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FERAL AFRICAN BEES AUGMENT NEOTROPICAL COFFEE YIELD

David W. Roubik

Abstract

No previous work describes natural history of coffee pollination in semi-natural habitats, but without intrusion of hived bee colonies. In Panama highlands having feral honeybees since 1985, the fruit and seed set of *Coffea arabica* was monitored during 1997 in bagged and open flowers on 558 shrubs in 11 transects within a range of 13 km, at elevations of 1300-1600 m. Caturra varieties were studied either next to old forest or in more open, mosaic habitats, while Catimor, an interspecific hybrid grown in "sun" plantations, was studied at a single site. Four honeybee hives were kept in the Catimor plantation.

Bees, the common visitors, were most abundant on flowers near old forest. Significant native visitors included *Centris festiva, Bombus pullatus, B. volucelloides, Trigona fulviventris, T. nigerrima,* and T. (*Tetragonisca) angustula*, but *Apis mellifera scutellata* made >95% of all flower visits in all areas. Visitation was not accurately measured by number of bees per flowering shrub, compared to bees per flower. Neither was the value of open pollination adequately gauged within a single branch with bagged and open flowers, compared to bagged and open branches on the same shrub. Flowers of *C. arabica* were found to be distylous, with 11 individual shrubs having short-styled flowers. Their fruit set and seed set, both in bagged and open flowers, was no different from the more common long-styled plants.

Caturra and Catimor showed over 25% fruit retention increases from pollinating visits by bees. For the former, seeds were over 25% heavier and developed faster from open pollination. Yield benefit from open pollination, chiefly by feral African bees, was 56%. Older plants, however, did not respond by increasing fruit set, nor did Catimor produce heavier fruit when pollinated by bees.
Key words: pollination, coffee

Introduction

The foremost tropical cash crop, *Coffea arabica* has surprisingly not been studied as to natural pollinators and their impact without introduced bee hives present, either in its native Africa or other tropical mainland areas (Free 1993; Smith *et al.* 1992; Wrigley 1988; Alvarado and Rojas 1994; Clifford and Wilson 1985; Amaral 1960; Badilla and Ramírez 1991; Nogueira-Neto and Filho 1959; Sein 1959). Maturation of coffee berries requires seven months. Fruit retention is apparently enhanced by degree of outcrossing (Free 1993) although *C. arabica* is self-fertile. In Panama I experimentally excluded visitors from flowers and compared berry production to normal, open flowers. Visitors were observed by old-growth forests and in agricultural areas. Not unexpected was discovery that feral African honeybees visited these African shrubs. However, naturalized African honeybees constituted most visitors and made nearly all the pollinating visits. Their impact, far greater than anticipated, suggests that many of the hundreds of crops visited and potentially pollinated by *Apis* are now experiencing changes in productivity in tropical America (Roubik 1989, 1995; Freitas and Paxton 1998). At coffee, flower visitors before invasion of the neotropics by *Apis melifera*, which only occurred in the last 45 years, were probably a diverse group and were still found at flowers near forest.

Materials and Methods

I studied one of the most common modern cultivars of *Coffea arabica* (Rubiaceae) used in the tropics "Caturra" and also "Catimor" — an interspecific backcross of *C. canephora* to *C. arabica*, which thrives, depending on adequate fungicide application, in sunlight (Alvarado and Rojas 1994; Smith *et al.* 1992; Clifford and Wilson 1985; Perfecto *et al.* 1996; Greenberg

et al. 1997). I established study transects in February 1997 in the western Panama province of Chiriquí, at 1300 to 1600 m elevation (9'80" N). This area is within 30 km of Costa Rica and touches Amistad National Park. Average annual rainfall is 1300-1800 mm with temperatures during the study ranging from 14 to 24° C. Sites were in extensive coffee growing regions at the foothills of the Talamanca mountain range.

Coffee begins flowering during dry season in response to showers, usually one week after a substantial rain, often after true bud dormancy (Clifford and Wilson 1985). Flowering begins synchronously within individual plantings and finishes after three days. Flowering then ceases for a few to several weeks, until again triggered by rain. For example, in the primary study area, consisting of 100 ha over 5 km in both relatively open and shaded plots ranging from 1300 to 1500 m elevation, coffee flowered a mode average of four times in each year during 1993 to 1997 (R. Hartmann, personal communication). One to five flowerings occurred during these five years, between January and early May. During my study, the first flowering on 20 January was small. The second and third occurred on 2-7 March and 23-26 March, and the last on 1-4 April. The second and fourth were the year's largest. We observed animals visiting flowers during the last three flowerings. The parallel study of Catimor was initiated on10 March. Flowering plants of a commercial coffee company, Durán, Lot 94, were observed for visitors during one of the year's two largest flowerings, on 11-13 March.

Study plantings and honeybee colonies

In the Caturra plantings, trees from the original forest were present, 20 to 35 m in height. These were managed for shade characteristics deemed correct for Caturra. The ten study transects, designated A-J, were of 9 to 25 coffee shrubs, using every tenth shrub where adjacent plants and rows were separated by 1 to 1.5 m. Transects were not made on edges of plantings. Over 95% of the plants were relatively young Caturra. Interspersed on some transects were older individuals of "Arábigo" or "Criollo Híbrido" which occurred in plots G, D, C, J and H. Several in D and J were over 30 years in age. All except 'I' were less than 500 meters from forest, and plots D and J were within 50 m of extensive primary forest. Study transects having several shade trees above the coffee were in all but plots E, F, A, B and (due to clearing in March) plot C. Plot D had one feral colony of honeybees nesting at ground level in one extreme. The 10 transects were oriented so that they remained at an even distance from forest, or extended perpendicular to it.

A 100% Catimor planting consisting of 2-y old shrubs constituted the Catimor site. Grown on terraced hillsides covering 10 ha, plants were separated by 1-2 m and had no shade during times of maximum daily insolation (1000-1400 h). The nearest forest was five km distant. Six small areas were selected on a transect 300 long, perpendicular to a line of four honeybee hives placed at 150 m from the end study plot. No insecticides or herbicides were used in plantings but fungicides were applied after April. In addition, Catimor was artificially fertilized. Caturra plantings were given some organic compost before flowering.

For Caturra, 12 honeybee hives were present at a lower elevation approximately 2 km from the study plots. No other managed bee hives existed within over 4 km. All honeybees in mainland Panama have been the African or 'Africanized' *Apis mellifera scutellata* since 1985 (Roubik and Boreham 1990). In Chiriqui African colonies are numerous in the wild, yet no European colonies have been present since 1985, and only 400 African bee hives were maintained by local coffee producers in the entire region in 1997 (Mr. M. F. Pardo, Duran Coffee, personal communication). To assess the degree of honeybee specialization on pollen from coffee flowers, two managed hives in the Duran planting, and two near forest where coffee plantings were few were kept with pollen traps during the April flowering (courtesy of M. Pardo). The pollen pellets were examined using a light microscope and standard palynological techniques (Amaral 1972; Roubik and Moreno 1991).

Pollination experiments and fruiting success

Open and bagged pollination experiments were made using branches with dense mature buds that were selected one or more days before flowering on 120 Caturra plants and 20 Catimor plants in 9 total plots, with an additional 24 Caturra plants included prior to April flowering. Open mesh tents were also placed over 10 shrubs in two Caturra plantings. A total of 30,861 (34% bagged) flowers on 447 branches were studied in Caturra plots and 8,289 (41% bagged) on 104 branches were followed in the Catimor plot. Bag mesh material was nylon with 1.25 mm openings. In Caturra plots A and B, both regular and very fine (0.25 mm) mesh bags were used on each plant, to assess the consequences of limiting wind pollination within fine mesh bags. Microhabitat conditions within a planting were scored as either relatively sunny or shaded. The shaded coffee shrubs had trees within 10 m.

One month after major flowering ended bags and tents were removed and total small green ovules at bases of wilted flowers was counted from bagged and open flowers. Flower numbers were written on masking tape at the base and tip of each treatment inflorescence series, and also on plastic flagging tape. Larger fruit, resulting from flowering before March, were removed. In addition, a total of 45 branches had both open and bagged flowers (bagged inflorescences were outermost on branches).

A total of 551 branches on 164 plants were monitored for developing fruit. In both Catimor and Caturra plantings, further sporadic flowering occurred after bags and tents were removed. A large flowering took place in the Catimor planting during late April. No attempt was made to remove these flowers or their fruit. For subsequent analysis of augmented fruit yield due to open pollination, the assumption was therefore made of equal flowering on portions of a given plant used for bagged and open pollination treatments, after the initial recording of flower number. Fruit retention and maturation were scored during May, June, August and October. All green, ripening fruit or red, mature fruit were counted on marked treatment branches. Fruit were also weighed during the last two censuses. To sample fruit weights, at least 40 of the largest fruit from bagged or open flowers were selected from 8-10 plants in each plot. An equal number of each category was taken from a given plant. Random subsamples of 10 to 20 fruit were then weighed in the field with a Pesola balance, to the nearest 0.2 g. In addition, fruit and seed weights were scored for 100 fruit from 12 plants, to test for relationship between fruit and seed weight.

Flower visitors and floral rewards

Bee visits and behavior (tempo of visitation, collection of nectar or pollen, interspecific aggression, floral corolla perforation) were recorded during two to four days in flowering episodes and included the same focal plants used for fruiting studies. Total open flowers, including day-two flowers that have wilted anthers but continue to secrete nectar (Nogueira-Neto and Filho 1959) were estimated on each plant monitored for visitors. The number of bees and other animals was scored during a brief inspection of labeled transect plants, usually in less than a minute, as all study transects were walked two or three times a day. To supplement the focal plant approach, unlabelled plants nearby were monitored if, on a given day, flowers on a labeled plant were fewer than 80. Honeybee visitation tempo was recorded by timing five consecutive visits to flowers. A different bee was chosen each time, until at least 100 had been observed on more than one day and during each hour in which visits occurred (0730-1630). Nectar sugar concentration was measured in brix units with a hand-held refractometer corrected for temperature by extracting nectar from bees (see Nogueira-Neto and Filho 1959) collected from mid morning until early afternoon (0900-1400).

Genetic variation in plantings

To explore the possibility that genetic variation differed greatly within Catimor and Caturra plantings and between the two principal cultivars, 25 individual plants were sampled along a continuous transect from two areas of both Caturra and Catimor plots. Horizontal starch gel eletrophoresis was used on fresh leaf samples prepared with tris-maleate grinding buffer and

run on 300 ml gels of 13% starch, using tris-citrate tray and gel buffers of pH 8.2 (Kephart 1990). Enzyme systems assayed were 6-phosphogluconate dehydrogenase (6-PGD), acotinase (ACO) and diaphorase (DIA). Each had shown variation in preliminary assays using leaf samples of Caturra. Gels were run for 7 hours at 75 volts, 50 milliamps.

Results

Fruit retention and yield

Ratios of open-pollinated to bagged flower fruit retention are given in Table 1 and Fig 1, for fruit counted on 24 August or 18 October (largest sample sizes were used). Plots averaged from 5% less to 56% more fruits produced from open pollination. Ninety-seven shrubs were included in the final census, including 464 branches. The grand mean of fruiting augmentation in individual plots was 17.08%. However, only plots E, F, A, B and 'Duran' had yields that were significantly increased by open pollination (t-test, one-tail comparison to a population mean of 1). Mean increase in this subset was 26%. Because comparison of bagged and open flowers on the same branch showed much higher fruit retention for open flowers (mean = 62% greater, n = 23), fruit set increases were computed only from pollination treatments including entire branches.

The ANOVA comparison of fruit set showed significant plot differences (df = 7, 90; F = 3.15, p = 0.005), but only between two Caturra plantings. Differences between plot F (full sun) and plots D and J (older plantings, considerably shaded) were significant at 95% confidence by Scheffe a-posteriori tests (Table 1). Significant variation in fruiting related to plant age was found within Caturra (Scheffe test, Table 2), although no difference existed between younger Catimor and Caturra plantings. Fruit set was moderately higher for plants in sunnier conditions (Table 2). A factorial ANOVA showed no significant interaction effect of plot and shade conditions on yield (F = 0, df = 4, 4, 85, p = 0.73). Fruit set also was uninfluenced by bag mesh size. No differences were observed in fruit retention from flowers bagged with fine or larger mesh (paired t-test, 2-tail, p = 0.30, N = 28).

The fruit set did not differ among plants with typical long styles, or shorter styles. Of 164 Caturra, 20 had flowers with short styles. Short-styled plants were found in plots H, D, G, J, and I. Stigmas rested on petal surfaces in newly opened flowers, as well as in day-2 flowers. The tent placed over eight shrubs in plot G contained both a large short-styled plant and a normal plant of similar size. Their proportional yield per flower did not differ (Wilcoxon signed ranks, z = 0.94, p = 0.35, n = 31). Among other plots no difference was found in fruit retention ratio on open and bagged branches of short-styled shrubs, compared to adjacent, normal, long styled focal plants (z = 0.245, p = 0.81, n = 26).

Mature seed weights were over 25% greater in open-pollinated Caturra and Arabigo of all experimental plots (paired t-test, 1-tail, p = 0.0001, n = 416), but not for Catimor. Regressing seed weight on fruit weight produced a line with slope greater than one ($r^2 = 0.82$, $p < 0.001$, n = 112), showing that an increase in fruit weight was met by a similar and greater increase in seed mass.

Flower visitors and behaviour

All 11 transects revealed visits to coffee flowers by *Apis mellifera* L., *Trigona nigerrima* Cresson, *T. (Tetragonisca) angustula* (Lat.), *T. fulviventris* Guérin-Meneville, *T. corvina* Cockerell and *Bombus volucelloides* Gribodo. Bees collected nectar, were seen with full coffee pollen loads and the visits of the first and last, in contrast to the other species, were rapid. At the Caturra plots, African honeybees visited five flowers in an average of 26.4 sec, SD 6.9, n = 127, while at Catimor, visits were significantly shorter (20.7 sec, SD 6.8, n = 189; p = 0.0001, Wilcoxon signed ranks). Some *Bombus pullatus* Franklin, *B. ephippiatus* Say and *B. volucelloides* Gribodo, both queens and workers, visited five flowers in less than 11 seconds, but my observations were limited. Similarly rapid was *Centris festiva* F. Smith, seen in plots H and D. Other, less common visitors were *T.* (*Tetragona) dorsalis* Friese, *T.*

amalthea Olivier, *Eulaema polychroma* (Mocsáry), *Melipona panamica* Cockerell, *Nannotrigona perilampoides* (Cresson), *Epicharis rustica* (Olivier), *Centris, Lasioglossum, Augochlora, Partamona bilineata* (Say), *Scaptotrigona subobscuripennis* (Schwarz), *Paratrigona ornaticeps* (Schwarz) and *Brachygastra*. All bees but *Centris* and *Epicharis* are social and *Brachygastra* is a social 'honey wasp'. Five nests of *Melipona, T. corvina, Partamona* and *T. angustula* were found in original forest trees felled in plot C during the study. The crowned woodnymph (Trochilidae) was observed in plot D. Syrphid flies of several genera, as well as hesperiid, ithomiine, danaid, and heliconiine butterflies also occasionally visited coffee flowers. Visits of most taxa could not have been a significant factor, and their numbers were far too low to be tested as to relevance in coffee pollination. In contrast, total observed *Apis* numbered 1415 and native bees 511, but two-fifths the latter were *T. corvina* and *T. fulviventris* which perforated flowers for nectar. *Trigona corvina* foraged in aggressive groups.

If nesting near coffee plantations, the honeybee harvested almost exclusively coffee pollen during the major flowering period in April. Pollen specialization by honeybees from hives in the Catimor planting was indicated by over 95% coffee pollen, with seven other pollen types observed. In contrast, colonies separated by a distance of several km from the coffee growing areas intensively harvested native tree pollen, with coffee pollen comprising under 5% of incoming pollen during the same interval.

Visitation rates

The number of bees per coffee plant or bees per flower varied appreciably among plots and sunny or shaded shrubs (ANOVA, Tables 1, 2). On a per-plant basis, Catimor plants had significantly more bees, but this comparison proved inadequate to assess differences in floral visitation (Table 1). Scheffe a-posteriori comparisons showed a statistical difference in bees per flower only in plot D, which had the most honeybees, native bees, was shaded, and was close to old forest. In general, there were more *Apis* per flower and more native bees per flower in shaded conditions and near forest, although the average number of flowers per shrub was higher in sunny plots more distant from forest (ANOVAs, $p = 0.0001$, Table 2). When the near-forest component was removed by excluding plots J and D, *Apis* per flower had no significant variance due to sun or shade ($df = 1,491$, $F = 2.73$, $p = 0.1$). A weak but significant positive correlation was seen between *Apis* per flower and flower number on coffee shrubs (adjusted r-squared = 0.10, $p = .0001$, $n = 696$). Adjustment in visits per flower for the Catimor plants, where *Apis* was 27.5% more rapid in flower visitation, did not change the ANOVA results — only plot D had significantly more visits than all other plots except J (Table 1).

Other general results

Fruit from open and bagged flowers ripened at different rates, evident in red coloration and also in greater weights among open pollinated fruit ($df = 9$, $p = 0.0001$, t-test, 1 tail, comparison of ratios of open to bagged weights to a population mean of 1.0, $n = 416$). Fruit drop was pronounced during the first three months after flowering, with initial fruit set at 91% (Durán) and 85% (Caturra plots); only a 2-3% decrease was detected between August 22 and 18 October.

The isoemzyme results merely confirmed that single plantings of coffee were not clones. Neither DIA nor 6-PGD were monomorphic isoenzymes in Catimor (5 of 35 individuals polymorphic) and plots D, G and J of Caturra (2 to 8 of 25 individuals polymorphic). Resolution was poor for ACO.

Nectar sugar concentration averaged 36% (SD 8%) for Caturra ($n = 305$ bees) and 27% (SD 4%) in Catimor ($n = 41$).

Discussion

This Panama study is a sample representing tropical, continental America in 1000-1500 m elevations at which Arabica coffee is generally cultivated, but where honeybees were previously absent or ecologically irrelevant. While Catimor is not suitable for export on the international market, its shrubs yield more berries per hectare (Alvarado and Rojas 1994). The present study suggests that Caitmor productivity is less on a per flower basis, compared to young Caturra, but its increased fruit set in response to open pollination is similar (Table 1).

Neotropical studies of coffee pollination show varied results and some ambiguity (McGregor 1976; Free 1993), and none was conceived to address natural history questions where pollinators had not been displaced by hives of bee colonies or wholesale habitat manipulation. Augmented fruit retention and larger size seem to result from outcrossing (Nogueira-Neto and Filho 1959; Raw and Free 1977; Badilla and Ramirez 1991). However, such research was conducted in the absence of what is likely the primary flower visitor of *Coffea* in the Neotropics — the feral African honeybee, *Apis mellifera scutellata* Lat. Furthermore, experimental studies have utilized cages remaining in place for several weeks to months. After a few weeks for coffee, which requires several months to produce mature fruit (Wrigley 1988), potential negative influence of shading from cages is expected (Corbet and Delfosse 1984). Caged plants studied by Raw and Free (1977) showed lower fruit retention, even if pollinating bees were introduced into them during flowering, compared to open-pollinated shrubs. In addition, either branches or entire plants have been covered to exclude pollinators, with results that differ five-fold in the implied value of pollinators (Amaral 1960). Claims persist for nearly a doubling of "yield" among widely varying "natural outcrossing" levels (Badilla and Ramírez 1991; Reddy *et al.* 1988; Free 1993). If yield refers to fruit retention, then these claims are not justified. If yield refers to the mass of a coffee bean produced per flower, then the present study gives some confirmation. But if such statements refer to older individual plants, they are patently false.

Apis mellifera scutellata, the east African honeybee (Hepburn and Radloff 1998), was the preeminent flower visitor of *Coffea arabica* despite the presence of dozens of other animals. Coffee is visited by many pollinating native social bees and wasps in the neotropical mainland, particularly *Trigona, Melipona*, and other Meliponini (Nogueira-Neto and Filho 1959; Martinez-Hernandez *et al.* 1993) and as documented for the first time in this study, *Bombus* and *Centris*. Compared to these native neotropical insects, the African honeybee quickly saturates rich resource patches such as flowering coffee plantations, by having large colonies, large flight range and an extremely effective recruitment system (Roubik 1989). Honeybee visits to any flower in any plot totaled over 40 in a day and did not differ significantly among most plots. Regardless of proximity of the known hives, honeybees evenly dominated the coffee landscape. Their pollen in hives near coffee plantings was found to consist of over 95% coffee pollen, while coffee pollen was less than 5% of total pollen from hives well separated from coffee plantations. This indicates opportunism as well as the likelihood that bees visiting the flowers came from close by. The honeybees were 82% of bees at flowers, and considering a much faster tempo in visitation, accounted for >95% of actual visits. Studies with none of the native bee genera present, but with European honeybees on Caturra, have shown the 16-17% fruiting augmentation that I observed (Badilla and Ramírez 1991; Free 1993; Sein 1959; Nogueira-Neto and Filho 1959) strongly suggesting the honeybee alone can account for at least this degree of seed set increase.

Variation in seed set on the same branch demonstrated that at the ramet level, allocation of nutrients shifted considerably toward open pollinated fruit. Fruit set showed a 62% increase among open-pollinated flowers, compared to 17% mean augmentation for single-treatment branches. Wind excluded by fine mesh bags appeared insignificant as a pollinating agent. Autogamy by gravity was possibly a large component of pollination. As these authors make clear, open pollination can change both the outcome and origin of pollen transferred to stigmas. Artificial pollination experiments would be necessary to determine whether outcrossing versus improved pollination with self-pollen were the primary benefits derived

from open pollination. Such benefits, seen not only in fruit retention over the long maturation period, but also in faster growth and greater seed and fruit mass, are thought to derive primarily from pollen brought from other shrubs by flower visitors (see Free 1993; McGregor 1976). Although six of nine study plots displayed only moderate or insignificant increase in fruiting success due to open pollination, the developmental rate and weight of ripe berries increased a mean of 23% among all open-pollinated Caturra plantings. Combined with mean numerical increase of 27% in fruit retention (where statistics were significant) open pollination could result in over 56% increase (1.23 x 1.27) of fruit mass and yield. As indicated by the results, within berries the seed mass increased more steeply than fruit mass.

The potential gain from pollinators was greater in Caturra plots. Even though the most productive plots in Caturra plantings were those receiving more sun, this was not due to more bee visitation or applications of fertilizer, and was thus potentially due to greater insolation during fruit maturation. Although Catimor plants did not evince increased berry weight from open pollination (means 1.6 and 1.75 g, n = 44), fruit set increased by 17% from open pollination. Because Catimor is derived from an interspecific hybrid, the negligible size response to open pollination may be linked to this variable. According to a-posteriori comparisons in ANOVA (Table 1), Catimor did not differ appreciably from Caturra in the seed retention increase resulting from open pollination.

The preliminary results from allozymes suggests both cultivars were genetically variable within distances of 25 m and therefore recombination potentially occurred via bees. Genetic monomorphism is unlikely to explain lack of response to outcrossing within some plots, particularly because less responsive plots had both short-styled plants and mixed cultivars present. No published work has mentioned distyly in *C. arabica*, but the decreased distance between stigma and anthers, compared to normal long-styled flowers, neither caused a reduction in development of selfed seed in covered plants, appreciable differences in mature berry weights in covered plants (means 1.67 and 1.72 g, n = 20), nor differences in seed set among open plants. Berry weights among open-pollinated plants were not compared. Observed increase in seed size among open pollinated Caturra did agree with individual berry weight increases implied by Badilla and Ramírez (1991), Nogueira-Neto and Amaral (1959, data re-analyzed using a 1-tail t-test on average weights of berries per plant), and Raw and Free (1977).

Past neotropical studies suggest honeybees are principal pollinators of coffee. Such findings were arbitrary because *Apis mellifera* had no independent or well established feral populations. This bee entered Panama in 1982 and became established for the first time in the wild (Boreham and Roubik 1987; Roubik and Boreham 1990). In Chiriquí Province, where the local fire department recorded honeybee 'cases' since 1957 feral *Apis* in the highlands also was unprecedented. Before 1967 there was one colony recorded in David, Chiriquí, while between 1977 and 1986 there were 706, virtually all in 1985 and 1986. Yearly data for 1993-1995 show 179 to 268 colonies recorded in the provincial capital (archives of the David, Chiriqui, fire department).

Significantly more bees, both native and African, were present on coffee flowers near forest. In younger plantings this should result in higher fruit production. Yet the highest visitation rate was not correlated with any benefit from open pollination in plots near forest. The oldest Caturra plants were present there, and productivity declines with plant age in coffee (Alvarado and Rojas 1994; Wrigley 1988; Clifford and Wilson 1985). My observations also suggest that sun or shade conditions were unlikely to influence flower choice by bees because exclusion of the sites by forest resulted in no analysis showing different visitation between sun and shade conditions. Bees were thus distributed fairly evenly over plots, despite a total spread of 13 km and the presence of known hives or feral colonies next to some plantings. Honeybee colonies seem to exist throughout the area. Pollen analysis strongly suggests they take the closest forage. Furthermore, visits seemed linked to the presence of nest sites and bee colonies in plot C, where tree removal may have caused

reduced visitation by native bees (Table 1). Another potential cause of diminished fruiting with more bee visits is nectar robbing by *Trigona*, but further studies are necessary (Roubik 1989; see also Nogueira-Neto and Filho 1959). Slower visitation rate of honeybees at Caturra flowers may have been related to a nectar quality higher than that of Catimor. Nectar quality of Caturra was the same found in one of its progenitors, Bourbon, in Brazil (Nogueira-Neto and Filho 1959), thus the conditions studied in Panama could well be applicable to many areas in the neotropics.

In conclusion, while feral African honeybees in the Amazon produced a decline in fruit production in a native leguminous shrub (Roubik 1996), evidence presented here shows this exotic bee sustained and extended a positive pollination impact on a plant from its native environment.

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TABLE 1. Final fruit retention increase on branches of *Coffea arabica* due to open pollination, the observed visitation by native and African bees, and flowering characteristics of 11 study plots in Chiriquí, Panama (plot means). Yields of plots A and B were pooled, from a single planting. For sample sizes, N = branches, n = shrubs. Statistical differences are indicated.

Plot	Mean	Mean		*Apis* and Native Bees	
	Fruit Set	Flowers	(open/bagged), N,n	on shrubs	*Apis* shrub^{-1} bees flower
A	1.20**	77,10	1449	1.98	14, 5
B	1.20**	50	2118	1.97	11,10
C	1.16	20,11	416	0.63	17,1
D	1.03	139,24	327	1.63	66? , 53?
E	1.14*	87,9	1759	1.43	12,14
F	1.56**	72,10	1700	2.07	15,7
G	1.17	26,9	748	0.89	15,7
H	----	33	870	1.36	15,7
I	----	27	977	1.04	15,18
J	0.95	65,9	750	2.27	41,21
Dur	1.17*	101,16	1222	3.73?	42,4

**p < 0.005, t-test, 1-tail
*p < 0.06, t-test, 1-tail
? p < 0.05, Scheffe a-posteriori F test, Model 1 ANOVA, (Table 2)
+ bees per 10,000 flowers, left column *Apis*, right column native bees

TABLE 2. ANOVA (Model 1) of differences among fruit yield in coffee plantings related to bee visitation, sun or shade conditions, numbers of flowers open on study trees, and cultivar. A posteriori comparisons among groups are Scheffe tests at the 95% significance level. All yields are proportional numbers of mature berries from open compared to bagged flowers on individual plants, considering means when multiple branches were used.

Factors Compared	df	F	P	Scheffe F
Plot • yield	7,90	3.2	0.005	plot F: D, J
Cultivar • yield	2,95	4.9	0.01	Caturra age
Plot • Apis/plant	10,686	15.5	0.0001	Duran: all
Plot • Apis/flower	10,686	66.5	0.0001	plot D: all but J
Plot • native bees/flower	10,686	8.0	0.0001	plot D:A,B,E,F,Dur
Sun or shade • yield	1,96	3.84	0.053	
Sun or shade • Apis/flower	1,695	66.5	0.0001	
Sun or shade • Apis/flower*	1,29	1.79	0.19	
Sun or shade • native bees/fl	1,692	38.86	0.0001	
Flowers/plant • sun or shade	1,550	110.15	0.0001	
Flowers/plant • plot	10, 540	23.1	0.0001	

*recorded in plot D only, single day

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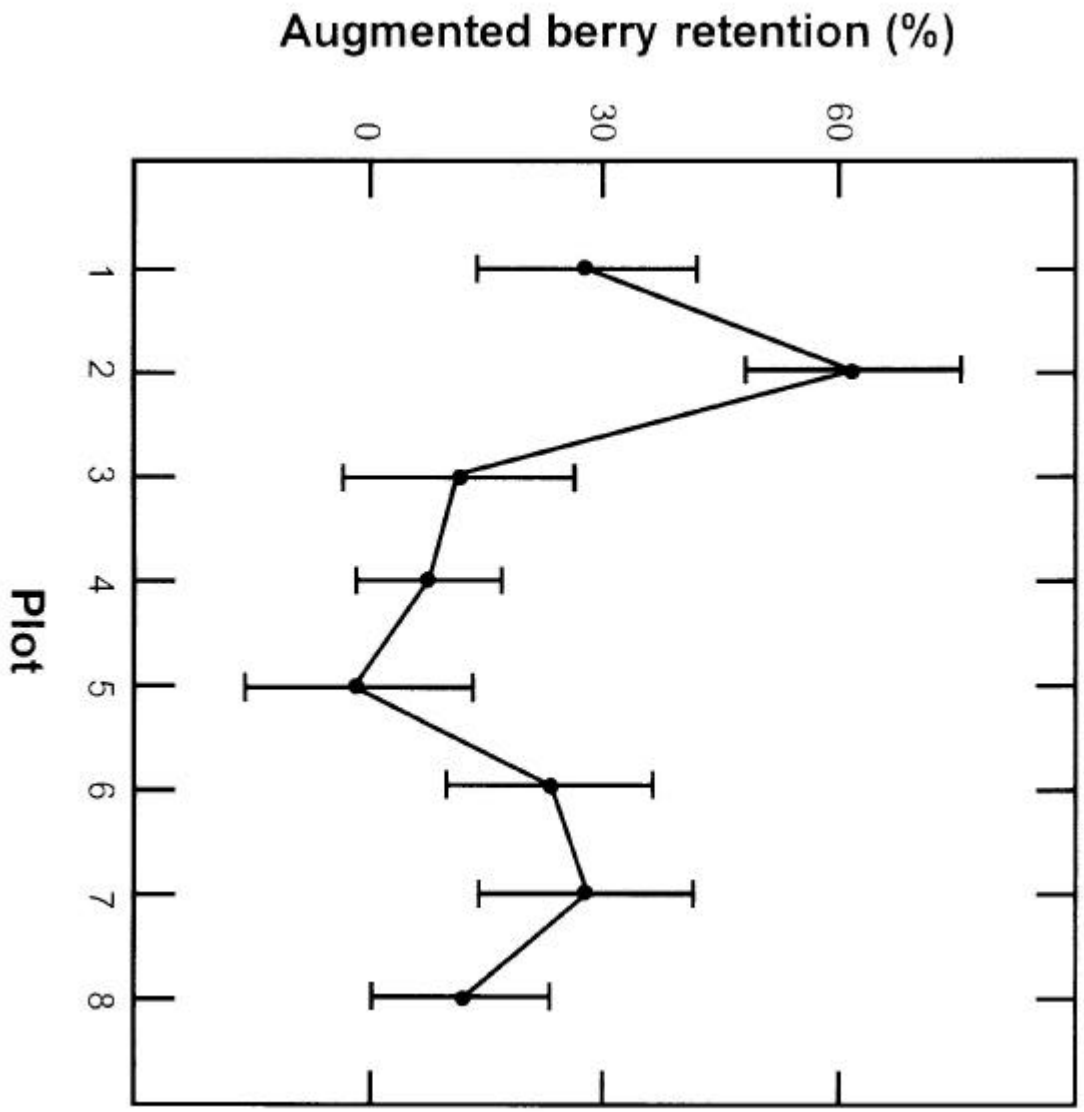

FIGURE 1. Mean augmentation in fruit retention, at maturity, of *Coffea arabica* in response to pollination by feral honeybees, *Apis mellifera scutellata*, and native pollinators in Panama. Bagged and open branches on 97 shrubs were compared (n = 9 to 24 per transect). Plots 4 and 5 included older, Arabigo cultivars (8 to 60 years) with relatively young Caturra; plot 8 was Catimor (2 years old), and the remainder were Caturra (6 to 8 years). Plots 1,2,6 (two adjacent transects combined) and 8 demonstrated statistically increased fruit retention in the open pollination treatments (paired t-test, one-tail, $p < 0.06$).