

resumed mate-finding and self-advertisement as soon as copulation was complete.

Using an approach based on game theory³⁴, I compared the effects of guarding versus searching on the fitnesses of male Idaho and Belding's ground squirrels (Table 2). These analyses suggest that mate guarding in Idaho ground squirrels is evolutionarily stable, largely because (1) locating receptive females is time-consuming for males and requires them to range widely (Table 1), which is dangerous, (2) obtaining sexual access to guarded females is difficult for all but the largest males, (3) unguarded females will mate multiply (Fig. 1a), thus diluting the first male's paternity, and (4) the longest (last) guarding male sires the majority of the litter (Fig. 1b). In contrast, conditions 1, 2, and 4 do not apply in Belding's ground squirrels and, as a result, resumption of mate searching after copulating is the evolutionarily stable state. The phenotypic costs and genetic consequences of mate guarding versus resuming searching merit investigation in other animals. □

Note added in proof: D. W. Foltz and P. L. Schwagmeyer have just reported³⁵ that $75 \pm 0.8\%$ ($n = 8$) of 13-lined ground squirrel

litters are sired by a female's first mate; this species thus closely resembles *S. beldingi* in both male post-copulatory behaviour and sperm usage pattern (Table 2).

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TABLE 2 An analysis of mate guarding behaviour versus resuming mate searching subsequent to copulating for male Idaho ground squirrels and Belding's ground squirrels, using game theory to find the evolutionarily stable state.

<i>S. brunneus</i>	<i>S. beldingi</i>
For guarding to be evolutionarily stable,	For not guarding (resuming searching) to be evolutionarily stable,
(1) $E(G, G) > E(N, G)$	$E(N, N) > E(G, N)$
Is it? If so,	Is it? If so,
(2) $[(g)(\Delta p)(l)]/t_g > [(1 - \Delta p)(l)]/t_s$	$[(1 - \Delta p)(l)]/t_s > [(g)(\Delta p)(l)]/t_g$
(3) $[(0.73)(0.83)(5.20)]/2.90 > [(0.43)(4.40)]/0.40$	$[(1)(0.57)(4.40)]/3.50 > [(0.43)(4.40)]/0.40$
(4) $1.1 > 0.7$	$4.7 > 0.7$
(units: offspring per hour)	(offspring per hour)
Conclusions	
Guarding is evolutionarily stable	Searching is evolutionarily stable

Schwagmeyer and Parker⁷ adapted the 'optimal diet' model of MacArthur and Pianka³⁶ to explore the relative payoffs of mate guarding versus resuming searching by male 13-lined ground squirrels (*S. tridecemlineatus*), a species in which males do not guard. They showed that guarding a female who has just been mated (G) is evolutionarily stable against invasion by non-guarding behaviour (N) when, in a population of guards, the expected reproductive benefits per unit time from guarding $E(G, G)$, exceed the expected gains per unit time from leaving the female and resuming searching $E(N, G)$, (inequality 1 for *S. brunneus*). Likewise, a non-guarding population (for example, *S. beldingi*) is resistant to the invasion of guarding behaviour when $E(N, N) > E(G, N)$. Expected gains from G and N behaviour depend on the parameters in inequality 2. For *S. brunneus*, these parameters are: g , the probability that a male can successfully guard his mate from other males, estimated as: $19/26 = 0.73$ (assuming that overthrown males gain no further matings); Δp , the increase in the probability of paternity due to guarding, calculated as: $1 - [\text{probability of paternity if the male does not guard}] = 1 - [(0.2) \times (\text{the likelihood that the abandoned female mates once more}) + 0.1 \times (\text{the likelihood that she mates twice more})] = 1 - [(0.2)(5/7) + (0.1)(2/7)] = 0.83$; see Fig. 1); l , the average litter size (5.2); t_g , the mean length of time a female is guarded (2.9 hours); and t_s , the mean time it takes a searching male to acquire a subsequent mate (estimated as 1.3 hours, the time it took defeated males to locate a new female). Note that both t_g and t_s are estimated conservatively relative to the inequality being examined; furthermore, predation risks, which make searching even more unfavourable, are not considered in the model. For *S. beldingi* the parameters in inequality 2 are defined similarly, but calculated differently: g is assumed to be 1.0 (that is, if males did guard females, they would do so effectively; this is the most conservative assumption relative to the inequality); Δp is calculated from the relative frequency of mating with 1–5 males³³ and the probability of paternity of the first male given that the female he leaves mates with 0–4 males subsequently (these values are $[(0.16)(1) + (0.26)(0.6) + (0.26)(0.3) + (0.26)(0.1) + (0.06)(0)] = 0.43$, so $\Delta p = 0.57$), l is 4.4 (ref. 31); t_g is assumed to be the length of the receptive period (3.5 h; ref. 30); and t_s is 0.4 hours.

Foraging specialization without relatedness or dominance among co-founding ant queens

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HYPOTHESES on the evolution of sociality in the Hymenoptera have focused on two non-exclusive selective processes. First, individuals may help relatives to enhance inclusive fitness (kin selection^{1,2}). Second, group living may be so highly advantageous that competitively inferior individuals are forced into subordinate roles through social competition^{3–7}; in this hypothesis, subordinates help dominants in the expectation that they may benefit from the group's resources if the dominants lose status or die. Many

social Hymenoptera associate predominantly with close relatives^{8,9}, which precludes an effective comparison of kin selection and social competition. Here we report on the existence of foraging specialists among unrelated co-foundresses of the leaf-cutter ant *Acromyrmex versicolor*; such task specialization leaves the forager at a relative fitness disadvantage within her foundress association. Contrary to the predictions of social competition theory, individuals specialize independently of competitive ability (as measured by relative body size) or reproductive status (as measured by ovarian condition) and without conflict. The selective basis of foraging specialization may lie in the intense competition that occurs among newly founded colonies engaged in reciprocal brood raiding.

In many ant species colonies are initiated by multiple foundresses¹⁰. As in other co-founding ants, *A. versicolor* foundresses do not associate preferentially by collection locale in laboratory experiments, suggesting that associations need not consist of close relatives^{11,12}. To confirm this, we estimated within-group relatedness^{11,13} from 26 field-caught foundress associations using allozymes as genetic markers. Of 30 tested, one locus was polymorphic¹⁴. Co-foundresses were no more closely related than randomly selected queens ($\hat{r} = -0.12$, s.e. = 0.03, estimated by a jack-knife over groups¹⁵). The negative \hat{r} and small s.e. imply that genotypes are distributed more evenly across groups than would be expected under random association. The negative \hat{r} is probably a sampling artefact caused by small group size ($N = 3.8$) and unequal allele frequencies; we do not infer that kin avoid each other¹⁶. We conclude that associations constitute random samples of the population, precluding kin selection as an explanation for social traits¹⁷⁻¹⁹.

Among co-founding ants, *A. versicolor* is unique in that foundresses regularly leave the nest to forage before the emergence of the first workers. Foragers are exposed to greater risks of predation and parasitization, and to greater thermal and physical stresses than their sedentary nest-mates²⁰⁻²². Nonetheless, leaves procured through foraging are shared communally in a single fungus garden. Foraging thus enhances colony fitness at the expense of a forager's relative intracolony fitness^{18,19}. As among co-founding wasps, foraging is a task in which specialization might indicate an incipient reproductive division of labour^{5,23}, a likely precursor to the evolution of permanent worker sterility which is characteristic of most social hymenoptera^{5,20,23,24}.

To study the distribution of foraging effort within colonies, we established eleven colonies, each with three newly mated foundresses collected immediately after a mating flight on 23 September 1987 at North Scottsdale, Arizona. To ensure substantial size variation within each association, the mass of each foundress in an association was arranged to be at least ± 1 standard deviation (equal to 1.04 mg) from the mass of the other two foundresses. Foundresses were marked, housed in 'ant

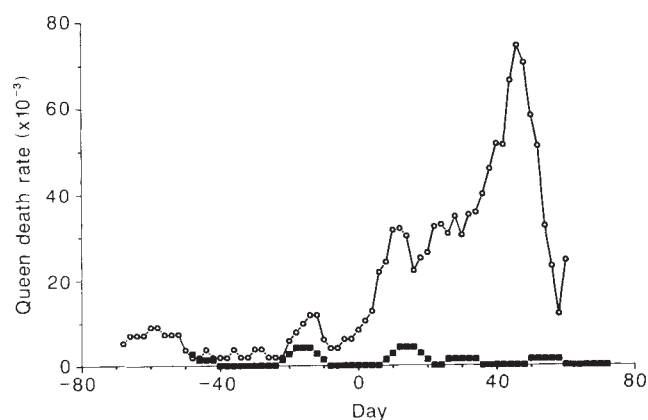


FIG. 1 Comparative rates of foundress mortality in *A. versicolor* (squares) and the ant *Veromessor pergandei* (circles), which displays more typical behaviour for cooperatively founding ants (data for *V. pergandei* from ref. 25). Queen death rate is calculated as the percentage of all the foundresses alive at the start of a 2-day period who died during that period; it is displayed as a 3-point moving average. All observations in each nest are standardized to day of first worker emergence (day 0) in that nest. *V. pergandei* and most other cooperatively founding species reduce to secondary monogyny soon after first worker emergence²⁸.

farms' and offered fresh native vegetation in attached foraging arenas, according to standard procedures²⁵. Farms and associated arenas were placed on a mechanized circular surface which rotated under a video camera. Foraging trips taken by each co-foundress in each association were censused from video records of 6-hour foraging sessions (57 sessions over 14 weeks). Sessions began immediately after colony formation and ended when workers assumed foraging tasks. Farms were not offered food between sessions. In each association virtually all foraging trips (average was 165 ± 69 trips per farm) were performed by a single foundress ($P < 0.001$ in each case); the only exceptions occurred in two associations where a single secondary forager appeared after the death of the first foraging specialist.

Another 34 farms were similarly established to see if specialization in foraging was a function of potential competitive ability, as measured by relative size. These farms were spot-sampled 8 times per day for 15 weeks to estimate the number of foraging trips taken by each foundress. Chi-square analyses indicated the existence of a foraging specialist in 44 of the 45 farms in the two samples combined; the role of foraging specialist was independent of initial relative size (Table 1). At the conclusion of these experiments, all co-foundresses from 18 associations were dissected to measure primary oocyte number and size

TABLE 1 Social correlates of reproductive status among *A. versicolor* co-foundresses

	Relative initial mass*			Foraging status	
	Large	Medium	Small	Forager	Non-foragers
Forager	18	16 ($X^2 = 2.36$; NS)	10		
Number of primary oocytes (\pm s.d.; N)	8.2 (2.9; 18)	8.6 (1.9; 18) ($F = 0.01$; NS)	8.4 (2.1; 18)	8.6 (2.2; 18)	8.5 (1.9; 35) ($t = 0.17$; NS)
Primary oocyte length, mm (\pm s.d.; N of queens)	0.51 (0.11; 16)	0.53 (0.12; 16) ($F = 0.70$; NS)	0.56 (0.17; 16)	0.52 (0.10; 16)	0.54 (0.12; 32) ($t = 0.38$; NS)
Number of total oocytes (\pm s.d.; N of queens)	18.56 (13.32; 18)	20.28 (16.43; 18) ($F = 0.06$; NS)	19.50 (14.56; 18)	20.37 (15.34; 19)	18.94 (14.32; 35) ($t = 0.34$; NS)

* Each foundress in each association was ≥ 1 s.d. in initial mass from the other 2 foundresses in that association, such that the total number of 'large', 'medium' and 'small' foundresses was the same over all foundress associations.

(routine assays of reproductive conditions^{20,26,27}). Reproductive condition was independent of body size and foraging specialization (Table 1); all foundresses had well developed ovaries and therefore presumably functioned as queens. During spot sampling, farms were examined for evidence of aggression that might induce a 'loser' to become a foraging specialist; in addition, the interiors of two colonies were videotaped for an average of 79 h per colony. We never saw aggression among foundresses, nor acts of ritualized dominance such as occur among some Polistine wasps^{5,23,27} (for example, asymmetric antennation, allogrooming or trophallaxis). Access to brood or fungus, the principal resources of a colony, was never contested by, nor denied to, any co-foundress. Unlike other cooperatively founding ants^{25,28} and some bees²⁰ and wasps²⁹, *A. versicolor* foundresses do not fight on first worker emergence (Fig. 1), and they share resources cooperatively for at least 1.5 yr in laboratory colonies.

The primary benefit of Hymenopteran foundress associations is believed to be defence against enemies^{20,27,30}; in some ants, the enemy is conspecific. Newly founded nests are often clumped spatially, and they engage in reciprocal brood raids; colonies with more workers (and queens to produce them) tend to prevail^{10,25,31}. This pattern is seen clearly in *A. versicolor*, where newly founded colonies are highly clumped¹², yet adult colonies are territorial³²; from a group of new colonies, only a single adult colony will survive. We marked workers in 16 ant farms and paired them to common foraging areas. Brood, leaf and fungus raids occurred. Of 163 raids, 131 involved marked workers; these workers always displayed fidelity to their natal colony. Fighting among workers, and between workers and foreign queens, was common. In each pairing only a single colony survived.

As only one colony from an initial cluster of colonies will survive to adulthood, relatively small differences in colony efficiency could cause large differences in ultimate colony reproductive success. An increase in foraging efficiency should translate to a similar increase in quality of initial raiding force and, ultimately, success in eliminating rivals. Foraging social insects enhance their efficiency through experience^{26,33,34}. An *A. versicolor* foraging queen gains experience as she gathers leaves; to refuse further foraging squanders the former resource. Yet each queen should prefer her colony mates to forage, but the simultaneous expression of such preferences would reduce colony fitness; energy and time spent in intragroup conflict over task allocation would limit the colony's future competitive potential^{11,35}. Under these circumstances, a foundress may be relatively indifferent as to whether she is the one that suffers the mortality risk associated with foraging, because the colony will either succeed as a unit or (more probably) fail as a unit. □

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Glycine enhances NMDA-receptor mediated synaptic potentials in neocortical slices

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ONE class of excitatory amino-acid receptors, the *N*-methyl-D-aspartate (NMDA) receptors, mediates transmission at a small, but important, group of synapses in the neocortex^{1–3}. These receptors are implicated in neuronal plasticity during development in young mammals and in memory acquisition in adults^{4–6}. Recently, responses of isolated membrane patches to NMDA were shown to be greatly enhanced by glycine⁷. This, together with the demonstration that the strychnine-insensitive glycine-binding site is distinct from, but linked to, the NMDA receptor⁸ has excited intense interest in glycine as a synaptic modulator. Before proposing a physiological function, however, it is important to determine whether glycine could enhance synaptic responses to NMDA receptor activation in intact, adult tissue. An earlier study⁹ failed to demonstrate enhancement of NMDA responses when glycine was applied and it was proposed that in intact tissue the high-affinity glycine site was already saturated by endogenous glycine. It remained possible that glycine concentrations can be maintained at low levels close to synaptic receptors. We have examined responses of neurons in slices of adult neocortex to focal applications of excitatory amino acids and glycine and report enhancement by glycine of NMDA receptor-mediated excitatory postsynaptic potentials.

So that small synaptic responses could be recorded intracellularly under controlled conditions, we used slices of adult neocortex, which does not contain any strychnine-sensitive glycine-binding sites¹¹. The perfusing fluid was delivered at a low flow rate (less than 0.3 ml min⁻¹) to allow metabolic products, transmitters and modulators to be controlled by natural release, degradation and uptake processes, rather than by the perfusion system.

In all cells tested in which rapid-onset, repeatable responses to electrophoretically applied excitatory amino acids could be evoked, glycine enhanced responses to NMDA (mean increase in amplitude 100.00 ± 65.75% s.d., range 22–284%, *n* = 38), but produced no significant change in responses to quisqualate (mean increase 4 ± 28.54%, range, 50% decrease to 20% increase). The effective glycine concentration is not known, but maximal effects were produced with ejection currents of less than 4 nA (Fig. 1). The responses when glycine was dissolved in acidic and alkaline solutions were similar. The effects of