Ovipositor Length in a Guild of Parasitoids (Hymenoptera: Braconidae) Attacking *Anastrepha* spp. Fruit Flies (Diptera: Tephritidae) in Southern Mexico

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ABSTRACT In southern Mexico, four native and one introduced species of Opiinae (Braconidae) attack larvae of *Anastrepha* spp. fruit flies. There is a substantial overlap in the hosts of the parasitoids, and every species has been collected from fruit flies attacked by at least one or two other species. The ovipositors of these braconids have a broad interspecific range of lengths, some are less than the length of the abdomen, and others, several times the length of the abdomen. The following three hypotheses are proposed to account for this variety of lengths: (1) Because of differences in the host stage attacked, there are differences in host vulnerability; i.e., mature host larvae feed at greater depths within fruit pulp and can be best reached with a longer ovipositor. There is an implication that competition among the wasp species has selected for foraging on different host stages and that this diversifying selection has resulted in different ovipositor lengths. (2) Although longer ovipositors increase host range and thus have competitive advantages, they may be heavy, awkward, and expensive to move around. If so, species with longer ovipositors might have to invest more in locomotion (reflected in wing size) and less in reproductive capacity (numbers of mature eggs held in the ovarial calyx). Balancing selection would then maintain both short ovipositor-small winged-high fecundity species and long ovipositor-large wing-low fecundity species. (3) Although there are niche overlaps among the species, each has a "core environment" determined by factors such as temperature, humidity, seasonality, and host diversity. Ovipositor lengths have evolved to met the requirements of these specialized environments, and are not due to interspecific competition mediated by ovipositor length; i.e., there has been no diversifying or balancing selection for differences in ovipositor length. Hypothesis number 1 fails because all the species attack similar host stages. Neither was there support for hypothesis number 2. There were no correlations between wing size, or potential fecundity, and ovipositor length. The lack of correlation between species-pairs niche overlaps and differences in species-pairs relative ovipositor length is most consistent with hypothesis number 3. That is, because species with similar ovipositors are neither more or less likely to co-occur in the same samples from various fruits and locations than species with different ovipositor lengths it may be that species interactions are unimportant in the evolution of ovipositor lengths. If so, the lack of a pattern of competition made easily recognizable by differences in ovipositor length could influence biological control tactics. For example, if it is difficult to predict the abilities of newly introduced species to integrate in the existing guild of natural enemies, it may be more prudent over the short term to concentrate on the conservation of the natural enemies already present rather than pursue the "classical" introductions of new species.

KEY WORDS *Diachasmimorpha*, *Doryctobracon*, *Opius*, *Utetes*, biological control, interspecific competition

THE OVIPOSITORS OF parasitic Hymenoptera are tools that reflect the manner by which species reach and pierce the integuments of their hosts (Price 1972, Quicke et al. 1999). Length is one functional feature of ovipositors that exhibits considerable interspecific variation. Those that are carried outside of the abdomen range from small and barely noticeable to prodigious projections, such as those of the Peruvian ichneumonid *Dolichomitus hypermeses* Townes and the Japanese braconid *Euurobracon yokohamae* Dalla Torre, that extend eight to nine times the length of the insects' forewings (van Achterberg 1986).

It might be expected that various parasitoids exploiting the same insect would have ovipositors of similar lengths. However, it is not unusual for species with common hosts to have substantially different ovipositor lengths (e.g., Heatwole and Davis 1965, Price 1972, Brandl and Vidal 1987). This suggests differences in how these parasitoids gain access to and/or handle their common hosts. Knowledge of behavioral and ecological differences inferred from ovipositor lengths can perhaps inform biological control programs, and suggest which candidates for introduction

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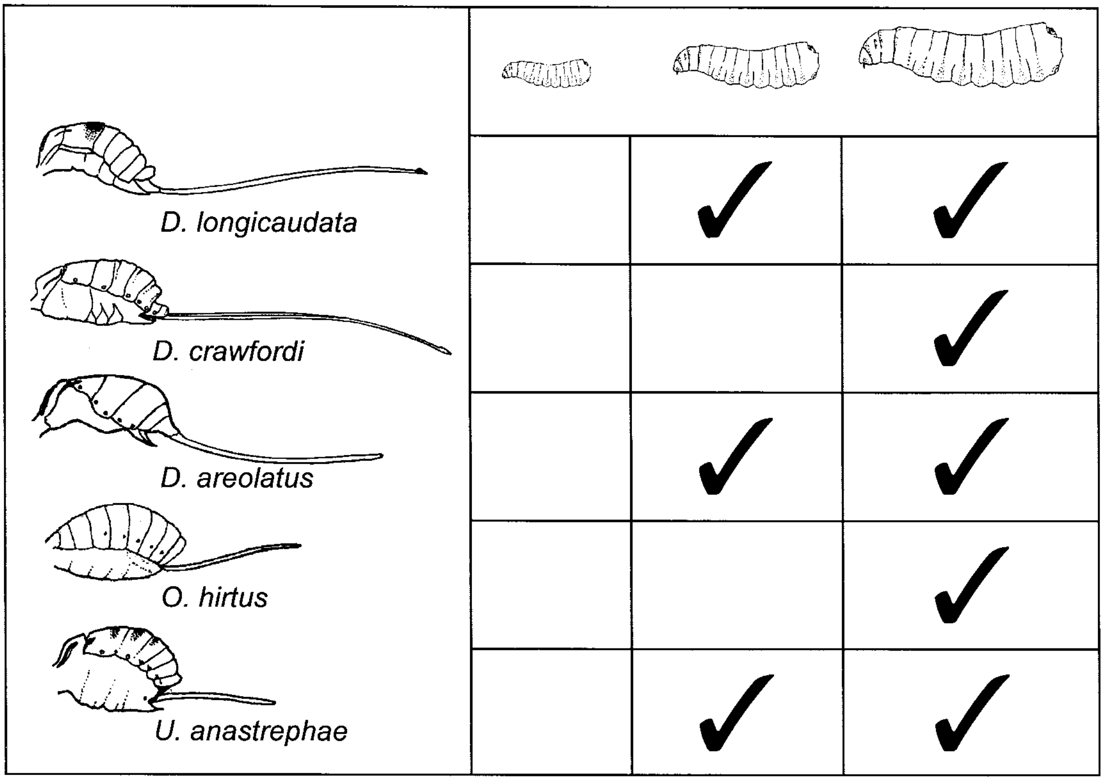

Fig. 1. Female abdomens and ovipositors of the various common species of *Anastrepha*-parasitoids in Veracruz, Mexico. Although not drawn strictly to scale, the different insects are similar in size when they develop in the same species of host. Larval flies represent, in ascending size, the first, second, and third instars of development. A check means that the parasitoid is known to develop successfully after oviposition in that particular instar host (abdomen by K.V.; of larvae adapted from White and Elson-Harris 1992).

might cause the least disruption to an existing suite of natural enemies (Price 1972).

An example of parasitoids with shared hosts, but different ovipositor lengths, occurs in the Mexican state of Veracruz where 10 species of Hymenoptera attack tephritid flies of the genus *Anastrepha* (e.g., Lopez et al.1999). Among these parasitoids is 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 yr ago. All are solitary, endoparasitic koinobionts that oviposit in frugivorous tephritid larvae and complete development within the host puparia.

These species, both native and exotic, are geographically widespread and attack a wide range of fruit flies in a diversity of fruits (table 1 cited in Wharton and Marsh 1978, Lopez 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 (Sivinski et al. 1997, Lopez et al. 1999). For example, *U. anastrephae* and *D. areolatus* are commonly found attacking *Anastrepha obliqua* (Macquart) in the same *Spondius mombin* L. fruits (Sivinski et al. 1997). But while they have many similarities in terms of 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.*

In the following, we describe the ovipositor lengths, wing sizes and shapes, body weights, and numbers of mature eggs in the calyx of the ovaries of the native species within the Veracruz *Anastrepha*-parasitoid guild and of the introduced opiine *D. longicaudata.* We then propose three hypotheses to account for differences in their ovipositor lengths.

Hypothesis Number 1. *Different Parasitoids Species Attack Different Host Instars and These Differ in Accessibility. Species that Specialize in Less Accessible Hosts Require Longer Ovipositors:* Multiple species cannot coexist while simultaneously exploiting an identical resource (Volterra 1926, Gause 1934). Yet it is common, even typical, for insects to be attacked by more than one species of parasitoid (Godfray 1994). These potentially competing species presumably partition the shared resource through specialized foraging that has evolved through diversifying selection. That is, each exploits the host under a different set of circumstances; e.g., different times and places, to avoid competition. In parasitic Hymenoptera, these different tactics may result in differences in the morphological structures used to locate and oviposit into the host in its various states (e.g., Price 1972). Although all the *Anastrepha*-parasitoid species exploit tephritid larvae in fruits, different instar larvae may occur at different depths within fruits (Calkins and Webb 1988). If so, those species that attack shallow-dwelling early-instar larvae may need only a short ovipositor to reach their hosts. This hypothesis is similar to that proposed by Price (1972, 1975) to account for the differences in ovipositor length among the parasitoids of the Swaine jack pine sawfly, *Neodiprion swainei* Middleton. Some species attack pupae buried in leaf litter, 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.

Price (1975) further elaborated on the relationship between accessability and reproductive morphology by arguing 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. Because less accessible hosts are typically more mature, and because inevitable mortality occurs over the developmental period of the host, older, less accessible hosts should be less abundant than younger, more accessible hosts as well. Both of the these 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 length and the numbers of ovarioles per ovary (which reflects the potential for egg production). In terms of Mexican fruit fly parasitoids, if short ovipositor species can regularly attack younger larvae (or a greater range of larval ages) then they are predicted to carry more mature eggs than species with longer ovipositors.

Hypothesis Number 2. *Long Ovipositors are Expensive to Produce and Maintain, and Direct Resources Away from Fecundity and Toward Locomotion. Long and Short Ovipositors May Represent Different Investment Strategies:* The ovipositor may represent a considerable expense, both to construct during ontogeny and to carry and manipulate during adult life. Although species with short ovipositors may not be able to reach certain deep-dwelling hosts, they may be better able to invest their material resources and energies toward foraging for hosts and fecundity (e.g., Masaki 1986). If so, we predict that species with short ovipositors relative to body size attacking the same stage of the host as long ovipositor species will carry more mature eggs. Because the burden of movement with an ovipositor falls only on females, we also argue that females will invest more than males in organs of locomotion, such as wings, and that this sexual dimorphism in investment in wings will be disproportionately great in species with long ovipositors. We follow Price (1972), who noted that the wings of females were largest relative to the male's in species with the most widely dispersed hosts, in the use of wing-sexual dimorphism as a means of estimating female investment in movement. In terms of coexistence among potential competitors, "the costly ovipositor"argument suggests that some species trade access to deep-dwelling hosts for cheap mobility and high fecundity, and that competing long-ovipositor species are able to coexist by having access to deep-dwelling hosts that are unavailable to short-ovipositor species.

Hypothesis Number 3. *Despite Overlap in Host Ranges, Each Species has Specialized Foraging Areas; if the Fruits within These Specialized Areas Differ in Size or Penetrability, Then the Hosts They Contain Differ in Accessibility. This Difference in Host Accessability Leads to Differences in Ovipositor Length:* Rather than a generalization concerning the evolution of ovipositor length across species, the "specialization" hypothesis posits that different ovipositor lengths have evolved in a variety of unrelated situations. Although there is considerable overlap in the distributions and host ranges of the five species, each also has areas of specialization. *Utetes anastrephae* tends to be somewhat more common in the interiors of certain trees than does *D. areolatus* (Sivinski et al. 1997), and is typically found only in tree species with relatively small fruit (Lopez et al. 1999, Sivinski et al. 2000). However, *D. areolatus* has the broadest host range of any of the Mexican species and is often the dominant parasitoid in *Anastrepha* parasitoid guilds throughout tropical America (Lopez et al. 1999 and citations). In Florida, it and *D. longicaudata* have been introduced to suppress populations of the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Baranowski et al. 1993). *Doryctobracon areolatus* has been displaced from the southern portion of Florida by *D. longicaudata,* but maintains itself in the northern portion, apparently because of a greater tolerance for low temperatures and superior foraging ability in environments with low host plant diversity (Eitam 1998). In Mexican surveys, *D. crawfordi* is the native species that most commonly attacks *Anastrepha* infesting exotic, commercial fruits such as oranges (*Citrus sinensis* L.) (Crawford 1927, Lopez et al. 1999). It is also abundant in native yellow chapote (*Sargentia greggii* Coult.) and is found to a lesser extent in *Anastrepha* spp. in guava, *Psidium guajava* L. and *Tapirira mexicana* Marchard (Plummer and McPhail 1941, Lopez et al. 1999). It appears to be limited by severe heat and low humidity, is rarely seen in the field during the dry season, and is relatively abundant at high altitudes (Darby 1933, Darby and Knapp 1934, Sivinski et al. 2000). In the Veracruz survey (Lopez et al. 1999) summarized in Table 1, *Opius hirtus* had the narrowest host range, being recovered only from *Anastrepha alveata* Stone in the native fruit *Ximenia americana* L. In other areas, it is the only common parasitoid of *Anastrepha cordata* Aldrich in *Tabernaemontana alba* Mill, and in still

Table 1. The tephritid-host fruits in Veracruz State, Mexico, on which the various braconid parasitoids forage, and the *Anastrepha* species present in the various host fruits (modified from Lopez et al. 1999)

Parasitoid	Fruit species	*Anastrepha* species attacked
Doryctobracon areolatus (Szepligeti)	*Spondias purpurea* L. *Spondias mombin* L. *Ximenia americana* L. *Tapirira mexicana* Marchard *Psidium sartorianum* (Berg.) *Ndzu.* *Psidium guineense* Sw. *Citrus sinensis* (L.) Osbeck *Myrciaria floribunda* (West) O. Berg *Mangifera indica* L.	*A. alveata* Stone *A. bahiensis* Lima *A. fraterculus* (Wiedemann) *A. ludens* (Loew)
Doryctobracon crawfordi (Viereck)	*Psidium guajava* *Psidium sartorianum.* *Psidium guineense* *Citrus sinensis* *Tapirira mexicana*	*A. ludens* *A. obliqua* (Macquart) *A. striata* Schiner *A. fraterculus*
Opius hirtus (Fisher)	*Ximenia americana*	*A. alveata*
Utetes anastrephae (Viereck)	*Spondias purpurea* *Spondias mombin* *Ximenia americana* *Tapirira mexicana* *Psidium guajava* *Psidium sartorianum* *Psidium guineense*	*A. alveata* *A. fraterculus* *A. obliqua* *A. striata*
Diachasmimorpha longicaudata (Ashmead)	*Syzgium jambos* L. *Spondias mombin* *Tapirira mexicana* *Psidium guajava* *Psidium guineense* *Psidium sartorianum* *Citrus sinensis* *Mangifera indica*	*A. ludens* *A. obliqua* *A. striata* *A. fraterculus*

other locations it has a wide host range and has been reared from the puparia of additional *Anastrepha* spp., the papaya fruit fly, *Toxotrypana curvicauda* Gerstaeker, and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (M.A. and J.S., unpublished data; Wharton 1983).

If there are differences in fruits in the specialized, relatively nonoverlapping, portions of each species' niche then the ovipositor lengths of each may simply reflect the resulting differences in host accessability. These critical differences in fruits might be in terms of size or penetrability. Long ovipositors can buckle when forced into a tough substrate (Quicke et al. 1999) and could be maladaptive even in larger fruits if their rinds are hard. While interspecific competition may have been important in defining the niches of the various species and which fruit are most commonly foraged upon, there would be no subsequent direct divergent or balancing selection for ovipositor length. That is, the ovipositor of a particular species is its present length because of selection in the context of oviposition substrate and not due to interactions with competing *Anastrepha*-parasitoids. For example, *O. hirtus* attacks the monophagous tephritid *Anastrepha cordata* Aldrich as it develops in *Tabernaemontana alba* Mill. (Hernández-Ortiz et al. 1994). It is the only parasitoid to commonly do so, and because 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. This substrate-hypothesis is distinct from hypothesis number 1, which argues that it is the nature of the host and not the nature of the fruit that determines ovipositor length.

Materials and Methods

Source of Insects. Specimens of *D. areolatus, D. crawfordi, O. hirtus*, *D. longicaudata* and *U. anastrephae* used for the measurement of ovipositor length, wing size and shape, and number of mature oocytes, were obtained from colonies maintained at the Instituto de Ecologia over periods of several years on the larvae of *A. ludens*. Because various *Anastrepha* spp. reach different sizes, and host size influences parasitoid size, the standardization of hosts facilitated morphological comparisons of parasitoids. Egg sizes of *D. areolatus*, *D. crawfordi*, and *O. hirtus* were obtained from colony specimens at the Instituto de Ecologia. Egg sizes of *D. longicaudata* were obtained from specimens reared on the larvae of *A. suspensa* in a colony maintained at the Florida Department of Plant Industry (Gainesville, FL) for a period of over 8 yr and from the Instituto de Ecologia colony. Additional *D. areolatus* and all *U. anastrephae* egg measurements were obtained from field-collected specimens that had developed in *A. suspensa* feeding in *Eugenia uniflora* L. (Hendry County, FL, June 1999). The eggs of *D. areolatus* obtained from wild Florida material and from Mexican colony specimens were compared to standardize egg measurements made in the Florida

Table 2. Mean and standard error of ovipositor lengths (number in sample) of the common Opiinae parasitoids of *Anastrepha* spp. fruit flies in southern Mexico, and of other variables that may have co-evolved with ovipositor lengths

	Diachasmimorpha longicaudata	*Doryctobracon areolatus*	*Doryctobracon crawfordi*	*Opius hirtus*	*Utetes anastrephae*
Ovipositor length, mm	5.27	3.77	5.39	2.20	1.57
	0.08	0.04	0.08	0.03	0.04
	(31)	(28)	(13)	(40)	(20)
Body wt, mg	5.19	5.12	5.25	5.47	2.86
	0.21	0.27	0.30	0.21	0.15
	(33)	(26)	(13)	(40)	(20)
Female wing loading	0.36	0.32	0.26	0.28	0.26
	0.008	0.01	0.01	0.01	0.02
	(33)	(26)	(12)	(40)	(20)
Female wing area (mm^2)	7.38	7.83	10.0	9.54	5.62
	0.16	0.16	0.17	0.18	0.12
	(33)	(28)	(13)	(40)	(20)
Male wing area, mm^2	5.87	7.12	8.17	7.91	5.01
	0.11	0.14	0.18	0.19	0.11
	(27)	(30)	(33)	(20)	(20)
Mature eggs/ovary	39.7	23.5	14.5	14.2	5.91
	2.09	1.15	1.23	0.66	0.16
	(11)	(10)	(11)	(11)	(11)
Egg length, mm	0.64	1.13	1.26	0.74	0.45
	0.008	0.01	0.02	0.02	0.007
	(35)	(40)	(67)	(88)	(28)
Egg width, mm	0.08	0.10	0.13	0.14	0.15
	0.002	0.003	0.004	0.003	0.002
	(35)	(40)	(67)	(88)	(28)
Egg volume, mm^3	0.005	0.009	0.02	0.01	0.007
	.0002	0.0005	0.001	0.0007	0.0003
	(35)	(40)	(67)	(88)	(28)

All specimens developed in *A. ludens.*

and Mexico laboratories (see next section "*Measurement of Eggs and Ovaries*"). All female specimens were between 5 and 10 d of age and had been maintained in the presence of males.

Measurement of Eggs and Ovaries. All of the species had similar ovary morphology, with two ovarioles per ovary. All were apparently synovigenic, with maturing oocytes present along the lengths of the ovarioles. The numbers of mature oocytes stored in the ovarian calyx were counted in dissected specimens under a binocular microscope. Egg length and greatest diameter were measured by first projecting an image of a dissected egg via a projection microscope, tracing the outline on paper, scanning the image into a computer, and then using Sigma Scan software to make both the measurements and compare them to a standard line of known length. We are aware that a number of circumstances might result in the increased production, expenditure, or absorption of eggs (e.g., Charnov and Stephens 1988). Thus, the numbers of eggs cached by any particular female parasitoid might vary over time, and this complicates determining the number of mature eggs "representative" of a species. However, in defense of our methods, egg numbers within species were relatively constant (see Results). All the species were reared and held under similar colony conditions, and we assume that these conditions had similar effects on the propensities of females to produce and cache eggs.

Measurement of Wings. As in the above, images of dissected wings were projected onto paper and measured with a computer. Forewing length was defined as the distance from the wing tip to the junction of the cubital and media veins, area was the region apical to the junction of the basal and medius veins, and width was the longest line perpendicular to the long axis of the wing. Hindwing length was defined as the distance from the wing tip to the junction of the medielle and nervellus veins, area was the region apical to the junction of the mediella and nervellus veins, and width was the longest line perpendicular to the long axis of the wing. Wingloading, the wet weight of the insect divided by total fore and hind wing areas (mg/mm^2), is a simple ratio of the flight surface available to propel a unit of body mass (e.g., Wickman 1992). As noted earlier, sexual dimorphism in wing area was used to estimate sexual differences in locomotory requirements (see Introduction). This would be complicated if the wings of one sex were adapted for some function other than flight. In *D. longicaudata* males beat their wings rapidly during courtship, producing a sound ("song") and perhaps fanning pheromones toward the female (Sivinski and Webb 1989). It is not known if male wings are modified to sing or disperse pheromones in this species, and the sexual behaviors of the other species are undescribed. Because of the potential for misinterpretation, two measurements of female investment in wings, sexual dimorphism in area and wing loading, were used in tests of hypothesis number 2. Female wing loading would not be influenced by signaling elaborations of male wings.

Measurement of Ovipositors. Ovipositor sheaths from the tip to the point of origin on the venter of the abdomen were projected onto paper, measured by computer, and compared with a line of known length. Ovipositor sheaths are slightly shorter than the ovipositors themselves, which arise more anteriorly on the abdomen, but are easier to measure. In measuring the sheath rather than the ovipositor we have traded precision for a relatively small underestimation of length.

Measurement of Body Weights. Wingless specimens preserved in 70% ethanol were placed on filter paper for 1 min to remove excess fluid, and then weighed to the nearest 0.1 mg on an electronic balance.

Statistical Analysis. All statistical tests were preformed with SAS computer programs (SAS Institute 1989). Relationships between two morphological or ecological variables were examined by correlation (PROC CORR) and those involving three variables by multiple regression (PROC GLM; type III sum of squares).

The methods of Southwood (1987) were employed to address species packing, i.e., the extent to which particular pairs of species were found together or apart. Data were obtained from a previously published survey of the parasitoid fauna in 26 species of fruit as they occur at various altitudes and at different times of the year in the state of Veracruz, Mexico (Sivinski et al. 2000). Only fruit samples that contained at least one species of braconid parasitoid were considered ($n = 207$). First, a 2×2 contingency χ^2 test was performed comparing the numbers of samples in which species A and B occurred separately, together, or not at all. If the test was significant, it was further determined if the species exhibited a "repulsion" (contingency table cells $bc > ad$) or an "affinity" ($ad > bc$).

The resulting χ^2 values were then used to calculate "coefficients of mean square contingency" [$Cab = /(\chi^2/\chi^2 + \mathrm{n})$]. These values have the same range as a correlation coefficient and allow the comparison of various species-pairs. The sign of the coefficient (+ [affinity] or − [repulsion]) was based on the ratio of *ad: bc* in the contingency table. To discover if relative ovipositor length was related to the degree species-pairs bore an "affinity" or exhibited a "repulsion" for one another, the *Cab* values for the various species-pairs were correlated to length of the ovipositor of the shorter species relative to that of the longer species (mean shorter/mean longer). *Opius hirtus* was not considered in these calculations, because empty cells within the contingency tables precluded χ^2 testing.

Results

Hypothesis Number 1. *Different Parasitoid Species Attack Different Host Instars and These Differ in Accessibility.* All of the braconid species under consideration have been colonized at the Instituto de Ecologia and all develop in second and third instar larvae capable of feeding deeply inside of infested fruits [Fig. 1; additional information on the host instars attacked is available for *D. areolatus* (Eitam 1998), *U. anastrephae* (Matrangolo et al. 1998), and *D. longicaudata* (Lawrence et al. 1976)].

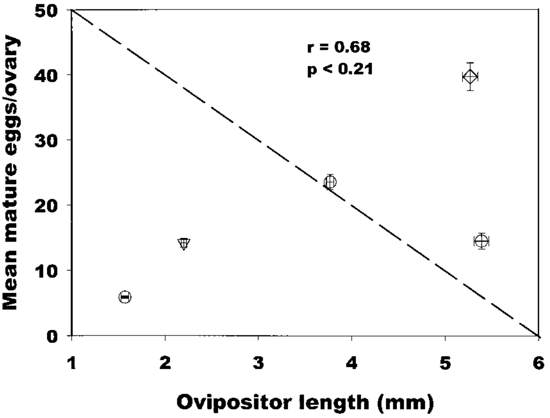

Fig. 2. Relationship between mean ovipositor length and the mean numbers of mature eggs held in the ovarial calyxes (bars represent standard errors). Diamond symbol represents the exotic species *Diachasmimorpha longicaudata,* and the triangle symbol, the relatively specialized native species *Opius hirtus.* Dashed line represents the predicted relationship of the two variables based on the correlations described by Price (1972); i.e., that species with longer ovipositors typically attack less accessible hosts, and so have fewer oviposition opportunities and carry fewer eggs.

In addition to evidence from laboratory rearing procedures, the morphologies of the internal female reproductive tracts are inconsistent with the hypothesis that short-ovipositor species are adapted to exploit easily accessible hosts. Price's hypothesis that species with longer ovipositors attack less accessible hosts and so should carry fewer mature eggs was not supported in the braconids under consideration. While all species have two ovarioles per ovary, the numbers of mature eggs cached in the calyx of the ovary was relatively constant among individuals within species and bore no correlation to ovipositor length (Fig. 2).

Not only is there no correlation between fecundity and ovipositor length, there is a suggestion that species with longer ovipositors have greater oviposition opportunities. An extensive, multiyear survey of fruit fly parasitism in a wide range of Mexican-native and introduced fruits recovered all five of the braconids under consideration (Lopez et al. 1999). Using this data, we found a significant positive relationship between mean size (weight) of the fruits in a particular sample and the mean ovipositor lengths of the parasitoids that developed in the tephritid larvae from the sample (Fig. 3; ovipositor lengths determined in the current study).

Hypothesis Number 2. *Long Ovipositors are Expensive to Produce and Maintain, and Direct Resources Away from Fecundity and Toward Locomotion.* This hypothesis predicts that females with longer ovipositors require larger wings to forage in a manner comparable to a short-ovipositor species, and that this might be reflected in a greater sexual dimorphism in total wing area. Because of the purported greater in-

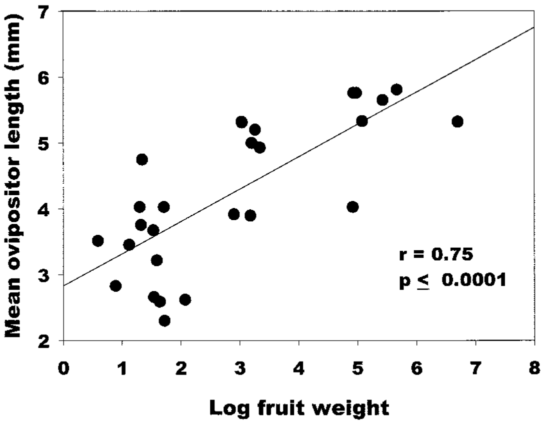

Fig. 3. Relationship between the log mean weight of fruits of various species and from various locations in southern Mexico and the mean lengths of the ovipositors of the parasitoids recovered from the samples (fruit and parasitoid species composition data from Lopez et al. 1999; mean ovipositor data from the current study).

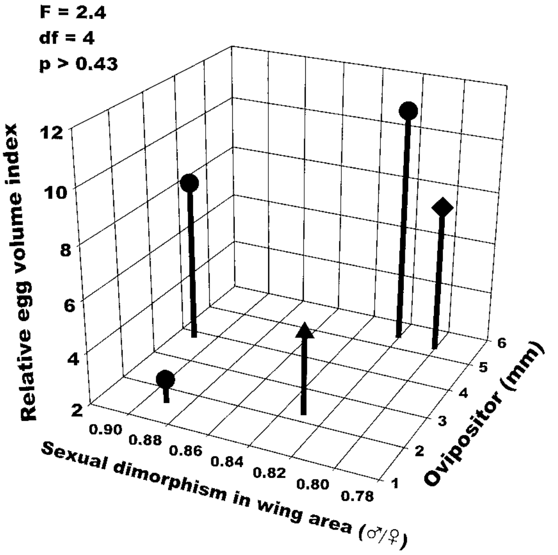

Fig. 4. Relationship between mean ovipositor length, the sexual dimorphism in forewing area, and the relative egg volume index (the estimated volume of mature eggs held in the ovarial calyxes/mean adult female body weight * 100). Diamond symbol represents the exotic species *Diachasmimorpha longicaudata,* and the triangular symbol, the relatively specialized native species *Opius hirtus.* The hypothesis that ovipositor maintenance would direct resources away from egg production and toward greater investment in female wings predicts a regression line that arises at the near-upper left of the field and declines toward a point in the far-lower right.

vestment in locomotion there would be less resources to invest in gametes (egg number * egg volume). Unfortunately, this long ovipositor-small egg number hypothesis makes some similar predictions to hypothesis number 1 in the sense that both argue that species with relatively long ovipositors would be expected to carry relatively few mature eggs. That is in terms of hypothesis number 1, if deep-dwelling, mature larvae are more difficult to reach, then host-handling time would increase and the number of eggs required per unit time might decrease. Thus, hypothesis number 2 should be examined in light of the failure of hypothesis number 1 described above (i.e., that there is no correlation between ovipositor length and the developmental stage of the host attacked).

In terms of a multivarient regression, hypothesis number 2 predicts that as ovipositor length increases there should be a concurrent decline in male wing area relative to female wing area and a decrease in total gamete volume. This was not so for wing sexual dimorphism (Fig. 4; with sexual dimorphism in wing loading substituted for sexual dimorphism in wing area, $F = 11.8, P > 0.21$), and for total gamete volume, the opposite was significantly the case (Fig. 5).

Hypothesis Number 3. *Despite Overlaps in Host Range, Each Species Has Specialized Foraging Areas; If the Fruits in These Areas Differ in Size or Penetrability, Then the Hosts They Contain Differ in Accessibility.* In most cases, pairs of parasitoid species obtained from samples of various fruit species and from different times of the year and altitudes exhibited "repulsion," i.e., they were significantly more likely to occur apart than would be expected by chance. This suggests that the species typically occupy niches that are substantially different from one another in terms of fruit-host and fly-host, and/or altitude and season. Exceptions are the propensity of *U. anastrephae* and *D. areolatus* to co-occur, and the lack of any significant relationship between *U. anastrephae* and the exotic *D. longicaudata.*

Is the degree to which pairs of species are found together influenced by their relative ovipositor lengths? The lack of a correlation between the degree of overlap among the species pairs and their relative ovipositor lengths fails to support the hypothesis that niche separation is due to a history of selection for different ovipositor lengths (Fig. 6). That is, if disruptive selection for ovipositor length had resulted in niche divergence there should be a positive relationship between the degree of difference in the relative ovipositor lengths of any two species and the degree of overlap in their association. Thus, species with the most dissimilar ovipositors would be the most likely to co-occur within a particular sample. This is not the case, either when all species are considered together or when the exotic *D. longicaudata* is excluded.

In addition to the lack of a positive correlation, the absence as well of a negative correlation suggests that ovipositor length is not an important determinant of niche boundaries; i.e., species with similar ovipositors lengths do not more commonly co-occur than those with dissimilar lengths. This general absence of relationship between differences in ovipositors and species co-occurrence is consistent with the hypothesis that ovipositor length has neither evolved in the context of interspecific competition nor has it been an

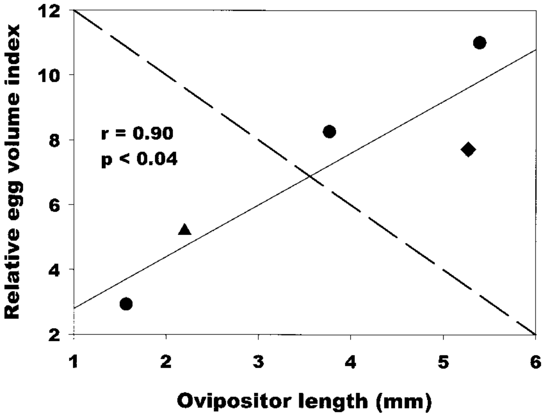

Fig. 5. Relationship between an egg volume index (the mean estimated volume of mature eggs held in the ovarial calyxes/mean adult female body weight * 100) and ovipositor length. Diamond symbol represents the exotic species *Diachasmimorpha longicaudata*, and the triangle symbol, the relatively specialized native species *Opius hirtus*. The egg volume index, unlike egg number considered in Fig. 2 is an estimate of available resources directed toward eggs; i.e., egg number is insufficient for this purpose because eggs vary in size among the species (see Table 2). Dashed line represents the prediction of the hypothesis that the maintenance and movement of longer ovipositors would direct resources away from fecundity and toward locomotion.

important preadaptation that influenced the evolution of the niche boundaries.

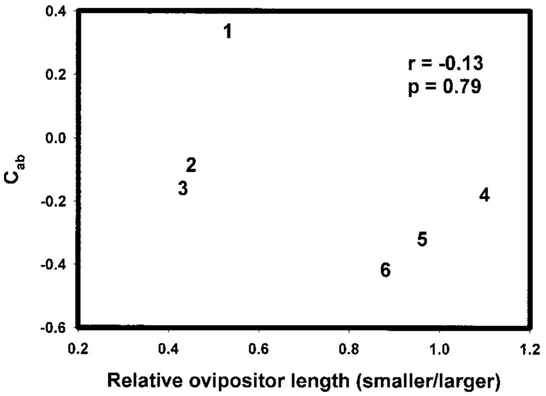

Fig. 6. Relationship between the *coefficient of mean square contingency* (=Cab; a measurement of the likelihood two species are likely to be found together in a sample), and relative ovipositor length (smaller species of a pair/larger species of a pair). Species with similar ovipositor lengths are neither more or less likely to co-occur than species with dissimilar ovipositor lengths. Numbers refer to particular pairs of parasitoids: 1 = *D. areolatus* and *U. anastrephae;* 2 = *D. longicaudata* and *U. anastrephae;* 3 = *D. crawfordi* and *U. anastrephae;* 4 = *D. longicaudata* and *D. crawfordi;* 5 = *D. longicaudata* and *D. areolatus;* 6 = *D. areolatus* and *D. crawfordi.*

Discussion

The four native and one exotic braconid species attacking *Anastrepha* spp. in Veracruz State have a considerable potential for overlap in host ranges; i.e., each species is capable of locating and developing in hosts that harbor at least one, and sometimes as many as three, of the other parasitoid species. Yet despite their many similarities, their ovipositors differ substantially in length. Such differences among potentially competing parasitoids attacking other host insects are typically due to the various species exploiting distinct host ages which differ in accessability (e.g., Brandl and Vidal 1987, Price 1975, Heatwole and Davis 1965). This does not seem to be the case among species of the *Anastrepha*-parasitoid guild. All attack and are capable of development in relatively mature host-larvae capable of dwelling deep in fruit pulp. Short-ovipositor species are rarely found in larger fruits, presumably because they have difficulty reaching hosts, and this limitation on their foraging raises the question of how they persist, and even flourish, if they are in competition with long-ovipositor species.

An alternative hypothesis, that long ovipositors are expensive to produce and maintain, and that they, and the wings required to carry them, absorb resources that could be used to produce more and/or larger eggs, was not supported. There was no evidence that short ovipositor-small winged-high fecundity parasitoids coexist with long ovipositor-large winged-low fecundity parasitoids through balancing selection.

The hypothesis most consistent with our findings is that ovipositors have evolved to meet special, presently unspecified, needs within niches that originally diverged on the basis of phenomena unrelated to host accessability, perhaps factors such as temperature, humidity and/or host-fruit abundance and diversity. That is, ovipositor lengths may not have evolved through divergent or balancing selection due to interspecific competition, nor were ovipositor lengths apparently important preadaptations in the evolution of the niche. They have simply evolved to meet the peculiar, noncompetitive conditions in which particular species found themselves. If so, the competition the various species face in regions of niche overlap is insufficient to significantly affect lengths that are adaptive in regions of nonoverlap. For example, the very short ovipositor of *U. anastrephae* appears to limit the variety of host-infested fruits it can forage upon; i.e., it is limited to attacking larvae in small fruits. However, we would suggest that competition with species with longer ovipositors is relatively unimportant compared with some unknown advantages this particular form of ovipositor has in the core of its species' niche. Thus, it remains a common and widespread species despite the apparent drawback of a reduced host-range.

If ovipositors in the Mexican *Anastrepha*-parasitoid have evolved due to "special-needs" selection pressures in isolation from other species, this knowledge could influence the strategy of fruit fly biological control in southern Mexico and elsewhere in Latin America. For one thing, it might make the introduction of new species, compatible with the existing guild, less predictable. For example, Price (1972) suggests that the species most likely to integrate successfully into a guild of parasitoids attacking the Jack Swain jack pine sawfly would be those whose ovipositor fit within relatively large gaps in the preexisting range of ovipositor lengths. This assumes that ovipositor length influences competition, and if this were not the case, as may be true in the Mexican Opiinae, then ovipositor length would not be a good predictor of competition or coexistence.

The different outcomes of interactions between *D. longicaudata* and *D. areolatus* in the USA and Mexico may be an example of the unpredictable effects of mixing species with poorly understood specializations. *Diachasmimorpha longicaudata* appears to have had a major impact on the distribution of *D. areolatus* in Florida (Eitam 1998); as noted earlier, *D. areolatus* has been replaced in the southern portion of its potential range by *D. longicaudata.* Florida is a region where both species were recently introduced, and where neither would be expected to be uniquely well adapted to particular niches through lengthy selection. In Mexico, where *D. areolatus* has had the opportunity to evolve in concert with native fruits and host-flies, it and *D. longicaudata* are broadly sympatric (e.g., Lopez et al. 1999, Sivinski et al. 2000). That is, *D. areolatus* may be sheltered from competition from *D. longicaudata* because it is well adapted to a special set of local conditions.

Phylogenetic constraints are a fourth and previously unaddressed influence on ovipositor lengths in the *Anastrepha*-parasitoid guild. Constraint hypotheses posit that ovipositor lengths have not been sensitive to recent selection pressures, perhaps because co-adapted gene complexes do not allow direct exposure of length to selection or because there is no genetic variation within a lineage on which selection for length can act. For example, there are no species of *Doryctobracon* with short, *Utetes*-like ovipositors, and it is possible that the genetic structure of the clade does not allow the evolution of such a species. If there were some other overriding *Doryctobracon*-quality that favors members of the genus in the Veracruz environment, then long-ovipositor species will occur whether long ovipositors are optimal or not. In its strongest form, this argument suggests that ovipositor length is not an important constraint on foraging and that it is other, undefined, traits that determine the distributions and host ranges of the various species. However, we would argue that the strong correlation between ovipositor length and the size of host-fruits in which larvae are attacked implies that ovipositor length is an important limitation on foraging.

Lack of easily discernable ecological and morphological patterns in the organization of the *Anastrepha*-parasitoid guild suggests a cautious approach to biological control. In our opinion, unexplained complexity in distributions and oviposition tactics may make parasitoid conservation an attractive alternative to the immediate and indiscriminate introduction of new parasitoids. Conservation of *Anastrepha*-parasitoids may be particularly fruitful due to numerous, generally monophagous, nonpest *Anastrepha* that develop in native fruits and share natural enemies with pest species (M.A. and J.S., unpublished data). The replanting of disappearing native fruits in the vicinities of orchards may increase the numbers of parasitoids, prevent the accelerating decline of a portion of the local insect fauna, and eventually supply farmers with a renewable source of valuable timber. Seedlings of native fruits are presently being supplied to farmers in parts of Veracruz in an attempt to test the efficacy of this control strategy.

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