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THE ECOLOGY OF SOME NORTH AMERICAN DACETINE ANTS

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INTRODUCTION

The tribe Dacetini is composed of a moderate number of unusual forms characterized by a tendency toward extreme reduction in the number of antennal segments, elaboration of the apparently predacious mandibles, and development of a wide diversity of types of bizarre cephalic hairs. It has recently been intensively revised by W. L. Brown (see 1948, 1949 for major changes), who finds that it is predominantly tropical and contains several large, abundant genera plus a quantity of small, very poorly known ones. Some of the larger genera have penetrated temperate zones and one at least (*Smithistruma*) has undergone considerable speciation there. Phylogenetic trends as outlined by Brown (1948 and *in litt*)[1] include reduction in size, shortening of the mandibles, and a shift from an epigaeic to a hypogaeic mode of life. All of the forms found thus far in the United States belong to four dominant, relatively specialized genera. *Strumigenys* F. Smith is represented by one species, *S. louisianae* Roger, extending from tropical America into the southern states. *Trichoscapa* Emery is also represented by its single species *T. membranifera* Emery, a tropicopolitan tramp which has been collected frequently in the Gulf States. *Quadristruma* Brown is known at this time in the United States from a single record of *Q. emmae* (Emery) from Homestead, Florida; it has probably been introduced. *Smithistruma* Brown is represented by no less than 22 endemic and one possibly introduced species. These are found over the entire United States but are very scarce west of the Mississippi and in the extreme north. Even though it tends to be replaced by *Strumigenys louisianae* in local areas in the Gulf States, *Smithistruma* is by a wide margin the dominant genus in the United States.

Preliminary work by L. G. and R. G. Wesson (1936, 1939) and Brown (1950) on several species of *Smithistruma* and by Wilson (1950) on *Strumigenys louisianae* seemed to indicate that the diets of these two genera are restricted mostly to entomobryoid Collembola, a specialization certainly as aberrant as the structural modifications which characterize these ants. Brown (*in litt*) has recently determined that the Australian genera *Orectognathus*, *Alistruma*, *Clarkistruma*, and *Epopostruma* possess similar food preferences; this is especially significant in view of the fact that the first genus is one of the most primitive in the tribe.

Because it was Dr. Brown's original plan to correlate the evolution of food habits with dacetine phylogeny, the present study of North

[1]See also Brown's recent revision of the world *Smithistruma* (Amer. Midl. Nat., 50: 1–137, 1953). This contains a recapitulation of dacetine classification along with an abundance of field data on the North American species.

American forms was initiated to complement his work in Australia, and a great emphasis has been laid on food habits alone. Certain data accumulated on other aspects of ecology have been mostly incidental but are included here, along with what meager conclusions can be drawn from them, because they represent the first information of this sort published on the tribe.

In the present study the most efficient observation nest developed for the small North American forms was a little plaster of Paris Janet nest four inches long, three inches wide, and three-fourths of an inch deep. This was cast in the bottom of a square ice-box dish, and the top surface was scraped to extreme smoothness with a glass plate as soon as the plaster began to harden. The food chamber was about half an inch deep and occupied half the space of the nest. Brood chambers and interconnecting galleries were excavated in the plaster with a fine knife and made to simulate the natural nests as much as possible. The ants were transferred to this type of nest in the following manner: the original nest was taken entire from the field to the laboratory and carefully dissected; the adults and brood were removed individually with forceps or aspirator to another container and dumped together into the food chamber. The plaster nest was then covered with a single plate of glass and placed on some moistened strips of cloth. The Forel Arena technique was found to be impractical in transferring such small, delicate ants, since these are poorly organized and very sensitive to the slightest dessication. Also, if portions of the original nest were placed in the food chambers to facilitate rapid transfer, the ants tended to group permanently around and under these instead of moving into the brood chambers.

FOOD HABITS[2]

Food preferences were determined primarily by introducing as wide a variety of substances as possible into the food chambers and observing the reactions of the foraging workers as they encountered them. It was quickly established that the dacetines are exclusively predacious, so that after a short time the experiments narrowed down to the introduction of small organisms only. Those organisms captured by the ants, carried to the brood chambers, and presented to the larvae were classified as "accepted"; those ignored by the ants despite frequent contacts over a reasonable length of time were classified as "rejected." Both "accepted" and "rejected" organisms were retrieved and preserved for later identification. In the case of prey which had been taken to the brood chambers and covered with larvae, this removal often proved to be a delicate operation. Best results were obtained by brushing the larvae aside with a dry needle and picking out the prey with a needle made slightly adhesive with alcohol.

In must be emphasized that since adults were rarely observed in the act of feeding, the food preferences to be discussed apply essentially to the larvae. There is, however, considerable evidence that the adults feed on the same captured prey as the larvae, only much more sparingly.

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[2]Appreciation is expressed to Miss Grace Glance, Collembola specialist of the United States National Museum, for the determination of the Collembola collected in connection with this study.

Strumigenys louisianae Roger

A total of seven colonies of this species from several localities in southern and central Alabama were studied over a period of a little less than a year. As noted in my preliminary paper (1950), the principal food appears to be certain groups of Collembola, although a few other arthropods are taken occasionally, especially if they are dead or injured. The original list of accepted and rejected organisms has been incorporated into the much more extensive one given below.

ACCEPTED ORGANISMS

Collembola
- Entomobryidae: *Entomobrya, Lepidocyrtus, Orchesella, Tomocerus, Pseudosinella.*
- Isotomidae: *Isotoma.*
- Sminthuridae: *Ptenothrix.*

Entotrophi
- Japygidae: *Japyx.*

Dictyoptera
- Termitidae: *Reticulitermes.*

Psocoptera
- Psocidae.

Hymenoptera
- Formicidae: *Solenopsis* and *Monomorium* larvae.

Diptera
- Psychodidae, Phyllomyzidae.

Symphyla
- Scutigerellidae: *Scutigerella.*

Acarina—unidentified.

REJECTED ORGANISMS

Collembola
- Poduridae: *Neanura, Hypogastrura.*
- Onychiuridae: *Onychiurus.*
- A wide variety of other groups, including most of the orders of insects, numerous mites, annelids, isopods, nematodes, spiders, pseudoscorpions, millipedes, and centipedes.

By far the most preferred prey of this species are entomobryoid and symphypleonan Collembola, and these were used to maintain the colonies in the present study. Other arthropods were treated in a somewhat desultory fashion by the ants. When a half dozen or so termites were placed in the food chamber of a nest, they were attacked at once, and although one or two usually succeeded in escaping and hiding under debris, the majority were killed within several hours. Some of the corpses were carried to the brood chambers and consumed, while others were left undisturbed in the food chamber. Psocids and small flies were usually either ignored or half-heartedly attacked by the ants, and those carried to the brood chambers were then only occasionally partly consumed. *Japyx* were vigorously attacked by the ants, which appeared to have an especial antipathy toward these insects, and like the termites they rarely survived more than several hours in the food chamber of a sizeable colony. Legs and antennae were often consumed by the adults and larvae, but the bodies were almost never disturbed.

Only several mites were accepted over the entire period of observation. Since the debris in the food chambers almost always swarmed with a substantial number of species in several families, the possibility must be considered that the *Strumigenys* regularly accept certain forms but reject the majority. There is some evidence that mites are normally accepted in nature (see below). Symphyla were consistently accepted and eaten, to the extent that they seemed to be preferred almost as much as Collembola. Small ant larvae were also readily accepted, possibly suggesting that the *Strumigenys* may on occasion behave as thief ants, although no evidence of this was seen in the field.

A spot check of the food-chamber experiments was attempted by placing a Janet nest containing a colony of *Strumigenys* in a terrarium partly filled with fresh humus and leaf litter, which were taken from several areas and replaced periodically. Occasionally bits of wood containing termites were also added. The ants were allowed access to this material through galleries leading to the outside of the nest. Their prey, checked daily over a two-week period, consisted at least of eleven entomobryids, seven isotomids, four mites, and one symphylan. Except for the unexpected large proportion of mites, this sample is consonant with the prey specificity exhibited by colonies confined to the artificial nests. Attempts were made to established two colonies in Janet nests in the field at the original nesting sites, but in both cases they quickly migrated out and could not be found in the immediate vicinity.

The *Strumigenys* are bolder and more direct in their manner of stalking prey than the other dacetines studied. This trait is perhaps a result of their more efficient mandibles, which are extremely long and supplied with prominent apical teeth. They can be opened to almost a 180° angle and operate very much as miniature animal spring traps. When approaching a collembolan, the worker *Strumigenys* moves slowly and cautiously spreading its mandibles to the maximum angle and exposing two long hairs which arise from the paired labral lobes. These hairs extend far forward of the ant's head and apparently serve as tactile range finders for the mandibles. When they first touch the prey, its body is well within reach of the apical teeth. A sudden and convulsive snap of the mandibles literally impales it on the teeth, and drops of haemolymph often well out of the punctures. If the collembolan is small or average in size, the ant lifts it into the air and curls its gaster forward in an attempt to sting, a surprisingly awkward motion in this species and the other dacetines studied, for in many catches observed it did not appear that the sting entered the body of the prey at all. Nevertheless, all but the largest Collembola are quickly immobilized by this action, and struggling is feeble and short-lived. Apparently the prey are only paralyzed and not killed outright, since most can be prodded into feebly moving even after they have been carried into the brood chamber.

A great deal of individual deviation from the typical hunting behavior occured in the nests under observation. Sometimes workers were much less stealthy in their approach and seemed almost to charge their prey. Frequently they seized Collembola when these insects blundered into them. Dead Collembola were not stalked but were directly picked up after a brief inspection.

Nothing resembling concerted or coordinated stalking on the part of several workers was observed. Hunting in general appeared to be rather haphazard, a condition accentuated by the apparent inability of the ants to recognize the presence of insects more than about a millimeter away. Occasionally workers were seen to stalk and strike Collembola which had already been captured by other workers and were being transported to the brood chambers.

Field observations on the food habits of these tiny and secretive ants are understandably meager. At two localites in Alabama, Gulf State Park and Mobile, stray workers were observed carrying entomobryids. On one occasion, in Mobile, a worker was found carrying a small *Campodea*. As mentioned in my preliminary paper on this species, one nest collected at Tuscaloosa, Ala., contained recognizable insect remains in the galleries; these were identified as belonging to three entomobryoid genera, *Entomobrya*, *Proisotoma*, and *Isotoma*.

Larvae are fed by being placed directly on the prey. As many as ten or more may be piled at first on the same collembolan, and since they are active feeders they may wholly consume a small individual within several hours. The final fragments of the insect are held aloft, ponerine fashion. No case of ingluvial feeding of the larvae by the workers was ever observed, although occasionally workers were seen passing food in this manner.

Trichoscapa membranifera Emery

Two colonies of this species, respectively from Escambia Co. and Tuscaloosa Co., Alabama, were studied during an eight-month period.

ACCEPTED ORGANISMS

Collembola
- Entomobryidae: *Entomobrya*, *Lepidocyrtus*, *Orchesella*, *Tomocerus*, *Pseudosinella*.
- Isotomidae: *Isotoma*, plus one unidentified genus.
- Sminthuridae: *Ptenothrix*.

Entotrophi
- Campodeidae: *Campodea*.

Dictyoptera
- Termitidae: *Reticulitermes*.

Hymenoptera
- Formicidae: *Monomorium* larvae.

Symphyla
- Scutigerellidae: *Scutigerella*.

Acarina—unidentified.

REJECTED ORGANISMS

Collembola
- Poduridae: *Neanura*.
- A diversity of other invertebrates similar to those offered to *Strumigenys louisianae*.

The food preferences of the *Trichoscapa* proved to be about the same as for *Strumigenys*, with a little less latitude in the acceptance of non-collembolan groups. As in *Strumigenys*, mites were taken only on several occasions from a constant supply of diverse forms. Termites were usually ignored, never attacked so persistently as by *Strumigenys*,

and only occasionally were carried into the brood chambers and eaten. *Japyx* were killed but not transported or eaten. *Monomorium* larvae were eaten, but *Solenopsis* larvae were rejected by the *Trichoscapa* brood even though they had been transported by the workers. *Campodea* and *Scutigerella* were both readily accepted.

The *Trichoscapa* are the most active of the dacetines studied and show unexpected pugnacity under certain conditions. *Japyx* and termites were frequently attacked in the artificial nests with a viciousness approaching that of some of the more aggressive larger myrmicines. The little dacetines actually rushed at these insects when they contacted them, seizing hairs or appendages and doubling up in an effort to sting. Although they lacked a weapon of shock such as the mandibles of *Strumigenys*, they were able to panic fairly large individuals and dispose of them as quickly as this other genus. Since insects combatted in this fashion were rarely eaten, it is assumed that such aggressive behavior is used in the defense of the nest.

Stalking of Collembola is in an entirely different mood and is usually executed with far more caution and deliberation than the *Strumigenys* ever show. The *Trichoscapa* worker rarely recognizes an insect until it actually comes in contact with it, but it is very sensitive to nearby movement and probably depends a great deal on this in spotting prey. As soon as the worker becomes aware of the presence of a collembolan, it "freezes" in a lowered, crouching position and holds this stance briefly. If the collembolan is to its back or side, the worker now turns very slowly to face it. Once it is aligned with the collembolan, it begins a forward movement so extraordinarily slow that it can be detected only by persistent and careful observation. Several minutes may pass before the ant finally maneuvers over less than a millimeter's distance to come into a striking position, and it may be remain in this position for as much as a minute or more. During this time the collembolan may move away for one reason or another, in which case the ant rarely attempts to follow but begins to forage anew. Unlike *Strumigenys*, the *Trichoscapa* open their mandibles only to about a 60° angle. Tactile labral hairs are present and eventually come to touch the prey. The mandibular strike is as sudden as that of *Strumigenys*, but since it is usually directed at an appendage, it does not have the same stunning effect on the collembolan. These insects often struggle vigorously to escape, but the ants are very tenacious and retain a fast grip until they are able to sting their prey into immobility.

Unusual behavior in foraging workers was sometimes observed. Occasional bold *Trichoscapa* were seen to approach their prey rapidly and attempt to seize a hair or appendage, and these were frequently successful. Sometimes workers would "freeze" when Collembola were moving rapidly around them and wait without moving, apparently in anticipation of ambushing the animals as these blundered into their mandibles.

Details of larval feeding seem to be similar to those in the case of *Strumigenys*. In addition, the *Trichoscapa* were never observed to participate in any sort of trophallaxis, either between workers or between workers and larvae. As a rule, the *Strumigenys* appeared to be the more efficient in catching Collembola in the artificial nests. Specifically,

when fresh batches of Collembola were placed in the food chambers, colonies of *Strumigenys* were definitely able to accumulate these insects in their brood chambers faster than were *Trichoscapa* colonies of comparable size. However, it is obvious that this difference cannot be taken as a true indication of the relative efficiencies of these two genera under natural conditions, which involve a more scattered food supply and much longer periods of time.

Smithistruma rostrata (Emery)

Seven colonies from several localities in central and northern Alabama were studied over a period of nine months.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya*, *Lepidocyrtus*, *Orchesella*, *Tomocerus*, *Pseudosinella*, *Pseudosira*.
Isotomidae: *Isotoma*.
Sminthuridae: *Sminthurinus*, *Ptenothrix*.

REJECTED ORGANISMS

Collembola
Poduridae: *Anurida* (*Brown, 1950*), *Neanura*, *Achorutes*.
A variety of other invertebrates similar to those offered *Strumigenys louisianae*.

In marked contrast to the preceding two species, *Smithistruma rostrata* appears to feed strictly on Collembola. Organisms other than the preferred Collembola were completely avoided in the artificial nests and rarely attacked even when they ventured into the brood chambers. Otherwise, this species is essentially similar to *Trichoscapa membranifera* in details of stalking behavior and larval feeding and in the total absence of trophallaxis. Field data on the food habits of this and other species of *Smithistruma* are virtually lacking. On one occasion, near Old Fort, North Carolina, a worker was observed carrying an entomobryid toward its nest nearby.

Smithistruma brevisetosa (M. R. Smith)

One colony of this species from Tuscaloosa, Alabama, was studied over a period of six months.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya*, *Orchesella*.
Sminthuridae: *Ptenothrix*.

REJECTED ORGANISMS

Collembola
Poduridae: *Neanura*.
Onychiuridae: *Onychiurus*.
A variety of other invertebrates similar to those offered *Strumigenys louisianae*.

This species appears to be identical in food habits to *Smithistruma rostrata*.

Smithistruma missouriensis (M. R. Smith)

One colony from the Chilhowee Mountains of eastern Tennessee was studied for a period of about a month.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya, Tomocerus, Pseudosinella.*
Poduridae: *Achorutes.*

REJECTED ORGANISMS

Collembola
Poduridae: *Neanura, Achorutes.*
A small variety of other invertebrates, including isopods, mites, nematodes, and a few small insects.

Only one individual of *Achorutes* was taken by this colony, a remarkable exception to the general rule of Collembola specificity.

Smithistruma talpa (Weber)

One colony from the Chilhowee Mountains of Tennessee was studied for a period of about a month.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya, Orchesella, Tomocerus, Pseudosinella.*
Isotomidae: *Isotoma.*
Sminthuridae: *Sminthurinus.*
Entotrophi
Japygidae: *Japyx.*
Campodeidae: *Campodea.*
Symphyla
Scutigerellidae: *Scutigerella.*

REJECTED ORGANISMS

Collembola
Poduridae: *Neanura, Achorutes.*
Onychiuridae: *Onychiurus.*
A small variety of other invertebrates similar to those offered the *Smithistruma missouriensis* colony.

Japyx and *Campodea* were captured and carried to the brood chambers but later discarded. *Scutigerella* were readily accepted and eaten. Perhaps in agreement with its broader food perferences, this colony was more active and aggressive than the other *Smithistruma* studied. Its food habits were otherwise similar to those of *S. rostrata.*

Smithistruma clypeata (Roger)

Two colonies from central Alabama were studied over a period of approximately six months.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya, Lepidocyrtus, Lepidocyrtinus, Orchesella, Tomocerus, Pseudosinella.*
Sminthuridae: *Sminthurinus, Ptenothrix.*
Entotrophi
Japygidae: *Japyx.*
Campodeidae: *Campodea.*

REJECTED ORGANISMS

Collembola
Poduridae: *Neanura.*
A variety of other invertebrates similar to those offered *Strumigenys louisianae.*

One *Campodea* and two small *Japyx* were captured and eaten. These two colonies apparently had food preferences almost as broad as the *Sm. talpa* but were not nearly so active. Food habits were otherwise the same as in *Sm. rostrata*.

Smithistruma dietrichi (M. R. Smith)

One colony from the Chilhowee Mountains of Tennessee was studied for a period of about a month. Unfortunately, it was accidently destroyed before poduroid Collembola could be introduced, so that Collembola specificity was not checked.

ACCEPTED ORGANISMS

Collembola
Entomobryidae: *Entomobrya, Orchesella, Pseudosinella.*
Isotomidae: *Isotoma.*
Sminthuridae: *Sminthurinus.*
Entotrophi
Japygidae: *Japyx.*
Symphyla
Scutigerellidae: *Scutigerella.*

REJECTED ORGANISMS

A small variety of other invertebrates similar to those offered the *Sm. missouriensis* colony.

The several *Japyx* and *Scutigerella* given the colony were totally consumed. Outside of the acceptance of these forms, the food habits of this species appear to be about the same as those of *Sm. rostrata*.

DISCUSSION OF FOOD HABITS

Smithistruma (*Wessonistruma*) *pergandei* (Emery) was studied in some detail by L. G. Wesson (1936), who concluded that it fed exclusively on Collembola. While his experiments present strong evidence that Collembola are the primary food source, they are actually too limited to exclude the possibility that non-collembolan groups are also accepted. In addition, Wesson failed to identify the Collembola accepted, thereby leaving no clue to family specificity. In a later paper (1939), the Wesson brothers listed the following species as Collembola feeders: *Sm. rostrata* (Emery), *Sm. pulchella* (Emery), *Sm. reflexa* (L. G. and R. G. Wesson), and *Sm. talpa* (Weber). Again the prey were not determined and no real evidence was presented that these species are restricted to a collembolan diet. This early work, however, is still of considerable importance beyond its pioneering nature, because it lends to the impression that food habits are uniform throughout the genus.

The Wessons' observation of stalking behavior agree fairly well with my own. A typical catch by *Sm. pergandei* was described as follows: "The moment the worker scents a springtail which is one to four mm. away, depending on its size, she stops suddenly, slowly exploring her antennae in its direction. Having waited for a few minutes, she moves by slow advances to within 1 mm. of it. Then she folds her antennae, lowers her head to the ground and moves imperceptibly in the direction of the springtail until her mandibles almost touch it. Then she waits until the springtail *moves* against her mandibles. When this happens, she strikes, seizing the springtail in her

mandibles, piercing it with her sharp maxillary lobes, then drawing it back and stinging. If, on the other hand, the springtail fails to move, she arouses it by vibrating her antennae around it."

It is doubtful if the ants are able to sense Collembola more than a millimeter or so away, and this species is very exceptional if it waits for its prey to blunder against its mandibles before striking. All of the dacetines observed in the present study followed through the mandibular strike whether their prey moved or not; ambush as described above was unusual. Apparently the Wessons missed the significance of the labral lobes, which they mistook for the maxillae. These evidently function as tactile range finders for the mandibles, are relatively flexible organs, and are probably quite unable to pierce the integument of a collembolan.

Perhaps the most striking feature of the food habits of the dacetines studied is the specificity of preference for certain taxonomic groups within the Collembola. Why the poduroid Collembola are totally ignored while the other groups form the main dietary staple of these ants is not at all clear and remains a very significant problem. It appears to me that the most outstanding difference between the accepted and rejected groups which would be perceptible to one of these ants is in the degree of activity: the poduroids are as a rule extremely sluggish and slow-moving, whereas most other Collembola are wary and capable of rapid movement. It is possible that the poduroids produce a repugnant odor or fluid on the surface of their bodies. This is a fairly common phenomenon in sedentary terrestrial animals which are subject to much predation and tends to replace the ability to take rapid flight. If it does occur in the poduroids, the secretion must be relatively strong, for the ants apparently recognize these insects upon contact and never make an attempt to stalk them.

In some published notes on the behavior of *Strumigenys louisianae*, W. S. Creighton (1937) proposed the interesting hypothesis that this species immobilizes its prey and enemies by spraying them with a toxic fluid. He had come to this conclusion on the basis of two consistent observations made while the *Strumigenys* attacked some small, delicate *Brachymyrmex* which had been placed in their nest: the *Strumigenys* were able to kill these ants rapidly without doing much mechanical injury to their integument, and the *Brachymyrmex* engaged in exaggerated self-cleaning after each attack. W. L. Brown (1950) favored Creighton's idea of a toxic spray and suggested that this might originate from the paired labral lobes. No absolute proof has yet been adduced for or against such a hypothesis, but I am inclined to believe that either it is produced in microscopic amounts or it does not exist at all. Very early in the present study it was noted that workers of *Strumigenys* and *Trichoscapa*, and to a less extent those of *Smithistruma*, tended to be unusually aggressive while in the confines of the brood chambers. When the glass cover was moved over their heads they often attacked it, snapping at it with their mandibles and attempting to sting it. As this occurred I watched for signs of droplets appearing on the glass, but these were never apparent, even at magnifications of 60x. Also, fine bits of cobaltous chloride paper thrust at attacking workers did not pick up visible amounts of moisture. It is very probable that Dr.

Creighton underestimated the ability of these ants to injure and cripple insects with the use of their mandibles alone, for the shocking effect of the mandibular strike appears to be considerable. In my nests smaller Collembola usually yielded at once without a struggle when struck on the body, while larger insects such as *Japyx* were often thrown into a complete and immediate panic, reactions which can hardly be attributed to a tiny amount of fluid. It is curious that Dr. Creighton did not mention whether his *Strumigenys* employed their stings, because this was normal behavior in my colonies and played an important part in defense and the capture of larger prey.

One of the most characteristic features of dacetine ants is the widespread possession of concentrations of well developed and frequently aberrant hairs on the head. These are especially abundant on the clypeus, and the resemblance of many of them to the hyphae and fruiting bodies of fungi has led Brown (1950) to propose that they may serve as tactile or visual lures for the Collembola on which the dacetines feed. This is certainly a logical and tempting hypothesis, but one that would be very difficult to prove or disprove. In my own observations nothing resembling luring was ever found, although it is readily admitted that the conditions under which the Collembola were introduced into the artificial nests and the bright light required to watch them were hardly conducive to normal feeding behavior on the part of the Collembola. On the other hand, it seems very likely that under natural conditions a luring mechanism would add little to the efficiency of the ants in stalking prey, primarily because they seek their prey actively and need only to keep it from bolting before they seize it. Brown evidently conceived of the investiture as a lure while under the erroneous impression, given him by the Wessons' original observations, that some dacetines such as *Smithistruma* rely on ambush to catch Collembola. A more logical function of the investiture would be to deceive the Collembola with its fungus-like appearance as the ant approaches and thus prevent it from becoming frightened and moving away before the ant can spring the mandibular trap. A possible example of such of a function was noted in the case of *Smithistruma dietrichi*, which possesses a sparse cluster of long, filiform hairs around the anterior margin of its clypeus. Workers of this species were observed as they stalked Collembola, palpating them lightly with their antennae and frequently brushing them with their clypeal hairs. The latter contacts were irregular and apparently accidental, and did not seem to be tactile in function. The significant thing is that these contacts did not frighten the Collembola, which were very wary and ordinarily bolted when brushed by mites or other Collembola. Another point in favor of this interpretation is that if the cephalic hairs of dacetines truly mimic parts of fungi, this mimicry probably is tactile and not visual in nature. Collembola are provided with ocelli only, organs generally thought to be incapable of form preception. But even if they were capable of distinguishing the shape of the hairs, they would receive little opportunity to do so, since both Collembola and dacetines are predominantly hypogaeic. Thus the Collembola would have no incentive for going to the dacetines on the basis of the form of the hairs alone and could be deceived only by actually touching the hairs.

Foraging activity under natural conditions is a subject which has received scant attention in the previous literature. Smith (1930), the Wessons', Brown, and Creighton all have agreed that the United States dacetines are cryptobiotic and hypogaeic, rarely if ever appearing in the opening. In the case of *Trichoscapa membranifera* and the species of *Smithistruma* there is little doubt that this is for the most part true. Stray workers of these two genera are found typically in very hidden, protected places, as under the bark of rotting logs and stumps, under stones, and in the lower strata of leaf litter. *Strumigenys* workers, however, are also found frequently in open situations and apparently normally forage there even during the day. They have been taken abundantly in thin leaf litter in a number of localities, sometimes many feet from the parent colony. Others have been found occasionally in such situations as well tended lawns, piles of garbage, and on exposed roots in wooded areas.

LIFE HISTORIES

North American dacetine colonies are uniformly small, the majority containing between 25 and 100 workers and one to several mother queens. The largest colony of *Strumigenys louisianae* I have collected contained 181 workers, 119 larvae, and one queen. The larger of the two *Trichoscapa membranifera* colonies collected in Alabama contained 36 workers, two larvae, and one queen. Smith (1931) has reported a colony of this species from Mississippi with 75 to 100 workers. The largest *Smithistruma* colony I have collected was one of *Sm. pergandei* from western North Carolina; it contained 146 workers, and undetermined number of larvae and pupae, four alate queens, and one dealate queen. It appears that the species of *Smithistruma* tend to have larger colonies in the northern part of their ranges, where Brown (*in litt.*) has found colonies of a hundred or more workers to be very common. The largest of many collected in Alabama by Mr. B. D. Valentine and myself contained only 62 workers (*Sm. clypeata*).

The small colony size appears to be the result of a low rate of oviposition, combined with a further reduction of the total number hatching through consumption of some by the adult ants. The number of eggs present in a colony over a period of time fluctuates around what appears to be a nearly constant mean. This is illustrated by the following daily counts from two *Smithistruma* colonies. *Sm. rostrata:* 1, 1, 2, 6, 7, 7, 7, 5, 6, 7, 7, 2, 1, 7, 3. *Smithistruma brevisetosa:* 10, 7, 4, 8, 5, 3, 5, 6, 6. These counts are approximately representative for colonies of average size of all the species studied.

Examination of a substantial accumulation of records made in several states by B. D. Valentine, A. C. Cole, D. W. Pfitzer and myself has shown that winged forms appear at definite and restricted intervals in the year. They are produced by *Strumigenys louisianae* in the Gulf States predominantly in the last half of June and first half of July. They are produced by all the native *Smithistruma* for which records are available mainly during late August and early September, there being little difference in this respect between the northern and southern segments of the populations. The only winged form of *Trichoscapa membranifera* from the United States with which I am

familiar is a queen mentioned by Smith (1931), who took it as a stray on July 18, in Mississippi.

New colonies are apparently formed at least partly through swarming in the typical formicid manner. Male *Strumigenys* reared in the laboratory showed swarming behavior on one occasion after the nest had been freshly mositened and warmed somewhat. They ran rapidly back and forth in the lighted food chamber and vigorously attempted to take flight. In the field, stray dealate queens of the following species have been taken; *Strumigenys louisianae, Trichoscapa membranifera* (Smith, 1931), *Smithistruma* (*Wessonistruma*) *angulata, Sm.* (*W.*) *pergandei, Sm.* (*Smithistruma*) *bimarginata* (Wessons, 1939), *Sm.* (*Sm.*) *dietrichi, Sm.* (*Sm.*) *margaritae, Sm.* (*Sm.*) *pulchella.* Some evidence exists that the young queens forage and capture Collembola for their first brood. The Wessons observed dealate queens of *Smithistruma talpa* (= *medialis*) hunting in a fashion similar to that of the workers. In my own nests several *Smithistruma rostrata* mother queens deprived of workers foraged some within the limits of the brood chambers and succeeded in capturing

TABLE I

DURATION OF LIFE STAGES OF THREE DACETINE GENERA

	DURATION IN DAYS		
	Egg	Larva	Pupa
Strumigenys louisianae.....	12	29	12
Trichoscapa membranifera..	13	19	19
Smithistruma rostrata.....	9	31	19
Smithistruma clypeata.....	14	25	14

a few emtomobryids which they fed to their brood. A dealate queen of *Strumigenys louisianae* taken as a stray in the field and maintained for a few weeks in an artificial nest foraged continually in the food chamber and was observed on two occasions carrying entomobryids. She was actually watched in the process of catching one of these; her stalking movements resembled in every way those described previously for the workers of this species. If it is true that dacetine queens found colonies in a partially claustral manner and depend on hunting to nourish their first brood, this represents another remarkable trait for the tribe and would be the only instance with which I am familar of this type of behavior in the Myrmicinae.

An attempt was made to determine the approximate duration of the different life stages of the three genera considered in this study. For this purpose nests were maintained at a nearly constant temperature of 27° C, which was ascertained by trial and error to be reasonably close to the optimal range of the species reared. The data obtained for workers are summarized in the accompanying table. In addition, queen pupae of *Strumigenys louisianae* took 12 days and male pupae 13 days to develop. In reality, these data are of such a limited scope and the conditions of constant temperature under which they were obtained so unnatural that they cannot be considered as showing significant differences between species, but they may be taken as approximations for the three genera as a whole.

NESTING HABITS

Most of the dacetines known from the eastern United States are very highly restricted in habitat. This is evidently due more to the selection by the ants of particular micro-ecological conditions than to the effects of any gross factors of the physical environment. Specifically these conditions appear to be a high degree of humidity, which must be maintained nearly constant, plus a favorable nesting medium of readily workable yet firm material, such as humus and punky wood. Thus the ants are not restricted to any particular forest cover, but they do tend to be more abundant in those plant associations which provide the best types of rotting logs and stumps, the right degree of shade to allow moisture retention in those logs and stumps, and possibly also the most favorable topsoil and leaf litter. In general, the dacetines are most common in fairly dense mixed mesophytic woods, where they nest in moist, "Passalus-stage" rotten wood, in rotting twigs and small branches on the ground, and to a lesser extent under rocks sunk shallowly into the soil. Where pine logs and stumps are common, these are preferred. In the Southeast at least, the very best place to look for these ants is the high ground of swamps with mixed forest cover. Here they may compose in some spots upwards of five percent of the total ant population. Frequently, however, the habitats which appear to be most favorable for dacetines do not always offer a rich Collembola supply and these arthopods are often the most abundant in places where few or no dacetines occur.

As might be expected from its tramp distribution, *Trichoscapa membranifera* appears to be the most adaptable dacetine in the eastern United States. Colonies have been collected from all the situations typical for the tribe, as well as from the bulb of a gladiolus (Smith, 1931) and under bits of slate in a cultivated field. This species also probably has the least strict moisture requirements, venturing often into relatively dry, open soil. *Strumigenys louisianae* also occurs in all the typical dacetine habitats, and colonies have also been found in such situations as debris in a knothole of a living tree (Pfitzer, personal communication), in leaf litter at the base of a tree, and in soil covered only by moss. *Smithistruma rostrata* was the most adaptable species studied in its genus. Colonies were found in rotting logs and stumps in twigs and small branches buried in leaf litter, in old, crumbling sweetgum burs, and even in exposed leaf mold. There is considerable evidence that the species of *Smithistruma* tend to specialize further in selection of nesting sites, each one being restricted primarily either to rotten wood or to the bottom of surface rocks. This has been considered at length by W. L. Brown in his revision of the genus (1953, ref. in footnote 1) and will not be covered here.

The dacetines construct their own nests, occasionally utilizing preformed cavities as starting points. They may be one to several brood chambers, all of which are kept immaculately clean. They are flat and oval in shape and rarely exceed five centimeters in greatest diameter. Galleries are nearly always very short and indistinct. In my artificial nests, excavation was most frequently conducted by the *Strumigenys*, which often burrowed galleries straight through the soft plaster of Paris, so that the walls had to be continually patched to prevent the ants from escaping. The *Trichoscapa* and *Smithistruma*

limited themselves to building walls and enclosures with the debris available in the nests. One small *Smithistruma reflexa* colony built within a brood chamber a small igloo-shaped structure which completely covered the queen and brood.

MYRMECOPHILES

North American dacetines are almost totally free of myrmecophiles, a condition probably due to the small size of the colonies and the virtual absence of trophallaxis. Several truly myrmecophilous mites, identified by Dr. E. W. Baker as nymphs of the family Laelaptidae, were found in a colony of *Strumigenys louisianae* taken near Georgiana, Alabama, and were maintained in an artificial nest with the ants for a period of two months. During this interval they were extremely sedentary, spending most of the time riding on the bodies of their hosts. One individual remained on the ventral surface of the postpetiole of the queen and was never seen to move from this position. The ants appeared to be completely indifferent to the mites' presence and in return received no visible harm from them. The food of the mites could not be positively determined, but on several occasions individuals were observed moving their mouthparts over the surface of a packet of eggs. It is possible that they were feeding on the collaterial products of the queen.

DISCUSSION

The dacetines are in many ways among the most aberrant and specialized of ants, for nearly all of the details of their biology reflect their peculiar predacious habits. Colonies are exceptionally small, the larvae feed directly on the prey brought in by the workers, there is practically no trophallaxis, mymecophiles are very scarce, and the adult ants themselves have undergone such extreme modifications in morphology and behavior that they function as little more than living Collembola traps. In many aspects of their biology the dacetines resemble the Ponerinae, although they are undoubtedly far more specialized.

One of the most interesting features of the tribe which has not yet been considered is the ability of moderately large numbers of species to occupy the same immediate habitats, even though they are ecologically very uniform. In North America at least, the Formicidae as a whole seem to comply with the well demonstrated principle that ecologically identical species cannot occupy the same niche indefinitely; that is, within a given localized area one or a limited number of species will come to predominate because they possess a competitive superiority in the particular ecological conditions of the area. Thus it is evident that the number of species of a genus which can occupy a given habitat is a function of the degree to which its species compete there. The degree of competition would in turn be dependent on at least two characteristics of the species. First, the greater their diversity in such features as nesting site preferences, food habits, size, etc., the less would be the competition. Second, the greater the density of the total population of the genus, the greater would be the competition. Genera such as *Camponotus* and *Pheidole* are represented in many habitats by large numbers of species perhaps because these tend to be ecologically

diverse; in *Pheidole* there is also considerable variation in size. Genera such as *Myrmica* and *Formica* contain numerous species, but in any given restricted area it is difficult to find more than several which are truly abundant. This may well be due to their tendency toward ecological uniformity. As populations become excessively dense, as has happened occasionally following the introduction into new areas of such forms as *Pheidole megacephala*, *Iridomyrmex humilis*, and *Solenopsis saevissima*, the number of competing species becomes drastically reduced.

The unusual sympatry of the dacetines may be partly a result of their low population densities. Colonies of these ants are probably as abundant as those of many other common tribes, but the total number of workers is significantly lower because of the small average colony size. This allows a good representation of species within a single habitat without too great a population pressure resulting.

SUMMARY

1. A study was made of the ecology of eight North American species of dacetine ants, including *Strumigenys louisianae*, *Trichoscapa membranifera*, and six native *Smithistruma*. Food habits were emphasized.

2. The main dietary staples of these ants are entomobryoid and symphypleonan Collembola. Poduroid Collembola are consistently rejected. *Strumigenys* and *Trichoscapa* show the greatest latitude in food preferences, accepting occasionally Symphyla, Thysanura, termites, and mites. *Smithistruma clypeata*, *Sm. dietrichi*, and *Sm. talpa* may also take Symphyla and Thysanura, but less readily.

3. The hunting behavior of these dacetines is described in detail. All rely on stealth and actively stalk their prey, using their paired labral lobes as tactile organs, and seizing the prey with a convulsive snap of their mandibles.

4. No evidence of a toxic spray as suggested by Creighton (1937) was found. The bizarre cephalic hairs may mimic parts of fungi, as Brown (1950) has speculated, but they cannot serve as visual lures and probably do not serve as lures of any kind, but rather may be used to deceive Collembola being stalked by the ants.

5. Notes on life histories, nesting habits, and myrmecophiles are given. There is some evidence that colonies are founded in a partially claustral manner and that the queens hunt Collembola for their first brood.

6. The high degree of sympatry of ecologically uniform species in the Dacetini is emphasized. It is suggested that this may be partly a result of unusually low population densities.

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