8. L. C. Drickamer, *Folia Primatol.* **21**, 61 (1974).
9. M. Kawai, *Nihonzaru no Seitai (Ecology of Japanese Monkeys)* (Kawade-shobo Shinsha, Tokyo, 1969), p. 300.
10. T. Tanaka, K. Tokuda, S. Kotera, *Primates* **11**, 113 (1970).
11. G. Teleki, E. E. Hunt, Jr., J. H. Pfifferling, *J. Hum. Evol.* **5**, 559 (1976).
12. C. B. Clark, in *Primate Bio-Social Development: Biological, Social and Ecological Determinants*, S. Chevalier-Skolnikoff and F. Poirier, Eds. (Garland, New York, 1977), p. 235.
13. J. Altmann, in *Ontogeny of Behavior*, G. Burghardt and M. Bekoff, Eds. (Garland, New York, 1978).
14. See for example the following, S. B. Hrdy, *Folia Primatol.* **22**, 19 (1974); S. M. Mohnot, *Mammalia* **35**, 175 (1971); M. B. Parthasarathy and H. Rahaman, in *Congr. 5th Int. Primatol. Soc., Nagoya* (1974), abstracts, p. 128; R. Rudran, *Folia Primatol.* **19**, 166 (1973); Y. Sugiyama, *Primates* **5**, 7 (1964); in *Social Communication Among Primates*, S. Altmann, Ed. (Univ. of Chicago Press, Chicago, 1967), p. 221.
15. W. Angst and D. Thommen. *Folia Primatol.* **27**, 198 (1977).
16. M. Chapman and G. Hausfater, in preparation.
17. This research was supported by PHS grant MH 19617 and NSF grant BNS-76-06259. We gratefully acknowledge the cooperation of the government of Kenya and especially that of Joseph Kioko, warden of Amboseli National Park.

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# Competitive Interactions Between Neotropical Pollinators and Africanized Honey Bees

Abstract. *The Africanized honey bee, a hybrid of European and African honey bees, is thought to displace native pollinators. After experimental introduction of Africanized honey bee hives near flowers, stingless bees became less abundant or harvested less resource as visitation by Africanized honey bees increased. Shifts in resource use caused by colonizing Africanized honey bees may lead to population decline of Neotropical pollinators.*

If two species compete for a resource, it must be limiting in such a way that an increase in resource harvest by one species corresponds to diminished harvest by the other. Competition also occurs if resource harvest remains stable but harvest cost increases. The evidence of interspecies competition for food is usually circumstantial, and, despite extensive treatment of the subject, few field studies clearly demonstrate its importance (*1*). The Old World honey bee *Apis mellifera* is thought to displace native pollinators from both floral resources and geographic areas (*2*). During a study of competition between Africanized honey bees (feral hybrids of African and European *A. mellifera*) and native pollinators, I manipulated the number of Africanized honey bees foraging on certain flowering plants in French Guiana, South America. The experiments demonstrated that Africanized honey bees sometimes compete with native bees by diminishing their foraging success at flowers. Previous studies on the impact of introduced *A. mellifera* on the foraging activity of indigenous pollinators have not been made (*3*).

My study was conducted along a forest-savanna transition zone near Kourou, French Guiana, between November 1976 and June 1977. Introduced European honey bees were rare in French Guiana, and Africanized honey bees arrived in 1974 (*4*). The density of Africanized honey bee colonies was quite low at the time of the experiments. Feral Africanized honey bee swarms were captured and transferred to hives; each contained 6,000 to 15,000 bees when used in the experiments (*5*).

Hives of Africanized honey bees were introduced and later removed near patches of flowering plants visited by Africanized honey bees as well as stingless and other bees, wasps, and flies (Table 1). During periods when Africanized honey bee hives were present and absent, numbers of floral visitors were recorded in plots of *Mimosa pudica* (Fabaceae), *Melochia villosa* (Sterculiaceae), *Rhynchospora globosa* (Cyperaceae), and *Borreria* species (Rubiaceae) (*6*). I used different sizes and numbers of plots within patches of each plant species, and this permitted sufficiently large but accurate counts of foragers on flowers differing in spatial distribution (*6*). Foraging bees collected only pollen from *Rhynchospora* and *Mimosa*, but collected both nectar and pollen from the other flowers. Africanized honey bees from feral colonies foraged on all flowers except *Rhynchospora* when the experiments began, but had been in the area less than 2 years.

I began to take a census of foragers in the morning as flowers opened or first presented pollen and nectar. Bees depleted *Rhynchospora* and *Mimosa* pollen by midmorning, and few bees collected pollen on *Melochia* and *Borreria* after this time. However, the *Borreria* continued providing nectar and were visited in the early afternoon. During each day, forager counts were made at regular intervals for 80 to 180 minutes. Thus, five to ten separate counts were obtained on a daily basis of foragers in each plot within a larger patch of each plant species. Plots of *Mimosa* varied greatly in floral density over time, and flower counts in each were made daily. Floral densities remained stable in other species patches. Estimated mean total flowers in combined plots ranged from 843 in *Mimosa* to 27,000 in *Borreria*.

Additional measurements of pollen harvest were taken for stingless bees visiting *Mimosa* and Africanized honey bees foraging on *Rhynchospora*. I hypothesized that duration of floral visits varied with pollen abundance on *Mimosa* and measured the time spent visiting five flowers for 50 bees of the *Melipona* species with Africanized honey bees present and absent. Measurements were made during the first hour of foraging on 16 days when Africanized honey bees foraged and 4 days during their absence. Pollen harvest by two Africanized honey bee colonies visiting *Rhynchospora* was quantified by counting the number of foragers returning to each with pollen of this species for two 1-minute periods every 20 minutes.

Stingless bees became less abundant when Africanized honey bees increased in numbers on *Melochia villosa* (Table 1 and Fig. 1). Removal of Africanized honey bee hives led to reversal in abundance trends among Africanized and stingless bees ($P < .05$ in a nested analysis of variance; nested groups were comprised of days when Africanized honey bee hives were present or absent). The mean daily number of foraging Africanized honey bees dropped from 111.3 to 72.0 and that of stingless bees increased from 23.3 to 61.0 after Africanized honey bee removal. Figure 1 illustrates the relationship between Africanized and stingless bee abundance on *Melochia* (*7*). At low densities of each forager class, usually occurring at the first observations made at recently opened flowers, there was no negative numerical interaction. But at high densities of Africanized honey bees, their numbers increased as stingless bees became less abundant.

Africanized honey bee numbers changed significantly on *Rhynchospora* and *Mimosa* during the experiments (Table 1), but no significant change in numbers occurred within patches of *Borreria*, and competitive effects could not be assessed at this resource. The daily mean number of bees returning to Africanized honey bee hives with *Rhynchospora* pollen was 5187 ± 423 (S.D.). These were the only Africanized honey bees foraging on *Rhynchospora*, and their removal should have affected pollen availability, but no significant regres-

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sion was obtained between their numbers and those of *T. clavipes* on this resource. Native bees maintained stable densities on *Rhynchospora* and *Mimosa* (Table 1). However, mean duration of floral visits on *Mimosa* by *Melipona favosa favosa* increased from 29.35 to 40.16 seconds ($P < .001$, *t*-test) and that of *M. fulva* from 18.86 to 23.08 seconds ($P < .01$, *t*-test) when Africanized honey bees were removed (*8*). Since a decrease in the mean number of Africanized honey bees from 9.6 per 100 flowers to 0.0 corresponded to increased visitation time per flower among *Melipona*, it appears that the bees responded to increased pollen abundance in this manner, but not by recruiting more foragers. A linear relation was found between Africanized honey bee and *Melipona* abundance on *Mimosa*, suggesting that Africanized honey bees did not reach densities sufficient to depress the number of *Melipona*.

Africanized honey bees and stingless bees (Meliponinae) recruit nest mates to resources if foraging is profitable, and the extent of this response will vary according to bee species and resource type (*3*). Thus, stingless bees foraging on *Rhynchospora* and *Melochia* did not respond similarly to changes in Africanized honey bee abundance, in part because of their different recruitment systems or differing responses to pollen or nectar rewards. Similarly, *Melipona* foraging on *Mimosa* did not encounter sufficient increase in pollen abundance to respond by recruiting more nest mates. Increasing the abundance of pollen by removing Africanized honey bees did not lead to increased recruitment by stingless bees, but probably prolonged foraging by individuals. Since my observations of foragers on flowers were of fixed duration, extension of the pollen collection period after removal of Africanized honey bee hives would have gone undetected. Information revealing competition for pollen was lost since measurement of total colony resource harvest by stingless bees could not be included.

Reciprocal shifts in resource use do not always imply competition, but, when induced experimentally, these prove that resources are limiting and, hence, that competition occurs. At the population level, competition may not be statistically evident (for example, by change in population growth rate or size) unless extensive. However, increased time and energy expended searching for new resources, or continuing use of the same resource at increased cost, must influence individual expenditure for other activities. The time and energy available to an organism are finite, and all activities are linked in this sense (*9*). Local reduction in resource availability must in some way affect survival, growth, or reproduction. To maintain that adjustment to the presence or activity of an introduced competitor is accomplished without cost seems unrealistic. Furthermore, extensive and sustained competition between Africanized and stingless bees is likely since they are generalists and overlap greatly in time and place of foraging (*10*). Competitive superiority is a necessary attribute of a species able to establish residence in a saturated community (*11*) and, at floral resources, is likely to be of major importance to colonizing Africanized honey bees. Nevertheless, Africanized honey bees did not attain numbers on *Mimosa* large enough to depress the abundance of foraging *Melipona*. In this instance, either pollen was not greatly attractive, or *Melipona* depleted available pollen to levels at which Africanized honey bees could not forage profitably.

Foraging on *Melochia* became less profitable for stingless bees when Africanized honey bees were most numerous, but the specific causes are not clear. It is not known whether stingless bees switched to other resources or whether they ceased to forage during this period. However, it would be maladaptive for

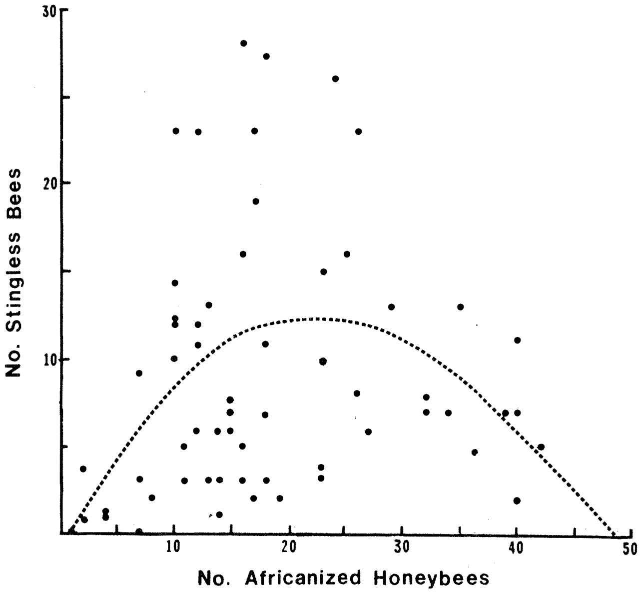

Fig. 1. The relations of Africanized and stingless (meliponine) bee abundances on flowering *Melochia villosa*. The dashed line is a quadratic polynomial (given by $y = -0.516 + 1.08x - 0.023x^2$) which gave the best fit to the points (*7*).

Table 1. *F* ratios for mean daily forager number during the presence of and after removal of Africanized honey bee hives. A nested two-level analysis of variance of forager numbers was performed for three forager classes. Nested groups of days were compared in which introduced hives of Africanized honey bees were present or absent. Subgroups within each group were censusing times. Degrees of freedom are *Mimosa* (1,12), *Rhynchospora* (1,18), *Melochia* (1,8), and *Borreria* (1,12).

| Forager class | Floral resource | | | |
|---|---|---|---|---|
| | *Mimosa** | *Rhynchospora* | *Melochia* | *Borreria* |
| Africanized honey bees | | | | |
| During | 9.6 | 81.5 | 111.3 | 371.0 |
| After | 0.0 | 7.5 | 72.0 | 365.0 |
| *F* ratio | 25.78† | 27.89† | 8.11‡ | 0.05 |
| Stingless bees§ | | | | |
| During | 25.3‖<br>32.0¶ | 65.6 | 23.3 | 124.5 |
| After | 19.1‖<br>44.5¶ | 100.0 | 61.0 | 189.5 |
| *F* ratio | 2.10‖<br>2.26¶ | 1.08 | 6.80‡ | 14.5† |
| Other native foragers | | | | |
| During | Not present | Not present | 51.8 | 22.5 |
| After | | | 60.1 | 59.0 |
| *F* ratio | | | 2.32 | 11.89† |

*Bees per 100 flowers. †$P < .001$. ‡$P < .05$. §*Mimosa: Melipona fulva* and *M. favosa favosa; Rhynchospora: Trigona (Tetragonal) clavipes; Melochia: M. fulva* and *T. (Trigona) cilipes; Borreria: M. fulva, M. favosa favosa*, and *T. (Trigona) cilipes*. ‖*Melipona fulva*. ¶*Melipona favosa favosa*.

foragers to ignore a resource where they had previously obtained a reward. To explain the results, I postulate that stingless bees abandoned the study plots. During the 75 hours in which Africanized honey bees were observed, I saw no aggression by the bees. Africanized honey bees also fail to exhibit interspecific aggression at artificial nectar feeders (*10*). If Africanized honey bees interfered with stingless bees, this was incidental to their foraging or involved a subtle chemical interaction.

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### References and Notes

1. H. G. Andrewartha and L. C. Birch, *The Distribution and Abundance of Animals* (Univ. of Chicago Press, Chicago, 1954); J. H. Connell, in *Ecology and Evolution of Communities*, M. L. Cody and J. Diamond, Eds. (Belknap, Cambridge, Mass., 1975); J. A. Wiens, *Amer. Sci.* **65**, 590 (1977).
2. Displacement of meliponines by European *A. mellifera* is mentioned by H. L. Schwarz [*Bull. Am. Mus. Nat. Hist.* **90** (1948)]. Displacement of wasp pollinators by Africanized honey bees has been inferred [G. T. Prance, *Biotropica* **8**, 235 (1976)]. *Apis mellifera* was thought to displace native *A. cerana* in Japan [S. F. Sakagami, *J. Anim. Ecol.* **28**, 51 (1959)].
3. C. D. Michener. *The Social Behavior of the Bees* (Belknap, Cambridge, Mass., 1974).
4. O. R. Taylor, *Bee World*. **58**, 19 (1977).
5. Hives measured 42 by 22 by 24 cm and contained up to 38,000 cells on six combs.
6. The number of days introduced Africanized honey bee hives were present of the total days each resource was censused were 22/27, *Mimosa*; 6/12, *Melochia*; 2/4, *Borreria*; and 3/6, *Rhynchospora*. Two colonies of Africanized honey bees were introduced near *Rhynchospora*, five near *Borreria*, two at first and then four in separate 3-day periods near *Melochia*, and ten hives were introduced near *Mimosa*. Hives were positioned in shaded areas adjacent to flowers and were well separated. Four large plots of *Borreria* and *Rhynchospora* were sampled, totaling 179 $m^2$ and 485 $m^2$, respectively; 10 plots totaling 73 $m^2$ were used for *Melochia*, and 12 plots totaling 9 $m^2$ were used for *Mimosa*.
7. Regression analysis was performed with the Honeywell 6660 computer and the Biomedical Sciences (BMDP) polynomial regression package at the University of Kansas. The program compared linear and curvilinear regression lines for goodness of fit. The $F$ ratio for reduction of residual error by the parabola fitted to *Melochia* data was significant at $P < .001$, but by a chi-square test, an insignificant amount of the variance in the $y$-variable was explained ($P < .005$).
8. A $t$-test comparison of means with unequal variances was used [R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969)].
9. S. C. Stearns, *Annu. Rev. Ecol. Syst.* **8**, 145 (1977); T. W. Snell and C. E. King, *Evolution* **31**, 882 (1977).
10. D. W. Roubik, in preparation.
11. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
12. I thank R. Jander, C. Michener, G. Eickwort, O. Taylor, N. Slade, G. Schlager, G. Gamboa, and M. Gaines for their comments. Supported by U.S. Department of Agriculture grant 12-14-7001-363 (O. Taylor, principal investigator) and NSF predoctoral grant DEB 76-22386.

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## Opiate Effects After Adrenocorticotropin or $\beta$-Endorphin Injection in the Periaqueductal Gray Matter of Rats

Abstract. *Injections of adrenocorticotropic hormone (ACTH) into the periaqueductal gray matter of drug-naive rats resulted in a dose-dependent opiate abstinence syndrome characterized by fearful hyperreactivity and explosive motor behavior. Injecting shorter chains of ACTH caused attenuated forms of this behavior. Injections of $\beta$-endorphin at this same site caused opposite behavior: sedative, analgesic, and catatonic. If the effects of morphine are mediated by two classes of receptor) and the other which is not stereospecific and naloxone-insensitive—the endogtor)—and the other which is not stereospecific and naloxone-insensitive the endogenous ligand of the second receptor may be ACTH. The neuropeptides ACTH and endorphin may be part of an integrated neuromodulatory system, and the opiate abstinence syndrome may be the result of an altered interaction between the two receptor systems.*

We have previously reported (*1*) that morphine effects in the central nervous system (CNS) appeared to be mediated by two classes of receptors: an endorphin receptor that was naloxone-sensitive, showed stereospecific affinity for opiates, and mediated the analgesic, catatonic effects of morphine; and a second receptor that was naloxone-insensitive, showed nonstereospecific affinity for opiates, and mediated the hyperexcitability [explosive motor behavior (EMB)] induced by morphine. We hypothesized that animals given morphine systemically did not normally manifest EMB because of a masking inhibitory action exerted by the endorphin receptor, which was simultaneously activated by morphine. Furthermore, since the morphine abstinence syndrome is similar or identical to the behavioral syndrome of EMB, we suggested that opiate abstinence symptoms might be due to morphine exciting the second receptor when naloxone blockade of the endorphin receptor ended the inhibitory action. However, the endogenous ligand for the second receptor was not known.

We now report that injections of the endogenously occurring peptide adrenocorticotropic hormone (ACTH) in the periaqueductal gray matter (PAG) of opiate-naive rats result in behavior similar to the opiate abstinence syndrome. We suggest that the mechanism underlying opiate abstinence behavior may consist of the stimulation by morphine of an ACTH receptor after removal (by naloxone blockade) or weakening (by tolerance development) of the inhibitory action of the endorphin receptor. This implies that the multiple pharmacological effects of opiates are dissociable and mediated by separate receptors; that is, narcotic analgesia is mediated by the endorphin receptor, and narcotic dependence by the ACTH receptor.

Adult male Wistar rats, weighing approximately 300 to 350 g, were each surgically implanted with bilateral intracerebral cannulas aimed at PAG sites (*2*). The guide cannulas were made of 30-gauge stainless steel tubing (outer diameter = 0.30 mm); the tips were aimed at sites just lateral to the aqueduct: 1 mm anterior to lambda, 0.75 mm lateral to the midline, and 4 mm below the level of the skull surface (we used horizontal head position, with bregma and lambda at the same horizontal plane). Injection needles were prepared from 35-gauge stainless steel tubing (outer diameter = 0.13 mm) and calibrated to extend precisely 2 mm beyond the tip of the guide cannula. From 5 to 7 days elapsed before any testing was conducted. Placement of cannulas was subsequently histologically verified in all animals.

Injection of ACTH(1–24) in the PAG resulted in all nine animals becoming hyperreactive to previously neutral auditory and visual stimuli and making 60-cm-high leaps in repeated attempts to escape from the plastic bin. (Normal rats are incapable of such high leaps.) Other signs of excitation such as tachycardia, tachypnea, and hyperthermia were also observed. Onset of jumping occurred approximately 10 minutes after the injection and lasted approximately 30 minutes; after this time other signs were observed, such as wet-dog shakes, teeth chatter, ear blanching, abnormal posture, squeal on touch, scratching, grooming, and exploration (rearing on hind legs) (*3*). These behaviors have been termed recessive signs and are suppressed during the period of occurrence of dominant signs such as jumping (*4*). Injections into the PAG of lower doses of ACTH(1–24) or of shorter chains of the peptide, such as melanocyte-stimulating hormone ($\alpha$-MSH), which coincides with ACTH(1–13), and ACTH/MSH(4–10) resulted in an immediate onset of recessive signs lasting approximately 20 minutes, but never in the dominant sign of jumping. These results (Table 1) suggest that the longer chain ACTH(1–24) resulted in fuller expression of the abstinence syn-

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