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SEASONAL LIFE HISTORY AND NEST ARCHITECTURE OF A WINTER-ACTIVE ANT, *PRENOLEPIS IMPARIS*

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SUMMARY

In north Florida (USA), foraging and above-ground activity of the ant *Prenolepis imparis* Say begins in November and ends in March or early April when the workers seal the nest until the following November. During this winter foraging period, workers' gasters become enormously corpulent through deposition of fat, doubling to tripling worker lean weight. The colony remains reproductively inactive until late August or early September when the queen's ovaries develop and she lays eggs. The single pulse of brood is probably reared on material derived from the corpulent workers. When the workers reopen the nests in November, most of the brood are callow workers or sexuals and all of the previous year's workers are again lean, their nutrient stores having been converted to new workers. The old workers become foragers while the callows become corpulent for the next year. Workers thus live between 1 and 2 (or more) years. Most nests are polygynous, and all queens contribute to the egg pool, though probably not equally.

The nests are 2.5 to 3.6 meters deep and consist of horizontal-floored, slightly domed chambers connected by a single vertical tunnel. As the worker population grows, total chamber floor area is increased by adding more chambers and by enlarging chambers, changing their shape from simple, nearly circular to lobed, 'pseudopodial' shapes. No chambers were found less than 60 cm below the ground surface, and most were in the bottom half of these deep nests, keeping most of the nest between 16 and 24° C, year-round.

Among the 9 colonies sampled, the number of workers varied from 560 to over 10,000. An incipient colony contained 33 nanitic workers and a single queen. Using the annual increase in worker population, the largest colonies were estimated to be 7 to 9 years old. Young, replete workers were found in the deeper chambers, while the previous years' workers (now foragers) were more abundant near the surface. The peculiar life cycle of this winter-active ant is discussed as an avoidance of competition with other ants by foraging during the cold season.

ZUSAMMENFASSUNG

Lebenszyklus und Nestbau einer kryophilen Ameise
Prenolepis imparis

Die Ameise *Prenolepis imparis* Say ist in Nord-Florida (USA) nur im Winter an der Erdoberfläche aktiv. Das Sammeln von Nahrung beginnt im November und endet im März oder Anfang April; danach verschließen die Arbeiterinnen das Nest bis zum November. Während der Periode des Nahrungssammelns wird die Gaster der Arbeiterinnen enorm dick, so daß das Gewicht dieser Arbeiterinnen sich verdoppelt oder verdreifacht. Die Gewichtszunahme wird durch den stark entwickelten Fettkörper verursacht und nicht durch die Füllung des Kropfes, wie man früher glaubte. Die Kolonie zieht bis Ende August oder Anfang September keine Brut auf, erst dann beginnen sich die Ovarien der Königin zu entwickeln und sie legt Eier. Diese Brut wird wahrscheinlich mit einem Sekret ernährt, für das die Energiespeicher der dicken Arbeiterinnen mobilisiert werden. Wenn die Nester im November wieder geöffnet werden, dann besteht der größte Teil der diesjährigen Brut aus jungen Arbeiterinnen oder Geschlechtstieren. Die Arbeiterinnen des Vorjahrs sind wieder mager, da sie ihre Fettkörperreserven an die Larven verfüttert haben. Diese alten Arbeiterinnen beginnen dann, Nahrung zu sammeln, während die jungen Arbeiterinnen für das nächste Jahr gemästet werden. Die Lebensdauer einer Arbeiterin beträgt also ein oder zwei Jahre oder mehr. Die meisten Nester sind polygyn, alle Königinnen sind fertil, doch legen sie vermutlich unterschiedlich viele Eier. Die Koloniegründung erfolgt wahrscheinlich pleometrotisch.

Die Nester befinden sich sehr tief im Boden, sie reichen bis zu einer Tiefe von 2.5 m bis 3.6 m. Die Kammern haben einen waagerechten Boden und eine leicht gewölbte Decke, sie sind durch einen einzigen senkrechten Gang miteinander verbunden. Die Gesamtfläche der Kammern ist mit der Arbeiterinnenzahl korreliert. Die Nester werden vergrößert, indem sowohl neue Kammern gebaut als auch vorhandene Kammern erweitert werden. Wenn Kammern vergrößert werden, dann wird die ursprüngliche Kreisform pseudopodienartig ausgelappt. Es wurden keine Kammern in einer geringeren Tiefe als 60 cm gefunden, die meisten Kammern befanden sich in der unteren Hälfte dieser tiefen Nester, wodurch im größten Teil der Nester das ganze Jahr über eine Temperatur zwischen 16° und 24° C herrscht.

Die 9 ausgegrabenen Nester enthielten zwischen 560 und über 10.000 Arbeiterinnen. Mit drei voneinander unabhängigen Bestimmungen der jährlichen Zunahme der Arbeiterinnenzahl wurde das Alter des größten Kolonie auf 7 bis 9 Jahre geschätzt. Die Arbeiterinnen waren in den Nestern spezifisch verteilt. Junge, gemästete Arbeiterinnen wurden in den tieferen Kammern gefunden, während sich die Arbeiterinnen des Vorjahrs, die jetzt Sammlerinnen waren, häufiger in der Nähe der Oberfläche aufhielten. Es wird diskutiert, daß die Lebensweise dieser kryophilen Ameise und speziell das Nahrungssammeln während der kalten Jahreszeit die Konkurrenz mit anderen Ameisen mindert.

INTRODUCTION

Among the ants, a wide variety of adaptations allows exploitation of an extraordinary diversity of habitats, food sources, shelters and seasons (WILSON, 1971). *Prenolepis imparis* is peculiar among ants in its preference for cooler rather than warmer temperatures (WHEELER, 1930 ; TALBOT, 1943a).

Foraging takes place at temperatures at which most other species of ants are inactive. During mid-summer on the other hand, *P. imparis* nests are inactive above ground. TALBOT (1943a, b) reported on the nest structure, colony size, foraging, temperature preferences and seasonality of *Prenolepis imparis* in Missouri and Ohio. Her data describe a species of modest colony size (average, 1,500 workers) and nest depth (maximum, 1.3 m), without hibernation, but with a distinct estivation period. As an apparent adaptation for this estivation, most workers (average 78 %) were in the "replete" state. Both TALBOT (1943a) and WHEELER (1910, 1930) assume repletion to be the result of a crop greatly distended with stored liquid food, as in species of *Myrmecocystus* (WHEELER, 1930). During estivation, eggs are laid and reared, and new workers emerge in September (in Missouri). Sexuals overwinter in the nest and mating flights take place on the first warm spring day.

P. imparis occurs more or less from s. Ontario to Colima, Mexico, and from coast to coast (WHEELER, 1930) Talbot studied the ant in the northern part of its range in Ohio and Missouri where its estivation is only a marginally noticeable one or two months. In north Florida, the ant is absent above-ground for 7 to 8 months, foraging only during the winter. I became curious what this ant did for 3/4 of a year, sealed in its underground chambers. By excavating nests throughout a year, I have discovered a number of interesting features on which I report here.

MATERIALS AND METHODS

During the winter of 1984-85, active nests of *P. imparis* were marked at two sites in the Apalachicola National Forest, near Tallahassee, Florida, USA. At both sites, the vegetation consisted of longleaf pine (*Pinus palustris*) forest with an understory of scattered scrub oaks and a ground cover of wiregrass (*Aristada stricta*). The soil was deep sand whose clay content increased somewhat at depths of 2 to 3 m.

All surface signs of activity ceased by early April, so that only staked nests could be found. These were dug at intervals throughout 1985. A vertical shaft large enough to accomodate a ladder was dug to one side of the nest. Chambers were exposed by lifting off one horizontal layer at a time. All ants were collected, the perimeter of each chamber was exposed and its horizontal projection traced on transparent acetate. Chamber depth from the surface and compass orientation were noted.

Queens were dissected and the degree of ovarian development assessed by counting the number of active ovarioles and the number of vitellogenic follicles. The contents of the queen's spermatheca were dispersed in 1 ml 0.5M NaCl and the sperm counted in a hemacytometer.

A total of 10 nests were excavated in six different months. Two of these were incipient nests and were excluded from the main analysis, two were dug in February and two in November. For analysis of worker populations, colony architecture, queen number, etc., the sample size was 8 to 10, but for analysis of the seasonal cycle, the sample size was only 1 for 4 of the six sampled months. The amount of effort and time (2 days) per excavation simply precluded larger sample sizes. Acceptance of the seasonal data as meaningful depends in part on their agreement with general patterns among other ants, and with published data on *P. imparis* (TALBOT, 1943a, b). The fact that the sequence of states from month to month form such a regular progression also strengthens the conclusions.

RESULTS

Seasonal Life History

Seasonal activity and foraging

One of the most striking characteristics of *P. imparis* is that it is apparent only during the winter and early spring. In north Florida, workers are active above-ground between early November and early April. Their reappearance in the fall is signaled by the reddish soil they excavate from their deep nests and scatter along short trails or in broad patches on top of the light-colored, sandy soil. The workers remain active above-ground all

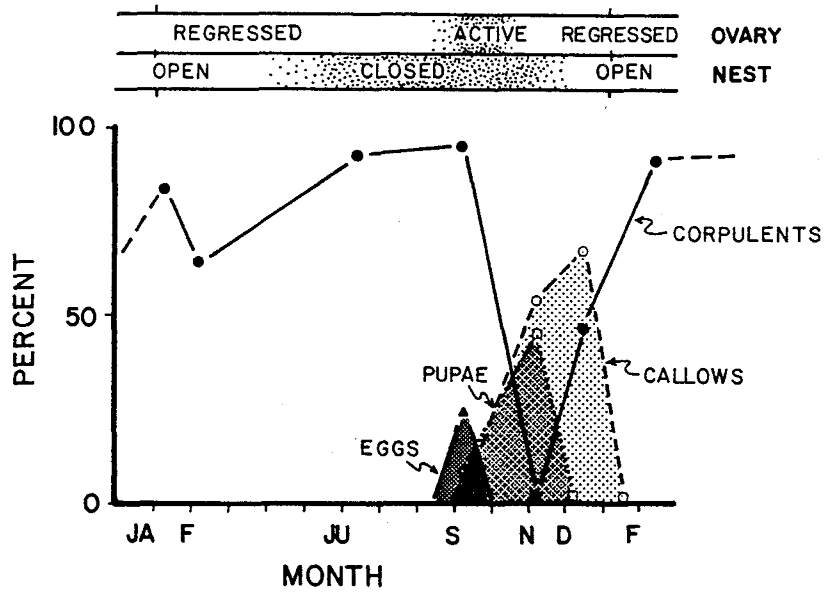

Fig. 1. — Seasonal brood production and worker corpulence, both as % of colony, in *Prenolepis imparis*. The corpulent workers provide the material for the production of a single pulse of brood. The queen's ovaries are active only in September (upper bar). The nest is open during the winter (Nov.-early April) and is sealed for the 7 to 8 warm months (lower bar). Only sampled months are labeled.

Abb. 1. — Brutproduktion und Anteil gemästeter Arbeiterinnen im Verlauf des Jahres bei der Ameise *Prenolepis imparis* (Angaben in Prozent der Kolonie). Die gemästeten Arbeiterinnen speichern das Material für die Aufzucht der ersten Brut. Die Ovarien der Königin bilden nur im September Eier (obere Reihe). Das Nest ist nur im Winter offen (November bis Anfang April) und bleibt während der 7 bis 8 warmen Monate geschlossen (untere Reihe). Nur diejenigen Monate sind gekennzeichnet, in den Proben gesammelt wurden.

winter, foraging whenever the temperature permits, even near freezing. Perhaps as protection for workers caught outside the nests by low temperature, most colonies have a number of short (up to 10 cm), dead-end vertical tunnels in the vicinity of their nest entrances. In March and April, worker activity declines above ground, and by mid-April, most nests have sealed their entrances for the summer. Rains wash away the excavated soil so that, unless marked, the nest cannot be found again until November. What do the ants do underground all summer ? The excavation of nests throughout one year has clarified the basic features of this estivating ant's life cycle.:

Seasonal Brood Production

P. imparis produced only a single brood per year, and it did so by using worker fat and nutrient reserves stored for 9 to 10 months. The rearing of this brood commenced in late August or early September and was complete by the time the nests were reopened in early November (*fig. 1*). In keeping with this pattern, the queen's ovaries were active only in the nest sampled in September, and both eggs and larvae, but almost no pupae were present. In none of the other 7 nests did I find a queen with active ovaries. By November, the nests (n = 2) contained abundant pupae and callow workers, but no larvae. Both nests also contained male pupae and callows. By December, pupae were almost absent, but callow workers made up almost 60 % of the worker force. Callows were no longer recognizable as such in the January nest, which contained only queens and workers, but no brood. This was also the case for the nests dug in February and June.

How do these ants manage to raise large numbers of new ants even though their last taste of foraged food lies at least 5 months behind them ? The answer lies in the storage of large amounts of worker fat and other nutrients (*fig. 2*) which are then drawn upon many months later for brood rearing. Many researchers have noted the " replete " nature of *Prenolepis* workers, but like WHEELER (1930), all assumed the repletion to result from liquid food stored in a distended crop. In actuality, " replete " workers contain enormously hypertropied fat bodies, but not unusually distended crops, as a quick dissection will show. Foragers are always lean and weigh about 2.0 to 2.2mg. Corpulent workers weigh up to 8 mg, and average about 5.4 mg.

The corpulence of workers showed a seasonal cycle which was exactly complementary to that of brood rearing (*fig. 1*). At the end of the foraging in April, over 90 % of all workers were distinctly corpulent, and remained so until brood rearing began in September.

Figure 3 shows the progress of fattening during the foraging season. By late February, fattening was essentially complete. By November when foraging began again and there were no more feeding brood in the the nest (i.e., no larvae), there were no longer any recognizably corpulent workers.

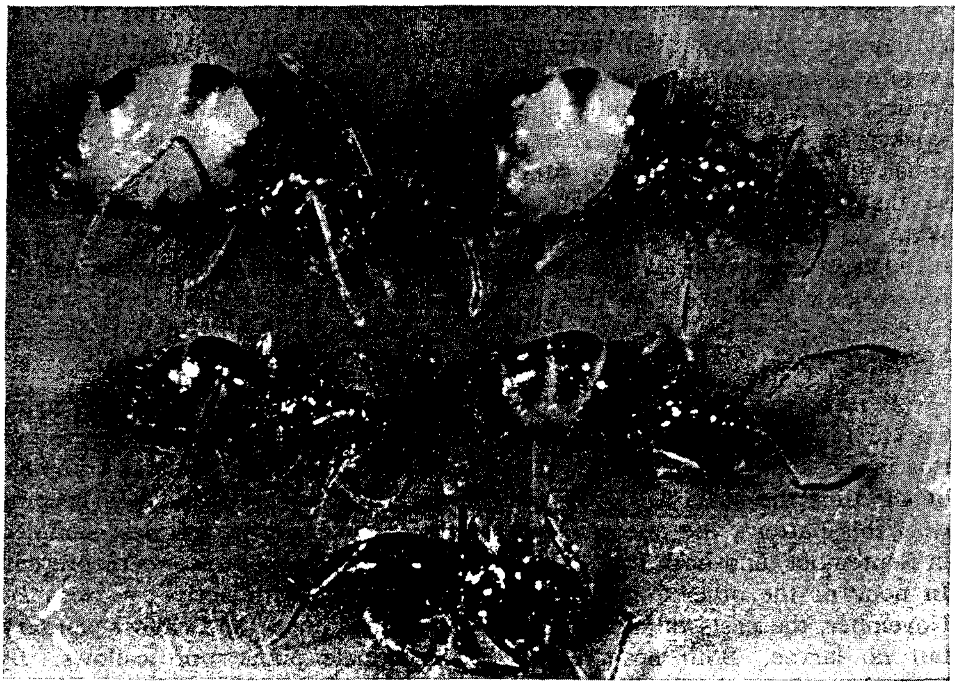

Fig. 2. — Workers of *Prenolepis imparis* showing varying degrees of corpulence. Foragers (bottom, center) are derived from the previous year's corpulent workers after weight-loss during brood rearing. The two fattest workers (top row) probably weight about 6 mg., while the forager weighs about 2 mg.

Abb. 2. — Unterschiedlich dicke Arbeiterinnen von *Prenolepis imparis*. Sammlerinnen (unten, Mitte) stammen von dicken Arbeiterinnen des Vorjahrs ab, die bei der Aufzucht der Brut abgemagert sind. Die zwei dicksten Arbeiterinnen (oben) wiegen ungefähr 6 mg, während die Sammlerin etwa 2 mg wiegt.

Pesumably, all this material was consumed in the production of brood. About a month later in December, when the workers had been foraging for about a month, about 20 % of the workers were distinctly corplent (*fig. 3*). None, however, were as heavy as workers in later months ($\overline{X}$ = 4.0 mg in December vs. 5.5 mg in September) indicating that the corpulence was still increasing in response to food intake.

Workers for fattening were not selected at random, but consisted entirely of callow workers, essentially all of whom became corpulent. This is apparent from the December nest in which all 4,888 workers showing signs of corpulence were callow, though 2,150 callows did not yet show signs of corpulence. Non-callows were never corpulent. Foragers seen at the surface were always very dark colored, never callow.

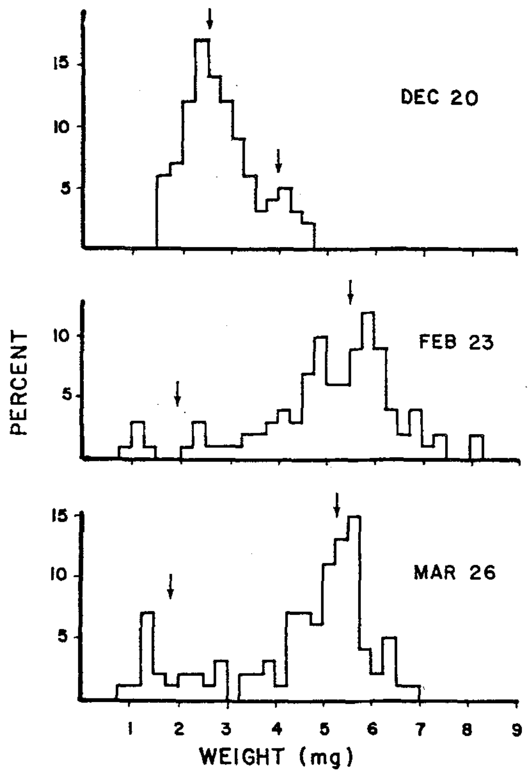

Fig. 3. — The increase of worker corpulence during the foraging period shown as weight-frequency. The mean weights for workers above and below 3 mg are indicated by arrows. Foraging begins in November when the callows emerge. By late February, fattening is complete. At this time, only foragers weigh less than 3 mg.

Abb. 3. — Die Verteilung der Arbeiterinnengewichte zeigt die zunehmende Dicke der Arbeiterinnen während der Sammelperiode. Die Durchschnittsgewichte der Arbeiterinnen oberhalb und unterhalb von 3 mg sind durch Pfeile angegeben. Das Sammeln von Nahrung beginnt im November, wenn die Brut schlüpft. Ende Februar sind die jungen Arbeiterinnen gemästet. In dieser Zeit wiegen nur Sammlerinnen weniger als 3 mg.

The simplest explanation of these observations is that each brood of workers functions as corpulents during their first 10 months of adult life. After giving up their reserves to brood rearing, they function as foragers until they die. In summer, a small fraction (less than 10 %) of workers are not corpulent. If we assume that these are surviving foragers, they must have eclosed about a year before their corpulent nestmates, making them almost two years old. How much longer they can survive is not possible to say, for as the corpulent workers become lean, they become indistinguishable from older sisters.

What is the quantitative relationship of nutrients stored to brood reared ? This was estimated from the number of workers, their estimated lean weight and the mean weight of corpulent ants. Reserve storage was estimated as the percent of the total worker live weight which was reserves. Storage after brood rearing in November is zero percent. By December, it had climbed to 22 % and when brood rearing commenced in September, over 60 % of the live weight of workers was stored fat. In others words, the average worker carried 1.5 times its lean weight in stored reserves.

Data from the two November nests allowed the estimation of efficiency of new ant production from this stored material. By assuming that these nests also entered brood rearing with 60 % stored reserves (3.5 mg per worker), it was possible to estimate the total weight of reserves they used to produce the observed weight of callow workers, pupae and males. These calculations indicate that *P. imparis* was able to convert 86 to 93 % of the stored material into new workers, or almost 1.5 times the workers' lean weight in new workers. These calculations ignore the contribution of water content, based as they were on live weights. In spite of the crudeness of estimation it is clear that the efficiency of conversion to new workers was very high.

Sexual production and colony founding

Sexuals were produced in the same brood as workers and were mostly adults by mid-November. Both November colonies contained males only, while the February colony contained 146 females and one male. The December colony contained no alates, even though it was the largest colony. Apparently not all mature colonies produce sexuals every year. I did not observe mating flights, but it is likely that they take place in the early spring, as reported for the Missouri populations by TALBOT (1943a).

A single incipient colony consisted of two small chambers, one at 18 cm depth containing a single queen and 14 workers, only one of which was corpulent, and a second at 39 cm contained 19 workers, 18 of which were corpulent. Headwidth frequency distribution showed that all 33 workers were clearly nanitic (mean headwidth = 0.68 mm; S.D. = 0.034) (*fig. 4*, upper). When lean, these workers weighed only 0.58 mg (S.D. 0.062 mg). As corpulent workers, their weight increased by 1.7 to 7.4 times, with a mean of 3.8 times. The mean weight of corpulent nanitic workers was 2.19 mg (S.D. 0.91 mg). The total weight of workers was about 51 mg, of which 44 mg (85 %) was corpulents which stored 32 mg of recoverable material. The colony was excavated in early April, making it likely that it was founded earlier in the same winter.

A young colony excavated in mid-January showed 3 modes in the headwidth-frequency distribution of its workers (*fig. 4*, lower). The smallest mode coincided with that of the incipient colony above, and the largest with a typical mature colony. This suggested that this colony was in its third year, or at least its third generation of workers, each incrementally larger than the previous generation. This colony contained 756 workers of which 475 (63 %) had headwidths distinctly smaller than normal workers in mature nests (*fig. 4*). The deeper of the two chambers (92 cm) and the 10 cm tunnel below it contained 15 queens with high sperm counts (means = 2.46×10^5; S.D. = 0.63×10^5; n = 13), possibly indicating recent mating. The large number of queens may account for the relatively large size of this young colony.

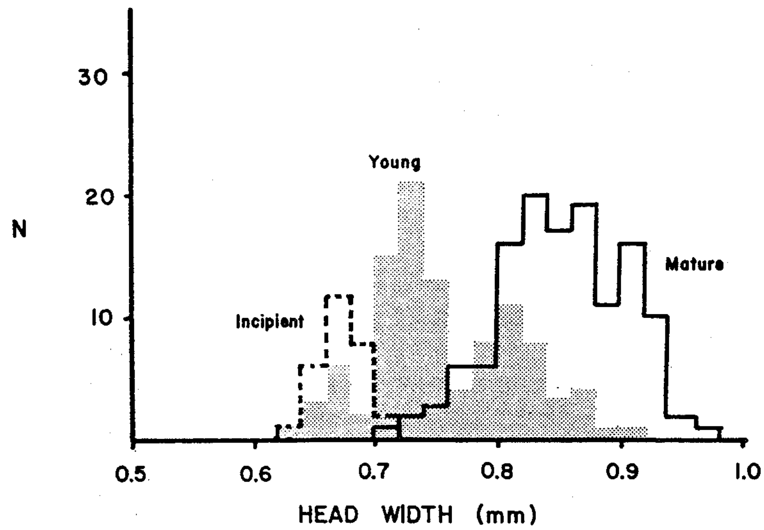

Fig. 4. — Comparison of size-frequency distribution among a mature, a young and an incipient colony of *P. imparis*. The incipient colony contained only a single mode of nanitic workers. In addition to nanitic workers, the young colony had produced a second, larger modal class and a third one within the size-range of the mature colony. Sample means of headwidths of workers in mature colonies (n = 130) are about 25 % larger than the nanitic class in the incipient colony (n = 33). The middle mode is 7 % larger than that of the nanitics.

Abb. 4. — Größenverteilung der Arbeiterinnen in einer reifen, einer jungen und in einer neu gegründeten Kolonie von *P. imparis*. Die neu gegründete Kolonie enthielt nur eine einzige Sorte von Arbeiterinnen. Die junge Kolonie hatte außerdem noch eine zweite, größere Arbeiterinnensorte produziert sowie eine dritte Sorte, die etwa gleich groß waren wie die Arbeiterinnen einer reifen Kolonie. Die mittlere Kopfbreite der Arbeiterinnen einer reifen Kolonie (n = 130) liegt um etwa 25 % über der Kopfbreite der Arbeiterinnen einer neu gegrüdeten Kolonie (n = 33). Die mittelgroße Arbeiterinnensorte ist um etwa 7 % größer als die Arbeiterinnen einer neu gegründeten Kolonie.

Queens

Colonies of *P. imparis* in north Florida were predominantly polygynous. Only two of the 8 older nests had a single queen. Queen number ranged from 1 to 6 with a mean of 4.14 (S.D. = 2.27). Queens had developed ovaries and were lying eggs only in the September nest. The number of vitellogenic oocytes (an index of egg-lying rate) in these 6 September queens varied from 57 to 220, indicating that either some queens are reproductively dominant, or that egg laying of individual queens may not be in phase.

The ovary of *P. imparis* consists of 18 to 25 rather long ovarioles. The queens, like the workers, contained a great deal of fat body throughout most of the year. This showed some decline during the egg-laying period, but queens never became as lean as workers.

Fig. 5. — View into the hole resulting from a complete nest excavation. The bottom chamber of this nest was 3.3 m. deep. The nest was in the square cut excavation at the bottom of the photo.

Abb. 5. — Blick in die Grube nach der vollständigen Ausgrabung eines Nestes. Die unterste Kammer dieses Nestes lag in 3.3 m Tiefe. Das Nest befand sich in dem viereckigen Ausschnitt am unteren Rand der Photographie.

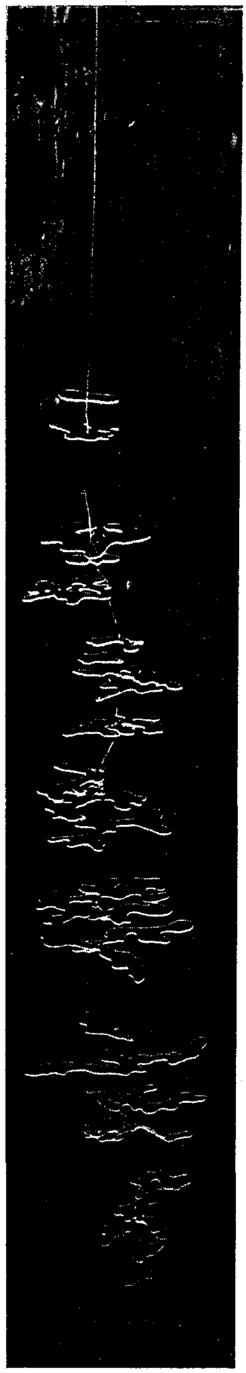

Fig. 6. — Model of the 2.4 m deep January colony showing the central vertical tunnel along which the chambers are arranged. This nest contained 31 chambers with a total area of about 1,800 cm^2, and housed 8,700 workers and 6 queens. The larger chambers are at mid-depth, but there are no chambers shallower than 60 cm. This nest reached to the water table, possibly explaining why it was not deeper.

Abb. 6. — Modell eines 2.4 m tiefen Nestes, das im Januar ausgegraben wurde. An dem zentralen, senkrechten Gang befinden sich die einzelnen Kammern. Das Nest enthielt 31 Kammern mit einer Gesamtfläche von ca. 1 800 cm^2, 8 700 Arbeiterinnen und 6 Königinnen. Die größeren Kammern befanden sich in mittlerer Tiefe, die oberste Kammer lag 60 cm unter der Oberfläche. Das Nest reichte bis zum Grundwasserspiegel, was möglicherweise erklärt, warum es nicht tiefer war.

Colony populations and colony age

All together, the colonies constitute a haphazard sample of the population of colonies from which they were sampled. As might be expected for stable populations, the number of workers varied widely from a low of about 600 to a high of 10,300 (mean = 3,790 ; S.D. = 3,650 ; incipient colony not included). Colonies with as few as 1,500 workers were capable of producing a few alates (November nest 1), while larger colonies can produce at least 20 % as many males as workers (November nest 2).

How old are these colonies ? The annual rate of increase in worker population can be computed for the nests containing callow workers (Nov., Dec.) by dividing the number of old workers (non-callows) into the number of new workers (callows and worker pupae). The values were 2.3 and 2.0 for the two mid-size November colonies, and 2.2 for the large December colony. These values are for the beginning of the foraging season, of course. By the end, most of the old workers will have died, leaving a colony population about twice as large as the previous year. Colony age can be approximated by the number of divisions by 2 required to reduce the worker population to approximately that of the first brood in a newly founded nest (ca. 25-50). This calculation suggested that a colony of 9 or 10 thousand workers is 7 to 9 years old.

Nest Architecture

The nests of *P. imparis* were impressive by their scale and neat organization. Even the nest with only 600 ants was 2.4 m deep, while the deepest nest bottomed out at 3.6 meters (mean = 2.83 m ; S.D. = 0.48 ; n = 8) (*fig. 5*). A tall ladder was a necessity for entry and (more importantly) exit from the excavation.

The basic structure of *P. imparis* nests is a vertical tunnel joining domed, horizontal-floored chambers about 1 cm high and of variable area and shape (*fig. 6*). The vertical tunnel may be continuous through several or all chambers, so that a straw may be slipped all the way down, or the next down-leg may be offset so that a straw will slip only from chamber to chamber. The former pattern was common, while the latter seemed to occur mostly in the upper chambers of some nests.

One of the most striking features of the nests is that even the shallowest chambers were quite deep (*fig.* 7), compared to other species of ants. No nests had chambers shallower than 60 cm, and 3 had none shallower than 120 cm. Once chambers began, they occured with fair regularity along the vertical tunnel.

Chamber area showed some regularity of pattern with respect to chamber depth. The smallest chambers tended to be the shallowest and deepest ones,

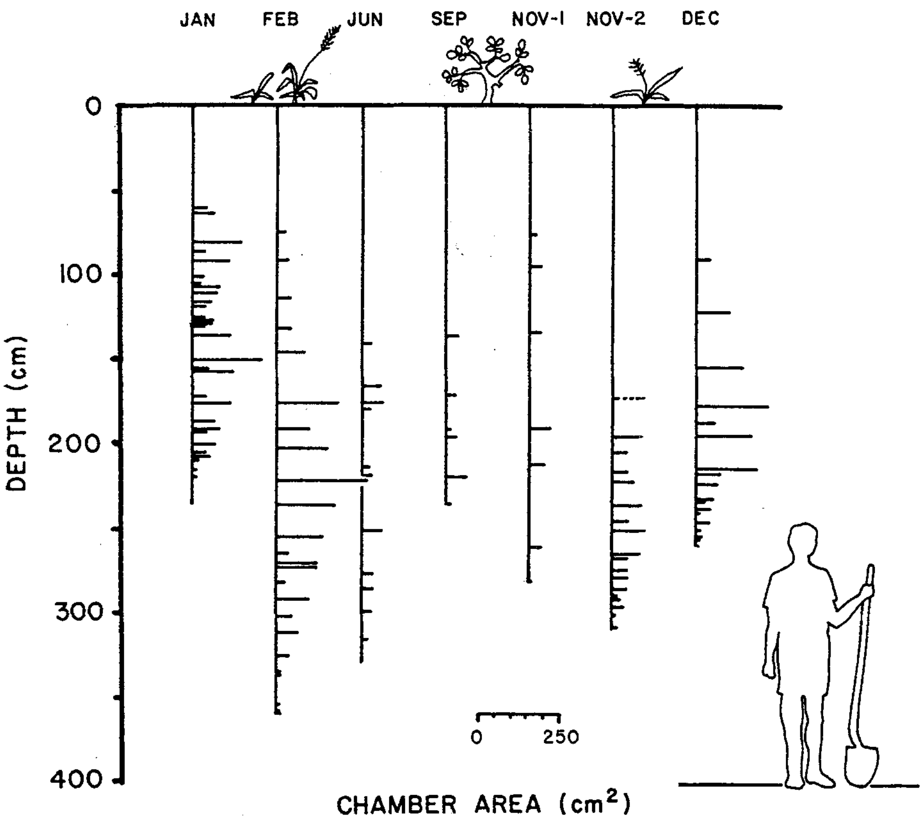

Fig. 7. — Schematic scale representation of the nests of *Prenolepis imparis*. Depth of chambers below the surface is to the same scale as the silhouette of a 5½ ft (1.6 m) tall man. Chamber area is represented by horizontal lines according to the indicated scale. The sampling month is indicated. Two nests were sampled in November. Nov.-2 was not yet open and was struck accidentally during excavation of Nov.-1, missing its upper chambers.

Abb. 7. — Schematische Darstellung der Nester von *Prenolepis imparis*. Die Tiefe der Kammern ist auf der linken Skala angegeben, rechts zum Vergleich die Silhouette eines 1.6 m großen Menschen. Die horizontalen Linien zeigen die Flächen der Kammern (untere Skala). Der jeweilige Monat, in dem die Nester ausgegraben wurden, ist oben angegeben. Im November wurden zwei Nester gefunden. Das Nest Nov-2 war noch nicht offen und wurde zufällig während der Ausgrabung von Nest Nov-1 entdeckt, wobei die oberen Kammern zerstört wurden.

while the largest chambers were found in the middle depths between these two (*fig.* 7).

Total chamber area (cm^2) showed a strong relationship to the number of workers in a colony ($A = 0.15\ W + 285$; $R^2 = 0.82$) (*Fig. 8*). Each worker increased chamber area by 0.15 cm^2. This area increase seemed to be al-

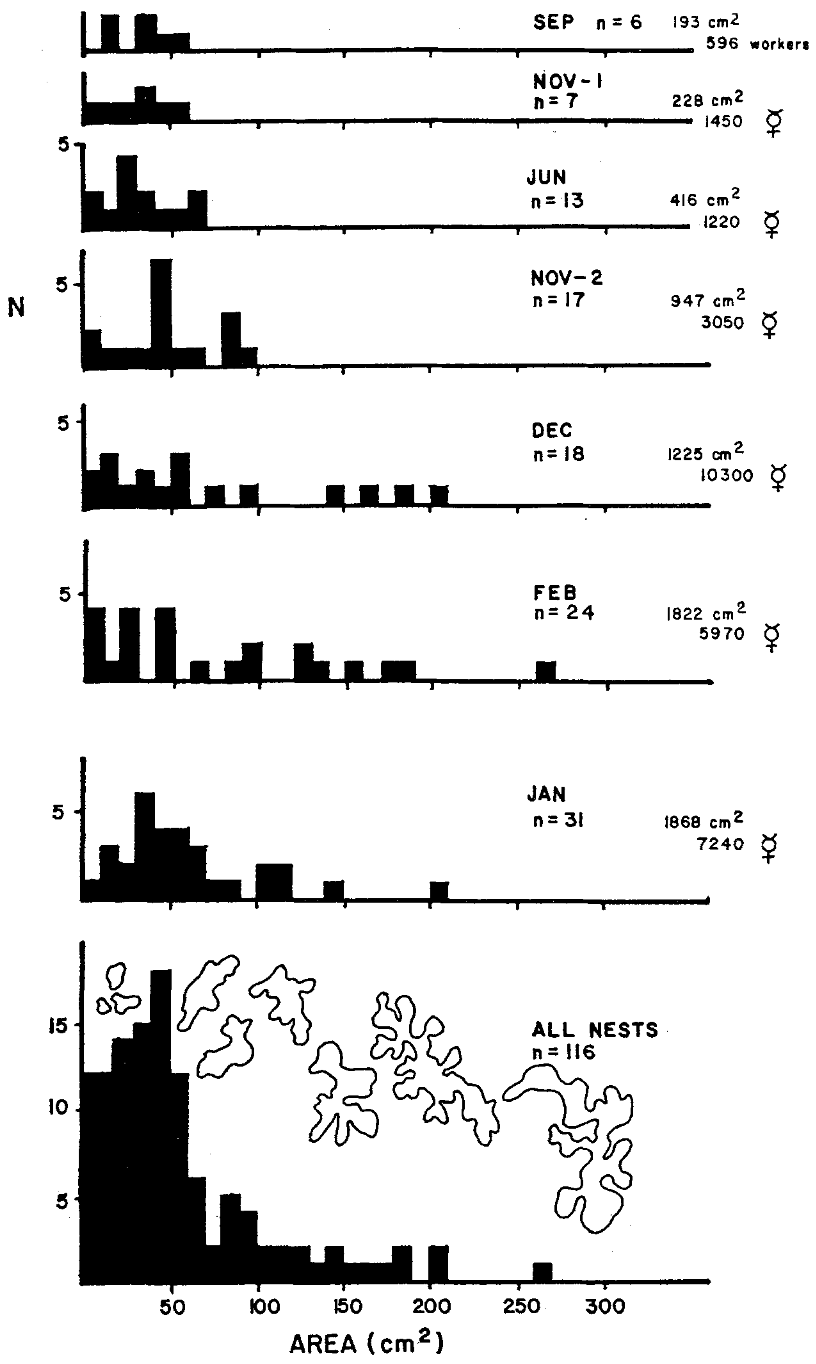

Fig. 8. — Chamber area-frequency distribution for the nests of *Prenolepis imparis*. The distributions are strongly skewed because colonies construct only a small number of chambers larger than the modal class. Number of chambers, workers and total chamber area are indicated. Arranged in order of increasing colony size from top top to bottom. The bottom histogram also shows representative outlines for chambers of increasing area, roughly in line with the abcissa scale.

Abb. 8. — Größenverteilung der Fläche der Nestkammern von *Prenolepis imparis*. Die Verteilung ist asymmetrisch, weil die Kolonien nur wenige größere Kammern besitzen. Die Anzahl der Kammern, der Arbeiterinnen sowie die Gesamtfläche der Kammern sind angegeben. Die Kolonien sind von oben nach unten entsprechend ihrer Größe angeordnet.

located first to increased numbers of chambers, and second to increasing the area of particular chambers (*fig. 8*) so that large colonies showed a dramatic increase in the mean size of their largest chambers. The chamber area/frequency distribution is therefore strongly skewed.

As chambers increased in size, their horizontal projections also changed shape. Small chambers were nearly circular, but larger chambers had ever more complex perimeters (*fig. 8*, bottom). Chambers tend to become enlarged by pseudopod-like extensions of portions of the perimeter. The complexity of this perimeter was estimated by computing the ratio of the measured perimeter to the perimeter of a circle of equal area. This ratio (P) showed a high correlation to chamber area (A) according to the regression $P = 0.011\,A + 1.24$; $R^2 = 0.67$. (A is in cm^2). For example, a 200 cm^2 chamber had about 3.5 times the perimeter of a 200 cm^2 circle, but this ratio was only 1.7 for a 50 cm^2 chamber.

Distribution of workers

In all colonies but November nest 2, the workers became more and more concentrated as the dig descended, so that the bottom chambers were often completely packed with ants. This could easily have been the result of driving the ants downward through the disturbance created by digging, a suspicion also expressed by Talbot (1943a). To test whether this was so, a variation of the standard digging method was applied to a single colony on Feb. 23, 1986. On the first day, a 3 m deep shaft was sunk adjacent to the nest, but the nest was not cut into. The hole was covered with plywood, and the ants left for 4 days to reassort themselves in what was hoped would be a natural way. The hole was then re-entered, the chambers located by just cutting into them from the vertical face. Sheets of metal were driven horizontally into wall so that they transected the tunnels connecting the chambers and prevented ants from moving from chamber to chamber. Ecavation then proceeded as before.

The distribution of workers in this " barrier nest " was similar to that in most of the other digs (*fig. 9*). Furthermore, if the disturbance of digging drove the ants downward, they would accumulate in the tunnels above the barriers. Only three of the nine barriers showed some accumulation, indicating that some downward movement occurred, but it was not massive. The distribution of workers in the 8 " non-barrier " nests can thus be taken as reflecting actual distribution. A Kolmogorov-Smirnov goodness-of-fit test indicates that the distribution of workers in the barrier and all non-barrier nests except Nov. 2 are significantly different from uniform distribution ($p < 0.001$). The barrier nest was, however, significantly different from the mean of the other nests (minus the Nov-2 nest) indicating that digging may have had a significant effect on worker distribution. Nevertheless,

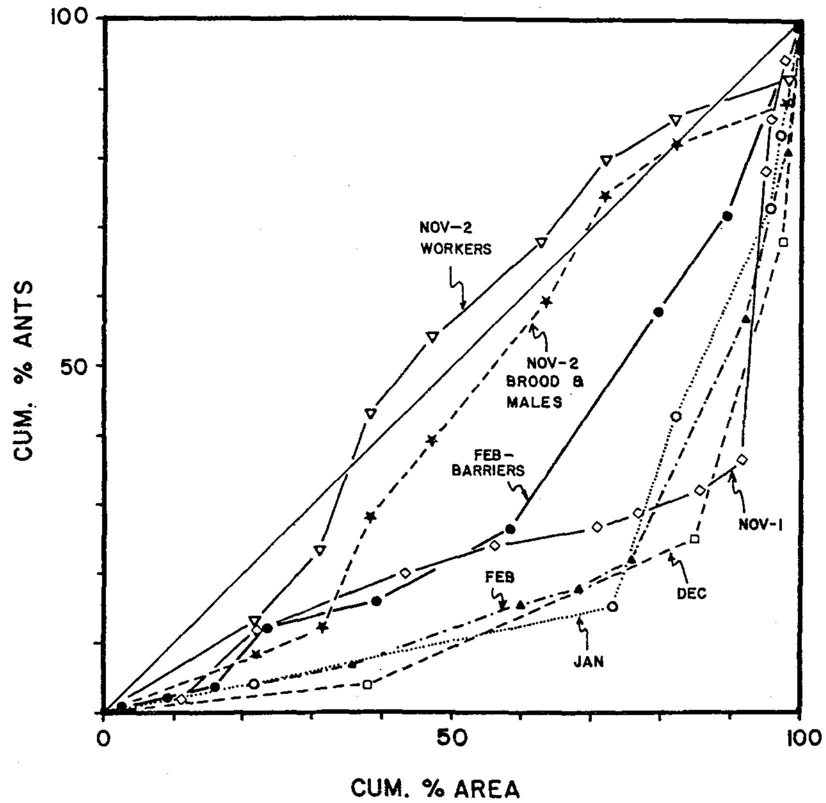

Fig. 9. — For most nests, as the excavation proceeded downward, chamber area (as % of total) cumulated much more rapidly than did the fraction of the worker population. Workers were ever more densely packed in the deeper chambers, and this was true even when workers were prevented from moving down in the nest before excavation (Feb.-barriers ; see text). The diagonal line represents the case in which workers are evenly distributed in the chambers, i.e., area and workers cumulate at the same rate. Such a distribution was observed only for the Nov-2 nest.

Abb. 9. — Im Verlauf der Ausgrabung summiert sich die Kammerfläche (Prozent der Gesamtfläche) schneller als die Anzahl der Arbeiterinnen (Prozent der Gesamtzahl) ; d.h. es befinden sich mehr Arbeiterinnen in den tiefen Kammern, und zwar auch dann, wenn die Arbeiterinnen vor der Ausgrabung daran gehindert wurden, nach unten auszuweichen (Feb-barriers, s. Text). Die Diagonale gibt die Gleichverteilung der Arbeiterinnen in den Kammern an. Eine solche Verteilung wurde nur in dem Nest Nov-2 gefunden.

these resembled the barrier nest much more than they did uniform distribution (*fig. 9*).

Figure 9 shows that as one proceeded downward in the nest, chamber area cumulated more rapidly than did worker number (both expressed as

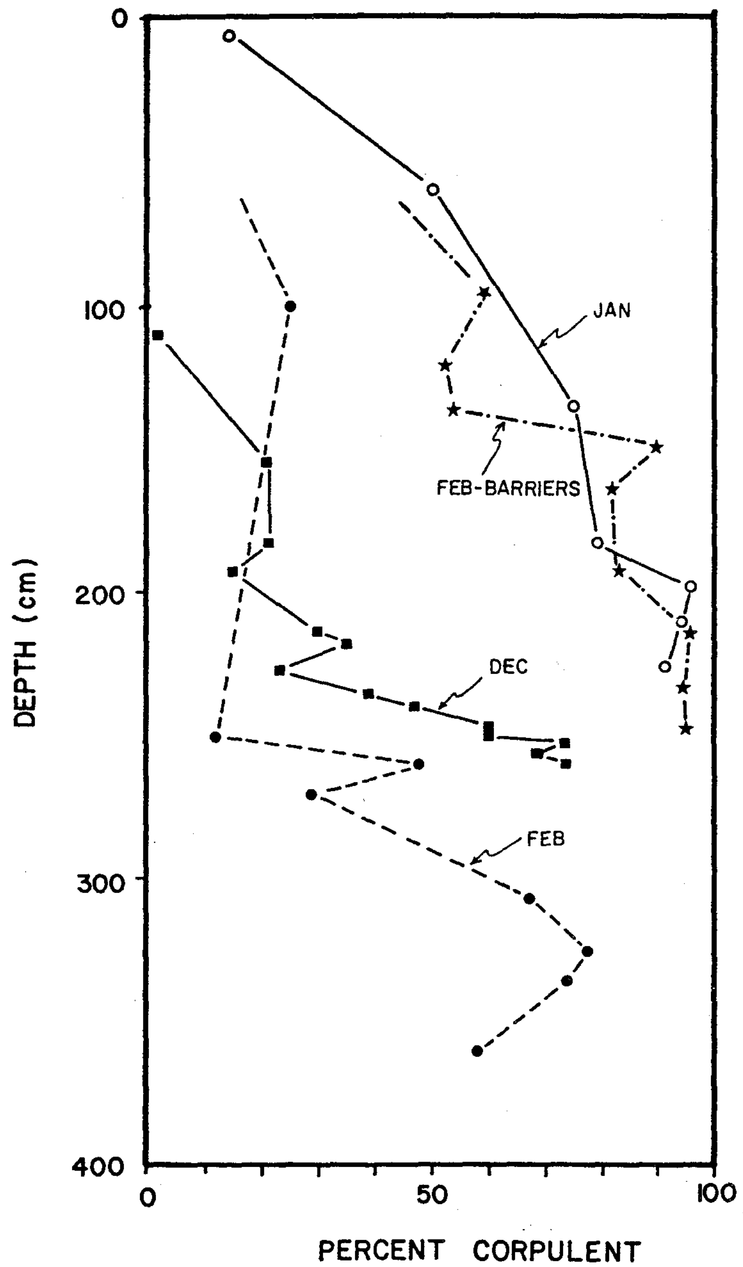

Fig. 10. — The percent of workers that were corpulent in relation to chamber depth. The deeper the chamber, the greater the fraction of workers which were corpulent. In Feb-barriers nest workers were unable to travel between chambers (see text). Similarity of worker-distribution of this nest and others confirms that distributions are not artifacts caused by excavation.

Abb. 10. — Prozentuale Häufigkeit der dicken Arbeiterinnen in den verschieden tiefen Kammern. Je tiefer die Kammer, desto größer war der Anteil der dicken Arbeiterinnen. In einem Nest wurden Barrieren eingebaut (Feb-barriers, s. Text), so daß es den Arbeiterinnen unmöglich war, zwischen den Kammern hin- und herzulaufen. Die Verteilung der Arbeiterinnen in diesem Nest ist ähnlich der in anderen Nestern, so daß die Verteilung der Arbeiterinnen nicht durch die Ausgrabung verursacht wurde.

percent of total). The only exception to this was the November nest 2 whose distribution did not differ significantly from uniform (that is, chamber area and worker number cumulated at identical rates. Kolmogorov-Smirnov Test). This was also the only nest which contained a substantial fraction of brood and alates (35 %), implying that chambers are fully and evenly utilized only for brood rearing. When brood or alates were not present in large numbers, the workers packed into the bottom of the nest, often completely filling the lowest chambers, a condition noted by both DENNIS (1941) and TALBOT (1943a). Thus, the density of ants over all chambers was usually between 3 and 8 ants/cm^2 (overall mean = 6.7 ants/cm^2), but in the bottom chambers it was usually between 15 and 50 ants/cm^2.

Both callows and corpulent workers were more represented at greater depths (*fig. 10*). As noted above, callows became corpulent, so the distribution of these two types is essentially the same. In most nests, 70 to 95 % of workers in the bottom chambers were callow and/or corpulent. These were, of course, the youngest workers, indicating strong stratification by age within the nest. Such stratification has been noted in other species as well (PORTER and JORGENSON, 1981 ; MIRENDA and VINSON, 1981).

The effect of this worker distribution was to keep most of the nest population in a zone of modest annual temperature fluctuation (*fig. 11*). Below 200 cm, the temperature varied less than 8° C. while at 50 cm it varied 13° C. For most of a typical colony the temperature never exceeded about 25° nor fell below about 16° C. The annual temperature wave lagged with depth so that the gradiant overturned twice each year. It is interesting that the brood were reared during the fall turn-over when the gradient was weak or disorganized.

DISCUSSION

Prenolepis imparis possesses a number of interesting and special features : 1) It forages exclusively in the cool months when most other ants are less active or inactive ; 2) its workers store more than twice their weight in fat and nutrients ; 3) eight months of the year are spent sealed in the nest with no food intake ; 4) during the last two months of this period, a single brood almost twice the weight of the (lean) worker population is reared ; 5) young workers become corpulent, storing material for the next year's brood, while the previous year's workers become lean and forage ; 6) in north Florida, the nests are very deep, keeping the ants in a zone of moderate seasonal temperature fluctuation.

My findings differ from those of TALBOT (1943a, b) and DENNIS (1941) in several interesting ways. While the arrangement of chambers and tunnels was similar in all areas, in north Florida the nests were almost 3 times as deep as in Missouri or Ohio and 4 times as deep as in Tennessee. In part,

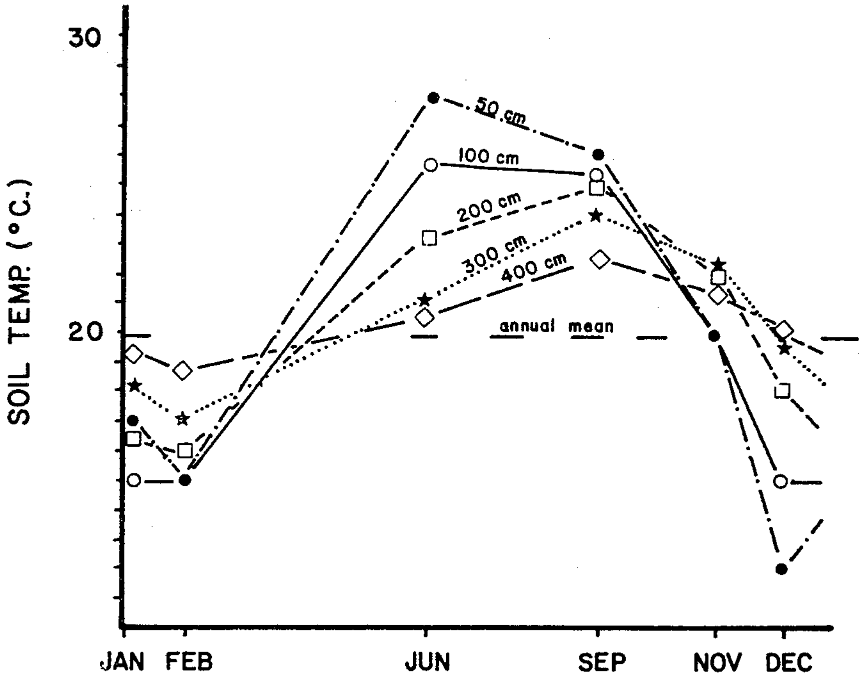

Fig. 11. — Seasonal fluctuation of soil temperatures in relation to depth. Temperatures were measured during nest excavations. Several temperatures at 300 and 400 cm were derived by extrapolation from shallower temperatures. The annual mean for 1983-5 is indicated.

Abb. 11. — Jahreszeitliche änderungen der Bodentemperaturen in verschiedenen Tiefen. Die Temperaturen wurden während der Ausgrabungen gemessen. Verschiedene Temperaturen in 300 cm und 400 cm Tiefe wurden von Temperaturen in flächeren Bodenschichten extrapoliert. Die durchschnittliche Jahrestemperatur für 1983-5 ist angegeben.

this may represent the difference between north Florida sand and the clay soils of the other study areas, but the fact that the upper chambers were never less than 60 cm deep in Florida, but only a few cm in Missouri, Ohio and Tennessee argues that temperature may play an important role in chamber distribution and depth. Temperature almost certainly plays a role in the length of the estivation period : 1 to 2 months in Ohio, 7 to 8 months Florida. It is the extreme length of this period that makes it so obvious that the brood reared at its end are reared entirely on stored body substance. TALBOT did not recognize that all callows function as " repletes " (actually corpulents) during their first year and foragers during their second. In her study, the fraction of corpulents never dropped below 67 %, while in mine, none were present at the end of brood rearing. In both localities, brood-rearing took place in the two months before the nest was re-opened in autumn.

However, while in the northern localities this was all of the two-month estivation, in Florida, it occupied only the last 25 % of this period.

Resumption of foraging in both areas corresponds roughly to the appearance of pupae and callows in the nest. In TALBOT's study, many still had larvae through the middle of the nest re-opening period. Perhaps this resumption of foraging before completion of brood-rearing accounts for the presence of repletes at this time. In Florida, brood-rearing is complete when nests are reopened and corpulents are therefore absent.

Queen number is dramatically higher in n. Florida than any of the northern populations. Both TALBOT (1943a) and DENNIS (1941) reported that 2 of 17 and 1 of 11 nests had two queens. The rest were monogynous. In n. Florida by contrast, 6 of 8 mature colonies were polygynous. Average queen number was over 4. The single " 3-year " colony contained 15 queens.

The key adaptation which allows *P. imparis* to indulge in this lifestyle is the ability to store large amounts of material in the hypertrophied fat body of workers. A similar type of storage was described in *Formica japonica* by KONDOH (1968b) and in *F. ulkei* by HOLMQUIST (1928, in KONDOH, 1968a). Arguing that the nature of the stored material was not known to be only fat, KONDOH developed an " index of corpulency " for relative weight on a given body size. For *F. japonica*, corpulent workers weighed about twice as much as lean, while for *P. imparis* this factor is about 2.5. Both *F. japonica* and *F. ulkei* become corpulent in the autumn and lose corpulency during the rearing of the next summer brood, a period during which workers forage. In *F. japonica* and *F. ulkei*, it is thus not possible to say unambiguously that the corpulence of workers provides material primarily for brood rearing rather than hibernation. In *P. imparis* on the other hand, this is obvious because brood rearing completely precedes foraging.

Many ants have workers which store liquid food in greatly distended crops (repletes) (WHEELER, 1910 ; WILSON, 1971), and until now, the workers of *P. imparis* were mistakenly assumed to be repletes as well (TALBOT, 1943a, b ; WHEELER, 1930). A number of advantages of storing fat over ordinary repletion suggest themselves : possible spoilage is avoided, the caloric concentration is probably higher, and the material can be more rapidly mobilized into secretory products. How the fat is mobilized for larval and queen use is, of course, completely unknown.

Foragers of *P. imparis* have long been known to be able to forage at very low temperatures, almost to freezing (TALBOT, 1943b ; WHEELER, 1930). In fact, they vanish into their nests before the spring warms the soil surface very much. Despite this obvious forager preference for cold temperatures, the non-foraging nest population is not exposed to particularly low temperatures. At the same instant that foragers may be making their mollasses-paced foraging trips at 1 or 2° C on the ground surface, workers deep in the nest are basking in a balmy 18 to 20° C. It is possible that foragers shuttle back and forth between these extremes. Whether they show unusually wide ranges of temperature adaptation is not known, but they are capable of movement at refrigerator temperature, when ants such as *S. invicta* are completely immobile. BRIAN (1983) and WHEELER (1930) speculate that most ants, including tropical ones, are thermophilic and may be limited by availability of warmth. Almost all ants active in cool places or seasons attempt to maximize exposure to high temperatures. This contrasts sharply with *Prenolepis imparis* whose temperature preferendum is for lower, rather than higher temperature (TALBOT, 1943b).

Chambers excavated in the earth are one of the commonest nest forms among the ants. Their form and depth vary enormously, and although much descriptive work has been published (BRIAN, 1983), no comprehensive review of nest architecture exists. Organization and form of underground chambers may vary from the sponge-like thermoregulatory mounds of *Solenopsis invicta*, to the swarms of ovoid chambers of *Atta* spp. (MOSER, 1963), the complex systems of multiple tunnels and chambers of some *Formica* spp. (TALBOT, 1948) and *Pogonomyrmex occidentalis* (LAVIGNE, 1969) or the " shish-kabob " nests of *Prenolepis imparis* (TALBOT, 1943) with its single, central tunnel connecting a stack of horizontal chambers. The deepest reported nests are probably those of *Atta* spp. which regularly descend to more than 4 m. (MOSER, 1963), but these are also species with enormous worker populations. Among species with more modest colony size, *Formica japonica* and *Messor aciculatum* descend to over 3 m. (KONDOH, 1968; KUBOTA, 1948, cited in KONDOH, 1968). *P. imparis* matches these species in depth of nest, at least in n. Florida.

Judging from the nests of *P. imparis* colonies of various sizes, nest depth increased to nearly its full extent early in colony life, a fact also noted by DENNIS (1941). Next, the number of small chambers increases, while increase in the area of individual chambers takes place mostly in rather large colonies. When chambers are enlarged, this is accomplished by " pseudopod-like " extensions of the perimeter. Ants must concentrate their excavation efforts on parts of the perimeter, rather than distributing them evenly around the walls of the chambers. The chamber shape represents the physical outcome of the social organization of labor in the nest. Nest structure must surely feed back upon how efficiently the ants carry out vital colony functions and allocations. The fact that, at least in *P. imparis* several nest architectural parameters grow at different rates during different phases of the colony life cycle, implies that there may be regular effects of these parameters on other aspects of social biology.

The packing of the majority of workers into the bottom of the nest, leaving the upper chambers sparsely populated or even empty, is somewhat puzzling. Why do the ants have so much unused chamber area ? The single nest showing uniform distribution among chambers was also the only one which contained a large amount of brood and alates. This indicates that the ants may spread out only when they need the space for efficient brood care. During the foraging season and estivation on the other hand, corpulent workers make up an increasing fraction of the ever more densely packed workers in the deeper chambers. It is likely that the vertical distribution of corpulent workers is simply the distribution of callows. A similar pattern has been noted in *Pogonomyrmex occidentalis,* in which workers pack into the bottom chambers for hibernation (LAVIGNE, 1969). Callows are also more abundant in the deeper chambers of *Pogonomyrmex badius.* In all ants investigated to date, young workers move from the brood area to the nest perimeter and out as they age, paralleling the change in their major tasks from brood care to general nest duties to foragers. In *P. imparis,* this movement is upward and, because the generations are so discrete, probably takes place in cohorts rather than gradually, resulting in the observed worker distribution. While it seems logical that chambers are enlarged in response to increased worker number, this population increase takes place before the nest is opened and the chambers enlarged. After opening, many of the chambers which are candidates for enlargement are probably sparsely occupied because workers move to the bottom of the nest after brood production. The density of ants in chambers is thus most even during brood production when the nest is closed and no increase in area is possible. When nest enlagement does occur it is in preparation for the brood to be produced almost a year later. It is space which remains unutilized until that time.

The incipient and " 3-yr old " colonies (*fig. 4*) leave the question of pleometrotic founding unanswered. The multiple queens in the latter could have been added post-founding. Until a colony builds up a sufficient worker force to excavate a deep nest, it must estivate near the surface, subject to higher temperatures ($> 26^{\circ}$).

It is interesting that even under these conditions nanitic workers appear to be able to live into the colony's 3rd year (or generation), in spite of the low expected longevity associated with their small body size. The first two generations each produce workers larger than themselves, trading size for numbers. Perhaps this trade-off must be accomplished in stages, accounting for the 3 distinct sizes of workers in this young nest.

While WHEELER (1930) claims the entire USA and parts of Ontario and Mexico for *P. imparis'* range, there is little information on the types of habitats in which it is found within this range. In Arizona, I have found it high in the Chiracahua Mts. In Colima, Mexico, it also occurs at 7,500 ft. elevation. It seems likely that the ant occurs only at higher elevations in the tropical and subtropical parts of its range, keeping it in the cooler habitats. While perhaps cool enough for *P. imparis'* taste, these tropical habitats are also much less seasonal. It would be interesting to determine how the colony cycle is modified for these conditions.

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References

BRIAN M.V., 1983. — *Social Insects: Ecology and Behavioral Biology*, Chapman and Hall, NY.

DENNIS C.A., 1941. — Some notes on the nest of the ant, *Prenolepis imparis* Say. *Ann. Entomol. Soc. Am., 34*, 83-86.

HEADLEY A.E., 1949. — A population study of the ant *Aphaenogaster fulva* ssp. *aquisa* Buckley. *Ann. Entomol. Soc. Am., 42*, 265-272.

KONDOH M., 1968. — Bionomic studies on the colony of an ant species, *Formica japonica* Motschulsky. I. Nest structure and seasonal change of the colony members. *Jap. J. Ecol., 18*, 124-133.

KONDOH M., 1968. — Bionomic studies on the colony of an ant species, *Formica japonica* Motschulsky. 2. Allometric study of the body weight and the corpulency relating to the body size of workers. *Jap. J. Ecol., 18*, 171-179.

LAVIGNE R.J., 1969. — Bionomics and nest structures of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am., 62*, 1166-1175.

MIRENDA J., VINSON S.B., 1981. — Division of labour and specification of castes in the red imported fire ant, *Solenopsis invicta* Baren. *Animal. Behav., 29*, 410-420.

MOSER J.C., 1963. — Contents and structure of *Atta texana* nest in summer. *Ann. Entomol. Soc. Am., 56*, 286-291.

PORTER S.D., JORGENSON C.D., 1981. — Foragers of the harvester ant, *Pogonomyrmex owyheeis*: a disposable caste? *Behav. Ecol. Sociobiol., 9*, 247-256.

TALBOT M., 1943a. — Population studies of the ant, *Prenolepis imparis* Say. *Ecology., 24*, 31-34.

TALBOT M., 1943b. — Response of the ant *Prenolepis imparis* Say to temperature and humidity changes. *Ecology., 24*, 345-352.

TALBOT M., 1945. — Population studies of the ant, *Myrmica schencki* ssp. *Emeryana* Forel. *Ann. Entomol. Soc. Am., 38*, 365-372.

TALBOT M., 1940. — The slave-making ant *Formica sanguinea subintegrata* Emery, its raids, nuptial flights and nest structure. *Ann. Entomol. Soc. Am., 33*, 560-577.

TALBOT M., 1948. — A comparison of two ants of the genus *Formica*. *Ecology., 29*, 316-325.

WHEELER W.M., 1910. — *Ants: Their structure, behavior and development*, Colombia Univ. Press.

WHEELER W.M., 1930. — The ant *Prenolepis imparis* Say. *Ann. Entomol. Soc. Am., 23*, 1-26

WILSON E.O., 1971. — *The Insect Societies*, Belknap Press, Harvard.