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ORIGINAL RESEARCH ARTICLE

Comparisons of pollen substitute diets for honey bees: consumption rates by colonies and effects on brood and adult populations.

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Summary

Commercially available pollen substitute diets for honey bees (*Apis mellifera* L.) were evaluated for consumption and colony growth (brood and adult populations) and compared with pollen cake and high fructose corn syrup (HFCS). Two trials were conducted; the first for 3 months during the fall and winter and a second for 2 months in the summer. Three diets were tested in Trial 1 (Diet-1, Diet-2, and Diet-3 (liquid and patty form)) and Diet-2 and Diet-3 (patty) in Trial 2. In both Trials, Diet-2 and Diet-3 patty were consumed at rates that were comparable to pollen cake. Colonies consumed significantly less Diet-1 than the other diets. There was a significant relationship between the amount of diet consumed and the change in brood area and adult population size in both Trials. Colonies fed Diet-3 patty produced significantly more brood than those fed pollen cake or any other diet in Trial 1. The lowest brood production occurred in colonies fed Diet-1 or HFCS. Adult populations in colonies fed Diet-3 liquid or patty did not differ from those fed pollen cake, and were significantly larger than colonies fed Diet-1 or Diet-2. In Trial 1, when some pollen was being collected by colonies, Diet-2 and Diet-3 did not differ from pollen cake in brood or adult population growth.

Comparación de dietas a base del sustitutivo de polen para abejas: tasas de consumo por colonia y efectos sobre la población adulta y la cría.

Resumen

Se evaluaron dietas a base de un sustitutivo de polen comercial para abejas (*Apis mellifera* L.) para consumo y crecimiento de la población de abeja adulta y cría comparándolas con una dieta a base de pastel de polen y jarabe de maíz con alto contenido en fructosa (HFCS son sus siglas en inglés). Se realizaron dos experimentos: el primero durante tres meses en otoño y el invierno y el segundo durante dos meses en verano. Se aplicaron tres dietas en el primer experimento, denominadas Dieta 1, Dieta 2 y Dieta 3 (en forma líquida y semisólida), mientras que en el segundo experimento se aplicaron las Dietas 2 y 3 (en forma semisólida). La Dieta 2 y 3 semisólidas fueron consumidas en porcentajes similares al pastel de polen. Las colonias consumieron en menos cantidad la Dieta 1 en comparación con las otras. Hubo una relación significativa entre la cantidad de Dieta consumida y los cambios en el área de cría y el tamaño poblacional de la abeja adulta en ambos tratamientos. Las colonias que consumieron la Dieta 3 semisólida, tuvieron un significativo incremento en la producción de cría al contrario de aquellas que se alimentaron con el pastel de polen ó cualquier otra Dieta en el experimento 1. La producción de cría más baja se observó en las colonias con la Dieta 1, a base de alta

fructosa. La población de abeja adulta en las colonias que se alimentaron con la Dieta 3, líquida ó semisólida no presentó diferencias de aquellas que se alimentaron con pastel de polen, y fueron significativamente más grandes que las colonias que consumieron la Dieta 1 ó 2. En el experimento 1, cuando algo de polen fue recolectado por las colonias, las Dietas 2 y 3 no presentaron diferencias con respecto a la Dieta con el pastel de polen en el crecimiento poblacional de la abeja adulta y la cría.

Keywords: colony, brood rearing, nutrition, *Apis mellifera*, protein, supplementary feeding

Introduction

Honey bee (*Apis mellifera* L.) colonies need pollen and nectar to fuel foraging flights, generate heat to thermoregulate their nest, and to rear brood. Nectar is a carbohydrate source, while pollen supplies the bees with the protein, lipids, vitamins and minerals needed to rear larvae (DeGroot, 1953; Manning, 2001). The quality of pollen affects the number of eggs that are laid by the queen and the proportion that are reared to adults (Allen and Jeffree, 1956; Doull 1973; Hellmich and Rothenbuhler, 1986). For colony productivity, it is critical that honey bees have access to high quality nutritional sources.

Meeting the nutritional requirements of commercially managed colonies has become more challenging, especially if they are used for pollination. Colonies are placed in monocultures where the amount of pollen might be limited or nutritionally inadequate. Land-use practices also affect the diversity and availability of flowering plants that supply nectar and pollen (Kremen *et al.*, 2007). During times when insufficient amounts of pollen are available from plants, commercially produced bee diets can supplement the available pollen and provide a practical method for sustaining brood rearing in honey bee colonies (Matilla and Otis, 2006).

Beekeepers feed colonies to stimulate brood rearing in the late winter or early spring, or to relieve dietary stress during times when adequate pollen from blooming plants is not available or is of marginal nutritional value (e.g. Nabors, 2000; Matilla and Otis, 2006). The purpose of our study was to evaluate different commercially available bee diets by measuring consumption and colony growth (brood and adult populations) and comparing them to pollen and a carbohydrate only diet of high fructose corn syrup (HFCS).

Materials and methods

Colonies and trials

The first trial in this study was conducted for 12 weeks from November 2006 until February 2007 in an Adee Honey Farm apiary at Arvin, California. The second trial was conducted with a different set of colonies at the Carl Hayden Bee Research Center apiary in the Santa Rita Mountains in Arizona for 6 weeks from June until August 2007. Trial 1 was ended just before moving the colonies into almond orchards for pollination. Trial 2 was ended when flowering plants became available to the bees and supplemental feeding was no longer necessary. European honey bee (*Apis mellifera ligustica*) colonies were used in both trials. The colonies were maintained in two deep Langstroth hive bodies. Measurements of brood and bee population size were made at the start of the study, and colonies were equalized to ensure similar numbers of bees and brood. Feeding treatments were assigned randomly to the colonies in both trials. Twenty colonies were used for each diet treatment in Trial 1 and six for each treatment in Trial 2.

Diets and their formulations

In Trial 1, colonies were fed one of three commercial diets (Diet-1, 2, or 3), a mixture of pollen collected by colonies in southern Arizona and formed into pollen cakes, or HFCS (Pro-Sweet liquid sugar blend; Mann Lake Ltd. Hackensack, Minnesota, USA). In Trial 2, colonies were fed Diet-2, Diet-3 (patty) or pollen cake. The commercial diets did not contain any natural pollen.

Diets were fed in either solid patty or liquid form. The commercial diets were purchased as patties (Diet-2) or mixed according to the manufacturer instructions (Diet-1 and Diet-3). Based on the protein and carbohydrate percentages of the diets, after mixing the Diet-1 patties contained about 26% protein and 42% carbohydrate, and Diet-3 was 16.5% protein and 66% carbohydrate. Diet-2 patty was 8.31% protein and 75.97% carbohydrate (analysis by Midwest Laboratories Inc., Omaha Nebraska, USA).

Patties were weighed prior to feeding them to colonies. Each patty weighed about 454 g with a thickness of 0.65 cm. Diet-3 liquid was made by mixing 227g of diet powder into 3.8 l of HFCS. The liquid was fed to colonies in division board or hive top feeders immediately after being mixed.

Diet consumption and growth rates of colonies were compared with HFCS alone (negative control) or pollen (positive control). Colonies fed HFCS received 3.8 l of a 10% solution of Cargill Number 55 syrup (Cargill Inc., Minneapolis, Minnesota, USA) in division board feeders. The pollen fed as the positive control was collected by bees in the Sonoran desert in Arizona, USA. Pollen was combined with equal parts (by weight) of granulated sucrose, Drivert sugars (a mixture of equal parts of sucrose and dry fructose) and tap water. The mixture was made into patties (hereafter referred to as pollen cakes) by first combining the pollen with water until the pollen pellets were suspended. The entire amount of sucrose was then added to the pollen slurry and mixed until smooth. Drivert sugar then was added and mixed until the batter had a dough-like consistency and pulled away from the sides of the bowl. The mixture was rolled between two sheets of wax paper into 454g patties with a thickness of 0.65 cm. Pollen cakes and other diets in patty form were stored in a -20°C freezer until fed to colonies. Patties were thawed prior to placing them into colonies. All the colonies fed patty diets were also given 3.8 l of a 10% solution of HFCS in in-hive feeders at 3 week intervals.

Feeding regimes and estimates of consumption

In Trial 1, colonies were fed diets in either patty form (Diet-1, 2, or 3 patty or pollen cake) or liquid feed (Diet-3 liquid or HFCS).

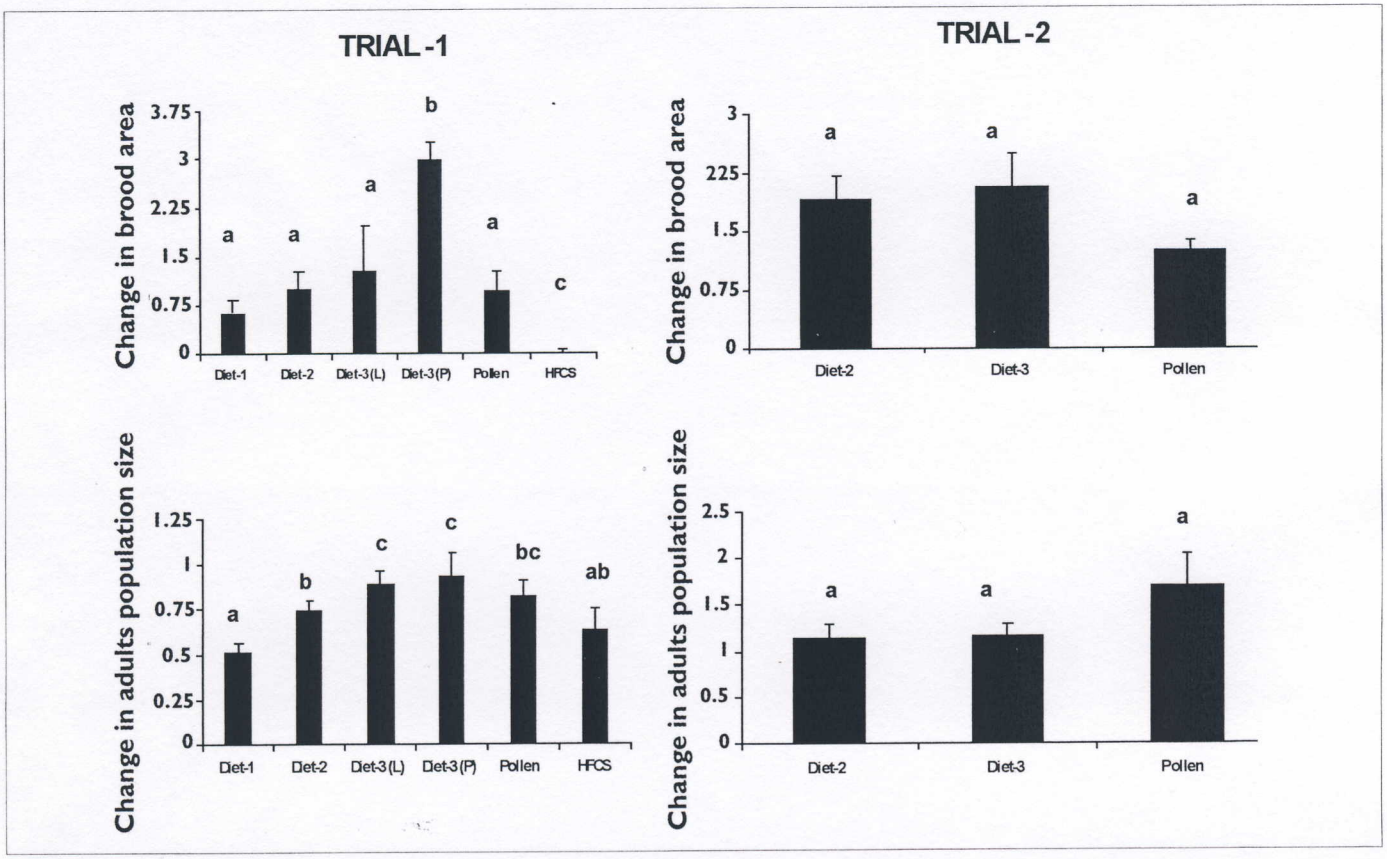

Fig. 2. Average proportional change in brood area and adult population size in European honey bee colonies fed different diets for 12 weeks in Trial 1 and 6 weeks for Trial 2. Proportional change in brood area (B) or adult worker population (A) was estimated in colonies using the equation: [B(t+1) / B(t)] and [A(t+1) / A(t)] where B(t) or A(t) are the population estimate at the start of the study and (t+1) is the estimate at the end. Diet-3 (L) is a liquid formulation of Diet-3, Diet-3 (P) is a solid patty formulation. HFCS is high fructose corn syrup. Columns labelled with the same letters are not significantly different at the 0.05 level as determined by a Fisher's LSD test. There were no difference among diets in their effects on brood or adult population change in Trial 2 ($F = 2.39$, d.f. = 2,16, $p = 0.123$; $F = 2.05$, d.f. = 2,17, $p = 0.159$ respectively).

Discussion

Pollen substitute diets can be effective in stimulating honey bee colonies to rear brood (Mattila and Otis, 2006; Nabors, 2000; Standifer *et al.*, 1973), but they must be both palatable to bees and nutritious. All diets tested here with the exception of Diet-1, were similar to pollen cake in their consumption by bees. However, not all diets were equally effective in stimulating brood rearing or population growth of adult bees. Diet-2, Diet-3 and pollen were consumed at equivalent rates in both Trials. In Trial 1, however, significantly more brood was reared and there were larger adult populations in colonies fed Diet-3 patties compared with those fed the other diets. These results suggest that differences in the nutritional quality of the diets (i.e., amounts of protein and carbohydrate) and perhaps the digestibility and accessibility of their nutrients to worker bees influence the amount of brood that can be reared even when consumption rates are similar.

In addition to nutritional factors, brood rearing and population growth in colonies are affected by the quality of the queen and the size of the adult worker population (Winston, 1987; DeGrandi-Hoffman *et al.*, 1989). In our study, the average initial adult population size was similar across all diet treatments, so the effects should have been the same regardless of the diet being fed. There might have been some variation among queens in the number of eggs they could potentially lay per day and this might have affected our results. Because of the highly significant slopes in lines describing the relationship between the amount of diet consumed and the increase in brood areas and adult populations, we can, however, be confident that the diet being fed had a large influence on brood production and colony population growth.

The availability of natural pollen differed during the two Trials and this might have affected the response of the colonies in terms of brood rearing and adult population growth. In Trial 1, the only food source available to the bees was the diets we fed, and colonies differed in brood production and adult population growth. In Trial 2 when some flowering plants were in bloom and bees could collect pollen and nectar from the field, brood rearing did not differ among the diets. Apparently if some pollen is available, diets can work equally well provided they are consumed at sufficient rates. This might be because nutrients that are missing in some diets are provided in the pollen collected by the bees. Alternatively, some nutrients in diet supplements might not be digested as readily as when they are present in pollen. For example, linoleic acid and manganese in diets do not accumulate in bees to the levels found when they are fed pollen (Manning, 2007).

Adult bee populations did not increase during the 12 week study period in Trial 1 (i.e., all averages were <1.0) (Fig. 2). Adult populations were about 50% of their starting size in colonies fed either Diet-1 or the HFCS control. The smallest declines in adult populations occurred in colonies fed Diet-3 in either liquid or patty form or in those fed pollen cake. Adult populations increased during Trial 2, where there were no significant differences in the percent increase in adult population size among the different diets ($F = 2.05$, d.f. = 2, 17, $p = 0.16$).

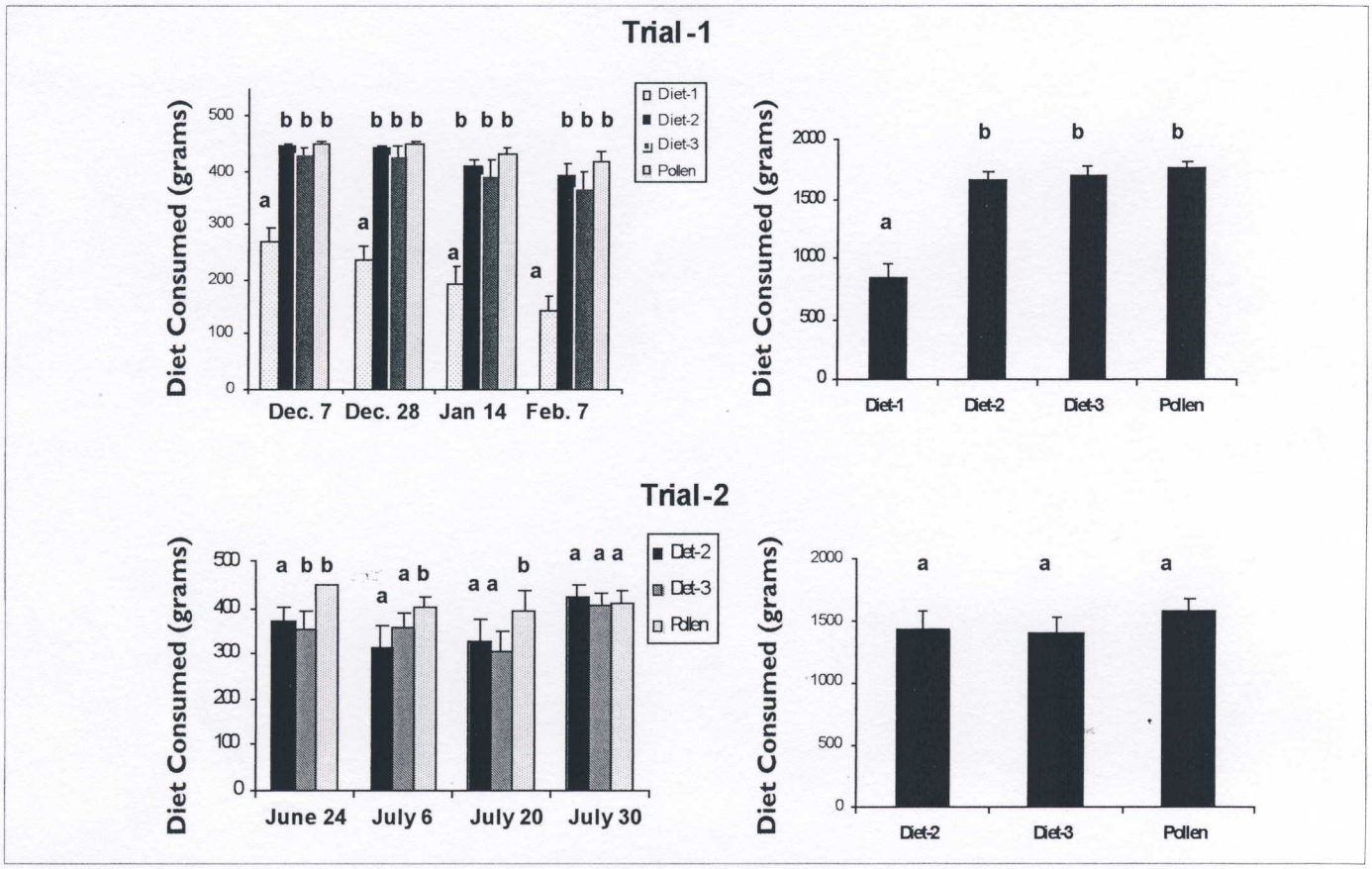

Fig. 1. Average amounts of honey bee diets consumed by colonies during 3 week intervals and for the 12-week study period in Trial 1 and at 10-12 day intervals and for the 6 week study period for Trial 2. Columns labelled with the same letters are not significantly different at the 0.05 level as determined by Fisher's LSD test. No significant differences were found in the amounts of the different diets consumed during Trial 2.

Table 1. Linear regressions of the change in honey bee brood area and size of the adult population in colonies fed different supplemental diets over a 12 week period for Trial 1 and a 6 week period for Trial 2.

Type of diet	Trial	Brood area				Adult population			
		Slope	T	d.f	p	Slope	T	d.f	p
Diet-1	1	0.062	4.28	18	<0.0001	0.063	16.06	18	< 0.0001
Diet-2		0.093	7.52	1	<0.0001	0.075	19.64	17	<0.0001
Diet-3 (liquid)		0.317	8.06	13	<0.0001	0.255	11.52	16	<0.0001
Diet-3 (patty)		0.165	7.65	12	<0.0001	0.086	11.67	16	0.0001
Pollen cake		0.078	4.56	12	0.001	0.079	14.48	16	<0.0001
Diet-2	2	0.143	9.70	5	<0.0001	0.105	13.15	5	<0.0001
Diet-3 (patty)		0.148	8.55	5	<0.0001	0.103	11.65	5	<0.0001
Pollen cake		0.108	12.3	6	<0.0001	0.130	7.70	6	<0.0001

Colonies were fed liquid diet (3.8 l) at 3 week intervals. Before feeding the colonies, the unconsumed portions of the patty diets were removed from the colony and weighed to estimate consumption. The amount of liquid Diet-3 consumed was estimated by subtracting the amount still in the feeder from the initial amount (i.e., with 3.8 l of diet). New liquid feed or patty then was placed in each colony. In Trial 2, consumption of Diet-2, Diet-3 patty or pollen cake was measured at 2 week intervals using the same protocol as described above for Trial 1.

Brood and adult bee estimates

Brood measurements were made just prior to the first feeding, midway through the study, and three weeks after the last feeding. Measurements were made using a grid with 5 cm x 5 cm squares that covered the entire side of a comb. The grid was placed over each side of a brood comb and the number of squares with brood was counted. Measurements of all frames with brood were summed for each colony. Adult bee populations were made by estimating the number and area of comb covered with bees. We totalled the area covered with bees for all frames to estimate the number of frames in the colony covered with bees.

Statistical analysis

The amount of diet consumed by colonies for each feeding interval was compared using a two-way analysis of variance with sampling interval and type of diet as factors. The weight of diet consumed during the study period was compared among treatments using a one-way analysis of variance. A t-test was conducted to determine whether there was a difference in consumption of the Diet-3 liquid when it was fed in either top or in-hive feeders.

Change in brood area (B) or adult worker population (A) was estimated in colonies using the equation: [B (t+1) / B (t)] and [A (t+1) / A (t)] where B (t) or A (t) are the population estimate at the start of the study and (t+1) is the estimate at the end. Changes in brood area and adult population were compared among diet treatments using one-way analysis of variance.

We determined whether there was a significant correlation between total amount of each diet consumed per colony and the increase in either brood area or adult population size using linear regression. Data were log transformed prior to the analysis to normalize variation. Separate analyses were conducted for each Trial.

Results

Diet consumption

During Trial 1, flowering plants were not in bloom and the only carbohydrate and protein sources for the bees were from the diets we provided. Colonies typically consumed more than 400g of Diet-2, Diet-3 or pollen cake during each 3 week interval between feedings compared with less than 300g of Diet-1 (Fig. 1). A two-way analysis of variance indicated that patty diet consumption was affected by the type of diet ($F = 110.97$, d.f. = 3, $p < 0.0001$) and time when it was fed ($F = 8.13$, d.f. = 3, $p < 0.0001$), but not by interactions between the two ($F = 0.94$, d.f. = 9, $p = 0.49$). Colonies consumed significantly less Diet-1 than the other diets during each feeding interval and during the 12 week study period ($F = 48.4$, d.f. = 3, 71, $p < 0.0001$). Consumption of Diet-2 and Diet-3 was similar to pollen cake. (Fig. 1). Colonies fed liquid Diet-3 consumed an average of 12.1 l when fed with bottle feeders and this was significantly greater than the average amount (7.04 l) consumed when fed using the division board feeder ($t = 6.69$, $p < 0.0001$, d.f. = 7).

In Trial 2, some pollen was being collected by colonies, but the bees still consumed more than 300g of the diets we fed them every 2 weeks. Consumption rates were affected by type of diet ($F = 4.36$, d.f. = 2, $p = 0.017$) but not the week of feeding ($F = 2.66$, d.f. = 3, $p = 0.056$) or interactions between the two factors ($F = 0.75$, d.f. = 6, $p = 0.608$). Colonies consumed more pollen cake than either Diet-3 or Diet-2 until the fourth week of the study. Over the entire 6 week period, however, the average amount of diet consumed by the colonies did not differ among the various types ($F = 0.7$, d.f. = 2, 16, $p = 0.513$) (Fig. 1).

Change in brood and adult bee populations

The average brood area and adult population size at the beginning of the study did not differ among groups of colonies chosen for each type of diet in Trial 1 (adult population: $F = 1.76$, d.f. = 5, 102, $p = 0.129$; brood area: $F = 0.85$, d.f. = 5, 102, $p = 0.515$) or Trial 2 (adult population: $F = 0.16$, d.f. = 2, 17, $p = 0.85$; brood area: $F = 0.45$, d.f. = 2, 16, $p = 0.65$). In Trial 1, colonies had an average of 8.7 frames of adult bees and 134 cm^2 of sealed brood, and in Trial 2, 8.0 frames of adult bees and 512 cm^2 of brood. Changes in brood areas and adult population sizes did not differ between colonies fed liquid Diet-3 in either in-hive or top feeders ($t = 1.41$. $p = 0.2$, d.f. = 8; $t = -0.45$, $p = 0.66$, d.f. = 17 respectively) so data were combined for subsequent analyses.

There was a positive relationship that was highly significant ($p < 0.001$) between the amount of food consumed and increase in brood area and change in adult population for all diets in both Trials (Table 1). Brood in colonies was affected by whether or not a pollen substitute diet was being fed. Only 31% of the colonies fed HFCS still reared brood by the end of the study compared with more than 90% of the colonies fed Diet-2, Diet-3 (patty or liquid) or pollen cake. Eighty four percent of the colonies fed Diet-1 were rearing brood by the end of the study.

In Trial 1, colonies fed Diet-3 patty had more than twice as much brood at the end of the study period than at the start and this increase was significantly greater than for the other diets (Fig. 2). Brood areas increased slightly (change in brood > 1.0) in colonies fed Diet-1, Diet-2, or liquid Diet-3 over the treatment period and were not significantly different from colonies fed pollen cake. Brood measurements taken midway through the trial (data not shown) indicated that there was a slight increase in the brood area in colonies fed Diet-1, but by the end of the study, brood areas declined in those colonies. Brood areas in colonies fed pollen cake declined midway through the trial, but then increased and by the end of the study were at levels that did not differ from other protein sources except Diet-3 patty. Colonies fed HFCS declined throughout the study and by the end brood areas were significantly smaller than colonies fed other diets. In Trial 2, there was no significant difference in brood area among colonies fed the different diets ($F = 2.08$, d.f. = 2, 16, $p = 0.16$) (Fig. 2).

The performance of all diets was compared with pollen cake because we expected pollen to be the most palatable and stimulate the greatest increases in brood rearing and adult population growth. Diet-3 patty, Diet-2 and pollen cake were equally palatable in our trials. Brood rearing in colonies fed Diet-2 was similar to pollen cake. However, in Trial 1 of our study the increases in brood area in colonies fed Diet-3 were significantly greater than in those fed pollen cake. There are several possible explanations for this result. One possibility is that the pollen lost some of its nutritional value while in storage (Hagedorn and Moeller, 1968a). Amounts of some key nutrients such as pantothenic acid are reduced in stored pollen (Hagedorn and Moeller, 1968b). The pollen we used was less than a year old and was kept frozen but might have had some degradation of nutrients that could account for the lower brood rearing rate. The pollen that was collected also could have had limited amounts of key nutrients to rear brood because of the floral sources. The pollen was collected in the Sonoran desert of Arizona (USA) where plant species are known to have relatively low protein levels (Schmidt *et al.*, 1987). Another possibility is that the bees in colonies fed pollen cake were stimulated to rear more brood than they could sustain. Colonies fed pollen cake usually consumed the entire portion given to them during the 3 week interval. In the absence of pollen caused by rapid consumption of the pollen cake, the workers might have consumed larvae and thus reduced the brood area until more food was provided (Schmickl and Crailsheim, 2001; van der Steen, 2007).

Our study indicates that with adequate nutrition, colonies can be stimulated to rear brood and sustain it even in the late fall or early winter when brood rearing rates are at their lowest. This finding is particularly important for the management of colonies used for pollination of crops that bloom in the late winter like almonds or in the early spring such as many fruit crops.

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