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OBSERVATIONS ON LEPTOTHORAX DULOTICUS.¹

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In a previous paper (Wesson, 1937), a new species of *Leptothorax* was described, and shown to be dulotic or slavemaking. This was evident from the fact that it was found in a mixed colony containing, besides workers and a dealate female of the new species, workers of both *L. curvispinosus* and *L. longispinosus*, and from the fact that *duloticus* workers were observed to remove pupae from a nest of *curvispinosus* and carry them back to the home nest. Subsequently, in 1937, I was able to find 3 fine, additional colonies within 200 feet of the spot where the type colony was taken. Two of these colonies, containing respectively 40 and 47 *duloticus* and 50 and 70 *curvispinosus*, were transferred to an artificial nest where it was possible to observe their behavior and also to compare them with *Harpagoxenus americanus* (Wesson, 1939) which was being studied at the same time. These observations are presented below.

I. OBSERVATIONS ON WORKERS DEPRIVED OF THEIR SLAVES.

Twenty workers of *L. duloticus*, together with about 15 medium-sized larvae, were separated from their slaves. Workers and larvae were placed in a bottle which was connected with a darkened chamber by a 2-in. tube through the cork. The bottle was placed in a strong light. At first the *duloticus* clustered in small groups in the bottle. A few of the ants, especially the darker, older ones persisted in running around and up the sides of the bottle. One or 2 carried a larva apiece to a pile. Several workers found the dark chamber and continued making trips between it and the bottle where most of the workers were clustered. They would go to the dark chamber, stay in it for 10 or 15 seconds, then return to the

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bottle where they would run about among the other workers, and again go to the chamber. Finally, $2\frac{1}{2}$ hours after the ants had been put into the bottle, a worker picked up a larva and carried it from the bottle through the tube into the dark chamber. Three minutes later the same worker picked up a callow in the bottle and carried it by the mandibles into the chamber. This worker then ceased her activity and remained in the chamber. When there was no more activity during the next hour, the rest of the workers were placed in the dark chamber while the larvae were placed in the tube just beyond the entrance to the chamber. Within half an hour the larvae were carried into the chamber. At first, larvae were carried in sporadically and by only 2 workers, but gradually several more joined them and trips became more frequent. The chamber containing the *duloticus* and larvae was then placed in a foraging box where the ants could obtain food and water. The majority of the workers remained at all times quiescent in the nest, but during the day 4 or 5 workers could usually be seen outside the nest simultaneously. The *duloticus* drank water and sugar syrup placed in the foraging area, and fragments of *Formica* pupae presented to them were carried into the chamber where they were eaten. The foraging was done listlessly, however, and with none of the bustle and energy of *L. curvispinosus* workers. At no time was a worker observed to lead another to the syrup or to the water tube. The larvae were frequently licked by the *duloticus* workers, but did not thrive. Within $2\frac{1}{2}$ weeks 8 had dried entirely, while the remainder were so shrunken that it was obvious that they had not been fed by the *duloticus*.

From the above experiment it seems probable that: (1) *L. duloticus* is an obligatory slavemaker, dependent on its host species, *L. curvispinosus* or *L. longispinosus*, for the rearing of its brood. This was shown by the inefficient foraging, and the comparative neglect of the larvae. (2) *Duloticus* remains so primitive that many of its ancestral formicine instincts are still present, though in attenuated form. Such instincts are those of foraging and of deporting other workers and larvae to a new nest (distinct from the deportation that occurs during a slave raid). These instincts are probably not manifest under normal conditions, but may be called into play by the removal of the slaves.

II. SEASONAL CYCLE.

The 2 *duloticus* colonies referred to above were kept through the winter following their capture, so that it was possible to observe the complete seasonal cycle. I present this in outline form, taking

from my notes selected data on a single *duloticus* colony. Since the dates given for the development in the artificial nest do not correspond to those obtaining under natural conditions, the series is "dated" by the parallel development of *curvispinosus* brood at the same time and under similar conditions.

March 1, 1938. Colony contains 28 *duloticus* workers, 1 dealate *duloticus* queen, about 40 slaves and 10 small larvae (about $\frac{1}{4}$ the size of a worker). Larvae in the *curvispinosus* colony about the same size.

March 15. Growing season begins.

March 20. *Duloticus* colony: larvae unchanged in size; 1 egg. *Curvispinosus* colony: larvae growing; a few eggs.

March 25. *Duloticus* colony: larvae unchanged; 12 eggs. *Curvispinosus* colony: larvae half grown; many eggs.

April 3. *Duloticus* colony: larvae unchanged; 30 eggs. *Curvispinosus* colony: many larvae nearly grown; many eggs.

April 10. *Duloticus* colony: larvae unchanged; about 40 eggs, a few of which are hatched; 4 *duloticus* workers scouting in the box in which the nest chamber is placed. *Curvispinosus* colony: 6 larvae in the semipupal stage.

April 15. *Duloticus* colony: larvae growing slowly; many eggs hatched; 3 workers scouting. *Curvispinosus* colony: a few pupae and many semipupae.

April 22. *Duloticus* colony: larvae nearly as large as the *curvispinosus* slaves; larvae hatched from the eggs growing rapidly (about 35); 6 to 8 workers scouting. *Curvispinosus* colony: many pupae, a few of them coloring.

April 29. *Duloticus* colony: original larvae, quite large; 35 new larvae as large as the workers; 15 workers scouting. *Curvispinosus* colony: many pupae coloring yellow, some emerging.

May 6. *Duloticus* colony: original larvae in semipupal stage; 35 large larvae and many smaller larvae and eggs present; 15 to 20 workers scouting. *Curvispinosus* colony: pupae emerging rapidly; nuptial flights.

May 10. *Duloticus* colony: 18 semipupae; many other larvae of all sizes. *Curvispinosus* colony: first batch of pupae nearly all emerged; nuptial flights over.

May 16. *Duloticus* colony: 2 female, 4 worker pupae; 20 semipupae, 30 large or medium-sized larvae; many workers scouting. *Curvispinosus* colony: entered on the "summer period"; larvae pupating and pupae emerging continually.

May 30. *Duloticus* colony: 2 female, 1 male, about 45 worker pupae, a few semipupae and larvae; 15 to 20 workers scouting.

June 10. *Duloticus* colony: 5 or 6 pupae emerged; scouting activity of the workers declining.

June 21. *Duloticus* colony: most of the pupae emerged; 3 or 4 workers scouting.

June 27. *Duloticus* colony: all but 1 or 2 pupae emerged; the brood consisting of 2 winged females, 1 male, and about 50 workers. On this day and thereafter there is no more scouting activity on the part of the workers. A few larvae and eggs are present which apparently are not growing. This completion of the emergence of the brood and the cessation of scouting activity would take place under natural conditions, so far as I can determine, between August 5th and 10th.

September 4 and 5. *Duloticus* colony: nuptial flights.

The development of the brood and the onset and cessation of scouting activity in *L. duloticus*, it will be noted, is the reverse of what it is in *Harpagoxenus americanus* (Wesson, 1939). The two forms may be contrasted as follows:—*duloticus*: brood develops principally from eggs laid the same spring; *americanus*: brood develops from larvae produced the previous summer; *duloticus*: nuptial flights take place in September; *americanus*: nuptial flights take place immediately after emergence of the winged brood; *duloticus*: workers begin scouting in the spring about the time that the eggs laid at the commencement of the season begin to hatch, and cease on the emergence of the brood in midsummer; *americanus*: workers begin scouting after the emergence of the brood and continue to do so until fall.

III. SLAVE RAIDS.

I have observed but 3 slave raids by *L. duloticus*. Since the 3 were very similar, only 1 is described as follows:—

April 27, 1938. A *duloticus* colony, containing 28 workers, a queen of *duloticus*, and about 40 *curvispinosus* slaves, was placed at one end of a box. At the opposite end (14 in. distant) was placed a *curvispinosus* colony containing 30 workers, a dealate queen, about 80 pupae, and some larvae. Both the *duloticus* and *curvispinosus* were nesting in small, glass-covered wooden chambers designed to imitate the natural nesting sites of the ants. The room in which the box was placed had been cool in the morning, but became much warmer during the afternoon. At 1:30 P.M. (temp. 73° F.) 2 *duloticus* workers emerged from the nest. By 2:15 (temp. 79° F.) 6 *duloticus* were scouting. Meanwhile, most of the remaining workers in the nest tended to cluster just inside the entrance. The scouting workers walked rather slowly and hesitatingly over the floor and sides of the nest, and reminded one

strongly of the appearance of a foraging *curvispinosus* worker. At 2:20 a scout met a *curvispinosus* worker near the latter's nest, and started to examine it. Then the *curvispinosus* attacked, and the scout turned and fled. A few minutes later another scout reached the *curvispinosus* nest, wandered over it a few minutes, left it but soon returned. At 2:35 she came upon the entrance. Very cautiously she inserted her antennae, then turned before the *curvispinosus* were aware of her presence, and went directly to the home nest at a fairly rapid pace. In the home nest she briefly combed her antennae, then ran about excitedly among the other workers that immediately began crowding forward in and about the entrance. Two minutes later she emerged and proceeded toward the *curvispinosus* nest followed by 18 *duloticus* and 5 or 6 *curvispinosus* slaves. The army consisted of a loose, rather rapidly moving file, about 5 in. in length, somewhat bunched in front but more straggling behind. The scout, now the leader of the file, moved with a peculiar, stiff-legged gait, with gaster deflected sharply downward, apparently depositing a scent trail. She moved rather slowly when she became a little in advance of the rest of the file, but fairly rapidly when touched on the gaster by following workers. Two or 3 *duloticus* and most of the slaves became lost from the file and returned to the home nest. The leader reached the *curvispinosus* nest in about 20 sec., climbed the front face of the nest and immediately plunged into the entrance, closely followed by 4 workers, and, at a little distance, by 6 or 7 more. Just inside the entrance the first *duloticus* workers encountered fierce resistance from the *curvispinosus*. With these the *duloticus* immediately grappled, biting and stinging viciously. They did not obtain the close, bulldog grip employed by *curvispinosus* workers when fighting one another, but attempted to seize their opponents, pull them within reach of their stings, then release them. Seven or 8 *duloticus* soon pushed into the *curvispinosus* nest, but it took nearly 3 minutes of fierce fighting before they were definitely masters of the situation. Once in control, and no longer strongly resisted by the *curvispinosus*, they ran about in the nest with excited, rather jerky movements, but showed little or none of the erratic, nip-jerk movements of the black slave-maker, *Harpagoxenus americanus*. They continued to bite and sting the *curvispinosus* workers, but did not retain their grips. By this time, the *curvispinosus* had had enough and fled carrying with them what brood they were able to snatch up. The *duloticus* continued to run excitedly about the nest attacking the few *curvispinosus* that remained, but gradually their excitement subsided. After a while, several *duloticus* dragged dead or injured *curvispinosus* out of the nest and dropped them. During the entire raid,

10 *curvispinosus* workers were killed and 4 or 5 so badly injured that they died in a few hours. No *duloticus* workers were killed or incapacitated. At first, the *duloticus* showed little or no interest in the *curvispinosus* brood, and did not pay any attention to it until they had complete possession of the nest. At 3:10 the first worker emerged carrying a pupa, and others followed singly soon afterward. Two *duloticus* workers, returning to the home nest with brood, brought back auxiliary files to the captured nest, the first comprising 6 *duloticus* and 4 *curvispinosus*, the second, 3 and 1. The *duloticus* continued to transport brood until about 4:30 at which time all pupae, larvae and eggs had been removed from the *curvispinosus* nest. The *duloticus* seemed reluctant to leave the nest, however, and 6 of them remained in it over night. During the following day the *curvispinosus* nest was gradually deserted.

The *duloticus* raid may well be compared with that of *Harpagoxenus americanus* (Wesson, 1939) which enslaves the same species as does *L. duloticus*. The raids of both species are very similar in form: a scout discovers a *curvispinosus* colony and returns to the home nest for an army. The army, led by the scout to the *curvispinosus* nest, kills or drives away the adults, bringing back the brood to the home nest at leisure. Both exhibit a reluctance to leave the captured nest after the *curvispinosus* brood has been removed. The raids of the 2 species differ, however, in many details: the *duloticus* scout is much more timid than the *americanus* scout, and consequently the *duloticus* depend more upon the concerted action of an army; an *americanus* scout will occasionally attack a small or poorly-defended *curvispinosus* colony without recourse to the home nest for assistance; the *duloticus* army moves in a loose, rather straggling file; the *americanus* move somewhat more slowly, but in a close, compact file; the *duloticus* army enters the *curvispinosus* nest by sheer force, biting and stinging the workers and driving them from their nest; the tactics of the *americanus*, on the other hand, consist in nipping at the *curvispinosus* and jerking them around, a worrying process which so excites the *curvispinosus* that they soon flee in a panic. This is more effective as it requires fewer workers and less time to rout the *curvispinosus* colony; *duloticus* workers show little interest in the *curvispinosus* brood until they have complete possession of the nest; *americanus* workers, on the other hand, begin to examine the brood almost as soon as they enter the *curvispinosus* nest; the *duloticus* take the entire captured larval brood to the home nest; the *americanus* usually neglect the very small larvae and eggs (but, in this connection, it should be recalled that *duloticus* begins raiding much earlier in the year than ameri-

canus and at a time when the *curvispinosus* brood may consist principally or entirely of larvae). I have not determined whether the *duloticus* reject captured male and female pupae as do the *americanus*.

IV. OBSERVATIONS ON MIGRATORY FEMALES.

The nuptial flights took place from the 2 colonies in the artificial nest on September 4th and 5th, 1938, at about 3:30 P.M. Both days were clear and warm (about 82° F.), but not sultry or humid. The box in which the nests were placed had remained in the sunlight during the early morning and in strong, diffuse daylight during the late morning and afternoon.

In an attempt to determine the method of colony formation, 4 females were very carefully dealated at 4:30 and placed in a box containing a *curvispinosus* colony (1 dealate female, 7 workers, 15 pupae and 1 or 2 larvae). For 2 hrs. they ran quite actively over the sides and top of the box; then their activity began to subside and they showed a disposition to gather in crannies or in corners. This change was noted even though the nest was kept warm and illuminated under an incandescent light bulb in order to eliminate any influence due to the fading of daylight. By 8:00 P.M. all the females had taken shelter in cracks or in small sections of hollow weed stems provided them. They remained hidden during the night and did not reappear until the middle of the following afternoon, about the time that the nuptial flight had taken place the preceding day. Again they ran rapidly and somewhat erratically around the nest, taking shelter after a few hours, to repeat the performance on the next day. When they were active during the late afternoons, the females ran about over the *curvispinosus* nest, but showed little interest in it. Occasionally a female came upon the entrance and inserted her antennae, but invariably fled precipitately when snapped at by the *curvispinosus* workers. A group of 5 *curvispinosus* pupae in a small chamber was made accessible to 1 of the females. She entered, walked about in the nest chamber, "sniffed" casually at the pupae, and left, after being in the chamber about 20 to 30 seconds. Two pupae were offered to a female after she had taken refuge in a stem for the night. She smelled them rather casually and, after a few minutes, dragged them part way into the entrance, but deserted them when she left the twig on the following afternoon. On succeeding days the females spent more and more time in their hiding places and finally ceased entirely their afternoon sallies about the box. At no time did they show any interest in the *curvispinosus* nest.

Although these observations are inconclusive as to the method of colony formation of the *duloticus* female, they do indicate that shortly after the nuptial flight *duloticus* females make no attempt to establish a colony by driving away the adults and usurping the brood and nest of a *curvispinosus* colony. This is especially important in view of the fact that such a method is strikingly exhibited by females of *Harpagoxenus americanus* (Sturtevant, 1927; Creighton, 1929; Wesson, 1939), and may indicate a significant difference in the origin and development of slavemaking behavior in the two forms. Other possible methods of colony formation by *duloticus* females are:

(a) The solitary female hibernates and attacks a *curvispinosus* nest the following Spring. This is suggested by elimination, lack of evidence and the fact that the nuptial flight takes place late in the season.

(b) The female seeks out a nest-founding *curvispinosus* female and cooperates with her in rearing a brood. This is doubtful, since the activity of the migratory females falls off steadily and sharply on the days following the nuptial flight.

(c) The female establishes a nest and rears a brood independently. I know of no known instance of such behavior on the part of a parasitic ant species.

V. TYPE LOCALITY.

Over 200 colonies of *Leptothorax curvispinosus* and 10 to 15 of *L. longispinosus* have been examined in several counties of Southern Ohio. Yet only in the type locality have any colonies been found that contain *L. duloticus*. Here, in an area of about 1,000 sq. ft., 4 colonies out of about 20 examined were found to contain *duloticus*. One of these, the type colony, was quite small, containing but 4 workers and a queen of the slavemaker, and was the only one to contain both *curvispinosus* and *longispinosus* slaves. Two others were much larger, containing about 40 workers and a queen of *duloticus*, and numerous *curvispinosus* slaves. The fourth colony was not taken, but was known to be *duloticus* from the presence of scouts about the entrance, and was assumed to be a rather large one from the number of foraging slaves. The small colony mentioned above was nesting in a large oak gall, while the other 3 were nesting in cavities in dead sticks on the ground. No colonies of *Harpagoxenus americanus* were found. The locality was on a steep, dry hillside thickly covered with small oak trees in which were intermingled a few pines and small maples. The ground vegetation consisted of scattered, low bushes, seedling trees and a few herbs. The

shallow, sandstone soil was thickly covered with dead leaves or pine needles. Independent *L. curvispinosus* colonies were numerous, but quite small, living for the most part in hollow acorns or twigs. The few *L. longispinosus* colonies, also quite small, were found principally in the bark or lichen at the base of the pine trees. Possibly the presence of numerous, small colonies of the host species is necessary for the survival of *L. duloticus*.

VI. OBSERVATION OF DULOTICUS QUEEN EATING EGG OF SLAVE.

On placing 1 of the *duloticus* colonies under a microscope on April 17, 1938, I observed a *curvispinosus* slave with gaster flexed forward between her legs in the act of laying an egg. When first seen the egg was about half extruded. The *duloticus* queen meanwhile was in front and a little to one side of the worker, and observing the act intently by continually examining the worker and the egg with her antennae. Not once during the several minutes required to extrude the egg did she turn from the worker. The queen snatched the egg from the worker as soon as it was laid, and devoured it on the spot. Holding the egg to her mouth parts with her fore tarsi, she consumed it in about 5 minutes. Since the eggs laid by unfertilized workers normally produce only males, and since no *curvispinosus* males appeared in the colony, it is evident that few or no eggs laid by *curvispinosus* workers survived, possibly because of being eaten by the *duloticus* queen. Whether this behavior by the queen is widespread among ants, or is a peculiarity of this species, I do not know. The observation is described for any interest it may have.

VII. DESCRIPTION OF MALE.

The following is a description of the male of *L. duloticus* which was not available at the time of the description of the worker and female (Wesson, 1937).

Male (Fig. 1). Length, 2.8-3.0 mm. Mandibles long, with broad blades, the terminal tooth sharply mucronate, penultimate tooth prominent, the basal teeth obsolete. Anterior border of the clypeus sinuate laterally, projecting and feebly emarginate in the middle; clypeal disk oval, slightly broader than long. Frontal carinae circular, partially enclosing the antennal insertions. Antennae 12 jointed, the scape as long as the first 4 funicular joints; first funicular joint pyriform, second to sixth funicular joints small, subequal, seventh funicular joint larger, the 4 terminal joints forming a distinct

club which is slightly longer than the remainder of the funiculus. Mesonotum strongly convex anteriorly, rising abruptly from and projecting somewhat over the pronotum. Thoracic sutures very distinct, the Mayrian furrows strongly impressed throughout their length. Forewings with long radial cell which is narrowly open. Hind wings veinless. Epinotum bearing robust spines about as long as broad at the base. Petiole in profile short, $1 \frac{1}{3}$ times longer than broad, broadly convex on the anterior slope, steeper and concave on the posterior slope. From above the petiole is broad, the sides subparallel, slightly narrower anteriorly; node slightly compressed laterally, the superior border feebly emarginate. Petiole bearing a stout ventral downward projecting tooth. Postpetiole from above subrectangular, $1 \frac{3}{5}$ times broader than long and broader than the petiole in the same proportion, the anterior angles prominent.

Head opaque, coarsely and densely punctate, the punctures intermingled with fine, sparse, irregular rugae. Mandibles longitudinally striate. Clypeus, thorax, petiole, postpetiole and gaster shining; the clypeus with a few longitudinal rugae, especially on the sides; borders of the thoracic sutures and areas bordering wing insertions, irregularly sculptured; petiole and sides of the epinotum crenulate; gaster and the smooth portions of the thorax very finely and sparsely crenulate and with sparse punctures.

Hairs long, erect, slender, sparse on most of the body, shorter and more numerous on the posterior segments of the gaster, short and reclinate on the legs and antennae.

Color, brownish black; antennae, legs and mandibles pale yellow; clypeus and genitalia reddish brown.

From the male of *L. acervorum*, the male of *duloticus* differs in the long, subdentate mandibles, the presence of a distinct antennal club, the presence of a ventral tooth on the petiole, and the presence of prominent epinotal spines. From the male of *L. longispinosus* to which it also bears a striking superficial resemblance, especially in the shape of the antennae, it differs in the produced emarginate clypeus, the coarsely sculptured head, the presence of epinotal spines and a ventral petiolar tooth, and the entirely different petiole and postpetiole. From the male of *Harpagoxenus americanus* (Creighton, 1927), the *duloticus* male differs in the possession of a distinct antennal club; in having mandibles longer and broader but less dentate; in the entirely different shape of the clypeus; in the possession of acute epinotal spines; in the entirely different shape of the

petiole and postpetiole, the former armed ventrally; and in minor differences of sculpture and pilosity.

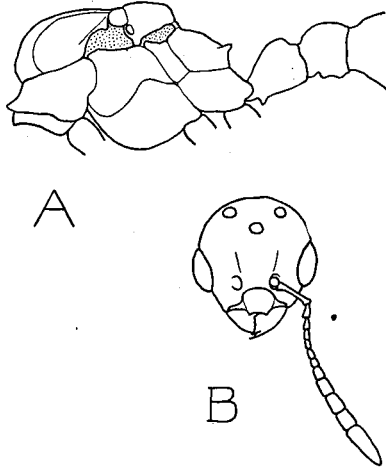


FIG. 1. A, Male of *Leptothorax duloticus* from the side; B, Head of same from the front.

SUMMARY.

1. Various observations on the behavior of *Leptothorax duloticus* are described, and, wherever possible, compared with those of *Harpagoxenus americanus*.

2. The male of *Leptothorax duloticus* is described.

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