Field Test of Resistance to *Acarapis woodi* (Acari: Tarsonemidae) and of Colony Production by Four Stocks of Honey Bees (Hymenoptera: Apidae)

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ABSTRACT Characteristics of four stocks of honey bees, *Apis mellifera* L., were evaluated in colonies managed commercially for honey production at three U.S. locations—one north-central location (Iowa) and two south-central locations (Mississippi, Texas). Stocks were compared for 1 yr beginning in October 1991 to determine the levels of infestation by tracheal mites, *Acarapis woodi* (Rennie), and to ascertain survival rates, levels of honey production, and sizes of adult and brood populations. Test stocks were ARS-Y-C-1 (*A. mellifera carnica* Pollman, imported from Yugoslavia), Buckfast (imported from the United Kingdom), Survivor (developed from colonies in a Louisiana apiary believed to have had severe tracheal mite infestation), and Unchallenged (developed from a feral Louisiana population never exposed to tracheal mites). Stocks initially were represented by 15–20 colonies at each location. After an initial inoculation of mite-infested bees in the autumn, infestation percentages increased more markedly in the susceptible (Survivor and Unchallenged) stocks than in the resistant (ARS-Y-C-1 and Buckfast) stocks. Mean infestation percentages in the resistant stocks remained <15% and thus were below levels associated with economic damage. Mean infestation percentages in susceptible stocks ranged from 13 to 95% at each site during the final 6 mo of the study. Numbers of mites per infested bee differed between stocks in 4 of 21 samples; mite numbers tended to be greatest in Survivor bees and least in Buckfast bees. Mortality increased more rapidly among susceptible colonies than among resistant colonies as infestation increased in 1992. Honey production was greatest by Buckfast, intermediate by Survivor, and least by Unchallenged and ARS-Y-C-1 colonies. Differences in population sizes of adult bees and brood occurred in approximately half of samples taken in spring and autumn; Survivor and Buckfast colonies were most populous. Stock characteristics showed no interaction of genotype with environment, i.e., location. Our results support the feasibility of an approach using genetically regulated resistance to manage problems caused by tracheal mites.

KEY WORDS *Apis mellifera, Acarapis woodi,* genetic resistance

GENETIC RESISTANCE OFFERS hope for an economical, nonpesticidal solution to problems caused to managed honey bees, *Apis mellifera* L., by endoparasitic tracheal mites, *Acarapis woodi* (Rennie). The possibility of genetically based variability for susceptibility to mite infestation was recognized as early as 1911 in Europe (Anderson 1930), soon after symptoms believed to be caused by tracheal mites first were observed in honey bees. Only recently, however, has rigorous testing demonstrated differential susceptibility among bee types (Gary and Page 1987, Clark et al. 1990, Page and Gary 1990, Milne et al. 1991, Szabo et al. 1991, Lin et al. 1992). This recent research has come in response to ongoing problems caused by tracheal mites in the United States and Canada (Otis 1990) during the last 9 yr. In Europe, tracheal mites currently are of little economic consequence (Otis 1990) after apparently having caused severe mortality of honey bee colonies in the United Kingdom early in the century. Differing degrees of mite-associated problems in honey bees of the New World versus in those of the Old World suggest that differential levels of resistance to tracheal mites may exist, but tests of this hypothesis have found neither strong nor ubiquitous resistance in Old World bees (Bailey 1965, 1967; Gary et al. 1990).

We sought to extend information about resistance to tracheal mite infestation in honey bees in a study with the following objectives: (1) under commercial beekeeping conditions, to measure tracheal mite infestation and other economically important traits of bee stocks likely to have resistance; then, if resistance is found, (2) to ensure that the genetic material conferring resistance is available to the beekeeping industry, and (3) to use appropriate stocks for further investigations into

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resistance. This report details the initial phase of the work, which was a field test involving four stocks managed commercially at several locations in the United States. The field test was prompted initially by availability for testing of an Old World stock, Buckfast, which is thought by the breeder to have tracheal mite resistance (Adam 1968). The stock was developed in England beginning about 1917 during the period of most severe mite-associated colony losses. Comparative resistance of this stock was documented recently when relatively low mite-infestation levels were observed in colonies from midsummer to late winter (Milne et al. 1991) and from autumn to spring (Lin et al. 1992), and in short-term exposure tests of individual bees (Lin et al. 1992). In our stock evaluation, we considered infestation patterns among experimental stocks and also tried to characterize the stocks involved more broadly by measuring colony survival and productivity. This approach allowed the possibility of tolerance to tracheal mites to be expressed if a stock performed well despite relatively high parasitism. The test was done in two widely separated geographic areas (north-central and south-central United States) to investigate possible environmental effects on stock performance.

Materials and Methods

Experimental Honey Bee Stocks. Two Old World stocks (ARS-Y-C-1 and Buckfast) and two New World stocks (Survivor and Unchallenged) were studied. ARS-Y-C-1 was composed of five colony lines of *A. m. carnica* Pollmann originally selected in Yugoslavia (Rinderer et al. 1993). ARS-Y-C-1 queens were imported in 1989, and the lines used in this study were chosen based on favorable traits observed during testing in two subsequent years.

The Buckfast stock was derived from queens imported from the United Kingdom (Buckfast Abbey, Buckfastleigh, Devon) in July 1990. Fourteen queens representing five Old World Buckfast breeding lines were introduced into colonies at the USDA honey bee quarantine station on Grand Terre Island, LA. Bees were held for a quarantine of 6 mo before propagation of test queens.

Five colonies that served as parental lines of the Survivor stock came from an apiary at Cade, LA, that had 25–50% colony losses during each of three consecutive winters (1987–1990). These losses presumably were caused in large part by tracheal mites because the apiary was near the site of initial detection of tracheal mites in the state in 1985 and the colonies were never treated with acaricides. In addition, symptoms of colony mortality we observed (bee populations dwindling in winter despite nests being well provisioned with food) are associated with tracheal mite parasitism (Otis and Scott-Dupree 1992). We chose colonies with relatively low tracheal mite infestation (averages of 3–12% of bees infested during July and September 1990) as Survivor stock parents. The Unchallenged stock originated from five feral colony sources near Leeville, LA, an area without tracheal mites when parental colonies were collected.

To produce test queens of each stock, queens were reared from one colony of one line of the stock and then naturally mated to drones from all five lines of the stock in isolation from other honey bees. Matings of groups of 100–150 queens per stock were scheduled sequentially for each stock during 2- to 3-wk periods in April, May, and June 1991. The isolated mating area was in the coastal marsh at Fourchon, LA. The area was surveyed for feral colonies before the matings by using direct searches, honey–syrup baits, inquiries to local residents and workers, and attempts at mating queens in the absence of supplemental drones. Three feral colonies were discovered and eliminated; no further colonies or foraging bees were seen within ≈10 km of the mating apiary, and the closest substantial honey bee population was ≈30 km away.

Experimental Colonies. Approximately 65 test queens (15–20 per stock) were introduced into small colony divisions during May and June 1991 by each of four cooperating commercial beekeepers (one each in Iowa, Minnesota, Texas, and Mississippi). Colonies were divided among two apiaries at each site, with similar numbers of colonies of each stock grouped together at each apiary. Colonies were managed by each beekeeper as was usual for their individual operation. Oxytetracycline hydrochloride (Terramycin; Pfizer, New York, NY) was applied in a powder mixture for disease control, but colonies were not treated against tracheal mites. At the time of queen installation, the 262 recipient colonies had tracheal mite infestations of 9 ± 13% (mean ± SD used throughout) based on examinations of 30 bees each; queens were assigned randomly to colonies. None of the beekeeping operations was known to have infestations of *Varroa jacobsoni* Oudemans at the beginning of the test. Because of rapid colony attrition during the early phase of the study, the Minnesota apiaries were dismantled after October 1991, and queens were used to augment apiaries at other sites. Thus, no data from Minnesota are presented.

In October 1991, after colony populations consisted entirely of offspring of test queens, we helped ensure that all colonies at each site were challenged with tracheal mites by inoculating with mite-infested bees. Worker bees were collected from infested colonies at Baton Rouge and shipped in cages to the test sites. At dusk, bees were sprayed with dilute sucrose syrup and a small cupful (≈100 g) was removed, weighed, and dispensed onto the tops of combs in the brood nest. The number of workers added per colony was 781 ± 66, of which 57 ± 9% were infested (based on an examination of 30 bees from each of 10 samples taken randomly during inoculation).

Two deviations from the general experimental plan were necessary. First, we intended that colonies in Iowa would winter on site. However, because of insufficient worker populations in some colonies in October 1991, all but 20 colonies (five of each stock) were moved to Louisiana for winter; they were returned in April 1992. Second, the discovery of *V. jacobsoni* in Texas late in the test led to treatment with fluvalinate (Apistan; Zoëcon, Dallas, TX) in August 1992.

Data Collection. Colonies were inspected and bees sampled for tracheal mite parasitism bimonthly from October 1991 to October 1992. Data were used only from colonies in which the original queen was verified during inspection. Colony characteristics such as relative defensiveness and the presence of microbial diseases were noted. To measure tracheal mite infestations, samples of 50–100 adult workers were collected from honey storage areas or the periphery of the cluster, stored on ice in the field, and then frozen until processed. Forty bees per colony were dissected, and, if infested, the tracheal trunks were excised from the thorax. Numbers of mites of all stages found between the spiracle and first branch of the tracheal trunk were counted at 60× magnification. No samples were collected from colonies in Iowa during December or February. Data are presented using terminology suggested by Margolis et al. (1982): mite prevalence is the percentage of bees infested with tracheal mites in a sample (colony), and mean mite intensity is the average number of mites per infested bee. The product of these parameters gives relative mite density (i.e., the mean number of mites per bee).

The population of adult bees in each colony was measured in autumn (October 1991 and 1992) and spring (February and April 1992, except that no Iowa colonies were measured in February, and only nonmigratory colonies were measured in Iowa in April). The population was quantified by estimating and summing the number of tenths of each comb (standard Langstroth frames) covered with bees. The sealed brood populations of colonies in Mississippi and Texas were measured in autumn and spring in one of two ways. In October 1991 and February 1992, the peripheries of all patches of sealed worker brood were traced onto waxed paper. For each patch, we estimated the percentage of sealed cells by counting sealed and open cells in three random 10-cell transects. Brood areas were later quantified by electronically digitizing the perimeter of each tracing, converting to area (square centimeters), adjusting for percentage fill, and summing patches for each colony. Brood areas were estimated in April 1992 by counting and summing tenths of comb sides covered with sealed brood. Small patches of brood were measured by counting the number of sealed cells and converting to sq cm by dividing by 4.219. Colonies in Iowa had very little or no sealed brood when inspected in October 1991 and April 1992. Honey production was measured by each cooperating beekeeper. Full honey storage chambers were weighed when harvested, and weights of empty chambers were subtracted.

Data Analyses. Mite prevalences and mean mite intensities within each time period at each location were subjected to one-way analysis of variance (ANOVA). Mite prevalences were transformed to $(x + 0.5)^{1/2}$ to help stabilize variances. For the dependent variable honey production, we tested for an interaction between stock and location; because none was evident, main effects were tested with a pooled residual error term. Populations of adult bees and of brood were compared among stocks by analysis of variance at each sample time for each location. When ANOVA for any parameter indicated a significant difference, means were compared by least squares means (SAS Institute 1990a); differences were considered to be significant at $\alpha \leq 0.05$. Survival times of colonies were compared among stocks with the product limit method (LIFETEST; SAS Institute 1990a); overlap of 95% CL was used as the criterion of similarity of survival curves of stocks. Pearson's correlation (SAS Institute 1990b) was used to determine the degree of association of colony survival times and honey production with mite infestation levels.

Results

Comparative trends of tracheal mite prevalences were relatively similar at each location during the year-long test (Fig. 1; Table 1). In general, ARS-Y-C-1 and Buckfast stocks had lower mite prevalences than did Survivor and Unchallenged stocks. Significant differences between these two groups were evident at each site within 2–6 mo after initiating the test in October 1991, and the magnitudes of differences increased through time. Prevalences tended to decrease during the summer of 1991 after the initial requeening of test colonies. In Iowa and Texas, mean mite prevalences in all stocks were very low (≤6%) through February 1992. Survivor and Unchallenged colonies then showed rapid increases in prevalence in summer. Results differed slightly in Mississippi in that mite prevalences generally rose during winter then declined in April before increasing during summer; Survivor and Unchallenged bees again showed much greater rises in prevalence. Mean prevalences in ARS-Y-C-1 and Buckfast colonies remained <15% at all sites throughout the study.

Trends of mean tracheal mite intensities among stocks were much less distinct than were patterns of mite prevalences. Differences among stocks in mean mite intensity occurred in 4 of 21 total sampling combinations of sites and times. Two trends were apparent. First, infested Survivor bees tended to have more mites than did infested bees of other stocks (noted in all four of the sampling times having differences). Second, infested Buck-

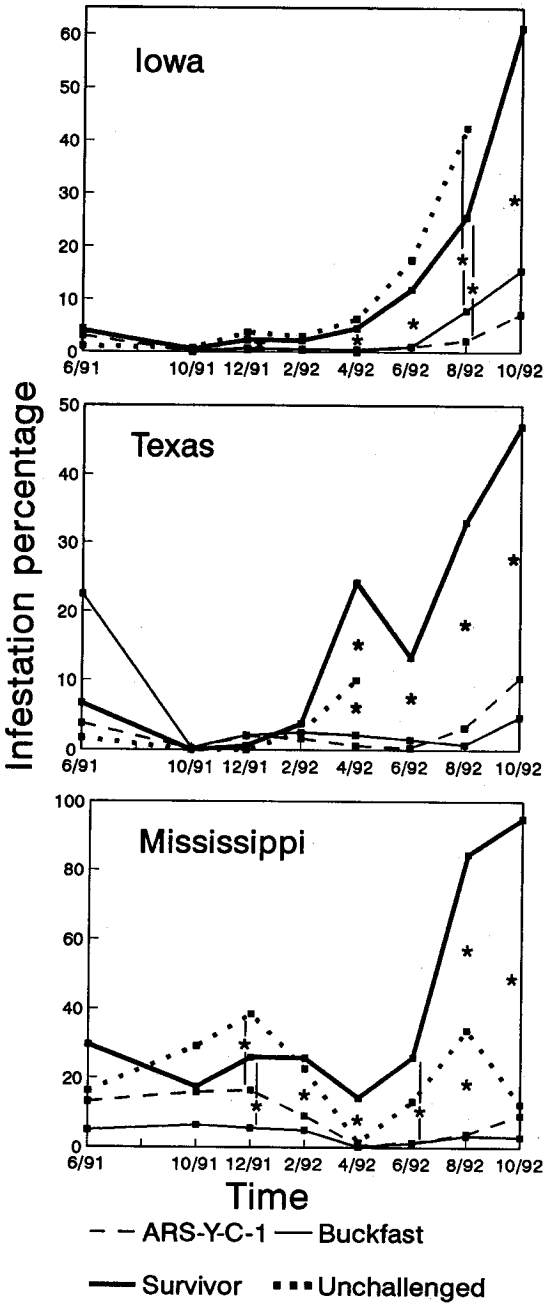

Fig. 1. Tracheal mite prevalence in four honey bee stocks located at each of three sites. At any sampling time, means that differ ($P \leq 0.05$) are separated by an asterisk or, if differing means are nonjuxtaposed, by an asterisk with lines indicating separation (see also Table 1).

fast bees tended to have fewer mites (noted in three of the four sampling times having differences). For all stocks, mean mite intensities generally were near 10 mites per infested bee and ranged from 5 to 20 mites per infested bee.

Colony mortality differed among the stocks (log rank $\chi^2 = 50.6$, df = 3, $P < 0.001$). ARS-Y-C-1 and Buckfast colonies had greater survival than Survivor and Unchallenged colonies (log rank $\chi^2 \geq 9.2$, df = 3, $P \leq 0.002$), especially during the last half of the test (Fig. 2). Colony survival time (of all stocks combined) was negatively correlated with mite prevalence during October, December, and February ($r = -0.181$ to -0.456, $n = 74$–129, $P \leq 0.040$). Colony attrition through queen supersedures was much greater than expected for young queens, especially near the start of the experiment. Queen losses may have resulted in part from inadequate matings at the isolated site.

Buckfast colonies produced significantly ($F = 4.53$; df = 3, 77; $P = 0.006$) more honey (34.2 ± 20.0 kg, $n = 32$) than Unchallenged (20.6 ± 17.2 kg, $n = 10$) and ARS-Y-C-1 colonies (17.6 ± 18.4 kg, $n = 23$). Survivor colonies produced quantities (31.2 ± 19.9 kg, $n = 18$) intermediate between Buckfast and the two other stocks. The rank of honey production by stocks was consistent at each site, with the exceptions that Unchallenged ranked last in Mississippi and that no Unchallenged colonies remained for honey production measurements in Texas. Mean honey production was greatest in Mississippi and least in Iowa. Based on honey production estimates of cooperating beekeepers for 1992, the average production of only the Buckfast colonies equaled or exceeded the average production of standard colonies used at each location. We found no evidence that tracheal mite infestation negatively affected honey production of surviving colonies. Production per colony within ARS-Y-C-1, Buckfast, and Unchallenged was not related ($r = -0.150$–0.160, $n = 10$–32, $P = 0.412$–0.658) to the mite prevalence found during the sampling period preceding the nectar flow period at each location (judged to be February in Mississippi, April in Texas, and June in Iowa). For Survivor colonies, mite prevalence preceding nectar flow and honey production were positively correlated ($r = 0.524$, $n = 18$, $P = 0.026$). Prevalences in colonies that survived to the nectar flow (i.e., mean ≤ 26% of workers infested in each stock) apparently were below the threshold for limiting productivity. Honey production of each stock was correlated positively with sealed brood population in the spring ($r = 0.506$–0.944, $n = 6$–22, $P < 0.001$–0.08).

Populations of adult bees differed among stocks for 6 of 11 samples (Fig. 3) and populations of brood differed for four of six samples (Fig. 4) taken in autumn and in spring. When differences occurred for either parameter, the trend was that Survivor or Buckfast colonies had larger populations than did ARS-Y-C-1 and Unchallenged colonies.

Some other general characteristics of the stocks became apparent while managing the colonies for a year. Notable observations were as follows. ARS-Y-C-1 bees were extremely calm and the stock was the least defensive of those tested. Bees wintered

Table 1. Results of ANOVA of tracheal mite prevalence among four honey bee stocks at three test sites

Time	Mississippi			Texas			Iowa		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Oct. 1991	2.85	3, 49 (B <U)	0.047	0.17	3, 34 (—)	0.918	1.98	3, 48 (—)	0.130
Dec. 1991	6.49	3, 45 (B <S, U; A <U)	0.001	0.56	3, 32 (—)	0.643	5.88	3, 44 (A, B <S, U)	0.002
Feb. 1992	9.31	3, 41 (A, B <S, U)	<0.001	0.73	3, 31 (—)	0.544	1.55	3, 27 (—)	0.225
Apr. 1992	18.01	3, 33 (A, B, S <U)	<0.001	66.29	3, 26 (A, B <U <S)	<0.001	5.96	3, 26 (A, B <S, U)	0.003
June 1992	5.03	3, 29 (A, B <S)	0.006	3.69	3, 23 (A, B <S)	0.041	8.23	3, 24 (A, B <S, U)	<0.001
Aug. 1992	52.79	3, 22 (A, B <U <S)	<0.001	8.11	2, 19 (A, B <S)	0.003	6.92	3, 20 (A <S, U; B <U)	0.002
Oct. 1992	71.10	3, 18 (A, B, U <S)	<0.001	4.77	2, 12 (A, B <S)	0.030	13.23	2, 13 (A, B <S)	<0.001

Mean separation shown in parentheses when $P \leq 0.05$ according to a least squares means approach (SAS Institute 1990a) following a significant ANOVA. A, ARS-Y-C-1; B, Buckfast; S, Survivor; U, Unchallenged.

in very tight, quiet clusters and consumed relatively little food. Poor surplus honey production often seemed to result from population growth being hampered in the spring because of a honey bound condition; that is, the cluster was confined low in the hive by a shell of unconsumed honey stored previously for winter use. ARS-Y-C-1 showed the greatest variability among stocks in honey production (coefficient of variation = 105); this variation suggests that production might be improved by selection within the stock. The countervailing results of good resistance to mite infestation but relatively poor honey production demonstrate that resistance to parasites is but one of many characteristics that can affect stock performance and suggests that broader investigations of the relationship between infestation and productivity are needed for ARS-Y-C-1.

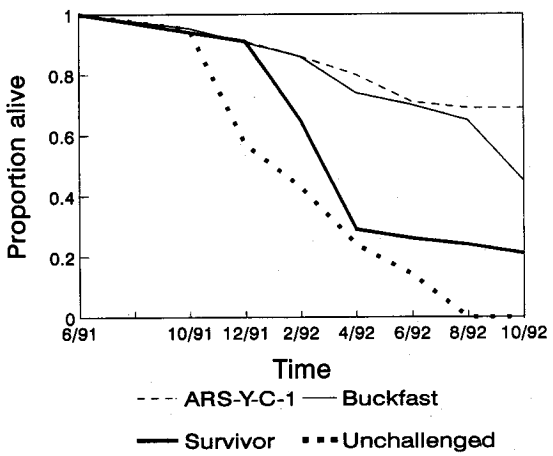

Fig. 2. Survival curves of colonies of the four honey bee stocks. The curves of ARS-Y-C-1 and Buckfast stocks differ (based on lack of overlap of 95% CL) from those of Survivor and Unchallenged stocks beginning in April 1992 and continuing throughout the remainder of the observations.

Buckfast had the most consistent within-stock behavior among test stocks. The bees usually were very calm on the combs and were defensive only infrequently. Colonies showed extensive pollen storage and relatively abundant drone production. They maintained quiet and tight winter clusters.

Survivor colonies were the least consistent behaviorally. Bees were much more active on the combs than were ARS-Y-C-1 bees and Buckfast bees. Large colonies were often good honey producers, but tended to be defensive. The bees were relatively active during winter, and colonies of this stock were usually the first to require supplemental feeding in the autumn and spring.

Unchallenged colonies were uniformly poor performers with consistently greater attrition of queens and colonies than shown by other stocks. Only two Unchallenged colonies survived with original queens until the end of the study. This stock had the most defensive bees tested and bees were active on the combs. We observed that microbial diseases were relatively frequent in Unchallenged bees.

Discussion

The field test revealed several differences in economically important characteristics of experimental honey bee stocks when colonies were managed commercially for honey production. Although stocks differed in the major traits we measured (resistance to mite infestation, honey production, and bee production), they performed similarly relative to each other in two widely separated geographic areas. This lack of interaction between genotype and environment indicates that the better-performing stocks could be expected to be productive under diverse beekeeping conditions.

ARS-Y-C-1 and Buckfast, two Old World stocks, were much less susceptible to tracheal mite infestation than were the two New World stocks. These results corroborate recent findings of comparative-

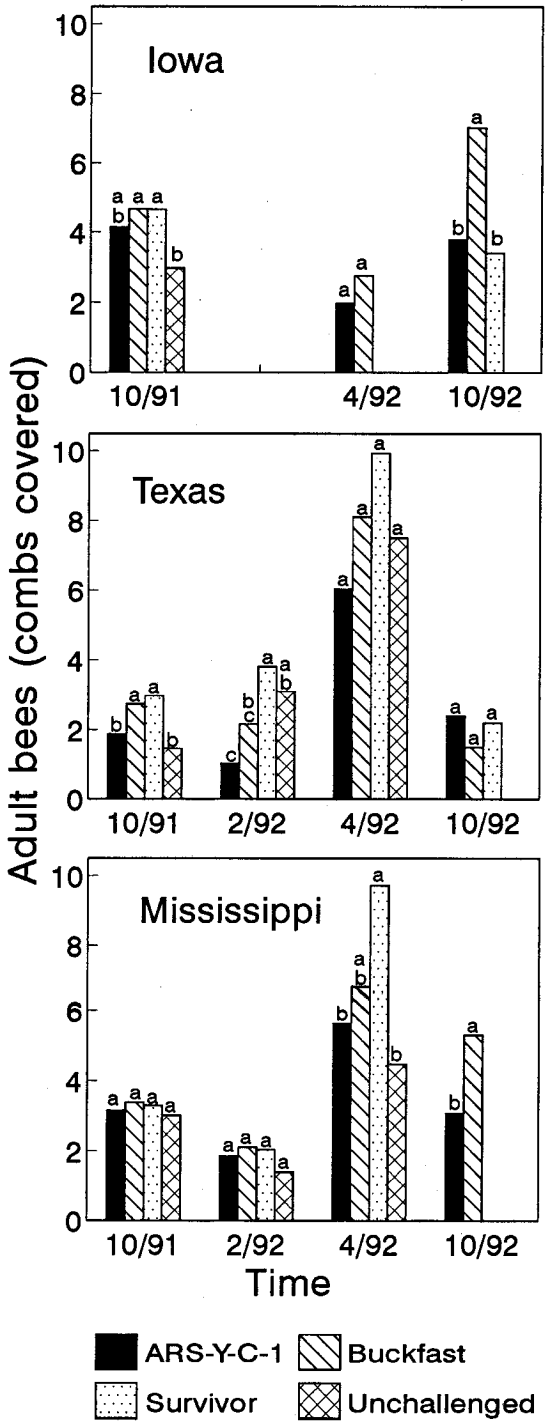

Fig. 3. Autumn and spring populations of adult bees in colonies of four honey bee stocks located at each of three sites. At any sampling time, means not sharing a common letter differ at $P \leq 0.05$.

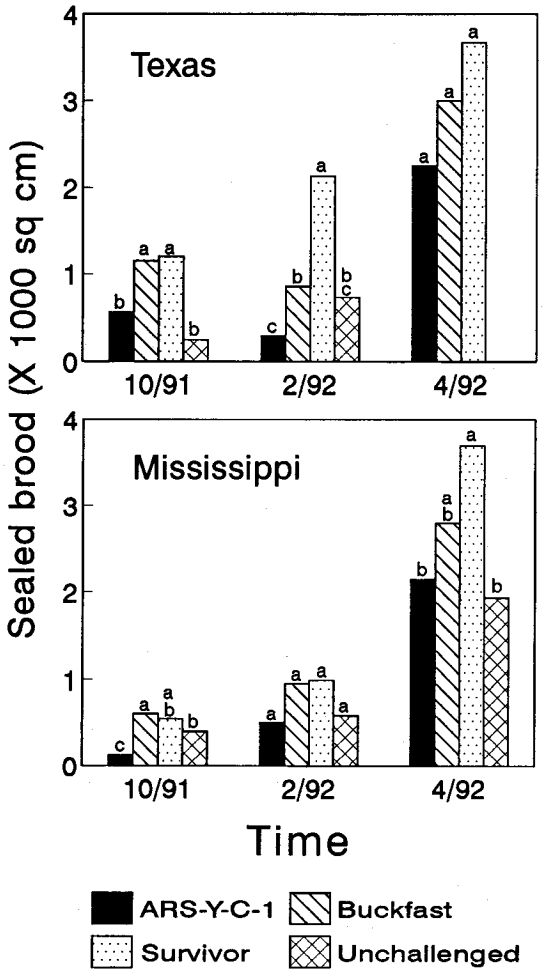

Fig. 4. Autumn and spring populations of brood in colonies of four honey bee stocks located at the two southern U.S. sites. At any sampling time, means not sharing a common letter differ at $P \leq 0.05$. Colonies in Iowa had no brood at the sampling times.

ly reduced infestation in ARS-Y-C-1 (Rinderer et al. 1993), in U.S. Buckfast (Milne et al. 1991), and in English Buckfast (Lin et al. 1992). The striking difference in susceptibilities of Old World and New World bees supports the hypothesis that bees existing in Europe have evolved a generally stable relationship with the parasite through relatively long-term natural and artificial selection.

Tracheal mite prevalences above ≈25% are associated with increased damage to honey bee colonies (Eischen et al. 1989, Furgala et al. 1989, Otis and Scott-Dupree 1992). Fewer ARS-Y-C-1 and Buckfast colonies (11 of 114, 10%) than Survivor and Unchallenged colonies (39 of 87, 45%) exceeded this threshold ($\chi^2 = 32.68$, df = 1, $P < 0.001$) during the test. Thus, while the Old World stocks were not immune to infestation, fewer mite control treatments would have been needed for these bees.

Among the New World bees, Survivor colonies were relatively susceptible to infestation even after presumably having been subjected to heavy tracheal mite infestations. Many Survivor colonies performed well (in production of honey, bees, and brood) despite this high infestation, suggesting that the bees had evolved some tolerance to the parasite. If tolerance exists, then measurements of infestation alone would not be a sufficient predictor of the impact of tracheal mites on all stocks of bees. However, this hypothesis needs to be tested before it could be concluded that putatively tolerant bees continue to perform well over longer periods or when faced with additional stress. The tolerance we observed may be a tenuous, temporary phenomenon, because many highly infested Survivor colonies died (or their queens were superseded) after the nectar flow in 1992.

In conclusion, rigorous research has verified that tracheal mites can cause devastating problems for honey bees in North America (Eischen 1987, Eischen et al. 1989, Furgala et al. 1989, Otis and Scott-Dupree 1992). Our findings of clear differential susceptibility among test stocks to mite infestation support the concept of an approach using genetically founded resistance to solve these problems. The germplasm of stocks resistant to infestation (ARS-Y-C-1 and Buckfast) is available commercially in North America and offers beekeepers a tool for use in recently advocated integrated approaches to managing tracheal mites (Fulton et al. 1991, Tomasko et al. 1993). Results of our field test suggest the need for investigations of mechanisms of resistance to tracheal mite infestation and of the long term effects of tracheal mites on bees of different genotypes, and the need for research on the relative economic worth of resistant stocks to beekeepers.

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