

Fruit Flies of the Genus *Anastrepha* (Diptera: Tephritidae) and Associated Native Parasitoids (Hymenoptera) in the Tropical Rainforest Biosphere Reserve of Montes Azules, Chiapas, Mexico

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ABSTRACT We report the results of a 2-yr survey that determined some of the host plant and parasitoid associations of *Anastrepha* fruit flies (Diptera: Tephritidae) in the “Montes Azules” tropical rainforest biosphere reserve (State of Chiapas, Mexico). We collected a total of 57.38 kg of fruit representing 47 native species from 23 plant families. Of these, 13 plant species from eight plant families were found to be native hosts of 9 species of *Anastrepha*. The following *Anastrepha* host associations were observed: *Bellucia pentamera* Naudin (Melastomataceae) with *A. coronilli* Carrejo y González; *Malmea gaumeri* (Greenm.) Lundell (Annonaceae) with *A. bahiensis* Lima; *Tabernamontana alba* Mill. (Apocynaceae) with *A. cordata* Aldrich; *Quararibea yunckeri* Standl. (Bombacaceae) with *A. crebra* Stone; *Ampelocera hottlei* (Standl.) Standl. (Ulmaceae) with *A. obliqua* (Macquart) and *A. fraterculus* (Wiedemann); *Zuelania guidonia* Britton and Millsp. and *Casearia tremula* (Griseb.) Griseb. ex C. Wright (Flacourtiaceae) with *A. zuelaniae* Stone; *Psidium sartorianum* (O. Berg.) Nied (Myrtaceae) with *A. fraterculus*; *Psidium guajava* L. and *P. sartorianum* (Myrtaceae) with *A. striata* Schiner; and *Manilkara zapota* (L.) Van Royen, *Pouteria* sp., *Bumelia sebolana* Lundell, and *Calocarpum mammosum* (L.) Pierre (Sapotaceae) with *A. serpentina* (Wiedemann). The following are new host plant records: *Malmea gaumeri* for *A. bahiensis*; *Quararibea yunckeri* for *A. crebra*; *Ampelocera hottlei* for *A. fraterculus* and *A. obliqua*; *Bumelia sebolana* for *A. serpentina*; and *Casearia tremula* for *A. zuelaniae*. *A. coronilli* is reported for the first time in Mexico. Infestation levels were variable and ranged between 0 and 1.63 larvae/g of fruit depending on host species. Larvae of eight species of *Anastrepha* on nine plant species from six plant families were found to be parasitized by *Doryctobracon areolatus* Szeplogi, *D. crawfordi* Viereck, *D. zeteki* Musebeck (new report for Mexico and northernmost record for the species), *Opius hirtus* Fisher, *Utetes anastrephae* Viereck (all Hymenoptera: Braconidae), and *Aganaspis pelleranoi* Brethes (Hymenoptera: Figitidae). Percent parasitism ranged from 0 to 76.5%. We discuss our findings in light of their practical (e.g., biological control) and theoretical (e.g., species radiation) implications and highlight the importance of these types of studies given the rampant deforestation of tropical forests in Latin America and the risk of extinction of rare fruit fly species that could shed light on the evolution of host plant and parasitoid associations within the genus *Anastrepha*.

KEY WORDS Tephritidae, *Anastrepha*, host–plant relationships, parasitoids, conservation

RAPID DEFORESTATION OF THE tropics may be causing the extirpation, perhaps even the extinction, of many fruit fly species (Diptera: Tephritidae) (Aluja 1999) and

also threatens the associated native parasitoid species (Hymenoptera). This is important because much of the information required to gain a more thorough understanding of fruit fly biology, ecology, and evolution is to be found in areas with unperturbed native vegetation. Therefore, one is confronted with the serious challenge of finding the few remaining pristine areas in which to study topics such as ancestral fruit fly host–plant and parasitoid associations, patterns of resource use, factors that regulate populations and niche partitioning, and adult behavior.

The types of information that can be gathered through surveys in areas with unperturbed native veg-

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etation and the potential uses to which it may be put can be illustrated by the work of Hernández-Ortíz and collaborators (Hernández-Ortíz and Pérez-Alonso 1993, Hernández-Ortíz et al. 1994). Their collections in a protected tropical evergreen rainforest (Estación de Biología Tropical "Los Tuxtlas," Veracruz, Mexico) discovered rare hymenopterous parasitoids such as *Microcrasis* sp., *Nealiolus* sp. (both Braconidae) and *Lopheucoila* sp. (Cynipidae), associated with various *Anastrepha* species. They also determined new fruit fly-parasitoid associations (e.g., *Anastrepha cordata* Aldrich-*Opius hirtus* Fischer) and fruit fly-host plant associations (e.g., *A. bahiensis* Lima-*Pseudolmedia oxyphyllaria* J.D. Smith [Moraceae]). Similarly, López et al. (1999) and Aluja et al. (2000a), collecting in isolated patches of tropical deciduous and sub-deciduous forests, discovered new fly host-plant and parasitoid associations such as those between *A. alveata* Stone, *Ximenia americana* L. (Olacaceae), and *Doryctobracon areolatus* Szépligeti (Braconidae); between *A. spatulata* Stone, *Schoepfia schreberi* J.F. Gmel. (Olacaceae), and *D. areolatus* and *D. toxotrypanae* Muesebeck (Braconidae); and between *A. ludens* (Loew) and *A. striata* Schiner and the pupal parasitoid *Coptera haywardi* Ogloblin (Diapriidae). These findings can aid the "biorational" control of pestiferous fruit fly species by improving the conservation of biological control agents (Aluja 1999, Sivinski et al. 2000). They also provide the samples needed for comparative studies aimed at understanding the evolution of *Anastrepha* behavior (Aluja and Norrbom 1999). For example, thanks to the efforts of Hernández-Ortíz and collaborators (Hernández-Ortíz and Pérez-Alonso 1993, Hernández-Ortíz et al. 1994), the habits of primitive *Anastrepha* species such as *A. cordata* were discovered, and this has allowed hypotheses about the evolution of oviposition behavior of flies in the genus *Anastrepha* (Aluja et al. 1999, Díaz-Fleischer et al. 1999).

Most published information on *Anastrepha* host-plant relationships and parasitoid associations has been recently summarized by Ovruski et al. (2000), Aluja et al. (2000b), Zucchi (2000), Uramoto et al. (2001), and Norrbom (2002, 2003). Several patterns arise from these reviews. Most species of *Anastrepha*, particularly those of no economic importance and even a few that are (i.e., *A. grandis* Macquart and *A. striata*), are either monophagous or stenophagous and have long adult lifespans (Aluja et al. 1999). The five most economically important *Anastrepha* species [*A. fraterculus* (Wiedemann), *A. ludens*, *A. obliqua* (Macquart), *A. serpentina* (Wiedemann), and *A. suspensa* (Loew)] are polyphagous, but at the local level, they behave more like stenophagous or oligophagous species. Host expansion to cultivated plants is a rare phenomenon, considering that there are >200 described and many undescribed *Anastrepha* species (Norrbom et al. 1999b, Norrbom 2002) and only 25 now infest plant species not originally from their native ranges (often commercially grown). The host plants are still unknown for many *Anastrepha* species (some hosts have been reported for 90 of the 204

[44%] described species, but even those species may have additional wild hosts). There is mounting evidence that one reason the host plants for many species are still undiscovered is that most efforts have been directed at surveys of commercial plants or those with similar types of fruit with the expectation of finding larvae in the ripening pulp of fruit. Too little attention has been paid to wild native plants, especially those with small fruits, and to examining immature fruits, seeds, and other plant parts (Aluja 1999). Recent surveys carried out in Mexico and Brazil have shown that there is a large suite of native hymenopterous parasitoids whose potential as biological control agents has been inadequately assessed because of overemphasis on exotic parasitoids (Ovruski et al. 2000). In the case of *Anastrepha*, 43 native parasitoid species have been identified, 58.1% of which belong to the family Braconidae, and 18.6, 11.6, 6.9, and 2.3% to the families Figitidae, Diapriidae, Pteromalidae, and Eulophidae, respectively (Ovruski et al. 2000). By far, the most widespread (and perhaps abundant) native parasitoids of *Anastrepha*, based on existing reports, are the braconids *D. areolatus*, *D. crawfordi* Viereck, and *Utetes anastrephae* Viereck, and the eucoiline figitid *Aganaspis pelleranoi* Brethes. These range from either southern Florida or equivalent latitudes in northern Mexico through northern Argentina (Ovruski et al. 2000). Finally, many wild plants serve as parasitoid reservoirs and should therefore be protected or cultivated (Aluja 1999).

In an effort to further contribute to our scant knowledge of *Anastrepha* diversity and host-plant and parasitoid associations in unperturbed habitats, we report findings of a 2-yr fruit collection carried out in the "Montes Azules" biosphere reserve (State of Chiapas, Mexico). Montes Azules is a 331,220 ha protected area within the Lacandon jungle (selva Lacandona) bordering Guatemala and a Mesoamerican biodiversity "hotspot" (Myers et al. 2000). This tropical rain forest holds 15% of Mexico's plant species, 50% of Mexico's 800 butterfly species, and the greatest diversity of bats in the country (Arriaga et al. 2000).

Materials and Methods

Study Area. We worked in the "Estación Chajul," located in Chajul, Chiapas (SE Mexico) and in several sampling points along the Lacantún river. Chajul is located between 16–17° N, between 90°30'–91°31' W (Fig. 1), and at an elevation of 140 m. Climate is defined mostly as warm humid (Am) with a mean annual temperature of 22°C and 1,500–3,000 mm rainfall, falling mostly between May and October (García-Gil and Hupb 1992).

Fruit Collection and Processing Procedures. Ripe, and on occasion, unripe fruit found on paths within and around the "Estación Chajul" were collected from branches and on the ground under the canopy of trees. The "Los Sótanos" ruins and "El Chaquistero," two other areas along the Lacantún River, were also sampled. These areas were accessed by boat from the "Estación Chajul" (≈45- and 90-min travel time to



Fig. 1. Map showing the location of Chajul and Montes Azules within the State of Chiapas, Mexico.

each disembarking site, respectively). Fruit was collected for ≈ 90 min while walking along a trail leading into the jungle from the point of disembarkation. Fruit collection comprised four sampling periods from late May to late August in 1999 and four sampling periods from early June to early December in 2000. Samples were taken to a temporary laboratory in the Estación Chajul. Samples were weighed and placed in plastic trays over plastic washbowls containing moist vermiculite as a pupation medium (for a detailed description of methods, see Aluja et al. 2000b). Particularly valuable samples were transported to a laboratory in Xalapa, Veracruz, Mexico, and treated as described above (in such cases, a subsample was taken to weigh individual fruit). Vermiculite was regularly inspected, and pupae were placed in 500-ml labeled plastic cups covered with a fine mesh. Pupae were held at $26 \pm 2^\circ\text{C}$ and 60–70% RH until adult fly emergence.

Processing of Data. Fruit infestation levels were calculated by dividing the total number of pupae obtained from a fruit sample by the sample's weight in grams. Percent parasitism was obtained by dividing the total number of adult parasitoids emerging from these pupae by the total number of pupae obtained from a fruit sample and multiplying by 100. Given that there were instances of parasitism by multiple parasitoid species in one fruit sample (but not in individual larvae [pupae]), we note that the percent parasitism value obtained this way is not species-specific, but an overall rate of parasitism. New host plant and distribution records for *Anastrepha* spp. and fruit fly parasitoids were established by consulting the host plant database for *Anastrepha* (Norrbon 2003) and *Toxotrypana* (Ovruski et al. 2000).

Insect and Plant Identification. Adult flies were identified by A.L.N., and voucher specimens were placed in the insect collection of the National Museum of Natural History, Smithsonian Institution, Washing-

ton, DC (USNM), and the Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico. Adult parasitoids were identified by R.A.W., and voucher specimens were placed in the insect collection of Texas A & M University (TAMU) in College Station, TX. Plants were dried and pressed at the Estación Chajul, Chiapas. Voucher specimens of plants not already represented in the permanent collection were kept in the IXAL herbarium. All plant names were verified using the U.S. Department of Agriculture GRIN online database (U.S. Department of Agriculture 2000).

Results

A total of 57.38 kg of fruit representing 47 species from 23 plant families was processed during this study (Table 1). Of these, 13 plant species from eight plant families were found to be natural hosts of nine *Anastrepha* species (Table 2). Larvae of eight species of *Anastrepha* on nine plant species from seven plant families were found to be parasitized by six species of hymenopterous parasitoids (Table 2). Fruit weight ranged between 3.4 g for the smallest fruits (e.g., *Brosimum alicastrum* Sw.) to 380 g for the largest fruits (e.g., *Pouteria* sp.; Table 3). Information on the fruiting phenology of those tree species bearing fruit found infested by *Anastrepha* spp. is provided in Table 4.

Only *A. obliqua* and *A. fraterculus* infested fruit from plants belonging to more than one plant family (Table 2). *A. serpentina* was found in four species of Sapotaceae, *A. striata* in two species of Myrtaceae, and *A. zuelaniae* Stone in two species of Flacourtiaceae. *A. bahiensis* Lima, *A. coronilli* Carrejo y González, *A. cordata*, and *A. crebra* Stone were all found infesting a single plant species.

Only *Psidium sartorianum* (O. Berg.) Nied. and *Ampelocera hottlei* (Standl.) Standl. hosted more than one species of *Anastrepha*: *A. striata* and *A. fraterculus* on *P. sartorianum* and *A. fraterculus* and *A. obliqua* on *A. hottlei* (Table 2). By contrast, up to four species of parasitoids were found infesting *Anastrepha* larvae stemming from the same fruit sample, and only in three cases was a single species of parasitoid associated with the *Anastrepha* larvae from fruit of a particular plant (Table 2).

Infestation levels by fruit flies were variable and ranged from 0 to 1.63 pupae/g of sampled fruit (Table 3). Percent parasitism was also variable and ranged from 0 to 76.5% (Table 3).

Discussion

Anastrepha fraterculus and *A. obliqua* were found to infest *Ampelocera hottlei* (Ulmaceae) for the first time. Fruit within the Ulmaceae are infested by flies in the genus *Rhagoletotrypeta* (Trypetinae: Trypetini) (Smith and Bush 1999) but had never been reported as hosts of flies in the genus *Anastrepha*. This finding is consistent with the polyphagous nature of both *A. obliqua* and *A. fraterculus*. *A. bahiensis* (polyphagous) and *A. zuelaniae* (restricted to feeding on plants in the family Flacourtiaceae) were found infesting

Table 1. Plant family, species, and sample weight obtained during four yearly fruit collecting periods in the tropical rainforest biosphere reserve of Montes Azules, Chiapas, Mexico, in 1999 and 2000

| Plant family | Plant species | Sample weight (kg) | Sampling periods |
|------------------|--|--------------------|---|
| Annonaceae | <i>Cymbopetalum mayanum</i> Lundell | 0.110 | 26/05–06/06/1999 |
| | <i>Malmea gaumeri</i> (Greenm.) Lundell | 1.250 | 16–26/08/1999 |
| Apocynaceae | <i>Taberna</i> sp. | 0.210 | 26/05–06/06/1999 |
| | <i>Tabernamontana alba</i> Mill. | 0.200 | 16–26/08/1999 |
| Arecaceae | <i>Bactris balanoidea</i> (Oerst.) H. Wendl. | 0.060 | 26/05–06/06/1999 |
| | <i>Desmoncus ferox</i> Bartlett | 0.080 | 01–16/07/1999 |
| Bombacaceae | <i>Quararibea yunckeri</i> Standl. | 0.160 | 22/07–02/08/1999 |
| Caricaceae | <i>Carica cauliflora</i> Jacq. | 4.003 | 26/05–06/06/1999 |
| Chrysobalanaceae | <i>Licania platypus</i> (Hemsl.) Fritsch | 1.830 | 26/05–06/06/1999 |
| | <i>Chrysolabanus</i> sp. | 0.020 | 26/05–06/06/1999 |
| Flacourtiaceae | <i>Casearia tremula</i> (Griseb.) Griseb. ex C. Wright | 0.320 | 16–26/08/1999 |
| | <i>Zuelania guidonia</i> (Sw.) Britton & Millsp. | 3.574 | 26/05–06/06/1999 01–16/07/1999 04/06/2000 |
| Clusiaceae | <i>Rheedia intermedia</i> Pittier | 0.160 | 26/05–06/06/1999 |
| | <i>Calophyllum brasiliense</i> Cambess. | 0.110 | 26/05–06/06/1999 |
| Fabaceae | <i>Inga punctata</i> Willd. | 0.040 | 26/05–06/06/1999 |
| | <i>Inga vera</i> Willd. | 0.370 | 16–26/08/1999 |
| | <i>Inga</i> sp. | 1.210 | 04/06/2000 |
| Lauraceae | <i>Nectandra salicifolia</i> (Kunth) Nees | 0.070 | 22/07–02/08/1999 |
| Malpighiaceae | <i>Byrsonima crassifolia</i> (L.) Kunth | 0.500 | 22/07–02/08/1999 22/07–02/08/1999 |
| Melastomataceae | <i>Bellucia pentamera</i> Naudin | 26.178 | 16–26/08/1999 29/10/2000 06/11/2000 04/12/2000 |
| | | 0.080 | 22/07–02/08/1999 |
| | | 0.070 | 26/05–06/06/1999 |
| | | 0.120 | 01–16/07/1999 |
| Meliaceae | <i>Guarea glabra</i> Vahl | 0.080 | 22/07–02/08/1999 |
| | <i>Abuta panamensis</i> (Standl.) Krukoff & Barneby | 0.070 | 26/05–06/06/1999 |
| | <i>Hyperbaena mexicana</i> Miers | 0.120 | 01–16/07/1999 |
| | <i>Brosimum alicastrum</i> Sw. | 0.940 | 26/05–06/06/1999 |
| | <i>Ficus petenensis</i> Lundell | 0.125 | 26/05–06/06/1999 |
| | <i>Brosimum panamense</i> (Pittier) Standl. and Steyerm. | 1.002 | 26/05–06/06/1999 |
| | <i>Ficus insipida</i> Willd. | 0.700 | 04/06/2000 |
| Moraceae | <i>Ficus maxima</i> Mill. | 0.200 | 04/06/2000 |
| | <i>Ficus</i> sp. | 0.100 | 04/06/2000 |
| | <i>Psidium sartorianum</i> O. Berg. | 1.310 | 01–16/07/1999 16–26/08/1999 |
| | <i>Psidium guajava</i> L. | 1.230 | 16–26/08/1999 |
| | <i>Passiflora ambigua</i> Hemsl. | 0.330 | 26/05–06/06/1999 |
| | <i>Passiflora</i> sp. | 0.090 | 04/06/2000 |
| | <i>Randia armata</i> (Sw.) DC. | 0.025 | 26/05–06/06/1999 |
| Rubiaceae | <i>Rubiaceae</i> sp. | 0.290 | 01–16/07/1999 22/07–02/08/1999 |
| | <i>Cupania</i> sp. | 0.040 | 04/06/2000 |
| Sapindaceae | <i>Cupania belizensis</i> Standl. | 0.040 | 26/05–06/06/1999 |
| | <i>Manilkara zapota</i> (L.) Van Royen | 3.035 | 26/05–06/06/1999 01–16/07/1999 |
| Sapotaceae | <i>Achras zapota</i> L. | 0.180 | 26/05–06/06/1999 |
| | <i>Pouteria</i> sp. | 1.150 | 01–16/07/1999 04/06/2000 |
| | <i>Pouteria durlandii</i> (Standl.) Baehni | 0.470 | 01–16/07/1999 22/07–02/08/1999 |
| Solanaceae | <i>Bumelia sebolana</i> Lundell | 0.600 | 16–26/08/1999 |
| | <i>Calocarpum mammosum</i> (L.) Pierre | 1.170 | 04/06/2000 |
| | <i>Solanum</i> sp. | 0.050 | 26/05–06/06/1999 |
| | <i>Solanum</i> sp. | 0.220 | 26/05–06/06/1999 26/05–06/06/1999 01–16/07/1999 |
| Ulmaceae | <i>Ampelocera hottlei</i> (Standl.) Standl. | 2.51 | 22/07–02/08/1999 16–26/08/1999 |
| Fabaceae | <i>Pithecellobium dulce</i> (Roxb.) Benth. | 0.850 | 04/06/2000 |

Malmea gaumeri (Greenm.) Lundell (Annonaceae) and *Casearia tremula* (Griseb.) Griseb. ex C. Wright (Flacourtiaceae), respectively. In both cases, the plants belong to genera previously unreported as hosts of these flies. *A. crebra* and *A. serpentina* were found feeding on *Quararibea yunckeri* Standl. (Bom-

bacaceae) and *Bumelia sebolana* Lundell (Sapotaceae), respectively. Both represent new host species records in plant genera previously known as hosts for these two *Anastrepha* species.

Our collection of *A. coronilli* is the first in Mexico. The distribution of this species had been thought to be

Table 2. Plant family, species, sample weight, number of yielded pupae, number of adult flies emerged from pupae, and number of adult parasitoids emerged from infested fruit sampled across the 2-yr sampling period at Montes Azules, Chiapas, Mexico

| Family | Plant species | Total no. of pupae | Fly species and sex ratio (M/F) | Parasitoid species and sex ratio (M/F) |
|-----------------|----------------------------|--------------------|---|--|
| Annonaceae | <i>Malmea gaumeri</i> | 21 | 5 <i>A. bahiensis</i> (1/4) | 9 <i>U. anastrephae</i> (6/3) 3 <i>A. pelleranoi</i> (2/1) |
| Apocynaceae | <i>Tabernamontana alba</i> | 30 | 10 <i>A. cordata</i> ^a (7/3) | 5 <i>O. hirtus</i> (2/3) 3 <i>D. zeteki</i> ^b (2/1) |
| Bombacaceae | <i>Quararibea yunckeri</i> | 3 | 1 <i>A. crebra</i> (0/1) | 1 <i>O. hirtus</i> (1/0) |
| Flacourtiaceae | <i>Zuelania guidonia</i> | 18 | 13 <i>A. zuelaniae</i> | 0 |
| | <i>Casearia tremula</i> | 18 | 8 <i>A. zuelaniae</i> (4/4) | 8 <i>O. hirtus</i> (1/7) 1 <i>D. crawfordi</i> (1/0) |
| Melastomataceae | <i>Bellucia pentamera</i> | 582 | 77 <i>A. coronilli</i> ^b (44/33) | 0 |
| Myrtaceae | <i>Psidium sartorianum</i> | 24 | 12 <i>A. striata</i> (6/6) 9 <i>A. fraterculus</i> (5/4) | 0 |
| | <i>Psidium guajava</i> | 3 | 2 <i>A. striata</i> (1/1) | 1 <i>D. crawfordi</i> (1/0) |
| Sapotaceae | <i>Manilkara zapota</i> | 235 | 187 <i>A. serpentina</i> (112/75) | 4 <i>D. crawfordi</i> (3/1) |
| | <i>Bumelia sebolana</i> | 97 | 14 <i>A. serpentina</i> (6/8) | 46 <i>U. anastrephae</i> (26/20) 14 <i>D. areolatus</i> (9/5) 9 <i>O. hirtus</i> (7/2) 2 <i>A. pelleranoi</i> (1/1) |
| | <i>Calocarpum mammosum</i> | 15 | 15 <i>A. serpentina</i> (11/4) | 0 |
| | <i>Pouteria</i> sp. | 260 | 190 <i>A. serpentina</i> (89/101) | 21 <i>D. crawfordi</i> (17/4) 1 <i>D. areolatus</i> (1/0) 3 <i>A. pelleranoi</i> (9/2) |
| Ulmaceae | <i>Ampelocera hottlei</i> | 856 | 311 <i>A. fraterculus</i> (149/162) 37 <i>A. obliqua</i> (13/24) | 127 <i>O. hirtus</i> (69/58) 52 <i>D. areolatus</i> (23/29) 27 <i>U. anastrephae</i> (17/10) 9 <i>A. pelleranoi</i> (6/3) |

New unpublished host associations are highlighted in bold.

^a New report for the State of Chiapas.

^b New report for Mexico.

restricted to Central America (Guatemala to Panama), Colombia, Surinam, and northern Brazil (Norrbon et al. 1999a, da Silva and Ronchi-Teles

2000). We also report *A. cordata* in the state of Chiapas for the first time, although Hernández-Ortiz (1992) had speculated that this particular species should be found in the state given its abundance in Central America (to the south) and its presence in Veracruz (to the north). Similarly, *A. zuelaniae* is reported for the first time in the state of Chiapas. Finally, we report for the first time in Mexico the presence of the braconid parasitoid *Doryctobracon zeteki* Muesebeck. The latter discovery also represents the northernmost record for this species that had been previously reported in Costa Rica, Panama, and Venezuela (Ovruski et al. 2000).

The largest species group of *Anastrepha* represented in our sample was the *fraterculus* group with five species (*A. fraterculus*, *A. obliqua*, *A. coronilli*, *A. bahiensis*, and *A. zuelaniae*). Both morphological and mitochondrial DNA phylogenies have shown that this is the largest species group in *Anastrepha* (McPherson et al. 1999, Norrbom et al. 1999b) and that it is the most derived (Norrbon et al. 1999b). Furthermore, *A. fraterculus*, formerly thought to be a single, wide-ranging species, is now believed to form a group of cryptic species with subtle morphological, genetic, and behavioral differences (Steck 1991, Selivon et al. 2001, Aluja et al. 2003). A similar case of cryptic speciation may be occurring among populations of *A. ludens*, another member of the *fraterculus* species group (Silva et al. 2001). Some of these cryptic species seem to exist in sympatry exploiting different hosts (Selivon et al. 2001). This suggests comparison with

Table 3. Species, fruit characteristics, degree of infestation, and percent parasitism for native plant species found to be natural hosts of *Anastrepha* in Montes Azules, Chiapas, Mexico

| Plant species | Average individual fruit weight g (±SD) | Number of pupae/g of fruit | Percent parasitism |
|----------------------------|---|----------------------------|--------------------|
| <i>Ampelocera hottlei</i> | 2.29 ± 0.45 | 0.850 | 76.47 |
| <i>Bumelia sebolana</i> | 2.10 ± 1.13 | 0.1616 | 73.20 |
| <i>Malmea gaumeri</i> | 1.30 ± 0.4 | 0.0168 | 57.14 |
| <i>Ampelocera hottlei</i> | | 0.2112 | 56.21 |
| <i>Casearia tremula</i> | 21.50 ± 6.45 | 0.0562 | 50.00 |
| <i>Quararibea yunckeri</i> | 2.79 ± 0.40 | 0.0187 | 33.33 |
| <i>Tabernamontana alba</i> | 25.53 ± 8.85 | 0.0500 | 26.67 |
| <i>Ampelocera hottlei</i> | | 0.1000 | 23.94 |
| <i>Ampelocera hottlei</i> | | 0.1617 | 10.91 |
| <i>Pouteria</i> sp. | 380 ± 119.6 | 0.2385 | 9.62 |
| <i>Ampelocera hottlei</i> | | 1.630 | 4.70 |
| <i>Manilkara zapota</i> | 63.6 ± 10.21 | 0.1126 | 1.76 |
| <i>Bellucia pentamera</i> | 12.60 ± 2.99 | 0.1000 | 0.00 |
| <i>Bellucia pentamera</i> | | 0.0242 | 0.00 |
| <i>Psidium sartorianum</i> | 2.89 ± 0.85 | 0.0240 | 0.00 |
| <i>Zuelania guidonia</i> | 17.44 ± 2.31 | 0.0217 | 0.00 |
| <i>Zuelania guidonia</i> | | 0.0147 | 0.00 |
| <i>Calocarpum mammosum</i> | 439.74 ± 69.2 | 0.0128 | 0.00 |
| <i>Bellucia pentamera</i> | | 0.0108 | 0.00 |
| <i>Psidium guajava</i> | 39.8 ± 11.72 | 0.0024 | 0.00 |
| <i>Zuelania guidonia</i> | 17.44 ± 2.31 | 0.0026 | 0.00 |
| Mean | | | 19.2 |

Data on independent samples provided (e.g., *A. hottlei*) to illustrate variability in rate of larval infestation and parasitism.

Table 4. Fruiting phenology of some *Anastrepha* spp. host plants in Chajul, Chiapas, Mexico*

| Fruit fly host plant species | Months | | | | | | | | | | | |
|------------------------------|--------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
| <i>M. zapota</i> | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>B. sebolana</i> | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>Z. guidonia</i> | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>A. hottlei</i> | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>C. tremula</i> | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>Q. yunckeri</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>P. durlandii</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>T. alba</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>P. sartorianum</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>P. guajava</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>B. pentamera</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| <i>M. gaumeri</i> | | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |

Months in which at least a few unripe or ripe fruit may be found are represented.

* Unpublished information provided by M. Martínez (Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México) and complemented by P. Sinaca (freelance consultant).

the recent radiations of the *pomonella* group in the temperate genus *Rhagoletis* (Feder 1995).

In the undisturbed tropical environment of the Montes Azules biosphere reserve, simultaneous infestation of the same host by different *Anastrepha* species seems to be the exception rather than the rule. Hernández-Ortíz and Pérez-Alonzo (1993) found a similar trend in a 5-yr fruit sampling survey carried out in a tropical rainforest environment in the state of Veracruz (only *A. fraterculus* and *A. striata* infested *Psidium guajava* L. at the same time). Similarly, in Montes Azules, we found a greater proportion of monophagous and oligophagous fly species than polyphagous species (57.9 versus 42.1%), an overall pattern in the neotropical genus *Anastrepha*, and in herbivorous insects in general (Jaenike 1990). Interestingly, the reverse numerical pattern is observed in perturbed agricultural settings in the same state of Chiapas. For example, in large scale mango orchards or mid-sized sapodilla, guava, or orange orchards, the predominant *Anastrepha* species were by far (60–95%) polyphagous (i.e., *A. ludens*, *A. obliqua*, *A. serpentina*, *A. fraterculus*) (Celedonio-Hurtado et al. 1995, Aluja et al. 1996). Perhaps there is greater specificity of tephritid flies in tropical unperturbed environments because of intense coevolution with their hosts, as hypothesized by Janzen (1970) for other herbivores. As a result, specialized species may have developed finer host finding mechanisms than generalist species. In this respect, we note that parasitoids were found, in general, attacking larvae in fruit belonging to more than one plant family, appearing not to be as specialized in terms of plant selection as their tephritid hosts.

Because host plants of monophagous *Anastrepha* species are widely distributed in space and time, and in vast rainforests, individual host trees can be extremely isolated, it is likely that population structure of a particular species is such that there are sub-populations closely associated with a particular tree. Furthermore, monophagous flies seem to have developed life strategies that allow them to survive until the next fruiting season of their host (e.g., extreme adult

longevity, dry season aestivation) (Aluja et al. 1999). In contrast, polyphagous species jump from host to host as the year progresses (Aluja et al. 1999). If multiple polyphagous species “accumulate” in particular hosts, they may at times face strong interspecific competition and high parasitism rates. The fruit of *A. hottlei* may represent such a case. The high levels of infestation discovered in this plant (up to 1.63 pupae/g of fruit, Table 3), the number of polyphagous species exploiting it (*A. fraterculus* and *A. obliqua*), and the high parasitism rates (up to 76%) may be an indication that this host is available at a time when other alternate hosts are scarce both for *A. fraterculus* and *A. obliqua* (Table 4). The other tree species fruiting when *A. hottlei* is available are either hosts of *A. serpentina* or *A. zuelaniae*, and with the exception of *B. sebolana*, none yielded considerable numbers of parasitoids (Tables 2 and 4). Keystone tropical plant resources support a broad spectrum of frugivores during times of food scarcity (Nason et al. 1998), and based on our evidence, it seems that *A. hottlei* may be playing the role of a keystone species for *A. fraterculus* and *A. obliqua* and their parasitoids. A similar case is represented by the myrtaceous *Myrciaria floribunda* (H. West ex Willd.) O. Berg, a plant commonly found in tropical, deciduous forests in central Veracruz, Mexico. As reported by Aluja et al. (2000b), this fruit is infested by *A. bahiensis*, *A. fraterculus*, and *A. obliqua* at a time during which no other fruit is available. The role of *M. floribunda* as keystone species is further supported by the fact that it is not only heavily infested by the above-mentioned *Anastrepha* species, but is also eaten by mammals that have little access to other food sources at the time of year this tree bears fruit.

An interesting host-use pattern detected in our study was that polyphagous species were not found exploiting hosts of monophagous species. Whether this is because of a higher competitive ability of monophagous species in their host plants or merely because they are better adapted to their host plant chemistry than less specialized polyphagous species needs to be investigated. More than 90% of shrub and tree species in Central American rain forests bear

small fleshy fruit. This pattern seems to be driven by animal seed dispersion (Levey et al. 1994), which is also thought to maintain high species diversity of tropical plants (Janzen 1970). Tephritid flies have been found to exhibit strong intra- and interspecific competition in such fruit, a phenomenon that in some cases may have reinforced host race formation (Averill and Prokopy 1987, Feder et al. 1995, Dukas et al. 2001). Strong interspecific competition for small fruit may help explain why polyphagous species such as *Ceratitidis capitata* (Wiedemann) have failed to fully colonize tropical rain forest environments in the Neotropics (Ronchi-Teles and da Silva 1996, da Silva and Ronchi-Teles 2000). Interspecific competition may have also played a role at selecting polyphagous species able to colonize novel hosts and exploit unoccupied niches. These traits would render them excellent candidates to become pests of fruiting plants introduced for agricultural purposes. The latter is supported by the fact that, of the seven economically important *Anastrepha* species, five are polyphagous. All of the above leads to the prediction that continued devastation of tropical environments will irreparably lead to the loss of numerous specialist fruit fly species, while a few generalist species, released from competition, will be able to survive and probably thrive in perturbed environments.

Percent parasitism averaged 19.2%, but reached 76% in some cases (*A. hottlei*). While evaluating parasitoid distribution along an elevational gradient encompassing highly disturbed areas and high altitude temperate regions in the state of Veracruz, Sivinski et al. (2000) found an overall parasitism rate of only 6%. In our study, *Anastrepha* larvae found in some large- and medium-sized fruit exhibited low parasitism rates (e.g., *Manilkara zapota* L. P. Royen and *Psidium guajava*). A similar pattern was detected in fruit with extremely hard skin (e.g., *Calocarpum mammosum* L. Pierre) or with a sticky surface (i.e., *Zuelania guidonia* [Sw.] Britton and Millsp.). However, *Anastrepha* larvae infesting small, soft-skinned fruit were at times highly parasitized. An unusual case of particular interest is represented by *A. serpentina*. This species is apparently exposed to low levels of parasitism in such large or hard-skinned fruit as *C. mammosum*, *Chrysophyllum mexicanum* Brandegee ex. Standl., *Pouteria durlandii* (Standl.) Baehni, and *Manilkara zapota* (M.A., personal observation), but in Montes Azules, parasitism levels were high in *Bumelia sebolana*, a plant with particularly small fruit for a Sapotaceae. The pattern observed here of high parasitism rates in wild trees bearing small fruit lends further support to the idea put forth by Aluja (1999) and later rediscussed by Montoya et al. (2000) of conserving areas of native vegetation near orchards to suppress pest populations of *Anastrepha* before adult individuals move to areas cultivated with exotic fruits.

It has been postulated that host shifts in the temperate tephritid genus *Rhagoletis* could have been driven to some extent by parasitism. For example, *R. pomonella* Walsh that shifted from hawthorn to apples may have differentiated from ancestral haw-

thorn infesting populations by exploiting enemy free space in the larger novel host, a situation thought to constitute a fitness tradeoff (Feder 1995). Whether parasitism is a driving force in generating diversity and specialization in *Anastrepha* remains to be proven, but widespread expansion of some species to novel, large introduced hosts, where they are not heavily parasitized, lends some support to this hypothesis.

Sechrest et al. (2002) found that biodiversity hotspots harbor greater amounts of evolutionary history than expected by species numbers alone. Our findings provide important information on the value of undertaking studies in such hotspots because, for example, new host associations and species interactions allow us to speculate about, if not to elucidate, ecological and evolutionary processes in insects and to gather useful information for the development of biorational pest management schemes in the tropics. The study of *Anastrepha* distribution and host range in Montes Azules proved to be extremely fruitful in gaining insight on ecological patterns such as host-parasitoid dynamics and tephritid life strategies. For example, it seems that monophagous species of *Anastrepha* dominate the Chiapas tropical rain forest environment and that some groups in the genus may be undergoing radiation, perhaps through chemical specialization to different plants or driven to some extent by competition and parasitism. Considering that previous estimates for the total number of flowering (fruiting) plants have gone from 250,000 to 320,000 (Prance 2001), we should expect to discover a considerable number of new specialist *Anastrepha* species through continued sampling in environments like Montes Azules. Because habitat destruction is the leading cause of species extinction (Pimm and Raven 2000), and given the rapidity of this process in tropical rain forests in Latin America, we can predict an important loss of monophagous species of *Anastrepha* unless serious conservation efforts modify this process. Such species may be too specialized to withstand accelerated loss of host plants in their native habitats. More thorough studies focused on the ecology of polyphagous species in rainforests might lead to a better understanding of the factors that transform certain tephritid species into agricultural pests of domesticated fruit. Ultimately they may shed light on methods to control pest species with minimal environmental impact while contributing to the conservation of nonpest species of tephritid flies and their host plants.

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