

NOTES ON THE EGG-EATING HABIT OF BUMBLEBEES.¹

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Among the older treatises on the biology of bumblebees, that of the Swiss biologist Huber (1802) occupies a preëminent position, partly because it is more comprehensive than those of earlier workers, but chiefly on account of the many new observations which are described by the author. Among other things, Huber (pp. 259-260) relates that, while engaged in egg-laying, the bumblebee queen is frequently molested by the workers who try to steal the newly-laid eggs in order to "drink the milky juice", and that the queen repels such offenders with great fury. About eighty years later, Huber's (1802) account was confirmed by the well-known Austrian bumblebee student Hoffer (1882-83), and a few years later also by Härter (1890, pp. 62-65). Hoffer (I, pp. 12-14) describes this interesting phase in the life-history of the bumblebee colony as follows: "While engaged in egg-laying, the queen usually is severely molested by the workers and the so-called small queens (and if she be one of the latter, even by the old queen), while the males, although coming into close proximity, do not cause the slightest trouble. In the case of *B. lapidarius*, I frequently observed small queens, or also common workers, force their heads between the cell-wall and the dorsal side of the abdomen of the egg-laying individual in the attempt to snatch the freshly-laid eggs from the cell*****; an endeavor in which they frequently succeeded to the great vexation of the egg-laying queen.*****"

"The proper number of eggs having been laid, the queen quickly withdraws her abdomen from the cell, and turning about quickly, first of all drives away the most obtrusive workers and other females, and closes the cell with wax*****; if the remaining individuals approach too close, she quickly makes an example by seizing the boldest individual with her legs and mandibles and engaging in a rough and tumble fight with her for a few moments, during which both individuals sometimes tumble

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to the floor over the other members of the colony. She then leaves the individual which has been chastized, and frequently severely bitten in this manner, and quickly returns to the cell to protect it against the onslaughts of others; occasionally, however, she is already too late, for some of the more active individuals have meanwhile opened it [the cell], and have taken out several eggs and devoured them.

"Punishment is almost always meted out only with the legs and mandibles, and the [chastized] individual, conscious of her guilt, does not even attempt to defend herself, all of her efforts being directed toward a hasty escape. This punishment sometimes is so severe that the poor creature is seriously wounded or even killed.*****.

"When, after such interruptions, the egg-laying queen has again returned to the cell,*****she opens the latter with her mandibles and lays more eggs*****, molested in the same manner as before*****; egg-laying completed, she remains near the newly-laid eggs for several hours. *****

"The attacks of the other individuals become less and less frequent, and finally cease altogether; and these same little insects which previously tried their very best to destroy the newly-laid eggs, now become attentive guardians and devoted nurses of their embryo brothers and sisters; they keep them warm and provide with tender solicitude for their nourishment."

Some twenty years after the publication of this description, the Russian psycho-biologist Wagner (1907) published a comprehensive treatise on bumblebees, in which he denies the correctness of Hoffer's (1882-83) observation, because Wagner (p. 90) found that whenever he opened an egg-cell in one of his bumblebee colonies, the workers invariably repaired the damage without molesting the eggs². Only once did Wagner (pp. 90; 111-112)

²In regard to these experiments of Wagner (p. 90), it may be stated that more than a century before it was discovered by Huber (1802) that bumblebee workers seldom show a desire to rob eggs after the latter are a day old. Huber (p. 260) says: "It seems that the old eggs are less sought after by the workers than those which are newly-laid; indeed I have seldom seen workers attack them the second day.

"I once tried to offer them old eggs just as they were attacking the fresh ones; they carefully closed up the first without attempting to eat them."

It seems probable therefore that the eggs which Wagner (p. 90) used in his experiments were not newly-laid eggs.

observe that an egg was sucked dry by a worker, but he believes that this was entirely due to the fact that the egg was accidentally injured, and that the worker, after having tasted the sweet juice, found the latter suitable as food. "If", says Wagner (p. 88), "this affair [the fight for the eggs] took place in the manner described by the author, bumblebee colonies could never become as populous as they actually are, since the eggs would be inevitably destroyed by one of the workers as soon as the queen takes up the pursuit of other obtrusive workers; this [the destruction of the eggs] naturally takes considerably less time than is required for a rough and tumble fight****, and for rolling about on the floor*****. During such encounters not only one, but five 'batches of eggs' can be despoiled." Wagner (pp. 88-89) therefore comes to the conclusion that Hoffer (1882-83) permitted himself to be deceived by the usual excitement among the members of a bumblebee colony when the latter is exposed to light.

Opposed to this negative evidence of Wagner (1907), we have the further positive evidence of Sladen (1912, pp. 51-52) who states that this fight for the eggs may be witnessed in the case of *Bremus (Bombus) lapidarius* and *Bremus terrestris* at the time the male and queen eggs are laid³, a statement which, as I have shown recently (1922a, p. 28), also applies to one—if not all—of our American species.

We now come to the more difficult task of interpreting this race-suicidal habit of bumblebees. After describing this unnatural (from the human standpoint) practice of bumblebee society with considerable detail, Huber (pp. 260-261) gives way to the following reflexions: "What is to be thought of Nature, when she seems to give to insects the faculty of destroying their own species, when she permits hivebees to kill their males, and gives bumblebees the right and the desire to devour the newly-laid eggs?"

³That "the fight for the eggs" probably occurs only at this period of the life-history of bumblebee colonies, is corroborated by my own observations (1922a, p. 28), and partly also by those of Harter (1890) and Lindhard (1912). Although I had about fifty incipient bumblebee colonies under close observation during the summers of 1922 (cf. 1923) and 1923, I failed to find any trace of such habit in the colonies during this period of their development.

“Would it not seem natural to conclude that she wishes to bring about total destruction? However, the species are conserved, the colonies multiply, the laws are not changed; on the contrary, it seems that it is by the sacrifice of a few that the conservation of the species is assured. Special observations show us that the hivebees only kill their males when the latter have become useless to their colony; they [the males] would consume a large quantity of provisions which the bees need for nourishment during the winter; and Nature prefers the conservation of the industrious ones to that of the males which no longer render any service after the time of reproduction.

“As for the pillage of the eggs of bumblebees, one must seek the cause further.

“It doesn’t seem of any usefulness to the colony itself; for the eggs which are subject to the gluttony of the workers are as much the eggs of the workers as eggs of males and females.

“But perhaps the Author of nature wished to diminish the number of ‘mellivores’ in that way.

“The bumblebees are the largest insects that feed on honey; and if their number trebled or quadrupled, other insects would not find any nourishment, and perhaps their species would be destroyed.

“This argument will have more force, if we notice with what care Nature has put limits on too great a population of bumblebees. These insects have several kinds of enemies; among others a pseudomoth and a big white caterpillar which feed on their wax, their pupæ, and sometimes themselves; they are even burdened with a numerous family of lice which attach themselves to their thorax, and which they carry off with them in the air.”

Although describing the egg-eating habit of bumblebees in great detail, Hoffer (1882-83) offers no explanation of this habit. However, a few years later, the well-known French bee student Pérez (1889), who was much interested in the observations of Hoffer (1882-83), ventured to discuss this interesting question. After quoting a large part of Hoffer’s (I, pp. 12-14) description, Pérez (p. 110 ff.) goes on to say: “But this return to better feelings [on the part of the workers] cannot make us forget

the wildness of the instinct which carried them away at a certain instant. That is one of the most astonishing habits among those which we owe to the observations of Hoffer, and one of the most inexplicable which the biology of bumblebees presents. That the egg-laying queen energetically defends her offspring, is such an ordinary and natural act that it cannot surprise us. As for the acquired instinct [of destroying the eggs], that is the natural consequence of the momentary cannibalism of the disappeared ones [instincts] when the indifferent mother abandoned her eggs to the voracity of her first-born. But why this fratricidal instinct, this passing madness, which for an instant interrupts and somewhat mars the upright and honest life of bumblebees? Indeed, in the case of the hivebee, we sometimes see the workers destroy, and without doubt also devour the eggs. But that only happens at a time when honey is abundant in the flowers, when the care of storing up as many provisions as possible, obliges them to sacrifice these objects of such tender solicitude ***. Here [in the case of bumblebees] the guilty ones have no such excuse. We are actually confronted with a case of plain gluttony. A freshly-laid egg is undoubtedly a delicacy which gives off an irresistible fragrance. That is perhaps all that we need to see in this habit; an imperfection of the social instinct which selection has not succeeded in correcting. The necessity of restricting too great a multiplication of the colony, cannot be entertained for a moment [as a possible explanation]. Here, as in the case of the hivebee, and elsewhere, a large population means riches and power. And if nature wished to moderate the increase, she had—without speaking of parasites—a much more simple and less savage means; that of restricting*****the number of eggs in the ovaries of the queen.

“That is not all. If we suppose that a restriction in the number of eggs is advantageous—which in some way would justify the fratricidal instinct of the workers—, of what use is the instinct of the mother which impels her to defend her eggs, an instinct which is diametrically opposed to the first? Why two instincts, not only contrary, but even contradictory? And if we accept that the voracity of the workers requires a corrective that the maternal instinct of the queen be from that time useful

to the species, we must agree that its adaptation is very defective. It would be better that the mother, less impetuous, would not leave the cell for an instant and would not engage in a fight with the aggressors. Not a single egg would be lost, and the covetousness of the evil-intentioned ones would not be satisfied. How are we to unravel this chaos? I give it up, as far as I am concerned. We delude ourselves, I believe, in wishing to seek perfection everywhere in nature, and under all conditions. Let us recognize that all is not for the best in the realm of the bumblebees anymore than in other realms."

Twenty-three years after the publication of this rather pessimistic speculation of Pérez (1889), another explanation was suggested by the late F. W. L. Sladen (1912).

After having given a detailed description of this strange habit of bumblebees in the first part (pp. 51-52) of his admirable treatise on bumblebees, Sladen (p. 257) says: "I think that the strange race-suicidal habit the *lapidarius* workers have of attempting to devour their mother's new-laid eggs is associated with the parasitism of *Psithyrus*. It is natural to suppose that workers that attempt to devour the eggs of their *Psithyrus* step-mother perpetuate their egg-devouring instinct through their sons that they sometimes succeed in rearing. In support of this view it is interesting to note that in nests of *B. latreillellus*, a species that is not preyed upon by any species of *Psithyrus*, I have never seen the queen's eggs molested by the workers."

As I have already pointed out elsewhere (1922a, p. 28), this explanation does not seem very plausible. It is a well-known fact that ants, even those belonging to species which are not molested by parasitic ants, frequently eat their own eggs (cf. Wheeler, 1910, p. 332). Moreover, I have frequently seen the workers of *Bremus fervidus* eat their mothers' eggs, and this species (cf. Plath, 1922b) probably does not suffer any species of *Psithyrus* to breed in its nests, a view which is supported by a large number of records (10 by Putnam (1864), "a large number" by Franklin (1912-13), and 33 by the writer) of *fervidus* nests, none of which were victimized by a *Psithyrus*.

In the same year in which Sladen (1912) published his work, another explanation was offered by the Danish biologist

Lindhard (1912). After quoting a part of Hoffer's (1882-83) description and giving a brief resume of Pérez' (1889) explanation, Lindhard (pp. 347-349) describes his own observations as follows:

"The *lapidarius* nest which is shown in Fig. 4 was without any wax covering or any other roof during the warm weather from the 10, to the 20-22, of August. When the lid of the box was opened and a glass plate removed, one could see all that took place in the nest. The bees did not let themselves be disturbed by the light⁴. Each evening, from about 4 o'clock until 7, egg-laying could be observed. Besides the old queen, as a rule, 2-4 large workers laid eggs, each one in her low, poorly-formed wax-cell. Generally there were 2-3 such small pots in use at the same time*****. The egg-laying workers were very uneasy, but did not bother one another very much, and only seemed to be shoving each other about in order to get a chance to lay eggs. If one succeeded in shoving another away from the cell, she, as a rule, took the other one's place. They [the workers] could also be seen shoving the queen about while she was engaged in egg-laying, but I did not see any worker try to take her eggs. Once she ran from one cell to another without closing the eggs, but a small worker went over at once and closed the cell without touching an egg. The queen however seemed nervous and jealous when one of the small females [workers] tried to lay eggs near her. I saw her one day shove a female [worker] away from a cell, carefully examine the eggs in the cell throw out three of them, bite the fourth one to pieces, and, after having chewed it together with a little pollen, lay it on top of a cell of a queen larva. The three other eggs were turned over and examined by two small workers and were dragged away.

"That was another explanation! Those were the unfertilized eggs which were used as food for the young queen larvæ.

"In the bumblebee colony the army of workers comes first⁵, in constantly increasing numbers, the individuals of each new batch being larger than those of the preceding one. The last

⁴This contradicts one of Wagner's (1907, pp. 88-89) assertions to which reference was made in the earlier part of this paper.

⁵This, as I have shown recently (1923, p. 332), is not always the case.

large workers or small queens in several species approach the old queen in size, and more or less of them lay eggs which are normally unfertilized. After these come the males, frequently in a large, homogeneous batch; but after this, the production of males in nests with a strong queen is very small. The young queens come forth 6-10 days after the males, and the production of queens continues as long as the old queen and the workers are in full strength, even if there are produced at the same time some workers and males. The number of large, egg-laying workers in a strong colony is now quite considerable. They lay only male eggs, and if all their eggs hatched, the number of males would be steadily increasing and would be many times as large as the number of young queens. But this is not the case; so there must therefore be some other use for these eggs, and, it seems, they must be used for food, and only those larvæ which receive such an extra albumen-rich food, become queens.

"If this theory is correct, *Bombus* and *Psithyrus* species are more closely related to each other than is generally believed. *Psithyrus* is accused of feeding its larvæ with the eggs of bumblebees and all of its own fertilized eggs become queens."

This explanation, in my opinion, seems to be the most plausible, and is very suggestive. If Lindbard's (1912) hypothesis is correct, we have here a similar state of affairs as in the case of certain ants (cf. Wheeler, 1910, p. 332) where the destruction of eggs insures the preservation of the species.

In this connection a few words may be said in regard to the food of hivebee larvæ. Dr. E. F. Phillips (1921, p. 111) has the following to say on this subject: "The feeding of the larvæ is one of the most ardently disputed questions in bee activity. The chief controversy arises over the source of the food, some authors claiming that it is a secretion of glands, while others maintain that it is regurgitated from the ventriculus." It seems that none of the investigators whom Dr. Phillips (pp. 111-116) mentions, have considered the possibility that the so-called royal jelly with which hivebees feed their queen larvæ may, at least in part, consist of malaxated eggs⁶, a surmise which is

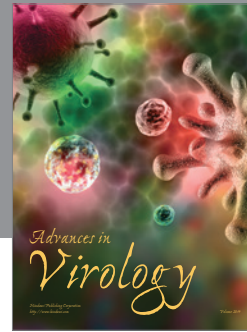
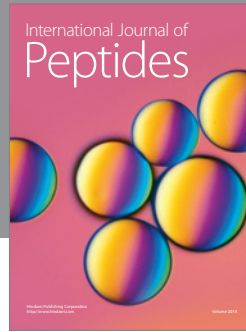
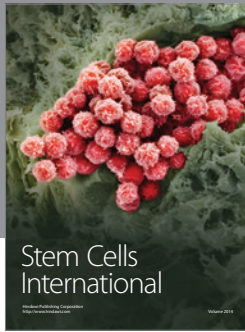
⁶That hivebees sometimes destroy eggs is asserted by Pérez (1899) in one of the preceding extracts.

further suggested by the similarity in color between this food-paste of hivebees and their eggs.

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