A COMMUNITY-ECOLOGY FRAMEWORK FOR UNDERSTANDING VECTOR AND VECTOR-BORNE DISEASE DYNAMICS

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ABSTRACT

The integration of community ecology into the understanding and management of vectors and vector-borne diseases has largely occurred only recently. This compendium examines a variety of community interactions that can affect vector or vector-borne disease dynamics. They include: the importance of risk of predation, risk of ectoparasatism, competition, interactions of competition with transgenic control, apparent competition mediated through vectors, indirect effects of pesticides, vector diversity, and parasite diversity within a vector. In this paper, we summarize these studies and introduce several additional important questions in need of further exploration.

Keywords: vectors, vector-borne disease, community ecology, apparent competition, dilution effect, Release of Insects carrying a Dominant Lethal, risk of predation, risk of parasitism

WHERE WAS YENTA THE MATCHMAKER?

Strangely, the marriage between community ecology and the study of vectors and vector-borne disease control came rather late, and until recently, both the eventual bride and groom seemed nearly oblivious to each other. Evidence that ecologists were nearly oblivious is obvious in the content of general ecology texts written in the 1970s, which present chapters dealing with effects of biotic factors such as predation, competition, and mutualism on populations and communities, but give little coverage to parasite or disease ecology (e.g., Odum, 1971; Pianka, 1974; Smith, 1974). Likewise, with the burden of vector and vector-borne disease control falling mostly on those trained in medical fields, community ecology theory was generally outside the mindset of most vector biologists. There were, of course, some flirtations with a community ecology perspective. For example, over a century ago, medical entomologists considered the concept of

zooprophylaxis (see Service, 1991)—the notion being that placing livestock in proximity to human habitation could lower biting rates by generalist vectors on humans (a prophetic example of "encounter reduction," which is one of several mechanisms of the "dilution effect" (Keesing et al., 2006)). And before the invention of the term "apparent competition" (sensu Holt, 1977) and its formal theoretical development, some mosquito control workers suggested that alternative prey in rice fields might allow mosquitofish populations to grow more quickly, ultimately causing greater predation intensity on mosquito larvae than if these alternative prey were absent (Hoy et al., 1972; Blaustein, 1992). But these exceptions failed to transform the flirtation to a serious relationship between disciplines.

We suspect that the development of DDT and other chlorinated hydrocarbons significantly contributed to the delay of the infusion of community-ecology approaches into vector control. These chlorinated hydrocarbons were initially seen as a cheap and effective way of vector control; with such "magic bullets", why bother with the subtleties of community interactions? It took several decades after the development of these insecticides to recognize (or at least acknowledge) that these broad spectrum, long-lived chemicals had massive, negative non-target effects (Carson, 1962; Graham, 1970), and a few additional decades passed before the development of "ecotoxicology", which gives serious consideration to indirect effects of these pesticides as they ramify through food webs (Relyea and Hoverman, 2006; Duquesne and Liess, 2010, this issue).

We (the authors of this current paper), who all started our academic studies in the 1970s, have witnessed a profound change in attitudes among academic ecologists: from largely ignoring applied problems such as pest and disease control, to now embracing such applied problems. Moreover, community ecology, theoretically and empirically, has advanced considerably in the last few decades (e.g., Morin, 2011), including the explicit integration of parasites into food webs and ecosystems (see e.g., Collinge and Ray, 2006; Ostfeld et al., 2008) so it now has even more to offer to the understanding of the dynamics and control of vectors and vector-borne diseases (e.g., Ostfeld et al., 2006; Ostfeld et al., 2008; Keesing et al., 2010).

The eventual marriage, of course, makes eminent sense. Vectors, reservoir hosts, and pathogens not only interact with each other, but are embedded in food webs and, like all other organisms, are subject to the direct and ramifying indirect influences of multiple food web components. Community structure varies greatly both spatially and temporally, and to better predict where and when vectors will thrive, or where and when outbreaks of vector-borne disease will occur—and how to prevent such outbreaks—mandates elucidating the influence of community structure on vector and vector-borne disease dynamics. The growth curves of vector and vector-borne disease papers that deal with community interactions (Fig. 1) dramatically illustrate that community-ecology approaches pervade current attempts to understand and control vector populations and vector-borne diseases. The curves for papers dealing with "apparent competition" and "dilution effect" reflect that these terms are now widely accepted. The concept of "competition" has, of course, been explored for many decades in ecology, and yet we see that only beginning in the 1990s was there a jump in such studies on vectors, with a
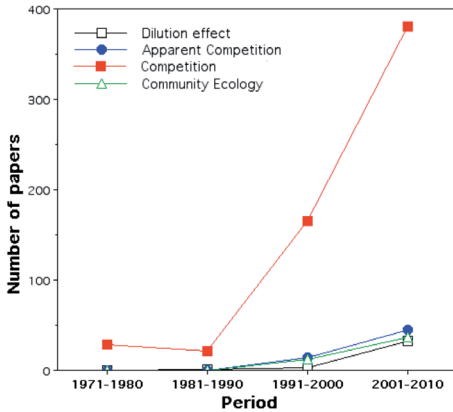
Fig. 1. Number of papers during ten year periods from ISI Web of Science on (1) "Dilution effect" and "disease*" and (vector* or tick* or mosquito*); (2) "Apparent competit*" and (mosquito* or vector* or tick*); (3) Competit* and (mosquito* or vector* or tick*); (4) "Community ecology" and (mosquito* or vector* or tick*).

further jump in the next decade. Moreover, this proliferation of studies of competition has not been matched by a comparable increase in more general analyses of the community context of vectors, in particular food web interactions – despite the fact that such interactions pervade the current discipline of community ecology (Morin, 2011).

SOME COMMUNITY INTERACTIONS

This compendium brings together a number of leading figures in the field, who present a diverse range of studies, including synthetic reviews, mathematical models, and original empirical research studies—that we believe collectively contribute significantly towards unraveling the importance of communities interacting to affect vector abundance, vector potential, and vector borne-disease. Although this compendium focuses on how community structure affects vectors and the diseases they transmit, we should not forget the flipside of the coin, namely, that etiological agents of infectious disease can have huge impacts on community structure (e.g., Lafferty, 2008). We begin the compendium by visiting this flip side:an essay by Bob Holt (Holt, 2010, this issue). He muses that the elimination of parasites could have far-reaching effects, on both ecological and evolutionary scales.

Three papers in this compendium (Kershenbaum et al., 2010; Roitberg and Mangel, 2010; Vonesh and Blaustein, 2010) consider the importance of predation risk. Early theoretical and empirical studies focused on predators' effects on prey populations via mortality from prey consumption. Yet predators not only affect their prey by consuming them, and thus inducing evolutionary counter-adaptations (gazelles are fast, turtles have shells, roses have thorns, and monkeys allogroom to remove ectoparasites), they also induce behavioral and physiological changes in response to perceived predation risk (Benard 2004; Morris et al., 2008; Whitman and Blaustein, 2009). Such changes, in turn, can affect prey populations (e.g., Spencer et al., 2002) and even community structure (Kotler and Brown, 2007). Over the past two decades, a growing number of studies have considered whether mosquitoes can detect risk of predation to their progeny

and choose oviposition sites accordingly. These studies have not been synthesized until now. Vonesh and Blaustein (2010, this issue) present a meta-analysis that shows that oviposition habitat selection by female mosquitoes, in response to perceived future risk of predation to their progeny is, in fact, common. Their meta-analysis examines various factors—life history and taxonomic—that might predict this behavior. One finding is that *Aedes* mosquitoes, which lay their eggs above the water line and hatch during subsequent floodings, are less likely to exhibit this behavior. However, mosquitoes such as *Anopheles*, *Culex*, and *Culiseta* species, which lay their eggs on the water surface, are much more likely to exhibit oviposition avoidance of aquatic predators that can harm their progeny. This is consistent with the prediction that oviposition avoidance in response to predators is more likely if the predation risk conditions at the time when the mother is assessing the habitat, predicts those conditions at the time when her larvae hatch and develop (Blaustein, 1999). Mosquito species whose eggs are laid directly on the water surface, with hatching occurring within 2–3 days of oviposition, should be better able to gauge risk of predation to their larvae, than species like *Aedes*, whose eggs are laid above the water line and do not hatch for weeks, months, or even years. One important consequence of this type of behavior is that it should alter how we interpret the effect of predators on mosquito populations. A mosquito population generally consists of terrestrial adults that may use a number of potential breeding sites. If oviposition across pools varying in predation risk is erroneously assumed to be at random, simple experimental designs that compare the number of larvae or adult emergence in predator-inhabited versus predator-free plots will likely over-estimate the effect of the predator on the adult mosquito population (Spencer et al., 2002).

Predation risk can also greatly affect foraging decisions by prey when foraging is risky (e.g., Stav et al., 2010). This has been demonstrated across many taxa (Brown and Kotler, 2004) but its role in affecting disease dynamics by, for example, limiting host movement, has received little attention to date. Kershenbaum et al. (2010, this volume) present models suggesting that risk of predation to a central-place forager that serves as a reservoir host can reduce disease spread. The model predicts that long-distance forays by a central-place forager such as the rock hyrax, which is a reservoir host of leishmaniasis, are reduced by risk of predation. This behavioral response in turn reduces disease transmission. When perceived risk of predation is high, the model predicts lower disease prevalence in the host and reduced disease cycling frequency. The paper presents an example of how anthropogenic activities can interact with host behavior and predation risk to affect infectious disease. In northern Israel, clearing of land for settlements and roads has altered the spatial configuration of rock piles (the habitat of hyrax), which interacts with predation risk to affect hyrax movement and, subsequently, disease dynamics.

A third paper in this collection (Roitberg and Mangel, 2010, this issue) also considers risk of predation in a theoretical framework. Mosquitoes should experience distinct risks of predation when they are resting, or looking for a nectar or blood meal, or searching for an oviposition site. Roitberg and Mangel construct models to assess how vector control methods, such as insecticide-treated bednets and insecticidal residual wall sprays, may interact with community dimensions—nectar-containing plants and risk of

predation—to affect foraging decisions by *Anopheles* mosquitoes. Insecticide-treated bednets increase emigration from a house, but risk of predation in the external environment reduces emigration rates by mosquitoes in search of nectar or blood meals. This approach shows much promise for dealing with the net effects of multiple, interacting factors—both anthropogenic and natural—in affecting vector behavior and population dynamics.

Like risk of predation, risk of parasitism should also be weighed by foragers when choosing foraging sites (Raveh et al., 2011). Yet, the effect of the risk of parasitism on habitat selection by hosts has received far less attention by researchers than has the influence of risk of predation on prey behavior and habitat choice. White-tailed deer serve as the primary reservoir host of several diseases transmitted by one of its ectoparasites, the lone star tick, *Amblyomma americanum*. Tick densities vary considerably in space within forests. Allan et al. (2010, this issue) find that deer spent less time foraging in areas with high densities of the lone star tick. Such a behavioral response to risk of parasitism should reduce disease transmission. Understanding when mammalian reservoir hosts detect risks of ectoparasitism, and gauging quantitatively how they manage this risk, can give a better understanding of pathogen transmission and disease dynamics.

Competition has long been recognized by ecologists as a major factor in structuring ecological communities (Elton, 1946). Prior to the last two decades, however, the importance of competition in affecting mosquitoes had rarely been considered (exceptions being container species; see below). Competition can affect mosquito survival, but competitive interactions can also strongly affect fitness and its vector potential (e.g., Bevins, 2008). In many types of mosquito breeding habitats, particularly those large in area or volume, taxonomically distant species have been shown to be strong competitors of mosquito larvae (reviewed in Blaustein and Chase, 2007). However, in small "container" habitats, interspecific competition among mosquito species is often very strong (Lounibos, 2002). With the recent widespread invasions of several container species such as *Aedes albopictus* and *Aedes japonicus*, there has been considerable interest in the competitive interactions between invasive and resident mosquito species (reviews in Lounibos, 2002; Juliano and Lounibos, 2005). Juliano (2010, this volume) uses results from published experiments that examined the strengths of both intra- and interspecific competition to conduct a meta-analysis examining competitive outcomes between the invasive *Aedes albopictus* and two resident mosquitoes, *Aedes aegypti* and *Aedes triseriatus*. He also assesses the role of food quality in determining the competitive outcome. The meta-analysis indicates that competition between *A. aegypti* and *A. albopictus* is context dependent; the latter has the competitive advantage when food quality is low, but no competitive advantage at high-quality food conditions. The analysis also indicates no competitive asymmetry between *A. triseriatus* and *A. albopictus*, regardless of food quality.

Another form of context dependence for competitive interactions among vectors may come from insect-sterile and transgenic-lethality techniques applied to one target vector species that competes with other species. Male sterilization techniques have been utilized for many years (Knipling, 1955). The basic approach takes advantage of the fact

that sterile males should effectively compete with wild nonsterile males for matings, which should in turn lower realized fertility of females and lead to a decline in the vector population, particularly when females mate only once. A more recent approach is the transgenic one, where incorporation of dominant lethal genes causes death in the *larval* progeny. This approach, referred to as RIDL® (Release of Insects carrying a Dominant Lethal), has great potential for vector control (Alphey et al., 2008). Optimally, in the case of mosquitoes, the lethal genetic effect should occur before the mosquito becomes an adult, when it becomes a nuisance and public health threat, but not before it can potentially compete with larvae of conspecifics and other mosquito species. When this can be arranged, the genetic modification does not just directly eliminate the individuals carrying the gene, but also degrades the environment for other vector larvae. Considerable theoretical work has established the benefits of transgenic control programs on the targeted vector species (e.g., Yakob et al., 2009), but the community ecological implications of such vector control remain largely unexplored. Bonsall et al. (2010, this issue) theoretically address this question here—and in particular the interplay of this technique with interspecific competition. Their models indicate that conventional and transgenic control techniques can readily affect the local coexistence and exclusion of vector species.

It is also common that different vector species share the same pathogen and the presence of multiple vectors sharing the same pathogen may affect disease dynamics. Lord (2010, this volume) examines this question with a model that considers arbovirus transmission, such as West Nile virus or St. Louis encephalitis virus, given two competent vectors with low seasonal overlap. Epidemics in the model runs varied considerably based on phenology of the vectors, but the overall result is that the action of multiple vectors resulted in multiple epidemic peaks. Lord points out that the model she presents does not consider interactions between the mosquito species, either at the larval stage or as adults. Yet such interactions may be relevant for the container species discussed in Juliano (2010, this issue) and Bonsall et al. (2010, this issue), and may then affect disease outcomes with multiple vectors. Incorporating these more complex interactions will be important in future research building on Lord's approach, articulating the relationship between vector species richness and the temporal dynamics of disease.

Host diversity may lead to a dilution effect, particularly if the additional hosts are refractory ones, or it may lead to apparent competition, particularly when the additional hosts are competent reservoirs that do not compete directly or exploitatively with the focal host (Keesing et al., 2006). Two host species that share a pathogen can be apparent competitors mediated by the disease agent; that is, host B allows the build up of the pathogen, which subsequently results in more disease prevalence for host A than would occur if host B were not present. This has been given considerable theoretical and empirical attention (references in Bonsall and Holt, 2010, this issue). However, the role of vectors on apparent competition between hosts has received considerably less attention. Bonsall and Holt (2010, this issue) suggest that apparent competition can be mediated by two mechanisms: (1) by reducing susceptible host fitness by feeding; (2) through the effects of disease transmission. They consider these possibilities in a mathematical

framework, and their paper provides an initial exploration of the ways in which apparent competition affects the dynamics of multi-vector communities. The models explored demonstrate that species exclusion can occur, even with purely frequency-dependent disease transmission (which in general is not expected to regulate hosts in single-host systems). The paper highlights the potential importance of understanding the detailed biology and dynamics of disease transmission within and between host species. An intriguing result is that sustained oscillations in disease prevalence can arise in vector-borne diseases in a multi-host context, even with density-dependent transmission. Together with Lord (2010, this issue)'s results, this suggests that multi-species vector-transmitted diseases can display a rich range of dynamical behaviors.

Pathogen diversity within a vector may result in a diversity of diseases transmitted to a host by a single vector bite. Arthropod vectors are commonly infected by more than one pathogen that they may be capable of transmitting to hosts. Pathogens that co-occur in arthropod bodies may interact in various ways, including competitively (Paul et al., 2002), and they may also co-infect mammalian hosts and may increase disease severity in the mammalian host. Civitello et al. (2010, this issue) consider whether co-infections in ticks deviate from the frequency expected from purely random association. They demonstrate with a meta-analysis that both negative and positive associations between pathogens occur in nature. A better understanding of the mechanisms for these associations can aid in understanding and controlling vector-borne diseases. For example, if certain pathogens tend to co-occur in individual ticks or other vectors, then hosts, including humans, might be expected to also become infected by both pathogens at higher frequencies than predicted by their independent transmission rates. Coinfections in hosts, including humans, can result in much different disease outcomes and prescribe different treatments than do a concatenation of single infections.

Chemical pesticides, besides killing vectors, can have many sublethal and indirect effects on vectors, interacting with other food web components. We summarized earlier the contribution of Roitberg and Mangel (2010) to this issue, where they examined by modeling how insecticide-treated walls and bednets could indirectly affect mosquitoes by changing their behavior and how they interact with other community components. Duquesne and Liess (2010, this issue) provide a complementary review, examining how pesticides in mosquito breeding sites can affect mosquito survival and vector potential by altering their competitive ability and vulnerability to predators. Broad-spectrum pesticides often kill antagonists (predators and competitors) of mosquito larvae. Because mosquitoes are early colonists of temporary water bodies, and can gauge risks of predation and competition when choosing an oviposition site, pesticide application may paradoxically cause local short-term reductions of mosquitoes but long-term regional increases in mosquitoes. Pest resurgence due to the killing of pest antagonists can be mitigated by using pesticides that selectively target the pest with little or no non-target effects. To date, arguably the most effective agent fitting this description is the biopesticide, *Bacillus thuringiensis israelensis*. This bacterium produces proteins that are toxic to mosquito and blackfly larvae and have little effect on nontarget organisms. It is now widely used for mosquito, blackfly, and chironomid control worldwide. Yoel Margalith,

whose laboratory discovered this bacterium and its larvicidal activity, passed away this past year and is eulogized in this compendium (Tsurim et al., 2010, this issue).

In summary, this compendium examines a variety of community interactions that can affect vector or vector-borne disease dynamics: the importance of risk of predation (Vonesh and Blaustein, Kershenbaum et al., Roitberg and Mangel), risk of ectoparasatism (Allan et al.), competition (Juliano), interactions of competition with transgenic control (Bonsall et al.), apparent competition mediated through vectors (Bonsall and Holt), indirect effects of pesticides (Roitberg and Mangel, Duquesne and Liess), vector diversity (Lord et al.), and parasite diversity within a vector (Civitello et al). We hope this compendium will spur continued expanded growth of work at the interface of community ecology and vector ecology/vector-borne disease. Many important questions remain to be addressed, and we conclude by sketching just a few questions in need of further exploration.

SOME FUTURE EXPLORATIONS

Generalist predators are common candidates for biological control. Clearly, pest control using generalist predators cannot be considered without considering the community as a whole, and may carry unanticipated risks under certain conditions. One example is the use of the mosquitofish, *Gambusia affinis*, as an introduced predator to control mosquitoes in rice fields. Rice fields generally are flooded for about four months before being drained to harvest the rice. Mosquitoes colonize through oviposition during these flooding phases. Despite the crowning of the mosquitofish as the "established predator" of mosquitoes in rice fields (Gall et al., 1980), the stocking of mosquitofish into this habitat for mosquito control is currently far from a sure bet. Indeed, experimental work has shown that although *Gambusia* can cause nearly 100 percent immature mosquito reduction in some rice fields (e.g., Hoy et al., 1971), in other cases *Gambusia*-stocked fields can yield *more* mosquitoes than other rice fields not stocked with this fish, even when mosquitofish are at very high densities (Blaustein, 1992). We also know that rice fields have rather complex communities (Lawler, 2001), with considerable among-field variation in community components including predator diversity and biomass, species sharing the same trophic level as mosquito larvae (exploitative and/or apparent competitors), intraguild predators, algal species composition, and nutrient levels. All these components of rice fields themselves affect mosquito larvae and may interact strongly with *Gambusia* to alter its effectiveness on mosquito production in that field. The very name "mosquitofish" is a misnomer—this taxon is a generalist predator with no clear preference for mosquito larvae—and given that mosquito abundance is typically low compared to other potential prey items such as cladocerans and ostracods, this huge variance in mosquito control by *Gambusia* across experiments should not be surprising. The challenge then is to incorporate community ecology into better predicting under what conditions mosquitofish will be effective mosquito control agents, including what stocking densities are necessary based on community structure to achieve significant control in a reasonable amount of time. Do species sharing the same trophic level as mosquitoes

in rice fields initially act as apparent mutualists (reducing predation intensity on mosquitoes by serving as alternative prey for predators which can be satiated or switch in their foraging activities), and then transition to apparent competitors (controphic species that cause increases in the development and numerical responses of the predator ultimately may magnify predation imposed on mosquito larvae) (Blaustein and Chase, 2007)? Does higher productivity via bottom-up effects delay the switch from apparent mutualism to apparent competition? Oviposition site selection by mosquitoes in response to *Gambusia* may also play a big role in the overall effect of *Gambusia* on mosquito populations. Some mosquitoes may directly avoid *Gambusia*-conditioned water when ovipositing (Angelon and Petranka, 2002; van Dam and Walton, 2008). But mosquitoes may also avoid invertebrate predators (Vonesh and Blaustein, 2010, this issue) and competitors (e.g., Blaustein and Kotler, 1993; Duquesne et al., 2011). *Gambusia* may thus strongly reduce the impact of these antagonists (Bence, 1988; Blaustein, 1992), thereby countering any direct effects it may have on mosquito numbers. Thus, community ecology—both theory and empirical work—still has much to contribute to understanding when and how to use *Gambusia* and other biocontrol agents effectively.

The role of biodiversity in affecting vector-borne disease prevalence has been an intensively researched question over the last decade, and is very likely to remain so over the next decade. In theory, increases in biodiversity may either cause an increase or decrease in disease prevalence (Keesing et al., 2006, 2010). However, empirical studies almost exclusively find that high biodiversity tends to reduce pathogen transmission and that the loss of biodiversity can increase disease risk (Keesing et al., 2010). A major reason why this relationship seems so robust is that the species that remain, or even thrive, in ecological communities experiencing biodiversity loss tend to be those that amplify pathogen transmission. Apparent-competition effects (the obverse of the dilution effect) may be most likely between similar, taxonomically related hosts, and species-rich communities typically include many distantly related taxa. Examples of hosts fostering parasite transmission remaining in low-diversity situations include highly competent reservoirs for multi-host pathogens such as small rodents, bats, and urban-adapted passerine birds, as well as many vectors that are excellent colonizers. The underlying causes of these correlations between ecological resilience of species to anthropogenic change and their amplifying role in pathogen transmission is only beginning to be studied (Cronin et al., 2010; Keesing et al., 2010). This ongoing research emphasizes the critical importance of community assembly and disassembly rules in governing the effects of biodiversity change on disease transmission (Ostfeld and LoGiudice, 2003).

Is biodiversity also a causative factor in influencing vector abundance and vector potential? The influence of biodiversity on invasion success has been a hot topic of research in recent years (e.g., Kennedy et al., 2002). It is not rare to hear anecdotal observations like rarely finding mosquitoes in high densities in pristine rain pools, and finding high densities in only disturbed ones (A. Gasith, pers. commun.). With respect to mosquitoes, many studies have experimentally examined the effect of a single controphic species of mosquito larvae on invasion success, or larval performance of a focal species (Juliano 2010, this volume; also reviewed in Blaustein and Chase, 2007). Moreover, there is evi-

dence that community simplification due to pesticides (Duquesne and Liess, 2010, this issue), or pool desiccation (Chase and Knight, 2003) can cause outbreaks in mosquitoes. However, no studies, to our knowledge, have systematically examined how altering biodiversity (as measured for instance by species richness of resident guilds) alters invasion success. For example, do mosquito assemblages become saturated, or instead can interactions among resident species at times facilitate invasion by newcomers?

The theoretical studies in this compendium collectively point out a number of important directions for future work. For instance, the additional feedbacks that become possible in a multiple species setting may permit oscillations to arise that are not expected in simpler modules (Bonsall and Holt), or lead to complex patterns of temporal variation during an annual cycle (Lord). Understanding the dynamics as well as statics of multi-species vector–host systems is an important challenge, and one that is relevant to key applied questions such as the prediction and management of disease outbreaks.

These are but a few exciting potential topics for examining how community ecology affects vectors and vector-borne disease, and how we can use community ecology for predicting and managing vectors and vector-borne disease. We hope that this compendium provides a catalyst for a wide range of future studies at this interface.

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