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THE EVOLUTION OF OVIPOSITOR LENGTH IN THE PARASITIC HYMENOPTERA AND THE SEARCH FOR PREDICTABILITY IN BIOLOGICAL CONTROL

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ABSTRACT

Ovipositor lengths are thought to reflect the egg-laying and host-searching behaviors of parasitoids. For example, parasitoids that attack exposed foliage feeders often have short ovipositors compared to species that must penetrate a substrate to reach a host. However, the relationship between host accessibility and ovipositor length is not apparent in a guild of braconids that oviposits in the larvae of frugivorous Mexican tephritids. While the longest ovipositors are up to 5× longer than the shortest, all attack roughly the same stages of their shared hosts, often in the same fruits. Nor is there any evidence that the shorter ovipositors represent a saving of metabolic resources and energy that is redirected toward egg production or greater ability to move. It has been suggested that if the ovipositor length of an introduced parasitoid is substantially different from the ovipositors of species already present, then it is more likely to find an empty niche in its new environment, become established, and add to the control of its host. However, with the present lack of a simple explanation for the variety of ovipositor lengths within the Mexican guild it is not clear how predictive ovipositor length would be in this instance. Until the evolution and maintenance of the various lengths is better understood it may be more circumspect to practice fruit fly biological control through the conservation and augmentation of parasitoid species already present.

Key Words: Hymenoptera, Diptera, Ichnuemonoidea, Braconidae, Opiinae, Chalcidoidea, Tephritidae

RESUMEN

Se piensa que la longitud del ovipositor refleja el comportamiento de los parasitoides para ovipositar y buscar el hospedero. Por ejemplo, los parasitoides que atacan hospederos que estan expuestos sobre el follaje de que se alimentan a menudo tienen ovipositores cortos comparados con las especies que tienen que penetrar un sustrato para alcanzar al hospedero. Sin embargo, la relación entre la accesibilidad al hospedero y la longitud del ovipositor en un gremio de braconidos que oviposita en larvas de tefrítidos mexícanos fruteros no es evidente. Mientras que los ovipositores más largos son hasta 5 veces más largos que el más corto, todos atacan más o menos las mismas etapas del hospedero compartido, a menudo en la misma fruta. Tampoco hay evidencia que los ovipositores más cortos representan un ahorro de los recursos metabólicos y de energia que es redirijido hacia la producción de huevos o ha una mayor mobilidad. Se ha sugerido que si la longitud del ovipositor de un parasitoide introducido es significativamente diferente de los ovipositores de las especies ya presentes, luego es más probable encontrar en ese nuevo ambiento un nicho vacio, establecerse, y añadir para el control de su hospedero. No obstante, con la falta de una explicación sencilla para la variedad en la longitud de los ovipositores en el gremio mexícano, no es claro cuan predicible la longitud del ovipositor puede ser en este caso. Hasta que se entienda mejor la evolución y mantenimiento de las diferentes longitudes puede ser más prudente practicar el control biológico de la mosca de la fruta a travéz de la conservación y aumento de las especies de parasitoides ya presentes.

The extended-piercing ovipositor is perhaps the key innovation that led to the diversity and abundance of the parasitic Hymenoptera. It allows feats of carnivory that are difficult or even impossible for the other great parasitoid group, the Diptera, and underlies the evolution of the distinctive "wasp" morphology. The wasp-waist for instance, is a pivot that provides the flexibility needed to position the ovipositor/stinger at the most appropriate angle to reach the host or penetrate a cuticle (e.g., Quicke 1997).

While in essence a tube attached to a mobile "delivery system", it is an over simplification to imagine ovipositors as just biotic hypodermic needles (Quicke et al. 1999). They have external and internal structures that help steer them along

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their course, serrations hardened with heavy metal-protein complexes, internal channels that deliver venoms, and microsculpturing to help move eggs along often considerable distances (Quicke et al. 1999; Vincent & King 1996). However, one of their seemingly simplest properties, their length, has a number of complex ecological and behavioral implications.

Even a passing familiarity with the parasitic Hymenoptera reveals the considerable variety of ovipositor lengths within the group. Why do these egg-laying tools exist in all these various lengths? The obvious answer is "to do their job by reaching their hosts", recognizing that hosts have different types of bodies and cuticles, and occur in a diversity of environments, surrounded by different depths and forms of materials, from unobstructed air to solid wood. Price (1972; LeRalec et al. 1996) accounted for the differences in ovipositor length among the parasitoids of the Swaine jack pine sawfly, *Neodiprion swainei* Middleton, by considering the tasks facing the different species. Some attack buried pupae and others oviposit in larvae exposed on leaf surfaces (Price 1972). Those that lay eggs in pupae have long ovipositors, designed to reach through leaf litter, while those that attack foliage-feeding larvae have short ovipositors just long enough to penetrate the host's integument.

But, will ovipositors be lengthened to deal with every contingency the wasp might face? Or, assuming there are tradeoffs to ever increasing size, will selection favor a length for every species that is just sufficient to undertake the typical piercing-depositing job it is likely to face? Might there be an optimal length, neither a "deluxe" nor "economy" model? And if there is an optimal length, are the only factors of any importance in its evolution the type of host being exploited and the environment where the host occurs? The answer to the last question seems to be no—at least not all the time or in any straightforward manner. Consider for example the braconids attacking Mexican fruit flies (López et al. 1999).

In the state of Veracruz 10 species of Hymenoptera attack tephritid flies of the genus *Anastrepha* (e.g., López et al. 1999). Among these parasitoids are a suite of native opiine braconids: *Utetes anastrephae* (Viereck), *Doryctobracon areolatus* (Szepligeti), *Doryctobracon crawfordi* (Viereck), and *Opius hirtus* (Fisher). An exotic opiine, *Diachasmimorpha longicaudata* (Ashmead) originally from the Indo-Philippine region, was established in the region over 30 years ago (Ovruski et al. 2000). All are solitary, endoparasitic koinobionts (parasitoids whose hosts continue to develop after being attacked) that oviposit only in frugivorous tephritids and complete development within the host's puparium.

These species, both native and exotic, are geographically widespread and attack a wide range of fruit flies in a diversity of fruits (López et al. 1999; Sivinski et al. 2000). It is not unusual for several to occur in any particular locale, or even for more than one species to emerge from flies infesting a single piece of fruit; e.g., *U. anastrephae* and *D. areolatus* are commonly found attacking *Anastrepha obliqua* (Macquart) in the same *Spondius mombin* L. fruits (Sivinski et al. 1997) and up to 5 species of parasitoids have been recovered from a single piece of fruit (Lopez et al. 1999). But while they have many similarities with respect to host range, distribution, and life histories, there are substantial differences in their ovipositor lengths (Fig. 1). These range from being less than the length of the abdomen in *U. anastrephae* to several times the abdominal length in *D. crawfordi*.

While these sympatric parasitoids share overlapping opportunities for oviposition, it appears they are not able to take equal advantage of the pool of hosts (Sivinski et al. 2001). *Anastrepha* larvae infest fruits over a large range of sizes, from little tropical "plums" weighing a few grams to commercial mangos more than half a kilo in weight (López et al. 1999). All the braconids attack flies in the smaller fruits, but only those with longer ovipositors are common in larger fruits (Fig. 1). How do the short-ovipositor species persist, and even flourish? Could there be a cost to having a long ovipositor, one so great that an insect with fewer options for oviposition, but investing in "cheaper" equipment, is still able to compete?

There are certainly problems inherent in having a very long ovipositor. Occasionally, species such as the Peruvian ichnuemonid *Dolichomitus hypermenses* Townes and the Japanese braconid *Euurobracon yakohamae* Dalla Torre carry prodigious external ovipositors, up to 8 times as long as their bodies (e.g., Townes 1975; Fig. 2). Some African Torymidae (or perhaps aberrant Pteromalidae) with ovipositors between 5 and 6 times their body lengths, e.g., *Ecdamura* sp. and *Eukoebelea* sp., are the likely record-holders among the chalcidoids (Compton & Nefdt 1988). However, these are rare exceptions to the rule, and few ovipositors exceed the more modest relative length of 1.3 times the body (Townes 1975). One reason is that the greatest force can be applied to the ovipositor when it is held perpendicular to the cuticle of a host or to the surface of the surrounding medium, and to accomplish this the abdominal tip must be held at least an "ovipositor-length" above the surface (van Achterberg 1986). Females wielding moderately long ovipositors often assume a head down/abdomen in the air/tip toe position to gain the greatest possible elevation. But even if the optimal position can be attained, too great a force on too-thin an ovipositor can cause it to bend (termed Euhler buckling), and prevent effective penetration (Vincent & King 1996; Quicke et al. 1999). All other things being equal the danger of this buckling is greater the longer the ovipositor.

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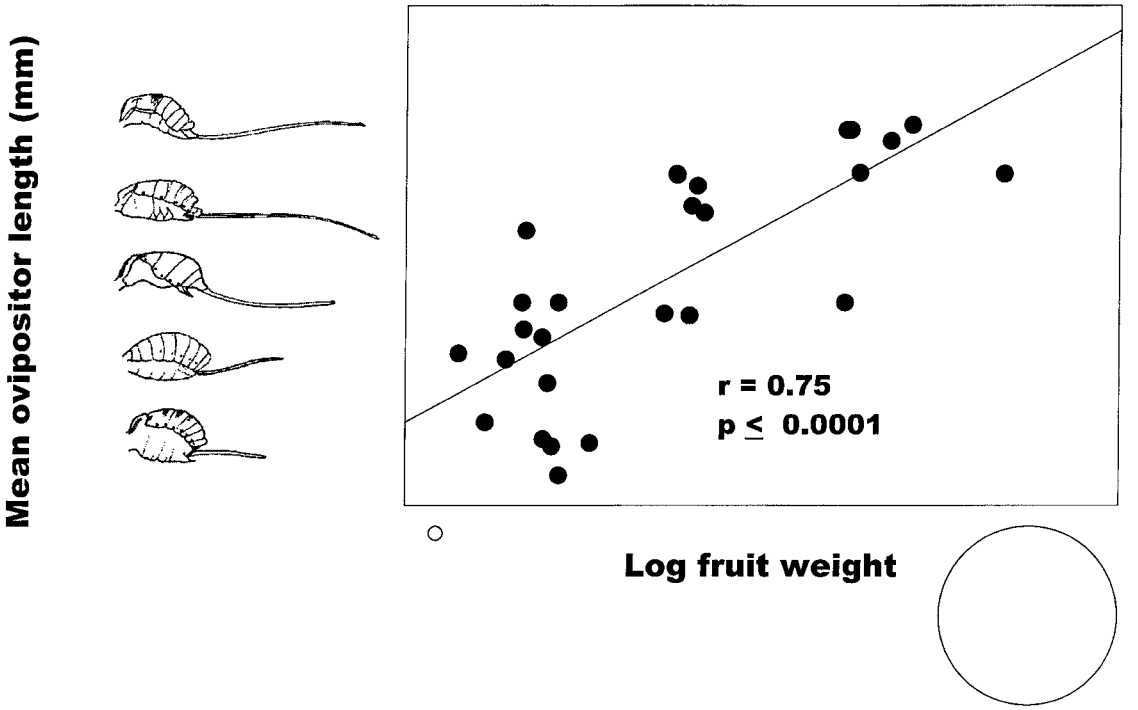


Fig. 1. The relationship between the mean size (weight) of a fruit sample containing tephritid larvae and the mean lengths of the ovipositors of the various parasitoids that attacked these particular larvae (see Sivinski et al. 2001). In general only parasitoids with longer ovipositors can exploit hosts in large fruits. The species, from top to bottom, are *Doryctobracon crawfordi*, *Diachasmimorpha longicaudata*, *Doryctobracon areolatus*, *Opius hirtus*, and *Utetes anastrephae*.

There are means of mitigating the positioning and buckling difficulties caused by extreme length. In *Megarhyssa* spp. ovipositors several times their owner's length can be effectively shortened by initially looping the shaft into a membranous sac at the tip of the abdomen (Townes 1975). The very long ovipositor of the parasitic orussid sawflies is coiled within the abdomen, and gripped by apodemes as it is extruded a bit at a time during drilling towards wood boring hosts. In this way the length of the exposed portion of the ovipositor is minimized, as is the problem of buckling (Cooper 1953; Quicke et al. 1999). In other instances, very long ovipositors are not used to penetrate tough substrates, but follow fissures or previously excavated tunnels through the medium surrounding the host. Under these circumstances, force and perpendicularity are not as critical and the ovipositor may meet the substrate at an angle of 120 degrees or less (van Achtenberg 1986).

In addition to exacerbating the penetration problems facing the ovipositor itself, increasing length can strain the "delivery system", the body of the wasp, by restricting movement, increasing wind resistance in flight, and making the insect more vulnerable to predators. Long ovipositors in a number of parasitoid taxa are held internally, e.g., that of the previously mentioned orussids is looped several times within the abdomen (Cooper 1953). All cynipoids and some chalcidoids carry the bulk of the ovipositor concealed in an internal pouch (Fergusson 1988; Quike et al. 1999). In chrysidids, platygasterids, and some scelionids the terminal abdominal segments telescope the ovipositor outward when in use and retract it when at rest (Kimsey 1992; Felid & Austin 1994). Even if not strictly internalized, the ovipositor is sometimes held out of the way by doubling its length back on the body. In the Vanhornidae it bends forward to rest in a groove on the ventral surface of the abdomen (Deyrup 1985). Leucospids carry the ovipositor curved over the dorsal surface of the abdomen, and in some platygasterids, such as *Inostemma*, the receptacle containing the internal portion of the ovipositor projects forward, "handle-like", from the base of the abdomen over the thorax (e.g., Goulet & Huber 1993).

No matter how useful it would be to have an ovipositor that could reach every host under the most difficult circumstances, it would seem that with all the problems, additional expenses and modifications that go along with size, the maximum length ovipositor may not be the optimal for

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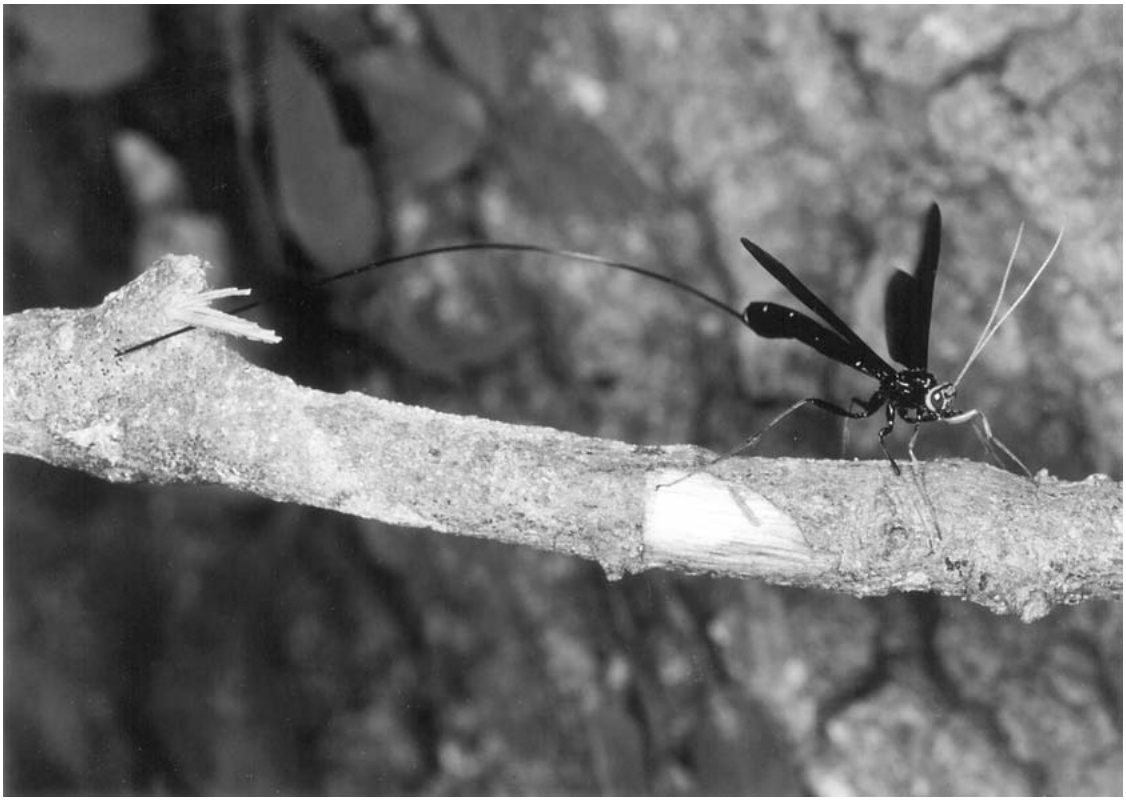


Fig. 2. A female *Megarhyssa atrata* (Fab.), a large ichnuemonid parasitoid with a very long ovipositor. The ovipositor can loop into a membranous pouch at the tip of the abdomen which shortens its exposed length. Such shortening prevents the ovipositor from buckling as it penetrates wood to reach the wasp's host.

the insect design as a whole. In terms of the Mexican braconids with the variety of ovipositor lengths, what might be the costs that prevent *D. crawfordi* (long) from displacing *D. areolatus* (medium) from displacing *U. anastrephae* (short)?

The energy and materials used to construct, maintain, and move an extended ovipositor could presumably have been spent elsewhere, perhaps in the production of more eggs, or in bigger flight muscles and better searching capacity. Of course, some fly larvae-hosts might be too deep in large fruits for the short-cheap ovipositor parasitoid to exploit, but access to these could be the benefit that makes it worthwhile for a competing species to continue to invest in a long-expensive ovipositor. That is, disruptive selection might result in a resource being shared by species with long and short ovipositors with few and many eggs, respectively.

The original prediction that fecundity should drop as ovipositors become longer, was made by Price (1973), who argued that if species with longer ovipositors deal with less accessible hosts, then, all other things being equal, handling time per oviposition should be greater and oviposition opportunities/unit of time should be fewer. In addition, since less accessible hosts are typically more mature, and because inevitable mortality occurs over the developmental period of the host, older, less accessible hosts should not be as abundant as younger, more accessible hosts. Both of the factors, longer handling time and fewer hosts, would contribute to lower potential rates of parasitism in species with long ovipositors. His hypothesis was supported by a strong negative correlation among species of Ichnuemonidae between ovipositor lengths and the numbers of ovarioles per ovary (which reflects the potential for egg production).

Is there a relationship between ovipositor length and fecundity in the Mexican braconids? No, there is not. The number of eggs does not significantly increase or decrease with ovipositor length. If there is a trend at all, it is in the opposite direction. The longer the ovipositor, the relatively more of the body is taken up by egg volume (No. of eggs*size of eggs) (Sivinski et al. 2001).

Though the "longer the ovipositor the lower the fecundity argument" is broadly supported when many species of Ichnuemonidae attacking a variety of host stages are considered, it is not as successful when looking at the one small guild of Braconidae attacking similar aged fruit flies un-

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der what seem to be similar circumstances. But are circumstances really so comparable after all? Despite overlaps in host ranges, each species has one or more specialized foraging areas within its niche. If the fruits within these specialized areas differ in size or penetrability, then the hosts they contain differ in accessibility, and this difference in host accessibility might lead to differences in ovipositor length. Maybe ovipositor lengths have evolved in a variety of unrelated situations, and each length is so well suited to this core ecological "stronghold" that whatever advantage or disadvantage it faces with competing species exerts a relatively trifling selection pressure. For example, the short-ovipositored *O. hirtus* attacks the monophagous tephritid *Anastrepha cordata* Aldrich as it develops in *Tabernaemontana alba* Mill. (Hernandez-Ortiz et al. 1994). For unknown reasons it is the only parasitoid to commonly do so, and since the pulp of this fruit is relatively shallow there may be no selection for a longer ovipositor in this particular, and arguably important, tritrophic interaction. There are any number of other such "specializations" such as greater tolerance for heat or ability to flourish at high altitudes (Sivinski et al. 2000).

While the diversity of ovipositors can form engaging intellectual puzzles, their different lengths also have broad practical, agricultural implications. These arise from the argument by Price (1972) that ovipositor length might be a means of predicting which newly introduced parasitoids will be able to avoid competition within an already existing guild of natural enemies, and so have the best chance of successful establishment and the provision of additional control.

At this point, let us make a somewhat lengthy digression to discuss the history of prediction in biological control. Predictability is a supreme virtue in an applied science such as entomology where we strive to find some way of saying that this good thing will happen and this bad thing will not. The search for biological predictability has become an issue of increasing importance in terms of both invasive species that arrive in new locations by accident and potentially beneficial arthropods deliberately moved from one place to another. As the world becomes more homogeneous through the spread of weedy species, the aesthetic appreciation of biological diversity increases along with greater awareness of its economic and ethical implications (widespread similarity mitigates the evolutionary potential of life). There is a growing cultural mandate to prevent the accumulation of potential pests and extraneous biological control agents (Simberloff & Stiling 1996; Thomas & Willis 1998). The latter always present some risk, no matter how small, of attacking nontarget insects or plants. In cases where nontargets have relatively slow rates of increase, "apparent competition", where an organism harbors a natural enemy that also attacks a more vulnerable species and as a result becomes a superior competitor, can be potentially devastating (Bonsall & Hassell 1997; Hudson & Greenman 1998). Even something that is initially safe may have the capacity to adapt to a more diverse environment and increase its host range (Willamson 1996).

A means of judging the present predictability of biological control is to compare the rates of establishment and resulting abundances of deliberately introduced natural enemies with the fates of "invasive" organisms that arrive in new areas largely by chance. It seems that establishing a beachhead is a long shot for an invading organism, and can be described by the "Rule of 10s". Willamson (1996) estimated that only 1 accidentally introduced animal or plant in 10 becomes established and only 1 out of 10 of these becomes abundant and pestiferous. Interestingly, the odds of a deliberately introduced biological control organism becoming common enough to exert an economic impact are only somewhat better, perhaps 3 in 10 become established and 3 of those effect control (depending on how success is measured). Apparently, there is often a far from complete understanding of the relevant ecology of natural enemies and their prey, and hence a long standing interest in why some natural enemies "work" and others do not.

Among practitioners of biological control there have been several attempts to collect and synthesize the attributes of successful natural enemies in order to focus explorations and make establishments more effective and environmentally safe. Propagule pressure, the size of the released cohort, is important to the outcome of natural enemy establishment. In a survey of Canadian programs, increases in the numbers of released insects, from <5000 to >30,000, improved success rates from 9% to 79% (Beirne 1975; Willamson 1996). If fewer than 800 individuals were included in individual releases success occurred 15% of the time compared to 65% if more than 800 insects were involved, and more than 10 releases gave 70% success compared to 10% for programs using fewer releases. When Goeden (1983) examined the insects introduced for weed control he found long attack season, gregarious feeding, and ease of colonization to be the most important contributors to success. The last of these has implications for propagule pressure.

In addition to how the craft of biological control is practiced there are some ecological generalizations concerning the vulnerability of insects to their natural enemies that might result in more predictable control. For example, biocontrol has tended to be more efficacious when applied against specialist herbivores rather than generalists and against exposed rather than concealed feeders (Gross 1991). Hosts that suffer high maximum parasitism rates, and by implication have

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fewer or less effective refuges to shelter within, are more likely to be successfully controlled (Hawkins & Gross 1992; Hawkins 1994). Within particular host taxa there are a number of even more specific correlations between vulnerability and type of natural enemy, and these relationships could be used to direct future establishment attempts. For example, Dyer and Gentry (1999) have examined the categories of predators and parasitoids that typically inflict high or low mortalities on Lepidoptera larvae with different morphological characteristics and defensive behaviors. Brightly colored larvae were likely to be rejected by wasps and bugs, but were attacked by ants and parasitoids, generalists were more likely to succumb to predation than to parasitoids, while hairy species were relatively immune to ants and bugs but fell victim to wasps and parasitoids, and so on. On the basis of their analysis they suggest that the generalist feeding habits of the infamous pest caterpillars of the genus *Spodoptera* (Noctuidae) are the reason they have not been successfully controlled by parasitoids, despite considerable efforts, and argue that in the future, predators, such as carabid beetles, might be more profitably employed.

In addition to morphology and ecology, the history of a pest and parasitoid interaction might be used to predict successful biological control. Hokkanen and Pimentel (1984) proposed that new associations between insects and natural enemies resulted in substantially greater mortality and a higher degree of pest suppression. The basis of their thesis was that long standing interactions will tend to be more benign since a prey species will have had ample opportunities to adapt to its hunter(s), but that it will be relatively defenseless when confronted with a novel set of weapons and hunting tactics. There are at least two criticisms of this theory. One is that the data used to substantiate the greater vulnerability of prey to new parasitoids can be reinterpreted to reach the opposite conclusion (Waage 1991). The second is that there is accumulating evidence that long term associations are typically more virulent than new ones: i.e., it is the natural enemies, including pathogens and parasites, that are ahead in arms races with their victims, and that familiarity has resulted in increasingly effective weapons and hunting tactics (e.g., Herre 1993; Ebert 1994; Kraaijeveld et al. 1998). While the opposite of earlier thinking, this emerging generalization of familiarity breeding lethality can be used as a predictive tool. It suggests that the closest possible match between the original populations of exotic pests and the populations of natural enemies that attacked them would tend to be most efficacious. However, as noted by Waage (1991), there seem to numerous exceptions to this rule of thumb, and in a practical sense one should not ignore any potential natural enemy regardless of origin.

There are also population characteristics, i.e., the distribution and abundance of a parasitoid in nature that might predict usefulness in a biological control program. Rare species on the periphery of host populations may be less competitive than other natural enemies, but be better foragers at low host densities. Such a species might do very well indeed if it could be introduced by itself into a new environment to deal with an exotic pest (e.g., Force 1974).

Now let us return to Price (1972) who reasoned that ovipositor length could be yet another means of estimating the likelihood that an exotic species would become established and whether it would disrupt the composition of an already existing native guild. He followed Hutchinson (1959) and Schoener (1965) who found that a "trophic apparatus", such as a bird's beak or an ovipositor, typically differs in size among sympatric species at the same trophic level, and that these differences in size are related to the differences in foraging behaviors that allow the species to coexist. A ratio of the larger to the smaller apparatus of 1.15 indicates sufficient niche separation in terms of the resource the apparatus is used to exploit. When ovipositor length ratios were examined in the guild of parasitoids attacking the Swaine jack pine sawfly, Price found that this threshold ratio was exceeded in comparisons among native species, but that the introduction of a European exotic had created a too close pairing of lengths between itself and a native species, and that there was already evidence of competitive displacement.

In the spirit of Price's search for predictability through ovipositor length, what do the various ovipositors of the Mexican braconids reveal about the potential for expansion through new introductions of this fruit fly parasitoid guild where it is already established, and about the use of its constituent species in future tephritid biological control programs elsewhere? There is the well-established relationship between ovipositor length and the size of the fruit a parasitoid can effectively forage upon. One might prefer to introduce a long ovipositored species such as *D. crawfordi* into new habitats dominated by large fruits. Other than this, there is little that can be said with certainty. There are obvious differences in ovipositor lengths, much as there are in Price's sawfly parasitoids. But, while the sawfly-parasitoid ovipositors are clearly due to distinct differences in foraging for different host stages, the same cannot be easily said for the Mexican tephritid-parasitoids. At this point it is difficult to say with any conviction how the various parasitoids manage to coexist in sympatry, and what role the differences in their ovipositors play in their coexistence.

If attempts were made to improve fruit fly biological control in Mexico are there "empty" niche spaces where exotic parasitoids would fit? Given our lack of understanding how the present diver-

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sity of tephritid parasitoids is maintained this is a troubling question to address. There is some circumstantial evidence of displacement of the long-ovipositored native *D. crawfordi* by the long-ovipositored exotic *D. longicaudata* (Sivinski et al. 1997), but the way in which this may have occurred remains obscure.

What is the best response to ignorance of the consequences of projected parasitoid introductions? More study is an obvious answer, but what if the sort of study that could predict success or dangerous failure requires time, and that during that period of study inactivity is impractical? We suggest that one way to deal with the present confusion and to best adhere with the applied-biology dictum of "do no harm" is to fully exploit what is already there; i.e., to conserve the existing guild and enhance its effectiveness through habitat manipulation.

For example, only 3.5% of the >200 species of *Anastrepha* are of any economic importance, yet a number of benign, generally monophagous, species developing in native fruits harbor the same parasitoids that attack notorious pests such as the West Indian fruit fly, *A. obliqua*, or Mexican fruit fly, *A. ludens* (Loew) (Aluja 1999). By encouraging the replanting of these sometimes endangered fruit trees in the vicinity of orchards it may be possible to support large numbers of parasitoids that will suppress pests that threaten crops destined for local consumption or markets (Aluja 1999). In addition to insect control and the conservation of disappearing plants and the flies and other arthropods associated with them, replanted fruit trees can be managed as timber and harvested for a profit. *Tapirira mexicana* Marchand, a tree that supports *A. obliqua* but also large numbers of 4 species of braconid parasitoids, has a wood equal in quality to mahogany (Terrazas & Wendt 1995).

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