

- (Tropical Fish Hobbyist, Neptune City, N.J., in press).
7. Personal communications: P. L. Colin on western Atlantic species, M. Schmale on western Atlantic Pomacentrinae, W. Douglas on western Pacific Apogonidae, B. C. Russell and B. Carlson on western Pacific Blenniidae, and J. Moyer on western Pacific Pomacanthidae.
 8. Eggs were collected from nests of 19 pomacentrins and five blenniids, and from males of two species of apogonids. A binocular microscope and a ruled ocular were used to measure live eggs. The same procedure was used by the investigators listed in (5).
 9. Because there are statistically significant differences in the egg size of pomacentrid subfamilies (R. E. Thresher, in preparation), analysis was limited to the Pomacentrinae, the only subfamily for which good comparative data are available. All other comparisons are at the family level.
 10. Komolgorov-Smirnoff test for unequal sample sizes.
 11. A. J. Southward and N. Demir, in *The Early Life History of Fish*, J. H. S. Blaxter, Ed. (Springer-Verlag, New York, 1974), pp. 53-68.
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 14. Average maximum adult sizes reported are as follows: (i) Pomacentrinae, $\bar{X}$ = 11.8 cm standard length (S.L.), variance = 14.8 in the western Atlantic, and $\bar{X}$ = 9.2 cm S.L., variance = 10.3 in the western Pacific ($P > .10$, Mann-Whitney U test); (ii) Apogonidae, $\bar{X}$ = 7.6 cm S.L., variance = 14.5 in the western Atlantic and $\bar{X}$ = 12.0 cm S.L., variance = 14.8 in the western Pacific ($P > .25$); and (iii) Blenniidae, $\bar{X}$ = 10.9 cm S.L., variance = 0.4 in the western Atlantic and $\bar{X}$ = 9.4 cm S.L., variance = 7.0 in the western Pacific ($P > .25$).
 15. The correlations between egg volume and adult size were statistically significant for both pelagic spawning families (Pomacanthidae, $r = .84$, $N = 10$; Acanthuridae, $r = .66$, $N = 5$) but not for demersal spawning families, on the basis of data for Pacific species only to avoid confounding interoceanic effects (Pomacentridae, $r = .11$, $N = 19$; Apogonidae, $r = .35$, $N = 6$; and Blenniidae, $r = .14$, $N = 13$).
 16. No data are available on annual or seasonal variations in egg volume for any reef-associated species, but seasonal variation, at least, appears to be minimal.
 17. R. E. Thresher, personal observations.
 18. G. Svardson, *Rep. Inst. Freshwater Res. Drottningholm* 29, 115 (1949); G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966), pp. 158-192; C. C. Smith and S. D. Fretwell, *Am. Nat.* 108, 499 (1974).
 19. R. E. Johannes (13) and P. F. Sale (3) both emphasize that coral-reef fishes are apparently under strong selection to maximize fecundity.
 20. For the Pomacentrinae, the only group for which such data are available, the mean size of smallest individuals for seven Atlantic species, recorded by A. R. Emery [*Bull. Mar. Sci.* 23, 649 (1973)], is 10.9 mm S.L. with a variance of 3.05 mm; the mean size at settlement for the only three western Pacific species for which data are available is 10.0 mm S.L. with a variance of 0.65 [R. E. Thresher, personal observations and references in (6)].
 21. D. H. Cushing, *J. Mar. Biol. Assoc. U.K.* 47, 193 (1967); T. B. Bagenal, *J. Fish Biol.* 3, 207 (1971).
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 23. The correlation between water column productivity and egg volume in reef fishes can be independently tested by measuring egg volumes in other areas of high plankton productivity, such as the Red Sea.
 24. J. M. Leis and J. M. Miller [*Mar. Biol.* 36, 359 (1976)] report that larvae of pelagic spawning and demersal spawning families at Hawaii are typically found in different planktonic environments. If a general rule, this difference might bear on the possibly different effects of plankton productivity on the two groups.
 25. R. E. Thresher, in preparation.
 26. The relation is probably a loose one, especially when one considers the probable complexity of interactions in the plankton and stochastic processes associated with larval survival and recruitment onto the reef.
 27. Studies on the dynamics of reef-fish communities emphasize the Pomacentrinae, benthic territorial damselfishes, as key species. This emphasis may, in fact, be maximizing differences be-

tween western Atlantic and western Pacific communities.

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Colony Defense by Africanized and European Honey Bees

Abstract. *Africanized and European honey bee (Apis mellifera) populations showed quantitative differences in colony defensive behavior. Africanized bees responded faster and in much larger numbers than European honey bees and produced 8.2 and 5.9 times as many stings during two different experiments. Times to react to alarming stimuli were negatively correlated with the number of bees responding and to the total number of stings. The number of bees responding was significantly correlated to the total number of stings only for the Africanized population.*

By 1990 (1), American agriculture may have to deal with the immigration of the Africanized bee, an insect with the potential to alter agricultural practices and significantly increase the cost of bee-pollinated food products. Honey bees (*Apis mellifera*) are not native to the Western Hemisphere, but were introduced to the Americas through importations of European stocks (*A. m. mellifera* and *A. m. ligustica*) since 1621 (2). In 1956, a variety from Africa, *A. m. scutellata* (formerly *adansonii*) (3) was introduced into Brazil for the purpose of improving honey production with a more

tropically adapted bee (4). The variety of honey bee resulting from the interbreeding of the established European and newly imported African types, referred to as the Africanized bee, has spread through much of South America and into Panama.

The Africanized bee has received considerable coverage in the popular press, from early stories about hoards of bees stinging victims to death and the subsequent "killer bee" label to more recent reports from Brazil that the bees are no longer a problem. The tendency to sting readily is the most objectionable charac-

Table 1. Correlations between defensive behavior measures in European (E) and Africanized (A) honey bees. Data are from experiment 1 only. Pre, before testing.

Item	Time to react to		Number of bees in picture at				Total number of stings
	Pheromone	Targets	Pre	30 sec-onds	60 sec-onds	90 sec-onds	
Time to react to Pheromone							
E	1.00	.01	-.15*	-.30†	-.29†	-.28†	.02
A	1.00	.29†	-.16†	-.41†	-.42†	-.32†	-.30†
Targets							
E		1.00	-.09	-.09	-.17†	-.16†	-.38†
A		1.00	-.09	-.15†	-.16†	-.08	-.18†
Number of bees in picture							
Pre							
E			1.00	.55†	.53†	.45†	.02
A			1.00	.76†	.66†	.53†	.13*
30 seconds							
E				1.00	.93†	.80†	.04
A				1.00	.94†	.76†	.31†
60 seconds							
E					1.00	.90†	.10
A					1.00	.83†	.31†
90 seconds							
E						1.00	.19†
A						1.00	.27†
Total number of stings							
E							1.00
A							1.00

Significant at * $P < .05$, † $P < .01$.

teristic of Africanized bees, one that is shared by the parental *A. m. scutellata* in South Africa (5). However, scientific data on stinging behavior of Africanized bees is limited (6–9), and there are none dealing with the stinging behavior of Africanized bees from the population in northern South America which is spreading toward the United States.

Stinging is only one possible final behavior in a sequence of acts by a honey bee that are collectively called defensive behavior (10). As part of our assessment of the potential impact of the Africanized bee on the American beekeeping industry, we quantified differences in defensive behavior, especially stinging, between European and Africanized honey bee populations.

Experiment 1 involved 150 large colonies in Baton Rouge, Louisiana, and 147 similar-sized colonies in Monagas, Venezuela. The Louisiana colonies had been established from various U.S. commercial honey bee stocks. The Venezuelan colonies had once contained European bees but were chosen on the basis that they had been allowed to breed freely for at least the past year with the feral Africanized bees which had been in the area for at least 2 years. All the hive entrances were made uniform (14 by 1.5 cm), and any additional openings were screened shut.

For experiment 2, 15 colonies of Africanized bees and 15 colonies of European bees were used. The colonies were equalized so that each consisted of 900 g of bees on three (43 by 20 cm) combs in new 20-liter hives, with entrances 3 cm in diameter. These colonies were established at a single location near Maturin, Monagas, Venezuela.

Each colony was tested twice in a standard, 90-second test sequence (11). Observations of defensive behavior were quantified in three ways. (i) The number of bees at the colony entrance was counted from photographs taken at 30-second intervals during the test. (ii) Two time measurements were made: the length of time until bees began to emerge after alarm pheromone was sprayed above the entrance, and the length of time it took the first bee to orient to and land on a moving target in front of the colony. (iii) The number of stings in the suede leather targets was counted.

An important consideration in evaluating colony defensive behavior is the temperature and relative humidity at the time of testing (4, 12, 13). The conditions during measurement of the Louisiana population (temperature, 25° to 36°C; relative humidity, 61 to 97 percent) were very similar to those in Venezuela (tem-

perature, 26° to 35°C; relative humidity, 61 to 92 percent). In experiment 2, bees were tested at one location and thus were in similar environments.

Means $\pm$ standard error (S.E.) for the seven measures of defensive behavior are shown in Fig. 1. Differences were determined by a one-way analysis of variance on log-transformed data. In both experiments, the Africanized bees responded more quickly to both pheromone and targets. In most instances during experiment 1, the responses of Africanized bees to the targets were immediate, and occasionally the targets were stung before they were placed at the entrance. This was in marked contrast to the European colonies where many bees continued to forage and did not respond at all.

In experiment 1, the Africanized colonies had significantly greater numbers of bees at the entrance at all times than the European colonies had. However, the numbers reported for the Africanized bees at the entrance were often underestimates of the numbers of bees respond-

ing, because immediately after the pheromone spraying many of these bees became airborne. In contrast, the European bees usually remained near the entrance until the targets provided a stimulus for orientation and attack.

The small colonies in experiment 2 had very few bees at the entrance at any time. The Africanized bees that did respond tended to fly away from the entrance, especially in the presence of a moving target, and thus were not included in the picture counts. These two conditions could explain the lack of a significant difference between the two populations for the preliminary (pre) and 90-second counts.

The total number of stings recorded from the large Africanized colonies of experiment 1 averaged 8.2 times greater than that recorded from European colonies and from the smaller colonies of experiment 2, averaged 5.9 times greater. However, the total number of stings produced by the Africanized bees in experiment 1 was probably an underestimation, especially for the most respon-

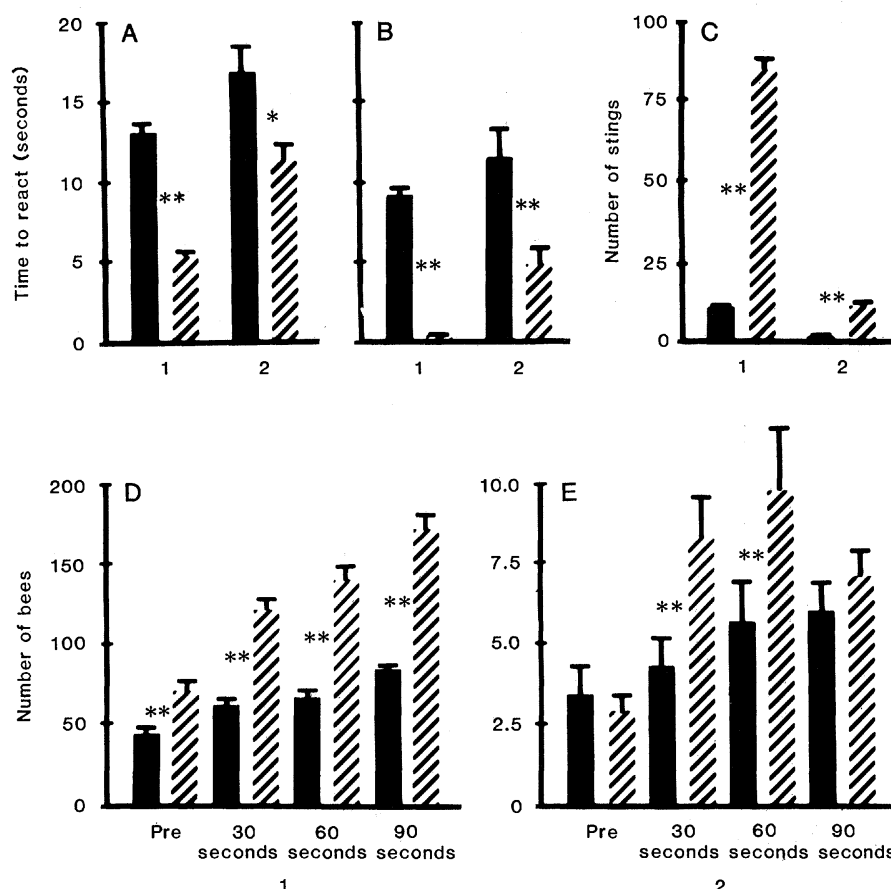


Fig. 1. Colony defensive behavior by European (solid bars) and Africanized (hatched bars) honey bees as measured by a standard test sequence during experiments 1 and 2. Values are means $\pm$ S.E. with paired means significantly different at * $P < .05$ and ** $P < .01$. Time to react was measured in response to (A) artificial alarm pheromone and (B) moving suede targets. (C) The number of stings in targets after 30 seconds. (D and E) The number of bees in a photograph of the colony taken before testing (Pre), and after 30, 60, and 90 seconds during experiment 1 (D) and experiment 2 (E). For experiment 1, 300 European colonies and 294 Africanized colonies were tested. In experiment 2, there were 30 colonies in each group.

sive colonies, because the targets were completely covered by bees within a few seconds of being presented. Since the bees remained on the targets (biting and stinging), other bees could not reach the surface with their stings.

Correlations between measures of all traits are presented in Table 1. Among the significant correlations, times to react were negatively correlated with numbers of bees and stings and positively correlated with each other, as would be expected. Bee counts and stings were positively correlated. A few correlations were not significant in one population, but significant for the other. The most notable differences were nonsignificant correlations in the European population between time to react to pheromone and either time to react to target or total number of stings, and between number of bees in pre, 30-second, and 60-second pictures and the total number of stings. These correlations were significant for the Africanized population. This difference reflects a greater proportion of Africanized bees participating in colony defense, as compared with European bees.

Other differences apparent in the responses showed by the two populations were not quantified in the test. The most obvious of these was the propensity for the Africanized bees to come out of the colony and fly. There were many more bees in the air and harassing the experimenters during tests of these colonies than during tests of the European colonies. In addition, Africanized bees at the entrance frequently attacked other bees—a behavior not exhibited by the European bees.

The number of stings in a leather ball was measured on colonies of bees in Brazil under temperature conditions (24° to 32°C) similar to those of our study (12). With adjustments for different target sizes, Africanized bees in northern and southern Brazil stung at rates of 0.32 and 0.26 stings per square centimeter in 30 seconds, respectively, whereas the Venezuelan population we studied averaged 0.85 stings per square centimeter in 30 seconds. This refutes the idea that the migrating bees have become milder through hybridization with "native" bees.

The measures of defensive behavior made during our studies indicate that the Africanized bee as it currently exists in Venezuela is significantly different from its European counterpart in the United States. The Africanized bees respond to colony disturbance more quickly, in greater numbers, and with more stinging. The impact of such a bee on the U.S.

beekeeping industry and agriculture would be considerable. Public response to the possibility of severe stinging and death would cause many beekeepers to give up beekeeping or reduce their colony holdings. The resulting reduction in honey production, and the loss of the major insect pollinator of many crops, would constitute a major expense for American agriculture.

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14. We thank R. Gomez and the Venezuelan Ministerio de Agricultura y Cria for laboratory and living quarters and equipment, and O. Taylor, University of Kansas, D. Pulido, Universidade de Oriente, and several Venezuelan beekeepers for access to Africanized colonies. In cooperation with the Louisiana Agricultural Experiment Station.

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Occlusal Variation Related to Soft Diet in a Nonhuman Primate

Abstract. Among 43 squirrel monkeys (*Saimiri sciureus*) raised either on naturally tough or on artificially soft foods, there are significant differences in occlusal features. Animals raised on soft foods show more rotated and displaced teeth, crowded premolars, and absolutely and relatively narrower dental arches. Dietary consistency may be a determinant of occlusal health.

The dental profession lacks consensus on reasons for the high prevalence of malocclusion in Western society (1). The condition is usually considered genetic (2, 3). Among suggested environmental correlates, an infrequently acknowledged idea is that forceful chewing stim-

ulates jaw growth—ensuring large arch space in relation to tooth size, thus preventing crowding—and guides proper eruption of permanent teeth and coordinated oral-facial growth. Studies of non-Western peoples (4) support this explanation: a sudden increase in occlusal

Table 1. Arch measurements of squirrel monkeys raised on natural hard diets ($N = 24$) and those raised on soft diets ($N = 19$). Values represent the mean $\pm$ standard deviation. Variance was homogeneous for all variables.

Variable	Measurement (mm)	
	Hard diet	Soft diet
Maxillary length to M ¹	17.27 $\pm$ 0.83	17.49 $\pm$ 0.62
Maxillary length to C ¹	9.76* $\pm$ 0.77	9.00 $\pm$ 0.76
Maxillary breadth at M ¹	18.33* $\pm$ 0.83	17.57 $\pm$ 0.75
Maxillary breadth at P ³	17.12* $\pm$ 0.89	15.54 $\pm$ 0.65
Mandibular length to M ₁	15.85 $\pm$ 0.87	15.51 $\pm$ 0.69
Mandibular breadth at M ₁	14.38* $\pm$ 0.65	13.56 $\pm$ 0.58
Palate height	3.99* $\pm$ 0.38	3.44 $\pm$ 0.28
Maxillary (M ¹) breadth/length ratio	1.056* $\pm$ 0.037	1.005 $\pm$ 0.045
Mandibular breadth/length ratio	0.908* $\pm$ 0.034	0.875 $\pm$ 0.028

*Mean significantly larger at $P = .01$.