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Species Interactions Among Larval Mosquitoes: Context Dependence Across Habitat Gradients

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Abstract

Biotic interactions involving mosquito larvae are context dependent, with effects of interactions on populations altered by ecological conditions. Relative impacts of competition and predation change across a gradient of habitat size and permanence. Asymmetrical competition is common and ecological context changes competitive advantage, potentially facilitating landscape-level coexistence of competitors. Predator effects on mosquito populations sometimes depend on habitat structure and on emergent effects of multiple predators, particularly interference among predators. Nonlethal effects of predators on mosquito oviposition, foraging, and life history are common, and their consequences for populations and for mosquito-borne disease are poorly understood. Context-dependent beneficial effects of detritus shredders on mosquitoes occur in container habitats, but these interactions appear to involve more than simple resource modification by shredders. Investigations of context-dependent interactions among mosquito larvae will yield greater understanding of mosquito population dynamics and provide useful model systems for testing theories of context dependence in communities.

Keywords

asymmetrical competition; community ecology; interspecific competition; predation; processing chain commensalism; vector ecology

INTRODUCTION

Interspecific competition, predation, and mutualism occupy the interface between population and community ecology and interact with one another to structure communities (2,31,33,69). These interactions are thus fundamental to community ecology and vital for understanding patterns of diversity (33,91). Besides being important ecological phenomena in their own right, species interactions are linked to behavioral and physiological ecology (105,125) and to energy flow within food webs and ecosystems (62). Thus, species interactions are important at all levels of organization within ecology and are central to understanding the ecology of any group or habitat, including mosquitoes, which are the focus of this review.

Apparent competition: a mutually negative interaction between populations of two species produced by each species increasing the abundance of a shared enemy and thus increasing predation

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

Commensalism: one species' population is positively affected by the abundance of another, whereas the second species' population is unaffected

Context dependence: occurs when abiotic or biotic conditions alter the strength or impact of population-level interactions or the nature of interactions

Competitive asymmetry: occurs when one species has a large negative effect on a competitor, which in turn has a small negative effect on the first species; results in a greater likelihood of competitive exclusion

Larval ecology of mosquitoes has been reviewed from multiple perspectives (20,77,89,106), but there has been no comprehensive review of the ecology of interspecific interactions of mosquitoes. Species interactions involving mosquito larvae are central to application of biological control of mosquitoes (13,53,104,107,134) and to some aspects of epidemiology of mosquito-borne pathogens (5,6). Mosquito larvae are also model systems for testing theory in behavioral (26,125), population (54), and community ecology (32,37,66,74,85,94,137). Thus, a synthesis of the literature on interactions among mosquitoes will be valuable to medical entomologists interested in the impact of interactions on adult production and to basic ecologists using mosquitoes as model organisms for testing ecological theory.

This review of species interactions among mosquitoes poses questions about the effects of ecological context on outcomes and importance of these interactions and the roles of species interactions in structuring mosquito assemblages. For competition, my emphasis is on mosquito-mosquito interactions, minimizing overlap with a recent review (20) of interactions of mosquitoes and controphic (i.e., in the same trophic level) nonmosquitoes.

ECOLOGY OF INTERACTIONS

Kinds of Interactions

Interspecific competition, apparent competition (69), predation, mutualism, and commensalism (33) are population interactions that structure ecological communities. As our understanding of community ecology has become more sophisticated, important questions about interactions have transcended whether a particular interaction is present to the context dependence of these interactions (2). Tradeoffs in species' success in interacting with competitors, predators, and physical variables can produce context dependence and can be important for stabilizing coexistence in communities (1,35,91). For example, competitive asymmetry (90) may be reduced or reversed in different environmental contexts (e.g., across a gradient of predation intensity), enabling competitors to coexist in a heterogeneous environment. Trade-offs across environmental conditions are one niche-based mechanism that can stabilize species coexistence and thus contribute to diversity (1,91). In contrast, if such trade-offs are absent or unimportant, and if all competitors are nearly equal (competitive symmetry), this would be consistent with neutral processes as the primary determinants of diversity (1,70,91). Thus, competitive asymmetries within any given context and trade-offs and context dependence across environmental gradients may provide insight into how assemblages of mosquitoes are structured.

Ecological Context and Species Interactions in Aquatic Communities

Ecological context not only affects outcomes of interaction among particular species, it may also influence the importance of different interactions along ecological gradients. Ecological context, specifically habitat size and temporal stability, influences the prevalence, pattern, and effects of species interactions across freshwater communities (140,142). Bodies of fresh water form a gradient from small and highly ephemeral to large and permanent. At the small, ephemeral end of this gradient, large long-lived predatory organisms (particularly fish) are

often absent, and aquatic organisms need to develop quickly. These conditions favor rapid growth and development, active foraging, movement, and competitive ability (140). As water bodies become larger and temporally more stable (i.e., less likely to dry or to freeze completely), an increasing array of larger, longer-lived predators can persist (140). This increase of diversity, number, and voracity of predators favors refuge use, inconspicuousness, predator deterrence, and slow growth and development (140). Thus, this view of aquatic communities postulates that environmental context determines the relative importance of predation and interspecific competition.

Organization of mosquito communities can be viewed in this same way (75,135), at least within two discrete habitat categories (89,129): containers (e.g., tree holes, bromeliad axils, and human-made containers) and pools (e.g., puddles, wetlands, and ponds) (23,24,32,88). This view of aquatic habitats leads to a prediction that interspecific competition among mosquitoes should control community structure in small ephemeral habitats, whereas predation should do so in large permanent habitats.

Throughout this review, I use the traditional classification of the genus *Aedes* (47).

INTERSPECIFIC COMPETITION

Kinds of Questions

Two types of ecological questions concern interspecific competition (57): (a) those concerning the impact in nature of competition and (b) those concerning the biological details of competition, such as context dependence, likelihood of competitive exclusion, mechanisms of competition, and responses to competition, all assuming that competition is important. To answer questions about impact in nature requires field experiments to manipulate species densities under realistic conditions (57). To answer questions about biological details requires more-complex experiments to manipulate other factors in addition to density (57). Some questions about biological details can be answered using experiments under less realistic, but more precisely controlled, laboratory conditions.

Competitive exclusion is most likely to occur when interspecific competition is highly asymmetrical (33,90,133). Exclusion can also occur when two species are similar in their interspecific effects but also have relatively low intraspecific effects (33,35). Investigation of the likelihood of coexistence versus exclusion can include evaluation of the roles of different biotic and abiotic variables in context-dependent outcomes of interspecific competition (e.g., along an environmental gradient, competitive advantage shifts from species 1 to species 2). Mechanisms of competition (e.g., interference or resources) and species responses to competition (e.g., altered survival, growth, and development) can be investigated in both the field and the laboratory.

Ecological Context and Interspecific Competition Among Mosquitoes

Despite many studies of interspecific competition among larval mosquitoes (Table 1), we have limited ability to determine whether these competitive interactions are more prevalent in small ephemeral habitats lacking large predators than in more permanent habitats. Our knowledge of interspecific competition among mosquitoes is largely derived from work on a few species of container-dwelling *Aedes*. One general conclusion from published investigations is that competitive asymmetry and context dependence of the degree and direction of the asymmetry are common, with both biotic and abiotic gradients affecting competitive outcomes.

Pools

Relatively little experimental work has been done on species from pools; all of it has been done in the laboratory with a few species of *Anopheles* and *Culex* (Table 1; details in Supplemental Table 1, follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). These species reside primarily in small ephemeral pools with relatively limited predator faunae or are extreme generalists in habitat use (e.g., *Culex pipiens*) (but see 20). Asymmetry of competitive interactions in small temporary pools has been demonstrated for *Anopheles* (86,87,122) and *Culex* (127), suggesting that for these species local competitive exclusion is a possibility. Developmental asynchrony modifies competition among *Anopheles*, and there is evidence for intraguild predation (33,69) and resource competition as interaction mechanisms (86,87).

Intraguild predation: killing and consuming potential interspecific competitors

In the absence of field experiments on interspecific competition, tests for intraspecific competition in pool habitats may yield evidence for the importance of competition. Intraspecific competition, probably for algal food, among *Anopheles gambiae* (s.s.) in small temporary ponds affects growth and development, but not survivorship, at approximately natural densities (56,109). Because *An. gambiae* and *An. arabiensis* often co-occur in small ephemeral pools (55), it seems likely that interspecific competition is also important in these pools. Field investigation of intraspecific competition between two chromosomal forms of *An. gambiae* yielded results consistent with significant competition in small ephemeral puddles but not in permanent rice fields (43). Further, the chromosomal form dominant in ephemeral puddles appears to be a competitor superior to the form dominant in permanent wetlands, which in turn has greater survivorship when predators are present (42,43), suggesting that intraspecific variation in *An. gambiae* follows the predicted pattern of competition dominating in small ephemeral habitats and of predation dominating in larger permanent habitats (140). These field experiments (42,43,56,109) with chromosomal forms of *An. gambiae* provide a perfect model for important experiments on interspecific competition among African *Anopheles* across the gradient from temporary to permanent ponds (50,124).

There have been no field experiments on interspecific competition among mosquitoes in permanent pools. Abundances of mosquitoes in permanent pools tend to be low, presumably because of predation (32,75,135), and it is possible that investigators have concentrated experiments on processes that seem more likely to be important in these habitats (i.e., predation). However, there is evidence for competition between mosquitoes and controphic tadpoles, snails, and cladocerans in permanent wetlands (20). Because many *Anopheles* and *Culex* are distributed across gradients of pool permanence and size (50,88,124), investigations of the trade-off between competitive success and invulnerability to predation for mosquitoes in pools should be productive.

Containers

Containers (e.g., tree holes and human-made containers) have been well studied, but the majority of investigations involved the invasive species *Aedes albopictus* (33 of 40 investigations, Table 1). Six of the remaining investigations involved *Ae. aegypti* or *Ae. triseriatus*. Another limitation is that most published work on competition among container mosquitoes relies on laboratory experiments (33 of 40 publications; Table 1), and all seven of the field investigations have involved *Ae. albopictus* (Table 1). Thus, our understanding of competition among container mosquitoes in nature is limited to a single invasive species. Of seven field experiments in containers, five show that interspecific competition is strong under field conditions (9,27,74,78,131) (Table 1).

Questions about biological details of competitive asymmetries, mechanisms, and context dependence have been investigated more frequently than questions of impact in nature (Table 1). Competitive asymmetry appears to be the norm, detectable in 31 of 35 experiments that could test for asymmetry (Table 1). Of unique species pairs tested in the laboratory, 11 of 12 show strong competitive asymmetry under at least some circumstances (Table 1). Thus, without some mechanism of coexistence we might expect competitive exclusion of one competitor under one set of environmental conditions.

Among container species, the dependence of outcomes on resource amount, type, and temporal input pattern (15,27,74,94,112,132,136,145) (Table 1;Supplemental Table 1) suggests that resource competition is a likely mechanism for these interactions and that differential resource use could contribute to local-scale coexistence of competitors. Water-borne interference (108,130,131) and size-dependent intraguild predation and hatch inhibition (45,46) have been demonstrated. A few investigations of apparent competition (36,74) and oviposition deterrence by competitors (100) have yielded little evidence for these mechanisms (Supplemental Table 1).

For the best-studied pair of competitors, *Ae. albopictus* and *Ae. aegypti*, competitive asymmetry is context dependent and significantly associated with the nature of the resource used (Table 2). The presence of rapidly decaying detritus types (e.g., animal detritus) tends to yield competitive equality or advantage for *Ae. aegypti*, and more refractory plant detritus (deciduous or coniferous leaves) tends to yield competitive advantage for *Ae. albopictus* (Table 2). Interspecific differences in starvation resistance of larvae of these species also depend on resource type (11). *Ae. albopictus* withstands starvation longer than *Ae. aegypti* when reared on oak leaves, but this difference is reversed when these species are reared on liver powder (11), suggesting a physiological basis for the detritus-type-dependent outcomes of interspecific competition.

Detritus types yield context-dependent competitive asymmetry for other species combinations (94,145) (Supplemental Table 1). Rapidly decaying detritus substrates (e.g., animal detritus and grass) yield large pulses of microbial growth and high nitrogen availability (110,144). An intriguing but little-investigated aspect of resource competition among mosquitoes is the hypothesis that the ratio of detritus types, or of nutrients from those types, determines the potential for competitive coexistence (133,145).

Context-dependent reversal of competitive asymmetry was also noted for abiotic factors (Supplemental Table 1) such as temperature (121, 132; but see 102) and drying (37). The latter experiment is unique because it uses caged populations of one or both competitors in all life cycle stages, allowed to compete over multiple generations. The filling schedule for containers within cages affected competitive outcome by imposing differential mortality on noncompeting eggs. This experiment shows the importance of linkages among life cycle stages and of trade-offs between competitive ability of one stage and environmental tolerances of other stages, a topic related to the general theory of coexistence of competitors (35, 37, 79).

Predators have context-dependent effects on outcomes of competition between container mosquitoes, with a trade-off between competitive success and the likelihood of surviving with predation (25,58,59) (Supplemental Table 1). *Ae. triseriatus* was involved in all three predation-competition trade-off investigations but perhaps surprisingly took on the role of both predation-resistant poor competitor compared with *Ae. aegypti* (58) and *Ae. albopictus* (59) and predation-vulnerable good competitor compared to *Orthopodomyia signifera* (30,93). These context-dependent results suggest that multiple container-dwelling species occupy positions along the continuum between vulnerable-competitive and resistant-noncompetitive. Field investigations in natural tree holes suggest that vulnerable-competitive species dominate

in predator-free, smaller, ephemeral tree holes and invulnerable-noncompetitive species dominate in predator-rich, larger, relatively permanent tree holes (23,24). This same trade-off is also observed along a gradient of permanence in groundwater pools (32), with competition occurring mainly between mosquito larvae and controphic nonmosquitoes.

The few investigations of the effects of protozoan parasites on competing mosquitoes yield some evidence for context dependence (Supplemental Table 1). Infection of *Ae. albopictus* with *Ascogregarina taiwanensis* decreased its competitive advantage over *Ae. triseriatus* infected with *Ascogregarina barretti* (3). In contrast, when both *Ae. triseriatus* and *Ae. hendersoni* were infected with *A. barretti*, the competitive advantage of *Ae. triseriatus* was enhanced relative to that observed when both species were uninfected, primarily because *A. barretti* has a more severe debilitating effect on *Ae. hendersoni* (36).

These experiments provide evidence that competitive asymmetry within one set of conditions and context-dependent competitive success across environmental conditions are common in mosquito assemblages. Trade-offs of competitive success across abiotic or biotic gradients suggest that species coexistence in container communities may be a function of niche-based organization of these communities rather than neutral mechanisms of species coexistence (91). Competing container mosquitoes are an attractive model system for field experiments testing ecological theory on context-dependent competition and coexistence.

Disseminated infection: an infection of a mosquito vector wherein the vector-borne pathogen has moved beyond the gut of the vector and, by reaching the salivary glands, can be transmitted by biting to a vertebrate host

Density-mediated effects: occur when species interactions result in effects on birth or death rates of one or both species

Trait-mediated effects: occur when species interactions alter behavior, morphology, or physiology of one or both species, often with consequences for population dynamics

Interspecific Competition and Disease

For *Ae. albopictus*, but not *Ae. aegypti*, competition increases the probability of acquiring disseminated infections of arboviruses (5,6). Because disseminated infection is required for virus transmission (5), competition among larvae may affect the probability of vector-borne virus transmission. These results may have important consequences for dengue transmission. *Ae. aegypti* is the main vector of dengue in most locations, but *Ae. albopictus* is also a competent vector and may be locally important (96). Invasion by *Ae. albopictus* can result in competitive replacement of *Ae. aegypti* (77,96), and when the two species can coexist, trait-mediated competitive effects could increase the vectorial capabilities of *Ae. albopictus* compared with that of *Ae. aegypti*. Thus, *Ae. albopictus* may assume a greater role in dengue transmission via both density-mediated and trait-mediated effects (21,117) of competition.

PREDATION

Kinds of Questions

Ecological questions about the role of predation parallel those posed concerning competition. The most basic question is whether predators have an important impact on mosquito populations in the field. This question is important for biological control (75), and impacts of particular predators have been reviewed recently (53,104,107,134) and hence are not addressed here. I focus on how ecological context may modify the importance of predation. The conceptual models (140) described above predict that predation should be more important in

relatively permanent large bodies of water. The effect of the physical environment on the role of predation depends critically on differential impacts of predation for multiple prey species (139), a phenomenon that is likely even without the ephemeral-to-permanent gradient. Differential impacts of predation can thus function as another niche-based difference among species along any gradient of predation (whatever its cause) in spatially heterogeneous communities (1,91,139). Context dependence of particular interactions may arise when habitat structure affects predation impact (67), when there are emergent multiple predator effects (MPEs) (126), or when mosquito density induces facultative predation or parasitism on mosquito larvae (137).

Emergent multiple predator effects (MPEs): occur when impacts of >1 predator type cannot be predicted by summing the effects of single predator types

Nonlethal, trait-mediated effects of the presence of predators on the success of potential prey (21,72,117) make context dependence likely. Nonlethal effects result from costs of predator avoidance (117) that can depend on risk from other enemies (126), resources (22), and time constraints (72). The mechanisms (e.g., behavior and life history) and magnitude (relative to lethal effects) of nonlethal effects of predators are thus contributors to context dependence.

Ephemeral/Competitive to Permanent/Predator-Resistant Gradient

The best evidence that ecological context affects the impact of predation along this gradient comes from field studies of both containers (23,24,51,96,129) and pools (32) and from some of the laboratory experiments summarized above (30,58,59). For pools, the effects of irregular drying on predator abundance and on production of mosquitoes have been documented (32), providing convincing evidence that position along the ephemeral-permanent habitat gradient controls the impacts of predation in nature. Similar manipulations of drying in containers have not been published, despite the small sizes of containers, which should make manipulation of drying or simultaneous manipulation of predators and competitors feasible. Field surveys have yielded evidence indicating that predation has a greater impact in more permanent containers (23,24,95,97). Manipulation of predation and habitat drying in mosquito-dominated containers is an opportunity for experimental field study of context-dependent predation.

Field surveys show that the competitively superior *Ae. albopictus* dominates in relatively predator-free human-made containers, but in predator-dominated tree holes *Ae. triseriatus* (a poorer competitor) (Supplemental Table 1) is codominant with *Ae. albopictus* (82, 99). This change in community composition has not yet been directly linked to temporal stability of these water-filled container types and may result from predator macrohabitat choice (82).

Habitat Structure

Experiments with the container species *Ae. albopictus* and *Ae. triseriatus* yielded no significant habitat structure effect on predation by *Toxorhynchites rutilus* or *Corethrella appendiculata* (4,73), two ambush predators with tactile detection of prey. Experiments with fish predators and habitat structure in pools have yielded variable results. There was no significant reduction in predator success for five fish species attacking *Culex* in simulated vegetation (71). Real vegetation density significantly affected consumption rates of *Culex* by *Gambusia holbrooki* and *Pseudomugil signifier*, but predation neither consistently increased nor decreased with vegetation density (141). Consumption by both predators was reduced at low vegetation density compared with both no vegetation and high vegetation densities (141). Real vegetation density had no effect on the consumption rate of *Culex* by the fish *Aphanius mento* (19). Consumption of *Culex* by *Gambusia affinis* was greater among rice plants or aquatic macrophytes compared with consumption rates in open water (92). There was a significant quadratic relationship of

survival of *Anopheles* to the density of filamentous algae in the presence of *Poecilia sphenops*, with low survival at either 0% or 100% cover of algae (61). In contrast, habitat structure significantly reduced the success of visually hunting hemipterans *Diplonychus* sp. (123) and *Notonecta undulata* (125) attacking *Culex*. Further investigations of the effects of habitat structure on the success of pool-dwelling invertebrate predators are needed. The variable results with fish predators indicate that more detailed evaluation of the patterns of context-dependent fish predation would be valuable, particularly because some fish are commonly used for biological control (13,134) and because the literature on biological control with *Gambusia* spp. suggests that control is most effective when vegetation is sparse or absent (reviewed in Reference 134). Finding appropriate ways to test whether contrasting predator hunting tactics (ambush versus pursuit; tactile versus visual) determine how habitat structure produces context-dependent predation (4) should be a high priority.

Emergent Multiple Predator Effects

Risk enhancement MPEs may arise due to conflicting prey responses to predators, whereas risk reduction MPEs often result from predator interference (e.g., intraguild predation) (126). Many mosquitoes co-occur with multiple predators (23,51,60,71,123,129,141), so MPEs seem likely.

In pools, the addition of *Gambusia* spp. sometimes fails to reduce mosquito abundance, which may result from emergent risk reduction MPEs via intraguild predation on invertebrates by *Gambusia* spp. (13,17). There was no evidence for a risk enhancement MPE for *Gambusia affinis* and *Gasterosteus aculeatus*, which have contrasting foraging locations, in a field experiment (113). *G. aculeatus* had no significant effect on mosquito abundances, and effects of *G. affinis* alone and with *G. aculeatus* were statistically indistinguishable (113). In contrast, strong emergent risk enhancement (>26%) was observed in experiments on *Gambusia* and the predatory hydrophilid *Tropisternus lateralis* preying on *Cx. tarsalis* (14) (Table 3).

Emergent MPEs arise in containers where intraguild predation is prevalent (51,60). In the most thorough investigation of MPEs on mosquitoes, size structure and differential size-dependent predation by *Tx. rutilus* and *C. appendiculata* preying on *Ae. albopictus* resulted in short-term risk reduction, but over the long-term the effects of the two predators were predicted by the multiplicative model (60). Intraguild predation among these predators is asymmetrical, with large *Tx. rutilus* preying on smaller *C. appendiculata* (95). MPEs on *Aedes* and *Culex* due to predation by *Toxorhynchites amboinensis* and *Mesocyclops aspericornis* in a variety of natural and human-made containers (119) include both risk enhancement and risk reduction (Table 3), but all estimated emergent MPEs were small (i.e., within $\pm 5\%$ of that expected based on a multiplicative model of multipredator effects) (Table 3). Similarly, predation on *Aedes* and *Culex* by *M. aspericornis* and *Toxorhynchites speciosus* (28) indicated small risk reduction MPEs of 1.9% to 3.7% relative to that expected from a multiplicative model (Table 3). MPEs among three species of copepods preying on early-stage *Ae. albopictus* (44) yielded a short-term (one-month) risk reduction of over 17% relative to the multiplicative model (Table 3). There was strong interference among copepod species, probably by intraguild predation (44). However, after two to four months, this MPE disappeared as copepod numerical responses eliminated young larvae in nearly all treatments (44). Thus, most documented emergent MPEs on mosquitoes are small short-term risk reductions via intraguild predation.

Nonlethal Effects

Nonlethal effects of predators on mosquito populations may arise from oviposition deterrence, which is well documented for pool-dwelling *Culex* and *Culiseta* (e.g., 7, 8, 18, 34, 48, 49, 84, 128). Nonlethal effects on larvae are caused by reduced movement, use of spatial refuges, and

reduced feeding in response to water-borne cues from predation for container species and *Cx. pipiens* (12,76,80-83,125,143).

Changes in larval behavior in response to predators would appear to come at a cost of reduced feeding (81); however, the demographic costs (life-history changes such as reduced growth and development) (72) of these behavioral changes have not been determined for mosquitoes. The effects of predators on mosquito life histories are sometimes present (12,61,98), but not necessarily associated with behavioral changes (66), and may be absent, even when predator-induced behavioral changes are expected to produce correlated life-history shifts (76). Whether predator-induced life-history shifts are, in general, products of behavioral change or true developmental changes remains unanswered. Estimating the demographic consequences of behavioral responses to predators, and the mechanisms producing life-history shifts in response to predators, is an important research direction for the future.

The flexibility of these mosquito responses to enemies when other constraints are present remains poorly investigated and is an important future research direction. If behavioral responses have costs such as reduced feeding, growth, or development, the larval response to the threat of predation should change with feeding conditions (22) and with time constraints of ephemeral habitats (72). For *Cx. pipiens* exposed to water-borne cues from *Notonecta undulata*, food shortage enhanced predator-induced reductions of development and growth rates (12). The possible impacts of time constraints on behavioral and life-history responses of mosquitoes to predators are uninvestigated. Mosquitoes should be useful model organisms for testing general predictions about how prey species balance conflicting demands of predator avoidance and foraging effort.

Adaptive manipulation of mosquito predator avoidance behavior by parasites is largely unstudied. A trematode using larval mosquitoes as an intermediate host, and requiring consumption of the mosquito by the definitive host, alters mosquito behavior to increase predation risk (138). In contrast, a nematode requiring survival of the mosquito for completion of development does not enhance antipredator responses of mosquito larvae to reduce predation risk (143). There is potential for behaviorally mediated MPEs to occur due to parasite manipulation of mosquito predator avoidance behavior.

Processing chain: a context-dependent interaction wherein one species exploits a resource but also modifies that resource, making some portion of it more available for another species; may result in commensalism or asymmetrical competition

BENEFICIAL INTERACTIONS

Processing Chains

Beneficial interactions involving mosquito larvae are predominantly processing chains, which are inherently context dependent (64,65). Many mosquito larvae consume fine particulate matter (106), yet most detritus enters aquatic environments as particles too large to be ingested by mosquito larvae (e.g., leaves and dead insects) (106). Microorganisms growing on detritus are fine particles and are consumed by mosquitoes, but shredders that chew large detritus also produce fine particles (feces or uningested material) (41,64). Context dependence arises because shredders (upstream consumers) (64) benefit fine-particle consumers such as mosquitoes (downstream consumers) (40,64) when consumer-independent processing (i.e., conversion to fine particles in the absence of the upstream consumer) is low but are detrimental when consumer-independent processing is high (64,65). Thus, this interaction varies from commensal to amensal, depending on the ambient rate of production of fine particulates.

Models of processing chains reveal several other environmental sources of context dependence (40,64,65).

Processing chains seem to be common for mosquitoes in containers, including pitcher plants (63), tree holes (25,40,41,114,115), and *Heliconia* bracts (64,111). Tests of predictions of models of context dependence (40,64,65) provide some support for these systems functioning as processing chains (63,114,115). Other results are inconsistent with predictions from simple processing chain models, especially observed negative effects of mosquito downstream consumers on upstream consumers in tree holes (40) and in pitcher plants (63). Such effects could result from interference competition (40). More sophisticated experimental tests of existing models and development of more detailed models incorporating additional mechanisms of interaction seem necessary for a full understanding of processing chains involving container mosquitoes. Processing chains are virtually uninvestigated for pool-dwelling mosquitoes.

CONCLUSIONS

Interspecific competition, predation, and beneficial interactions affect many organisms, including other aquatic invertebrates (64,105,126,139,140); hence, simply showing that these interactions affect mosquitoes is not a major scientific advance. Although documenting these effects for particular mosquito species may have practical importance, the important conceptual issues in the population and community ecology of mosquitoes involve how environmental context, including physical conditions and community composition, may alter the effects of species interactions on mosquito populations. This review suggests that, for communities distributed along environmental gradients of habitat size and permanence, the importance of different species interactions among mosquitoes changes in a manner consistent with the general theory developed for freshwater communities (140). Equally important, experimental investigations of particular species yield evidence for context-dependent effects of interspecific competition, predation, and processing chain commensalism. The laboratory investigations of context dependence summarized in this review, and future controlled experiments on similar questions, indicate the possibilities for context-dependent community effects on mosquitoes. However, well-designed field experiments on variation in biotic interactions across environmental contexts are needed to determine the realized importance of these effects. Interactions among mosquitoes can provide useful model systems for testing and developing ecological theory for context-dependent effects across gradients of habitat permanence, size, predation intensity, resource availability, or structural complexity.

Context-dependent interactions of mosquito larvae may be important for practical aspects of mosquito ecology, including control and forecasting. Controlling mosquitoes is costly in money, labor, and environmental impact, and understanding where and when success is most or least likely is vital for cost-effective applied ecology. Examples of context-dependent effects involving larvae that may have practical consequences include the following:

Habitat drying and desiccation of eggs can shift competitive asymmetry between *Ae. aegypti* and *Ae. albopictus* (37). Seasonal drought and temperature are correlated with their distributions and abundances (79). Climate may thus influence which of these dengue vectors dominates or whether they coexist, which may affect dengue transmission. Understanding how climate and competition interact to affect dengue transmission may be useful for targeting control efforts where and when dengue risk is greatest.

Gambusia affinis and *Gambusia holbrooki* are often used for biological control of mosquitoes (134), but the effectiveness of these *Gambusia* species depends on both vegetation (141) and other predators (13,14,134). Understanding context-dependent

predation may help to target *Gambusia* releases where conditions make reduction of mosquitoes by *Gambusia* more likely.

As we learn more about how biotic interactions of mosquitoes depend on ecological context, more of the practical implications of community interactions will become apparent.

SUMMARY POINTS

1. Mosquito assemblages are postulated to be organized along an ecological gradient, from small ephemeral habitats where interspecific competition dominates and large predators are uncommon to large permanent habitats where predation dominates.
2. Limited evidence suggests interspecific competition among mosquitoes is common in small pools.
3. Interspecific competition among container-dwelling mosquitoes is commonly asymmetrical, and ecological context often reverses asymmetries. Competitive container-dwelling mosquitoes dominate in ephemeral habitats, as predicted. Nearly all field investigations of competition and context-dependence focus on *Ae. albopictus*.
4. Interspecific competition among larval *Aedes* can have important trait-mediated effects on the vector potential of resulting adults, with unknown consequences for disease epidemiology.
5. Effects of predation are context dependent, with predation dominating community organization in more permanent pools and in larger, more permanent containers.
6. Effects of habitat structure on predator impact on mosquitoes vary and may depend on predator hunting tactics. Predators have nonlethal, trait-mediated effects on mosquito oviposition, foraging, and life history. The costs of these nonlethal effects and their dependence on resources and temporal constraints are largely unstudied.
7. Emergent MPEs on mosquitoes occur primarily through risk reduction via predator interference. Behavioral responses of mosquitoes to predators suggest the possibility of risk enhancement via conflicting responses to predators, but this has not been investigated.
8. Experiments on container mosquitoes support some of the theory on processing chains, but existing models do not account for some observed effects of mosquitoes on other taxa.

FUTURE ISSUES

1. How do interactions among mosquito larvae combine with ecological effects on eggs and adults to determine outcomes of those interactions at the population level? This question may yield important insights into how complex life cycles influence coexistence of competitors.
2. How do trait-mediated and density-mediated effects of larval interactions affect epidemiology of vector-borne disease? Future investigations should examine effects of larval interactions on adult size, longevity, probability of transmission, and feeding behavior.

3. What are the costs of nonlethal effects of predators on mosquitoes, and how do they interact with resource availability, time constraints, densities, and lethal effects to influence populations? Nonlethal effects of predators could yield indirect effects on interspecific competition, survivorship, and adult traits.
4. There is a general need for field experiments on competition, predation, and mutualism, and on their context dependence across species and habitats. Investigations of context-dependent competition and predation in pool-dwelling species and field manipulations of habitat permanence in containers should be high priorities.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Table 1
Summary of experimental investigations of competition among mosquito larvae^a

Species combination	Competition in nature ^b	Competitive asymmetry ^c	Context dependence ^d	Reference(s)
Pools: laboratory investigations of biological details				
<i>Anopheles arabiensis</i> , <i>Anopheles gambiae</i>	*	2/2	-	(122,87)
<i>Anopheles quadrimaculatus</i> , <i>Anopheles gambiae</i>	*	1/1	0/1	(86)
<i>Culex quinquefasciatus</i> , <i>Culex tarsalis</i>	*	1/1	-	(127)
<i>Culex pipiens</i> , <i>Culex restuans</i>	*	0/1	0/1	(118)
Containers: field investigations of impact in nature and biological details				
<i>Aedes albopictus</i> , <i>Aedes aegypti</i> , <i>Aedes triseriatus</i>	0/1	1/1	-	(68)
<i>Aedes albopictus</i> , <i>Aedes aegypti</i>	3/3	2/2	0/3	(27,74,78)
<i>Aedes albopictus</i> , <i>Wyeomyia</i> spp.	0/1	-	-	(100)
<i>Aedes albopictus</i> , <i>Aedes japonicus</i>	1/1	1/1	-	(9)
<i>Aedes albopictus</i> , <i>Tripteroides bambusa</i>	1/1	-	0/1	(131)
Containers: laboratory investigations of biological details				
<i>Aedes albopictus</i> , <i>Aedes aegypti</i> , <i>Aedes triseriatus</i>	*	4/4	0/1	(11,45,46,68)
<i>Aedes albopictus</i> , <i>Aedes aegypti</i>	*	4/8	3/4	(5,6,16,37,39,102,108,110)
<i>Aedes albopictus</i> , <i>Aedes triseriatus</i>	*	7/7	4/7	(3,15,59,94,112,132,145)
<i>Aedes albopictus</i> , <i>Aedes polynesiensis</i>	*	1/1	-	(103,120)
<i>Aedes albopictus</i> , <i>Aedes sierrensis</i>	*	1/1	0/1	(137)
<i>Aedes albopictus</i> , <i>Culex pipiens</i>	*	2/2	0/1	(29,38)
<i>Aedes albopictus</i> , <i>Tripteroides bambusa</i>	*	1/1	-	(130)
<i>Aedes albopictus</i> , <i>Wyeomyia</i> spp.	*	-	-	(100)
<i>Aedes aegypti</i> , <i>Aedes triseriatus</i>	*	1/1	1/1	(58)
<i>Aedes aegypti</i> , <i>Aedes notoscriptus</i>	*	1/1	1/1	(121)
<i>Aedes aegypti</i> , <i>Culex pipiens</i>	*	1/1	-	(116)

Species combination	Competition in nature ^b	Competitive asymmetry ^c	Context dependence ^d	Reference(s)
<i>Aedes triseriatus</i> , <i>Aedes hendersoni</i>	*	1/1	0/1	(36)
<i>Aedes triseriatus</i> , <i>Orthopodomyia</i> <i>signifera</i>	*	2/2	1/1	(30,93)
<i>Aedes japonicus</i> , <i>Aedes atropalpus</i>	*	1/1	-	(10)

“-”Indicate no investigations testing for the effect in that column.

^aDetails in Supplemental Table 1.

^bIndicates number of investigations showing competition in nature out of those that tested for such effects. Cells with an asterisk indicate that laboratory investigations cannot test for competition in nature.

^cIndicates number of investigations showing competitive asymmetry out of those that tested for such effects.

^dIndicates number of investigations showing context-dependent competitive asymmetry out of those tested for such effects.

Table 2

Dependence^a of competitive advantage on detritus type in field and laboratory experiments on *Aedes albopictus* and *Aedes aegypti*

Superior competitor	Detritus substrate ^b	Venue	Reference ^c
<i>Aedes albopictus</i>	Senescent live oak leaves	Laboratory	(11)
	Senescent live oak leaves + water in field containers	Field	(74)
	Senescent live oak leaves	Laboratory	(39*)
	Senescent avocado leaves + water in field containers	Field	(27)
	Dead <i>Drosophila</i> + crickets	Laboratory	(110*)
	Senescent live oak leaves	Laboratory	(110*)
	Senescent slash pine needles	Laboratory	(110*)
Equal	Yeast + wheat germ + baby cereal	Field	(68)
	Liver powder	Laboratory	(16)
	Dead <i>Drosophila</i> + senescent live oak leaves	Laboratory	(39*)
	Senescent live oak leaves + water from field containers	Laboratory	(102)
	Yeast: Lactalbumin + senescent live oak leaf infusion	Laboratory	(5)
	Yeast: Lactalbumin + senescent live oak leaf infusion	Laboratory	(6)
	Cut Zoisa grass	Laboratory	(110*)
<i>Aedes aegypti</i>	Sheep chow	Laboratory	(108)

^aDependence of the superior competitor (*Ae. albopictus* versus *Ae. aegypti*, and equal) on the type of resource (rapidly decomposing, high-quality versus slowly decomposing, low-quality substrate) was significant by 2×2 two-tailed Fisher exact test ($Df = 1$, $P = 0.0101$).

^bRapidly decomposing and high-quality substrates indicated in boldface type. Investigations that tested for the effects of physical factors or intraguild predation (37,45,46) are excluded.

^cPublications reporting multiple, related competition experiments with different detritus substrates are indicated with an asterisk.

Two- and three-predator emergent multipredator effects

Table 3

Ecological Context	Replicates	Observed										Multipredator effect	
		Predator #1			Predator #2			Predator #3		All predators			
		Control N prey ^a	N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	Expected proportion killed ^c		Observed - expected ^d
Predators: 1. <i>Gambusia affinis</i> , 2. <i>Tropisternus lateralis</i> . Prey: <i>Culex tarsalis</i> (14)													
Rice field	4	73.25	74.5	−0.017	41.25	0.436	-	-	-	22.25	0.696	0.427	0.269
Predators: 1. <i>Mesocyclops aspericornis</i> , 2. <i>Toxorhynchites speciosus</i> . Prey: <i>Aedes notoscriptus</i> , <i>Culex quinquefasciatus</i> (first instars) (28)													
Tires Jan.-May	25 to 26	45	3	0.933	17.5	0.611	-	-	-	2	0.956	0.974	−0.019
Tires June-Aug.	6 to 25	31	14.5	0.532	12.5	0.597	-	-	-	7	0.774	0.811	−0.037
Tires Sep.-May	3 to 60	37	7	0.811	13	0.649	-	-	-	3.5	0.905	0.933	−0.028
Predators: 1. <i>Mesocyclops aspericornis</i> , 2. <i>Toxorhynchites amboinensis</i> . Prey: <i>Aedes aegypti</i> and <i>Aedes polynesiensis</i> (119)													
Tires	44 to 673	32.3	1.3	0.96	12.6	0.61	-	-	-	1.5	0.954	0.984	−0.031
Metal drums	10 to 42	492.1	1.9	0.996	102.4	0.792	-	-	-	0	1	0.999	0.001
Ovitrap	341 to 467	25.2	2.6	0.897	10.7	0.575	-	-	-	0.7	0.972	0.956	0.016
Tree holes	159 to 287	12.4	1.1	0.911	8.1	0.347	-	-	-	0.1	0.992	0.942	0.05
Predators: 1. <i>Mesocyclops aspericornis</i> , 2. <i>Toxorhynchites amboinensis</i> . Prey: <i>Culex quinquefasciatus</i> (119)													
Metal drums	10 to 42	583.7	146.1	0.75	119.5	0.795	-	-	-	41.8	0.928	0.948	−0.02
Ovitrap	341 to 467	38.1	18.3	0.52	19.1	0.499	-	-	-	11.3	0.703	0.759	−0.056
Predators: 1. <i>Macrocyclus distinctus</i> , 2. <i>Megacyclops viridis</i> , 3. <i>Mesocyclops pehpetensis</i> . Prey: <i>Aedes albopictus</i> (44)													
Instars 1 and 2: July	5	8.44	0.76	0.91	0.9	0.893	4.11	0.513	1.55	0.816	0.995	0.995	−0.179
Instars 1 and 2: Aug.	5	20.04	0.04	0.998	2.4	0.88	0.25	0.988	0	1	1	1	0
Instars 3 and 4: July	5	14.66	0.09	0.994	1.55	0.894	3.66	0.75	0.11	0.992	1	1	−0.007

Ecological Context	Replicates	Control N prey ^a	Observed						Multipredator effect		
			Predator #1		Predator #2		Predator #3		All predators		Observed - expected ^d
			N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	N prey ^a	Proportion killed ^b	
Instars 3 and 4: Aug.	5	52.25	0.04	0.999	5.7	0.891	3.85	0.926	0.71	0.986	-0.014

^aThe mean numbers of larval mosquitoes present per replicate.

^bThe estimated proportion killed relative to control.

^cPredicted proportion killed from multiplicative model of multipredator predation (126).

^dThe MPE is quantified as: (observed proportion killed—expected proportion killed), so that positive values indicate multiple predator risk enhancement and negative values indicate multiple predator risk reduction.