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Author(s): C. R. Ribbands

Source: *Journal of Animal Ecology*, Nov., 1951, Vol. 20, No. 2 (Nov., 1951), pp. 220-226
Published by: British Ecological Society

Stable URL: https://www.jstor.org/stable/1541

THE FLIGHT RANGE OF THE HONEY-BEE

By C. R. RIBBANDS

Bee Research Department, Rothamsted Experimental Station, Harpenden

INTRODUCTION

There are numerous records in beekeeping literature of honey-bees gathering honey from good crops growing 5 miles or more from their hives. Eckert (1933) even recorded colony gains from crops growing 7 miles away.

The usual flight range has been believed to be less than this, but most authorities have agreed that it is considerable. In Britain, Manley (1948) wrote that it covered '5 to 6,000 acres at least' and Wedmore (1932, p. 95) considered that 'the economical distance for honey-gathering is about 1 to $1\frac{1}{2}$ miles'. N.A.A.S. Advisory Leaflet no. 344 (1949) stated that 'a locality that provides pollen and nectar continuously from early spring to autumn, within a radius of about 2 miles, is ideal for bees'. In the United States, Dadant (1946) suggested that apiaries might be placed 2–4 miles apart in hilly country, but that in open country they should be from 5 to 6 miles apart. Root (1947), however, stated that bees usually do not fly more than $1\frac{1}{2}$ miles. He added that they would not go more than half a mile if they could obtain sufficient nectar within that distance, but that usually there was insufficient pasturage there.

The present experiments demonstrate that the economical distance for honey-gathering is sometimes not more than one-quarter of a mile; they emphasize the importance of weather in determining the flight range of the honey-bee.

METHOD

Crops on well-defined areas, as far as possible in isolation from other nectar-producing crops, were selected. Three apiary sites were then chosen for each experimental crop—one on the edge of the crop, one $\frac{3}{8}$ mile from that edge and one $\frac{3}{4}$ mile from it (distances measured from 6 in. O.S. maps). The colonies of bees chosen for each experiment were first sited in one group upon some preliminary crop at least 5 miles away. They were weighed at the beginning and end of their sojourn there, and the gain or loss of each colony was calculated. These gains or losses were arranged in order of magnitude, and the colonies were divided into three subequal groups, in terms of these weights. One group was then placed at each of the experimental sites—0, $\frac{3}{8}$ and $\frac{3}{4}$ mile from the crop. Each colony was again weighed at the end of the flowering period of the experimental crop, and its net gain or loss calculated. From these changes the average gain or loss of each group was deduced, and comparison of these averages provided the required experimental result.

In 1949 all the colonies were removed to one site on a post-experimental crop, and subsequent weighings determined the gains or losses of each group upon that crop. The results were then analysed statistically; these analyses were ultimately discarded as unnecessary, in view of the consistency and magnitude of the results.

Eight experiments were conducted. The first six were made upon three permanent crops—apple, lime and heather—in 1949 and 1950. The identical sites were used in successive years. Two additional experiments were made upon annual crops—cabbage and onion—in 1949. They could not have been exactly repeated.

The description just given is of the general plan, but some slight modifications were necessary. For the heather and onion experiments no suitable site was obtainable at $\frac{3}{8}$ mile, so results at 0 and $\frac{3}{4}$ mile only are compared. In several experiments more bees were placed on the crop than at the distant sites, but the same attempt was made to produce a similar pre-experimental average for each group. In the second heather experiments an error vitiated this average, but this did not affect the final result.

THE EFFECT OF FORAGING DISTANCE UPON COLONY GAINS

The results from the apple crop are given in Table 1. The apples were grown in a modern cleanly cultivated 70-acre orchard. The bees at $\frac{3}{8}$ mile could fly to this orchard, to a much smaller orchard or to a group of willows about the same distance away in another direction; with this exception the competing flora was sparse, most of the area being ploughed. In 1949 there was a substantial gain in colony weight both upon the crop and at $\frac{3}{8}$ mile, but the gain at $\frac{3}{4}$ mile was less by 85%. In 1950 the small gain on the crop compared with a loss at $\frac{3}{8}$ mile and a substantial loss at $\frac{3}{4}$ mile. In 1950, when the gain obtained was smaller, the absolute effect of distance was greater—a difference of nearly 15 lb. instead of one of 11 lb. between the colonies on the crop and those $\frac{3}{4}$ mile away.

The results from the lime crop are given in Table 2. The site was a double avenue of lime trees, 1 mile long. Bees were placed under the line of trees, and the alternative sites were measured at right angles to the avenue, from its centre. There were no isolated lime trees on the experimental side of the avenue but there was a considerable competing flora. In cooler weather this was mainly blackberry, which grew in fair quantity near the that obtained at the crop, but during separate weeks this percentage varied from 1 to 79%. In both years the gains during the second week were substantially greater than those during the first week; although in both years the weather in the second week was better, this difference is mainly attributed to change in the state of the crop, which was at its peak of flowering during the second week. In the second week of 1950 the crop was greater

Table 1. *Gain in weight of colonies at apple crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb.: Before crop	During crop	After crop	Daily weather means
	1949:	11–22 Apr.	2–12 May	12 May–6 July	2–12 May
0	4	0	13·3 ± 2·7	46·5	sunshine 7·8 hr., max. temp. 58·1° F.
3/8	4	0·7	10·5 ± 2·6	40·3	
3/4	4	− 0·9	2·0 ± 1·4	50·0	
	1949–50:	2 Nov.–2 Feb. (winter loss)	28 Apr.–18 May	18 Apr.–1 May	28 Apr.–18 May
0	8	−16·5	3·0 ± 2·2	7·9	sunshine 4·9 hr., max. temp. 59·3° F.
3/8	4	−16·2	− 4·4 ± 1·6	11·9	
3/4	4	−15·9	−12·2 ± 1·1	6·9	

Table 2. *Gain in weight of colonies at lime crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb.: Before crop	During crop		
	1949:	16–28 June	28 June–7 July	7–15 July	Total
0	3	13·50	15·6 ± 2·1	40·2 ± 4·6	55·9 ± 6·0
3/8	3	16·9	10·3 ± 2·3	43·7 ± 7·6	54·0 ± 9·5
3/4	3	17·2	5·9 ± 1·6	26·5 ± 8·2	32·5 ± 4·2
Daily weather means:					
sunshine (hr.):			9·01	9·33	
anemometer mileage:			85	77	
max. temp. (° F.):			73·9	76·9	
	1950:	16–30 June	1–8 July	8–15 July	Total
0	4	1·9	9·9 ± 2·2	25·4 ± 4·2	35·3 ± 5·9
3/8	4	1·7	2·3 ± 1·2	22·1 ± 2·8	24·4 ± 3·4
3/4	4	1·3	−0·1 ± 1·2	20·2 ± 3·8	20·1 ± 4·8
Daily weather means:					
sunshine (hr.):			2·95	9·25	
anemometer mileage:			55	78	
max. temp. (° F.):			64·2	70·1	

3/4 mile site; there was an abundant supply of white clover throughout the experimental area, and on warmer days this was sometimes worked.

The results for both years are divided into two separate weeks. For each of the 4 weeks the bees at the crop gained more than those sited 3/4 mile away, but the magnitude of this difference varied considerably. The combined results from both years showed that the gain at 3/4 mile was 58% of and the effect of distance substantially less than in the first week of 1949. Weather conditions seem insufficient to account for this difference, which indicates that the effect of distance tends to be reduced when the quality of the crop improves.

The heather was dominant over the top of a Welsh moor, 1400 ft. high, and covered many hundreds of acres. The 3/4 mile site was in the valley at 800 ft., and the bees there had to fly uphill to their crop. In 1949 there was no competing flora, either in the valley or on the moor; in 1950 the valley held a good crop of white clover when the bees were transported there, and only the earliest heather flowers were then in bloom. Since it was thought that this might vitiate the experiment, all the colonies were weighed on 20 August when the white clover had finished, and the heather had just come into bloom. All colonies then showed losses, but those on the moor had lost least (5·5 lb. against 9·3 lb.), showing that no appreciable yield had been obtained from the white clover. In 1949, a superb heather season, the 15% difference between the two sets of colonies was not significant, but in 1950, a bad heather season, the final recorded gain $\frac{3}{4}$ mile from the crop was only 10% of the gain recorded at the crop.

The two experiments on annual crops were both conducted in 1949. They are recorded in Tables 4 and 5. The onions occupied a 15-acre field. There was some competition from clovers and hedgerow flowers, but none from other cultivated crops. The cabbages occupied an 8-acre field, with no competing crops. It had been intended to leave the bees here for a long period, but the severe losses led to quick removal to a more desirable site, to avoid possible starvation.

For the cabbage experiment colonies of widely varying size were used. Upon the crop the stronger colonies gained a little weight while the weaker ones lost slightly (individual change on cabbage, +0·8, +0·5, +0·4, −1·1, −2·75 lb., followed by gains of 14·9, 17·9, 23·6, 5·6 and 1·25 lb. respectively, upon the subsequent crop). Away from the crop the stronger colonies lost most (individual losses at $\frac{3}{8}$ and $\frac{3}{4}$ mile from cabbage, 5·0, 4·6, 3·6, 2·9 and 2·3 lb., followed by gains of 29·5, 26·6, 10·9, 16·5 and 6·7 lb. respectively, upon the subsequent crop).

The results demonstrate that increases in foraging distance were consistently associated with decreases in colony gains; the magnitude of this effect was, however, very variable. At one extreme (Table 1, 1950) a distance of $\frac{3}{8}$ mile eliminated any nectar gains, while at the other (Table 3, 1949) the colony gain was reduced by only 15% at $\frac{3}{4}$ mile.

A comparison of the total unweighted colony gains from all five crops in 1949 shows that the colonies at the crops gained 166$\frac{1}{4}$ lb., while those

Table 3. *Gain in weight of colonies at heather crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb.: Before crop	Mean gain of colonies in lb.: During crop	Daily weather means
	1949:	15 July–4 Aug.	4 Aug.–20 Sept.	
0	7	34·6	59·6 ± 5·8	sunshine 5·9 hr., anemometer mileage 190, max. temp. 64° F.
$\frac{3}{4}$	3	37·3	51·2 ± 2·1	
	1950:	1–15 July	4 Aug.–20 Sept.	
0	8	22·1	25·6 ± 1·2	sunshine 4·6 hr., anemometer mileage 379, max. temp. 60° F.
$\frac{3}{4}$	4	30·3	2·45 ± 0·7	

Table 4. *Gain in weight of colonies at onion crop*, 1949

Miles from crop	No. of colonies	Mean gain in lb.: Before crops 12 May–6 July	Mean gain in lb.: During crop 7–30 July	Daily weather means
0	4	50·9	38·0 ± 5·7	sunshine 7·5 hr., max. temp. 76·0° F.
$\frac{3}{4}$	4	51·8	30·4 ± 7·5	

Table 5. *Gain in weight of colonies at cabbage crop*, 1949

Miles from crop	No. of colonies	Mean gain in lb.: Before crop 10 Mar.–14 Apr.	Mean gain in lb.: During crop 28 Apr.–5 May	Mean gain in lb.: After crop 5–23 May	Daily weather means
0	5	−5·2	−0·4 ± 0·6	12·7	sunshine 6·6 hr., max. temp. 57° F.
$\frac{3}{8}$	2	−5·2	−4·8 ± 0·01	28·0	
$\frac{3}{4}$	3	−5·4	−2·9 ± 0·3	11·4	

$\frac{3}{4}$ mile from the crops gained only $113\frac{1}{4}$ lb.—a reduction of 32%. In 1950, a poor honey year, the colonies at the three crops gained 65·6 lb., while those $\frac{3}{4}$ mile from the crops gained only 11·8 lb.—a reduction of 82%. The breeding rate of a colony partly depends upon the quantity of incoming forage (Nolan, 1925), so that improved early gains produce an increased population of bees for subsequent foraging; these calculations make no allowance for any cumulative effect of distance which could thus be produced.

THE RELATION BETWEEN COLONY GAINS AND INCOMING PROVENDER

Consideration of the causes of the effects of distance should be preceded by an interpretation of the extent to which the data are related to the actual quantities of forage which were brought into the hive. Every day each colony consumed, for its sustenance, a considerable quantity of both honey and pollen. The quantity of food so dissipated depended both upon the number of bees and the quantity of brood in each colony, and probably ranged between $\frac{1}{2}$ and $1\frac{1}{2}$ lb. per colony per day. The duration of most of the experiments was so short that this loss was similar in each group of colonies, irrespective of their distance from their crop. Therefore an equal addition to all the colony net gains will provide an estimate of the proportion of forage brought in at each distance.

This factor helps to explain the sensitivity of colony net gains to weather factors, the magnitude of the distance effect, and the variation in that magnitude. For instance, if it is supposed that the cost of colony sustenance averaged 1 lb. per day during the first week of the 1950 lime crop, when the colony net gains varied with distance from 9·9 to $-0·1$ lb., the amount of forage carried into the hive (ignoring surplus water) would then only have ranged from 16·9 to 7·1 lb. Thus the colony net gain might have been eliminated by a 42% reduction in incoming provender.

Increases in incoming forage are at most slightly reflected in increased requirements for sustenance; they will therefore reduce the magnitude of the distance effect upon colony net gains. With the fullest possible allowance for this relation there is still a wide variation, not thus accounted for, in the magnitude of the distance effect, and this provides the clue to its main cause, a factor which is itself variable—the weather.

THE ROLE OF WEATHER IN PRODUCING THE EFFECT OF FORAGING DISTANCE

To obtain information concerning the effects of weather during the 1950 lime experiment, daily records were kept. One colony at each distance was weighed each evening at sunset. These records were compared with the daily weather statistics from Rothamsted Experimental Station, 4 miles away, and also with the gains from a colony at Rothamsted, close to another avenue of limes (Table 6). The record of the latter colony is not directly comparable with that of the others, because the weights were taken (for another experiment) at 9.30 a.m. each morning.

As expected, water-loss by evaporation from nectar during the night subsequent to a heavy crop substantially affected the daily evening weighings (10 July); in addition, there was evidence that substantial loss might also occur on at least the second night (comparison of colonies 8 July, when the poor performance of the at-crop colony could be attributed to water losses from gains of 5–6 July; size of losses on 11 and 16 July). Such continued water-loss makes it difficult to correlate daily changes in weather conditions with those in colony gains. A feature of the daily record is the considerable effect upon the total gain of a few outstandingly good days. After allowing for the subsequent loss of water the honey yield obtained on 9 July must have been a substantial percentage of the total yield. The effect of distance varies considerably from day to day. On 9 and 13 July it was not visible, but on 5, 6, 12 and 15 July it was substantial. In all the latter instances the effect can be attributed to unfavourable weather, but the major role was played by different weather components on different days.

The records from the colony in Harpenden have been included because they are believed to illustrate another aspect of the effect of distance. The main experiment was in a country district, not flooded with bees, but the Harpenden colony was sited on the edge of a residential area overpopulated with bees. This difference could explain how on the two best flying days (9 and 13 July) there were increased gains in the country colonies but not in the Harpenden colony; in the latter the better weather was counterbalanced by more intense competition from bees sited farther from the crop.

It was not possible to obtain daily records of colony gains during other experiments, because no portable automatic weight-recording apparatus was available. However, when the total colony gains in the various experiments are compared with the average weather conditions then experienced much of the variation of the magnitude of the distance effects seems explicable. The considerable effect of distance during the first week of the 1950 lime flow is associated with low temperature and sunshine records, and the difference between the two heather experiments with less sunshine, lower temperature

Table 6. *Comparison of daily colony gains during lime crop, with weather records from Rothamsted ($3\frac{1}{2}$ miles south)*

	July 1950														
	1–4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Sunshine (hr.)	—	**0·0**	**0·8**	6·1	9·1	**12·1**	7·0	6·5	8·4	**9·3**	12·2	**1·8**	10·3	4·6	**2·2**
Maximum temperature (° F.)	—	**62**	**65**	71	75	**81**	67	66	68	70	68	66	67	65	69
Rain, hours (including following night)	—	0	3·3	0	0	3·5	4·0	0·4	0·6	3·3	0	9·0	0·1	0·4	0
Anemometer mileage	—	41	21	26	29	40	111	101	**137**	**36**	93	84	82	119	**120**
Weather generally	—	Bad	Bad	—	—	Good	—	—	Bad	Good	—	Bad	—	—	Bad
Gain in lb.															
Colony at crop	6·25	6·6	3·25	0·25	1·0	9·55	−1·0	1·75	7·4	4·1	1·0	3·5	−4·6	1·05	2·1
Colony at $\frac{3}{8}$ mile	−5·25	2·1	1·6	2·5	4·5	14·5	−5·0	−0·4	3·6	8·2	−0·1	0·75	−1·75	−1·0	1·0
Colony at $\frac{3}{4}$ mile	−3·25	1·9	1·9	2·5	3·25	9·25	−3·6	−0·75	3·6	6·75	1·0	0	−2·6	−0·4	0·6
Colony in Harpenden	0·05	2·6	2·3	2·25	4·45	3·2	−1·25	0·55	1·45	2·0	2·05	−2·7		−0·1	−1·05

Table 7. *Calculated effect of foraging distance upon nectar intake*

Minutes for complete trip, including unloading; hive on crop	... ...	5	15	30	60	120	240
Percentage reduction in nectar intake	At $\frac{3}{8}$ mile	39	18	10	5	3	1
	At $\frac{3}{4}$ mile	56	30	18	10	5	3

Table 8. *Five-minute counts of returning bees, near sunset*

G.M.T.	Distance from crop on 12 July			Distance from crop on 14 July		
	0	$\frac{3}{8}$ mile	$\frac{3}{4}$ mile	0	$\frac{3}{8}$ mile	$\frac{3}{4}$ mile
8.30	666	512	272	1110	952	279
8.45	372	118	14	244	122	48
9.00	112	15	2	19	0	2
9.15	80	0	0	0	0	0

and more wind during 1950; a small distance effect during the onion experiment is associated with warm weather, and a considerable effect during the cabbage experiment with cold weather.

THE ROLE OF FLYING TIME IN THE EFFECT OF FORAGING DISTANCE

Causes other than weather may contribute to the distance effect; the most obvious of these is the time and energy wasted by bees in flying the required distance. The energy consumed is negligible (Beutler, 1950), but the time may be appreciable. Since bees fly at about 14 m.p.h. (Park, 1923) it will take them about $3\frac{3}{14}$ min. for a return trip of $\frac{3}{8}$ mile; it is easy to calculate the effect of this increased foraging time upon nectar intake (Table 7).

To obtain an estimate of the likely magnitude of this cause, a large number of bees working from a hive at the 1950 lime crop were individually marked, and on 12–13 July, in favourable flying weather (see Table 9), a continuous watch was kept on the hive entrance and the times of incoming marked bees were recorded. Thirty-two records were obtained. Since the longest and the shortest times were likely to be least reliable, since they might include bees missed during an intermediate return, or bees returning without a full load, the upper and lower eight records were discarded. In the remaining half the mean time for the complete trip (including unloading) was $40{\cdot}3 \pm 5{\cdot}9$ min.

With such a foraging time, and when the magnifying effect of colony sustenance on net gains is allowed for, the effect of distance upon colony gain might have been completely accounted for, in some experiments, without postulating any other influence.

OTHER EXPERIMENTAL FACTORS

A minor factor is the effect of distance upon colony flight near sunset (20.13 G.M.T.). This was investigated by making simultaneous counts of the numbers of returning bees, for 5 min. periods, at 15 min. intervals, at a hive at each distance from the 1950 lime crop (Table 8). These observations showed that flighting continued later at the colonies nearer to the crop. It is not unlikely that flighting from such colonies also commenced earlier in the morning.

Sometimes during heavy honey-flows new comb foundation had to be added to the colonies. In all such cases allowance was made for only the exact added weight, but the necessity for drawing new comb must have been a disadvantage. The colonies which gained most drew out most new comb, so this factor could only have tended to minimize the distance effect, and may be ignored.

Throughout the experiments every effort was made to keep all the colonies in a non-swarming condition. However, for the 1950 lime experiment owing to the bad weather in June it was found necessary to include, in each group, one colony which had just commenced to rear queen cells. These cells were cut out both at the commencement of the lime flow and at weekly intervals thereafter. Each colony with cells was the poorest member of its group; in the preliminary period the three cell-producing colonies had averaged 0·9 lb. more than the others, but during the fortnight of the lime experiment their mean net gain was $13{\cdot}3 \pm 3{\cdot}8$ lb., while the others gained $32{\cdot}7 \pm 3{\cdot}6$ lb. This happened in spite of the reduced breeding rates of the cell-raising colonies. It illustrates a practical consequence of Taranov's (1947) observation that swarm bees tend to cluster in the hive, and do not reinforce the foragers.

DISCUSSION

The present results must be compared with those obtained in the United States by Eckert (1933), and by Sturtevant & Farrar (1935). Eckert's work was done in Wyoming, where for three seasons he placed groups of colonies in an arid region, devoid of crops, at various distances at half-mile intervals from an irrigated area. Colonies within 2 miles of the irrigated area gained equally with those upon it. Sturtevant & Farrar compared a group of 30 colonies sited 1 mile within an irrigated area with a similar group sited $1\frac{1}{2}$ miles from the edge of the area ($2\frac{1}{2}$ miles from the first group). In 1931 the average gain of the distant colonies was 59% of the average gain (73 lb.) of those among the crops; 1932 was a better year, and between 22 June and 16 August (after making allowances in respect of stolen supers) the distant colonies gained 91% of the average gain (218 lb.) of the others. Sturtevant and Farrar (1935, p. 589) concluded that 'apiaries located out some distance from the nectar source may not always do as well as those surrounded by a considerable area of nectar-secreting plants', but 'if necessity requires the placing of apiaries appreciable distances away from the nectar source..., other things being equal, the beekeeper can secure a quite satisfactory honey crop'.

Such conclusions could not be derived from the present results. The explanation may lie in the different conditions of the American experiments, for they took place in a dry district where flying conditions were probably uniformly favourable, and the bees were sited in an area, but not upon a crop. The most valuable crops may have been at a distance from all the colonies, thereby reducing the differences between the relative mileages covered by the various groups. Lunder & Lunder (1946), working upon the heather crop in Norway, obtained a 37% decrease in yield when bees had to fly more than $1\frac{1}{4}$ miles to the crop—a result not inconsistent with my 1949 experience with heather.

The results emphasize that the optimum foraging range is much less than the maximum one. They illustrate the importance of weather in determining foraging range. The effect of flying time is proportional to the speed at which the crop is gathered; it is therefore most considerable in respect of pollen crops, which often take only a few minutes to collect (Ribbands, 1949). The relation of these results to problems of practical beekeeping will be discussed elsewhere (Ribbands, 1951).

ACKNOWLEDGEMENTS

I am pleased to acknowledge the helpfulness of the farmers who provided the apiary sites for these experiments, and the help given throughout the experiments by members of the Bee Department at Rothamsted. In particular, the heather experiments could not have been conducted without the willing assistance of Messrs M. Hassanein and J. S. Simpson.

SUMMARY

The gains in weight of groups of colonies of honey-bees sited on the edge of crops were compared with those of groups sited $\frac{3}{8}$ and $\frac{3}{4}$ mile away from the same crops. Experiments were repeated in two successive years, under different weather conditions.

Increased flying distance was consistently detrimental, but the magnitude of the effect varied considerably; the reductions in the gains ranged from 15% at $\frac{3}{4}$ mile to 100% at $\frac{3}{8}$ mile. In 1949 the reduction in total gains at $\frac{3}{4}$ mile from five nectar crops, was 32%; in 1950, from three crops, the reduction was 82%. Reduced colony gains of up to 25%, at $\frac{3}{4}$ mile from the crop, could be attributed to increased flying time. The greater reductions were associated with unfavourable weather. Distance also reduced colony flighting near sunset.

The effect of distance upon colony net gains is much greater than its effect upon the quantity of forage brought into the hive; an instance is cited in which colony gain could have been eliminated by a 42% reduction in incoming provender.

Colonies in a pre-swarming condition gained much less than 'balanced' ones.

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