Research Article

The Biology and Natural History of *Aphaenogaster rudis*

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Workers from the genus *Aphaenogaster* are among the most abundant ants in the hardwood forests of eastern North America. The biology of these so-called *rudis*-group ant species, including details about their sociometry, productivity, natural history, and behavior, are synthesized here using published and newly collected data. The latter was collected, in part, using an artificial field nest, and its construction and use are explained. Ants of the *rudis* group occur in high densities in forest habitats (0.5–1.3 nests m^2), have moderate sized colonies (population means from 266 to 613 workers per nest), and are keystone seed dispersers. Many aspects of their life history and behavior follow an annual cycle that tracks seasonal changes. These include foraging, reproduction, the production of new workers and nest migrations. This synthesis highlights what is known about these ants and reveals gaps in our knowledge that require further study.

1. Introduction

Sociometric data and natural history information about ants serve as the raw material for discovering patterns, formulating hypotheses, and planning experiments that examine a wide range of ecological, behavioral, and evolutionary processes. Seminal research investigating topics as diverse as population regulation [1], mutualisms [2], kin selection [3, 4], and sex-ratio evolution [5] illustrate how ant studies, using previously published or newly collected sociometry data, have made important contributions to understanding the function and evolution of biological systems.

Tschinkel has argued that myrmecologists have been negligent in collecting and reporting basic biological attributes of individual ant species [6, 7]. Also problematic is that the existing data for some of our better studied species are scattered among an eclectic collection of published studies. Collecting, cataloguing, and disseminating information regarding ant species' biological attributes are important tasks that need greater attention.

This paper provides an overview of the biology of *Aphaenogaster rudis (s.l)*. This ant is common in the hardwood forests of the eastern United States [8–11] and has been the subject of numerous ecological and evolutionary studies (e.g., [12–14]). Newly collected data and previously published information from dozens of studies are synthesized here to explain what is known about these ants. A description of an artificial field nest that facilitates collecting and studying whole colonies of this ant and data collected from these nests are also provided.

2. Materials and Methods

Data and observations from published studies and from three study populations in the state of Connecticut are used to describe the basic biology of a prototypical *rudis*-group ant. This term is used to refer to three different species, as explained in the taxonomy section. Details about the Connecticut study populations, methods used for finding, collecting, and sorting whole nests, and the construction and use of a newly developed artificial wooden field-nest are explained in the following.

2.1. Connecticut A. rudis Populations. The three populations for which new data are presented were located in Connecticut State Forests. These populations are referred to throughout this paper by the names of the forests where they occurred:

Nipmuck (Nipmuck State Forest, 41° 59′ 21″ N 72° 10′ 51″ W), Pachaug (Pachaug State Forest, 41° 36′ 8″ N 71° 53′ 22″ W), and Mohegan (Mohegan State Forest, 41° 39′ 59″ N 72° 4′ 59″ W). Each study site occupied a multi hectare section of mature forest dominated by hardwoods (primarily *Acer* and *Quercus* species) and containing a few small groves of conifers (*Tsuga canadensis* and *Pinus strobus*). These secondary forests are part of a New England landscape with a well-documented history [15].

Colonies were collected by digging up nests (see Section 2.2) in the three Connecticut populations in the spring, summer, and fall of 2001–2003. This field work, and nests collected during these field seasons and in 2004 and 2005 where artificial nests (see Section 2.4) were used for colony collections, are the source of data and observations reported on here as being from Connecticut.

2.2. Collection of Nests. Workers of the *rudis* group are among the most commonly encountered ants in the hardwood forests of southern New England. In late spring, summer, and early autumn, nests can be found in the soil, in dead wood on or near the forest floor, under and between rocks, and in the leaf litter. Foragers are readily attracted to many ant baits and nests can be located by following bait-laden foragers as they return to their colonies.

Soil nests have a single, small circular nest-entrance that is hidden under the leaf litter. In the summer these nests are compact and shallow (<15 cm deep). Whole colonies may be excavated from the soil by removing a single inverted cone-shaped plug of earth, centered on the nest entrance, from the ground using a full-sized shovel. Colonies nesting in other locations, for example, in downed wood or in the leaf litter, can be collected in their entirety by placing the ants and their nesting material into large plastic bags.

Field-collected nests can easily be separated from their nesting materials in the lab. Material from each field colony collected in Connecticut was spread across the bottom of 55 liter plastic bin that contained two artificial nests, sugar water, and water. Artificial nests consisted of foil covered test tubes with a moistened cotton ball. Small test tubes with water held behind a cotton plug, and a similarly arranged honey-water solution, served as a source of water and carbohydrates. The exposed nesting materials desiccated and within a few days workers would move the queen and brood into the nesting tubes.

2.3. Artificial Wooden Nests. Artificial field nests were constructed from two rectangular pieces of white-pine lumber measuring 12.7 × 22.8 × 2.54 cm. One piece of wood was partially excavated with a router to hollow out a U-shaped chamber, with an additional shallower cut made from the top edge of the U to the outer edge of the board (Figure 1). The second piece of wood was placed over the top of the hollowed out chamber, forming an enclosed nesting area with a single entrance. The two nest pieces were held together with two screws, secured with wing nuts, placed through predrilled holes in both boards.
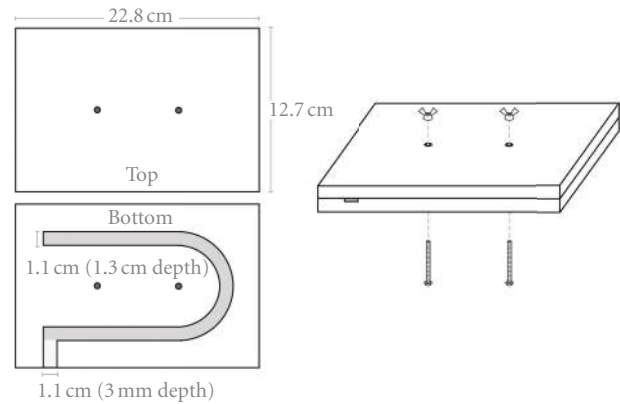

FIGURE 1: Artificial field nest. The U shape of the bottom half of the nest is excavated to a depth of 1.3 cm and the short section that connects the U to the exterior edge, shown in a lighter shade of gray, to a depth of 3 mm. Two holes drilled in each piece allow bolts to be used to hold the two boards together.

Twenty-five artificial nests were placed on the forest floor in the Mohegan study site in the spring of 2002. The following spring a majority of the nests were occupied by *rudis* group ants. These nests were collected in mid-August 2003 (Table 1) by placing each nest in a sealable plastic bag. The contents of each colony were processed (individuals counted and preserved) in the laboratory within a few days of collection. In 2004 additional nests were censused from the same forest, as detailed in Lubertazzi and Adams [14].

2.4. Worker Head Widths and Caste Dry Weights. Worker head width is commonly used as a reliable measure for assessing variability in worker size [16]. We measured the head widths of 25 randomly chosen workers from each of 39 colonies sampled from the Nipmuck and Pachaug forests. The head of each worker was removed from the body, placed frons side up on a glass slide and measured using a stereomicroscope at 90x magnification. The maximum width of the head was recorded to the nearest hundredth of a mm using an ocular scale. ANOVA was used to test if worker size varied between populations or among colonies within populations. The relationship between colony worker number and worker size was examined by regressing the average colony head width on colony worker number for 27 of the 39 colonies sampled. This reduced data set represented collections deemed to be of whole colonies.

A randomly chosen sample of 25 workers from each of eight preserved colonies was used to determine the average dry weight of workers. Individuals were oven dried for three days at 30°C then weighed to the nearest mg using a Mettler balance. The dry weight of 25 males and 25 gynes from the Nipmuck and Pachaug populations was similarly assessed. These individuals were collected and preserved in alcohol in August 2001. Collections were made one week prior to the time sexual adults were no longer found in field nests, which was presumably the time of the mating flight.

Table 1: Worker number and sexual production for colonies from artificial wooden nests collected in the Mohegan State Forest in August 2003. All colonies except G contained a queen.

Colony	Workers	Males	Females alates
1	568	68	4
3	660	111	5
4	544	18	17
5	907	75	0
7	322	1	0
8	760	1	0
10	479	0	0
A	827	0	0
C	498	58	0
E	473	140	0
G	183	0	0
H	395	0	0
J	644	112	0
V	563	0	0
X	1033	0	0
Y	846	72	0
Z	724	0	0

2.5. Nest Density Measures. Three Connecticut populations were sampled in July and August of 2003 to determine nesting density. Twelve haphazardly selected 3 m × 3 m plots (plots per forest: Nipmuck 5, Mohegan 3 and Pachaug 4) were intensively searched for nests and tallied. Each plot within a forest was located at least 30 m away from any adjacent plot.

2.6. Foraging Distances. Distances from randomly placed pecan sandies cookie crumb baits to a foragers' nest entrance were measured in July and August of 2003. From 5–10 baits were placed in a haphazardly fashion over a roughly 10 m square area of the forest floor and rechecked after 30 minutes. If a bait was being foraged upon one laden worker was followed back to its nest entrance. The straight line distance from the bait to the nest entrance was then measured to the nearest cm. The bait was checked for foragers from any other colonies and if present similarly followed and the distance measured. The next bait was then checked and similarly censused. Data was collected from all three Connecticut study populations (colonies sampled: Nipmuck, 22, Mohegan 17, and Pachaug 25). Foraging distances between populations were compared using ANOVA.

3. The *rudis*-Group Ant

North America is home to 26 validly named *Aphaenogaster* species and 4 undescribed forms [17]. One group of species, the *Aphaenogaster rudis-fulva-texanus* complex, comprises species largely confined to eastern North America [18]. Certain members of this group are impossible to separate morphologically [18–21]. Umphrey [18], seeking to define the species and range boundaries of the complex, developed and described complex morphological metrics, electrophoretic markers, and karyotype counts for identifying these ants. He defined and assigned coded names to ten forms with six being matched to named species and the remainder putatively representing undescribed species.

Ants from the genus *Aphaenogaster* are abundant in the wide ranging mesic hardwood forests of eastern North American. These ants have been the subject of dozens of published studies and are often identified and reported as *A. rudis*. Using range limits and habitat infinities provided by Umphrey [18] we can infer that these studies are likely to involve three species: *A. rudis* Enzmann or N22a in Umphrey's coding system, the undescribed form N17 and *A. picea* (Wheeler, W.M.) or N18. It is not possible to clearly distinguish these three forms from each other using morphological characters. This paper will describe the biology of these ants as a single prototypical species that will be referred to as a "*rudis*-group" ant. This name is used for practical convenience and not in a strict taxonomic sense. While many publications ascribe the name *A. rudis* to their study form the majority likely involve the two northern forms (N17 and N18). Our biological knowledge is therefore heavily biased by knowing more about populations that experience cooler temperatures and a shorter annual season of productivity than the lower latitude N22a (putatively the true *A. rudis*).

Further work is clearly needed to resolve the taxonomic and nomenclature problems within this complex. In light of these issues, it is imperative that future research involving ants from the *rudis-fulva-texanus* complex include the deposition of voucher samples in an accessible museum collection.

The ranges of the three *rudis*-group species overlap along some of their boundaries but are thought to be predominately allopatric [18]. N22a/*A. rudis* has the most southern distribution. It is found in the lower elevations of the Appalachians from Virginia to northeastern Alabama and within forests of the piedmont region of the Carolinas. Along the Maryland, Delaware, and New Jersey coastal plain, the range of N22a/*A. rudis* broadly overlaps with *A. carolinensis*. To the west N22a/*A. rudis* is found in the forests of Tennessee, Kentucky, southern Ohio, and southern Indiana and has been found as far west as Missouri. N17 and N18/*picea* are, respectively, western and eastern variants that occur to the north or at higher elevations than N22a. N17 is found in and to the north of Ohio, into Ontario, and possibly occurs as far west as Iowa. N18/*A. picea* is found within, east of, and north of Pennsylvania. It occurs in southeastern Ontario, Quebec and possibly the maritime provinces of Canada. Its preference for cooler mesic forests also allows this form to occur in higher elevation Appalachian mountain forests, potentially extending its range as far south as Georgia and Alabama. Studies cited in this paper that report on *A. rudis s.l.* are not believed to represent any other forms within the *rudis-fulva-texanus* complex. This is inferred from what is known about the other forms' ranges, habitat preferences and/or low nesting densities.

A. fulva may be found in low densities in some forests where *rudis*-group ants are common. The former can be

reliable identified from the latter by the heavily rugose mesopleural of its queens. Queens of *rudis*-group ants have a smooth mesopleura [17].

4. Colony Characteristics

4.1. Annual Colony Cycle. Mature *rudis*-group colonies exhibit an annual cycle of activity and productivity that tracks seasonal changes. The description outlined here arbitrarily starts with a renewal of colony activity in the spring and ends with winter diapause. Specific seasonal activities and responses are detailed, along with supporting data and information, in an idealized version of what occurs within the colony over the course of a full year. The seasons are used in a relative sense to indicate times of the year when temperatures are warming (spring), consistently supporting colony growth (summer), cooling (autumn), and cold (winter). The dates associated with these times of the year will vary according to the geographical location of a given population.

4.1.1. Spring. In Connecticut *rudis*-group workers are among the first ants to become active on the forest floor during the spring. Once the snow cover has gone and the ground is exposed, foragers can be found above ground on warm and sunny days of early spring (~15°C ambient temperature). Early spring activity explains, in part, Lynch et al.'s [22] finding in a Maryland ant community that a *rudis*-group ant was active for a greater portion of the year than other co-occurring ant species. Umphrey [18] suggested N18/*A. picea* was among the most cold tolerant North American *Aphaenogaster* species. This tolerance helps these ants be poised to begin their annual above-ground activities as early in the spring as possible.

As spring progresses entire colonies diurnally move back and forth from underground chambers to protected cavities near the surface, especially favoring locations warmed by sunlight. Daytime spring temperatures at the top of the leaf litter can reach 40°C and may be 20°C warmer than 15 cm below ground [23]. Exposure to these higher temperatures raises metabolic rates, restarting brood development and queen oogenesis.

Later in the spring the winter nest is abandoned for a new site on or near the ground surface. This switch in nesting location coincides with the ground surface and subsurface becoming consistently warmer than the more thermally stable, but now regularly cooler, underground nesting chambers. The spring-season nest migration of *rudis*-group colonies has been observed in Missouri [24] and Connecticut. Maintaining a high degree of flexibility in where and when they move their nests help *rudis*-group ants hasten their transition from winter diapause to summer productivity.

4.1.2. Summer. The abandonment of the winter nests putatively delimits a time when conditions become consistently conducive to colony growth. In Connecticut this point is reached in late May or early June. Some larval growth and egg production take place in the spring and fall but the bulk of egg laying, larval growth, pupation, and eclosion occurs during the summer. Productivity peaks in late summer and declines sharply in the fall [25, 26].

Maintaining the optimal temperature/humidity microenvironment for the brood and queen is an important focus of the workers. This may involve daily movements within the nest or, if a better nesting location is found, can include a summer-season nest migration [12, 27–29]. Structures such as downed wood that contain hollow chambers or loosely attached bark, areas between exposed rocks and the soil, and other similarly sheltered warm locations can all provide suitable nesting sites during the summer.

Food demands are highest during this season. Prior to the summer individuals had to rely on internal reserves, built up during the autumn, to sustain their low metabolic and developmental needs. During the warmer months food is now needed to supply nutrients to the brood, the queen, and the workers. Foraging, worker development, and the production of new sexuals (each explained in greater detail in sections that follow) all assume greater importance during the summer.

4.1.3. Autumn. The onset of shorter days and cooler temperatures leads to changes in nesting location and colony productivity. There is also a general slowing of overall colony activity. Above-ground or near-ground level nests are eventually abandoned for deeper below-ground nesting sites. This autumn nesting site is likely different from the nest used during the summer even if the summer nest contained soil chambers [24]. By October in Missouri [24] and Connecticut, *rudis*-group ants have all moved to what will be their underground winter nests.

Egg production decreases as temperatures decline, with oogenesis eventually stopping altogether. Colony activity slows [30], metabolic and development rates fall, and individuals increasingly rely on internally stored nutrients for their decreasing metabolic needs. Foraging slows and eventually ceases as the temperatures cool.

4.1.4. Winter. In winter months colonies avoid freezing temperatures by maintaining their nests below ground. Talbot [24] found the average depth of 5 winter colonies in Missouri to be 25 cm. Colonies in Connecticut appear to prefer deeper nests, to a depth of at least 50 cm. Developmental processes enter a diapause and worker activity within the nest is minimal.

4.2. Nesting Ecology. Downed wood provides a good nesting resource for *rudis*-group ants in Connecticut and in other locations [12, 31]. Limbs and boles greater than 10 cm in diameter and slightly decaying appear to be particularly favorable. In the Connecticut study sites almost all of these suitable nesting sites were occupied by a thriving *rudis*-group colony. Wooden nesting structures are often in short supply relative to the high density of nests (see below). The combination of the relative scarcity and suitability of

TABLE 2: The average number of workers per colony for various populations of *rudis*-group ants.

Population study	N	Mean	SE
Talbot 1951 [24]	71	352	38
Headley 1949 [25]	46	266	28.8
Mohegan SF 2003	17	613	53.5
Lubertazzi and Adams 2010 [14]	65	507	32.3
Morales & Heithaus 1998 [12]			
Fed colonies	24	457	59
Control colonies	27	360	46
Heithaus et al. 2005 [13]	36	601	56.1

wooden nest sites [31] likely contributes to the attractiveness of artificial wooden nests.

In mature hardwood forests in eastern Connecticut soil nests were common in the summer. Below-ground nest chambers are not likely to reach temperatures as conducive to larval developmental as can be found in ground surface structures or among the leaf litter [23]. Regardless of their limitations soil nests may be the only option available for many colonies.

Headley [25] described the structure of soil nests surveyed from central Ohio. A typical ground nest had a single entrance, which was an inconspicuous circular hole ~6 mm in diameter. A few nests had multiple entrances but in every case all the entrances for a single colony were located within 10 cm of one another. A central shaft, or a few bifurcating shafts, lead down from the entrance and connected the underground nest chambers. Chamber number averaged 6.5 and ranged from 2 to 17. The chambers' dimensions averaged 12 mm high, 12 cm wide, varied in length from 18 to 50 mm and were found from just below the surface to a depth of 84 cm. Similar ground nests were reported from Missouri [24] with notable differences being slightly shallower chamber depths and, on average, fewer nest chambers. In both studies some colonies were found inhabiting various co-opted cavities such as areas between rocks and in downed wood.

Ants of the *rudis* group maintain a concentrated central nest chamber regardless of where their nest is situated. In Connecticut the majority of the colony's biomass (brood, nurse workers, and idle foragers) was found within 20 cm of the queen.

The average density of nests was 0.5 nests/m² across three Connecticut populations, 1.3 nests/m² in Missouri [32], and 0.5 nests/m² in Ohio [12]. *Aphaenogaster* species are also known to be common in other forests [33, 34].

4.3. Colony Life Cycle.
The following provides a few details about nest founding, nest size, and productivity. The paucity of known details shows the need for further study and that there remains much to be learned about the basic biology of *rudis*-group ants.

4.3.1. Colony Founding. Two lines of evidence, genetic and observational, suggest that new colonies are begun claustrally by single queens. Genetic studies show that *rudis*-group nests contain workers produced from a single queen that has mated with one male (see the reproductive biology section). A few incipient colonies found in Connecticut contained a single queen and 25–35 minim workers. These colonies were discovered during mid-summer and were presumably founded the previous fall.

4.3.2. Productivity. Colony productivity can be highly variable among nests within and among populations. Worker number in mature colonies has been surveyed in a number of populations and ranges from a mean of 266 to 613 workers per nest (Table 2). Colonies with less than a hundred to more than a thousand workers can produce new sexuals (Figure 2(a)) but large colonies are more likely than small colonies to allocate energy towards reproduction (Mann-Whitney U-test = 460, $P < 0.04$). The number of reproductives produced is also highly variable among nests (Table 1 and [14, 24, 25]). Some large colonies produce no sexuals (Figure 2(b)), suggesting that mature colonies do not produce new sexuals every year.

5. Foraging Ecology

5.1. Foraging. Foraging distances (Figure 3) for three eastern Connecticut populations were similar among populations ($F_{2,61} = 0.04$, $P = 0.9$) and collectively averaged 57 cm (SD = 31). Despite this short foraging range the high density of nests provides for the abundant presence of *rudis*-group foragers across the forest floor.

The running speed of individual workers returning to the nest with food has been found to vary with the number of workers in a colony [35]. Laden foragers returned to their nest faster in colonies with 140–150 workers than in colonies with 30–40 workers.

Talbot [32] estimated that total worker density of a *rudis*-group ant, above and below ground, averaged ~425 workers m² in a Missouri woodland. In a Maryland forest *rudis*-group workers occupied 27% of ground baits [22]. In Connecticut more than half of the ground baits placed on the forest floor were typically found by these ants within 30 minutes.

Solid food is primarily brought back to the nest by individual foragers. Some recruitment of nestmates does occur at concentrated food finds (Lubertazzi, personal observation). A trail pheromone used for recruitment to food has been isolated from the poison gland of a *rudis*-group ant species [36]. The pheromone is a mixture of N isopentyl-2-phenylethylamine, anabasine, and anabasiene, and 2,3′-bipyridyl. Even with recruitment *rudis*-group ants do not maintain more than eight nestmates at a food item at any given time [22, 36].

Ants of the *rudis* group are timid when encountering workers of other species and do not defend foraging territories. These ants are readily displaced at large food items by a number of co-occurring ant species [22, 37]. Their propensity to avoid confrontations is also evident in their intraspecific interactions. It was not unusual to
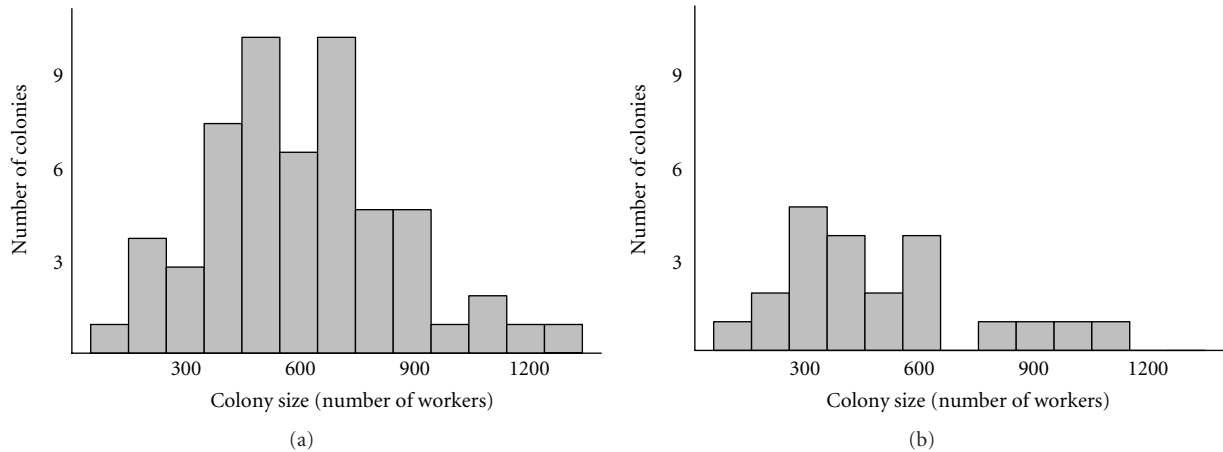
FIGURE 2: Distribution of the number of workers present in colonies that produced (a) or did not produce (b) sexual adults. Data are from Mohegan population trap nests collected in August of 2003 (17 colonies) and 2004 (65 colonies) [14].
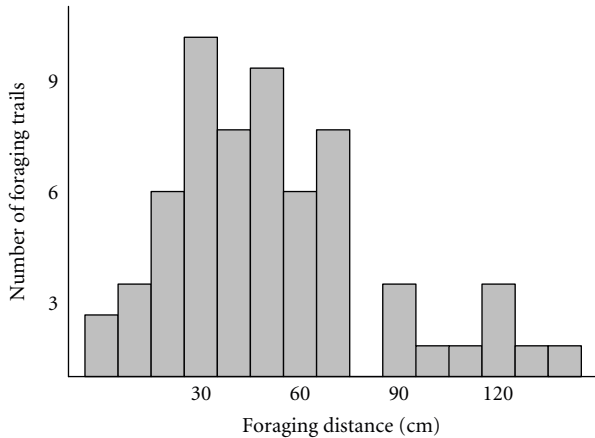

FIGURE 3: Distribution of the straight line distance, in cm, from a food item that attracted foragers to the nest entrance. Data were collected from three eastern Connecticut populations in July and August of 2003.

find individuals from two or three colonies of a *rudis*-group ant foraging on the same bait in Connecticut forests. Here and in Maryland paired individuals could occasionally be found engaging in paired battles that "involve long, seemingly inconclusive "wrestling" bouts that result in few if any casualties" [22]. In Connecticut, workers were observed indifferently walking around any intertwined pair of fighting ants that they encountered.

5.2. Diet. Ants of the *rudis* group are general scavengers. In Connecticut the majority of food items observed being carried by foragers were small invertebrates or parts of insects. Workers have been observed preying on termites (*Reticulitermes flavipes*) in the field in Connecticut and Indiana [38] and in a laboratory study [39]. Small invertebrates are likely the staple of their diet. Other food resources are also exploited and are clearly important, but are either temporally limited or spatially uneven in their availability. For example

a mushroom species is known to be foraged upon by a *rudis*-group ant [40]. This opportunistically encountered resource may provide nutrients that are not readily found in their typical diet but is unlikely to even be encountered within the foraging range of many colonies.

These ants are keystone seed dispersers in the mesic forests of eastern North America [41, 42]. Ants of the *rudis*-group move a majority of the diverse myrmecochorous seeds that are produced in these habitats. The collection of eliasome-bearing seeds by *rudis*-group ants is well documented, as is the floral diversity of myrmecochorous plants throughout these ants' ranges (e.g., [13, 43, 44]). Sexual production within colonies can be altered by elaiosome consumption [12, 45] despite the fact that colonies become satiated quickly when provided with myrmecochorous seeds. Seed foraging ceases within hours of a colony being presented with elaiosome-bearing seeds and this response can persist for many days [13].

Foragers opportunistically imbibe liquid food resources and behaviorally overcome morphological limitations in how much liquid can be held in their crops [46]. Foragers recruit nestmates to particularly rich finds and can also use absorbent objects to collect liquids [37]. Saturated materials are brought back to the colony and the liquids they hold are consumed within the nest. Workers can store an average of 0.13 mg of liquid in their crop but can transport up to 10 times this amount of liquid using an absorbent tool [37].

6. Reproductive Biology

6.1. Intra Colonial Social Structure. Colonies of *rudis*-group ants have a simple reproductive and social structure [47, 48]. There is one singly mated queen that is the sole reproductive in her nest. Young workers may have functional ovaries but worker eggs are either not produced or eliminated in queenright colonies [49].

Although Talbot [24] and Headley [25] both found some *rudis*-group ant colonies with more than one dealate queen, Crozier [48] suggested these did not represent polygynous

colonies. This was inferred from his genetic findings and observations that unmated *rudis*-group queens may spontaneously remove their wings in their natal nest. This dealation behavior was also noted by Haskins and Enzmann [50].

A few mature field colonies collected in Connecticut were found to contain numerous dealate queens after they had settled into artificial nests in the laboratory. In every case there were other winged queens present and unattached wings of queens were found in the sorting bin or in the artificial nest. Dealation was clearly occurring after the nests were collected from the field. This same behavior was observed in a few laboratory nests, originally collected in Connecticut, that had produced female reproductive.

In a few colonies the unmated dealates were left in the laboratory maintained nest. Behavioral differences between a colony's reproductive queen and her unmated dealate daughters were evident. When a reproductive queen moved within the nest and antennated a worker, the worker would typically lower her head and/or flee. Workers that initiated antennating a reproductive queen's body typically continued to investigate the queen with their antenna. Such attention lead to the queen attracting a retinue of workers when she remained in one part of the nest. Worker-to-worker interactions within the nest produced no alarm and always quickly lead to disinterest.

By contrast, dealates spend considerable time outside of the nest and appeared to be subordinate to the queen in their interactions. Antenna-to-antenna contact between workers and dealates always led to the dealates fleeing. Dealates overall were more worker-like in their actions. They were seen outside the nest, moved brood and never attracted a retinue. The one dealate behavior that was queen-like was the propensity to seek cover and remain motionless under an object when the nest was disturbed. Workers varied in their response to disturbance but were as likely to run around excitedly, pick up brood, or move outside of the nest into their foraging arena.

Worker-like behaviors in the dealates become more pronounced weeks after dealation, and, when left in the nest until the following spring, dealates no longer ran as quickly or as persistently from disturbances. In worker-dealate interactions the dealate still tended to move away from worker contacts. Workers reacted with greater alarm when they come in contact with a dealate than when contacting another worker but these differences were subdued when compared to similar interactions that occurred in the fall.

The reason(s) for the spontaneous dealation of gynes and any potential adaptive value of this behavior are unknown. It has been observed in species from other genera, for example, *Pogonomyrmex* (Bob Johnson, personal communication) and *Myrmica*, [51]. The aggressive reactions of *rudis-group* workers to dealates, the propensity of dealates to be found outside the nest in laboratory colonies, the usual absence of supernumerary queens in field colonies in Connecticut and Crozier's genetic data suggests that if dealation occurs in a naturally occurring colony these unmated gynes are likely driven out of their natal nest. Regardless, it is not possible to rule out that spontaneous dealation is the first part of a secondary reproductive strategy. Inbreeding within the nest,
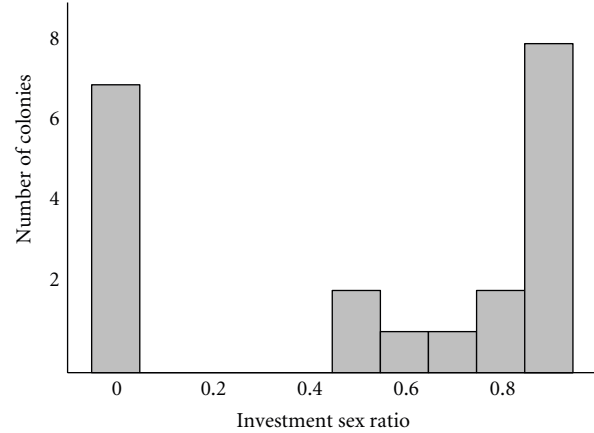

Figure 4: Distribution of colony-level sex ratios (female) for field-collected colonies without a queen based on data from Table 3. Colonies with a sex ratio of 0 produce only male reproductives.

dealates walking out of their natal nest and mating on the forest floor or colonies allowing unrelated males into the nest to mate with a newly dealate queen are all possibilities.

6.2. Sex Ratios. Sex ratios have been calculated for a number of *rudis*-group populations. The first such estimate, calculated to test hymenopteran sex ratio theory [5], was improperly derived. The 14-colony data set combined colony data from two states collected in two different years hence does not represent a population sex ratio. The first rigorous study of *rudis*-group sex ratios was a study examining the potential benefits of elaiosome food resources in an Ohio population [12]. Naturally occurring colonies presented with elaiosome-bearing seeds increased their reproductive allocation and had a more female biased sex ratio than control colonies. A follow-up study suggested the treatment response was a quantitative effect of adding more food rather than a result of specific nutrients contained in the elaiosomes [45].

A field study of a Connecticut Mohegan population also involved food supplementation [14]. No differences were found between control colonies and colonies provided with extra protein. Sex ratios were split (most colonies specialize in mostly male or mostly female investment) and the population sex ratio was estimated to be 0.86 (95% CI: 0.81 to 0.91). Colonies that produced larger broods invested slightly more in males.

The sex ratio of queenless field colonies was similar to those of queenright colonies (Figure 4, Table 3). Naturally occurring queenless colonies overall invested much more in female than male production. Workers in these colonies appear to be raising their recently lost mother's brood rather than raising their sons and nephews.

6.3. Mating. Mating flights have been described for a congener [52] but have never been described for any *rudis*-group ant. It is not known how far queens fly from their natal nests or if mating occurs on the ground, or elsewhere.

TABLE 3: The production of sexual adults in queenless field colonies. Data are from 4 populations: M: Mohegan SF (2004); N: Nipmuck SF (2001); O: Ohio (1949) [25]; P: Pachaug SF (2001).

Source	Workers	Males	Females
M	386	53	12
M	190	2	9
M	282	3	41
M	424	31	51
M	325	32	9
M	89	0	1
M	432	0	45
M	196	83	43
M	303	14	32
M	225	35	15
N	730	86	0
N	555	108	0
N	1211	6	35
N	387	33	0
O	138	6	0
O	119	6	0
O	328	3	0
P	327	20	20
P	587	0	17
P	556	0	14
P	472	28	0

In Connecticut it appears that populations have synchronous mating. Collecting whole nests from 3 different forests over numerous years revealed that winged reproductives disappeared from all the nests within a given population at the same time. New sexuals were typically gone from the Connecticut colonies, depending on the population and the year, sometime between late July and mid-August.

7. Caste Attributes

7.1. Larvae. G. C. Wheeler and J. Wheeler [53] studied and described the morphological and developmental characteristics of the egg and larval stages of *rudis*-group ants. There are four larval instars. First instar larvae were found to subsist on worker-provided liquid foods. Subsequent instars were also able to ingest solid foods [53, 54].

7.2. Workers. Fielde [54] found the developmental period for workers, from egg to eclosion, averaged 64 days (time for eggs to hatch: median = 19.5 days, $N = 22$; larval stage: median = 28.5 days, $N = 26$; pupal stage: median = 16 days, $N = 68$). Southerland [55] examined the influence of temperature on development time. She compared the productivity of artificially created *rudis*-group nest fragments (a queen and 50 workers) maintained at 15°C and 25°C. During 150 days at the cooler temperature no workers were produced. Brood were present and survived but no pupation occurred. Nests maintained at the warmer temperature were able to produce new workers.

The dry weight of Connecticut workers averaged 0.8 mg (SD = 0.16, $N = 200$; Figure 5(a)) and head width averaged slightly less than 1 mm (mean = 0.91, SD = 0.06, $N = 975$; Figure 6). Connecticut and Vermont [30] head width data showed workers form a single monomorphic caste. Worker head width in Connecticut did vary significantly among colonies within populations (Nipmuck population $F_{18,456} = 13.4$, $P < 0.01$; Pachaug population $F_{19,480} = 13.1$, $P < 0.01$) and between populations ($t_{973} = 5.96$, $P < 0.01$). These differences are presumed to be caused by environmental variation in food availability and temperature differences experienced among colonies. A regression of average colony worker head width on colony worker number was not significant ($N = 27$, $P > 0.3$).

Southerland [55] found that worker mortality was higher in laboratory nests maintained at 30°C than in nests maintained at 15°C. Field colonies collected in Connecticut and maintained in the laboratory contained workers that survived for more than a year. The average life span of a worker in a natural setting, where there are many risks, is undoubtedly less.

Workers possess functional ovaries but do not lay eggs when their colony has a healthy, fertilized queen [49]. Worker-produced males are also presumed to be uncommon in naturally occurring queenless nests (as discussed in the reproduction section).

Workers of the *rudis*-group exhibit little division of labor and can perform a total of 41 different behavioral acts [30]. In laboratory nests it was found that 75% percent of a workers' time is spent in nonsocial behaviors and most individuals are inactive most of the time. Worker activity levels and brood tending rates were higher in the summer relative to autumn [30].

7.3. Gynes. Low temperature and a sustained drop in metabolic rate are presumably necessary to induce gyne development, as has been found for other temperate ants [56]. New queens are thus produced from a subset of overwintered female brood. Workers are likely to play a role in determining which females develop into queens by altering the diet and/or temperature environments of select larvae [57].

Early-instar gynes resume development in early spring and in Connecticut eclose in mid-June. Fielde reported a single developing queen she observed spent 17 days in a pupal state [54]. Once eclosed gynes are presumably fed by their nestmates to increase their fat stores, which is typical for ant species in which queens found nests independently. Gynes collected from the Pachaug and Nipmuck forests averaged a dry weight of 6.5 mg (SD = 0.5, $N = 25$; Figure 5(b)).

Haskins [58] observed the survivorship schedule of 11 laboratory-housed queens, finding a median lifespan of 8 years and a maximum of 13. A number of eastern Connecticut colonies, mature when found and therefore at
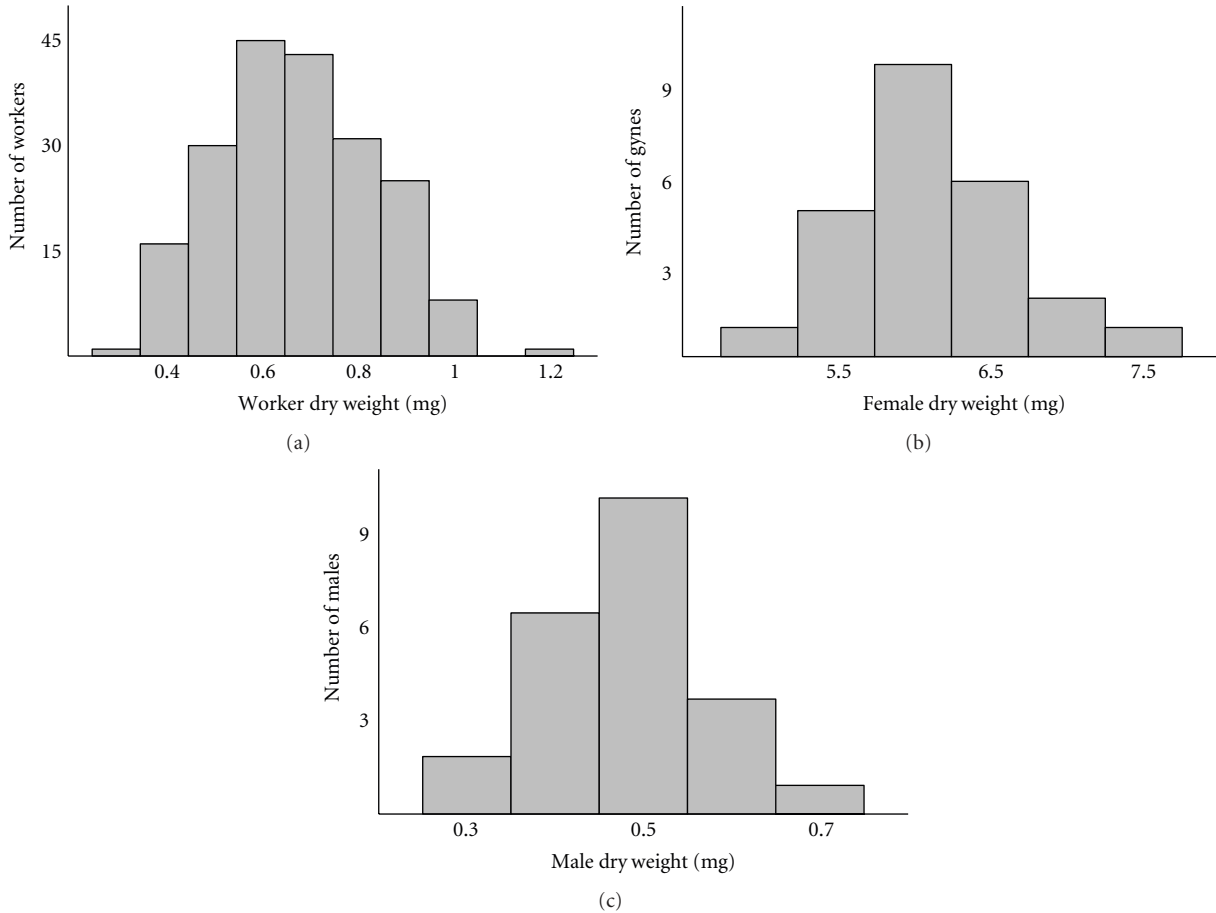
(a)

(b)

(c)

Figure 5: The dry weights of three adult *A. rudis* castes. (a) workers, $n = 200$; (b) gynes, $n = 25$; (c) males, $n = 25$.
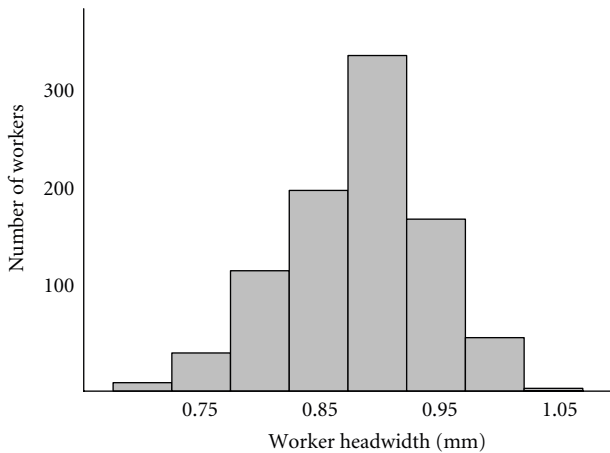

Figure 6: The distribution of the head width of 975 workers from 39 Nipmuck and Pachaug colonies.

least a few years old when collected, were maintained in the laboratory from 2001 through 2005.

7.4. Males. Males can be produced from unfertilized eggs of queens or workers but in queenright nests there is no worker reproduction [49]. Males collected from the Pachuag and Nipmuck populations averaged 0.6 mg dry weight (SD = 0.1, $N = 25$; Figure 5(c)). Fielde [54] reported that the median duration of the pupal stage for 3 males was 19 days. Males in queenright nests are thought to be produced from overwintered brood, passing through conditions similar to those experienced by gynes [24, 25]. Adult males leave the nest within a month of eclosing and their adult lifespan is likely brief. Once leaving the nest to mate, even if they avoid being killed by a predator, they will eventually succumb to starvation.

8. Conclusion

Ants of the *rudis*-group are an abundant component of the hardwood forests of eastern North America. Their ability to forage early in the spring, to readily move their nests, and to feed upon a wide range of resources plays a part in their success.

These ants can serve as a useful study system for investigating ecological and evolutionarily questions, and for learning more about basic ant biology. Ants of the *rudis* group are easy to locate and collect; the use of artificial wooden nests can facilitate their study in the field, colonies

can be readily maintained and studied in the laboratory, their colony size is such that many characteristics of whole colonies are amenable to direct measurement and the workers are not aggressive. Finally, with numerous aspects of their basic biology having been investigated this knowledge forms a solid foundation for planning future studies.
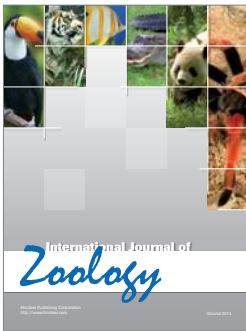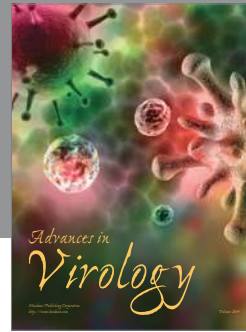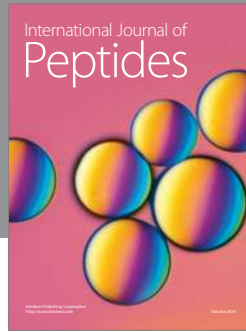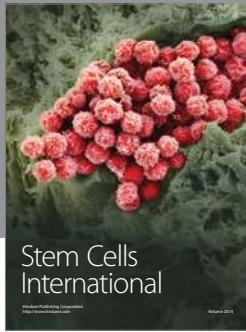
Acknowledgments

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