Utah State University

DigitalCommons@USU

Demography and Role of Herbivorous Ants in a Desert Ecosystem as Functions of Vegetation, Soil and Climate Variables

W. G. Whiteford

G. Ettershank

Recommended Citation

Utah State University
MERRILL-CAZIER LIBRARY

DEMOGRAPHY AND ROLE OF HERBIVOROUS ANTS IN A DESERT ECOSYSTEM AS FUNCTIONS OF VEGETATION, SOIL AND CLIMATE VARIABLES

Walter G. Whitford, Project Leader
and Carol Ann Kay
New Mexico State University

ABSTRACT

Studies of the critical thermal maxima and minima showed no differences in *Pogonomyrmex rugosus*, *P. californicus* and *Novomessor cockerelli*. These data indicate that seasonal and diet differences in foraging activity times in these species may be due to differences in water balance or interspecific competition. Forager numbers per colony in *P. desertorum* increased as fruit production increased during the growing season, substantiating the pattern observed in 1972 in *P. rugosus*, *P. californicus* and *N. cockerelli*. *P. rugosus* foraged at night in July but did not engage in nocturnal foraging in June. Nocturnal foraging in *P. rugosus* was suggested to occur in response to a high density food source. No nocturnal foraging was observed in *P. desertorum* and *P. californicus*. *Pheidole* sp. exhibited marked seasonal variation of foraging activity.

In watering experiments designed to modify climate, *P. desertorum* exhibited foraging response to reduced temperatures and lower saturation deficit with experimentals exhibiting greater activity. In *P. rugosus*, although experimental and control nests reached comparable temperature and saturation deficit, unwatered colonies remained essentially inactive while watered colonies exhibited high levels of activity.

Analysis of foraging data by a bi-quadratic multiple regression demonstrated that forage availability and colony satiation are the most important variables affecting foraging activity. Forage preference studies failed to conclusively elucidate factors involved in forage selection. Forage selection appeared to be a function of forage availability in *P. desertorum* and/or availability of those species of annuals which are dependable suppliers of seeds throughout the growing season. Seed production of *Eriogonum trichopes* and *E. abertianum* was measured for plants growing on the playa fringe. No correlation was found between canopy size and seed number. Numbers of mesquite seeds in the immediate vicinity of ten *Novomessor* nests ranged from 106 to 1,342 on a day in October, with a mean of 711.

V_{O_2} in *P. desertorum* and *Formica perpilosa* was significantly affected by VPD. V_{O_2} in *N. cockerelli* was affected only at the highest VPD and 35 C. *Trachymyrmex smithi neomexicanus* died at all T_a at VPD above 65 % relative humidity. A key to the worker ants of the Chihuahuan Desert IBP Validation Sites is presented in Appendix II.

INTRODUCTION

The ant community is a conspicuous part of desert ecosystems and the seed harvesting ants are an important segment of the ant community. Seed harvesting ants are also important components in other deserts of the world (Briese, 1973; Shaeta and Kaschef, 1971; Délye, 1967; and Szlep-Fessel, 1970). Therefore, studies on factors affecting the foraging activity and population dynamics of seed harvesting ants appear essential for understanding functional interrelationships of animals and plants in desert ecosystems and applying this understanding to the deserts of the world.

Previous studies were concentrated on factors affecting foraging in *Pogonomyrmex* sp. and *Novomessor cockerelli*, i.e., climate and relative abundance and pattern of seed distribution and their forage preference (Whitford, 1973). These studies suggested the need to examine other species, especially species of *Pheidole* and to further examine factors affecting forage preference and foraging behavior. In assessing these factors experimental approaches were used whenever possible as suggested by R. Chew (personal communication).

In addition to examining seed harvesting ants, we undertook studies of foraging ecology of two species of ants which appeared to be important on the Jornada Validation Sites. These studies utilized techniques developed for harvester ants and the results have been submitted for publication (Schumacher and Whitford, 1974).

OBJECTIVES

1. To test conclusions regarding the influence of climatic factors and forage availability and forage preference based on the 1972 studies using field experimentation.
2. To continue mark-recapture estimates of forager numbers with emphasis on *Pogonomyrmex desertorum*.
3. To obtain additional data on factors affecting nocturnal foraging in *Pogonomyrmex* sp. and *Novomessor*.
4. To continue studies of oxygen consumption as a function of temperature and saturation deficit and to initiate studies of thermal tolerance and water loss.
5. To examine the influence of climate and seed availability as factors affecting foraging in species of *Pheidole*. These studies were initiated but deemphasized because of problems of species identification in the field. C. A. Kay is currently working on a key to separate the species.

In addition to objectives stated as a result of 1972 studies (Whitford, 1973, pp. 61-62) the following was added.

6. To expand the analysis of factors affecting foraging behavior to include studies of other important species in the ant community.

METHODS

Our studies were centered around three sympatric genera of harvester ants which are important at the Jornada

Validation Site and which are widely distributed in desert areas in the United States and Mexico. One genus, *Pheidole*, has world-wide distribution in arid and semi-arid areas. Field studies were conducted on areas adjacent to the Jornada Validation Sites, 40 km NNE of Las Cruces, Dona Ana County, New Mexico.

CRITICAL THERMAL MAXIMA (CTMAX) AND MINIMA (CTMIN)

CTMax and CTMin were measured in ants acclimated to laboratory conditions. Ants were removed from nest boxes and placed in a beaker containing approximately 1 cm sand on the bottom. The beaker was placed in either a heating mantle or cooling coil where the rate of temperature change was controlled at 0.5 C per min. A thermistor was placed at the soil surface to measure the temperature, which was assumed to be the ants' body temperature. Silicon oil prevented ants from climbing the sides of the container. The temperature at which coordinated movement ceased was recorded as the CTMax or CTMin.

FORAGING ACTIVITY

Foraging activity was monitored using techniques described in Whitford (1973; DSCODE A3UEE03). In order to further evaluate the effects of saturation deficit level and soil surface temperature on foraging activity, areas were watered with between 500-1,000 gallons of water applied over a 20 m radius circle in a fine spray. Application of water was made in the evening on one day and foraging behavior monitored the subsequent day. Controls were colonies in the unwatered area.

FORAGE PREFERENCE AND SEED PRODUCTION

In order to examine the persistence of forage preference when the preferred forage species was not present, we selectively removed *Eriogonum abertianum* and E. *trichopes* from a 20 m radius circle with a nest of *Pogonomyrmex rugosus* at the center of the circle. Forage materials were collected from returning foragers at intervals over a two-month period. Forage materials were also collected from foragers of a control colony approximately 100 m from the experimental colony. Forage preference data were also collected on *P. desertorum* colonies in an area where *P. rugosus* was absent.

Densities of seed-producing plants were estimated on all study areas at monthly intervals and data on seed production calculated from regression equations (Whitford, 1973) and phenology. Because *Eriogonum abertianum* and E. *trichopes* produce seeds continually, rates of seed production by these forbs were estimated by litter traps placed under 10 individuals of each species. Seed production per unit time was estimated from the litter traps. Number of mesquite seeds around 10 nests of *Novomessor* were counted on one day in October.

OXYGEN CONSUMPTION

Variations in oxygen consumption as a function of temperature and saturation deficit were measured using the techniques in Ettershank and Whitford (1973). Oxygen consumption measurements were made on species on which foraging behavior had been studied. These data are presented in Appendix I.

RESULTS

CRITICAL THERMAL MAXIMA (CTMAX) AND MINIMA (CTMIN)

There was no significant difference in CTMax and CTMin between *P. rugosus*, *P. californicus* and *N. cockerelli*. These species are characterized by significant differences in foraging activity patterns as a function of soil surface temperature and saturation deficit (Whitford, 1973). Since these species do not differ physiologically in their ability to survive high temperatures or to be mobile at low temperatures, seasonal and diurnal differences in peak foraging times may be due to differences in water balance, or to niche compression due to interspecific competition. The latter could explain peaks of activity in early spring and late fall in *P. californicus* when ambient temperatures are low but in which active summer colonies forage at high temperatures and saturation deficits (Schumacher and Whitford, in prep.). These data suggest that further examination of physiological and behavioral responses in these ants could provide data valuable in assessing the role of interspecific competition in desert harvester ants.

MARK-RECAPTURE STUDIES

Mark-recapture estimates of forager numbers were obtained using the paint-spot techniques described in the 1972 report (Whitford, 1973; A3UEE15). We concentrated on estimates of forager colony size in *P. desertorum* because we had few data for that species in 1972. The pattern of increase in forager numbers in mid-summer was consistent with that seen in 1972 (Table 1). This increase is probably due to two factors: (1) increased availability of seed resulting in greater recruitment of foragers and (2) addition of workers due to reproductive activity in late spring and early summer. These data suggest that mark-recapture estimates of forager population size may be used to evaluate the impact of harvester-ant foraging on the ecosystem.

Excavation was again attempted to obtain estimates of total colony numbers. We encountered considerable difficulty in recovering ants from the excavation and have but one reliable count. The *P. rugosus* nest for which the count is reliable contained 3,639 workers and 321 larvae and pupae. This colony was excavated on September 15, 1973.

NOCTURNAL ACTIVITY

Additional data were required to assess factors affecting

nocturnal foraging in species of *Pogonomyrmex*. Consequently, six colonies of *P. desertorum* and three colonies of *P. rugosus* were observed for 3 min each, every 2 hr to assess foraging activity. Nocturnal foraging varied not only between species but also with respect to season. In June, there was no nocturnal foraging at soil surface temperatures and saturation deficits characterized by intense foraging activity in early July (Table 2). The absence of nocturnal activity in June may have resulted from a paucity of seeds or reflect satiation of the colonies. The only species of *Pogonomyrmex* which foraged at night was *P. rugosus*. One colony of *P. desertorum* was engaged in nest cleaning at 2300 hr on June 20. While no quantitative data were obtained, no foraging activity was noted in *P. californicus* at night.

FORAGING ACTIVITY -- *Pheidole* SPECIES

Studies of factors affecting foraging activity of *Pheidole* were complicated by our inability to separate species in the field and by the changes in foraging activity with season. In mid-summer there was a marked decrease in foraging activity. Foraging activity continued at higher temperatures and saturation deficits in April and May than in early August (Table 3). The seasonality of foraging activity in species of *Pheidole* is of considerable interest and will be investigated further. In late September and early October, the activity of *Pheidole* reached a peak coincident with the shift in activity from *P. desertorum* to *P. californicus* (Schu-

macher and Whitford, in preparation). Studies of *Pheidole* will be re-initiated in early spring of 1974 using the field keys for identification prepared by C. A. Kay (see Appendix II).

FACTORS AFFECTING FORAGING ACTIVITY

The results of watering experiments in foraging activity in *Pogonomyrmex desertorum* are summarized in Figures 1 and 2, and on foraging activity in *Pogonomyrmex rugosus* in Table 4. The foraging response of *P. desertorum* can be represented as a plane resembling a normal curve with an optimum soil surface temperature range between 25 C and 45 C (Figure 1). It is more difficult to assess the response to saturation deficit since saturation deficit varies directly with temperature. These data suggest that saturation deficits and soil surface temperature act primarily as thresholds for activity. Since the rate of movement and thus foraging rate in ants is temperature dependent at least up to some maximum, when watering resulted in lower soil surface temperature, i.e., 25 C as to 35 C, foraging activity was greater in controls than experimentals. In one set of experiments three colonies of *P. desertorum* received less than half the water applied to two other *P. desertorum* nests. Although there was no difference in soil surface temperature or saturation deficit, 49 C and 36 g·m^3 at 1500 hr, the colonies which received heavy watering exhibited activity $\bar{x} = 3.5 \cdot min^{-1}$ while activity was absent in the other colonies. This indicates that the temperature and/or humidity in surface chambers may be significant factors affecting foraging activity.

Pogonomyrmex rugusus exhibited a marked response to increased soil moisture or to conditions in the surface galleries (Table 4). In almost every experiment, watering in the evening resulted in frenzied activity the next day. Although the control and experimental nests reached comparable temperatures and saturation deficits (Table 5), the unwatered colonies remained essentially inactive.

Table 1. Forager colony size in three species of *Pogonomyrmex* as estimated by mark-recapture studies and the Lincoln index (forager colony estimates ± the standard error are presented; an * indicates colonies adjacent to the bajada study site)

Date	P. desertorum	P. californicus	P. rugosus
May 24, 1973 *	158 + 55		
	210 + 84		
	152 + 34		
May 29, 1973 *	168 + 42		
	258 + 140		
June 18, 1973	133 + 39		431 + 143
July 8, 1973 *	913 + 330		
	353 + 125		
	817 + 455		
	439 + 138		
July 10, 1973	506 + 212	107 + 22	645 + 176
	246 + 68	130 + 52	
	409 + 135		
	202 + 29		

Table 2. Nocturnal foraging activity in two species of harvester ants, *Pogonomyrmex rugosus* (POG-RUG) and *Pogonomyrmex desertorum* (POGDES). Foraging activity was recorded as a function of time, soil surface temperature (T_S) and saturation deficit (SD)

Hour	T_s°C	SDgms·m^{-3}	Date	Mean number to nest·min^{-1} POGDES	POGRUG
1900	34	25.8	June 20, 1973	0	0
2100	22	16.3		0	0
2300	18	13.5		0	0
0400	14	10.1	June 21, 1973	0	0
0600	12	7.5		0	0
2000	30	26.0	July 6, 1973	0	83
2400	29	20.0		0	67
0200	26	15.0		0	31
0400	26	15.0		0	22
0600	24	9.8		0	0
0800	23	16.9		6	6

Examination of data on the effects of soil surface temperature and saturation deficit on foraging activities in harvester ants provided no assessment of the relative importance of these factors as regulators of foraging activity. Therefore, these data were analyzed by a biquadratic multiple-regression to evaluate the contribution of these factors as regulators of foraging activity. This equation is of the form:

$$y = B_0 + b_1 x_1^2 + B_2 x_2^2 + B_3 x_1 + B_4 x_2 + B_5 x_1 x_2$$

where y = foraging activity, x_1 soil surface temperature and x_2 saturation deficit. The correlation coefficients obtained by this analysis are provided in Table 5.

In all species studied, saturation deficit and soil surface temperature accounted for between 10 and 40% of the variation in foraging activity. The data for *Novemessor cockerelli* for July included only measurements taken during the day, and in mid-summer this species is primarily nocturnal. The low r^2 values for all months taken together probably result from differences in forager recruitment with season, and seasonal shifts in forage availability.

This analysis plus experimental data on foraging patterns, watered colonies and qualitative observations suggest that these physical factors act primarily as a threshold or 'on-off' switches and only secondarily as rate regulators. We have recently shown a marked seasonality in the activity of *P. desertorum* and *P. californicus* (Schumacher and Whitford, unpublished data). However, the two most important regulators of foraging intensity appear to be: (1) the degree of satiation of the colony and (2) the availability of suitable forage. In studies

of foraging territories we found that several colonies were "uncooperative" after our initial tests. These colonies were invariably the most active during the initial trials, then ceased foraging after one or two days. When the surface granaries of these colonies were opened they were filled with the dyed seeds used in experiments.

When foraging intensity was compared over three summers, 1971-1973, the importance of forage availability and colony satiation are apparent. Drought conditions in 1971 resulted in the absence of annual forbs and grasses and reduced fruiting in shrubs. In *P. rugosus* and *N. cockerelli*,

Table 4. The effects of watering on environmental parameters affecting foraging activity in *Pogonomyrmex rugosus* colonies (T_{soil} = soils surface temperature; Sat. Def. = saturation deficit; Exp. = watered colonies; Cont. = unwatered colonies). Data are summarized from four dates in June and July, 1972

Hour	T_{soil}°C Exp.	Cont.	Sat.Def.gm·m³ Exp.	Cont.	Activity No. to nest·min⁻¹ Exp.	Cont.
0730	20	25	6	8	70	0
0830	23	30	14	18	107	0
0900	15	35	13	15	148	0
0930	25	32	12	14	101	0
1030	35	52	25	33	1	0.3
1130	26	37	13	17	111	0
1130	30	38	25	31	245	0
1230	40	55	29	48	260	0
1330	54	62	30	31	31	0
1330	46	44	40	43	271	0
1430	49	61	36	36.4	40	0
1500	50	63	38	39	10	0
1630	30	32	14	14	218	0.3

Table 3. The effects of temperature and saturation deficit on foraging activity in *Pheidole*. The numbers in the table refer to the number of individuals on a 3 cm segment of a foraging trail at one point in time

Soil Surface Temperature	0-5(N)	6-10(N)	11-15(N)	16-20(N)	21-25(N)	26-30(N)	31-35(N)	36-40(N)
10-15								
16-20								
21-25		1.6 (4)						
26-30		1.9 (4)						
31-35			1.5 (8)	0 (8)		* 5 (1)	* 3 (1)	
36-40					1.7 (4)	0 (4)	* 2.5 (2)	
41-45						0 (4)		
46-50							0 (4)	
51-55							0 (4)	
56-60								

* Indicates data for May.

maximum foraging rates at moderate soil surface and saturation deficits were 4·min^{-1} (Whitford and Ettershank, 1972). In 1972 annual forbs and grasses fruited from late March through September, and the maximum foraging rates at moderate soil surface temperatures and saturation deficits in *P. rugosus* and *N. cockerelli* were 60·min^{-1} and 140·min^{-1}, respectively (Whitford, 1973). In 1973, a year similar to l972 with respect to fruit production by annuals, most *P. rugosus* were inactive at moderate conditions and *N. cockerelli* exhibited reduced activity. There appeared to be no significant difference in foraging activity in *P. desertorum* and *P. californicus* in 1972 and 1973. However, in 1971 we recorded very few active colonies of *P. desertorum*.

FORAGE PREFERENCE AND SEED PRODUCTION

The experiments designed to evaluate shifts in forage preference when the preferred species were reduced in availability were inconclusive (Table 6). The failure of this approach was primarily due to the absence of foraging activity in *P. rugosus* colonies during much of June and July and the absence of foraging in *P. desertorum*, possibly due to disturbance in the experimental area. In addition,

Figure 2. The effects of watering on soil surface temperature and foraging intensity in *Pogonomyrmex desertorum*. Method of presentation is the same as in Figure 1.

Table 5. Correlations obtained for the effect of saturation deficit and soil surface temperature on foraging activity derived from a biquadratic regression model

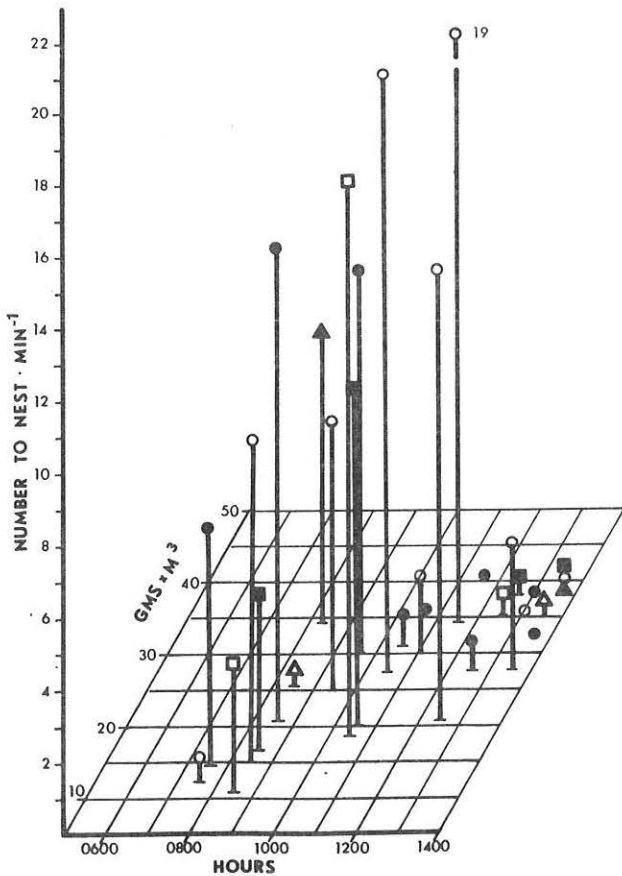| Time Period	Number of Observations	R^2
Novomessor cockerelli		
June to November	249	.075
June	31	.38
July	122	.09
August	47	.32
Fall	49	.35
Pogonomyrmex rugosus		
June to November	222	.07
June	38	.49
July	81	.21
August	34	.14
Fall	69	.11
Pogonomyrmex californicus		
June to November	93	.11
July	25	.18
August	30	.20
Fall	38	.26
Pogonomyrmex desertorum		
June to November	101	.06
July	34	.28
August	28	.33
Fall	39	.22

Figure 1. The effects of watering on saturation deficit and foraging intensity in *Pogonomyrmex desertorum*. Solid symbols indicate watered plots; open symbols controls. Paired symbols indicate data from a single experiment.
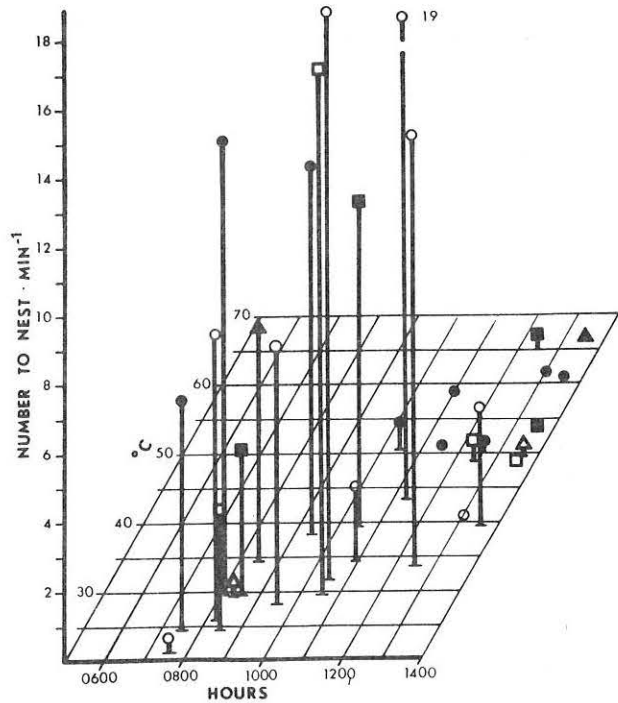
removal of *Eriogonum* spp. from the experimental area did not result in removal of surface seed remaining from the 1972 growing season. The assumption that these fruits would not be used as forage proved erroneous. Future studies on forage preference will have to be conducted in completely cleared arenas using combinations of natural seeds and fruits.

Additional studies on forage preference were conducted on an area adjacent to the bajada site where *P. desertorum* is essentially the only harvester ant species present. We did, however, locate two *P. californicus* near the bajada study area. The May samples showed that *P. desertorum* was removing fruits in relation to their approximate relative abundance. The spring annuals *Descurainia pinnata* and *Cryptantha crassisepala* were stem-cured at that time and large quantities of fruit were on the soil surface. In addition there were noticeable quantities of seed of *Erioneuron pulchellum*, *Eriogonum abertianum*, *Baileya multiradiata* and others remaining in areas of accumulation on the soil surface from the previous growing season. By July, most of the seeds of spring annuals were dispersed, except for the fruits of *C. crassisepala* which were extremely abundant on the site (Tables 7 and 8) and all of the *Eriogonum* spp. were in flower and fruit (Table 8). The forage preference again appeared to be related to relative abundance of fruits.

The foraging behavior of *P. desertorum* on this area was different than on the playa areas. *P. desertorum* was rarely observed to forage in the canopy of forbs on the bajada. It's foraging behavior on the bajada was similar to that of *P. rugosus* on the playa area. The lack of late summer data for this area precludes testing the generalization that harvester ants continue to forage on fruits of species which are dependable suppliers throughout the summer growing season preferentially over those which pulse seeds during the season.

Eriogonum *Seed Production*

Ten *Eriogonum trichopes* plants on the playa fringe were selected at random in June, 1973. Seeds from these plants were collected over a period of time in order to correlate numbers of seeds per plant with canopy size.

Table 7. Forage selection by *Pogonomyrmex desertorum* during the growing season, 1973, adjacent to the bajada

Forage item	Percent of total	
	May	July
Cryptantha crassisepala	11.3	14.8
Descurania pinnata	13.2	
Eriogonum abertianum	9.4	16.3
Eriogonum rotundifolium		1.4
Erioneuron pulchellum	35.8	7.7
Erigonum trichopes		54.5
Other *	18.9	4.6

* Other is Baileya multiradiata, Cassia bauhinoides, Hilaria mutica Astralagus allochrous.

Table 6. Percent composition of fruits of *Eriogonum abertianum* and *E. trichopes* of the total fruits foraged by *Pogonomyrmex* sp. in an experimental area and a control area

DATE	POGRUG				POGDES				POGCAL			
	ERIABE		ERITRI		ERIABE		ERITRI		ERIABE		ERITRI	
	CON	EXP	CON	EXP	CON	EXP	CON	EXP	CON	EXP	CON	EXP
June 6	53.5		0		41.1	66.7	2.9	12.5				
June 18	61.9		0		46.8		6.3					
July 10					28.6		21.2		4.7		85.7	
July 11					32.4		37.5		0		55.5	
July 14	52.6		7.0		18.6		32.7		11.8		43.8	

POGRUG = *Pogonomyrmex rugosus*
POGCAL = *P. californicus*
POGDES = *P. desertorum*
ERIABE = *Eriogonum abertianum*
ERITRI = *Eriogonum trichopes*
EXP = Experimentally manipulated area
CON = Control area

Table 8. Densities and phenology of annuals on the study areas during the peak foraging period of harvester ants, 1973. Study sites are indicated at the top of each section; A+ in phenology indicates flower and fruiting or mature fruits present

Species	May 22, 1973 Total Density Plants/ha	Phen.	June 28, 1973 Total Density Plants/ha	Phen.	July 23, 1973 Total Density Plants/ha	Phen.
PLAYA SITE						
Allionia incarnata					27.55	+
Ammocodon chenopodiodes			31.91	0	27.55	0
Astragalus tephrodes	19.26	0				
Astragalus wooteni	67.42	+			27.55	0
Bahia absinthifolia	9.63	0			55.10	0
Baileya multiradiata	221.54	+	638.16	+	633.68	+
Cassia bauhinoides	86.69	+	95.72	+	82.65	+
Chenopodium incanum	86.69	0				
Croton pottsii	67.42	0	31.91	0		
Crypthantha angustifolia	57.79	+				
Crypthantha crassisepala	19.26	+			82.65	0
Desurania pinnata	57.79	0				
Eriogonum abertianum	606.81	+	797.70	+	192.86	+
Eriogonum rotundifolium	192.64	+	606.25	+	2,947.98	+
Eriogeron divergens					27.55	0
Eriogonum trichopes			319.08	+	137.76	+
Erioneuron pulchellum	57.79	0			303.06	+
Iva ambrosifolia					27.55	0
Lepidium sp.	19.26	0				
Mentzelia albicaulis	9.63	+	63.82	+		
Nama hispidum	134.85	+	159.54	+	27.55	+
Oenothera sp.	28.90	0				
Perezia nana	28.90	0	127.63	+		
Salsola kali	134.85	+				
Sphaeralcea subhastata	19.26	+	31.91	0		
Verbena wrightii	9.63	+				
Verbena ambrosifolia	77.06	0				
Xanthocephalum sarothrae			95.72	0		
PLAYA CLEARED SITE						
Amaranthus blitoides					129.82	0
Ammocodon chenopodioides					64.91	+
Astragalus sp.			152.42	0		
Astragalus allochrous			101.62	0	64.91	0
Bahia absinthifolia			50.81	0	129.82	+
Baileya multiradiata			457.27	+	389.46	
Cassia bauhinoides					129.82	+
Croton pottsii			50.81	0		
Crypthantha crassisepala			50.81	0		
Eriogonum abertianum			558.89	+	389.46	+
Eriogonum rotundifolium			1,422.62	+	389.46	+
Eriogonum trichopes			558.89	+	194.73	+
Erioneruon pulchellum			406.46	0	194.73	0
Gilia opthalmoides			50.81	0		
Kallstroemia parviflora			.		64.91	+
Mentzelia albicaulis			50.81	0	64.91	0
Nama hispidum			101.62	+	259.64	+
Salsola kali			50.81	0	129.82	0
Tidestromia lanuginosa			50.81	+		
Zinnia grandiflora			101.62	0		

Table 8 (continued)

Species	May 22, 1973 Total Density Plants/ha	Phen.	June 28, 1973 Total Density Plants/ha	Phen	July 23, 1973 Total Density Plants/ha	Phen.
BAJADA SITE						
Ammocodon chenopodioides			40.53	0		
Astragalus allochrous			121.60	0		
Astragalus tephrodes					41.22	0
Astragalus wooteni	30.02	0			41.22	0
Baileya multiradiata	82.45	+	40.53	+	120.07	+
Crypthantha angustifolia	1,855.06	0				
Crypthantha crassisepala	123.67	+	891.70	0	720.44	0
Crypthantha sp.	494.68	0				
Dithyrea wislizenii	41.22	+				
Eriogonum abertianum	371.01	+	364.79	+	330.20	+
Eriogonum rotundifolium	82.45	0				
Eriogonum trichopes	2,968.09	+	2,877.75	+	2,281.39	+
Eriogeron divergens					60.04	0
Erioneuron pulchellum	82.45	0	243.10	0		
Gilia opthalmoides		+	121.60	+		
Solanum elaegnifolium					180.11	0
Xanthocephalum sarothrae			40.53	0		

To catch the seeds as they fell, squares of metal screen with raised sides and covered with cheesecloth were placed under each plant. On June 18 and on two subsequent dates at intervals of 21 days, each plant's maximum height and width were measured; the cheesecloths were removed, taken to the laboratory, and all *Eriogonum trichopes* seeds were taken out and counted.

For each date, the average height and width of the plants and the average number of seeds per plant were determined, after which canopy sizes and the regression equation relating them to seed numbers were calculated. The average number of seeds per day was also calculated for each plant by dividing the number of seeds on a certain date by the number of days since the last collecting date.

The same methods were used to determine seed production in *E. abertianum*, the only difference being that the first collecting date was July 13 and there was only one other collecting date, July 30.

The data obtained are summarized in Tables 9 and 10. There was no correlation in either plant species between canopy size and seed number, as seen in the r^2 values for the *E. trichopes* and *E. abertianum* regression equations (Table 11). There was a general increase of seeds of *E. trichopes*, however, over the sampling period, but this was not true of *E. abertianum*.

Seeds found Around Novomessor Nests

In order to determine the amount of mesquite seeds

Table 9. *Eriogonum trichopes* seed production on the playa fringe in 1973

Date	Plant #	Maximum Ht (cm)	Maximum Wt (cm)	# Seeds	Average #seeds/day
730618	1	30	55	129	
	2	30	51	357	
	3	32	54	319	
	4	56	69	39	
	5	54	54	41	
	6	38	47	151	
	7	30	64	856	
	8	18	40	57	
	9	30	51	101	
	10	38	52	333	
	$\bar{x}$ = (S.E.)	35.6 ± 3.7	53.7 ± 2.6	238.3 ± 7.9	
730711	1	33	70	170	8.1
	2	34	63	681	32.4
	3	16	49	123	5.9
	4	53	78	927	44.1
	5	47	75	816	38.9
	6	35	56	99	4.7
	7	30	65	1,303	62.0
	8	20	40	143	6.8
	9	34	51	119	5.7
	10	36	53	598	28.5
	$\bar{x}$ =	33.8 ± 3.5	60 ± 3.9	497.9 ± 135.6	
730801	1	36	70	464	22.1
	2	34	66	679	32.3
	3	22	48	872	41.5
	4	54	77	1,040	49.5
	5	54	75	1,444	68.8
	6	43	51	671	32.0
	7	30	67	1,542	73.4
	8	20	42	337	16.0
	9	30	60	582	27.7
	10	41	59	1,236	58.9
	$\bar{x}$ =	36.4 ± 3.7	61.5 ± 3.7	886.7 ± 131.2	

Table 10. *Eriogonum abertianum* seed production on the playa fringe in 1973

Date	Plant #	Maximum Ht (cm)	Maximum Wt (cm)	# Seeds	Average #seeds/day
730713	1	9.5	9	25	
	2	12.5	14.5	51	
	3	10.5	13	68	
	4	10.5	10	60	
	5	13	14.5	170	
	6	13.5	16	112	
	7	12	10	17	
	8	9.5	8.5	22	
	9	12	13	26	
	10	12.5	15	13	
		$\bar{x}$ =11.6	12.4	56.4	
		$\pm$ 0.5	$\pm$ 0.9	$\pm$ 15.9	
730730	1	14	13	5	0.3
	2	14	20	42	2.5
	3	11	16	3	0.2
	4	13.5	14	6	0.4
	5	14	18	9	0.5
	6	16	22	23	1.4
	7	13.5	15	39	2.3
	8	13	14.5	4	0.4
	9	14	23	15	0.9
	10	16	24	26	1.5
		$\bar{x}$ = 13.9	18	17.5	
		$\pm$ 0.5	$\pm$ 1.3	$\pm$ 4.5	

Table 11. Regression of seed numbers vs canopy size and correlation coefficients (r^2 values) for *Eriogonum trichopes* and *E. abertianum* plants on the playa fringe in 1973

Eriogonum trichopes

Date	Regression equation	r^2 value
730618	$Y_{\#seeds} = -18.7 + 0.11X_{canopy\ size}$ (cm^2)	0.099
730711	$Y_{\#seeds} = -169.3 + 0.23X_{canopy\ size}$ (cm^2)	0.38
730801	$Y_{\#seeds} = 321.4 + 0.18X_{canopy\ size}$ (cm^2)	0.24

Eriogonum abertianum

Date	Regression equation	r^2 value
730713	$Y_{\#seeds} = -5.4 + 0.49X_{canopy\ size}$ (cm^2)	0.26
730730	$Y_{\#seeds} = -9.2 + 1.9\ X_{canopy\ size}$ (cm^2)	0.18

collected by *Novomessor* ants, all the seeds found in the immediate vicinity of 10 *Novomessor* nests around the playa fringe were collected one day in October. Each site was recorded and the number of seeds around each nest were counted.

The number of seeds per nest ranged from 106 to 1,342 with a mean of 711 (Table 12 and Figure 3). One seed weighs an average of 0.045 g and this value was used to calculate the weight of the seeds around each nest.

A number of authors have commented on the nutritious nature of mesquite seeds (in abstracts listed in Schuster, 1969), therefore the *Novomessor* ants probably obtain many nutrients and much energy from these seeds.

Table 12. Number and weight of mesquite seed around ten *Novomessor* nests on the playa fringe in 1973

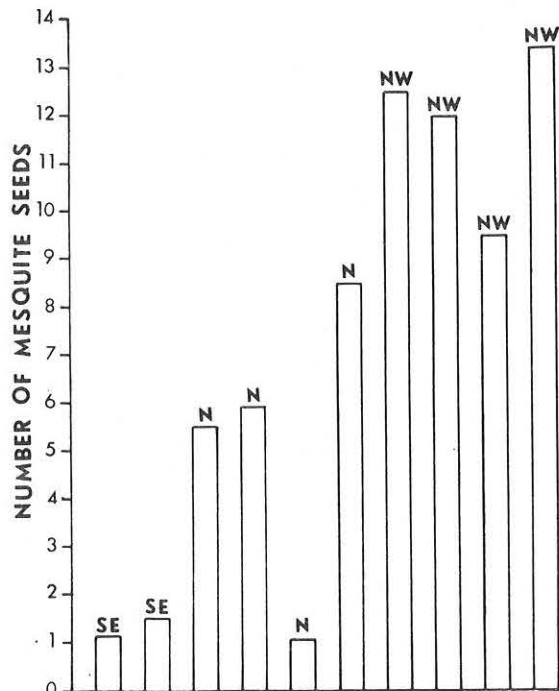| Date	Site	#of Seeds	Weight of Seeds (gms)
731006	PL 50S14	111	5.0
	PL 40W63	106	4.8
	PL 50S14	144	6.5
	PL 40W63	586	26.4
	PL 30SW51	1,195	53.8
	PL 20W51	1,253	56.4
	PL 30W63	557	25.1
	PL 40W63	859	38.7
	PL 30SW51	957	43.1
	PL 20SW51	1,342	60.4

Figure 3. Numbers of mesquite seed hulls found around the preiphery of *Novomessor cockerelli* nests. Letters above the bars indicate sector of playa fringe where nests were located.

ACKNOWLEDGEMENTS

LITERATURE CITED

BRIESE, D. 1973 An ant community of a semi-arid ecosystem. Preprint Ph.D. dissertation. Australian National University.

DÉLYE, G. 1967. Physiologie et comportement de quelques fourmis (Hym. Formicidae) du Sahara en rapport avec les principaux facteurs du climat. Ins. Soc. 14:323-338.

ETTERSHANK, G., and W. G. WHITFORD. 1973. Oxygen consumption of two species of *Pogonomyrmex* harvester ants (Hymenoptera:Formicidae). Comp. Biochem. Physiol. 46A:605-611.

SCHUMACHER, A., and W. G. WHITFORD. 1974. The foraging ecology of two species of Chihuahuan desert ants: *Formica perpilosa* and *Trachymyrmex smithi neomexicanus* (Hymenoptera:Formicidae). Submitted to Ins. Soc. In Press.

SCHUMACHER A., and W. G. WHITFORD. Spatial and temporal variation in Chihuahuan desert ant faunas. In prep.

SCHUSTER, J. L. (ed.). 1969. Literature on mesquite. Special Report 26. Int. Center for Arid and Semi-Arid Land Studies. Texas Tech. Univ. 84 pp.

SHAETA, M. N., and A. H. KASCHEF. 1971. Foraging activities *Messor aegyptiacus*. (Hymenoptera:Formicidae). Ins. Soc. 18:215-226.

SZLEP-FESSEL, R. 1970. The regulatory mechanism in mass foraging and the recruitment of soldiers in *Pheidole*. Ins. Soc. 17:232-244.

WHITFORD, W. G. 1973. Demography and bioenergetics of herbivorous ants in a desert ecosystem as functions of vegetation, soil type and weather variables. US/IBP Desert Biome Res. Memo. RM 73-29. 63 pp.

WHITFORD, W. G., and G. ETTERSHANK. 1972. Demography and role of herbivorous ants in a desert ecosystem as functions of vegetation, soil and climate variables. US/IBP Desert Biome Res. Memo. 72-32. 15 pp.

APPENDIX I

INFLUENCES OF TEMPERATURE AND HUMIDITY ON OXYGEN CONSUMPTION OF FIVE CHIHUAHUAN DESERT ANTS*

ABSTRACT

Oxygen consumption in five sympatric species of Chihuahuan Desert ants was measured at three relative humidities at 15, 25 and 35 C. The rate of oxygen consumption (QO_2) exhibited non-linear increase in *Formica perpilosa, Pogonomyrmex desertorum, Novomessor cockerelli,* and *Trachymyrmex smithi neomexicanus,* but was linear in *Pogonomyrmex californicus.* Vapor pressure deficit had a significant effect on QO_2 of *P. desertorum, T. s. neomexicanus* and *F. perpilosa,* but not on the other two species. Activity increased at higher vapor pressure deficits in *P. desertorum, N. cockerelli* and *T. s. neomexicanus.* The highest vapor pressure deficits at 35 C resulted in deaths of all species except *P. californicus* and *T. s. neomexicanus* died at intermediate and high vapor pressure deficits at all temperatures.

INTRODUCTION

Studies have shown that rates of O_2 consumption of ants generally increase with air temperature (Stowtzoff, 1909; Dreyer, 1932; Kennington, 1957; Golley and Gentry, 1964; Schmidt, 1966; Ettershank and Whitford, 1973; Kay, in prep.). Ettershank and Whitford (1973) found that O_2 consumption of *Pogonomyrmex rugosus* also increased with vapor pressure deficit, but that O_2 consumption of *P. maricopa* was unaffected by vapor pressure deficit. Kay (in prep.) found that rates of O_2 consumption of some species of *Myrmecocystus* were elevated in dry air. Ants of the genera *Pogonomyrmex* and *Myrmecocystus* are commonly encountered throughout the deserts of the southwestern United States and northern Mexico, where avoidance of water stress would be of major ecological importance.

In the present study, rates of O_2 consumption were measured over a range of air temperatures and humidities for five sympatric species of Chihuahuan desert ants, *Pogonomyrmex californicus, P. desertorum, Novomessor cockerelli, Trachymyrmex smithi neomexicanus,* and *Formica perpilosa.* The five species normally forage over different ranges of soil surface temperature and humidity. *Pogonomyrmex californicus* and *P. desertorum* are harvester (seed gathering) ants that can forage at soil surface temperatures exceeding 50 C and vapor pressure deficits as high as 40 mm Hg (unpubl. data). Most of the range of *P. californicus* lies in California, Nevada and Arizona, although the range extends into southwestern New Mexico, western Texas and northern Mexico (Cole, 1967). *Pogonomyrmex desertorum* is found in southern Arizona and New Mexico, western Texas and to about latitude 21° in

Mexico (Cole, 1967). *Novomessor cockerelli* are primarily nocturnal, forage on both insects and plant parts and are seldom active on the surface at soil surface temperatures above 35 C or vapor pressure deficits over 30 mm Hg (unpubl.). The geographic range of the species closely coincides with that of *P. desertorum* (Creighton, 1955). *Trachymyrmex smithi neomexicanus* grow fungus and forage on debris at about the same soil surface temperatures and vapor pressure deficits as *N. cockerelli* (Schumacher and Whitford, 1974). The species is known from specimens taken by Cole (1952, 1953) in southern New Mexico. *Formica perpilosa* forage on plant and insect exudates and on whole insects (LaBerge, 1952). Workers forage almost independently of soil surface temperature and humidity apparently because they usually forage in shrubs (Schumacher and Whitford, 1974). The species is widely distributed from Kansas to California and from Colorado into northern Mexico (Gregg, 1963).

This study was designed to evaluate the response of oxygen consumption to temperature and humidity to examine the potential physiological basis for differences in foraging behavior of ant species.

METHODS

Worker ants of all five species were aspirated from the soil surface at their nest entrances during the months of September, October and November, 1973. Additional *Pogonomyrmex desertorum* were obtained at depths of 20 to 100 cm from an excavated nest. All ants were captured on or near the IBP Chihuahuan Desert Jornada Validation Site, ca. 40 km NNE of Las Cruces, Dona Ana County, New Mexico. Ants were transferred to plastic boxes lined with moist paper toweling and left in the laboratory overnight (ca. 24 C) with no food. Rates of O_2 consumption were measured the following day. Measurements of oxygen consumption were made at three air temperatures, 15, 25 and 35 C, in a Gilson Differential Respirometer. Humidity was controlled and CO_2 absorbed by 0.3 ml of 5, 40 or 100% KOH by volume pipetted onto folded filter paper in the center well (Ettershank and Whitford, 1973). Table 1 contains a condensed version of the table of Ettershank and Whitford (1973) showing relative humidities and vapor pressure deficits obtained by using the three concentrations of KOH at each of the three temperatures.

Ten or fifteen ants, depending on size, were aspirated into the vessels. Because *F. perpilosa* shows size polymorphism, only ants of approximately the same size were placed in a single vessel. Before each measurement, the reaction vessels were equilibrated to the respirometer bath temperature, first for 45 min open to the outside air and then for 15 min closed. The amount of O_2 removed was then recorded at

---

APPENDIX I

30-min intervals for 1 hr. Activity was estimated near the end of the hour period by counting the number of ants crossing a line on the reaction vessels in 1 min (Ettershank and Whitford, 1973). Between measurement periods, the vessels were disconnected from the respirometer to allow air exchange, and weak or dying ants were removed and counted. An ant was considered to be weak and dying if locomotion was impaired.

Measurements were made on the same ants at three consecutively increasing temperatures. Most data were collected between 0930 hr and 1930 hr, but some data for *N. cockerelli* were collected between 2100 hr and 2230 hr. At the end of an experiment the ants were killed with chloroform, counted and dried to a constant weight at 57 C. A complete set of 45 determinations, five for each temperature and humidity combination, was obtained twice for *P. desertorum*, once using foragers and once using ants collected from within a nest. The 45 determinations were made only on foragers of the other four species. Additional determinations were made at 35 C for *N. cockerelli* and *F. perpilosa* to replace unusable data from vessels containing weak or dying ants.

Volumes of O_2 were converted to $\mu l \cdot hr^{-1}$ and $\mu l (mg \cdot hr)^{-1}$ STP. Activity indices were calculated by dividing the activity counts by the total number of ants per vessel. A data point was excluded from analyses if any ants were dying at the end of a measurement period. Stepwise multiple regression analyses (Draper and Smith, 1966) were used to examine possible effects of temperature, vapor pressure deficit, dry weight, and number of ants per vessel on O_2 consumption. Vapor pressure deficit rather than relative humidity was used as the humidity regressor variate because vapor pressure deficit gave a measure of the drying power of the air air. The number of ants per vessel varied slightly due to miscounts and death of individuals. An F test was used to test for heterogeneity of variance, and t' was calculated to compare means of samples with unequal variances (Steel and Torrie, 1960). The 0.05 probablility level was used for tests of significance.

Rates of O_2 consumption during the first 30 min of a measurement period were not significantly different from rates during the second 30 min. Therefore, all results were based on data from each complete 1-hr period. Mean rates of O_2 consumption for the five ant species are presented in Figure 1. Because rates of O_2 consumption for *P. desertorum* foragers were not significantly different from rates for *P. desertorum* workers collected from beneath the surface, the two data sets were combined. *Formica perpilosa*, the only formicine species, had mean rates of O_2 consumption and sample variances that were higher at all temperatures than those of the four myrmicine species.

The best multiple regression analyses of O_2 consumption as a function of temperature, vapor pressure deficit and body dry weight are presented in Table 2. Number of ants per vessel did not significantly affect O_2 consumption of any of the species. A regression model using log O_2 consumption did not fit the *P. californicus* data because O_2 consumption was linearly related to temperature over the 20 degree range of tests. The other four species had nonlinear responses of O_2 consumption to temperature. A model using log O_2 consumption vs. temperature, log vapor pressure deficit and log dry weight, best fits the data sets of those species.

Temperature had a highly significant regression coefficient for all five species. Dry weight significantly affected O_2 consumption of *P. desertorum*, *N. cockerelli* and *F. perpilosa* only. Most of the workers of *P. californicus* and *T. s. neomexicanus* were from the same colonies. Very little weight variation occurred within a colony, which probably accounted for the nonsignificant dry weight coefficients for those two species. The vapor pressure deficit regression coefficients were highly significant for *P. desertorum* and *T. s. neomexicanus* and significant for *F. perpilosa*. Oxygen consumption of *P. californicus* was apparently unaffected by vapor pressure deficit. The vapor pressure deficit regression coefficient for *N. cockerelli* was not significant. However, at 35 C, O_2 consumption data for

Appendix I. Table 1. Percent by volume of potassium hydroxide (% KOH) used at a temperature (T_a) to attain the corresponding vapor pressure deficit in mm Hg (VPD) and percent relative humidity (RH) (modified from Ettershank and Whitford, 1973)

| | T_a °C | | | | | |
| | 15°C | | 25°C | | 35°C | |
KOH %	RH	VPD	RH	VPD	RH	VPD
5	82	2.3	90	2.4	85	6.3
40	65	4.5	70	7.1	65	14.8
100	0	12.8	0	23.7	0	42.2

APPENDIX I
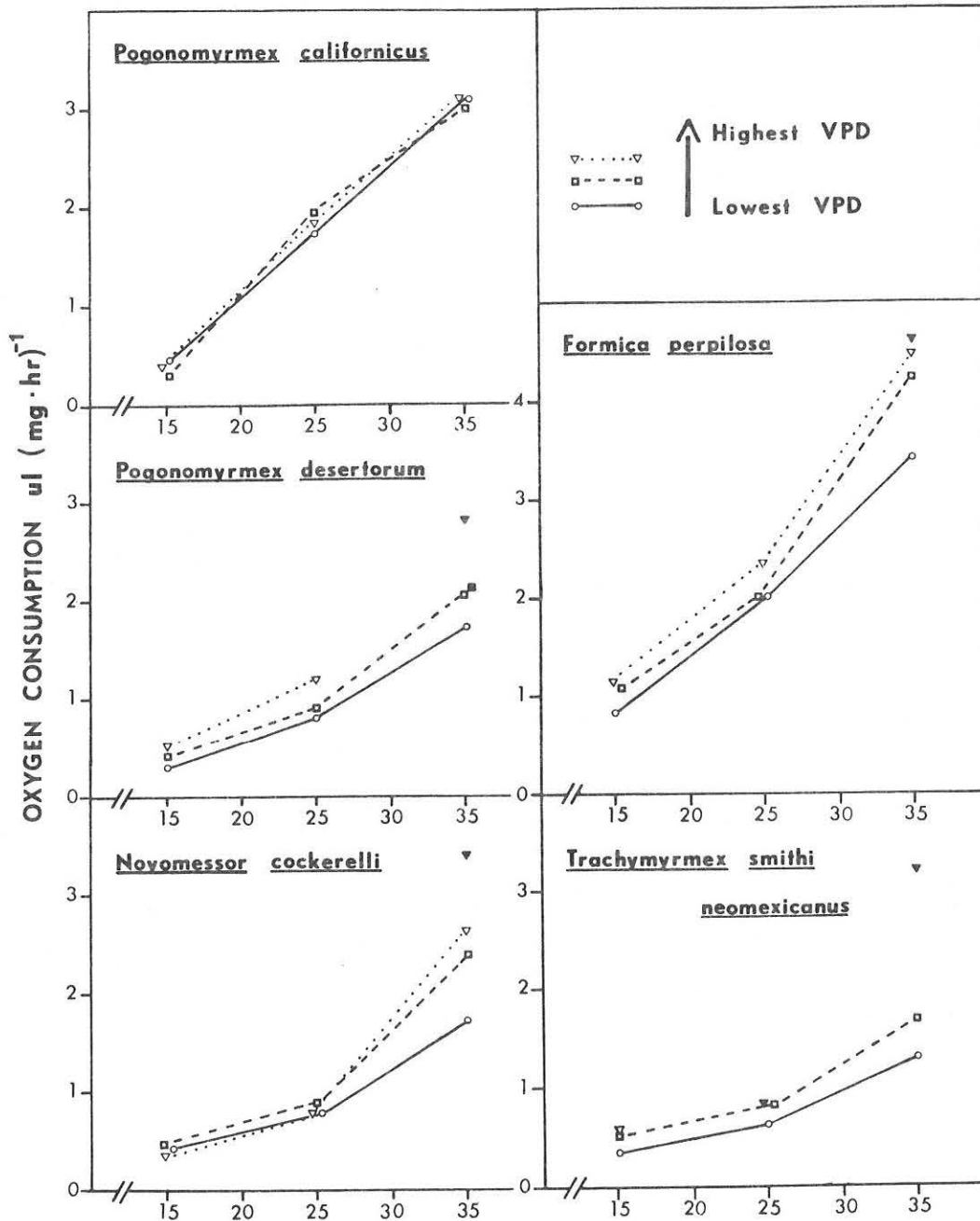
Appendix I. Figure 1. Mean rates of O_2 consumption of five species of Chihuahuan Desert ants as a function of temperature and vapor pressure deficit. Solid symbols represent data from vessels containing dying ants.

N. cockerelli from vessels containing 100% KOH had a sample variance and mean that were significantly greater than the sample variance and mean of data from vessels containing 5% KOH (F[5,4] = 32.2, p < 0.0005; t' = 3.34, 0.02 < p < 0.05).

Table 3 presents Q_{10} values for O_2 consumption over the ten degree intervals between experimental temperatures. The Q_{10}'s of *P. desertorum* and *F. perpilosa* were unaffected by temperature and humidity. The Q_{10}'s of *P.* *californicus* decreased with temperature but were unaffected by vapor pressure deficit. The Q_{10}'s of *N. cockerelli* and *T. s. neomexicanus* increased with temperature at all vapor pressure deficits, but the increase was greatest in dry air.

Figure 2 gives activity indices of the five species as a function of temperature and humidity. Workers of *P. californicus* were more active than those of the other four species. Activity of *P. californicus* was unaffected by vapor

APPENDIX I

Appendix I. Table 2. Multiple regression analyses of oxygen consumption (μ l/ant· hr): temperature (C), vapor pressure deficit (mm Hg), and dry weight (mg) for five species of ants (T_a = air temperature; VPD = vapor pressure deficit; DW = body dry weight; b = coefficient; F = partial F ratio; df = degress of freedom; p = probability level of F)

	Pogonomyrmex californicus	*Pogonomyrmex desertorum*	*Novomessor cockerelli*	*Trachymyrmex smithi neomexicanus*	*Formica perpilosa*
Multiple R^2	.958	.917	.936	.897	.918
Standard Error Est.	.3229	.0849	.0845	.0767	.0886
Dependent variable	O_2 cons	$\log_{10}O_2$ cons	$\log_{10}O_2$cons	$\log_{10}O_2$cons	$\log_{10}O_2$cons
Constant (b°)	-2.1587	-.9202	-1.4253	-.8025	-.5259
Independent variables:					
T_a, b_1	.1849	.0310	.0333	.0217	.0295
F	983.87	540.77	385.49	139.99	208.01
df	1, 43	1, 70	1, 39	1, 26	1, 37
p	<.0005	<.0005	<.0005	<.0005	<.0005
$\log_{10}$VPD, b_2		.2112		.2571	.0828
F		49.91		25.68	4.16
df	Not sig.	1, 70	Not sig.	1, 26	1, 37
p		<.0005		<.0005	.025<p<.05
$\log_{10}$DW, b_3		.7576	2.0055		.4491
F		22.89	34.71		29.76
df	Not sig.	1, 70	1, 39	Not sig.	1, 37
p		<.0005	<.0005		<.0005

pressure deficit but was greatest at 25 C. Workers of *P. desertorum* were also quite active with peak activity at 25 C. Activity of *P. desertorum* greatly increased at high vapor pressure deficits. Because the same activity patterns were found both for *P. desertorum* foragers and for workers collected beneath the surface, the two data sets were combined. Workers of *N. cockerelli* and *F. perpilosa* were less active. Both species increased activity with temperature. Workers of *N. cockerelli* also increased activity at high vapor pressure deficits. Workers of *T. s. neomexicanus* were

very inactive under all conditions, but activity increased slightly at high vapor pressure deficits.

Figure 3 shows the number of weak or dying ants in reaction vessels expressed as a percentage of the total number of animals at each set of experimental conditions. No workers of *P. californicus* died throughout the experiment. Only one ant, an *F. perpilosa* at 35 C, died in vessels containing 5% KOH. All species except *P. californicus* had losses at 35 C and 100% KOH. Some

Appendix I. Table 3. Q_{10} values of oxygen consumption versus temperature (T_a) and vapor pressure deficit (VPD) for five species of ants

T_a interval °C	VPD mm Hg	*Pogonomyrmex californicus*	*Pogonomyrmex desertorum*	*Novomessor cockerelli*	*Trachymyrmex smithi neomexicanus*	*Formica perpilosa*
15 - 25	highest	4.2	2.3	1.9	1.4*	2.0
		5.8	2.1	1.8	1.5	1.7
	lowest	3.8	2.5	1.9	1.8	2.4
25 - 35	highest	1.7	2.4*	3.3	3.7*	1.9
		1.5	2.3	2.7	21.	21.
	lowest	1.8	2.2	2.1	2.1	1.7

* questionable values from chambers containing weak ants.

APPENDIX I
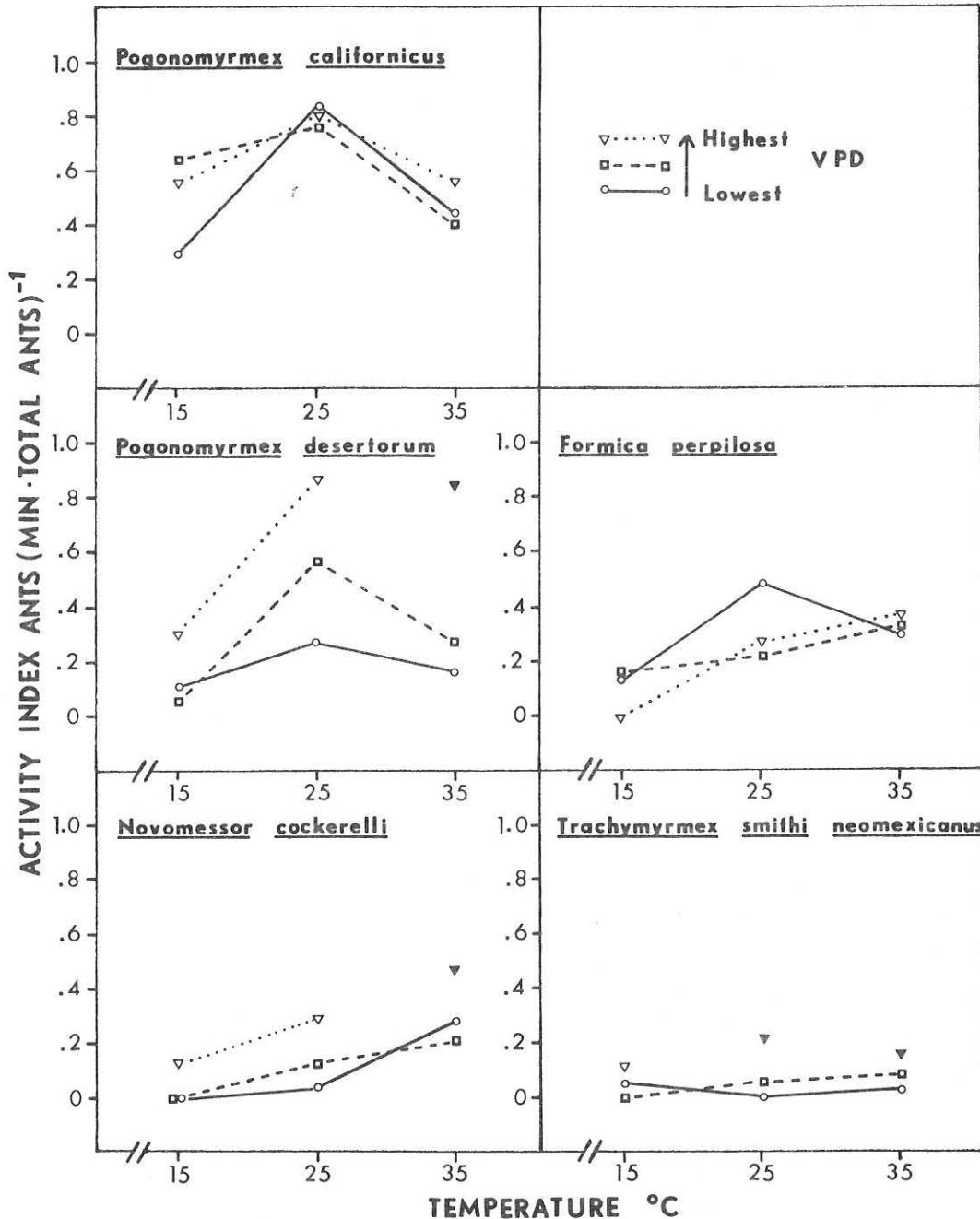
Appendix I. Figure 2. Indices of activity of five species of Chihuahuan Desert ants as a function of temperature and vapor pressure deficit. Each point is the mean of several counts made during O_2 consumption measurements. Solid symbols represent data from vessels containing dying ants.

workers of *F. perpilosa* and *N. cockerelli* died at 35 C in vessels containing 40% or 100% KOH. Workers of *P. desertorum* died at 25 C in vessels containing 100% KOH and at 35 C in vessels containing 40% or 100% KOH. Workers of *T. s. neomexicanus* died at all three temperatures in vessels containing 40% or 100% KOH.

DISCUSSION

Rates of O_2 consumption presented here for the four

members of the subfamily Myrmicinae (*P. californicus, P. desertorum, N. cockerelli* and *T. s. neomexicanus*) are comparable to rates of O_2 consumption reported by Ettershank and Whitford (1973) for *Pogonomyrmex rugosus* and *P. maricopa*. Rates of O_2 consumption given by Golley and Gentry (1964) for minor workers of *Pogonomyrmex badius* are approximately 100 times larger than rates for workers of *P. californicus* and *P. desertorum*, even though *P. californicus* workers and *P. badius* minor workers are of approximately the same size. On a weight basis, rates of O_2

APPENDIX I
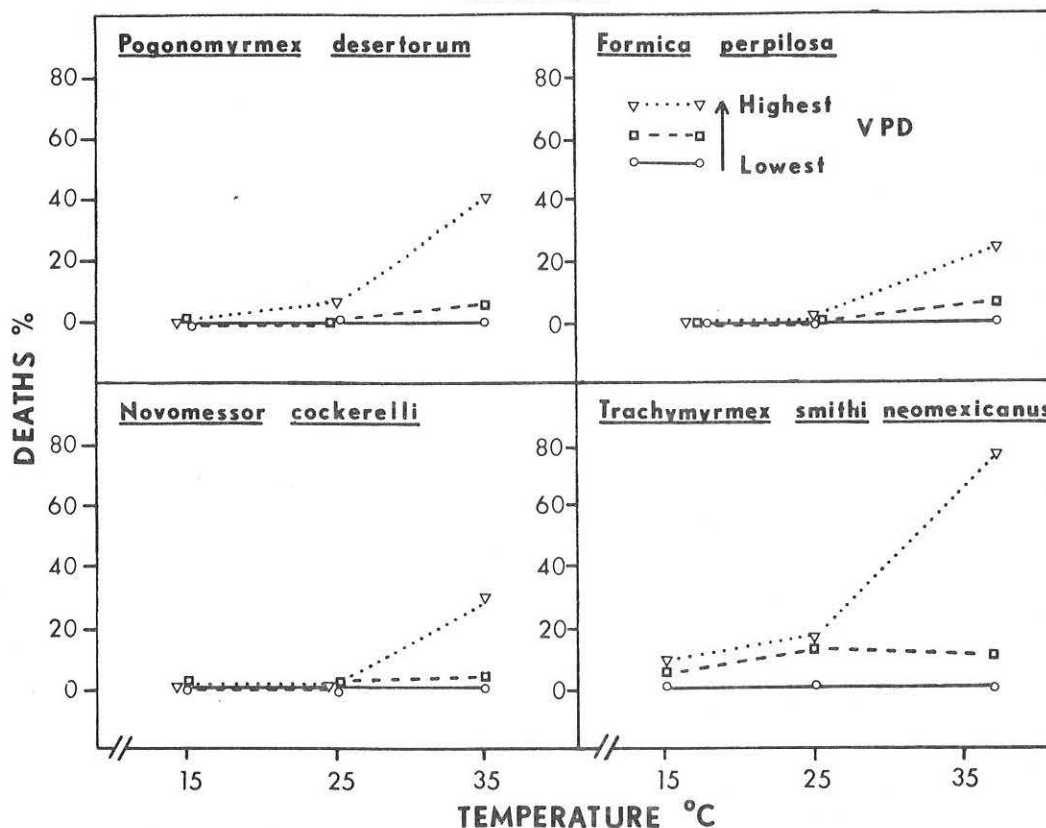
Appendix I. Figure 3. Mortality of four species of Chihuahuan Desert ants during O_2 consumption measurements, as a function of temperature and vapor pressure deficit. Number of dying ants expressed as a percentage of total number of experimental animals.

consumption for *F. perpilosa* and for other formicine ants (Dreyer, 1932; Kennington, 1957; Kay, in prep.) are slightly higher than rates for myrmicine ants (excluding data for *P. badius*). Ettershank and Whitford (1973) suggested that desert-adapted ants may have lower rates of O_2 consumption than ants such as *P. badius* found in more mesic habitats. However, *Formica ulkei* (Dreyer, 1932) and *Camponotus pennsylvanicus* (Kennington, 1957), which are also found in mesic environments, do not have especially high rates of O_2 consumption.

Ettershank and Whitford (1973) found that rates of O_2 consumption ($\mu l \cdot [mg \cdot hr]^{-1}$) for *P. maricopa* (mean dry weight = 3.69 mg) were generally higher than rates for *P. rugosus* (mean dry weight = 4.65 mg). They suggested that, on a weight basis, O_2 consumption of *Pogonomyrmex* may decrease with increasing dry weight. Rates of O_2 consumption for *P. californicus*, the smallest of the four desert *Pogonomyrmex* (Table 2), were higher than rates for *P. rugosus*, *P. maricopa* or *P. desertorum*. *P. desertorum*, however, had lower rates of O_2 consumption than *P. maricopa* even though *P. desertorum* is the smaller of the two ants (Table 2). In the present study, activity might have had a greater effect on O_2 consumption than weight. Workers of *P. californicus* had higher rates of O_2 consumption on a weight basis and were more active than workers of the other three myrmicine species tested. Workers

of *T. s. neomexicanus* had very low rates of O_2 consumption and were almost totally inactive.

Only *P. desertorum* and *T. s. neomexicanus* greatly increased O_2 consumption with vapor pressure deficit. Both of these species increased activity in dry air; therefore, increased activity might have caused increased rates of O_2 consumption. *N. cockerelli* also increased activity in dry air. *F. perpilosa* was the only species for which increased rates of O_2 consumption with vapor pressure deficit were not accompanied by increased activity, but the large sample variances of the *F. perpilosa* data made interpretations difficult. Neither activity nor O_2 consumption of *P. californicus* seemed to be affected by vapor pressure deficit. Other insects are more active in dry air than in moist, (Buxton and Lewis, 1934; Kay, in prep.). Ettershank and Whitford (1973) found, however, that activity of *P. rugosus* decreased with increased vapor pressure deficit.

In this study, the species that greatly increased O_2 consumption with vapor pressure deficit also appeared to be more severely stressed by high vapor pressure deficits (Fig. 3). Workers of *P. desertorum* and *T. s. neomexicanus* which greatly increased O_2 consumption at high vapor pressure deficits also had high death rates in dry air. Death rates as well as rates of O_2 consumption of *N. cockerelli* and *F. perpilosa* increased to a lesser extent with vapor pressure

APPENDIX I

deficit. No workers of *P. californicus* died under any of the experimental conditions nor was O_2 consumption of that species significantly affected by vapor pressure deficit. Kay (in prep.) found that three species of *Myrmecocystus* with high death rates in dry air at 35 C increased O_2 consumption with vapor pressure deficit, but that a fourth species with a lower death rate did not significantly increase O_2 consumption with vapor pressure deficit.

Ettershank and Whitford (1973) suggested that *P. rugosus* may increase O_2 consumption at high vapor pressure deficits to provide metabolic water to replace water lost by evaporation. Increased O_2 consumption with vapor pressure deficit found for Myrmecocystus (Kay, in prep.) supports that hypothesis. Other investigators (Barton-Browne, 1964; Edney, 1967) have also suggested that metabolic water may be used by insects to maintain water balance, but little direct evidence exists to support the suggestion. Because increased activity might have caused the increased O_2 consumption seen in the present study, it is impossible to say whether or not the present data support the hypothesis. Ettershank and Whitford (1973) suggested that a mechanism for increasing metabolic water production may be better developed in ants such as *P. rugosus* that inhabit very xeric environments. Data presented here do not clearly support that idea. The data do suggest that increases in O_2 consumption with vapor pressure deficit probably were either directly or indirectly related to increased water stress. Increased stress may have caused increased activity, which in turn may have elevated O_2 consumption.

Pogonomyrmex californicus are found in some of the hottest desert areas in the United States (Cole, 1967). Workers of *P. californicus* forage at much higher soil surface temperatures and vapor pressure deficits than workers of *P. rugosus* or *P. desertorum* (unpubl. data). Like its close relative, *P. maricopa* (Cole, 1967), *P. californicus* did not increase O_2 consumption with vapor pressure deficit (Ettershank and Whitford, 1973). Workers of *P. californicus* may have lower desiccation rates than workers of many other desert ants, which may allow *P. californicus* to withstand high vapor pressure deficits.

The detrimental effect of high vapor pressure deficit on workers of *P. desertorum* was surprising. Workers normally forage at vapor pressure deficits as high as those that caused death in this study. However, foragers in nature may be exposed to high vapor pressure deficits only for short periods of time. The apparent intolerance of *P. desertorum* to desiccation might at least partially explain differences in foraging activity between *P. desertorum* and *P. californicus* in relationship to temperature and humidity (unpubl. data). No data exist at present to explain the high activity of *P. californicus* and *P. desertorum* at 25 C, but 25 C may be close to the lower foraging threshold of both species.

Rates of O_2 consumption of *N. cockerelli* were elevated at high vapor pressure deficits only at 35 C. The pattern was reflected in the Q_{10} values for the species which increased in dry air over the 25 C to 35 C interval. Deaths also occurred only at 35 C. Since workers of *N. cockerelli* normally do not forage at vapor pressure deficits above about 30 mm Hg (unpublished data), these ants avoid conditions that might cause water stress.

Trachymyrmex smithi neomexicanus was very intolerant of high vapor pressure deficits at all temperatures. Increases in O_2 consumption at high vapor pressure deficits apparently did not provide enough metabolic water to replace losses by evaporation. Workers of this species forage only at low soil surface temperatures and low vapor pressure deficits and therefore avoid unfavorable conditions (Schumacher and Whitford, 1974). Schumacher and Whitford (1974) found that workers of *T. s. neomexicanus* had a mean critical thermal maximum of 36.4 C and that individual ants died below 35 C. During the present study, workers remained for two or more hr at 35 C in humid air without fatalities. Schumacher and Whitford (1974) believed that individual ants were weak at the beginning of critical thermal maximum experiments. Those ants might have desiccated in transit to the laboratory, and desiccation may have influenced critical thermal maximum values. However, in this study the Q_{10} of *T. s. neomexicanus* increased with temperature in humid air. The increase might have been caused by high temperature stress.

Workers of *F. perpilosa* and of three diurnal species of *Myrmecocystus* (Kay, in prep.) died in dry air at 35 C in almost equal numbers during O_2 consumption measurements. As Schumacher and Whitford (1974) and Kay (in prep.) have noted, these formicine ants forage in the vegetation on liquid food and therefore can forage almost independently of soil surface temperature and vapor pressure deficit. The four formicine ants were not as adversely affected by high vapor pressure deficits as were some myrmicine ants that forage on the ground (Fig. 3). *Formica perpilosa* and the three diurnal *Myrmecocystus* (Kay, in prep.) may use metabolic water to alleviate water stress.

Délye (1968) found that upper lethal temperatures of Saharan ants were no greater than those of more mesically adapted members of the same genus. Species of *Pogonomyrmex* and *Myrmecocystus* had critical thermal maximum values apparently characteristic of the genus as a whole (unpubl. data). *Novomessor cockerelli* had a mean critical thermal maximum of 51.7 C although workers of the species seldom forage at soil surface temperatures above 35 C (unpubl. data). Although foraging activity of ants has generally been characterized in terms of temperature, desiccation at high vapor pressure deficits may set upper limits on foraging conditions of some species. Data from the present study, from the study of Ettershank and Whitford (1973), and from the study of Kay (in prep.) suggest that degree of tolerance to desiccating conditions can vary greatly among ants, even of the same genus. Délye (1968) found that Saharan ants had less permeable integuments than non-desert adapted species. Some desert ants may increase metabolic water production as they desiccate, but other factors such as integument permeability, must also be important to desert survival.

APPENDIX I

LITERATURE CITED

BARTON-BROWNE, L. 1964. Water regulation in insects. A. Rev. Ent. 9:63-82.

BUXTON, P. A., and D. J. LEWIS. 1934. IV-Climate and tsetse flies: Laboratory studies upon *Glossina submorsitans* and *tachinoides*. Phil. Trans. Roy. Soc. London, Ser. B. 226:175-240.

COLE, A. C. 1952. A new subspecies of *Trachymyrmex smithi* (Hymenoptera:Formicidae) from New Mexico. J. Tenn. Acad. Sci. 27:159-162.

COLE, A. C. 1953. Studies of New Mexico ants. VI. The genera *Solenopsis*, *Monomorium*, *Mrymecina*, and *Trachymyrmex* (Hymenoptera:Formicidae). J. Tenn. Acad. Sci. 28:299-300, 316.

COLE, A. C. 1967. *Pogonomyrmex* harvester ants. Univ. of Tenn. Press, Knoxville.

CREIGHTON, W. S. 1955. Studies on the distribution of the genus *Novomessor* (Hymenoptera:Formicidae). Psyche 62:89-97.

DÉLYE, G. 1968. Recherches sur l'écologie, la physiologie et l'éthologie des Fourmis du Sahara. Thèse présentées a la Faculté des Sciences de l'Université d'Aix-Marseille.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York.

DREYER, W. A. 1932. The effect of hibernation and seasonal variation of temperature on the respiratory exchange of *Formica ulkei* Emery. Physiol. Zool. 5:301-329.

EDNEY, E. G. 1967. Water balance in desert arthropods. Science 156:1059-1066.

ETTERSHANK, G., and W. G. WHITFORD. 1973. Oxygen consumption of two species of *Pogonomyrmex* harvester ants (Hymenoptera:Formicidae). Comp. Biochem. Physiol. 46A:605-611.

GOLLEY, F. G. and J. B. GENTRY. 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius* Ecology 45:217-225.

GREGG, R. E. 1963. The ants of Colorado. Univ. of Colo. Press. Boulder.

KENNINGTON, G. S. 1957. Influence of altitude and temperature upon the rate of oxygen consumption of *Tribolium confusum* Duval and *Componotus pennsylvanicus moduc* Wheeler. Physiol. Zool. 30:305-314.

LaBERGE, W. E. 1952. Locality records of two ants found in Kansas. J. Kans. Ent. Soc. 25:59.

SCHMIDT, G. H. 1966. Einfluss der Temperatur auf den Atmungsstoffwechsel der Puppen von *Formica polyctena* (Hymenoptera, Insecta). Helgolander Wiss. Meeresuntersuch. 14:369-380.

SCHUMACHER, A. M. and W. G. WHITFORD. 1974. The foraging ecology of two species of Chihuahuan Desert ants: *Formica perpilosa* and *Trachymyrmex smithi neomexicanus* (Hymenoptera:Formicidae). Insectes Sociaux. In Press.

SLOWTZOFF, B. 1909. Uber den gaswechsel der insekten und deren beziehung zur temperatur der luft biochem. Zeit. 19:497-503.

STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc. N.Y.

APPENDIX II

KEY TO THE WORKER ANTS OF THE
CHIHUAHUAN DESERT IBP VALIDATION SITES

WARNING: Nest surface structure varies with the location and age of an ant colony and with season. Use nest surface structure only as a clue to the identity of a colony.

1. Pedicel one segmented. Sting always absent (Figure 1a) 2

    Pedicel two segmented. Sting sometimes present (Figure 2a) 11

2. Odor of crushed ant usually not very noticeable but taste that of formic acid. Cloaca round and surrounded by a circle of hairs (Figure 1a) (Subfamily:Formicinae) 3

    Odor of crushed ant pungent and taste bitter (that of butyric acid). Cloaca slit-shaped and not surrounded by a circle of hairs (Subfamily:Dolichoderinae) 9

3. Workers tiny (less than 2.5 mm in length) and only slightly polymorphic (more than two distinct sizes within a nest). Color yellow . . . . *Lasius* sp.

    WARNING: In the field, workers of *Lasius* sp. resemble *Iridomyrmex pruinosum.*

    Workers large or medium sized and polymorphic. Larger workers greater than 5 mm in length. Color variable. 4

4. Dorsum of thorax convex, without a distinct depression (Figure 1b . . . . *Camponotus* sp.

    Dorsum of thorax with a distinct depression at the mesoepinotal suture (Figure 1a) 5

5. Workers bicolored; head and thorax reddish orange and gaster blackish. Nests usually located under shrubs. Maxillary palpi shorter than length of head (Figure 1a) . . . . *Formica perpilosa*

    Color not as above. Nests located in the open or occasionally at the base of a small plant. Maxillary palpi very long, much longer than length of head (Figure 1c) (Genus:*Myrmecocystus*) 6

6. Color yellow. Workers forage nocturnally 7

    Color blackish with head and thorax brownish. Workers forage diurnally 8

7. Larger workers greater than 7 mm in length. Color a dirty or orangish yellow. Nests located in sand, clay or gravel, and usually surmounted by a 6 to 16 cm cone of

small pebbles. The cone is occasionally absent . . . . *Myrmecocystus mexicanus*

    Workers less than 6 mm in length. Color a very pale yellow. Nests located in sandy areas with or without a small cone of sand . . . . *Myrmecocystus navajo*

8. Some hairs on the dorsum of thorax of larger workers long and slightly curved (Figure 1d). Nests of larger colonies surmounted by gravel-coated cones up to 40 cm in diameter . . . . *Myrmecocystus depilis*

    All hairs on dorsum of thorax short and straight (Figure 1e). Nests usually not surmounted by a large cone . . . . *Myrmecocystus mimicus*

    WARNING: individuals of *M. depilis* and *M. mimicus* sometimes cannot be distinguished. Check several ants from each colony. Newly established colonies of diurnal *Myrmecocystus* may have nest cones similar to those of *Conomyrma. Conomyrma* may be recognized by its characteristic odor and by the presence of an epinotal projection (Figure 1f).

9. Workers tiny, less than 2.2 mm in length. Color yellow or yellowish brown. Epinotal (propodeal) projection absent. Nest entrances usually surrounded by a crater about 3 cm in diameter. See warning in couplet 3 . . . . *Iridomyrmex pruinosum*

    Workers greater than 2.8 mm in length. Color orange with a blackish gaster or entire ant blackish. Epinotal projection present (Figure 1f). Nest entrances usually surrounded by a crater greater than 5 cm in diameter. (Genus:*Conomyrma*). See warning under couplet 8 10

10. Color of head and thorax a clear orange; color of gaster blackish. . . . . *Conomyrma bicolor*

    Color variable but usually blackish; head and thorax never a clear orange . . . . *Conomyrma insana*

11. Compound eyes reduced to single, small pale facet (Figure 2g). Color blackish organe. Nests usually located under shrubs. Workers forage nocturnally in large columns about 5 cm wide and many meters long. Ants carnivorous, usually preying on other ants. Workers occasionally seen at dawn carrying prey slung under their bodies. (Subfamily:Dorylinae) . . . . *Neivamyrmex nigrescens*

   Compound eyes black and composed of more than 5 facets. Color, nests and habits variable. Workers

APPENDIX II

capable of foraging individually; columns when occurring usually not attaining dimensions of those described above (Subfamily:Myrmicinae) 12

12. Head disproportionately large with an indention dividing the top of the head into two lobes (Figure 2b). Antenna 12 segmented. Sting absent. Color brownish orange. Ant (major worker) often associated with small ants with normal heads (minor workers). (Genus: *Pheidole*) 26

Head not disproportionately large or bilobed. If slight indentation present in top of head, antenna 10 segmented and sting present. Color variable 13

13. Workers usually 5.5 mm in length or greater. If length approaching 5 to 5.5 mm, psammophore (long hairs on the under side of head) well developed (Figure 2a) 14

Workers small, less than 5 mm in length, or dimorphic (of two distinct sizes). If dimorphic or polymorphic, minor workers less than 4 mm in length. Psammophore always very poorly developed or absent 18

14. Head approximately oval; length (excluding mandibles) much greater than width. Hind legs greater than 10 mm in length, appearing excessively long and spindly. Psammophore and sting absent. Color a solid reddish black. Gait awkward and stumbling. Nests usually surmounted by large, irregular gravel mounds with large entrances, 1 to 4 cm in diameter . . . . *Novomessor cockerelli*

Head approximately square; length (excluding mandibles) equal or less than width. Hind legs less than 9 mm in length, not appearing excessively long. Psammophore and sting present. Color, gait and nests not as above (Genus:*Pogonomyrmex;* Subgenus: *Pogonomyrmex*) 15

15. Workers bicolored; head and thorax black or dark reddish black and gaster orangish brown. Nest entrances surrounded by large gravel disc up to 1 m in diameter . . . . *Pogonomyrmex rugosus*

Workers orange. Nest entrances surrounded by crater of soil, partial crater or nothing 16

16. Epinotal (propodeal) spine present (Figure 2a). Workers forage with gaster approximately horizontal or somewhat lowered . . . . *Pogonomyrmex desertorum*

Epinotal spine absent. Workers often forage with gaster elevated 17

17. Length usually greater than 8 mm. Head width greater than head length (excluding mandibles). Rugae (ridges in exoskeleton) of head fine (greater than 3 rugae per 1 mm). Colonies composed of less than 500 workers. Workers always move with gaster greatly elevated . . . . *Pogonomyrmex apache*

Length usually less than 7 mm. Head width and head length approximately equal. Rugae of head coarse (less than 3 rugae per 1 mm). Colonies usually composed of 1,000 or more workers. Workers sometimes move with gaster elevated . . . . *Pogonomyrmex californicus*

18. Gaster spatula shaped (compressed dorso-ventrally) (Figure 2f). Postpetiole attached to the dorsal surface of first gastric segment. Color reddish black with gaster somewhat darker. Nests located in woody plants or at the base of woody plants . . . . *Crematogaster* sp.

Gaster not dorso-ventrally compressed. Post-petiole attached to anterior end of gaster. Color variable. Nests usually located in soil 19

19. Workers approximately monomorphic (of one basic size). Length 3.8 mm or greater. Color not yellowish orange. Legs not excessively long. Workers usually forage individually 20

Workers polymorphic (of more than two sizes), dimorphic (of two distinct sizes) or rarely apparently monomorphic. Length 3.7 mm or usually much less. If length approaching 3.7 mm, color yellowish orange and legs appearing excessively long. Workers often forage on trails 21

WARNING: Major workers may not be above ground.

20. Color reddish brown. Exoskeleton with rugae, pits and epinotal spines only. Nest entrances inconspicuous, with or without small cones of soil. Workers usually forage diurnally or crepuscularly on small seeds. Antenna 12 segments . . . . *Pogonomyrmex (Ephebomyrmex) imberbiculus*

Color a dull black. Exoskeleton with numerous spines and bumps. Nest entrances often surrounded by dry leaves. Excavated soil often piled to one side of entrance.   Workers usually forage crepuscularly or nocturnally on plant debris. Forage often carried over body like a sail. Antenna 11 segmented . . . . *Trachymyrmex smithi neomexicanus*

WARNING: Couplets 21 through 28 refer to ants that are sometimes difficult to distinguish in the field.

21. Workers polymorphic or almost monomorphic, none with disproportionately large heads. Color a solid
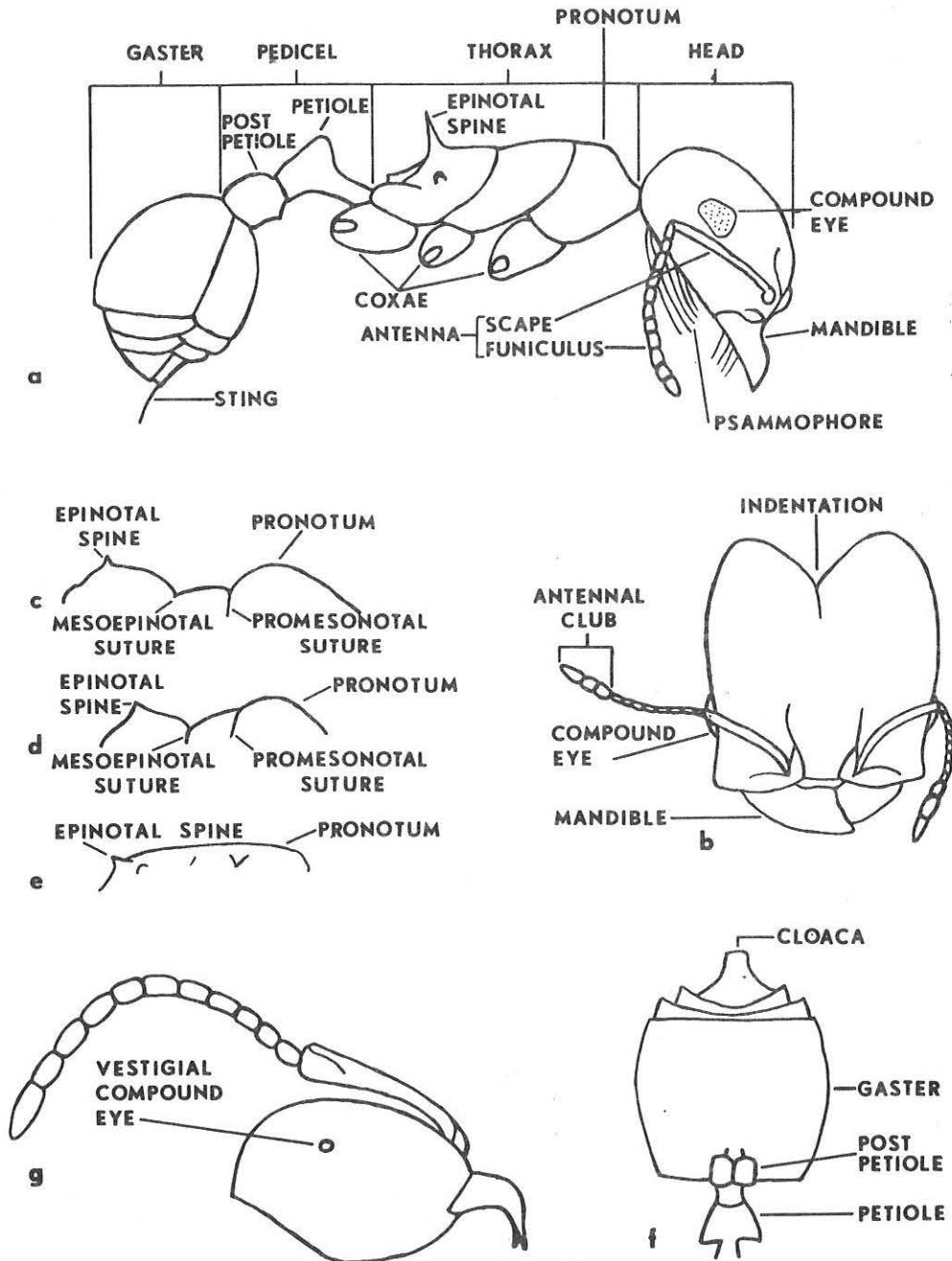
APPENDIX II

yellow or yellowish brown with gaster dark brown. Antenna 10 segmented with a 2 segmented antennal club. Sting present. (Genus:*Solenopsis*)..........22

Workers dimorphic or occasionally monomorphic; major workers when present with disproportionately large heads. Color of minors variable; black, orangish yellow or rarely pale yellow. Antenna 12 segmented with a 3 segmented antennal club (Figure 2b). Sting usually absent. See warning under couplet 19......24

22. Eyes reduced to less than fifteen facets. Color pale yellow. Workers only slightly polymorphic. Length less than 2.5 mm (Subgenus:*Diplorhoptrum*).........
................................*Solenopsis krockowi*

WARNING: Members of the subgenus *Diplorhoptrum* cannot be distinguished in the field. Other species besides *S. krockowi* are found in Dona Ana County, New Mexico.

Eyes with more than 30 facets. Color yellow, yellow with gaster darker or yellowish brown with gaster dark brown. Workers polymorphic. Length of some workers greater than 3 mm. See warning under couplet 19 (Subgenus:*Solenopsis*)........................23

23. Color yellow or yellowish brown with gaster usually darker. Eye of largest workers separated from mandibular insertion by a distance one-and-one-half times the maximum eye diameter.....*Solenopsis xyloni*

Color yellow; gaster never dark. Eye of largest workers separated from mandibular insertion by a distance twice the maximum eye diameter...........
................................*Solenopsis aurea*

WARNING: The color of *Solenopsis xyloni* is variable. Occasionally the gaster of individual workers is not darker than the head and thorax. Look at several ants from a colony.

24. Workers monomorphic and less than 2.5 mm in length. Colonies small and rare (less than 100 ants per colony). Sutures on dorsum of thorax indistinct or absent (Figure 2e). Sting present. (Genus:*Leptothorax*)..........25

WARNING: In the field *Leptothorax* may closely resembe *Pheidole* or *Solenopsis*.

Workers dimorphic; majors with disproportionately large, bilobed heads. Colonies of moderate size (several hundred workers per colony) and usually numerous. Sting absent. Two distinct sutures present on dorsum of thorax (Figures 2c, 2d). (Genus:*Pheidole*).

...................................26

25. Color pale yellow.................*Leptothorax* sp.

Color black......................*Leptothorax* sp.

26. Color of major and minor workers yellowish orange to brown. Hind legs of minors greater than 4 mm in length, appearing excessively long. Head of minor workers approximately tear-shaped, length (excluding mandibles) much greater than width. Antennal scapes of majors (Figure 2a) reaching to corners of head. Nests usually surmounted by irregular craters, 15 cm or greater in diameter, with a large opening, 2 or more cm in diameter............*Pheidole desertorum*

Color of minor workers brownish black. Color of major workers brown, orange or blackish brown. Hind legs of minors less than 3 mm in length, not excessively long. Head of minors not tear-shaped; length (excluding mandibles) usually approximately equal to or slightly greater than width. Antennal scapes of majors reaching less than one-half of the distance to top of head. Nest surface structure variable; entrance less than 0.5 mm in diameter....................................27

27. Color of major orange. Head width of major greater than 2.1 mm. Head length of major (excluding mandibles) greater than 2.2 mm. Length of major greater than 6.5 mm in length. Length of minor greater than 2.5 mm. Epinotal (propodeal) armature of minor a tiny slender spine (Figure 2c). Excavated soil usually piled to one side of the nest entrance. Majors above ground only after rains..........*Pheidole militicida*

Color of major orangish brown. Head width of major less than 1.5 mm. Head length (excluding mandibles) of major less than 1.7 mm. Length of major less than 5.5 mm; length of minor less than 2.2 mm. Epinotal armature a small, blunt spine (Figure 2d). Excavated soil usually found as small crater around nest entrance. Majors commonly forage with minors.....28

28. Head (excluding mandibles) length of majors greater than 1.5 mm; head width of majors greater than 1.3 mm. Length of majors greater than 4.7 mm. Length of minors greater than 1.8 mm. Transverse rugae (ridges in the exoskeleton) absent on top of head of major.....
................................*Pheidole xerophila*

Head width of majors less than 1.1 mm; head length (excluding mandibles) of majors less than 1.2 mm. Length of minors less than 1.7 mm. Length of majors less than 4.3 mm. Transverse rugae present on top of head of major..................*Pheidole rugulosa*

APPENDIX II
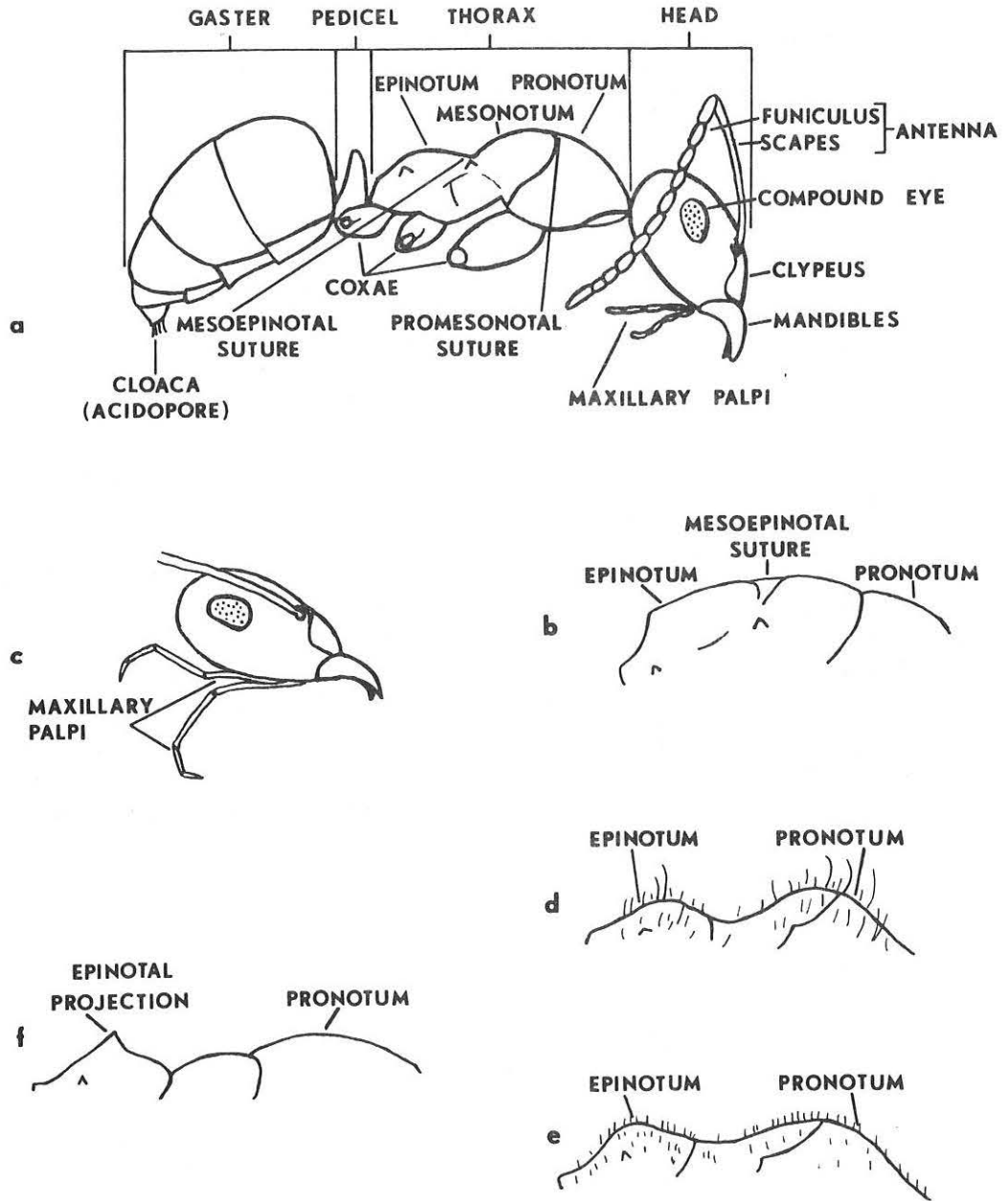
Appendix II. Figure 1. External morphology of Subfamily Formicinae, illustrated for use in association with the Key to Worker Ants.

APPENDIX II

Appendix II. Figure 2. External morphology of Subfamilies Dorylinae and Myrmicinae, illustrated for use in association with the Key to Worker Ants.