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.

ANITA M. COLLINS
THOMAS E. RINDERER
JOHN R. HARBO
ALAN B. BOLTEN*

United States Department of Agriculture, Agricultural Research Service, Bee Breeding and Stock Center Laboratory,
Baton Rouge, Louisiana 70808

References and Notes

1. O. R. Taylor, *Bee World* **58**, 19 (1977).
2. E. Oertel, *Proc. La. Acad. Sci.* **9**, 71 (1945).
3. F. Ruttner, *Proceedings of the 25th International Congress on Apiculture* (1975), p. 325.
4. C. D. Michener, *Annu. Rev. Entomol.* **20**, 399 (1975).
5. D. J. C. Fletcher, *ibid.* **23**, 151 (1978).
6. C. D. Michener, chairman, *Report of the Committee on the African Honey Bee* (National Technical Information Service, Springfield, Va., 1972), pp. 8–92.
7. G. W. Consenja, *Rev. Brasil. Entomol.* **16**, 13 (1972).
8. L. S. Gonçalves, W. E. Kerr, J. Chaud Netto, A. C. Stort, *Congr. Brasil. Apic.* **2**, 211 (1973).
9. A. C. Stort, *J. Apic. Res.* **13**, 33 (1974).
10. A. M. Collins, T. E. Rinderer, K. W. Tucker, H. A. Sylvester, J. J. Lackett, *ibid.* **19**, 224 (1980).
11. A. M. Collins and K. J. Kubasek, *Ann. Entomol. Soc. Am.* **4**, 355 (1982). A picture of the bees around the entrance was taken before testing. Timing of the test began when 0.8 ml of an artificial alarm pheromone (isopentyl acetate in paraffin oil 1:100 by volume) was sprayed over the entrance. At 30 seconds, the second photograph was made, and the colony was given a physical jolt by shooting it with a glass marble (1.9 g, 2.3 cm in diameter) propelled by a slingshot. The third photograph was taken at 60 seconds, and the suede targets were moved into place, one 2 to 6 cm in front of the entrance and a second 25 cm farther away. These two blue suede targets (5 by 5 cm) were clipped to the arms of a battery-operated device that swung them vertically 20 cm about 120 times per minute during the 60- to 90-second interval. At 90 seconds, the targets were removed and the final photograph was taken. A pair of targets was used only once and replaced for each test sequence.
12. M. A. Brandeburgo, L. S. Gonçalves, W. E. Kerr, *Cienc. Cult. (São Paulo)* **29**, 750 (1977).
13. A. M. Collins, *J. Apic. Res.* **20**, 13 (1981).
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.

* Present address: Department of Zoology, University of Florida, Gainesville 32611.

12 May 1982

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 stimulates 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 ± standard deviation. Variance was homogeneous for all variables.

Variable	Measurement (mm)	
	Hard diet	Soft diet
Maxillary length to M^1	17.27 ± 0.83	17.49 ± 0.62
Maxillary length to C^1	9.76* ± 0.77	9.00 ± 0.76
Maxillary breadth at M^1	18.33* ± 0.83	17.57 ± 0.75
Maxillary breadth at P^3	17.12* ± 0.89	15.54 ± 0.65
Mandibular length to M$_1$	15.85 ± 0.87	15.51 ± 0.69
Mandibular breadth at M$_1$	14.38* ± 0.65	13.56 ± 0.58
Palate height	3.99* ± 0.38	3.44 ± 0.28
Maxillary (M^1) breadth/length ratio	1.056* ± 0.037	1.005 ± 0.045
Mandibular breadth/length ratio	0.908* ± 0.034	0.875 ± 0.028

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

variation has been repeatedly observed in societies that become industrialized and diets shift to refined food. Some experiments on rats have shown similar results (*5, 6*), but rats are not appropriate models for occlusion in humans (*7*). Among primates the squirrel monkey (*Saimiri sciureus*) is an excellent human analog for masticatory studies. We report results of a study of growth and occlusal consequences of a soft diet in squirrel monkeys.

The animals were from two groups; one ($N = 22$) was raised in the wild on the raw and usually tough natural foodstuffs (*8*) before capture, and the other ($N = 17$) was raised in the laboratory on a soft artificial diet that contained 0.25 percent cholesterol (*9*). We added to each group two experimental animals raised under closely observed laboratory conditions on hard or on water-softened biscuits. Dental stone casts were made of adult animals and were sent to one of us (R.M.B.), who kept the records and documentation and provided the casts to the other (R.S.C.). The subjects thus were scored and sorted double-blind; occlusal variations from anatomically defined norms (*1, 10, 11*) were observed under an illuminating magnifier (*12*). A resulting contingency assortment showed that 19 animals raised on hard diets had no observable occlusal deviations and three had noticeable deviations from normal; four animals raised on soft diets had no occlusal deviations, but 14 did. These figures represent a statistically significant association between occlusal abnormalities and maintenance during growth on a soft diet (*13*). Deviations were analogous to common human malocclusions—mesially narrow and disproportionately long maxillary arches leading to upper incisor overjet forward over the lower incisors impacted malerupted premolars and second molars, malaligned crowded premolar rows, and crowded and rotated incisors. The tooth displacement count (*1, 11*) was significantly greater in animals on soft diets (Fig. 1), although the count did not approach the average of 5.1 for urbanized humans (*1*).

There are consistent metrical differences between the two experimental groups (Table 1). Medio-lateral arch breadths are significantly larger in animals on hard diets. Maxillary and mandibular arch lengths (from medial interincisal point to behind the first molars), on the other hand, are relatively unaffected by diet. This finding is consistent with similar experiments on rats (*5, 6*). Maxillary arch length to the canine tooth, which actually measures anterior arch breadth or squareness, does vary with diet. Palate height (perpendicular to M^1 occlusal surfaces) is greater in the group on hard diets. Breadth to length ratios eliminate sex dimorphic effects on the data; maxillary and mandibular relative breadth ratios are much greater in the animals on hard diets. The multivariate metrical pattern indicates pronounced differences (*14*).

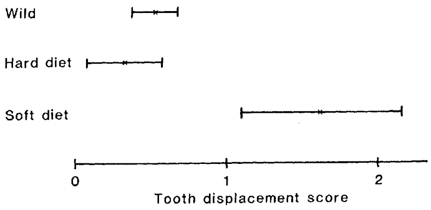

Fig. 1. The mean values and 95 percent confidence intervals for tooth displacement scores of 70 wild squirrel monkeys, 23 raised on hard diets, and 19 raised from immaturity on artificial soft diets.

Craniofacial growth coordination and morphological integration (measured by correlation) are known to break down in samples of humans with malocclusion (*15*); this is often attributed to so-called racial mixture. Bivariate correlations among metrical attributes are consistently lower in our soft-diet group, averaging .48; in contrast, the average for the wild monkeys was .68 (*16*). The most significant differences are in the two measurements of maxillary breadth in comparison to palate height: correlations are positive in the group on hard diets and negative in the soft-diet group (*17*). Again, multivariate tests confirm the significant pattern of differences (*18*).

Our results indicate a relation between dietary consistency (hence chewing forces) and occlusal development in these monkeys. The relation of masticatory demand to processed foods provides a consistent model for predicting the inevitable transition from predominantly good to bad human occlusion within one generation's time, as experienced by many societies (*4*) when the diets shift to soft, processed foods. This experiment involved a natural, noninvasive mechanism relevant to humans; other primate experimentation has involved radical methods such as cutting muscles, blocking nasal passages, or inserting oral implants (*19*), disruptions not generalizable to the average person.

Interproximal attrition and loss of arch space were negligible in our animals; periodontal disease, carious destruction, and tooth loss were present in both samples and actually greater in the group raised on hard diets. Therefore, these two frequently mentioned factors do not explain the observed differences. We conclude that chewing stress is an epidemiological factor with possible preventive implications for occlusal disorders.

ROBERT S. CORRUCCINI
Department of Anthropology,
Southern Illinois University,
Carbondale 62901
ROBERT M. BEECHER
Department of Anatomy,
Wright State University School
of Medicine, Dayton, Ohio 45435

References and Notes

1. Estimates vary but 30 to 50 percent of American youths show occlusion for which orthodontic treatment is considered highly desirable [J. Kelley and C. Harvey, *Vital and Health Statistics* (Series 11, No. 162, Public Health Service, Washington, D.C., 1977)].
2. A. Lundstrom, *Tooth Size and Occlusion in Twins* (Karger, Basel, 1948); R. Smith and H. Bailit, *Angle Orthod.* **47**, 65 (1977).
3. Recently heritability coefficients and genetic variance estimates for occlusion have been revised sharply downward [E. Harris and R. Smith, *Am. J. Orthod.* **78**, 155 (1980); R. Corruccini and R. Potter, *ibid.*, p. 140; R. Potter, R. Corruccini, L. Green, *J. Craniofacial Gen. Dev. Biol.* **1**, 217 (1981)].
4. A. Lombardi and H. Bailit, *Am. J. Phys. Anthropol.* **36**, 283 (1972); R. Corruccini and L. Whitley, *Am. J. Orthod.* **79**, 250 (1981).
5. D. Watt and H. Williams, *Am. J. Orthod.* **37**, 895 (1951); C. Barber, L. Green, C. Cox, *J. Dent. Res.* **42**, 848 (1963); W. Moore, *J. Zool.* **146**, 123 (1965).
6. R. Beecher and R. Corruccini, *Angle Orthod.* **51**, 61 (1981).
7. Rats have a mobile mandibular symphysis, diastema, and lack secondary Haversian remodeling.
8. The diet of wild *Saimiri* includes large insect and fruit species with chitin, cellulose, and rinds providing considerable masticatory resistance; the tooth morphology indicates adaptation to forceful chewing with molars loaded under high occlusal pressure [A. Rosenberger and W. Kinzey, *Am. J. Phys. Anthropol.* **45**, 281 (1976); see also (*10*)].
9. The animals were raised or acquired at Litton Bionetics and maintained on the special diets for research on atherosclerosis. Litton Bionetics shared tissues and provided all documentation on provenience, birth date, sex, response, and test dates. Animals not raised on the fudge-like test diet including lard were raised on water-softened monkey Chow.
10. J. Mills, *Dent. Prac.* **6**, 47 (1955); R. Kay, *Am. J. Phys. Anthropol.* **43**, 195 (1975).
11. L. Baume *et al.*, *Int. Dent. J.* **23**, 530 (1973); H. Draker, *Am. J. Orthod.* **46**, 295 (1960).
12. Occlusally abnormal animals showing more than one missing tooth were excluded from nonmetrical evaluation. Metrical observations, where involved, were taken with dial calipers calibrated to 0.02 mm.
13. $\chi^2(1) = 16.67$, $P = .0001$. Yule nonparametric correlation coefficient between hard diet and ideal occlusal state is .91. The standard for ideal occlusion was set by museum study of 70 adult squirrel monkeys captured in four South American countries (R. S. Corruccini, personal observations).
14. Discriminant analysis allocated 92 percent of the specimens to the proper sample; mean separation along the function was significant at $P = .0001$ ($D = 6.45$, $\chi^2(8) = 36.5$).
15. C. Lavelle, *Am. J. Orthod.* **61**, 29 (1972); C. Moorrees and R. Reed, *Am. J. Phys. Anthropol.* **12**, 77 (1954); S. Garn, *Am. J. Orthod.* **47**, 661 (1961). The same lowering of correlations was observed in rats raised on soft diets (*6*).
16. The difference is significant at $P = .05$ [$t(21) = 2.17$]. Since animals were randomly assigned to samples, this pattern does not result from genetic factors.
17. A deeply arched but narrow palate is similar to the human "maxillary collapse syndrome," the

most common occlusal syndrome among American youths (*1*); in monkeys on hard diets the palate broadens as it gets higher.

18. Principal components analysis shows higher covariance in animals on hard diets (eigenvalue one is 4.65 and 4.21 for monkeys on soft diets) and less dispersion away from that common growth vector (eigenvalue two is 1.11 and 1.34, respectively).
19. E. Harvold, K. Vargervik, G. Chierici, *Am. J. Orthod.*, **63**, 494 (1973); J. McNamara, *ibid.* **64**, 578 (1973); J. Hiniker and S. Ramsfjord, *J. Prosth. Dent.* **16**, 503 (1966); J. Charlier, A. Petrovic, J. Hermann-Stutzmann, *Am. J. Orthod.* **55**, 71 (1969).
20. Michael Freeman and Sally Stick provided technical help. This work was supported by NSF grants BNS81-19875 and DEB79-22186 to R.S.C. and by University Research Services of Wright State University.

5 April 1982; revised 29 July 1982

Associative Learning in Egglaying Site Selection by Apple Maggot Flies

Abstract. *Evidence is presented demonstrating that associative learning during oviposition in* Crataegus *or apple hosts can significantly influence the propensity of apple maggot flies to accept or reject these hosts in future encounters. The data suggest that within resource patches of a given host type there may be an enhancement of foraging efficiency.*

Insects of several orders undergo adaptive changes in behavior as a result of experience (that is, learning in its broadest sense) (*1*). For example, previous experience plays an important role in oviposition site preference pattern of certain hymenopterous parasitoids (*2*). The female, after having found and parasitized a few individuals of a given host type, learns to associate particular physical or chemical cues with that type, measurably increasing subsequent preference for it. Until now, the only strong evidence for associative learning in oviposition site selection in nonparasitoid insects is in *Drosophila* (*3*). Studies on butterflies (*4*) have been suggestive but inconclusive. In this report on oviposition of the apple maggot fly, *Rhagoletis pomonella*, into host *Crataegus* and apple fruit, we present data showing associative learning in egglaying site selection in a herbivorous insect.

Flies used in laboratory assays emerged from puparia formed by larvae that infested apples collected from Orchard Hill trees in Amherst. At the time these assays were begun, the flies were mature but had not been previously exposed to fruit (hence, "naive"). In the two-choice test, a randomly selected fly was caged with one apple and one *Crataegus mollis* fruit for as long as fruit visits continued. Each fly was removed 5 minutes after the last fruit visit. In other laboratory tests, each randomly selected fly was offered a single fruit and permitted to remain there until it either accepted the fruit (attempted oviposition) or rejected it (left without attempting oviposition). If the fly neither accepted nor rejected the fruit within 10 minutes, these data were excluded from the analysis.

Each fly assayed in field tests had just finished ovipositing in a Red Delicious apple on an Orchard Hill tree and was offered, under the same protocol as in laboratory tests, a single fruit for acceptance or rejection.

In the two-choice test in the laboratory (Table 1) flies demonstrated a significant ovipositional preference for *C. mollis* over apple (*5*). Similarly, in a one-choice test in the laboratory (Table 1) flies exhibited a significantly greater propensity to attempt egglaying in *C. mollis* than in apple. In contrast, in a one-choice test in nature (in which we offered fruits from the same batches and on the same days as offered in the laboratory), not one of 50 flies observed on apple trees attempted oviposition in *C. mollis* (Table 1) (*6*).

There are at least two possible explanations for the difference between these laboratory and field results. (i) The ovipositing flies on apple trees were individuals that had a propensity—either genetic or based on larval induction—to oviposit in apples or (ii) the ovipositing flies on apple trees had learned to accept apples and reject other potential hosts such as *C. mollis*. We believe the former explanation to be unlikely on the basis that (i) the flies observed in the laboratory originated as larvae the previous year from the same trees on which the flies observed in the field were found ovipositing; (ii) in laboratory assays, fewer than 3 percent of naive *R. pomonella* flies from different wild populations originating as larvae from apple exhibit-

Table 1. Acceptance of fruit for oviposition by *R. pomonella*. Flies tested in the laboratory were mature but had not been previously exposed to fruit. Flies tested in the field experiment were in an apple orchard that was at least 1 km from other fruit hosts of *R. pomonella*.

Test type	Fruit type	*N*	Percentage accepting fruit	*P**
		Laboratory experiments		
Two-choice	*C. mollis*	48	94	
	Apple	56	46	≤ .001
One-choice	*C. mollis*	50	90	
	Apple	50	36	≤ .001
		Field experiment		
One-choice	*C. mollis*	50	0	
	Apple	50	62	≤ .001

**P* values refer to comparisons between first and second items in each experiment.

Table 2. Acceptance of a fifth fruit for oviposition by trained (+) and untrained (−) flies. A fly was considered trained if it attempted oviposition in each of the first four fruits offered, and untrained if it did not attempt oviposition in at least one of the first four fruits offered.

First four fruits offered	Fly trained	Fifth fruit offered	*N*	Percentage accepting fifth fruit	*P**
		Experiment 1			
Apple	+	*C. mollis*	29	52	
C. mollis	+	*C. mollis*	47	91	≤ .001
C. mollis	−	*C. mollis*	29	83	≤ .025
		Experiment 2			
C. mollis	+	Apple	49	20	
Apple	+	Apple	26	92	≤ .001
Apple	−	Apple	49	49	≤ .01
		Experiment 3†			
Apple	+‡	*C. viridis*	15	6	
C. viridis	+	*C. viridis*	17	94	≤ .001

**P* values refer to comparisons with first item in each experiment. †All flies had trained on *C. viridis* and rejected apple when offered it as a fifth fruit 3 days prior to training under this protocol. ‡Nine of 24 flies failed to train on apple; 7 of 24 failed to train on *C. viridis*.