1985

Selection for high and low pollenhoarding honey bees

Richard L Hellmich, II, *United States Department of Agriculture*
Jovan M. Kulincevic, *Ohio State University*
Walter C. Rothenbuhler, *Ohio State University*

The Journal of Heredity 76:155–158. 1985.

Selection for high and low pollen-hoarding honey bees

Abstract: Pollen hoarding by the honey bee can be modified by selection. Two-way selection for honey bees that hoarded high and low levels of pollen in nucleus colonies was made for four generations. Two different lines of bees were produced in which high-line colonies hoarded significantly more pollen than low-line colonies. Rapid separation exhibited by the two lines suggests that the heritability of this trait is high (divergence $h^2 = 49.5$ percent ± 20.3 percent). Genetic gains of the lines were asymmetrical in which substantial progress was made during high-line selection, while little, if any progress was made during low-line selection. Polygenic inheritance involving additive genes was suggested by the steady improvement of the high line over the four generations of selection. Pollen-hoarding differences were confirmed in full-sized colonies when high and low full-sized colonies were monitored from July to October. High-line full-sized colonies averaged from two to 13 times as much hoarded pollen as the low-line full-sized colonies.

Richard L. Hellmich, II

Jovan M. Kulincevic

Walter C. Rothenbuhler

THE HONEY BEE can survive and flourish on every major continent except the Antarctic. This adaptability, at least partly, is due to the large number of individuals in a colony and to hoarding of food—both honey and pollen. This hoarded food enables the honey-bee colony to generate heat, rear brood, and survive periods when food is unavailable from plants. Diversity among honey-bee colonies, however, in amounts of honey and pollen hoarded is often high. Part of this variation may be attributed to chance orientation of honey bees to different flower sources and other environmental effects; but some variation seems likely to be genetic in origin. The purpose of this investigation was to study some of the genetic factors involved with pollen hoarding. Two-way selection was made for honey bees that hoarded high and low levels of pollen.

Racial variation in pollen-collecting activities of honey bees was observed by Hutson[4] and Filmer[3]. They noted that Caucasian bees foraged at lower temperatures than Italian bees. Differences in amounts of pollen hoarded by strains of honey bees were noted by C. G. Butler, in a personal communication to O. W. Park (see Rothenbuhler et al.[11]). He wrote: "We have data which show that some strains are, other things being equal, much more active pollen gatherers than others. For instance, the old English brown or black bee, with which we have worked, is an inveterate pollen gatherer and clogs the brood nest with pollen."

Mackensen and Nye were the first to select honey bees for pollen preferences. Two-way selection produced colonies with high percentages of alfalfa pollen-collecting bees and colonies with low percentages of alfalfa pollen-collecting bees[6]. During the sixth generation high and low alfalfa pollen-collecting lines had 86 percent and 8 percent, respectively, of their pollen foragers that collected alfalfa pollen[7]. A plateau was reached in both lines after six or seven generations of selection[9]. After making reciprocal crosses and backcrosses, Nye and Mackensen[8] hypothesized that the alfalfa pollen-collecting trait was dependent on several genes, each having an additive effect.

Our study involving high and low levels of hoarded pollen, was begun at the Ohio State University Bee Laboratory during the summer of 1978. Four generations of bees in small nucleus colonies were selected from 1979 to 1982 with the objectives of observing selection response and estimating the realized heritability of pollen hoarding. Pollen hoarding of high and low full-sized colonies was monitored from July to October in 1982.

Materials and Methods

The base population of honey bees (*Apis mellifera*) consisted of 34 full-sized colonies

The authors are affiliated with the Department of Entomology, the Ohio State University, Columbus, Ohio 43210. Dr. Hellmich is currently research entomologist at the Bee Breeding and Stock Center Laboratory, ARS, USDA, Baton Rouge, LA 70820. This paper is based on a dissertation submitted by the senior author in partial fulfillment of the requirements for the Ph.D. degree in entomology at the Ohio State University. This investigation was supported in part by cooperative agreement 12-14-7001-1004 with the United States Department of Agriculture, by the Ohio Agricultural Research and Development Center, and by the Louisiana Agricultural Experiment Station. The authors wish to thank Victor Thompson and M. Kim Fondrk for technical assistance with colony maintenance and instrumental inseminations. Dr. Hellmich also wishes to thank Drs. Cliff Kern and Mike Johnson for their enthusiasm and support. The Instruction and Research Computer Center at the Ohio State University provided computer facilities.

of commercial stock headed by natural-mated queens. During the summer of 1978 an estimate of the amount of pollen (nearest tenth of a comb) in each of these colonies was made at 10-day intervals. Figure 1 shows the average amount of pollen that was measured per colony over the summer season.

In the spring of 1979, three colonies, represented by the boxes labeled "H", provided queens and drones that were used to establish three sublines of high-pollen hoarders. Three colonies, represented by the boxes labeled "L", provided queens and drones that were used to establish three sublines of low-pollen hoarders. The best selections were not always made because sometimes the original queens failed or were otherwise unavailable.

A cyclic mating scheme was followed that was similar to the scheme used by Kulincevic and Rothenbuhler[5]. For example, to produce the first selected generation of the high line, "A" queens were mated with "B" drones, "B" queens with "C" drones, and "C" queens with "A" drones. For subsequent generations, queens were mated with drones to which they were least related. Each queen was artificially inseminated once, using semen from only one drone per insemination[12]. Because of the haploid nature of the drone[1,10], inbreeding of the queen does not occur until the fourth generation of this mating system (F_x = 9.4 percent). Worker (progeny of the queen) inbreeding occurs the third (F_x = 9.4 percent) and fourth (F_x = 13.3 percent) generations.

Each of the six sublines consisted of about eight five-frame nucleus colonies making a total of about 48 colonies tested each year. Colony inspections were made semimonthly from the middle of August to the middle of October. The amount of hoarded pollen in each colony was measured by a comb-sized grid marked off in square inches. (Square inches were converted to square centimeters.) Estimates of bee and brood amounts were made to the nearest tenth of a comb; and brood quality was estimated by ranking at 0.5 increments from 3.0 to 0 (where 3 = 95 to 100 percent and 0 = 30 to 40 percent of cells in broodnest occupied). Each generation the colonies within each subline were ranked based on the hoarded-pollen measurements. The colony with the largest amount of hoarded pollen within each high pollen-hoarding subline and the colony with the lowest amount of pollen within each low pollen-hoarding subline were selected to provide queens and drones for the next generation.

During the fourth generation seven full-sized colonies each of high- and low-pollen-hoarding lines also were tested. Queens of high-line colonies were sisters, and queens of low-line colonies were sisters; each was grafted from a selected third-generation queen from their respective line. High- and low-line queens were instrumentally inseminated with 5 μl of semen from multiple high- and low-line drones, respectively. Drones from each line were progeny of a selected third-generation queen from a subline that was least related to the grafted queens.

On May 29, 1982, each queen with 1.6 kg of worker bees was put into a 10-frame standard Langstroth hive. Worker bees were obtained from miscellaneous stock colonies; and the hives contained similar amounts of stored pollen and honey. The investigator was blind to the genetic origin of the queens in order to reduce measurement bias. Attempts to equalize colony populations of bees and brood within each genotype were made following June 8, June 17, and June 30 inspections. From mid-July to mid-October measurements were taken at two- or three-week intervals for amounts of hoarded pollen. Most of the original worker bees shaken into the colonies were probably replaced with new bees by the mid-July inspection.

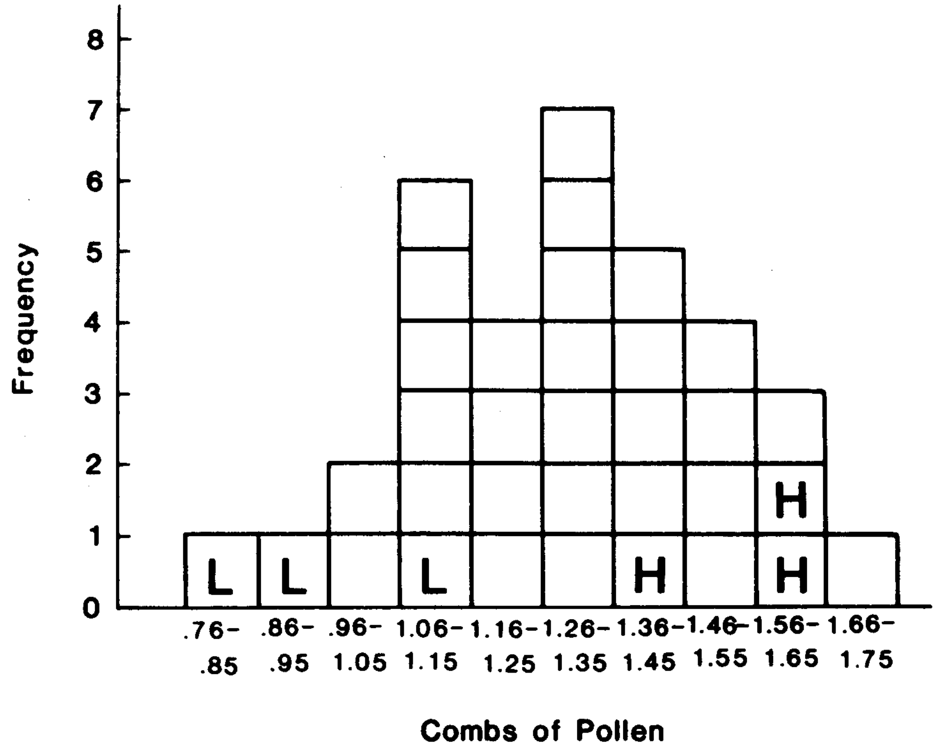

FIGURE 1 Frequency histogram: mean combs of pollen in each of 34 full-sized colonies (L = parents of low line; H = parents of high line).

Table I. Mean square centimeters of pollen and *t*-test results for seven high pollen-hoarding (HPH) and seven low pollen-hoarding (LPH) full-sized colonies for six inspection periods

Inspection	Date	HPH	LPH	$P > F$
1	7-15	1148	581	0.025
2	7-30	1690	652	0.01
3	8-16	2265	781	0.005
4	9-8	1077	148	0.001
5	9-29	2297	323	0.001
6	10-18	1877	142	0.001

Results

Two-way selection

Pollen hoarding by high and low lines was significantly different during each generation as indicated by the 95 percent confidence intervals from analysis of variance tests (see Figure 2). High-pollen hoarders averaged 78.7 square centimeters of pollen in the first generation, while low-pollen hoarders averaged 22.6 square centimeters of pollen—a difference of 56.1 square centimeters. Differences between lines increased in the second, third, and fourth generations: by the fourth generation, high-pollen hoarders averaged 287.1 square centimeters of pollen while low-pollen hoarders averaged 65.8

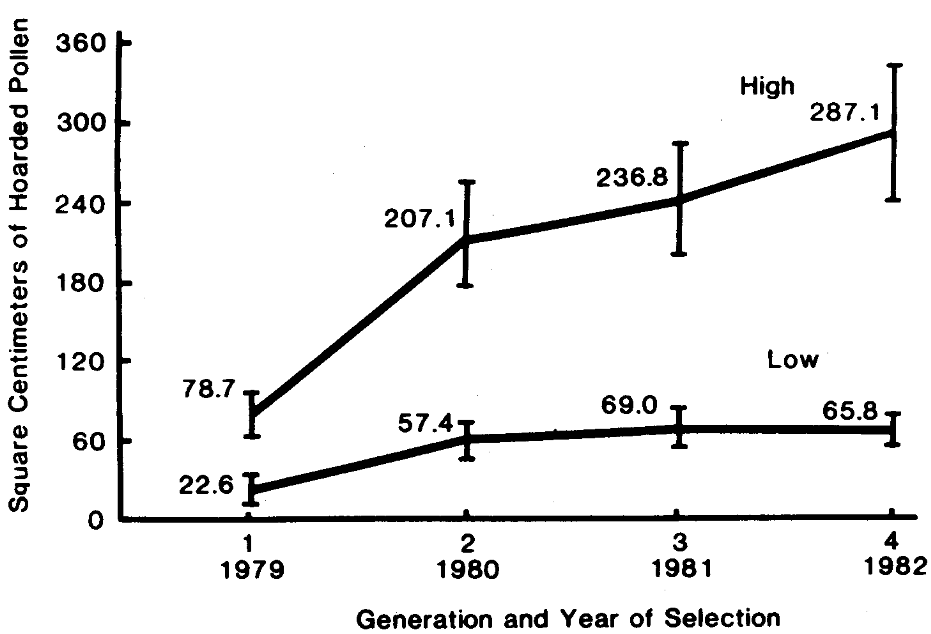

FIGURE 2 Two-way selection for high and low levels of hoarded pollen measured in square centimeters over four generations with 95 percent confidence intervals.

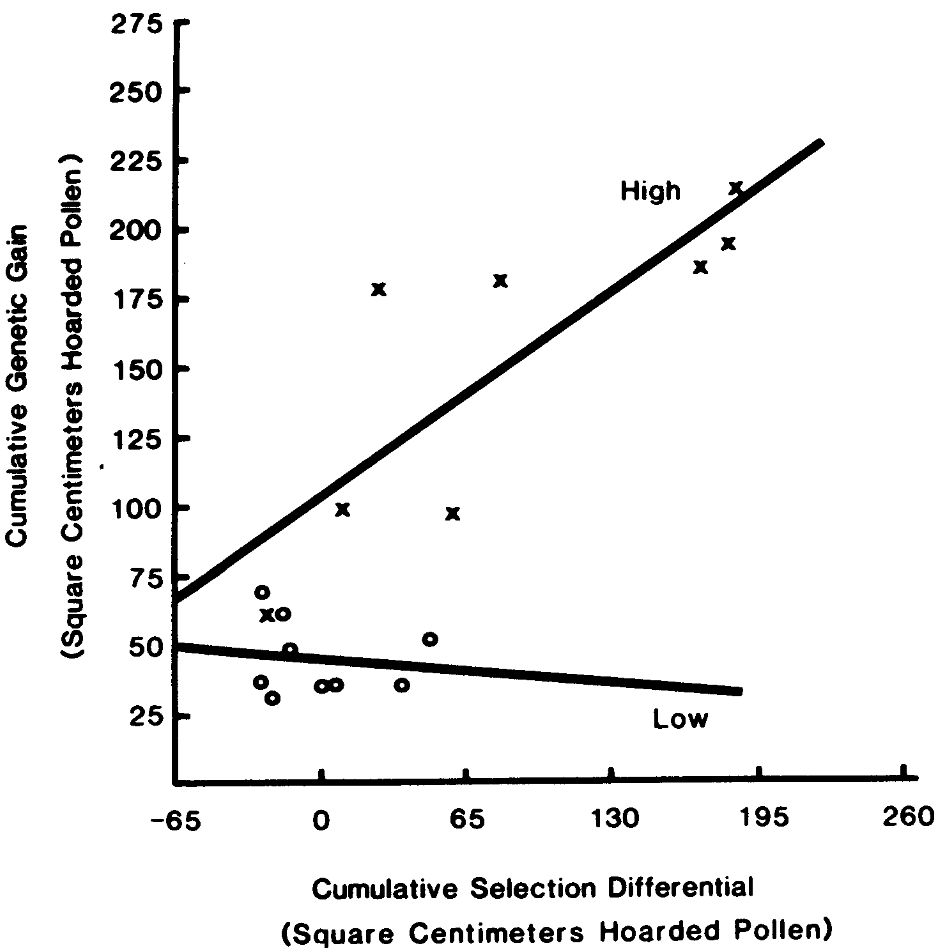

FIGURE 3 Cumulative genetic gain plotted against cumulative selection differential for pooled observations for high and low pollen-hoarding sublines over four generations of selection (x = high and o = low).

square centimeters—a difference of 221.3 square centimeters.

During each year of selection there were no significant differences between the high- and low-line bees in bee populations, amounts of brood, and quality of brood.

Realized heritability estimates were calculated from generation means plotted against a cumulative selection differential for both high- and low-pollen hoarders (see Figure 3). Systematic changes due to environmental influences are included in these estimates. The realized heritability estimate for high-pollen hoarders is 55.6 percent ± SE 16.1 percent; and the realized heritability estimate for low-pollen hoarders is 6.3 percent ± SE 19.0 percent. This estimate for low-pollen hoarders is not significantly different from zero. Heritability estimate of divergence is 49.5 percent ± SE 20.3 percent.

Full-sized colonies

Amounts of pollen hoarded by high- and low-pollen hoarders were significantly different during each of the six inspection periods (see Table I). High-line colonies hoarded from two times as much pollen during the first inspection (7–15) to 13 times as much pollen during the last inspection (10–18).

Discussion

Two distinctly different lines of honey bees were produced with two-way selection for high- and low-pollen hoarders. Marked separation exhibited by these lines suggests that the heritability of this trait is high. Genetic gains of the lines were different, but such asymmetrical progress was not unexpected (see, for example, Falconer[2]).

The inheritance pattern of the pollen-hoarding trait seems similar to the inheritance pattern Nye and Mackensen[8] hypothesized for the alfalfa pollen-collecting trait. Polygenic inheritance involving genes that are additive is suggested by the steady improvement of the high pollen-hoarding line over four generations of selection. Such inheritance also is suggested by hoarded-pollen data measured from random-mated colonies shown in Figure 1; these data are normally distributed.

If the trait is polygenic, continued selection for high-pollen hoarding may produce bees that hoard even more pollen. An upper limit to high-pollen hoarding would be reached when hoarding of pollen interfered with colony fitness. Colony fitness, probably, would be lowered if a colony reduced the space for brood rearing by filling the brood nest with pollen, or if a colony hoarded only pollen instead of honey. Colonies could survive under these conditions only if comb space for brood rearing and/or combs of honey were provided from an outside source.

There also is a lower limit to the amount of pollen that a colony needs for survival. Colony survival is decreased if pollen stores or honey stores are insufficient to ensure normal brood production or colony maintenance. Selection for low-pollen hoarders might have reached such a lower limit. Continued selection for the low pollen-hoarding trait, if they are near such a lower limit, is expected to produce little, if any, progress under the testing conditions used. Yet, selection for the tendency to hoard even smaller amounts of pollen might be possible, if colonies are given sufficient amounts of pollen to ensure colony survival. With this method further selection could produce honey bees that rarely hoard pollen.

Genetic variability of the pollen-hoarding behavior probably accounts for some of the honey bee's success. For example, in areas in which pollen dearths are frequent, high-pollen colonies would probably be more successful than low-pollen colonies; and in areas in which pollen sources are abundant, low-pollen colonies would probably be more successful than high-pollen colonies. Many behaviors contribute to the success of the honey-bee colony: nectar hoarding, thermoregulation, and colony defense—to mention just a few. But pollen-hoarding is one of the most important behaviors because pollen provides the chief source of protein, fats, and minerals to the honey-bee diet.

References

1. COLLINS, A. M., T. E. RINDERER, J. R. HARBO, and M. A. BROWN. Heritabilities and correlations for several characteristics in the honey bee. *J. Hered.* 75:135-140. 1984.
2. FALCONER, D. S. Introduction to Quantitative Genetics, 2nd ed., Longman Group Limited, Burnt Mill, Harlow, Essex, UK. p. 190-192. 1981.
3. FILMER, R. S. New Jersey State Agric. Exper. Sta., 52nd Annual Report. p. 228-238. 1931.
4. HUTSON, R. New Jersey State Agric. Exper. Sta., 51st Annual Report. p. 176-182. 1930.
5. KULINCEVIC, J. M. and W. C. ROTHENBUHLER. Selection for resistance and susceptibility to hairless-black syndrome in the honey bee. *J. Invert. Path.* 25:289-295. 1975.
6. MACKENSEN, O. and W. P. NYE. Selecting and breeding honey bees for collecting alfalfa pollen. *J. Apic. Res.* 5:79-86. 1966.
7. —— and ——. Selective breeding of honey bees for alfalfa pollen collection: sixth generation and outcrosses. *J. Apic. Res.* 8:9-12. 1969.
8. NYE, W. P. and O. MACKENSEN. Selective breeding of honey bees for alfalfa pollen: fifth generation and backcross. *J. Apic. Res.* 7:21-27. 1968.
9. —— and ——. Selective breeding of honey bees for alfalfa pollen collection: with tests in high and low alfalfa pollen collecting regions. *J. Apic. Res.* 9:61-64. 1970.
10. POLHEMUS, M. S., J. L. LUSH, and W. C. ROTHENBUHLER. Mating systems in honey bees. *J. Hered.* 16:151-155. 1950.
11. ROTHENBUHLER, W. C., J. W. GOWEN, and O. W. PARK. Recent work in honey-bee genetics, with preliminary consideration on the breeding of honey bees for pollination. Proc. 8th Ann. Mtg. N. Cent. States Br. Ent. Soc. Am. p. 45-46. 1953.
12. ——. A technique for studying genetics of colony behavior in honey bees. *Am. Bee J.* 100:176-198. 1960.