AN ANALYSIS OF THE FACTORS INVOLVED IN THE FORMATION OF A CLUSTER OF HONEYBEES *(APIS MELLIFERA)*

by

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(with 1 fig.)

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INTRODUCTION

The development by honeybees of the habit of clustering together has undoubtedly played an important part in their successful colonisation of many parts of the world. Clustering results in the maintenance of a favourable temperature in the brood-areas of their nests and enables the adults to survive under conditions which would be fatal to the individual insects. Few attempts have been made to determine the factors which result in worker honeybees being attracted towards each other to form a cluster. Stray worker bees are strongly stimulated to join a cluster if a queen is present in it (BUTLER 1954a) but, under natural conditions, queenless clusters are sometimes formed (SCRIVE 1948), thus demonstrating that the presence of a queen is not essential to cluster formation.

SLADEN (1902) observed worker honeybees fanning currents of air over their exposed scent-producing (NASSANOFF) glands at the entrance to their hive and suggested that the scent thus dispersed attracted other members of their colony. VON FRISCH and RÖSCH (1926) provided experimental evidence in support of this hypothesis, and noted that worker honeybees sometimes exposed their NASSANOFF glands without fanning their wings. LECOMTE (1950) found that bees which were scattered in a darkened arena clustered together provided that a certain minimum number of individuals were present; and he concluded that one of the stimuli leading to this result was olfactory and originated in the bee's abdomen but did not mention the

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NASSANOFF gland in this connection. He decided that the vibrations produced by a cluster of bees also acted as an attractive stimulus, but was unable to demonstrate that either an olfactory or vibratory stimulus, by itself, was sufficient to cause scattered bees to cluster together. He therefore concluded that both these stimuli have to be applied simultaneously to induce clustering.

At intervals since the autumn of 1951 the authors have reinvestigated this problem in an attempt to obtain further information about the factors which stimulate worker bees to cluster together, and which enable individual bees to locate in darkness a cluster which has already formed nearby.

GENERAL METHODS

Most of the experiments were performed in wooden arenas, each 47 cms × 47 cms × 23 cms deep, with a glass lid which was covered with an opaque cloth to exclude all light, except during brief periods of observation. Usually 2 wire-gauze cages (5.0 cms high × 7.6 cms long × 1.3 cms wide) were placed on the floor of the arena so that they were equidistant from its centre, from the walls nearest to them, and from each other. One of these cages contained the supposed stimulatory substance and the other served as a control. Worker honeybees, taken at random from a queenright colony, were lightly anaesthetised with carbon dioxide and scattered in the arena. Most of these bees soon recovered from the anaesthetic and some, often many, of them formed a cluster on one or both of the cages. Not all the bees clustered at any one time, and during the course of an experiment a number of them died. Counts of the numbers of bees clustering on each cage were, therefore, made at regular intervals throughout the day. At the end of each day's experiments all the apparatus was thoroughly washed with water and dried.

In the statistical analysis of the results obtained the total counts made on one day were regarded as a single observation only. If many more bees were counted on the cage containing the supposed stimulatory substance than on the control cage, then, for this observation, the stimulus was regarded as having exerted a positive effect.

Each experiment was repeated until it could be asserted with a predetermined degree of confidence that the stimulus under investigation did or did not produce an effect of any magnitude. As explained above each experiment was scored as positive or negative. In the absence of any real effect the bees would be equally likely to cluster on either cage, so that positive results would be obtained in about 50% of all experiments. A stimulus producing a real effect would tend to increase this percentage. The number of experiments was determined in the light of the results as

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they were obtained, in such a way that the following statements were true: —
1. In the absence of any real effect (50% positives in the long run) the probability of wrongly asserting that a real effect existed was 0.05.
2. In the presence of a real effect large enough to give 85% in the long run the probability of wrongly asserting that no real effect existed was 0.10. For more marked effects this probability would be smaller.

PRELIMINARY INVESTIGATIONS

A. NUMBER OF BEES REQUIRED FOR CLUSTER FORMATION

Experiment 1. An empty wire-gauze cage was placed in the centre of the floor of each of three arenas, which contained 50, 150 and 200 bees respectively, and counts were made of the number of bees clustering on these cages. The experiment was repeated, 7 counts being made on each occasion. The results showed that individual honeybees would, under certain circumstances, come together to form a cluster even in total darkness, and that as the number of bees released in the arena was increased a significantly greater (0.01) proportion of them formed a cluster. The mean percentage of the bees which were clustering at the time of the observations was 25.7% in the arena containing 50 bees, 38.4% in the arena containing 150 bees and 55.8% in the arena containing 200 bees.

These conclusions are in general agreement with those of LECOMTE (1950) and led to the decision to use a minimum of 200 bees in each further experiment.

B. THE ATTRACTION TO A CLUSTER OF BEES IN THE ARENA

Experiment 2. Two cages, the sides of which were made of a single thickness of wire-gauze (4 meshes/cm.), were placed in an arena in which 200 bees had been scattered. One cage contained at least 100 bees, the other was empty. On each of nine trials many more of the bees in the arena clustered on the cage containing bees than on the empty cage.

Experiment 3. This was similar to experiment 2 except that the cages were made of a double thickness of wire-gauze. The space between the two layers of gauze was such (1.5 cm) that the bees outside the cages could not make physical contact with those inside them. This experiment was carried out nine times and, as in Experiment 2, on each occasion a larger number of bees clustered on the cage which contained the bees.

C. INTERCHANGE OF FOOD BETWEEN THE BEES IN THE CAGES AND THOSE IN THE ARENA

Experiment 4. In experiments 2 and 3 in which no food was supplied to the bees in the arena a total of 472 bees died in the arena when

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double-walled cages were used, compared with 222 bees which died when single-walled cages were employed. It seemed probable, therefore, that those bees which had clustered on the single-walled cages were fed by the bees inside and so were enabled to survive. In order to verify this a single-walled cage containing 200 well-fed bees was placed in one arena, whilst an empty cage was placed in another one. Two hundred bees were scattered in each arena. This experiment was repeated six times, each trial lasting between 24 and 48 hours. In each trial many more bees were dead in the arena which contained the empty cage than in the arena which contained the cage with bees. A total of 712 dead bees were counted in the arenas which contained the empty cages but only 140 dead bees were found in those which contained the cages that were full of bees. It was obvious that, in the latter cases, the bees in the cages must have given food to the bees outside them.

THE INFLUENCE OF HUNGER ON CLUSTER FORMATION

During experiments 2, 3 and 4 it was noticed that the longer the experimental bees had been without food the more readily they appeared to cluster on a cage containing other bees. On some occasions clusters first formed on both cages, but, after a time, those bees that were clustering on an empty cage left it in favour of the cage which contained bees. As it seemed probable that their behaviour might be explained by their desire for food, the following experiments were carried out to investigate this matter.

Experiment 5. Two cages, each containing 150 well-fed bees were used in an arena in this experiment. One cage had walls of a single thickness of wire-gauze and the other had double wire-gauze walls. In each of six trials many more of the bees in the arena were attracted to cluster on the cages with walls made of a single thickness of wire-gauze than upon the other cages. Since the only difference between the two kinds of cage was that the bees clustering on the cage with walls of a single thickness of wire-gauze could reach the bees inside with their tongues, and possibly with their antennae, whereas when double-walled cages were used this was not possible, it was concluded that the bees preferred to cluster on a cage with whose occupants they could make contact and by whom they could be fed. The following experiment was carried out to determine whether hungry bees were more attracted to a cluster than were well-fed bees.

Experiment 6. Two double-walled wire-gauze cages were placed in each of two arenas; one cage in each arena contained 150 well-fed bees, the other was empty. One group of 200 bees, which had been confined in a cage in the laboratory and starved for 18-24 hours was placed in one

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arena, and a similar but well-fed group from the same colony was placed in the other arena. The combined results of seven trials are given in Table 1.

Table 1. Influence of degree of hunger on clustering of bees on occupied and unoccupied cages.

	Cage containing bees	*Cage not containing bees*
No. of starved bees clustering	1,847	361
No. of well-fed bees clustering	1,484	467

Although there appeared to be a slightly greater tendency for the starved, in comparison with the well-fed, bees to cluster on the cage containing other bees, this difference was not significant so that it appears probable that desire for food is only a contributory factor in causing bees to join a cluster.

Experiments 7 and 8. Two cages, each containing 200 bees, were placed in the arena. These cages were single-walled in experiment 7 and double-walled in experiment 8. One of the cages contained bees which had been starved for 24 hours, and the other bees which had been fed for 24 hours. Each experiment was repeated six times, and on each occasion a greater number of bees clustered on the cage containing the well-fed bees.

Experiment 9. Two double-walled cages were placed in an arena. One was provided with a feeder containing sugar syrup whilst the other had an empty feeder. Both contained an equal number of bees taken at random from the same colony. The experiment was repeated ten times; on five occasions the largest numbers of bees clustered on the cages containing well-fed bees, whilst in the remainder clusters first formed on the cages containing unfed bees, but, later in the day, the bees moved over to the cages containing well-fed bees.

From the results of these experiments it became apparent that a group of well-fed bees was more attractive to individual bees than a group of starving bees. In further trials the temperature of the atmosphere in the two cages was kept at a constant level, nevertheless more bees clustered on the cages containing well-fed bees than on the one containing unfed bees, so that attraction to the fed bees was not entirely due to their higher temperature.

It was thought probable that the fed bees, by their greater activity, produced a greater degree of attraction than did the starved bees and that consequently the bees in the arena preferred to cluster on the cage which contained the fed bees. A further experiment was performed to investigate this matter.

Experiment 10. Two hundred bees were placed in one double-

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walled cage in the arena and 100 in another. Both cages were kept at the same temperature. In each of six trials larger numbers of bees clustered on the cages containing the greater numbers of bees, presumably because they were quantitatively more attractive.

THE INFLUENCE OF TEMPERATURE ON CLUSTER FORMATION

Experiment 11. Two cylindrical tins (each 7.5 cms in diameter and 14.0 cms high) were stood on end in a rectangular wooden arena at points, along one of its diagonals, equidistant from the centre and two corners. A small electric lamp was fitted inside one of the tins in order to raise its temperature to a higher level than that of the arena. The other tin was unheated. Two hundred bees which were scattered at random in the arena always clustered on the tins. In each of eight trials more bees clustered on the heated tin (mean of 31.5° C) than on the unheated tin (mean of 23.0° C). Part of the attraction of single bees to a cluster may, therefore, be considered to be due to the heat which it radiates.

INFLUENCE OF BEE SCENT ON CLUSTERING

Attempts were made to determine whether bee scent by itself has any influence on cluster formation. A cylindrical glass arena 31 cms in diameter and 23 cms high was used so that the whole apparatus could be thoroughly cleaned to remove any bee odours with which it might become contaminated. During experiments it was covered with opaque material to exclude all light.

Experiment 12. Two clean cages were placed on the floor of the glass arena. In one 50 bees, recently killed by severe cold, were placed; the other cage remained empty. Two hundred bees were scattered in the arena. This experiment was repeated seventeen times. On six occasions the bees showed a preference for the cage containing the dead bees, on five they showed a preference for the empty cage, and on the remaining six approximately equal numbers of bees clustered on each cage. It was concluded, therefore, that the dead bees were not attractive to the live bees.

Experiment 13. In this experiment both cages possessed double-walls of wire-gauze. One contained 50 recently excised scent (NASSANOFF) glands from newly killed bees, and the other cage contained the recently excised dorsal tergites, with adhering body fluids, of the second abdominal segments of 50 bees. In each of the six trials many more bees were counted on the cage containing the scent glands than on the one containing the tergites, so it appeared that the odour from the scent glands had attracted the bees. Since the freshly killed whole bees (Experiment 12) did not serve to

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attract live bees, it appears to be necessary for the surfaces of the scent glands to be exposed.

In attempts to obtain further evidence in support of this conclusion the following experiments with an olfactometer were carried out.

Experiment 14. The apparatus used is shown in Figure 1, and was constructed entirely of 'perspex'. Air was drawn through the apparatus as indicated by the arrows. In one of the limbs of the olfactometer the supposed attractive substance was placed. A quantity of cotton wool was placed in the other limb, the quantity being adjusted to equalise, as nearly as possible, the rate of flow of air along the limbs.

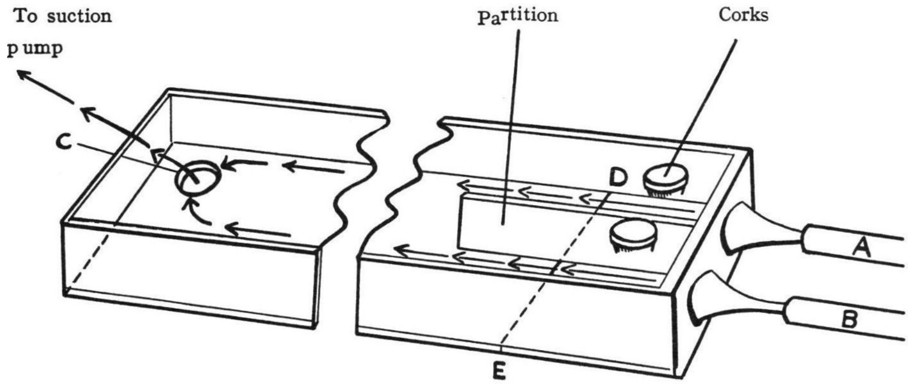

Fig. 1. *Olfactometer.* A & B are limbs of olfactometer. Line DE is recording line. Air current drawn through apparatus as shown by arrows.

Bees were introduced individually into the apparatus, with the minimum of disturbance through the aperture C. They walked to the beginning of the partition where they had to choose which limb to enter. In order to allow for a possible 'trial and error' response to the stimuli, the side of the partition a bee chose was not recorded until she had crossed the line DE. She was then removed and another bee was released in the apparatus. After ten trials the positions of the tubes A and B were interchanged, the entire apparatus was washed at the end of twenty trials, or whenever a bee had defaecated in it. All experiments were performed in a deep red light, to which honeybees show little reaction. The results obtained are shown in Table 2.

These data indicate that recently killed bees exerted no attraction but that the excised scent glands exerted a significant attraction. Similar results were obtained whether the scent glands were removed from bees belonging to the same or different colonies as the experimental individuals. Honey and crushed comb were also found to attract the experimental bees.

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Table 2. Olfactometer Experiments

Stimulus	*Trials* *Positive*	*Negative*	*Significant attraction to stimulus*
Dead bees (frozen)	11	19	No
Excised scent glands:			
1. From bees of same colony as those in olfactometer	68	16	Yes
2. From bees of different colony to those in olfactometer	25	5	Yes
Crushed comb	85	24	Yes
Honey	54	26	Yes

THE INFLUENCE OF VIBRATION ON CLUSTER FORMATION

Experiment 15. Two cylindrical tins were placed in a wooden arena. Between 200 and 500 bees taken straight from a hive were placed in one of the tins, the other did not contain any bees and served as a control. Some calcium chloride was placed at the bottom of the tin containing the bees (separated from them by wire-gauze) to absorb moisture and prevent them becoming unduly sticky. The tin containing the bees was ventilated by means of a long glass tube which extended through its lid and the roof of the arena. The rest of the apparatus was made air-tight so that no odour from the bees in the tin could escape into the arena.

Throughout the trials the temperature of the control tin was maintained at a slightly higher level than that of the tin containing the bees (mean of 1.6° C).

At intervals during the day, counts were taken of the number of bees which were clustering on each tin. The results are shown in Table 3.

When the mean temperature of the air inside the tin containing the bees remained, throughout an experiment, less than 4° C. above the mean temperature of the arena, more of the bees in the arena were usually attracted to the slightly warmer control tin. However, whenever the mean temperature of the air inside the tin containing the bees was 4° C. or more above that of the temperature of the arena more of the bees in the arena clustered on the tin which contained the bees, although the control tin was at a higher temperature.

Since the temperature of the air in the tin which contained the bees was some indication of their activity, the relatively higher temperatures appeared to be correlated with their greater activity and probably with the vibrations which their activities caused. It thus appeared probable that bees in the arena were attracted to cluster near the source of vibration, but only when

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the vibrations reached a certain intensity. In order to test this hypothesis an inanimate vibrator was used.

Table 3. Effect of vibration on cluster formation (Temperature data arranged in an increasing series.)

Mean temp. of tin containing bees (°C) above that of mean temperature of arena	*No. of trials*	*No. of trials in which greater no: bees clustered on tin containing bees*	*No. of trials in which greater no: bees clustered on empty tin*
0.0	1	–	1
1.0	1	1	–
2.0	1	–	1
2.5	2	1	1
3.0	7	–	7
3.5	3	–	3
4.0	2	2	–
4.5	2	2	–
5.5	1	1	–
6.0	2	2	–
6.5	2	2	–
8.5	1	1	–
9.0	1	1	–
9.5	1	1	–

Experiment 16. In this experiment a tin containing a mechanical vibrator producing dominantly 100 cycles per second was used instead of one containing bees. The temperature of the control tin was kept slightly higher than that of the experimental one. This experiment was performed on seven occasions and on six of them many more bees clustered on the tin containing the vibrator, but on the seventh no discrimination was observed. It was thus apparent that the bees clustered at the source of vibration.

THE INFLUENCE OF SIGHT ON CLUSTER FORMATION

All the experiments so far mentioned were carried out in total darkness, except for the brief periods when counts were being made. The following experiment was, therefore, performed to determine whether sight plays any part in enabling scattered bees to find and join groups of bees in the absence of all other known stimuli.

Experiment 17. Two cages (10 cms × 10 cms × 4 cms) each with the top and bottom made of glass, were suspended 0.5 cms above the glass roof of an arena. The cages were 10 cms apart and were equidistant from the centre of the roof. An open cylinder of wire-gauze was attached to the inside of the glass roof of the arena directly beneath each cage. The whole apparatus stood on a sheet of ground glass which was lighted from beneath

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by four equally spaced electric lamps; it was completely covered by a large opaque box, so that the electric lamps provided the only illumination. Two hundred bees were placed in one of the cages, the other remained empty and served as a control. Another 200 bees were scattered in the glass arena and counts were made every half-hour of the number of bees which had temporarily settled on the wire-gauze cylinders beneath each cage. In eight of eleven trials a greater number of individuals were counted on the wire-gauze cylinder which was directly beneath the cage which contained the bees. In one trial more bees were counted on the other cylinder, and in two trials approximately equal numbers were counted on both cylinders. It appeared probable, therefore, that, since all other stimuli had been eliminated, the bees were attracted by sight of the caged bees and clustered near them.

DISCUSSION AND CONCLUSIONS

LECOMTE (1950) found that a certain minimum number of bees must be present before a cluster is formed. His observations have been confirmed in the present work and it was found that within limits the percentage of bees which formed a cluster increased as the number of bees present was increased, presumably because larger clusters are quantitatively more attractive.

SLADEN (1902) concluded that the scent sometimes dispersed from the NASSANOFF gland of a bee attracted other bees towards it, and RIBBANDS and SPEIRS (1952) found that scent dispersed by bees faciliated the reorientation of other members of their colony to their hive entrance after its position had been changed. KALMUS and RIBBANDS (1952) demonstrated that foraging honeybees were attracted to dishes by the scent left on them by earlier foragers. In the present work it has been found that although the scent of whole dead bees was not attractive to individuals, the latter were attracted towards and clustered on cages containing freshly excised scent glands. Thus scent from the NASSANOFF gland probably plays an important role in cluster formation. It appears probable that the dead bees were not attractive to individual bees since contraction of their abdominal tergites on death led to masking of their scent glands and any scent present on the general body surfaces of the dead bees was apparently insufficient to attract other individuals. BUTLER and FREE (1952) found that when the guard bees of a colony examined 'intruder' bees which had inadvertently arrived at the wrong hive entrance, the latter contracted their abdominal segments. In the light of the present work it appears probable that this behaviour by intruder bees masks the scent to some extent, thus making it more difficult

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for the guards to appreciate their strange odours and distinguish them as intruders.

LECOMTE (1950) also found that whole dead bees were not attractive to isolated individuals and postulated that both vibratory and olfactory stimuli were required simultaneously to stimulate bees to form a cluster.

In 1948 AUTRUM and SCHNEIDER demonstrated that honeybees perceive vibrations through their legs. HANSSON (1951) and others have also concluded that bees possess little ability to recognise sounds. HANSSON (1951) showed that bees could not be trained to associate air-borne vibrations with food but could be trained to associate mechanical vibrations (perceived through their legs) with food.

In the present work it was found that individuals were only preferentially attracted to cluster on a tin containing bees when the bees inside the tin were sufficiently active to produce considerable vibration, but readily clustered on a tin which contained a mechanical vibrator. The vibrations produced by the bees forming a cluster are, therefore, likely to cause individual bees to join it.

In 1952 HERAN discovered that bees are able to perceive temperature changes of 0.25° C. with their antennae, and found that the temperature preferred by individuals varied from 31.5° to 37.5° C.

In our experiments at room temperature the bees preferred to cluster on tins which were a few °C. above the environmental temperature. It is probable, therefore, that the temperature of a cluster which is slightly higher than that of the environment, is one of the factors which attracts individual bees to join it. Bees preferred to join a cluster of well-fed bees rather than a cluster of hungry bees (even when unable to obtain food from them) probably because of their greater activity. Hungry bees preferred to join a group of bees from whom they could obtain food. The extensive food transmission that occurs continuously between the bees of a honeybee colony (NIXON and RIBBANDS 1952) may play an important part in attracting its members towards each other.

Since these experiments were completed BUTLER (1954a) has shown that queen honeybees secrete on the surfaces of their bodies a substance ('queen substance') which worker honeybees seek to obtain. So great is the worker honeybees' urge to obtain 'queen substance' that groups of queenless, broodless, workers will readily join strange colonies, which possess queens, in order to obtain it. BUTLER has suggested that this urge to obtain 'queen substance' is a powerful factor in maintaining colony cohesion, and has shown that worker honeybees cluster around a queen in order to obtain this substance.

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Von Frisch & Rösch(1926) found that when they covered with shellac the Nassanoff glands of bees which were foraging at dishes newcomers were still attracted towards them, and they supposed that this attraction was entirely visual. In the present study it has been found that individual bees are preferentially attracted by the sight alone of active bees. A similar result has recently been obtained by Butler and Tyndale-Biscoe (Butler 1954b) working with foraging wasps.

Thus individual bees are attracted to a cluster of their fellows by a variety of stimuli, each of which, provided it is of sufficient strength, serves as an attraction on its own. Mutual attraction as exhibited by honeybees is clearly an important adaptation to social life.

SUMMARY

1. It has been found that the stimuli of scent, vibration, and heat, which are produced by a cluster of bees, can each, provided they are of sufficient magnitude, attract individual bees to join it.

2. Bees can be attracted by sight alone towards actively moving bees.

3. Hungry bees prefer to join a cluster of bees from whom they can obtain food; and well-fed bees are more attractive to individual bees than are hungry bees, even when the individual bees are unable to obtain food from well-fed ones.

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ZUSAMMENFASSUNG

Von den Duft-, Vibrations- und Wärmereizen, welche eine Bienenansammlung aussendet, kann jeder, falls er stark genug ist, andere Bienen veranlassen, sich hinzuzugesellen.

Allein der Anblick sich bewegender Bienen kann Artgenossen anlocken.

Hungrige bevorzugen Haufen von Bienen, von welchen sie sich füttern lassen können; auch wenn sie nicht gefüttert werden, gehen sie lieber zu vollgesogenen als zu hungrigen Bienen.

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