

Annual cycles in worker size of the seed-harvester ant *Veromessor pergandei* (Hymenoptera: Formicidae)

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Summary. The seed-harvester ant *Veromessor pergandei* Mayr is primitively polymorphic; workers are monophasically allometric. There is a distinct annual cycle in mean worker body size that replicates across colonies and habitats (Fig. 1); this cycle occurs through alteration of the worker size distribution (Fig. 2). There is little, if any, morph-specific task specialization by workers suggesting worker size variance is a colony-level adaptation permitting maintenance of a large and constant worker force during periods of resource fluctuation. Smaller workers appear in the foraging force following the “triple crunch” of reduced seed availability, reduced favorable times to forage, and alate production during winter months. Adult and starting *V. pergandei* colonies exhibit strong intraspecific territoriality, suggesting the selective advantage for maintenance of a large and constant worker force. Such selective pressures may have provided the initial variance in worker size distributions that led subsequently to specialized caste-specific task performance in more distinctly polymorphic ant species.

Introduction

True polymorphism in ants is associated with remarkable correspondence between tasks and castes of a given species. Polymorphism is a colony-specific adaptation that only culminates in individual-specific task performance. Assuming monomorphism with little worker size variance as the primitive condition in ants (Wilson 1985), polymorphism must have originated in colonies with some amount of worker size variance but, by definition, with no morph-specific task performance. Forces enhancing worker size variance prior to the emer-

gence of castes are unclear. By altering worker size, a colony not only alters ability of workers to perform tasks (e.g. forage), but also energetic investment in individual workers. A worker force can be generated and maintained at less cost if worker sizes are correspondingly smaller. If resource levels available for worker production fluctuate, production of workers with corresponding fluctuations in their body sizes would permit maintenance of a given worker population in light of such resource changes. One of the most obvious competing demands on the resources available for worker production and maintenance is colony reproduction. Energetic costs for the production of sexual forms can be up to 60% of the worker biomass in a colony (reviewed in Nielsen 1978). If these sexuals are produced during periods of limited resources, the competing demands on worker production are even greater.

I have examined this trade-off in worker size in the desert seed-harvester ant *Veromessor pergandei* which displays considerable variance among workers of a single colony. Numerous authors have noted this variance and suggested possible adaptive advantages for it (Went et al. 1972; Davidson 1977, 1978; Bernstein 1979; Rissing and Pollock 1984). *Veromessor pergandei* is sympatric throughout much of its range with the seed-harvester ant *Pogonomyrmex rugosus* which is ecologically very similar (Davidson 1978, see also below) but which displays much less worker size variance and, as such, provides a comparison for studies on worker size variance in *V. pergandei*.

Methods

One hundred workers and forage items they carried were collected randomly approximately every 4 weeks from foraging columns of 4 *V. pergandei* colonies at the Desert Botanical Gar-

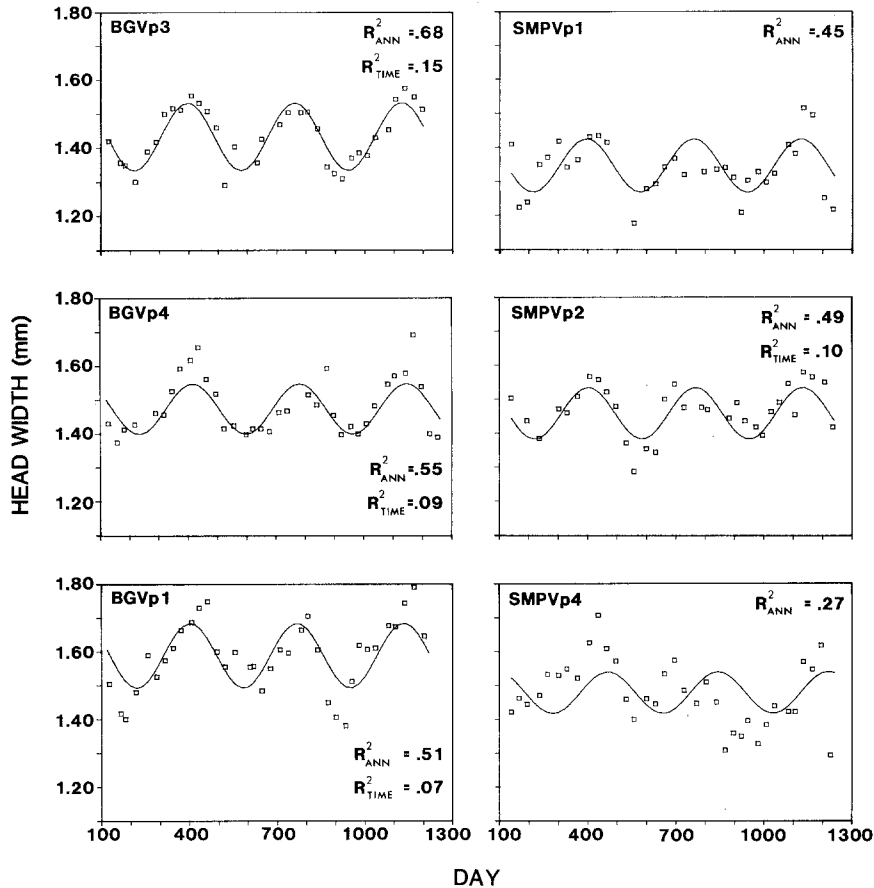


Fig. 1. Annual cycle of mean worker size (head width) at adult *Veromessor pergandei* colonies at the Desert Botanical Garden (BGVp nests) and Phoenix South Mountain Park (SMPVp nests). Curve is fitted annual cycle; R^2_{ann} is percentage of total variance explained by this fitted cycle. Points indicate mean of a sample of 35 foragers corrected for linear influence of time (in BGVp nests and SMPVp2); R^2_{time} is percentage of total variance explained by linear effects of time. Day 1 = 10 April 1982; Day 1300 = 23 July 1985

den, Phoenix, AZ (referred to as “BGVp1–4”) and from 3 colonies at South Mountain Park, Phoenix, AZ (“SMPVp1, 2 and 5”). The two sites are 17 km apart. Collections began in May/June 1982 and ended in May/June 1985. A fifth colony, BGVp7, apparently founded after the start of observations at the Botanical Garden, was added in 1983. Similarly, 100 workers (and forage items) were collected from 4 *P. rugosus* colonies at the Botanical Garden and two colonies at South Mountain Park. *Veromessor pergandei* colonies were generally active all year long while *P. rugosus* colonies displayed distinct annual activity cycles: collections for this species were limited to warm and generally moist periods. All samples were preserved; subsequently, random samples of 35 ants from each collection were measured (head width at widest point, HW). Additionally, all 100 workers collected each month for 1 yr (Dec 1983–Nov 1984) at BGVp1 were measured to examine annual changes in *V. pergandei* worker size distribution.

To identify possible “caste-task” correlation in *V. pergandei*, all seeds collected from BGVp4 and SMPVp2 from May 1982 to April 1985 were weighed individually; mean seed mass harvested (for samples with >20 seeds) was correlated with mean forager HW. Additional task performance on the basis of worker size was examined by collecting workers excavating nest material, cutting seeds from plants, defending the nest, or foraging at night and comparing their head widths with daytime foragers from the same nest.

Possible temporal processes (linear or cyclic) in the worker size-frequency distribution were analyzed through an iterative regression technique described by Pollock (Appendix). Each colony provides a time series with unique specifications. Similar

functions across these series thus provide independent evidence for a common biological process.

To examine whether young colonies exhibit different processes than their adult counterparts, an iterative dummy variable technique was applied to BGVp7. To identify when this colony began to exhibit an annual cycle (see below) this series was estimated as

$$y(t) = C + D + \sum_j f_j(t)$$

where

$$D = 0 \quad 0 < t \leq i$$

$$D = 1 \quad \text{otherwise}$$

and each $f_j(t)$ is an independent temporal function such that

$$f_j(t) = 0 \quad 0 < t \leq i$$

$f_j(t)$ = assigned temporal function (e.g. annual cycle) otherwise

i was iterated from the second to the last observation point. Iterations with high r^2 -values indicate the probable onset of the process(es) $f_j(t)$.

Results

There is a distinct, annual cycle in mean worker body size in colonies of *V. pergandei* (Fig. 1). This cycle, which explains up to 68% of total variance in mean HW, replicates across all colonies and

Table 1. Characteristics of the annual cycle in worker head width at *Veromessor pergandei* colonies at the Botanical Garden and South Mountain Park

Colony	Low point of cycle ^a	Range of cycle ^a (mm)	Intercept ^b (mm)	Coefficient of temporal trend ^c ($\times 10^{-4}$)
Adult colonies				
BGVp1	9 August	0.191	1.589	-0.183
BGVp3	2 August	0.199	1.433	-0.938
BGVp4	21 August	0.149	1.473	-0.767
SMPVp1	2 August	0.157	1.347	
SMPVp2	8 August	0.152	1.459	-0.728
SMPVp4 ^d	7 July ^d	0.122	1.479	
Other colonies				
BGVp2 (died)	9 August	0.100	1.396	-1.622
BGVp7 (newly founded) ^e	27 August	0.124	1.436	-0.115

^a See Appendix for method to calculate cycle low point and range (= amplitude $\times 2$)

^b Overall mean HW for this colony controlling for all identified temporal functions

^c Listed only if significantly different from 0

^d SMPVp4 had a 375 day cycle; low point is for first year, each subsequent year, low point is 10 days later

^e Cycle does not include first 4 data points

both habitats sampled. The annual cycle is similar in phase and range in all colonies (Table 1).

Mean head width of foragers at *V. pergandei* colonies is changed by altering the body size distribution of workers active outside the nest through the year (Fig. 2). At the low point in the cycle at BGVp1, for example, workers active outside the nest were predominantly ≤ 1.04 mm HW, generating a worker size distribution strongly skewed to that found when worker sizes were larger (compare June 1984 with December 1983; Fig. 2). This shift in the distribution of worker body sizes results in a corresponding cycle in worker variance: the coefficient of variance, CV, is high when mean head width is low and *vice versa*. This trend was found in all *V. pergandei* nests.

Worker size variance in *V. pergandei* colonies is greater than other desert seed-harvesters in the genera *Veromessor* or *Pogonomyrmex*, especially *P. rugosus* (Fig. 3, unpublished data). During the course of the annual cycle, worker size distribution at a given *V. pergandei* colony "slides" along the allometric line; at the height of the cycle, worker allometry is most like that of *P. rugosus* (Fig. 3). Variance in worker size distribution and allometry

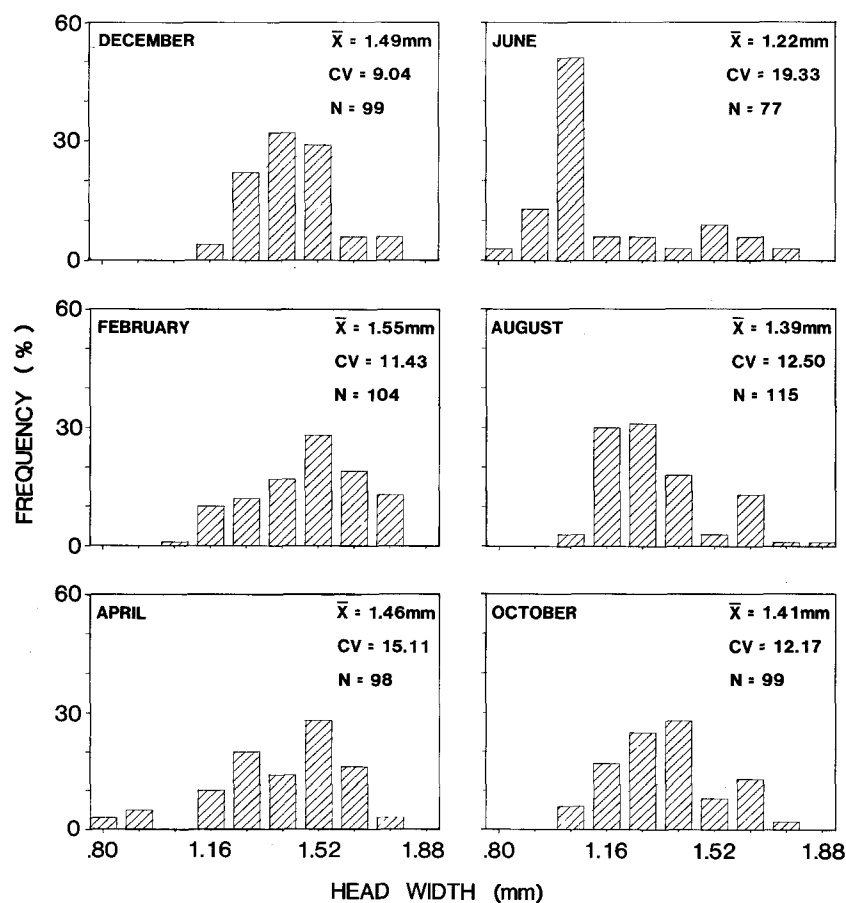


Fig. 2. Size frequency distribution of *Veromessor pergandei* foragers at BGVp1 during one year. CV = coefficient of variation

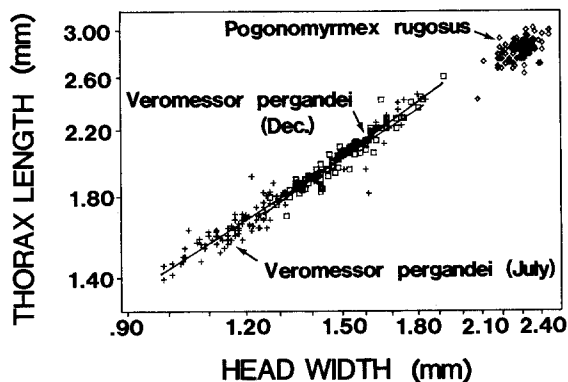


Fig. 3. Allometry of *Veromessor pergandei* and *Pogonomyrmex rugosus* workers at the Desert Botanical Garden. Workers of *V. pergandei* from the same nest (BGVp1) collected 6 months apart (Dec. 1983 and July 1984) are shown. Allometric equation for December *V. pergandei*: Thorax Length, $TL = 1.380 HW^{0.941}$, $N = 96$, $r^2 = 0.93$; for July: $TL = 1.435 HW^{0.837}$, $n = 104$, $r^2 = 0.93$; both the constant and the allometric coefficient are different for the 2 *V. pergandei* samples

is great enough to result in significantly different allometric equations for workers from the same nest through time (Fig. 3). t values for both constants and coefficients in Fig. 3 are greater than 3.55; $P < 0.001$.

Two *V. pergandei* colonies at the Botanical Garden show variations in the annual cycle of typical, "adult" colonies (Fig. 4). BGVp2 died during the study; while it displayed typical cycling of worker body size until early 1983, body sizes and foraging activity began to fall below normal levels after May 1983. Similarly, the newly founded colony, BGVp7, did not display any cycle in worker body size until August 1983. While the reproductive season of *V. pergandei* is January–March, BGVp7 did not reproduce in 1983 (Pollock and Rissing 1985). Subsequent to this, average worker body size reached that of other "adult" colonies on both study sites, and the annual cycle began. BGVp7 reproduced in 1984 and 1985.

Similar, but less dramatic trends are evident in several *V. pergandei* colonies. All *V. pergandei* colonies at the Botanical Garden and SMPVp2 exhibited a negative linear temporal trend (Table 1). BGVp2, the colony that died, exhibited the greatest temporal decline, while BGVp7, the new colony, exhibited the least. These trends suggest that all *V. pergandei* colonies at the Botanical Garden may be slowly dying. This effect of time on HW has been removed from Fig. 1 for the affected colonies through partial regression.

The annual cycle in *V. pergandei* worker body size is not consistent with or correlated with any task performed by individual workers examined.

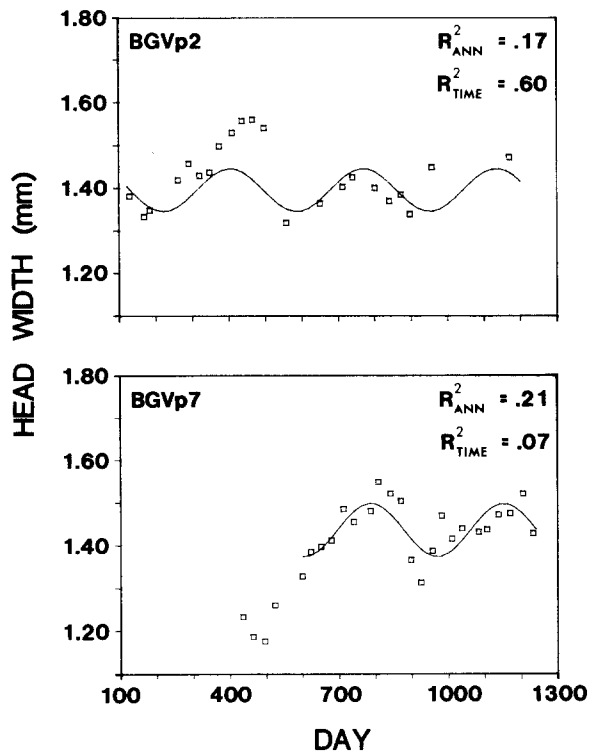


Fig. 4. Annual cycle of mean worker size (head width) at a dying (BGVp2) and a newly founded (BGVp7) *Veromessor pergandei* colony at the Desert Botanical Garden. Data points, fitted cycle and R^2 's as for Fig. 1

There is no correlation between mean worker HW and mean mass of seed harvested. For BGVp4, $r = -0.32$; $n = 27$ monthly samples (for a total of 1171 weighed seeds and 945 measured ants). For SMPVp2, $r = 0.07$, $n = 25$ monthly samples (1545 total weighed seeds and 875 measured ants). While a complete dietary analysis will be presented elsewhere (in preparation), *V. pergandei* and *P. rugosus* had similar diets during the 3-year study. *Schismus arabicus* is apparently preferred by both species and harvested predominantly in the Spring and early Summer. Apparently due to depletion of *S. arabicus* fruits, especially in the drought year 1984 (Rissing 1986), *S. arabicus* is replaced by *Pectocarya recurvata* and then by *Plantago insularis* at South Mountain Park by both ant species. The trend is similar for both species at the Botanical Garden where *S. arabicus* is replaced directly by *P. insularis*.

There is no consistent differential partitioning of nest excavation among *V. pergandei* workers (Table 2). Workers occasionally clip seeds from plants, especially *S. arabicus*. While there is some evidence that larger workers may preferentially perform this task, the data are conflicting (Ta-

Table 2. Task performance according to worker body size in *Veromessor pergandei* nests

Colony	Date ^a	Task ^b	Mean HW of ants performing task (mm ± SD; N)	Control ^c (mm ± SD; N)	<i>t</i> ^d	<i>P</i>
SMPVp1	8 Feb	NE	1.489 (0.155; 35)	1.516 (0.146; 35)	0.715	NS
SMPVp4	8 Feb	NE	1.510 (0.079; 35)	1.569 (0.220; 35)	1.415	NS
SMPVp5	8 Feb	NE	1.553 (0.209; 33)	1.479 (0.129; 35)	1.755	NS
BGVp1	10 Feb	NE	1.550 (0.213; 37)	1.536 (0.211; 35)	0.380	NS
BGVp3	10 Feb	NE	1.349 (0.184; 34)	1.458 (0.193; 35)	2.612	<0.02
BGVp7	10 Feb	NE	1.335 (0.133; 35)	1.342 (0.171; 35)	0.179	NS
SMPVp2	9 March	CS	1.634 (0.159; 32)	1.481 (0.230; 35)	3.203	<0.01
BGVp1	13 March	CS	1.576 (0.168; 35)	1.597 (0.182; 59)	0.559	NS
SMPVp4	15 April	CS	1.617 (0.131; 35)	1.650 (0.173; 35)	0.907	NS
BGVp1	16 April	NF	1.452 (0.272; 35)	1.426 (0.179; 35)	0.472	NS
BCVp12 ^e	6 July 76	F	1.190 (0.216; 58)	1.190 (0.162; 50)	0.016	NS
BCVp7 ^f	16 July 78	NG	1.345 (0.227; 52)	1.350 (0.216; 24)	0.104	NS
BCVp18 ^g	16 July 78	NG	1.246 (0.216; 46)	1.274 (0.226; 50)	0.616	NS

^a All dates in 1985 unless otherwise indicated

^b NE = nest excavation, CS = clipping seeds, NF = night foragers; F = fighters, NG = night guards (defend nest entrance, see Wheeler and Rissing 1975a)

^c Controls are daytime foragers from the same nest at the same time unless otherwise indicated

^d test for comparison of means (when samples had heteroscedastic variances, the *t*'-test of Sokal and Rohlf [1981] was used)

^e Collection of workers from a colony in Boulder City, Nevada fighting with *Solenopsis xyloni*; controls are foragers from this colony collected 13 days earlier

^f Collection from a colony in Boulder City, Nevada; controls are foragers from this colony collected 5 days earlier

^g Collection from a colony in Boulder City, Nevada; controls are foragers from this colony collected 26 days later

ble 2). Further, *S. arabicus* seeds mature and fall rapidly and sequentially from the parent plant providing a very brief period to perform this task; I have observed "clipping" on less than 10 occasions (always by less than 5% of the current foraging force) during several thousand hours of field observations.

Unlike *V. pergandei* which is active year round *P. rugosus* was active only during warmer seasons and, even then, much less predictably. This sporadic foraging activity precludes analysis of cycles in body size in this species due to extreme coliniarity between possible periodic functions (see Johnston 1984 for a discussion of such sample-induced multicoliniarity). Nonetheless, overall worker variability and hence any possible cycle in that variability for *P. rugosus* appears much less than that for *V. pergandei*. Overall mean CV for all *P. rugosus* colonies was 4.83 ($n=81$ monthly samples) and 12.11 for *V. pergandei* ($n=205$ monthly samples).

Discussion

The "polymorphism" of *V. pergandei* is primitive and more properly termed monophasic allometry (*sensu* Oster and Wilson 1978). Wilson (1985) has summarized the apparent steps involved in the evolution of polymorphism in ants starting with an initial increase in worker size variance and simple

allometry progressing through increasing bimodality of workers and culminating in one or two breaks in the allometric curve. Factors selecting for the initial increase in worker variance have not been clear. Long term data collected from individual *V. pergandei* colonies suggest that an initial advantage to increased worker size variance lies in its effect on maintaining the size of the overall worker force rather than creating individual workers more efficient at accomplishing specific tasks. This latter step, task performance based on individual worker size, should be evolutionarily subsequent to the initial forces selecting for increased variance.

Several aspects of *V. pergandei* natural history suggest the possible importance of a large, constant worker force. Colonies forage with a column extending up to 40 m (Wheeler and Rissing 1975a). Column direction can change daily, with a complete rotation about the nest every 2–3 weeks. Rate of rotation is dependent upon seed availability, but even in years of high seed production, the column continues to rotate (Rissing and Wheeler 1976) suggesting a multi-functional column. Contact with neighboring columns occurs regularly and results in fighting, frequently over long periods of time (Went et al. 1972; Wheeler and Rissing 1975a). Furthermore, foraging columns raid and destroy conspecific starting nests (personal obser-

vation). Such intraspecific aggression provides a colony with exclusive use of a foraging area. When seeds are limiting (see below) such exclusivity may prove advantageous.

Intra-colony aggression occurs among starting *V. pergandei* colonies as well. Workers from newly opened colonies engage in inter-nest brood raiding followed by worker defection from "defeated" colonies. Colony foundation by multiple queens, pleometrosis, is common in *V. pergandei* (Pollock and Rissing 1985). Pleometrotic colonies open faster and almost always (16 of 19 trials) defeat haplometrotic (single queen) colonies (Rissing and Pollock, in press). Production and maintenance of a large worker force via pleometrosis seems essential to the success of starting colonies. Whether adult or starting, the demands of territoriality would seem to provide an advantage to colonies with larger worker forces.

The "trunk trail" foraging system of *P. rugosus* contrasts with the territorial dynamics of *V. pergandei*. Trunk trails change slowly, if at all, suggesting seeds are much less limiting for the former (Hölldobler 1976; Davidson 1977). Rather than exclude conspecifics from an area for future exploitation, trunk trails appear to minimize contact and conflict with neighbors (Hölldobler 1976). *Veromessor pergandei* is most abundant in the Mohave Desert, which is physically and temporally less predictable than the Sonoran Desert, where *P. rugosus* is more common (Creighton 1950). Probability of limited nest sites and a less extensive and predictable food base in the Mohave (Tevis 1958; Davidson 1977) imply increased intraspecific competition for resources and consequently an increased need for maintenance of a large, more constant, worker force in *V. pergandei* relative to *P. rugosus*.

If *V. pergandei* worker size variance is a mechanism to maintain a constant, large worker force, size of developing larvae should be lowest when resources for worker production are most limited. Throughout the Mohave and drier portions of the Sonoran Desert seeds are produced in an annual Spring "pulse" in response to Winter rains (Beatley 1974; Nelson and Chew 1977). Decreasing availabilities of preferred seeds late in the year correspond to shifts to less preferred seeds and increasingly limited foraging times due to colder weather. At this same time *V. pergandei* reproductives are likely produced, for colonies release reproductives from late January–March (Pollock and Rissing 1985) and, as with most other ant species (Wheeler and Wheeler 1963), alate production should occur soon before this. While *V. pergandei*

colonies store seeds (see Fig. 5 of Wheeler and Rissing 1975b), these reserves must be drawn upon during Winter and cannot be replenished until subsequent weather changes and seed set. In short, *V. pergandei* colonies experience a "triple crunch" from November through February (reduced availability of seeds, especially preferred ones; reduced periods favorable for foraging; and alate production). Given the estimate of 60 days to go from egg to newly eclosed adult (Wheeler and Wheeler 1976) and some additional amount of time to go from nest worker to forager (for *Atta cephalotes*: 16 weeks from egg to forager [Wilson 1983]), workers produced during this "crunch" period should appear in the foraging force in late Spring and early Summer. Similarly, larger workers, fed by abundant seeds harvested during Spring, should appear in the foraging force in late Summer and early Fall. Both expectations correspond to observations reported here (Fig. 1).

Reproduction results in reduced production of large workers in other social insects. *Pheidole dentata* produces fewer soldiers during alate production (Johnston and Wilson 1985). Similar annual variation in caste proportions is correlated with seasonal production of alates in a termite (Bodot 1969). Starvation of a termite colony also results in a reduction of soldier production (Su and La Fage 1986).

Task specificity with primitive polymorphism

Given the primitive polymorphism of *V. pergandei*, task performance capabilities of workers should be broad with little morph-specific task performance. Correlation between forager size and seed size in this species is weak and frequently nonexistent (Davidson 1978; Gordon 1978; Rissing and Pollock 1984). Mean forager size in a given month is not correlated with mean seed mass harvested in that month (see above). Larger workers may preferentially clip seeds from plants during a brief period of time prior to seed fall (Gordon cited in Oster and Wilson 1978), but this is not always the case (Table 2) and seems unlikely to explain the entire adaptive value of *V. pergandei* worker size variance. Larger workers in column foraging species such as *V. pergandei* may travel greater distances for seeds (Bernstein 1979); this, however, does not occur in *V. pergandei* (Rissing and Pollock 1984). Other specific tasks such as nest excavation and colony defense are similarly independent of worker size (Table 2).

Variation in forager body size of *V. pergandei* across its geographic range has been interpreted

as a function of interspecific exploitative competition (Davidson 1978). While this hypothesis is not necessarily mutually exclusive with the intraspecific competition hypothesis proposed here, the degree of worker size variation within a single *V. pergandei* colony suggests point samples from many colonies are inadequate to test the interspecific hypothesis. For example, a single nest displays similar levels of variance in the course of 1 year as reported from the entire range of this species. Using the allometric equation: HW (mm) = 1.993 × mandible length (mm) - 0.217 ($r=0.98$, $n=94$; Rissing, unpublished data), the smallest and largest populations of *V. pergandei* reported by Davidson were from Barstow, CA (mean HW = 1.23 mm) and Gila Bend, AZ (mean HW = 1.42 mm) for a range of 0.19 mm. The mean range of the annual cycle of the 6 adult *V. pergandei* colonies in this study was 0.16 mm (Table 1). Size-frequency distributions implicating "character shifts" in response to other seed-harvester species (Fig. 3 of Davidson 1978) can be generated from a single colony during a single year (Fig. 2). Similarly, the CV, which varies geographically from 16.22 (Mojave, CA) to 8.55 (Casa Grande, AZ) for a difference of 7.67 and which appears correlated with the diversity of granivorous ant species within a habitat (Fig. 2 of Davidson 1978), varies up to 14.19 within a 12 month period at a single nest (for BGVp3, Oct. 1982 CV = 7.16; June 1983 = 21.35) and up to 13.52 when the linear trend on time (discussed above) is removed (for BGVp3, Oct 1982 CV = 7.02; June 1983 = 20.54). Mean greatest change in CV during any 12 month period in the 6 adult colonies studied was 11.67 (and 11.47 when the linear trend on time is removed). Some geographical variation in the size-frequency distribution of *V. pergandei* at the same time might also occur under the hypothesis proposed here if there is any corresponding variation in the timing and extent of seed production, winter limitations on foraging, and/or colony reproduction causing a shift in the phase of the annual cycle among distant sites.

The feedback and control mechanism(s) by which a social insect colony generates its size-frequency distribution of workers is poorly understood and quite intriguing (Wilson 1985). Under the hypothesis proposed here for *V. pergandei*, feedback is immediate, and control is simple and direct: when resources are limiting, reduce larval nutrition to maintain worker number. If, however, colonies are producing workers in anticipation of future seed availability, feedback and control is complex and the annual cycle in worker variance found here more difficult to explain. Given the

somewhat surprising inability of species much more polymorphic than *V. pergandei* to respond to strong selection to adjust ratios of newly produced workers (e.g. removal of >90% of the leaf-cutting size class in *Atta cephalotes* [Wilson 1983] or near continual exposure to a major predator [Johnston and Wilson 1985]) such overt control of worker sizes produced by a *V. pergandei* colony seems unlikely.

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Appendix

On the use of time series analysis in social insect colony demography

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Any periodicity may be given the form

$$k * \sin(2\pi * (t + B)/P) \quad (1)$$

where

k = the period's amplitude,

t = time,

B = a constant which defines the zero point of the cycle as $-B$

(Since the temporal scale must have an arbitrary origin,

B is always contingent on this origin.), and

P = the cycle's period.

For any given period both k and B must be estimated. (1) may be re-written as

$$k * \sin(2\pi * (t + B)/P) = k * (\sin 2\pi t/P) * (\cos 2\pi B/P) + k * (\cos 2\pi t/P) * (\sin 2\pi B/P)$$

Let

$$\beta_s = k * (\cos 2\pi B/P), \quad \beta_c = k * (\sin 2\pi B/P) \quad (2)$$

then

$$k * \sin(2\pi * (t + B)/P) = \beta_s * \sin 2\pi t/P + \beta_c * \cos 2\pi t/P$$

Let the original time series be indexed by $y(t)$. Then to test whether this series exhibits a cycle of period P we need only estimate

$$y(t) = C + \beta_s * \sin 2\pi t/P + \beta_c * \cos 2\pi t/P$$

through standard regression techniques (Johnston 1984). Significant t-values for either β_s or β_c indicate the presence of a cycle of period P . When both are significant k and B may be recovered from (2) as

$$B = (P * \tan^{-1}(\beta_c/\beta_s))/2\pi$$

$$k = \beta_s/\cos(2\pi B/P) = \beta_c/\sin(2\pi B/P)$$

so that the cycle may be expressed in the simple form of (1). Ignoring the sign of the amplitude, the low point of a cycle is then given as

$$t_{\text{low}} = (I + 3/4) * P - B$$

where I is an integer. When $k < 0$ the observed low point will be phase shifted by $-P/2$.

Without an a priori defined cycle, P must be derived in an exploratory fashion. The series may be submitted to a spectral analysis (Koopmans 1974) or, alternatively, a series of regressions may be performed where the period of the i th regression is given by

$$P_{i+1} = P_i + \Delta t, \quad P_0 = \Delta t$$

where Δt is a fixed increment. An increasing r^2 indicates the iterative regressions are in the neighborhood of a true periodicity; further iterations using smaller increments within this neighborhood permit a finely tuned estimate of this periodicity. Once a period is identified, the residuals from this estimate may be examined for further cycles. Thus through a set of imbedded iterative regression techniques (Mosteller and Tukey 1977) several cycles may be identified until the residuals appear exhausted.

Upon completion a fully specified time series has the form

$$y(t) = C + \sum_{i=1}^N k_i * \sin(2\pi(t + B_i)/P_i) + f(t) + e(t)$$

where P_i is the i th of n cycles identified and $f(t)$ represents any non-periodic temporal functions, such as a linear trend.

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