

EXTRA-COLONY ALTRUISM IN THE BUMBLEBEES: MISBEHAVIOUR OR ADAPTATION ?

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L'altruisme extra-colonial chez les bourdons: erreur comportementale ou adaptation ?

Résumé: Cinq cas particulièrement intéressants d'altruisme extra-colonial ont été mis en évidence chez les bourdons *Bombus pascuorum* Scopoli pendant des expériences en milieu naturel sur l'orientation des pourvoyeuses durant le retour au nid et le fourrage. Dans l'un des cas, la pourvoyeuse a commencé à approvisionner une autre colonie de la même espèce. Dans quatre autres cas, les pourvoyeuses ont approvisionné alternativement leur colonie maternelle et une petite colonie orpheline de *B. terrestris*. L'une de ces fourrageuses est devenue, par la suite, une soigneuse du couvain dans le nid de *B. terrestris*. Les implications de ces observations pour la compréhension des causes à court et à long terme de ces comportements d'aide extra-coloniaux chez les bourdons sont discutées dans le cadre:

- (1) de l'hypothèse d'un artéfact
- (2) de l'hypothèse d'une erreur comportementale
- (3) de l'hypothèse d'un abri temporaire
- (4) de la théorie de sélection de parentèle
- (5) de l'hypothèse du cleptoparasitisme
- (6) de l'hypothèse de l'intégration au niveau super-société

Mots-clés: *Bombus*, *Bombus pascuorum*, *Bombus terrestris*, aide extracoloniales, cleptoparasitisme, altruisme réciproque

Summary: Five particularly interesting cases of extra-colony altruism were recorded in the bumblebees (*Bombus pascuorum* Scopoli). In one case, a forager of *B. pascuorum* drifted to another colony of the same species. In the remaining four cases, workers of *B. pascuorum* foraged alternatively for their maternal colony and a small queenless colony of *B. terrestris*. One of these bees was also observed to take care of the brood of *B. terrestris*. The implications of these data for the understanding of proximate and ultimate causal factors of extra-colony helping behaviour in the bumblebees are discussed.

Key words: *Bombus*, *Bombus pascuorum*, *Bombus terrestris*, extra-colony helping behaviour, cleptoparasitism, reciprocal altruism.

INTRODUCTION

Bumblebees are able to distinguish between members of their own colony and strangers from other colonies by means of chemoreception (FREE, 1958a). However, strangers of the same or even of a different species are sometimes accepted by a colony and join its activities (SLADEN, 1912; FREE, 1958a; FREE and BUTLER, 1959; HASSELROT, 1960; ALFORD, 1975). The behaviour of bees which leave one colony and join another is called traditionally the drifting (cf. FREE, 1958). Using the terminology of more recent theories of social behaviour, working for a strange colony may also be labelled the extra-colony altruism, or the extra-colony helping behaviour.

Presently, I would like to report five particularly interesting cases of extra-colony altruism, observed in the bumblebees *Bombus pascuorum* Scopoli during a series of field experiments on their nest site and food source orientation, and to put forward several hypotheses concerning the proximate and ultimate causal factors of drifting in the bumblebees.

MATERIAL AND METHODS

The experiment was carried out in an orchard in Mrozy (central-eastern Poland) during August 1979. A large colony of *B. pascuorum* was found in a pine forest about 35 km to the east from Mrozy on 9th August. It was confined to a double-chamber observation hive and transferred to Mrozy. All the collected bees (a foundress queen, 105 workers, 12 males and 2 young queens) were marked individually with paint. On 13th August, the hive was installed in the orchard, and opened. To test the nest site orientation of the bees, a 1m x 1m vertical board with 4 circular entrance holes, arrayed as a matrix of 2 rows and 2 columns, was placed in front of the hive. Only one at a time of these holes led to the hive via a 60 cm long rubber pipe, the others led to similar pipes opening into empty air. To test the orientation at the food source, another 1m x 1m vertical board was installed about 7 m from the hive. Four pieces of honeycomb, one of them filled always with sucrose solution, the others empty, were offered to the bees on small shelves fixed to that board.

During the experiment, three other bumblebee colonies were also present in the orchard: another colony of *B. pascuorum* (at the start of the experiment on 13th August, it consisted of a foundress queen and of 37 workers), a colony of *B. lapidarius* Müll. (a queen and 33 workers on 13th August), and a small queenless colony of *B. terrestris* (on 13th August, only 3 workers were present, but they continued to forage and to take care of the brood). These colonies were reared in the Department of Apiculture of the Institute of Horticulture and Agriculture in Pulawy. Wild living queens were captured in the spring and confined to large outdoor cages equipped with hives. At the beginning of June, the starting colonies were transferred to Mrozy (about 150 km to the north-east) in their original nest boxes, and allowed to forage freely in the orchard. The hive containing the observed colony of *B. pascuorum* was installed about 4 - 5 m from the hives housing the other colonies. The entrance holes of all the hives faced the same direction (south).

The experiments were carried out during 16 consecutive days. The bees were observed almost uninterruptedly from about 10 a.m. to the dusk. However, on some days the attention of the observer was focused mostly on homing behaviour of the bees, and on the others, on their foraging behaviour. Thus, only a part of the returns to the nest and of the foraging trips was recorded.

RESULTS

During the experiments, five cases of drifting were observed:

Case 1: "Yellow-Blue". That bee was profoundly disoriented at its first return to the nest after its opening at its new site in Mrozy. After about 2 hours of repeated unsuccessful attempts to reach its own nest, both via the holes in the board and via the ventilation windows of the hive, it entered the hive of the other colony of *B. pascuorum*. Before the dusk, it made 3 foraging trips for pollen for its adoptive colony, and spent the night in its hive. On the next day, after one observed foraging trip for its new colony, it was caught and introduced directly into its own hive. It made one foraging trip for it, but then it returned to its new colony. However, on the next day it attempted again to enter the hive of its maternal colony, but did not succeed, and was never seen again.

Case 2: "White". That bee was marked on 18 August. On 21 August, it was observed to make one foraging trip for its own colony, and then one for the colony of *B. terrestris*. At dusk, it was found in the hive of *B. terrestris*, caught, and placed in its own nest. During the next 8 days, it foraged exclusively for its own colony (297 foraging trips recorded). However, on the last day of the experiment, the change of the position of the hole leading to the nest provoked profound disorientation of that bee. After repeated unsuccessful attempts to reach its own nest, it entered again the hive of *B. terrestris*. On the return from its next foraging trip, it attempted again to reach its own colony, but without success, and finally it entered again the hive of *B. terrestris*. Then, it foraged twice for *B. terrestris*; then, it attempted again to reach its maternal colony; succeeded; and made 3 further foraging trips for it before the end of the experiment.

Case 3: "Pink-Blue-Green". On 14 - 16 August, it made at least 8 foraging trips for its maternal colony. On 21 August at dusk it was found in the hive of *B. terrestris*. On the next day it made 22 foraging trips for *B. terrestris*, and then it returned spontaneously to its own colony, and made 4 foraging trips for it before the dusk. During the next 7 days, it made at least 352 further trips for its maternal colony.

Case 4: "Red". On 14 August, that bee made 2 foraging trips for its own colony. On 16 August, it made 1 foraging trip for *B. terrestris*. On 17-21 August, it kept working alternatively for these two colonies (17 August: 2 trips for *B. terrestris*, one for its own colony, then 3 for *B. terrestris*; 18 August: 16 trips for *B. terrestris*, one for its own colony, 2 for *B. terrestris*, 4 for own colony; 19 August: 3 trips for own colony. 20 August: no foraging observed; 21 Au-

gust: one trip for own colony, one for *B. terrestris*, one for own colony, and then 11 trips for *B. terrestris*). During the next four days, "Red" worked exclusively for the colony of *B. terrestris* (328 foraging trips recorded). It disappeared three days before the end of the experiment.

Case 5: "Red-Brown". It was marked on 18 August. On 19 August it made two foraging trips for its own colony, then one for *B. terrestris*, then one for its own colony again, and then it drifted finally to the colony of *B. terrestris*, and before the dusk performed for it 13 foraging trips. During the next 8 days it made for that colony at least 198 further foraging trips. Moreover, on 26 August at the dusk it was also observed to act as a house-bee for *B. terrestris* (warming the brood).

DISCUSSION

As it seems, the present data throw some light on proximate and ultimate causal factors of drifting in the bumblebees. Several hypotheses may be put forward to account for that behaviour:

(1) **The "artifact" hypothesis.** No data concerning the occurrence of drifting of workers between wild bumblebee colonies are known to me. The conditions of the present study were unquestioningly to a large degree artificial: the observed colonies were all transferred from other sites and housed in artificial domiciles placed only few metres apart. As known, in the honeybees such conditions favor drifting, absent or infrequent between wild colonies (cf. FREE, 1958b). Thus, it may be argued that the present data should be treated simply as artifacts, and as such dismissed from further considerations.

However, in many respects the conditions of the present study were much less distant from the conditions of life of wild living colonies than it may seem. As for the high density of colonies, I observed similar concentrations of nests in wild habitats, too. From the point of view of homing behaviour, transferring a colony to a new site and/or placing it in a domicile amounts to a radical change in the surroundings of the nest entrance. Such changes occur frequently under natural conditions, too, for instance, as a result of heavy rainfall, wind, grazing, haymaking, etc., and bumblebees are well adapted to them, responding to them by orientation flights (cf. FREE and BUTLER, 1959; ALFORD, 1975). In the present case, homing was made purposefully difficult by providing four entrance holes; hence, the disorientation of some bees. However, profound disorientation following the changes in the surroundings of the nest entrance is not infrequent in the case of wild colonies, too (ALFORD, 1975).

Moreover, numerous examples show that sometimes important insights into the mechanisms of animal behaviour may be gained in spite of, or even *thanks* to artificial study conditions, as in such situations some potentialities, otherwise hidden, may reveal themselves. Thus, for instance, the present data imply, at least, that workers of *B. pascuorum* certainly do *not* follow the rule: "Never work for a strange colony".

(2) The "misbehaviour" hypothesis. According to this hypothesis, drifting has no adaptive significance: bumblebees drift simply by mistake. A number of indirect arguments in favour of this hypothesis can be found in the literature on drifting in the honeybees. Thus, when hives are arranged in repetitive patterns, honeybees tend to drift to hives occupying similar positions in the pattern to their own. Facing hives in different directions and painting them different colours reduces drifting (FREE, 1958b).

On the other hand, entering a strange nest, by mistake or not, is not equivalent to joining a colony: at the best, it may constitute the first step in the process of the adoption of the bee. Once in, the bee can easily recognize the nest as not its own by its odour. As known, bumblebees may visit regularly strange nests to rob them for their own colony (FREE and BUTLER, 1959).

The cases of "Yellow-Blue" and "White" reported presently demonstrate also unequivocally that drifting cannot be reduced simply to erroneous homing. Both these bees entered a strange nest only after prolonged unsuccessful attempts to reach their own nest. They were all the time perfectly aware of its location; they were just unable to enter it.

These data suggest thus also that the inability, permanent or temporary, to enter the parental nest may be one of the causal factors of drifting.

In terms of its proximate mechanisms, drifting would thus represent the decrease of the selectiveness of the responses contributing to the homing behaviour of the bumblebees, following the prolonged impossibility to respond to the "proper" set of releasers, a phenomenon well known in ethology.

The question of ultimate causal factors of bumblebee drifting is much less clear. What can the bee gain by working for a strange colony, even if it cannot reach its own nest? In contrast to that, the costs of drifting are obvious. They are related to at least two factors: 1°, deserting the maternal colony; 2°, helping its present or future competitors.

The importance of these costs is difficult to estimate. However, if drifting occurs in response to the inability of a worker to reach its own colony, either, as it often happens, the nest has been destroyed, or the bee is profoundly disoriented. In both cases the bee is, thus, at least temporarily, incapable of helping any more to its own colony. As for the costs related to helping competitors of the maternal colony, their role is probably limited by the fact that the bumblebees are, as a rule, fairly efficient at resource partitioning (cf. MORSE, 1982).

As for the possible benefits of extra-colony altruism, the following hypotheses may be put forward:

(1) The "temporary shelter" hypothesis. As demonstrated by the behaviour of all five bees observed drifting in the present experiment, and, particularly, "Pink-Blue-Green" and "Red", drifting is not irreversible: the bee may eventually return to its own colony. In the meantime, by working for a strange colony the bee "pays" for shelter and protection.

(2) The "kin selection" hypothesis. By working for a strange colony of the same species, the bee may actually help to propagate some of the genes identical to its maternal colony.

(3) The "cleptoparasitism" hypothesis. As demonstrated by the case of "Red-Brown", foraging for a small queenless colony may be followed by a rise in its dominance hierarchy to the position of a house bee. As known, in queenless colonies dominant workers begin to lay (FREE, 1955; HONK, van *et al.*, 1982), and such colonies are able to rear males (ALFORD, 1975). By drifting to a small queenless colony, even of a different species, the worker gains thus the chance to produce sons, profiting, moreover, from the help of subordinate workers. Bumblebee queens are well known usurpers of nests of other females, including those of a different species. They accept the workers already present, and take care of the brood left by the former queen, to profit subsequently from their help (SLADEN, 1912; VOVEIKOV, 1953).

3. The "super-society" hypothesis. Recently, the fundamental role of reciprocity in insect social behaviour was stressed, among others, by JAISSON (1985) and HAMILTON (1987). Jaisson (1985) put forward the hypothesis postulating the existence in social insects of super-society level of organization, the "society of societies", giving as the possible examples the enormous federal coalitions of colonies amongst certain highly evolved ant species.

If, as it seems, bumblebees really follow generally the rule: "Under certain conditions you may work for a strange colony", as a consequence a loose and rudimentary super-social structure, based on the ties of the potential reciprocal extra-colony helping behaviour, is created in bumblebee communities. Helping a strange colony would thus contribute not so much to helping the competitors of the maternal colony, as to helping its potential reciprocators. The fact that all five bees observed drifting in the present study kept working alternatively for two colonies supports this hypothesis, too.

To conclude, I would like to stress two points:

1*) the hypotheses discussed above are not mutually exclusive: all of the discussed factors may play some role in bumblebee drifting;

2*) the aim of this discussion was to open some questions, and not to answer them. All the discussed hypotheses remain to be confirmed (or falsified) by more detailed observations, preferably using wild colonies not transferred from their original nests.

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