

FOOD PREFERENCES OF THE COLORADO POTATO-BEETLE, *LEPTINOTARSA DECEMLINEATA* SAY.

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The experiments¹ here described were undertaken some years ago (1923-25), but no account of them was published at that time as a report on work of a somewhat similar nature by others appeared while my own was still in progress. More recently one or two additional papers relating to the choice of food-plants by the Colorado potato-beetle have been published and the whole question appears worthy of review with incorporation of the data secured by the present writer.

Aside from its importance as an insect pest of cultivated potatoes the Colorado potato-beetle is of particular interest on account of an apparent shift in its food-habits which occurred less than a century ago when it was first noted as feeding on the foliage of the potato. However, the food preferences of this beetle are not so clear as might appear from this statement and they have already furnished interesting material for study at the hands of several entomologists in this country and in France where the species has been naturalized since about 1920.

The potato-beetle was described by Thomas Say in 1824 from the western plains region and was regarded by him as native to the United States. There seems to be no reasonable doubt that this supposition was in error and that the original habitat was Mexico. At the time of its discovery by Say and for several decades later the beetle appears to have restricted its feeding to the foliage of a common weed of the Southwest, *Solanum (Androcera) rostratum*. This plant in turn is of Neotropical origin and is thought to have preceded the beetle, and to have become naturalized in the United

¹ I wish to express my gratitude to the Elizabeth Thompson Fund for a grant which made possible the construction of a series of large outdoor cages in which the breeding experiments were conducted.

States at a much earlier date. Its spread may have followed the trails of the early Spanish explorers aided by the bur-like fruit which is readily transported on the fur of animals or clothing of man. Later this plant became more sparingly naturalized further northward and eastward under locally arid conditions like those prevailing on waste land or railroad ballast. That this plant may be actually native to the drier parts of our southwestern states is quite possible, but at any rate it appears to have been the preferred food-plant of the potato-beetle during the earlier half of the nineteenth century. There is also a native potato in this same region, *Solanum fendleri* Gray, *nec* Heurck & Muel. (*S. tuberosum boreale* Gray) which extends from Western Texas to Arizona and Mexico in moist transition areas but there are apparently no records that indicate whether or not this wild potato has ever served as a food-plant for the beetle. That it might do so is very likely since it is very similar to the cultivated form, although as the two plants (*S. fendleri* and *S. rostratum*) do not occur under similar ecological conditions passage from one to the other could not commonly occur.

Before 1860 the potato-beetle found a highly acceptable food-plant in the potatoes that were cultivated in the region where it then occurred and it was recognized as early as 1859 as an established pest in gardens. Thenceforth it spread into the eastern and southern states and later to the Pacific region. It has continued to prefer the potato to other species of the genus *Solanum* (*s. lat.*), although several other genera of Solanaceæ are sometimes attacked in a more sporadic way. Thus it is well known that the larvæ are frequently destructive to egg-plants (*Solanum melongena*) in gardens and that they appear occasionally on tomatoes (*Lycopersicum esculentum*), ground cherry (*Physalis* spp.) and on certain varieties of cultivated tobacco (*Nicotiana*) that develop a low nicotine content in the leaves.

The sporadic occurrence of the beetle on some of its less favored food-plants may indicate the presence of separate strains or genetically distinct types, especially as it cannot always be traced to the absence of the preferred potato food-plants in the immediate vicinity.

With this question in mind a series of 24 species of So-

lanum were secured as seed and plants were raised in the greenhouse. These were then set out in the open² at the time the first seasonal brood of beetles appeared and a number of adults (ten) were placed on the foliage of each plant. From these preliminary tests it was at once evident that there was a wide variation in the readiness with which the beetles fed upon the several species of *Solanum* that were offered to them. Omitting the potato which was suffering heavily from beetle feeding throughout the neighborhood at that time, several species were greedily accepted and voraciously fed upon. Among the species tested these were notably *S. (Androcera) rostratum*, *S. dulcamara*, *S. melongena* (garden egg-plant), wonderberry³, *S. marginatum*, and *S. subinerme*.

Several were absolutely refused, including *S. nigrum*, *S. pseudocapsicum*, *S. barbisetum*, *S. granuloso-leprosum*, the garden tomato (*Lycopersicum esculentum*) and three unidentified Panamanian species.

Intermediate with reference to feeding were *S. pyracanthum*, *S. atropurpureum* and an unidentified Panamanian species.

As a result of these preliminary tests nine species were selected for further experimentation, as follows: "wonderberry", *S. (Androcera) rostratum*, *S. subinerme*, *S. marginatum*, *S. dulcamara*, *S. torvum*, *S. barbisetum*, *S. melongena* and *Lycopersicum esculentum*.

The last-mentioned species was added, although the beetles had previously refused to feed upon it, because of an infestation called to my attention by Professor W. E. Castle, who noticed the familiar beetles and larvæ destroying the

²On the grounds of the Bussey Institution at Forest Hills, Boston, Mass. where the entomological laboratories of Harvard University were located at that time.

³This plant was secured from a seedsman as Luther Burbank's "Wonderberry" which is according to botanists a form of *Solanum nigrum*. However, as noted below, the potato-beetle does not feed on the wild form of this species and cannot develop on it, a fact also attested by Trouvelot ('33) and his co-workers who attempted unsuccessfully to rear this insect in France on European plants of this cosmopolitan *Solanum*. The wonderberry is said to have originated as a hybrid between *S. villosum* and *S. guineense* (cf. Whitson & Williams, "Luther Burbank," vol. 6, pp. 105-133 (1914)). The latter name has been applied to both *S. nigrum* and *S. aggregatum*, so the nativity of the wonderberry is hopelessly shrouded in doubt, but it appears that it is not identical with *S. nigrum* as has been assumed.

foliage of tomato plants in his garden in Belmont, near Cambridge, Mass. On account of this unusual occurrence it appeared that we might have chanced upon a mutation in choice of food and a part of the colony was transferred to one of the large screened cages⁴ with a few healthy tomato-plants. They continued to feed and it appeared that some of the larger larvæ had entered the soil to pupate although the majority died before attaining full growth. However, no adults of a second generation appeared in the cage and the soil was left undisturbed until the following summer which likewise brought forth no beetles. This second year a similar infestation occurred in Professor Castle's garden, but we made no further transfers as it was evident that the beetles could not maintain themselves on tomato even though certain adults had developed a taste for it. In France Trouvelot and Thénard ('31) have similarly noted the disappearance of the larvæ from tomato plants and they attributed this to the difficulty experienced by the larvæ in maintaining their foothold while crawling on the coarsely hairy leaf stalks. This has been later questioned, however, by others working in the same region. Feytaud ('23) noted earlier that the adult beetles in France eat tomato foliage avidly, a statement that could certainly not be applied generally to the potato-beetle population in America. Quite recent studies in France substantiate this as they have shown that certain varieties of tomato are readily eaten while others are not.

Laboratory experiments by McIndoo ('35) showed that both adults and larvæ are to a surprising extent attracted to tomato leaves when permitted to choose between potato, horse-nettle (*Solanum carolinense*), *S. dulcamara* and tomato. Although showing much irregularity, a considerable number (± 9.6 -12%) of beetles and many larva (15%) came to rest on the tomato leaves. As the species is unable to survive on tomato it is clear that when tomato is as readily available as other acceptable species that there is a consistent weeding out in the general population of those beetles

⁴ These cages were four feet square at the top and bottom with vertical sides eight feet high, covered completely with bronze window screening except on the bottom which was sunk to a depth of eight inches in the soil of the garden. They thus maintained the plants and insects under practically out-door condition throughout the year.

that are attracted to tomato. Even granting that the inability to mature on tomato is not absolute it is obvious that natural selection will completely prevent the development of any strain attracted to this plant for oviposition.

The relation of the potato-beetle to tomatoes is an extreme case of mistaken instinct, but the broods in our other cages showed that a similar less pronounced relationship prevails with at least some other species of *Solanum*. As mentioned in a preceding paragraph nine species on which the beetles fed readily were set out in separate breeding cages in the spring of 1923. Each cage was supplied with twenty beetles (ten of each sex). No further attention was paid to them except to note the progress of the experiment and to replace from a reserve stock any plants that suffered excessive defoliation. Replenishment was necessary especially in the case of *S. rostratum* as these plants were smaller and appeared to grow less vigorously.

Numerous larvæ developed in all of the nine cages and beetles of a second generation appeared in all of them. Plants were kept growing in the cages until the end of the season and outdoor conditions prevailed during the winter.

The following season (1924) the cages were again supplied with plants of the same species, but, of course, no further beetles were added. Beetles appeared in all but four of the nine cages. These four included *S. marginatum*, *S. barbisetum* and the two unidentified Panamanian species, indicating that the beetles had not survived the first year on these plants.

In the spring of the following season (1925) only the five remaining cages were planted as before and three of these failed to develop any adult beetles. These were "wonderberry", *S. torvum* and *S. dulcamara*, showing that under the conditions of the experiment the beetles had been unable to maintain themselves on these three species beyond the second season.

At this time (1925) only the two remaining cages produced beetles of the spring brood and the experiment was carried no further as it appeared clear that the beetles were able to continue on these plants. They were *S. rostratum*, the plant believed to be the original food-plant and *S. melongena*, the egg-plant. We know of course from innumerable obser-

vations that the beetles maintain themselves indefinitely on potato.

It thus appears that not only do the beetles evince a differential choice among various Solanums and other solanaceous plants as was first clearly shown by Trouvelot, *et al.* ('33a), but the choice of the beetles is not always compatible with the larval requirements in the way of food. Thus even if the beetles are unable to maintain themselves for more than a year or two on plants that they will quite willingly attack we may readily understand how the potato-beetle and similar insects fail to widen their range of food-plants even though the instincts of the adults may vary considerably in directions incompatible with larval food requirements. What happens in such cases is that a certain proportion of the population is doomed to extinction due to faulty instinct of the parents in selecting unsuitable food-plants. If the environmental resistance rates high or the "viscissitudes of life" are excessive, as is usually the case, this factor plays an important part in the economy of the insect, but in the case of pests of agricultural crops where this environmental resistance is lessened by an excessively increased food-supply it becomes of very minor importance.

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