

NATURAL HISTORY OF THE ANT *PHEIDOLE DESERTORUM*
WHEELER IN A DESERT GRASSLAND HABITAT

BY KEN R. HELMS

Department of Zoology
Arizona State University
Tempe, AZ 85287-1501, U.S.A.*

ABSTRACT

Pheidole desertorum colonies are large for the genus; the number of adult workers in established colonies ranges from 2,460–24,814. They are nocturnal during summer and are predators and scavengers on arthropods. Both minor and major workers forage, although foraging by majors appears to occur primarily when food is abundant. Young major workers may function as repletes. The adult major/minor worker ratio varies greatly among colonies; much of that variance appears explained by colony size and maturity of adult colony reproductive broods. Most colonies produce reproductives each year and colony sex ratios are extremely sex-biased. Mating season begins following summer rainfall. Males and gynes fly prior to sunrise; males form aerial swarms which gynes enter. Mating occurs on the ground, then gynes fly away, presumably to suitable colony founding sites. Colony foundation is normally haplometrotic, although pleometrotic queen associations with workers are found.

INTRODUCTION

Ants in the genus *Pheidole* occur nearly world-wide and are common in such diverse habitats as deserts and tropical forests. There may be as many species in *Pheidole* as occur in any other ant genus (Wilson, 1976; Hölldobler and Wilson, 1990). However, little is known about the natural history of most species.

*Correspondence: E-Mail: agkrh @ ASUVM.inre.asu.edu

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Pheidole desertorum occurs in northern Mexico and the southwestern United States (Arizona, Nevada, New Mexico, Oklahoma, and Texas [Krombein 1979, Wheeler and Wheeler 1986]). There are notes on the natural history of *P. desertorum* (Cole, 1937; Creighton, 1950; Krombein, 1979; Wheeler and Wheeler, 1986) and the species has been included in the desert community ecology studies of Davidson (1977a,b). Their nesting biology and importance as prey for (and defense against) *Neivamyrmex* army ants have been studied extensively (Miranda, Eakins, Gravelle, and Topoff, 1980; Droual and Topoff, 1981; Droual, 1984). I studied a Chihuahua desert population of *P. desertorum* over a five-year period and have developed an account of major aspects of their natural history.

METHODS

The study was conducted from 1988 to 1992, primarily on a 0.8 km² site in the San Simon Valley, near Rodeo, New Mexico. The area is desert grassland (Miranda, et al. 1980), although shrubs are common, primarily Mormon tea (*Ephedra trifurca*), snakeweed (*Gutierrezia* sp.), and burroweed (*Haplopappus* sp.).

Pheidole desertorum colonies are nocturnal during summer and were located at night with peanut butter baits set at 3.5m intervals along randomly selected transects and at 3.5m equidistant intervals within 105 × 105m grids (100 baits per grid) (Helms, 1994). Most colonies were left intact and monitored in the field. Colony reproductive status was assessed as described by Helms and Rissing (1990) and Helms (1994). A subset of colonies was collected with traps that exploit this species' nest evacuation response to attack by *Neivamyrmex* army ants (Helms and Rissing, 1990). After collection, female alates (referred to here as gynes) and males were removed and counted. The remaining workers and brood of each colony were divided into 20 groups of equal weight. The workers and brood in each group were counted until the cumulative mean number of major and minor workers and brood changed by 5% or less over two consecutive groups (i.e., until the mean numbers of individuals per group stabilized). Total number of majors, minors, and brood within each colony was then estimated by multiplying the cumulative mean numbers by 20. Samples of adults and pupae of each caste were dried at 50°C and body mass measured (± 0.01

mg). The headwidths of additional samples of major and minor workers were measured above the eyes (± 0.01 mm).

RESULTS AND DISCUSSION

General Description

As in most members of the genus, *P. desertorum* has a dimorphic worker caste consisting of large (major) workers (or soldiers) and smaller (minor) workers (Tables 1, 2). However, the appearance of workers is atypical for the genus. As noted by Wheeler and Wheeler (1986), major workers of *P. desertorum* are large compared to those of most species in the genus, but their heads are not as greatly enlarged relative to the body. Minor workers are also large for *Pheidole* and have unusually long legs and antennae. Wheeler and Wheeler (1986) described major workers as appearing superficially similar to *Pogonomyrmex* and minor workers as resembling *Aphaenogaster*.

Colony Locations, Size, and Density

Pheidole desertorum nests in the soil; nests were most often found at the base of shrubs and clumps of grasses. However, nest site location varies according to habitat. Not far from the study site, in the foothills and valleys of the Chiricahua Mountains of Arizona, nests are often located under large stones, which are uncommon on the grassland site. Nests under stones are also reported from other Arizona locations (Cole, 1937) and from Nevada (Wheeler and Wheeler, 1986).

Colonies have multiple nests (Droual and Topoff, 1981), up to seven in my study. In general, only one nest is occupied at any one time, although emigrations between nests are common, particularly when the soil is moist (Droual and Topoff, 1981). Maintenance of multiple nests appears important in providing refuge when the colony is attacked by *Neivamyrmex* army ants (primarily *N. nigrescens*) (Mirenda, et al. 1980; Droual and Topoff, 1981; Droual, 1984).

Consistent with earlier work, *N. nigrescens* appeared to be an important predator on *P. desertorum* during this study. Raids on *P. desertorum* (and other *Pheidole*) were observed in 1991 and 1992;

Table 1. Worker body size in *Pheidole desertorum* measured by headwidth above the eyes (H.W.) in millimeters.

Colony	Colony Size		Mean H.W.		Mean H.W.		Limits	N ^c	Limits	N ^c
	In Total No. of Adult Workers	Workers	of Major Workers (S.D.) ^{a, b}	Workers (S.D.) ^{a, b}	of Minor Workers (S.D.) ^{a, b}	Workers (S.D.) ^{a, b}				
A9 ^d	2851		1.43 (0.06)		1.33-1.53		0.59 (0.01)	25	0.56-0.62	25
A4	6830		1.55 (0.04)		1.49-1.61		0.67 (0.04)	25	0.61-0.74	25
X1	8181		1.56 (0.05)		1.37-1.63		0.62 (0.03)	30	0.55-0.68	25
X3	8349		1.56 (0.03)		1.46-1.59		0.63 (0.03)	25	0.57-0.66	24
A6	13966		1.55 (0.04)		1.47-1.65		0.62 (0.03)	25	0.56-0.68	25

^a S.D. = standard deviation.

^b Major and minor worker headwidths were tested for deviation from normal distributions in each of the five colonies and found not significantly different ($P > 0.2$ in all cases, Kolmogorov-Smirnov goodness of fit tests).

^c Number of individuals measured per colony.

^d Reproductively immature colony.

Table 2. Pupal and adult dry weight (mg) and standard deviation (S.D.) in *Pheidole desertorum*. Values are means across colonies, i.e., the sum of the mean of each colony divided by the number of colonies. Adult (post-pupal) individuals are a representative sample from colonies; they include younger (callow) as well as older individuals in the approximate frequency of their occurrence.

	Pupa Dry Weight (S.D.) ^a	N ^b	Adult Dry Weight (S.D.) ^a	N ^b	T _½ ^c	P ^d	Mean % Adult Increase Over Pupal Weight ^e
Gynes (N=9 ^f)	2.81 (0.52)	23.9	7.04 (1.73)	27.2	0	<0.005	150.5
Males (N=9 ^f)	1.12 (0.18)	34.4	1.16 (0.15)	40.0	9	NS	3.6
Major Workers (N=15 ^f)	0.97 (0.36)	38.1	2.11 (0.68)	64.9	1	<0.005	117.5
Minor Workers (N=20 ^f)	0.23 (0.04)	93.4	0.27 (0.05)	97.5	34	<0.005	17.4

^a Standard deviation of the mean values among colonies.

^b Mean number of individuals measured per colony.

^c Test statistic from Wilcoxon's signed-ranks test for paired comparisons (Sokal and Rohlf, 1981).

^d Probability that adult dry weight is greater than pupa dry weight (tests are one-tailed). NS = $P > 0.05$.

^e [(mean adult weight - mean pupal weight) / mean pupal weight] × 100.

^f Number of colonies from which individuals were measured.

N. nigrescens were sometimes found bivouacked within *P. desertorum* nests.

Colony density is high on the grassland site, and colonies can be much larger than proposed by Creighton (1950). Fifty-six and 92 *P. desertorum* colonies were found within the two 105 × 105m grids. Mean number of adult workers per colony censused was 9,881 (Table 3).

Territoriality

Of those colonies located along transects, I assessed 61 for internest movement at least once per week over a one-month period (June 8–July 8, 1989); 37 emigrated between nests at least once. Those colonies moved an average of 2.90m (S.D. = 2.10m) from their original nest location. Average distance from the original nest location to that of their nearest known conspecific neighbor along transects was 14.59m (S.D. = 3.34m). Of those colonies which emigrated more than once, the last known move was toward or back into the original nest in 12 of 21 cases (also see Droual and Topoff, 1981).

Nests of colonies are clumped away from their neighbors, consistent with the hypothesis that colonies actively avoid one another or with the hypothesis that foundress nests rarely survive if they are located near established nests.

Workers from neighboring colonies fight when they encounter one-another at baits. Fights often result in death, and fighting persists until one colony dominates the bait. Fighting at baits was also observed between *P. desertorum* and other ant species, primarily *Pheidole hyatti*, *Pheidole xerophila*, and *Solenopsis* sp. *Pheidole desertorum* nearly always displaced other *Pheidole*; however, *P. desertorum* were often displaced when *Solenopsis* sp. was present.

Foraging Behavior and Diet

Only minor workers leave the nest at the start of foraging activity (shortly after sunset). However, major workers leave the nest and come to baits; their foraging role may be associated with exploiting clumped or otherwise abundant food sources. Workers forage to baits in diffuse columns, with majors and minors returning to the nest with food. However, not all majors are moving in the column or collecting food; nonforaging majors may be defend-

Table 3. Census data from *Pheidole desertorum* colonies. Numbers in parentheses are the number of pupae, other numbers are the number of adults.

Colony	Number of Minor Workers	Number of Major Workers	Number of Gynes	Number of Males	Collection Date
A10	2,150 (630)	310 (122)	0	0	7/5/88
A9	2,593 (1,012)	258 (237)	3 (0)	0	7/17/88
A4	5,217 (713)	1,613 (0)	0	45 (490)	6/15/88
X1	6,584 (2,561)	1,597 (144)	0 (1)	763 (313)	7/12/88
X3	6,655 (2,028)	1,694 (133)	127 (71)	0	7/7/88
CY29	8,599 ^(a)	1,812 ^(a)	66 (144)	0	6/28/91
A8	9,617 (3,045)	1,450 (775)	9 (0)	696 (15)	7/22/88
A6	11,696 (2,683)	2,270 (414)	218 (28)	0	7/9/88
A5	20,174 ^(a)	4,640 ^(a)	375 (60)	0	7/18/88

^aPupae not censused.

ing the column and the food source. These different foraging roles of *P. desertorum* majors and minors are similar to those found for *Pheidole pallidula* and *Pheidole teneriffana* (Szlep-Fessel, 1970).

Pheidole desertorum are predators and scavengers at the grassland site. Workers return to nests with a variety of arthropods (and parts). Those recognized were grasshoppers, beetles, termites, and bugs primarily. With the arrival of the first rains of summer, alate termites are captured in great numbers and stored in nests with the wings removed. Alates (primarily males) of other ants are scavenged during the rainy season. During spring and late fall (dry, apparently food-limited periods), it is common to find exoskeleton parts of workers of other ants (often recognized as *Pogonomyrmex*) within nests.

Pheidole desertorum from the same general location as this study were identified as seed-harvesters by Davidson (1977a,b). However, I never observed workers carrying seeds, and seeds were found rarely in nests and only in small numbers. In June 1989, I presented four colonies with cracked wheat, rolled oats, and whole seeds of Bermuda grass and Kentucky blue grass; such seeds are harvested readily by desert seed-eating ants and are small enough to be transported by *P. desertorum* workers (Taylor, 1977; Rissing, 1981; Rissing, personal communication). *Pheidole desertorum* frequently encountered the seeds but never collected them.

Food Storage

Long-term food storage in *P. desertorum* may be accomplished by replete workers. Those workers are majors with distended (approximately 1.5 to twice normal size) gasters, whose behavior is sluggish. The gaster of these workers holds a golden-colored, oily substance enclosed in a structure separate from the crop and the rest of the alimentary tract (Cover and Helms, unpublished). In *Pheidole pallidula*, major workers with distended gasters store lipids whose energy is somehow transferred to nestmates (Lachaud, Passera, Grimal, Detrain, and Beugnon, 1992).

In *P. desertorum*, major workers with distended gasters are young and not pigmented fully. Since major workers more than double their dry body weight following pupation (Table 2), it is possible that young major workers serve in energy storage, with that role diminishing as energy is transferred to nestmates later in the majors' lifespan. Young minor workers can also have distended gasters, and the dry body weight of minor workers also increases following pupation, but to a lesser extent than majors (Table 2).

The Frequency of Major and Minor Workers

The percent of adult workers that were majors varied greatly among colonies (9.0 to 23.6%; Table 3). Two colonies were small and presumably young; one produced no reproductives and the other produced only three gynes (Colonies A9, A10; Table 3). The percent of adult workers that were majors was less in these colonies (9.0 and 12.6%) than in the remaining mature colonies. However, there was also substantial variation among mature colonies; the percent of adult workers that were majors ranged from 13.1–23.6% (Table 3). This variation is associated with difference among colonies in age of their reproductive broods. Increasing maturity of reproductive broods is correlated with decreasing adult major/minor ratio (Fig. 1A) and increasing major brood production (Fig. 1B).

It appears that production of sexual broods may limit production of major workers, and the adult major/minor ratio decreases with increasing duration of reproductive effort. Major worker mortality likely contributes to this decline. However, as a reproductive brood becomes increasingly mature, the production of majors increases, and the major/minor ratio is presumably restored. Similar effects

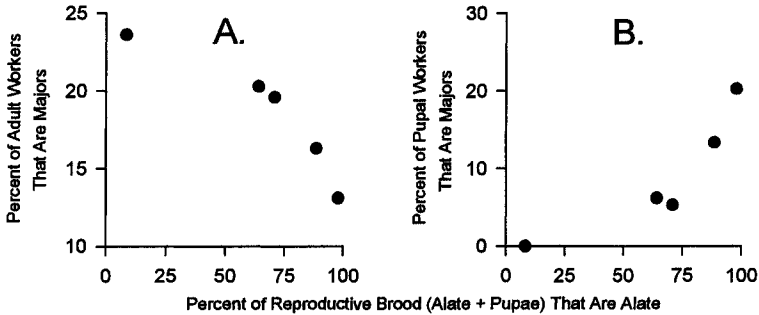


Fig. 1: Percent of adult and pupal workers that are major workers as a function of the maturity of *Pheidole desertorum* reproductive broods. A. Kendall's coefficient of rank correlation = -1.0 , $P = 0.05$. B. Kendall's coefficient of rank correlation = 0.8 , $P = 0.10$. Data are from colonies A4, X1, X3, A8, and A6 in Table 3.

of reproduction on the major/minor ratio have been found for *Pheidole dentata* (Johnston and Wilson, 1985).

Reproduction

Most colonies in the population produced sexuals each year. In 1991, 255 of 287 colonies had alates. The time of year at which gyne and male eggs are produced is not known; gyne and male pupae can be found in nests by mid-May. Most sexual forms are pigmented fully and mature by early to mid-July. Colonies can also produce a second reproductive brood. Reproduction was assessed in late July and early August 1991 in 25 colonies with a mature reproductive brood in early July; 10 of these colonies had an additional reproductive brood consisting primarily of individuals not pigmented fully (callows) and/or pupae. Worker pupae were observed throughout the period when reproductive brood occurred.

Pheidole desertorum gynes are much larger than males (Table 2). Gynes and males also differ greatly in temporal changes in body mass. Body mass of males remains essentially unchanged following pupation, while gynes experience a dramatic increase (Table 2). Mean dry weight of 60 gynes (30 from each of two colonies) collected as they emerged on the surface to fly was 8.75mg; given a mean gyne pupa dry weight of 2.81mg (Table 2), gynes more than triple their pupal dry weight before flight. This

substantial temporal increase in gyne body weight may be the rule in ant species with independent colony foundation (see, e.g., Keller and Passera, 1989; Tschinkel, 1993).

The Sex Ratio

The sex ratio of reproductive broods is extremely biased; 145 of 146 colonies whose sex ratio was assessed where at least 50 reproductives were observed produced either only gynes, only males, or a sex ratio extremely male-biased (on average, > 97% males) (Helms and Rissing, 1990; Helms, 1994; also see Droual, 1982). Such dimorphism among colonies in the sex ratio also occurs in *Pheidole xerophila tucsonica* (Helms and Rissing, 1990), *Pheidole hyatti* (Helms, unpublished data), and perhaps *Pheidole dentata* (Johnston and Wilson, 1985).

The frequency of gyne-specialist and male-specialist colonies found within the *P. desertorum* population was very near equal (171 gyne-specialist and 177 male-specialist colonies; Helms, 1994). In addition, 144 of 151 colonies specialized in the same sex over each consecutive year during a two to five year period (Helms, 1994).

Mating Flights

Mating season begins following the first substantial rainfall in July. Alates begin emerging on the surface one and one-half to two hours before sunrise. They begin to fly from the nest perimeter approximately 45 minutes prior to sunrise until just before sunrise. Alates often climb blades of grass, stones, or other objects before taking flight. Flights generally occur when there is substantial soil moisture, it is warm, and there is no breeze. Conditions in which mating flights were observed are summarized in Table 4.

After leaving the nest, males form aerial groups (swarms) which hover approximately 2-5m above the ground; swarms occur simultaneously at various locations throughout the site. No distinguishable topographic feature was associated with swarm location. Observed swarms were not large; five to approximately 50 males were observed. Swarms did not persist beyond one-half hour past sunrise. Gynes fly into swarms and hover with males; they often left those swarms without mating. No more than two gynes occurred in a swarm at any one time. In three cases observed, there

Table 4. Environmental conditions at one hour prior to sunrise when *Pheidole desertorum* mating flights were monitored in July 1991.

Date	Precipitation	Depth of Soil Moisture (cm)	Temperature (°C)	Estimated Wind Speed ^a	Mating
	In 24 hours Prior (mm)				Flights Observed
7/10	2.5	4	16.5	10–15	No
7/15	4.5	4	19.0	0–5	Yes
7/16	0.0	2	19.0	5–15	No
7/20	3.0	2	19.0	15–20	No
7/21	15.5	15	20.0	0–5	Yes
7/22	0.0	1	–	0–5	Yes
7/23	0.0	<1	16.5	0–5	No
7/25	9.5	8	17.0	0	Yes
7/31	10.0	5	19.0	0–5	Yes

^a In miles per hour.

was physical contact between a gyne and male, and they dropped immediately to the ground where mating occurred. One mating lasted five minutes, 23 seconds. In two of three matings observed, the gyne appeared to terminate mating by biting the male on the gaster; all three gynes flew away after mating. One gyne momentarily reentered the same swarm prior to departing.

The flight of gynes following mating could be common in desert *Pheidole*. While it does not occur in *Pheidole sitarches* (Wilson, 1957), it occurs in *P. desertorum*, *P. hyatti* (Helms, unpublished data), and *P. xerophila tucsonica* (Johnson, personal communication). *Pheidole* gynes could mate with multiple males. Allozyme data show that multiple mating might occur in *P. desertorum*, but if so, it appears rare (Helms, 1994). Therefore, flight after mating may occur primarily for dispersal to colony founding sites.

Colony Foundation

Pheidole desertorum foundress nests were observed after initiation of the mating season and were discovered only under large piles of old cow dung (approximately 25cm or more in diameter). However, incipient colonies were rarely found, and given the locations of adult nests, most queens on the site may attempt colony

foundation at the base of shrubs and clumps of grasses. Foundress nests under cow dung may indicate that colony foundation will occur under stones in areas where they are present.

Foundress queens of *P. desertorum* sometimes join others within a single founding nest; of 12 foundress nests discovered in 1991, nine had one queen, two had two queens, and one had three queens. Minim workers were present in two of the pleometrotic groups. Pleometrotic groups were collected and kept in the laboratory; only single queens remained alive after two months following collection. However, allozyme data suggest multiple reproductive queens might sometimes occur within a single adult nest in the field (Helms, 1994). Pleometrotic groups in nature may sometimes persist into the colony reproductive stage.

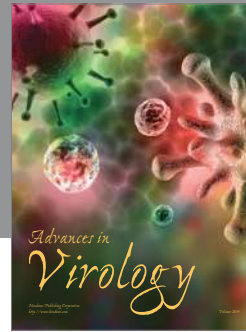
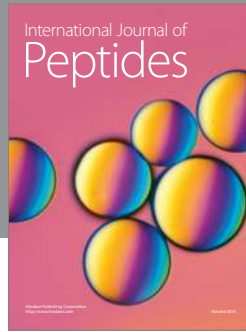
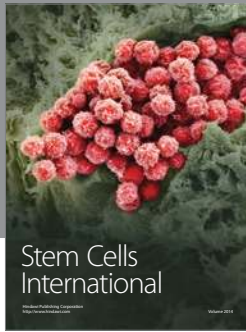
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