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## COMPETITIVE DISPLACEMENT AND REDUCTION

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## INTRODUCTION

The purpose of this chapter is to review the literature for evidence of competitive displacements of mosquitoes and to consider whether and how this phenomenon may be applied towards mosquito control. Competitive displacement is considered biological control in the context of a broad definition of the discipline, which includes conservation, augmentation, and introduction of natural enemies of pests or vectors (Lounibos and Frank 1994). Because partial reductions of pest or vector populations are desirable and competitive displacements are unlikely to be complete, the term competitive reduction is coined to apply to any diminution of mosquito populations effected by interspecific competition less than local extinction. After reviewing origins of the concept, examples of inadvertent competitive reductions of mosquito populations, and a trial for biological control, I examine potential mechanisms, which are important to understand if competition is to be manipulated in the interests of mosquito control. The final sections of this chapter will consider opportunities and obstacles facing the development of this technique.

## THE CONCEPT

Competitive displacement is based upon the ecological principle that different species cannot simultaneously occupy the same niche (DeBach 1966). Seeds of the concept date at least to Darwin (1859), and 20th-century authors, such as Grinnell (1928) and Gause (1934), have been credited with permutations. Hardin (1960) called the principle competitive exclusion based, in part, on various studies of competing laboratory populations in which one or another species eventually went extinct.

The older literature cites relatively few examples of competitive displacement observed in action in nature. Connell (1961) demonstrated by means of exclusion experiments on rocky seashores that the intertidal distribution of 2 barnacle species was determined by interspecific competition. However, the contemporary distributions of these species are the result of competition having gone to completion in evolutionary time. Documentation of competitive exclusion in nature is possible when an accidentally or purposely introduced species displaces an ecological homolog over a relatively quick time span. However, some instances of competitive displacement may occur in time frames that exceed ordinary observation periods, rendering documentation and experimental validation of causes less tractable.

Well documented cases of competitive displacement occurred after the importation of *Aphytis* spp. parasitic wasps which serially displaced one another after introductions of different exotic species for biological control of the California red scale (DeBach 1966). Although competitive displacement was not the intention of the *Aphytis* spp. introductions, observant entomologists recognized that the principle underlying displacement of wasps might

be useful for biological control of pests or vectors by replacement with an inoffensive ecological homolog (e.g., Furman et al. 1959, DeBach 1964, Turnbull 1967).

Competitive displacement has appeared in recent limelight in the context of biological invasions and human-induced habitat modifications, both of which may threaten biodiversity if vulnerable or endangered species are displaced (e.g., Mack et al. 2000). Indeed, the concept of importing non-indigenous species for biological control has come under fire because of the potential undesirable effects of predation, parasitism, and competition on non-target native fauna and flora (Simberloff and Stiling 1996, Ewel et al. 1999). A recent review of competitive displacement among insects and arachnids confirmed that in the majority of instances, exotic species displaced native species or previously established invaders (Reitz and Trumble 2002).

## INADVERTENT COMPETITIVE REDUCTIONS OF DISEASE VECTORS BY HUMAN INTERVENTIONS

A diverse literature documents the occurrence of competitive reductions of mosquito populations following human-assisted habitat changes or establishments of invasive species. Several of these reductions involved malaria vectors of the Maculipennis Complex of *Anopheles* in southern Italy. The salt-tolerant vector *An. labranchiae* was largely replaced by the less dangerous and zoophilic *An. hispaniola* by means of desalination (*bonfica*) of larval habitats (Missiroli 1939) and DDT spraying targeting the vector species (Trapido and Aitken 1953). Interestingly, this shift in balance between the 2 anopheline species in southern Italy was impermanent, as documented by increases during the ensuing 35 years in numbers of sites occupied by *An. labranchiae* and the disappearance of *An. hispaniola* from Sardinia (Marchi and Munstermann 1987). The recrudescence of *An. labranchiae* in Sardinia has occurred close to new human settlements, where *An. hispaniola* was not known to occur (A. Marchi, pers. comm.). Therefore, recent changes in the relative abundances of these 2 species in southernmost Italy may not be associated with competitive interactions.

In an experiment conducted in the 1950s to control malaria in southern Kenya and northern Tanganyika (now Tanzania), residual house spraying with dieldrin led to the virtual disappearance of the vector *An. funestus* and its replacement in outdoor resting shelters by the related, but zoophilic, species *An. rivulorum* (Gillies and Smith 1960). Because larvae of the 2 species frequently co-occur, these authors conjectured that interspecific larval competition had suppressed *An. rivulorum* numbers prior to the high mortality suffered by *An. funestus* from insecticide treatments. The decreases in *An. funestus* abundance released *An. rivulorum* from competition and the predominance of the former species in niches previously shared by both species.

*Anopheles funestus* and *An. rivulorum* belong to the same species group (Coetzee and Fontenille 2004), and are both closely related to *An. parensis*, another exophilic, East African species whose abundance on the Kenya Coast increased following house-spraying to reduce malaria transmission by *An. funestus* (Gillies and Furlong 1964). One concern following such shifts in species composition is whether the presumed non-vector species might assume vector status over time or upon closer inspection. Although *An. parensis* has not been incriminated as a malaria vector, even when collected indoors (Kamau et al. 2003), *An. rivulorum* has been shown to transmit *Plasmodium falciparum* to humans in eastern Tanzania (Wilkes et al. 1996).

Conspicuous shifts in the abundance of container-inhabiting *Aedes* mosquito species have been associated with human-assisted invasions of the broadly distributed *Ae. aegypti* and *Ae. albopictus* (Lounibos 2002). *Aedes aegypti*, indigenous to Africa, is believed to have become

established in tropical Asia towards the end of the 19<sup>th</sup> century (Smith 1956). In cities such as Kuala Lumpur and Calcutta, the spread of the domestic form of *Ae. aegypti* coincided with reductions in the urban range of the related, native container inhabitant *Ae. albopictus* (Gilotra et al. 1967). In Shanghai where *Ae. aegypti* did not successfully invade, *Ae. albopictus* was more common in domestic habitats than in localities in sympatry with *Ae. aegypti*, suggesting that competitive interactions influenced distributions (Gilotra et al. 1967).

*Aedes albopictus* spread from Asia into Pacific Islands during periods of social upheaval and human migration associated with World War II, leading to reductions by this invasive species of island-endemic mosquito species, such as *Ae. guamensis*, presumably by interspecific competition (Rozeboom and Bridges 1972). Where insecticide treatments had previously suppressed *Ae. aegypti*, such as in Guam or Manila, *Ae. albopictus* was observed to spread into urban niches vacated by insecticide-induced population reductions of its interspecific competitor (Gilotra et al. 1967). Following its invasion of North America in the 1980s (Hawley et al. 1987), *Ae. albopictus* rapidly reduced the range and abundance of *Ae. aegypti* throughout most of the southeastern USA (Hobbs et al. 1991, O'Meara et al. 1995). The latter is the best documented example of a naturally occurring competitive reduction, including many experiments conducted to test hypothetical competitive mechanisms (Juliano and Lounibos 2005).

## A FIELD TRIAL OF COMPETITIVE REDUCTION FOR MOSQUITO CONTROL

Laboratory experiments at Johns Hopkins University showed that *Ae. albopictus* would competitively displace cage populations of *Ae. polynesiensis* (Gubler 1970a). The displacement mechanism was presumed to be sterility induced by asymmetric reproductive competition (Gubler 1970b), interspecific larval competition (Lowrie 1973), or a combination of the two (Gubler 1970a).

Based on the consistent outcome of interspecific competition in the laboratory, non-native strains of *Ae. albopictus* were released on a sparsely populated atoll in the Pacific Ocean to reduce local populations of *Ae. polynesiensis* by interspecific competition (Rosen et al. 1976). The justification for this scheme was replacement of an important vector of human filariasis in Oceania by a non-vector of this parasite. Although the released *Ae. albopictus* dispersed broadly on the atoll, establishments were transient and disappeared within 2 years after the experiment, with no detectable effect on *Ae. polynesiensis* populations (Rosen et al. 1976). Although the authors conjectured about possible causes, they were ultimately unable to explain the failure of *Ae. albopictus* to colonize the target habitats.

## MECHANISMS OF COMPETITIVE REDUCTION

If competitive reduction is to be used for biological control, understanding its modes of action will be critical for predicting and facilitating successful deployments. Here, mechanisms are differentiated more broadly than a recent review, which embraced all in the context of exploitative (resource) or interference competition (Reitz and Trumble 2002). These authors point out that multiple mechanisms may underlie many examples of competitive displacement.

### Reproductive Competition

Asymmetric mating interference, whereby males of one species mate with a related species and produce inviable or less fit hybrid offspring, has been proposed as a method for the biological control of pests and vectors (Ribeiro 1988) and as a mechanism that maintains parapatric distributions of related species in nature (Ribeiro and Spielman 1986). Reproductive competition through the production of inferior or inviable zygotes has also been central to some proposed and field-tested genetic techniques for mosquito control (e.g., Lorimer et al. 1976).

Although there is some evidence to support the occurrence of this mechanism, also known as satyrization, in natural populations of ticks and tsetse flies (Ribeiro 1988), its importance as a population reduction mechanism among mosquitoes remains unsubstantiated. Among some non-vector arthropods, interspecific matings in hybrid zones where native and invasive species meet yield offspring with heterotic vigor (Perry et al. 2001), contrary to predictions of satyrization models.

Spielman and Feinsod (1979) suggested that infertile interspecific matings maintained the parapatric distribution of *Ae. aegypti* and *Ae. bahamensis* on Grand Bahama Island, but no data were presented to support this hypothesis. Nasci et al. (1989) claimed that asymmetric reproductive competition favoring *Ae. albopictus* was responsible for the demise of *Ae. aegypti* in the southeastern USA following the invasive spread of the former species in the 1980s. However, experimental evidence reported by these authors to support this claim has not been reproducible (Harper and Paulson 1994, Estrada-Franco and Craig 1995)

### Apparent Competition

Apparent competition occurs through the differential effects of a parasite or predator on 2 co-occurring species (Holt and Lawton 1994). Preliminary explanations for the recent range reductions of *Ae. aegypti* in the USA invoked the asymmetric effects of a protozoan parasite, *Ascogregarina taiwanensis*, which hitchhiked to North America with *Ae. albopictus* and is, supposedly, pathogenic only to *Ae. aegypti* (Craig 1993). However, field surveys after the establishment of *Ae. albopictus* in Florida found a low prevalence of this parasite infecting co-occurring *Ae. aegypti* (Garcia et al. 1994, Juliano 1998), and outdoor experiments in tires where the 2 species co-occur in Florida did not support a role for apparent competition mediated by *A. taiwanensis* as a mechanism explaining the outcomes of interactions between these 2 *Aedes* species (Juliano 1998).

### Egg Hatching Inhibition

A novel hypothesis by Edgerly et al. (1993) suggested that *Ae. albopictus* larvae differentially suppress hatching of eggs of *Ae. aegypti* and *Ae. (now Ochlerotatus) triseriatus*. Although this 'discretionary' hatching favored the invasive species in laboratory experiments, no field data are available to evaluate whether interspecific hatching inhibition operates in nature with potential for affecting population reductions.

### Oviposition Deterrence

Oviposition site selection by the mosquito *Culiseta longiareolata* in temporary pools is deterred by the presence of its potential competitor, the toad *Bufo viridis* (Blaustein and Kotler 1993). This example shows that physical displacement may occur even before the competing life stages, such as larvae, encounter one another. Models indicate that shifts in habitat selection based on interspecific effects on oviposition strategies may prominently influence population sizes of the competing species (Spencer et al. 2002).

### Larval Resource or Interference Competition

In traditional views, competition has been viewed as either exploitation, wherein individuals compete for limiting food resources, or interference, whereby individuals inhibit the growth and development of competitors by physical or chemical means (Morin 1999). Both types are known to operate among larval mosquitoes (e.g., Dye 1982, 1984; Broadie and Bradshaw 1991, Juliano 1998) and may act concurrently in the same system.

Interspecific larval competition was proposed as a likely mechanism to explain the invasion success of *Ae. aegypti* in Asia, based on the superiority in laboratory experiments of this

invading species in competition with the native *Ae. albopictus* (Moore and Fisher 1969). Although *Ae. aegypti* larvae consistently prevailed over *Ae. albopictus* in the presence of nutritious, artificial food (e.g., Black et al. 1989), this competitive outcome was inconsistent with the population reductions of *Ae. aegypti* by *Ae. albopictus* in the southeastern USA during the late 1980s and early 1990s (Hobbs et al. 1991, O'Meara et al. 1995). However, in competition experiments using leaf litter as the basal resource, *Ae. albopictus* larvae were consistently superior to *Ae. aegypti* in growth and survivorship parameters (Barrera 1996, Juliano 1998), and analyses of population growth trajectories demonstrated that interspecific larval competition was the most logical explanation of the population declines of *Ae. aegypti* in containers containing leaf litter substrates (Juliano 1998). The same competitive outcome was observed in experiments conducted in nature that manipulated resident populations of these 2 species in Brazil (Braks et al. 2004), demonstrating the generality of this result between continents and founding populations of different genetic origin (Birungi and Munstermann 2002).

The current distributions of *Ae. aegypti* and *Ae. albopictus* in the USA, where the former species is now restricted to urbanized, subtropical sites, is believed to reflect a state of relatively stable equilibrium, where zones of co-existence and exclusion are associated with different environmental conditions, as in other, well-studied regions where these species are sympatric or parapatric (e.g., Fontenille and Rodhain 1989). Experiments at exclusion and coexistence sites indicate that higher egg mortality of *Ae. albopictus* in drier, hotter environments mitigates the competitive advantage of that species in its larval stages (Juliano et al. 2002). Thus, although sites of co-existence and exclusion may be similar in aquatic environments (Juliano et al. 2004), differences in aerial environments may determine the impact of interspecific larval competition among sites. Therefore, abiotic and biotic factors may influence the outcome of competitive reductions through effects on different life history stages.

Superiority of *Culex quinquefasciatus* in larval competition with *Cx. tarsalis* was demonstrated in laboratory experiments by Smith et al. (1995) and suggested as a mechanism to account for a shift in the balance of these 2 species in light trap collections during the last 2 decades in the California valley. However, the shift in numbers in traps may also reflect the consequences of human-induced habitat changes that favor increases in the eutrophic larval environments preferred by *Cx. quinquefasciatus*.

Although interspecific larval competition is apparently an important reduction mechanism, the predictability of encounters in nature based on the outcomes of laboratory experiments has proven elusive. In addition to the failed predictions of release experiments (Rosen et al. 1976) and invasions (e.g., Moore and Fisher 1969, Black et al. 1989), the competitive reduction of *Oc. triseriatus* from tire habitats by invasive *Ae. albopictus* predicted from laboratory microcosm experiments (Livdahl and Willey 1991) did not occur in Florida (Lounibos et al. 2001). Possible mechanisms to explain the unexpected co-existence of these 2 species in nature include differential habitat selection (Lounibos et al. 2001) and asymmetric vulnerability to native predators (Griswold and Lounibos 2005). Interspecific larval competition may also account for instances where reductions of resident container mosquitoes did not occur after an invasion, e.g., in Florida bromeliads where native *Wyeomyia* spp. are superior to *Ae. albopictus* in competing for larval resources (Lounibos et al. 2003).

### Interphyletic Larval Competition

A potential objection to the use of competitive reduction for the biological control of mosquitoes arises if the superior competitor could also become a pest or disease vector. This criticism has been raised, for example, about the attempted competitive reduction of *Ae. polynesiensis* by *Ae. albopictus* (Rosen et al. 1976), because the latter species is a known dengue vector (Hawley 1988). Although most classical research on competitive displacement

considered only ecological homologs (DeBach 1966), recent findings from 3 different ecosystems show that larval mosquitoes may suffer from interphyletic competition with larval anurans.

In temporary pools in Israel, toad tadpoles may retard the development of *Cu. longiareolata* larvae (Blaustein and Margalit 1996). In more permanent water bodies in Australia, sympatric species of frog tadpoles suppress the survival and development of *Cx. quinquefasciatus* and *Oc. australis* larvae (Mokany and Shine 2003a,b). An important consideration is that the suppression of mosquito growth by frog larvae occurs at high resource levels, the competitive interaction probably being mediated through a yeast or fungus (i.e., a case of “apparent competition”) which lives mutualistically in tadpole guts but inhibits mosquito growth (Mokany and Shine 2003a). In contrast, the competitive reduction of *Cu. longiareolata* by *B. viridis* toad tadpoles is eliminated at high resource levels (Blaustein and Margalit 1996).

Although the extent of interphyletic competition unfavorable to mosquitoes awaits and warrants further research, experimental releases of larval anurans for competitive displacement of mosquitoes could have broad appeal owing to their innocuous nature and conservation concerns for this group of vertebrates (Stuart et al. 2004). Because larval anurans will eventually emerge from aquatic habitats, additional releases may be necessary for mosquito control, although adult anurans often return to larval sites to lay eggs (L. Blaustein, pers. comm.)

## MAINTAINING COMPETITIVE REDUCTIONS

Not surprisingly, the maintenance of competitive reductions is dependent on the persistence of conditions that permitted the shift in population dominance between species. For example, the recrudescence of *An. labranchiae* in Sardinia after anti-malarial campaigns (Marchi and Munstermann 1987) may be facilitated by habitat alterations and increased human settlement, and the replacement of vector by non-vector anopheline species, as witnessed in East Africa (Gillies and Smith 1960, Gillies and Furlong 1964), might not persist without subsequent insecticide applications to suppress the vector species.

However, the outcomes of other inadvertent competitive reductions, such as that of *Ae. aegypti* by *Ae. albopictus* in the USA (Lounibos 2002) appear to be relatively stable, not requiring interventions for persistence. Nevertheless, field tests of promising candidates for biological control by means of competitive reduction should be performed under conditions of controlled immigration, such as on islands (e.g., Rosen et al. 1976) where many of the cited examples of inadvertent competitive reductions were documented (Table 1).

## ORGANISMIC RESEARCH AND BIOLOGICAL CONTROL

The conclusions about mosquito larval suppression by anurans arose through insights from community ecological observations and simple but well designed experiments. Although the potential application of these recent findings for mosquito control remains uncertain, it can be safely said that too little ecological and behavioral research is currently conducted to elucidate possible weak links with potential for biological control. Past appeals for more natural history research devoted to biological solutions applied to mosquito control (e.g., Laird 1959) have been overshadowed by attention to “high-tech” methods, even though these may be decades away from field testing (Smith 2004).

Incremental increases in understanding have been achieved through experimental investigations concerning the reductions of *Ae. aegypti* populations by *Ae. albopictus* (Juliano 1998, Juliano et al. 2002, 2004; Juliano and Lounibos 2005). Understanding why other resident container mosquito species have not been displaced by *Ae. albopictus* (Lounibos et al. 2001,

2003), and predicting the outcome of introducing a new species (by invasion or intentional introduction) requires a detailed knowledge of the natural history and plasticity of the invading and resident species of the biological community. However, if appropriate groundwork is done, biological control trials of competitive reductions could be more promising than that conducted by Rosen et al. (1976). Particularly if the favored organism is known to be unharmed, field trials should encounter less public resistance than speculative transgenic methods.

Field trials might also include environmental modifications that tip the balance in favor of the benign species, e.g., as occurred when desalination favored population replacement by a non-vector anopheline species in Italy (Missiroli 1939).

Finally, in light of the potential damage of introducing exotic species for biological control (Simberloff and Stiling 1996), competitive reduction trials should use native species, whose prevalence could be favored by augmentative or inundative releases.

## SUMMARY

Competitive displacement and reduction is based on a well established ecological principle wherein one species diminishes the abundance of another, usually related, species by means of competition. Unanticipated occurrences of competitive reductions are reasonably well documented among native and invasive populations of mosquitoes, especially when affected by human interventions. As confirmed by a recent review on arthropods (Reitz and Trumble 2002), larval resource or interference competition appears to be the most prevalent mechanism effecting displacement. The potential of competitive reduction for biological control is relatively untested and requires further ecological research.

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