STUDIES ON FREE COLONIES OF CRYPTOCERUS TEXANUS SANTSCHI (HYMENOPTERA: FORMICIDAE)

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For a number of years the writer has hoped to present habit data derived from a study of free colonies of Cryptocerus texanus. The need for such a study is apparent if papers previously published in this journal are consulted. Most of the reactions which Dr. R. E. Gregg and I discussed in our 1954 publication (1) were those of captive colonies of texanus installed in Janet or Field nests. The limitations of this type of study are shown by the fact that, after more than a year, during which time some of the colonies had been tested with a wide range of food, it was not even suspected that texanus subsists on pollen. In 1963 (2) after other inconclusive feeding experiments, the writer abandoned the artificial nests and installed colonies in sealed terraria that permitted limited foraging. The responses of the foragers, which at first seemed to be entirely without point, were finally recognized as activities which resulted in the collection of pollen grains. While their was no reason to suppose that this pollen gathering was an abnormal response, there was good reason to suspect that the process might show interesting new features when carried on by a free colony. Some of these are discussed in this paper. The period during which the free colonies were observed extended from late October to the middle of April.

It may be objected that the term "free colony" as used here is a misnomer. The writer has yet to find an undisturbed nest of texanus so situated as to permit easy and continuous observation. The ants are not found in young trees, presumably because these are avoided by the beetles whose abandoned larval burrows are used as nest passages by texanus. But an undisturbed nest of texanus in a dead limb well up in the crown of a large tree is very nearly inaccessible. And, even if one grants the unlikely possibility that the presence of the colony could be spotted from the ground, there would be no practical way to take advantage of the discovery. Since what was needed for the present study were nests at or below eye-level and since it appears that these are not to be had, a compromise was inevitable. When

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limbs containing colonies of *texanus* are pulled down the ants at first show little tendency to leave them. This suggested that if such limbs were wired on another tree at eye-level the ants might remain in them and continue their normal activities with the nest positioned so that these could be easily observed.

The first attempt at this had a discouraging outcome. Two days after a dead oak limb containing a texanus colony had been wired to a low limb of a Texas ebony tree, the ants moved out of the oak limb and, taking their brood with them, migrated into the upper part of the crown. Since by doing so they removed themselves from any possibility of further observation, it can only be conjectured that they occupied another burrow well up in the crown of the tree. Much better luck was had with two other colonies when the oak limbs in which they were living were wired, at eve-level to the branches of a grapefruit tree just outside our cottage in La Feria, Texas. This arrangement worked admirably, for although the ants explored many of the burrows in the tree, they remained in the oak limbs during a six months period of observation. Moreover, an examination of the colonies at the end of this time showed that they had done very well for themselves, even though living on a tree that is not ordinarily utilized as a nest site. Since the principal object of this study was to determine whether these colonies behaved differently from captive colonies, two control nests were set up in sealed terraria which were kept inside of the cottage.

It was soon clear that the two groups of nests reacted identically to light and temperature. Foraging, both in the free colonies and the captive colonies, was strictly confined to daylight hours. It would occur only when the temperature was 70°F (21°C) or higher. Because of the greater warmth of the cottage the captive colonies usually began foraging sooner than the free colonies and the latter would not forage at all on cool days. But it was equally clear that the free colonies were often restricted to the nest by another factor for, on very windy days they would not leave the nest, even though the light and temperature conditions were favorable. The foragers from a free nest are much more alert than those in sealed terraria. This alertness makes them hard to observe since they will usually show an avoidance reaction if the observer comes within a foot of them. They will move quickly to the opposite side of a leaf or twig or, when on large branches they may try to hide under bits of loose bark. But there is a much more significant outcome of this alertness for it clearly keeps them from being blown out of the tree. The foragers cling to leaves with the greatest tenacity when these are moved by

breezes. The result is, therefore, quite unlike that predicted by the writer in 1963, for the movement of the leaves does not displace the foragers on them. Since I expected that there would be numerous displacements, the ground below the tree was cleared of weeds and smoothed so that any fallen forager would be easily visible. But, although observations were made several times a day over a period of six months, not a single forager was ever seen on the soil at the base of the tree. This statement needs further consideration for the foragers not only managed to avoid being displaced from the tree but they also refused to leave when foraging brought them near the soil. The trunk of the tree in which the nests were placed consisted of a single, large basal trunk about eighteen inches high, which divided into two secondary trunks to form a Y. The crown of the tree was thus divided into two portions and the most certain way to get from one to the other was to travel down one arm of the Y and up the other. This the foragers from the free nests regularly did. But in passing from one arm of the Y to the other the ants were often within a foot of the soil. As they are clearly aware of the presence of an observer at that distance it is inconceivable that they should not have been aware of the soil below them. Yet no forager was ever seen to descend to it. Since texanus is not known to nest in grapefruit trees, there is a possibility that this behavior was abnormal. If so it seems odd that the abnormality should have prevented the ants from doing the one thing that might have led them to a more acceptable nest site. In my opinion their behavior was normal and, if this is correct, we now have support for the view that texanus forages only in trees and that its presence on the ground may be regarded as the result of an accident. Moreover, there is reason to believe that such accidents are much less frequent than was formerly supposed.

When a free colony of texanus is foraging actively it is impossible to keep track of the foragers, since they are scattered all over the crown of the tree. But if the beginning of foraging is observed in the morning it is possible to get some idea of the number of workers engaged in it by counting how many workers leave the nest before any return to it. On this basis the number of foragers was surprisingly small, for it appeared that there were seldom more than twenty outside the nest at the same time. More often there seemed to be no more than a dozen workers engagd in foraging. After a number of counts of this sort the writer came to the conclusion that even the most active of the free colonies must be a small one. It was, therefore, a surprise when this colony was exposed on April 11, to

find that it contained twelve queens, fifty-six majors and one hundred and twelve medias and minors. It is hard to explain why so few of the latter leave the nest but this behavior accords well with earlier observations on captive colonies, where the majority of the members spend long hours packed into a nearly immobile mass near the outer end of the nest passage. It is possible that with the higher temperatures which occur during the summer months a greater percentage of the colony engages in foraging. But in this connection it is well to remember that the colony exposed on April 11 contained ten pupae, one hundred and ninety-two larvae and one hundred and seventy-eight eggs. Despite the small number of foragers it is plain enough that their activities had brought through considerable winter brood and this is supported by callows and advanced brood taken from other nests as early as February 11.

It was originally supposed that the free colonies would have to be supplied with food, since the mature grapefruit leaf lacks pollentrapping hairs. The foragers from the free colonies soon overcame this difficulty by utilizing a transient pollen trap on the young leaves. Each of these has an expanded flange at either side of the petiole and before the leaf reaches full size there are sticky hairs on the lower surface of these flanges. Even though they are evanescent, these hairs supplied the colonies with sufficient pollen to keep them in good condition. The foragers from the free colonies also fed on honeydew when they could get it. Their reaction here was similar to that described by Creighton and Nutting for Cryptocerus rohweri in 1965 (3). The aphids (presumably A. sphaericola) had covered the leaf surface with a film of honey-dew and it was this, rather than the aphids which interested the texanus workers. The ants appeared to care nothing for the aphids, for they pushed them aside and walked over them in order to get at the honey-dew. The aphids plainly disliked this treatment for they would often withdraw their mouthparts and move to another part of the leaf. It seems well to note that in the Rio Grande Valley aphids are present in significant numbers only during two rather brief periods one in early spring, the other in the fall. If these same conditions hold over the entire range of texanus it is likely that honey-dew plays little part in its diet.

The control colonies had to be provided with food, but this difficulty was unexpectedly simplified when it was found that Tillandsias trap large numbers of pollen grains. There are two species of this epiphyte in the Rio Grande Valley, *T. usneoides* ("Spanish moss") and *T. recurvata* ("ball moss"). Each of these plants has elongate, strap-like leaves which are covered with a reticulum of thin, white,

semi-erect scales that largely conceal the green surface beneath them and give to the plants their characteristic grey color. Large numbers of pollen grains are trapped in the spaces between these scales and the ants have no difficulty extracting them. The advantages of using Tillandsias as a pollen source for captive colonies of texanus are outstanding. Since the epiphytes will stay fresh indefinitely, an ample supply can be kept on hand without difficulty and, when they are introduced into the terraria, there is no need to provide them with a water source. After a few weeks it became clear that the captive colonies could be kept in excellent condition with no food source other than the pollen grains trapped on the Tillandsia leaves. This was a most surprising discovery for, if captive colonies can subsist on nothing but Tillandsia-trapped pollen, free colonies should be able to do so as well.

The significance of this will be obvious to anyone who has tried to arrive at an explanation for the diversity of the trees in which the nests of texanus have been found. The first data on this, published by Dr. M. R. Smith in 1947 (4), appeared to indicate that texanus has no preference for a particular kind of a tree as a nest site. Five of the six trees carried in this list belonged to unrelated genera. By 1954 the number of records had risen to twenty-seven and with this increase there appeared the fact that some selective process must be involved in the nesting responses of texanus. In this second list seventeen of the records came from live-oaks and this disproportion (63%) was too great to permit the view that any tree is equally suitable as a nest site for texanus. At present the disproportion of records from live-oaks has risen to 71% and, in view of the fact that the remaining 29% of the records are spread over six different trees, it follows that the incidence of nests in live-oak trees is at least eight times greater than it is in any other tree. As soon as it was found that pollen grains are the principal food of texanus it became clear that the capacity of live-oak leaves to trap wind-blown pollen makes this tree an especially favorable nest site for texanus. This advantage is so striking that the difficulty is not to show why texanus usually nests in live-oak trees but to explain why it should ever nest anywhere else. There is a strong temptation to treat other records as accidents and sweep them under the rug, which was essentially what the writer did with them in 1963. If this is done one can then fall back upon the often cited but seldom proved explanation of host plant preference.

But the fact remains that *texanus* occasionally nests in other trees than live-oaks and, with an ant whose responses are as rigid as those

of texanus, it should be possible to account for why it does so. If the choice is made by the nest-founding female, we muse suppose that she is something of a botanical taxonomist, since the list of trees which she has "chosen" includes representatives of five Families². But the whole concept of host plant selection implies a narrow range of choice, seldom extending beyond a few species within a single genus. It should be obvious, therefore, that whatever the selective mechanism may be, it can hardly be a choice on the part of the nest-founding female.

It occurred to the writer that one possible selective device might be a marginal pollen supply in trees where the incidence of texanus colonies is low. Efforts to clarify this brought out several disconcerting items. The mature leaves of Texas ebony and mesquite appear to be completely devoid of hairs of any sort which might act as pollen traps. Moreover, in southern Texas, hackberry and mesquite trees usually shed their leaves by the end of December and remain leafless for the next two months. For a species which matures broad all year long and must forage all year long in consequence, a deciduous tree scarcely seems a logical nest site. But it is now clear that we need not look for pollen traps on the leaves of the trees in which texanus is nesting if these trees have Tillandsias growing on them. For the Tillandsias will trap enough pollen to supply the needs of the texanus colony and this supply will be equally effective whether the tree is evergreen or deciduous. There are thus two pollen sources to be considered and these are not necessarily interdependent. This can produce a survival differential which might be expressed as follows:

NEST SITE live-oaks with Tillandsias live-oaks without Tillandsias other trees with Tillandsias other trees without Tillandsias CHANCE FOR SURVIVAL
optimum
good
fair
little or none

On the basis of the above it is not necessary to attribute a capacity for the selection of suitable host plants to the nest-founding female. On the contrary she can be regarded as hampered in her nest-founding responses since she can no longer utilize soil as a place to found her nest. But, except for this limitation, we may suppose that her reactions at the end of a marriage flight are those of most nest-

²Colonies of *Cryptocerus texanus* have been found in live-oak and deciduous oaks (Fagaceae), Texas ebony and mesquite (Leguminosae), hackberry (Ulmaceae), prickly ash (Rutaceae) and Mexican persimmon (Ebenaceae).

founding females. If her main concern at this time is to put herself into a safe position as rapidly as possible, it is logical to believe that the nest-founding female of *texanus* would accept any cavity in plant tissue whose opening she could occlude. In securing her own safety the female has also provided for the initial development of the colony, since the occlusion that protects her from predators gives equal protection to her developing brood. But, thereafter, there should be a high mortality among these incipient colonies for, unless the female has occupied a cavity in a live-oak or in some other tree on which Tillandsias are growing, there is scant chance that the colony will reach maturity. If this view is correct the selection involved is not the choice by the female of a suitable host plant but the much more commonly encountered phenomenon which eliminates any organism that has placed itself in a position where survival is impossible.

There are features in the distribution of texanus which accord well with the above view. In the past twenty years the number of records for texanus has more than doubled and its range has been considerably extended by the addition of records from Mexico. With this additional information it has become clear that in the lower Rio Grande Valley the incidence of texanus is far less than it is in other parts of the range. This region of low incidence extends both north and south of the Valley proper and forms a band, about a hundred miles wide, in which it is exceedingly difficult to find colonies of texanus. During six winters of collecting in this area the writer has failed to take a single colony. Indeed, the one record of texanus from the Rio Grande Valley appears to be the Brownsville record published by M. R. Smith in 1936 (5). The only live-oaks in the lower part of the Valley are a few trees which have been brought in and planted around houses as ornamentals. For this reason alone it might be expected that texanus would not find the lower Valley a particularly favorable area in which to nest. But there is no lack of mesquite, Texas ebony or hackberry trees in the lower Valley and it is hard to see why these trees are so seldom utilized if nothing more than their presence is required. But while all three of these trees are widely and uniformly distributed throughout the lower Valley, the great majority of them are free from Tillandsias. The latter are very sporadic in the Valley, most of them being confined to a few isolated pockets near the river. If it is true that this restriction makes most of the trees in the Valley unsuitable as nest sites for texanus there is no need to look further for an explanation of its low incidence there.

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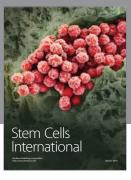
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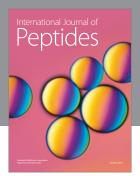
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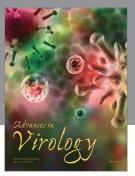
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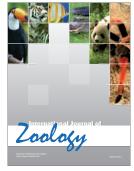


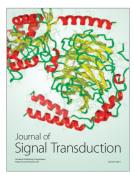














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