. Pinder et al. (2004, 2005) also found species richness of aquatic fauna in the Wheatbelt declined, and assemblage structure changed, in relation to salinity. Similarly, Pinder et al. (2004) also noted *Necterosoma penicillatus* Clark (Coleoptera: Dytiscidae) was common in saline wetlands.

A large amount of variability in mosquito density and richness was not associated with aquatic fauna. It is also possible this variation may be because of differences in nutrient sources between water bodies, reflecting variable proximities to agricultural inputs. The patches of remnant native vegetation, in which our quadrats were situated, were surrounded by sheep farms. We, however, attempted to minimize potential nutrient inputs from agricultural sources by separating quadrats from agricultural land by >100 m at each site. Additionally, topographical variation among sites was low and water bodies were fed predominantly by rainfall and groundwater sources, rather than runoff from agricultural land.

Unexplained variability in mosquito density may also be because of abiotic, habitat, or the variable temporal and spatial nature of ephemeral water bodies. More variation in mosquito density and the density of halotolerant species, *Ae. alboannulatus* and *Ae. camptorhynchus*, is associated with abiotic and habitat factors, than aquatic fauna (Carver et al. 2009a). Conversely, a greater proportion of variation in mosquito richness and density of halosensitive species, *Cx. australicus* and *Anopheles annulipes*, is associated with aquatic fauna than abiotic and habitat factors. These relationships may suggest that as salinity increases (particularly >10 gL⁻¹ TDS), a trophic cascade may occur, releasing competitively inferior halotolerant mosquito species, such as *Ae. alboannulatus* and the RRV vector, *Ae. camptorhynchus* (and possibly non-culicid Diptera), from interspecific regulation (Carver et al. 2009b). Herbst (2006), for example, examined trophic interactions between a predatory water boatman, *Trichocorixa reticulata* Guerin-Menaville (Hemiptera: Corixidae); brine shrimp, *Artemia franciscana* Kellogg (Anostraca: Pontellidae); and brine fly, *Ephydra gracilis* Packard (Diptera: Ephydriidae). Herbst (2006) found *T. reticulata* reduced the abundance of *A. franciscana* and *E. gracilis* at low salinities, but halosensitivity of *T. reticulata* resulted in predatory release and increased abundance of *A. franciscana* and *E. gracilis* at higher salinities.

Negative relationships between mosquitoes and competitor groups were not observed in this study. Relationships among *Culex globocoxitus*, *An. annulipes*, and competitor groups were positive, suggesting predators may regulate abundance of competitors across the landscape, but not these mosquitoes (Holt 1977).

Alternatively, resources (appropriate nutrients and habitat) may be a limiting factor of abundance and richness in ephemeral water bodies (Bradshaw and Holzapfel 1992, Yee et al. 2007). If resources are limiting, it suggests *Cx. globocoxitus* and *An. annulipes* do not interact with nonpredatory aquatic fauna. It is also possible interactions between mosquitoes and competitors are only weakly competitive and, as such, not significant in this study.

It has, however, been suggested mosquitoes will be excluded or avoid oviposition where the density of competitors increases (Blaustein and Chase 2007, Chase and Knight 2003, Greenway et al. 2003, Juliano 2009, Knight et al. 2004, Mokany and Shine 2003). This may explain the negative relationship between mosquito richness and the density of other taxa. Other taxa are composed of different functional feeding groups to mosquitoes and not directly considered competitors in this study. Some studies, however, have demonstrated reductions in mosquitoes, attributable to larval anurans and molluscs (Hagman and Shine 2006, Knight et al. 2004, Mokany and Shine 2003). Aquatic competitors of mosquitoes require better characterization.

Our designation of aquatic taxa into predator, competitor, and other groups was broad in this study because there is little specific knowledge about interactions between aquatic fauna and mosquito larvae in WA. Additionally, aquatic fauna were not discriminated to species in this study, and the niche range of individual taxonomic groups may be large in many cases. Furthermore, niches vary between culicid species (Liehne 1991, Merritt et al. 1992), potentially affecting the relationships of aquatic fauna to particular mosquito species. For example, competitors of *Aedes* sp. might be better classified as grazers (Merritt et al. 1992). In preliminary analyses, however, we examined a variety of group designations for aquatic fauna and their relationships to individual mosquito species and found the outcomes of this investigation were not affected. Additionally, there were no negative relationships between individual taxa and mosquito species. We argue that results presented in this study are generally representative of potential biotic relationships.

Relationships examined between aquatic fauna and mosquito larvae in this study were over a broad temporal period. Further research, particularly under controlled experimental settings, is warranted to control for variability between small ephemeral water bodies, to investigate positive and negative relationships between mosquitoes and aquatic fauna, and to affirm cause and effect. Notwithstanding a confirmed mechanism, however, neither individual predator or competitor taxa, nor other taxonomic groups, appear to broadly limit abundance of mosquitoes in ephemeral water bodies across the inland WA landscape. Rather, richness of predators and density of other taxa may be more important determinants of mosquitoes. For example, Greenway et al. (2003) found a negative relationship between mosquitoes and macroinvertebrate richness in constructed wetlands. We speculate that in addition to abiotic factors, such as salinity and

rainfall, numerous weak interspecific interactions with diverse taxonomic groups may be important determinants of mosquito abundance.

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Appendix 1. The classification of taxa (P, predator; C, competitor; and O, other taxa), no. of water bodies each taxonomic group occurred in, their mean densities (no. per m²) across all water bodies, and total faunal abundance (% of all fauna collected)

Group	Classification	Occurrence n (%)	Density		Total faunal abundance (%)
			Mean	SE	
Density (nonculicid)		180 (100)	9,491.66	2,528.29	98.51
Taxonomic richness (nonculicid)			6.62	0.21	
Predator density		158 (87.8)	33.60	9.58	0.35
Predator richness			2.28	0.13	
Competitor density		170 (94.4)	9,147.28	2,516.78	95.18
Competitor richness			2.27	0.07	
Other taxa density		172 (95.6)	285.26	44.77	2.98
Other richness			2.03	0.09	
Arthropoda (nonculicid)		180 (100)	9,481.60	2,528.35	98.41
Coleoptera		152 (84.4)	21.26	8.15	0.22
Dytiscidae		148 (82.2)	20.07	7.86	0.21
<i>Necterosoma</i>	P	53 (29.4)	7.05	2.98	0.07
<i>Antiporus</i>	P	35 (19.4)	0.87	0.31	0.01
<i>Rhantus</i>	P	31 (17.2)	0.36	0.14	<0.01
Bidessini	P	30 (16.7)	7.92	6.69	0.08
<i>Platynectes</i>	P	34 (18.9)	0.66	0.30	0.01
<i>Eretes</i>	P	2 (1.1)	0.00	0.00	<0.01
<i>Hyderodes</i>	P	11 (6.1)	0.02	0.01	<0.01
<i>Megaporus</i>	P	6 (3.3)	0.03	0.02	<0.01
<i>Lancetes</i>	P	4 (2.2)	0.01	0.00	<0.01
<i>Sternopriscus</i>	P	2 (1.1)	0.45	0.45	<0.01
<i>Limbodessus</i>	P	11 (6.11)	1.21	1.11	0.01
<i>Paroster</i>	P	27 (15.0)	1.48	0.56	0.02
Hydrophilidae		64 (35.6)	1.19	0.34	0.01
<i>Paracymus</i>	P	24 (13.3)	0.68	0.30	0.01
<i>Limnoxenus</i>	P	30 (16.7)	0.29	0.12	<0.01
<i>Berosus</i>	P	20 (11.1)	0.22	0.11	<0.01
Hemiptera		42 (23.3)	10.77	4.94	0.11
Corixidae	P	42 (23.3)	10.25	4.87	0.11
<i>Micronecta</i>	P	39 (21.7)	10.21	4.87	0.11
<i>Sigara</i>	P	3 (1.7)	0.03	0.03	<0.01
<i>Agraptocorixa</i>	P	1 (0.6)	0.01	0.01	<0.01
Notonectidae	P	10 (5.6)	0.52	0.22	0.01
Odonata	P	19 (10.6)	0.07	0.02	<0.01
Hydracarina	P	14 (7.8)	1.47	0.66	0.02
Trichoptera	O	6 (3.3)	1.14	0.86	0.01
Diptera (nonculicid)		162 (90.0)	268.83	44.79	2.80
Chironomidae	O	156 (86.7)	262.40	44.49	2.73
Dolichopodidae	O	17 (9.4)	1.18	0.53	0.01
Ceratopogonidae	O	14 (7.8)	1.44	0.76	0.02
Ephydriidae	O	32 (17.8)	1.77	0.69	0.02

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Appendix 1. Continued

Group	Classification	Occurrence <i>n</i> (%)	Density		Total faunal abundance (%)
			Mean	SE	
Phychodidae	O	2 (1.1)	0.04	0.04	<0.01
Tipulidae	O	1 (0.6)	0.81	0.81	0.01
Stratiomyidae	O	9 (5.0)	0.29	0.14	<0.01
Tabanidae	O	3 (1.7)	0.00	0.00	<0.01
Sciomyzidae	O	2 (1.1)	0.00	0.00	<0.01
Muscidae	P	1 (0.6)	0.03	0.03	<0.01
Empididae	O	10 (5.6)	0.86	0.54	0.01
Ostracoda	C	155 (86.1)	3,813.04	1,809.14	39.68
Copepoda	C	122 (67.8)	2,146.71	659.84	22.34
Conchostraca	C	14 (7.8)	1.03	0.48	0.01
Amphipoda	O	30 (16.7)	4.52	1.49	0.05
Isopoda	O	2 (1.1)	1.72	1.72	0.02
Decapoda	O	7 (3.9)	0.09	0.04	<0.01
Cladocera	C	117 (65.0)	3,186.51	1,114.66	33.16
Notostraca	O	1 (0.6)	0.07	0.07	<0.01
Mollusca	O	26 (14.4)	5.91	3.38	0.06
Annelida	O	13 (7.2)	1.14	0.68	0.01
Cnidaria	O	6 (3.3)	0.30	0.18	<0.01
Platyhelminthes	O	7 (3.9)	1.82	0.94	0.02
Chordata	O	28 (15.6)	0.88	0.46	0.01
Culicidae		155 (86.1)	143.03	44.65	1.49
Culicid richness			1.55	0.08	
<i>Ae. alboannulatus</i>		74 (41.1)	62.21	33.83	0.65
<i>Ae. bancroftianus</i>		1 (0.6)	0.01	0.01	<0.01
<i>Ae. camptorhynchus</i>		54 (30.0)	53.85	26.37	0.56
<i>Cx. australicus</i>		50 (27.8)	14.41	5.25	0.15
<i>Cx. globocoxitus</i>		37 (20.6)	9.12	5.16	0.09
<i>An. annulipes</i>		52 (28.9)	3.32	1.57	0.03
<i>Cs. atra</i>		3 (1.7)	0.11	0.08	<0.01
<i>Cq. nr linealis</i>		8 (4.4)	0.09	0.05	<0.01