

give preferential treatment to the ergatoids.

What selective pressures could cause the queens to adopt a worker-like appearance? Haskins and Haskins (1950) suggested that ergatoids are often found in "those forms in which wing-muscle degeneration does not occur and where foraging of the colony-founding queen is the rule". This may partly explain the frequent occurrence of ergatoids in the Ponerinae. The partially-claustral mode of colony foundation is a precarious strategy which is successful only within a certain range of ecological conditions (see 7.2.). The more advanced fully-claustral mode was derived through increased divergence in the size of queens and workers and the subsequent increased utilization of wing muscles by the lone foundress. An alternative evolutionary progression appears to have been loss of wings and reduction in thoracic musculature, i.e. the ergatoid strategy. Haskins (1970) presents evidence that in Myrmecia, the presence of wings is not always advantageous. Wingless and brachypterous females sometimes coexist with the normal forms, and they seem to be equally successful during colony foundation. The loss of wings in many ponerine ants affects the pattern of dispersal but not the partially-claustral mode of colony foundation. This suggests the nature of the selective advantages associated with the ergatoid modification. There may be a high mortality during aerial dispersal, or it may be safer to be mated near the nest. A change to colony fission may also be implicated, but the pattern of colony reproduction in species with ergatoids is very poorly understood. Ergatoids are often found in socially-parasitic myrmecines (Wilson 1971), and a consideration of their reproductive behaviour may indicate some of the evolutionary pressures involved with the loss of wings.

Where either colony foundation by winged queens or by ergatoid queens was unsuccessful, it is suggested that breeding workers assumed the reproductive role.

7.4. Transition from queenright to worker breeding system

The substitution of the queen caste by mated workers was made possible in the ponerines through a number of preadaptations. Workers in the phylogenetically-primitive formicid groups have retained functional ovaries and a spermatheca. In contrast, in the higher ants, the workers have often lost the ability to produce diploid eggs. The morphological differentiation between queen and workers is slight in the ponerines (Haskins 1970; Odontomachus, Brown 1976). Trophallaxis does not exist between ponerine adults, and this has two important consequences. Workers appropriate the food that is brought into the nests for themselves only and are thus able to accumulate fat reserves; this is then available if the ovaries become active. This is analogous to the situation in orphaned colonies of many species, where workers are able to produce male or trophic eggs, possibly because they no longer have to regurgitate to the queen. Absence of trophallaxis also implies that the queen has to ingest raw food, which limits her rate of egg production. The relatively small colony size may be an effect of the low fecundity of the queens. Colombei (1970) (in Brown 1976) estimated that a mature queen of Odontomachus troglodytes lays 2,5 eggs per day. The lack of a drastic divergence between queens and workers makes it more feasible for the latter to replace the queens. In addition, workers possess a pygidial gland, and the signal produced from it may enable the males to recognize suitable sexual mates (Chapter 6). At a functional level, worker reproduction necessitates colony reproduction through fission, and thus appropriate fragmentation mechanisms are required, eg. O. berthoudi has polydomous colonies, and Ward (1981a) observed frequent nest emigrations in the Rhytidoponera impressa group.

What was the reproductive system in those ancestral species which gave rise to breeding workers? Ward's (1981b, 1983) data on the Rhytidoponera impressa group suggest that evolutionary

changes followed path (b) in Figure 13; winged queens and gamergates occur in the same species (although they never coexist in one colony). I suggest an alternative pathway, which would involve a two-step process via path (a) and (c). Thus the hypothetical lost queen may have been ergatoid in some cases.

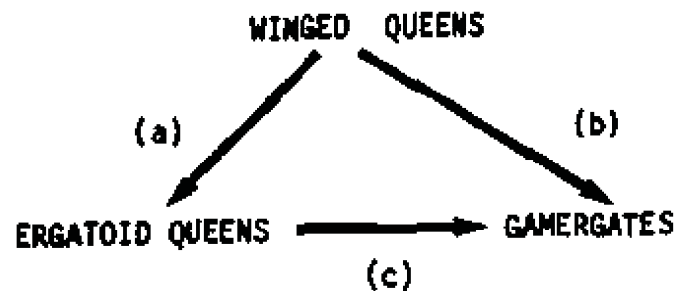


Figure 13 Hypothetical scheme of evolutionary changes leading to the disappearance of winged queens.

As was shown in 7.3., the change in queen morphology which occurred through the loss of wings (path (a), Figure 13) is a strategy very distinct from that of worker reproduction. Was the ergatoid strategy successful? Not many extant ponerine species have ergatoids, and there may be more species in fact that have gamergates. Loss of wings might be adaptive only under a narrow range of environmental conditions, and if these change the species are in an evolutionary cul-de-sac. The winged condition cannot be re-evolved, and worker reproduction may be the only solution.

The two alternative evolutionary schemes need to be considered in view of the necessary changes in male behaviour. The pattern of male dispersal must at all times be coadapted with the activities of the female partner. Many formicids disperse and mate on highly-coordinated mass nuptial flights, which act as an orientation cue for the sexuals from different colonies to meet. This mode of dispersal is however an advanced trait which

is not exhibited in the majority of queenright ponerine species (reviewed by Haskins 1970). I have witnessed the synchronized exit of male and female winged reproductives of the queenright Paltothyreus tarsatus in Mkuzi Reserve; this occurred at the end of a sunny morning following the first summer rains. The virgin queens landed singly on bushes and other vegetation. Individual females then presumably released a sex pheromone because flying males soon appeared and were observed to mate with them. This is similar to the behaviour in Amblyopone pallipes (Haskins 1978). Thus the males fly around searching for individual virgins, and the chances of success are enhanced because the alates of both sexes are active simultaneously.

In species with ergatoids the mating activities occur near the nests. Males locate their mates on the ground, and the latter seldom disperse very far from their nests. Males of Leptogenys use ground-laid recruitment trails to locate ergatoids (Maschwitz and Muhlenberg 1975). There is no reason to assume that the ergatoids (still a distinct reproductive caste, see 7.3.) do not leave their nests together with the males. The synchronization is probably mediated through the release of mandibular gland secretions by the males (Buschinger 1975). As a result males search for ergatoids when these are out of their nests and releasing sex attractants. The next step in the evolutionary series occurs when males use trails to orientate to foreign nests (as in Megaponera foetens, Longhurst and Howse 1979). Thus the male strategy now consists of finding nests, not individuals anymore. This switch in male behaviour has significant consequences for it brings the sexually-mature males in contact with the workers, a necessary prerequisite for worker mating.

In those species where the queen caste has disappeared, suitable workers are mated inside or in the vicinity of their nests. In O. berthoudi copulation occurs inside the nests, and this may suggest that they were derived from an ancestor with ergatoid reproductives. In Rhytidoponera metallica and R. chalybaea (Hölldobler and Haskins 1977, Ward 1981b), males copulate with workers outside the nest entrances, and this may be

related to the occasional presence of winged queens in these species (Whelden 1960, Ward 1981b). In R. chalybaea the virgin queens and the males leave the nests together. This may be associated (as in other Formicids) with the swarm of a large number of workers which mill around the nest entrances. These workers are of different ages and thus males can come across those that are sexually-attractive, again a prerequisite for worker reproduction.

7.5. Why have queens not re-evolved?

Crozier (1982) has pointed out that the evolutionary expectation in those species of Rhytidoponera where queens have been replaced by a "coterie of mated workers" is that queens should re-evolve. This has not happened in Ophthalmopone berthoudi (see 3.3.2.), where there is an obvious lack of specialization in the reproductive individuals. No morphological differentiation between breeding and sterile workers was ever detected. There is a pair of ovaries with three short ovarioles, and the large yolky eggs are laid singly and at a slow rate. The simplicity of the ovaries of the egg-layers reflects their worker nature and dictates cooperative breeding by multiple fertile individuals. Why does a secondary differentiation within the worker caste not take place? This would lead to the evolution of a class of fecund egg-layers with elaborate ovaries and possibly smaller eggs, and these would mate to the exclusion of all others in the colony.

Ponerine workers can produce trophic or male eggs in species which have retained queens. Workers lay haploid eggs in the absence of the female parent in Rhytidoponera purpurea (Haskins and Whelden 1965), and male as well as trophic eggs are produced in Odontomachus troglodytes (Colombei 1972a). This oogenesis may have formed the basis for the production of fertilized eggs. In O. berthoudi, slight physiological modifications throughout the worker caste made the ovaries more suitable for this purpose. Ineffective breeding workers are eliminated by natural selection

since they produce few or no eggs. However there has been no further elaboration of the reproductive organs, and there has been no reduction in egg size. There is no selective advantage for large yolky reproductive eggs being laid in a social environment (in contrast to the solitary mutillids, where large eggs need to be laid). As there is no trophallaxis between workers and queens in this ponerine species, the reproductive investment of each breeding worker is restricted by the amount of food it can acquire. A decrease in the energy used per individual egg should be selected for, since with the same expenditure of material, fecundity could be increased. It may be that the large eggs of O. berthoudi are a legacy of a past trophic function, and that this design could not be subsequently changed. Other species of ponerines with gamergate reproductives have large eggs (Paeters unpublished data). The eggs in the queenless Pachycondyla krugeri are large (1,6 x 0,6 mm), while the congeneric, queenright P. wroughtoni (Forel) has typically small Formicid eggs. Large eggs may be an inherent characteristic of worker reproduction in the Ponerinae.

Genetic changes which increase the fecundity of individuals should sweep through a population rapidly, since reproductive success is the only possible basis for the operation of natural selection (Williams 1966). Fecundity in species exhibiting maternal care is limited not just by the energetic cost of egg production, but also by the time and energy invested in brood care. Indeed, the survival of the offspring to breeding age is essential for the realization of reproductive success. Mothers of eusocial insects do not carry the burden of feeding their own offspring, since all the ants in the colony contribute to the rearing of the larvae. Hence there are fewer constraints on the size of their reproductive investments. There are small differences in ovarian activity among breeding workers of O. berthoudi (see 3.3.2.). Thus some individuals do produce more daughters than the average and these daughters have the same chance of reaching breeding age as the offspring of other egg-layers. In spite of the destruction of gene combinations during meiosis and recombination, fitter genotypes should increase their

representation in the nest population. The lack of marked differences in fecundity between the workers in the queenless colonies of O. berthoudi might be traced, firstly, to the nature of the control of their reproductive division of labour, and secondly, to a stabilizing selection which prevents specialization in their unpartitioned nest populations.

The salient feature of eusociality is the presence of individuals that are obligatorily sterile. Usually only the reproductive caste has an opportunity to engage in sexual reproduction. The sterile workers are restricted to performing all the other activities essential for colony maintenance. In O. berthoudi however, all the workers have the potential to become reproductive, and thus they can fulfil both functions in the colony. Insemination determines whether they fall into one category or the other. It is the limited period of male activity that restricts the incidence of mating, and only those ants which are present and which are sexually attractive during February to March can copulate with the males. Diploid eggs are laid for most of the year, thus producing a continuous sequence of young individuals. Since the workers live for less than one year, the short period of sexual receptivity of many individuals does not coincide with the mating season. The breeding workers would be expected to synchronize the production of their own offspring with the activity of males, but they do not appear to be able to time their egg-laying (i.e. by recognizing appropriate seasonal cues). As a consequence the timing of birth is not genetically controlled. The ants not born at the appropriate time of the year cannot become inseminated, and they remain non-reproductive. Thus a chance factor is introduced into the reproductive differentiation. Only a fraction of the sequentially-born daughters of "fitter" egg-layers can pass on their genes to the next generation. In addition, since the males cannot discriminate between potential mates on the basis of relative ovarian capabilities, all the workers of an appropriate age present in a nest have the same probability of becoming mated, including those with inferior ovarian apparatus. Since birth and mating are influenced by stochastic factors, many

superior gene combinations are lost. Furthermore, the less effective reproductive genotypes continue to circulate in the population because they are not selected against. Thus directional selection is expected to be ineffective in such a breeding system. It has not produced any changes over a great many generations. There may however also have been an opposing selective pressure acting against further reproductive specialization in the workers.

The genotype in O. berthoudi cannot become partitioned because of the nature of the control of oviposition, and this necessitates a "phenotypic compromise" between worker and reproductive attributes. The majority of the ants in these societies do not become reproductives, and they carry on their short lives as labourers. Colony survival is dependent on an effective worker force, especially since the breeding workers never leave the nests or participate in any of the maintenance activities. Ovarian improvements throughout the worker caste cannot be achieved at the expense of traits needed in non-reproductive colony members. In addition, if there are pleiotropic genes coding for fecundity or ovarian structure, these may have a negative effect on other characteristics needed for effective performance as a labourer. It is also possible that the mechanism of gene expression responsible for caste differentiation could not be re-evolved in this species. Selective pressures operate on a common worker "genetic programme" which must be sufficiently plastic to produce two functionally-distinct types of individuals. Thus only limited specialization is possible because of the lack of genetic compartmentalization.

Secondary reproductive differentiation in the worker caste could occur if there were only one generation of workers per year, since directional selection would then be effective. It is however impossible within the constraints of an existing eusocial system. As a result of the overlap of generations only a small sample of the workers can become mated. The social alterations exhibited by O. berthoudi were sufficient to enable continued survival in a particular environment. Since the

system works, directional selection pressures on it are unsuccessful. Were local conditions to become sub-optimal, this species might become extinct if survival were conditional on the development of a more efficient group of breeding workers.

These considerations suggest what the cardinal features of the evolution of a sterile caste in proto-formicid societies may have been. Haplodiploidy enables control of the sex ratio. While the timing and extent of haploid egg production were restricted, the production of female individuals was increased and staggered over the year. This gradually prevented many females from participating in sexual reproduction and hence forced them into the role of non-reproductive nestmates. Thus kin selection or queen oppression may not be responsible for the origin of castes with different reproductive potentials. Mechanistic explanations (Crewe 1982b) based on life history details can explain the control of the reproductive division of labour in O. berthoudi. They may similarly account for many enigmas surrounding the evolution of eusociality.

Crozier (1982) raised the question of what holds colonies of Rhytidoponera together in view of their very low intra-colony relatedness. This study on the biology of Ophthalmopone berthoudi indicates that colony odour is a fundamental aspect of eusocial organization. Despite the absence of the queen caste and a predicted low kinship within the colony, nestmate recognition maintains the social integrity of a group of workers. The viability of this eusocial alternative suggests that a reconsideration of some of the traditional views on the role of queens in the regulation of colonial life is timely.

APPENDIX A

Partial transcript from a computer-generated print-out, listing the activities performed by different ants from colony (3a) during an observation session (eg. 09A); repetitions and redundancies have been eliminated. First entry refers to the ants' colony (\$) and identity code, second entry to the activity observed, third entry to the nest in which active. Fourth and fifth entries are used when adults, brood or termites were transferred between nests; the former denotes the nest of destination and the latter the identity of marked recruits (when these were unmarked, it is indicated by XXX). The various activity codes are as follows: INS= found inside nest; ABO= unspecified above ground activity; EXC= excavating; CLE= nest sanitation; REC, EGG, LAR, COC, TER= adult, egg, larva, cocoon and termite transfer respectively; WAK= walking between nests; FOR= foraging; CAR= carried between nests. The location of the various nests is given in Figure 5; WWW refers to unknown above ground location.

DATA FOR DAY 09A

\$99	ABO	(Q)		
\$99	ABO	(P)		
\$101	ABO	(Q)		
\$103	ABO	(P)		
\$102	ABO	(P)		
\$107	ABO	(P)		
\$115	FOR	(Q)		
\$114	FOR	(P)		
\$117	ABO	(R)		
\$117	CAR	(R)	(P)	\$92
\$117	ABO	(P)		
\$117	WAK	(P)	(R)	
\$117	CLE	(R)		
\$117	CLE	(P)		
\$118	FOR	(P)		
\$33	ABO	(Q)		
\$33	ABO	(P)		
\$35	FOR	(Q)		
\$38	FOR	(P)		
\$39	ABO	(Q)		
\$39	ABO	(S)		

\$45	FOR	(Q)		
\$45	TER	(Q)	(P)	
\$36	LAR	(P)	(S)	
\$30	ABO	(S)		
\$30	ABO	(P)		
\$28	CLE	(Q)		
\$10	LAR	(P)	(S)	
\$10	REC	(P)	(S)	XXX
\$10	REC	(P)	(S)	\$157
\$10	CLE	(S)		
\$11	CLE	(P)		
\$11	CAR	(P)	(S)	
\$15	ABO	(P)		
\$21	FOR	(S)		
\$66	ABO	(P)		
\$63	CLE	(P)		
\$62	ABO	(P)		
\$61	CLE	(P)		
\$57	ABO	(P)		
\$55	ABO	(S)		
\$56	ABO	(P)		
\$53	ABO	(R)		
\$53	LAR	(P)	(R)	
\$53	CLE	(P)		
\$51	ABO	(P)		
\$72	TER	(P)	(R)	
\$75	FOR	(P)		
\$74	CLE	(P)		
\$92	REC	(R)	(P)	\$117
\$88	FOR	(P)		
\$88	ABO	(Q)		
\$118	FOR	(P)		
\$125	COC	(Q)	(P)	
\$125	WAK	(P)	(S)	
\$126	INS	(Q)		
\$130	WAK	(P)	(Q)	
\$132	ABO	(P)		
\$132	LAR	WWW	(Q)	
\$136	ABO	(P)		
\$142	WAK	(Q)	(P)	
\$147	CAR	(P)	(S)	\$208
\$149	INS	(Q)		
\$150	LAR	(P)	(R)	
\$151	ABO	(P)		
\$161	LAR	(P)	(S)	
\$189	CLE	(P)		
\$189	COC	(P)	(Q)	
\$158	INS	(Q)		
\$198	ABO	(P)		
\$205	CLE	(P)		
\$208	EGG	(P)	(S)	
\$186	INS	(Q)		

APPENDIX B

Partial transcript from a computer-generated print-out, summarizing the activities performed by different ants from colony (3a) over the entire October observation period. Entries correspond to those in Appendix A, except that the additional entry (no. 2) refers to the observation session (day; A= morning, P= afternoon) on which the activity was performed. Activity and nest codes are as in Appendix A.

\$11	04P	EXC	(Q)		
	04P	CAR	(Q)	(P)	\$70
	05A	ABO	(P)		
	05P	ABO	(P)		
	07A	CLE	(P)		
	07A	ABO	(S)		
	07P	ABO	(S)		
	08A	LAR	(P)	(S)	
	08P	CLE	(P)		
	09A	CLE	(P)		
	09A	CAR	(P)	(S)	\$2
	12A	ABO	(S)		
	13A	REC	(S)	(P)	\$203
	13A	REC	(S)	(P)	XXX
\$12	03A	FOR	(P)		
	08A	INS	(P)		
	09P	ABO	(P)		
	11P	FOR	(P)		
	12A	FOR	(P)		
\$13	not seen again				
\$149	09A	INS	(Q)		
	12P	INS	(S)		
\$150	07A	ABO	(P)		
	08A	ABO	(P)		
	08A	CLE	(R)		
	09A	LAR	(P)	(R)	
	09P	LAR	(P)	(R)	
	12A	ABO	(P)		
\$151	07A	LAR	WW	(R)	
	08A	ABO	(P)		
	09A	ABO	(P)		
	12A	ABO	(P)		

APPENDIX C

Soil temperatures at various times of the day during the month of April 1981. Measurements (in degrees Celsius) were taken on four separate days, with varying cloud cover. A digital thermometer with flexible thermocouples was used; these were placed in the following places: (A) on the surface and inside the entrance tunnel of an ant nest, (B) at three different depths in the soil profile.

(A)	Time of day	Ground surface temperature	Temperature 10 cm down nest entrance
	09h00	28,6	26,1
	10h00	36,5	28,1
	11h00	43,5	29,6
	20h30	27,6	32,5
	07h00	24,7	27,9
	08h00	27,4	28,0
	10h00	32,9	29,0
	11h00	35,9	30,4
	12h00	47,8	31,6
	15h00	48,0	37,0
	16h00	41,2	37,5

(B)	(- 10 cm)	(- 20 cm)	(-30 cm)
10H00	26,5	26,4	26,4
12H30	27,9	27,2	26,8

** air temperature: 27°C

Methods for gas chromatography

The mandibular gland secretions were extracted in pesticide residue-grade dichloromethane (Merck Chemicals, #6054). Either pairs of glands or single decapitated heads were used to prepare the extracts. The glands were dissected out of the heads of individual ants which had been immobilized by cooling, and were immediately placed in 10 μ l of dichloromethane inside 0,2 ml crimp top vials.

The extracts were analyzed on a Carlo Erba Fractovap 2150 gas chromatograph equipped with a flame ionization detector and a 25m x 0,2mm Carbowax fused silica capillary column (Hewlett-Packard). The column was held at 40°C for 5 min. after sample injection, and was then programmed for an initial temperature rise to 165°C at 1,3°/min, and a further rise to 200°C at 39°/min. Helium was used as the carrier gas at a flow rate of 1,5 ml/min. The retention times of the extract components and the areas beneath the peaks were calculated by a Hewlett-Packard 3390A integrator connected to the gas chromatograph.

APPENDIX E

Rainfall figures (in mm) recorded at the Mantuma weather station in Mkuzi Reserve, during August-November 1981 and 1982. Only heavy downpours (sometimes representing rain over a few days) are included, together with the monthly totals.

Date	Daily rainfall	Monthly totals
31st August 1981	31	38
10th September 1981	25	102
11th September 1981	31	
12th September 1981	38	
10th October 1981	12	70
11th October 1981	48	
20th November 1981	60	128
August 1982	--	0
September 1982	--	6
21st October 1982	27	81
1st November 1982	30	67
7th November 1982	24	

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Social organization, breeding biology and the process of reproductive differentiation in Ophthalmopone berthoudi Forel, a ponerine ant

Christian Paul Peeters

ADDENDUM

Contents

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Addition to p.11

There is strong evidence that the ants were not losing their marks with time:

(1) if it had occurred in the field, this would have resulted in some of the ants having unregistered colour combinations (unless the 2-4 marks on an individual flaked off simultaneously, which is very unlikely). On those occasions when nests were excavated at the end of an observation period, most of the marked ants were collected again (including some for which no activity data had been obtained). When colonies with marked ants were left in the field for a few weeks and even months, large numbers of individuals were re-collected with their previous colour combinations.

(2) it never occurred in laboratory colonies, where marked ants were observed continuously. There was frequent grooming of painted regions of the ants' bodies, without subsequent loss of the marks.

The cuticle in *O. berthoudi* is pubescent, and this explains why Humbrol paint adheres strongly to it. In contrast, marking of workers of *Plectroctena conjugata* was unsuccessful. Such ants have a shiny black cuticle, and it was found that the paint marks flaked off within days.

Addition to pp.47-48. Text should read as follows (p.47, line 26 onwards).

As the ants were released into the arena they soon met up and there were distinct antennations. The behaviour of the ants was monitored for 10-20 minutes, and in some tests the encounters were timed (Table 10a). The latter could not always be done precisely, especially since the beginning and end of an interaction are hard to determine. In addition there were sometimes two interactions occurring simultaneously, and then one had to be ignored. The intensity of the antennations could not be quantified, and thus additional descriptions are essential. A number of combinations of pairs of foragers were tested: (1) different nests from the same colony ($n=3$); (2) nests from different, but adjacent colonies ($n=4$)- in one of these it was suspected that colony fission had taken place in the recent past; (3) nests from different, distant colonies ($n=3$).

The initial interactions between workers from different colonies were characterized by prolonged and vigorous antennal "boxing" (Ward 1983); in subsequent encounters between the same individuals the duration of the antennation decreased (Table 10a). At the beginning of the tests there was no overt hostility between foreign ants, and they would walk away after their encounters. Some of the bouts of antennal boxing resulted in one of the participants adopting a submissive posture (see 2.3.6.). After some time however the repeated confrontations became more physical. There was momentary contact of the mandibles, the ants nudged heads or stood over one another's thoraces. Fighting sometimes followed; one ant held the other's mandibles (or their antennae or petiole) and lifted it off the ground. Some ants were dragged around. Tests involving adjacent and distant colonies gave similar results.

In contrast, all the interactions between nestmates were very short-lived (except for the first confrontation) (Table 10a), and they were of a different nature. When ants from distant nests within the same colony were tested, their interactions were sometimes initially slightly longer than those between

inhabitants of the same nest. After a few minutes however there were no more differences in the duration of the interactions. The lengths of the antennations cannot be compared statistically within and between tests. Times decrease with each encounter, and it is the entire sequence of antennation that must be considered. In addition, the number of encounters varies between pairs of ants in each test, because encounters in the arena occur randomly.

In summary, the main distinguishing feature between interactions involving nestmates and aliens was the end process; only in the latter did the repeated encounters lead to aggression.

Table 10a Length of the antennations between alien ants confined in a test arena. Two pairs of foragers were used in each recognition test; each pair belonged to the same nest. Different categories of nest relationships were tested: (a) distant nests within the same colony; (b) and (c) nests from adjacent colonies; (d) nests from distant colonies. Times are in seconds; "?" indicates an interaction that could not be timed.

(a)

	X1	X2	Y1	Y2
X1		1;0,5	2	6,5;?;?;2
X2			3,5;2;2;2	?;1;1,5
Y1				2,5;?;1,5;2,5; ?;1,5
Y2				

(b)

	A1	A2	B1	B2
A1		3;1,5;0,5; 1,5	5;2;1;2;1;?;2; 2;1,5;2;1,5;1	7;4;?;3;3;2,5; 1;1,5;1
A2			6;4;2;2;4;4;1; 5;2;1	3;1;5;4;2;1,5; 1;4;2;0,5;2
B1				2;?;2;1;2,5; 0,5;2;?;2
B2				

(c)

	D1	D2	B3	B4
D1		1;2;1;0,5; 2;?	4,5;2,5;4;?; 3;2;?;1;?	?;5;2,5;2,5;?
D2			4;5;4;7;?	5,5;5;5;3;3;2
B3				2;?;?;1
B4				

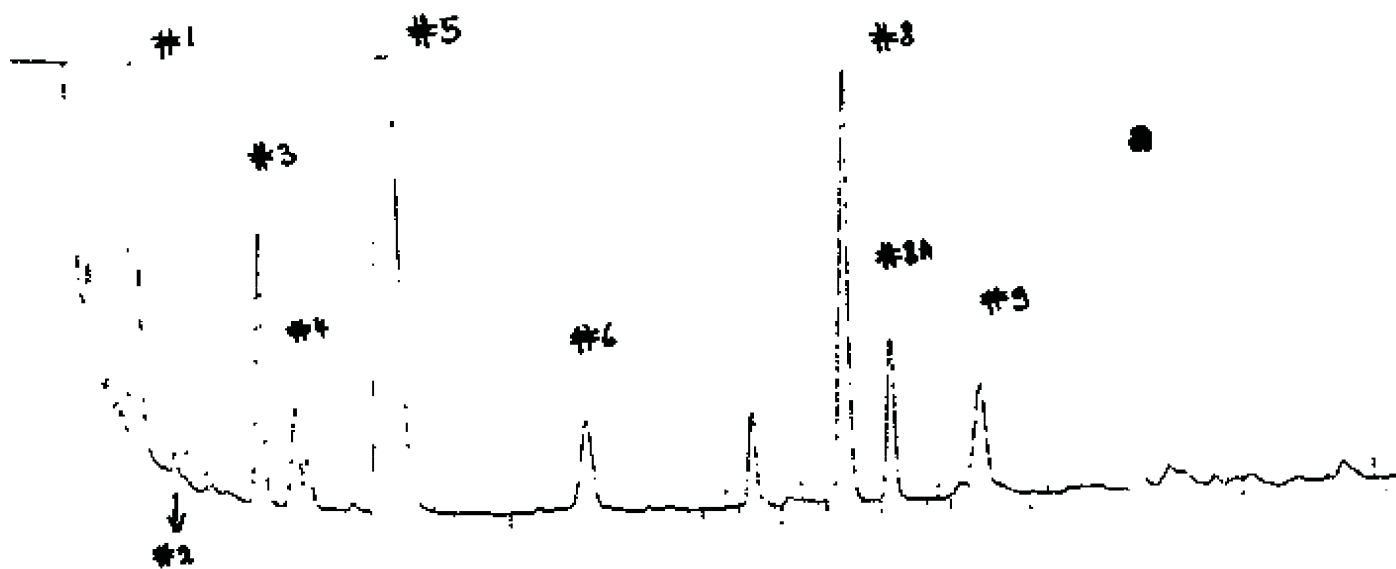
(d)

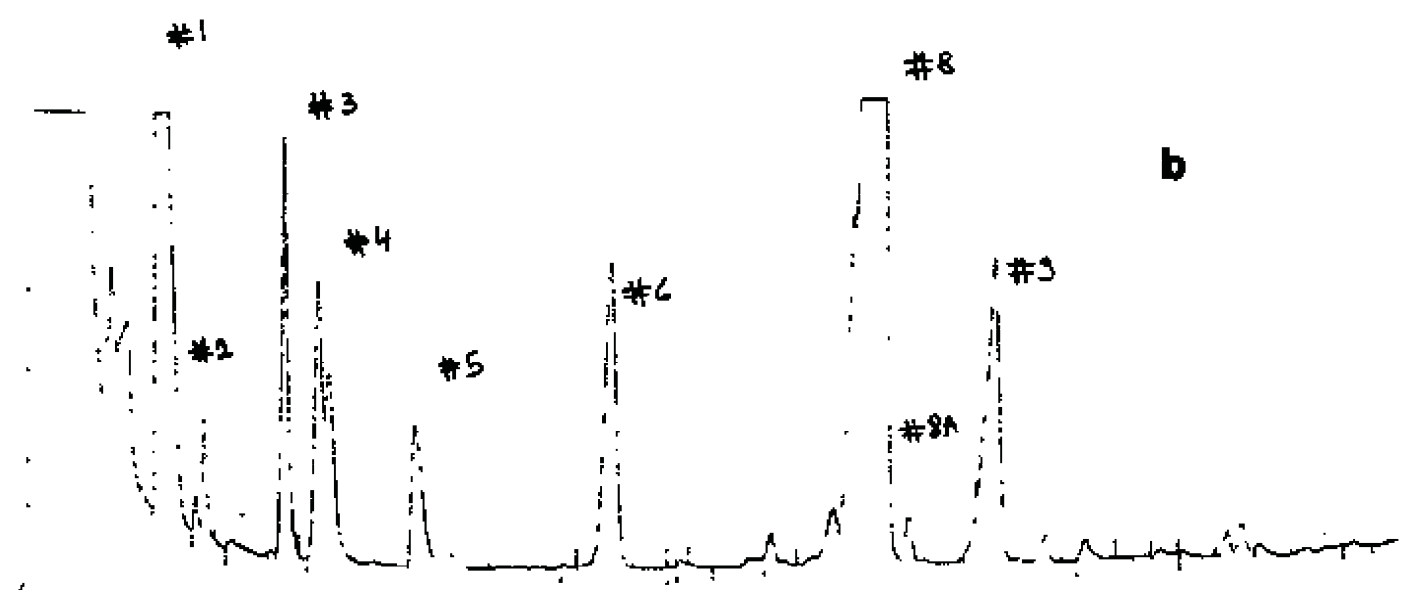
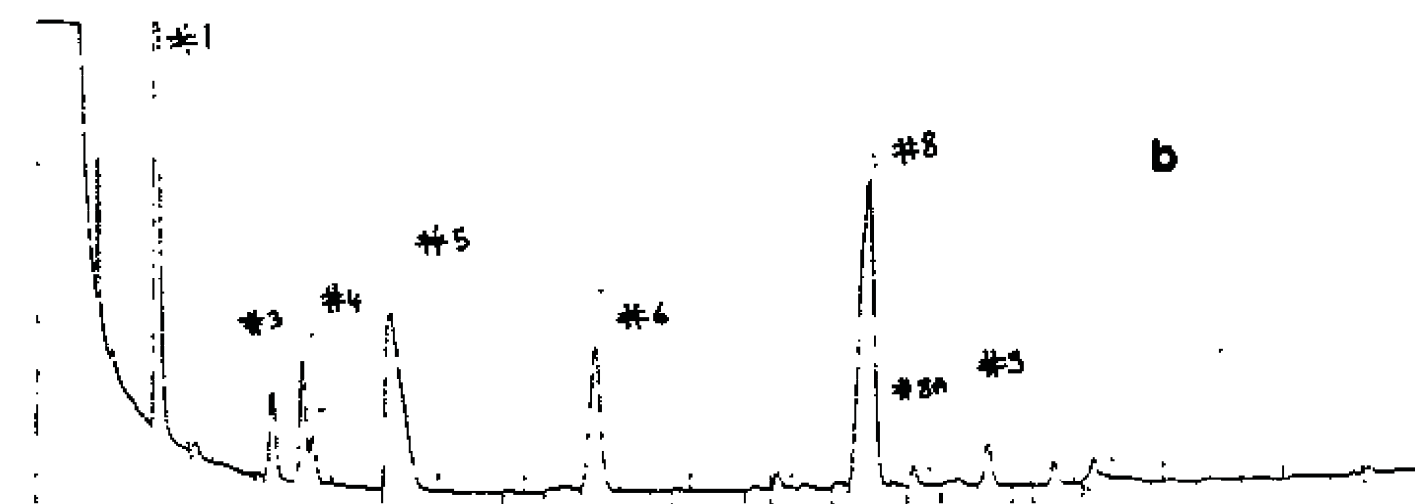
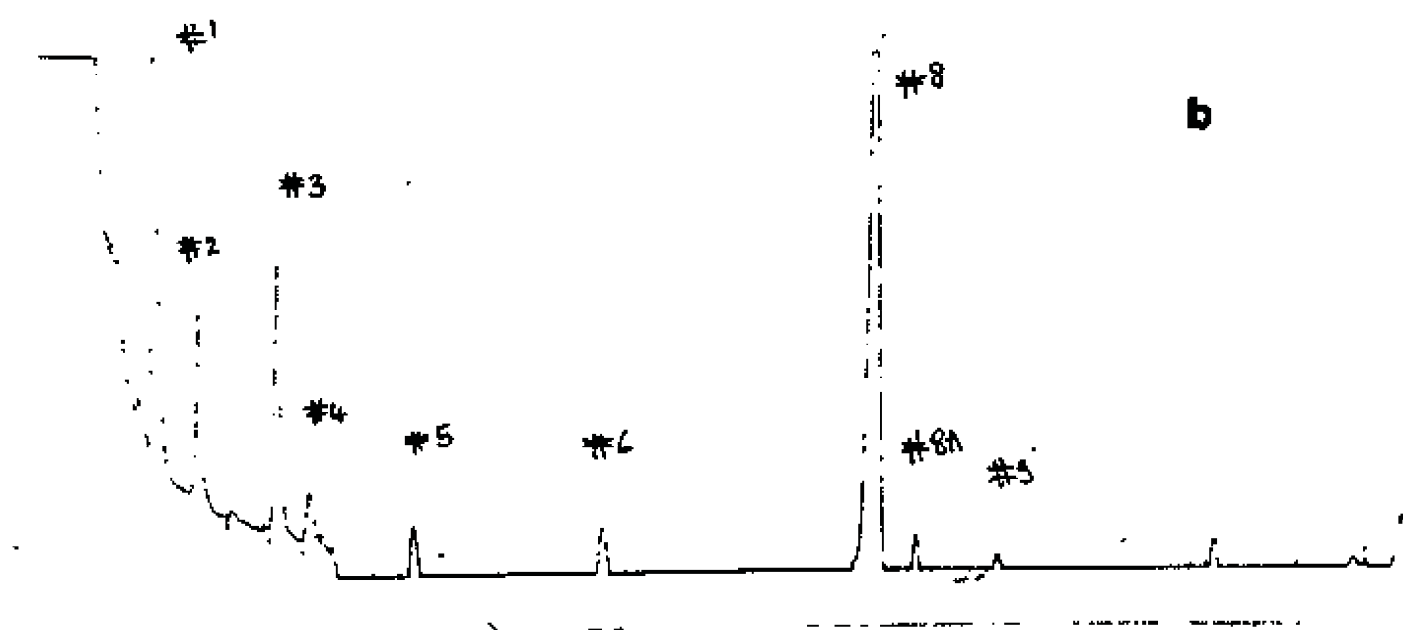
	A1	A2	C1	C2
A1		1,5	16;?;3	15;?;6;7;?;12
A2			10;2;?;10;5; 3;4;3;2;3	10;6;4;13;2;?; 4;5
C1				1;2;1,5
C2				

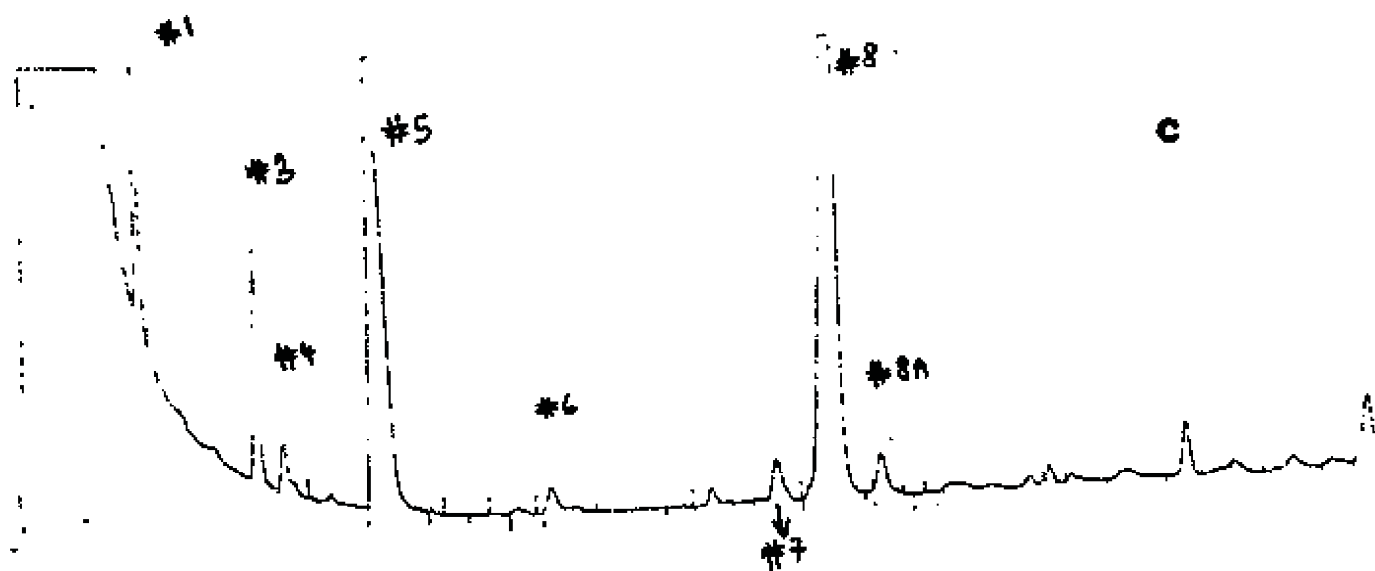
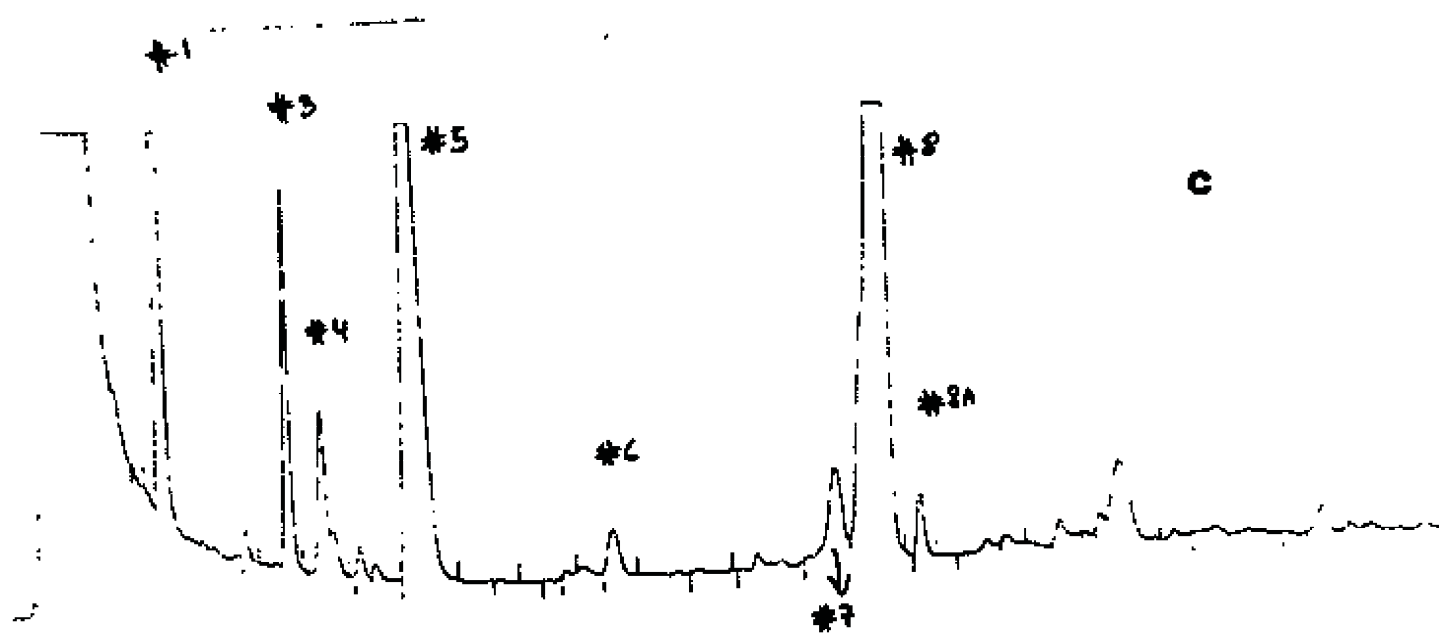
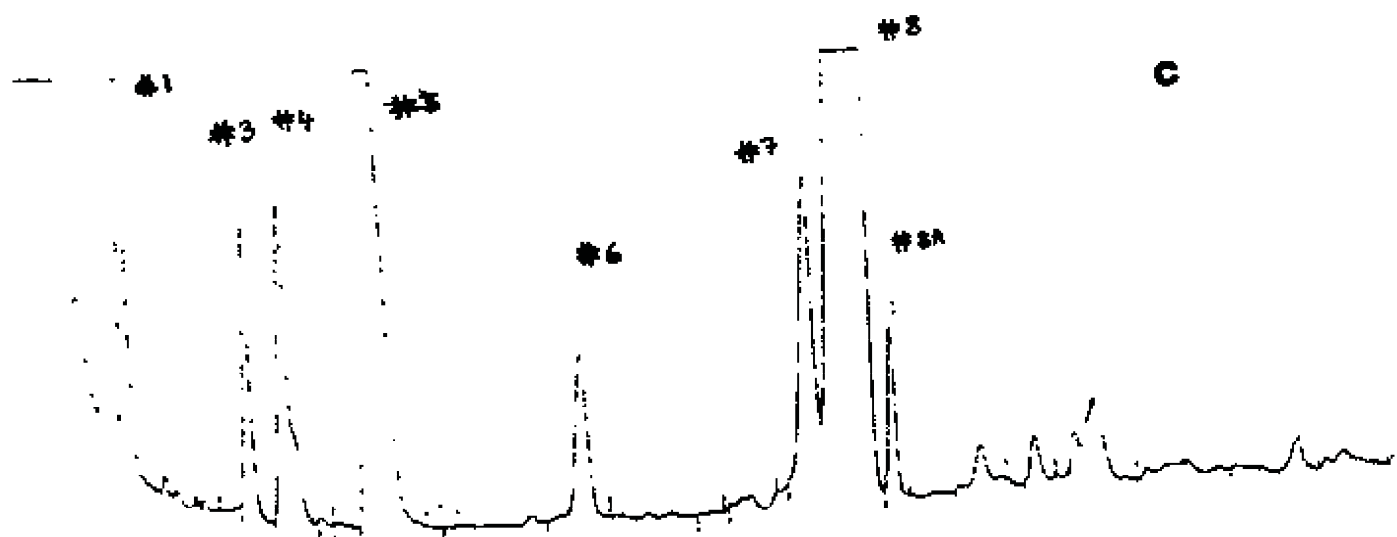
Addition to p.54 (Figure 6)

As stated in the text (p. 53), this analysis of the composition of mandibular gland secretions is preliminary. The extracts of over 10 individuals were analysed for each of the three categories of workers. These worker categories were arbitrarily constituted. A group such as the Innendienst workers included individuals with a substantial range of ages, and thus within-group variability could be expected. Notwithstanding, some consistent differences in the relative amounts of certain components were visually apparent between categories. None of the components have been chemically identified, and thus bioassays could not be attempted to determine which of the components are behaviourally important. The short reference to these incomplete results and the tentative suggestion of a change in the blend of components with age was merely intended to indicate that there may be pheromonal means through which within-nest recognition of individuals takes place.

Figure 6 Gas chromatograms of the mandibular gland secretions of three functional categories of workers of Ophthalmopone berthoudi (a) Innendienst workers, (b) foragers, (c) breeding workers.







Addition to p.77 (Standard deviations in Table 15)

Table 15 Measurements (with standard deviation) (in mm) of the head and gaster of breeding and sterile workers. Significance levels (*= $p < 0,05$; **= $p < 0,01$; ***= $p < 0,001$) computed for the means of two samples by t-test.

	sterile workers	breeding workers	t-value & significance
Sample size	29	10	
Mean length of head capsule	2,59 $\pm$ 0,07	2,58 $\pm$ 0,04	0,58
Mean width of head capsule	1,76 $\pm$ 0,06	1,78 $\pm$ 0,04	0,88
Mean height of 1st gaster segment	2,22 $\pm$ 0,13	2,35 $\pm$ 0,07	3,03 **
Mean length of 1st gaster segment	1,56 $\pm$ 0,11	1,73 $\pm$ 0,08	4,38 ***

TRANSCRIPT A

Computer-generated print-out, listing the activities performed by the marked ants from colony (3a) during October 1981. Each page refers to a different observation session (eg. 04A; A= morning, P= afternoon); repetitions and redundancies have been eliminated. First entry refers to an ant's identity code, second entry to the activity observed, third entry to the nest in which active. Fourth and fifth entries are used when adults, brood or termites were transferred between nests; the former denotes the nest of destination and the latter the identity of marked recruits (when these were unmarked, it is indicated by XXX; when these were marked but the code could not be read, it is indicated by X). A list is given to convert the colour codes used in the print-out to the identity codes used in the text (eg. GYX = \$31). The various activity codes are as follows: INS= found inside nest; ABO= unspecified above ground activity; EXC= excavating; CLE= nest sanitation; REC, EGG, LAR, COC, TER= adult, egg, larva, cocoon and termite transfer respectively; WAK= walking between nests; FOR= foraging; CAR= carried between nests. Nest entries refer to the following nests in Figure 5: ZE=(P); JU=(Q); AD=(R); DE=(S); OL=(XX); WWW refers to unknown above ground location.

YYY	\$1	RRB	\$57
YYR	\$2	RGY	\$58
YYG	\$3	RGR	\$59
YYX	\$4	RGG	\$60
YYB	\$5	RGX	\$61
YGY	\$6	RGB	\$62
YGR	\$7	RBV	\$63
YGG	\$8	RBR	\$64
YGX	\$9	RBG	\$65
YGB	\$10	RBX	\$66
YRY	\$11	RBB	\$67
YRR	\$12	RXB	\$68
YRG	\$13	R2	\$69
YRX	\$14	RXG	\$70
YRB	\$15	RXY	\$71
YXY	\$16	RXR	\$72
YXR	\$17	WWV	\$73
YXG	\$18	WVR	\$74
YXX	\$19	WWG	\$75
XYB	\$20	WWB	\$76
YBY	\$21	WWY	\$77
YBR	\$22	WBX	\$78
YBG	\$23	WBB	\$79
YBX	\$24	WBW	\$80
YBB	\$25	WBR	\$81
YBW	\$26	WBG	\$82
YWB	\$27	WRR	\$83
GYV	\$28	WRX	\$84
GYR	\$29	WRY	\$85
GYG	\$30	WRG	\$86
GYX	\$31	WRW	\$87
GGY	\$32	WYY	\$88
GGR	\$33	W2	\$89
GGG	\$34	WGG	\$90
GGX	\$35	W4	\$91
GRY	\$36	WCG	\$92
GRR	\$37	WGR	\$93
GRG	\$38	WGW	\$94
GRX	\$39	WGB	\$95
GXY	\$40	BBB	\$96
GXR	\$41	BBX	\$97
GXG	\$42	BBR	\$98
G2	\$43	BBW	\$99
Y4	\$44	BBG	\$100
R4	\$45	BGB	\$101
G4	\$46	BGX	\$102
B4	\$47	BGG	\$103
RYY	\$48	BGY	\$104
RYR	\$49	BGR	\$105
RYG	\$50	BRR	\$106
RYX	\$51	BRY	\$107
RYB	\$52	BRG	\$108
RRY	\$53	BRX	\$109
RRR	\$54	BYY	\$110
RRG	\$55	BYX	\$111
RRX	\$56	B2	\$112

BWB	\$113	G1R4	\$169
BWR	\$114	B1	\$170
BWG	\$115	B12	\$171
BWX	\$116	B1Y2	\$172
BWW	\$117	B14	\$173
R=RW	\$118	R1	\$174
R=RG	\$119	R12	\$175
R=RY	\$120	R1G2	\$176
R=RB	\$121	R1Y2	\$177
R=RX	\$122	R14	\$178
R=RR	\$123	R1G4	\$179
Y=YR	\$124	R1B4	\$180
Y=YW	\$125	R1Y4	\$181
Y=YX	\$126	G4Y5	\$182
Y=YG	\$127	G4R5	\$183
Y=YB	\$128	R4Y5	\$184
Y=YY	\$129	R4G5	\$185
Y=YRY	\$130	R4W5	\$186
Y=YGR	\$131	R4B5	\$187
G=GX	\$132	Y4G5	\$188
G=GR	\$133	Y4B5	\$189
G=GY	\$134	Y4R5	\$190
G=GG	\$135	B4W5	\$191
G=GW	\$136	B4Y5	\$192
B=BY	\$137	B4R5	\$193
B=BX	\$138	B4G5	\$194
B=BR	\$139	RXYR	\$195
B=BG	\$140	RXXG	\$196
B=BW	\$141	RXYB	\$197
W=WB	\$142	RXGR	\$198
W=WR	\$143	RXGY	\$199
W=WX	\$144	RXGB	\$200
W=WG	\$145	RXBR	\$201
W=WY	\$146	RXBG	\$202
G=GB	\$147	RXBY	\$203
G=GYR	\$148	RXRB	\$204
R=RGY	\$149	RXRY	\$205
R=RWG	\$150	RXRG	\$206
Y1	\$151	RYR	\$207
Y12	\$152	WXYR	\$208
Y1B2	\$153	WXGR	\$209
Y1R2	\$154	WXBR	\$210
Y14	\$155	WXRG	\$211
Y1R4	\$156	WXRY	\$212
Y1G4	\$157	WXRB	\$213
Y1W4	\$158	GXYR	\$214
W1	\$159	GXRG	\$215
W12	\$160	GXYR	\$216
W1R2	\$161	GXYG	\$217
W14	\$162	GXBG	\$218
G1	\$163	GXGB	\$219
G1R2	\$164	GXGR	\$220
G1Y2	\$165	GXGY	\$221
G1B2	\$166	GRBY	\$222
G14	\$167	GRYB	\$223
G1Y4	\$168	BXGR	\$224

BXGY	\$225
BXGB	\$226
BXRG	\$227
BXRY	\$228
BXRB	\$229
BXYG	\$230
BXYR	\$231
BXYB	\$232
BXWB	\$233
BXBW	\$234
BXBY	\$235

DATA FOR DAY 01A

B4	ABO	AD	
RBR	ABO	MZ	
YRB	ABO	ZE	
YYB	LAR	ZE	WN
YYX	EXC	AD	

DATA FOR DAY 02A

W4	ABO	ZE		
W4	EXC	ZE		
BRY	ABO	ZE		
GGR	EXC	ZE		
GGY	FOR	ZE		
GYX	ABO	ZE		
RRX	ABO	ZE		
WBR	ABO	ZE		
YBB	REC	ZE	AD	XXX
YBX	REC	ZE	WN	YXG
YGB	WAX	ZE		

DATA FOR DAY 03A

U4 FOR AD
 U2 FOR ZE
 U4 ABO JU
 U4 CLE ZE
 U4 ABO AD
 Y4 FOR ZE
 UDA ABO JU
 UDA ABO AC
 UDR FOR ZE
 UGY FOR AD
 URG ABO AD
 URX FOR ZE
 UYX ABO ZE
 UGR FOR ZE
 UGX EXC JU
 UGY FOR AD
 UGR ABO ZE
 URX FOR ZE
 UXC ABO ZE
 UYY ABO ZE
 RUB FOR ZE
 RUB ABO ZE
 RCG CLE AD
 ARG FOR ZE
 RRG ABO AD
 RRR FOR AD
 RRY ABO AD
 RRY CLE ZE
 RAL ABO AD
 RXY CLE ZE
 RYG FOR AD
 RYX ABO ZE
 RYX ABO AD
 RYX TER AD ZE
 RYX CLE ZE
 RUB FOR ZE
 RUB FOR ZE
 RUB ABO ZE
 RUB ABO ZE
 RGX TER JU ZE
 URX ABO ZE
 URY ABO ZE
 URY FOR WW
 RHG FOR ZE
 UWR ABO ZE
 UWR FOR ZE
 UWR ABO JU
 UYY ABO ZE
 YBB CLE AD
 YBR ABO ZE
 YBX ABO ZE

YGB CLE ZE
 YGB ABO ZE
 YGX ABO ZE
 YRX FOR ZE
 YRX FOR AD
 YJB ABO AD
 YJB ABO ZE
 YXR FOR AD
 YXR FOR ZE
 YYG ABO AD
 YYR ABO AD
 YYR REC AD WW XXX
 YYX ABO ZE
 YYX TER ZE AD
 YYY ABO ZE
 R=RR ABO ZE
 A=AY EXC JU
 Y=YY REC ZE WW XXX

DATA FOR DAY 04A

G4 ABO ZE
 R2 REC WW JU X
 R2 REC ZE JU ARR
 R2 CLE JU
 W4 FOR ZE
 Y2 ABO ZE
 Y2 FOR ZE
 Y4 FOR ZE
 BGR ABO ZE
 BRG CLE JU
 BRG ABO AD
 BRG REC AD WW XXX
 BRX ABO AD
 BRX ABO JU
 BRY ABO ZE
 BNX FOR ZE
 GGR ABO MI
 GRG FOR ZE
 GXG CLE ZE
 GYY ABO ZE
 RDX ABO ZE
 RGB ABO MI
 RGB ABO ZE
 RGG ABO ZE
 RCG REC ZE AD WRG
 RRG ABO ZE
 RRX FOR ZE
 RRY CLE ZE
 RRY EXC ZE
 RXG ABO AD
 RXG WAK AD ZE
 RYG FOR WW
 RYG FOR AD
 WBN ABO ZE
 WBN ABO ZE
 WBN CLE ZE
 WGN EXC ZE
 WRG CAR ZE AD RGG
 WRR CAR ZE JU R2
 WRY FOR ZE
 WRR ABO ZE
 WRR REC WW ZE
 YBG CLE AD
 YBA ABO ZE
 YGG ABO ZE
 YGG ABO ZE
 YGG CLE ZE
 YGY FOR WW
 YRB ABO ZE
 YRX ABO ZE
 YXY FOR ZE
 YXY CLE ZE

YYX ABO ZE
 YYY FOR ZE
 G*GY ABO ZE
 R=RG ABO ZE
 R=RG ABO JU
 R=RG FOR WW
 R=RX FOR ZE
 R=RX FOR JU
 W=NY FOR ZE
 Y=YB WAK ZE JU
 Y=YB LAR ZE JU
 Y=YA ABO ZE
 Y=YRY LAR ZE WW
 Y=YRY ABO JU

DATA FOR DAY 64P

G4 CLE WW
 G4 CLE ZE
 G4 EAC ZE
 R2 CLE ZE
 R2 EAC ZE
 R2 FOR JU
 R4 ABO ZE
 R4 FOR ZE
 Y2 FOR ZE
 B00 ABO ZE
 B2A ABO ZE
 DBX REC ZE JU RXG
 BRX ABO ZE
 G00 CLE ZE
 G00 FOR JU
 G0R FOR ZE
 GAR ABO JU
 GYC ABO ZE
 GYY ABO JU
 R0R FOR ZE
 R0X FOR WW
 R0Y ABO ZE
 R0G EAC ZE
 RRY CLE WW
 RRY EAC ZE
 RAX ABO ZE
 RXG CAR ZE JU DBX
 RXC REC JU ZE YRY
 RXG CLE ZE
 RXG REC ZE JU R0G
 XBR ABO ZE
 XGN ABO ZE
 XRG ABO ZE
 XRR ABO JU
 XRY FOR ZE
 XRG ABO ZE
 XHG ABO III
 XHK ABO ZE
 XHK CLE ZE
 XHR ABO JU
 XHR EAC JU
 XHR ABO ZE
 XYY FOR WW
 YBX CLE ZE
 Y0Y FOR ZE
 Y0G ABO ZE
 Y0X ABO ZE
 Y0X REC ZE JU XXX
 YRY ABO JU
 YAY EAC JU
 YXL FOR ZE

YAY CLE ZE
 YYC ABO ZE
 YYR ABO ZE
 YYR CLE ZE
 YYX FOR ZE
 YYY ABO ZE
 R=RG CLE ZE
 R=RX FOR R2
 R=RY ABO ZE
 Y=YB ABO ZE
 Y=YRY ABO WW
 Y=YRY CLE ZE

DATA FOR DAY 05A

B4 FOR AD
 G1 REC NW ZE R2
 G2 ABO ZE
 G2 FOR ZE
 G4 CLE AD
 R2 CAR NW ZE G1
 R4 CLE ZE
 W1 ABO ZE
 Y1 ABO NW
 Y2 FOR NW
 Y2 FOR JU
 Y4 FOR ZE
 BBW ABO AD
 BBX CAR JU ZE WGR
 BGG ABO ZE
 BRG CLE AD
 BRY ABO ZE
 BWR CLE NW
 BWW ABO ZE
 BWN ABO AD
 BYX ABO ZE
 GGG FOR JU
 GGR ABO ZE
 GGX ABO ZE
 GGY ABO AD
 GXG FOR ZE
 GXY CLE NW
 GXY CLE AD
 GYY ABO ZE
 GYY LAR ZE JU
 R14 ABO ZE
 RBR ABO AD
 RGG ABO ZE
 RRB ABO JU
 RRG CLE AD
 RRG LAR ZE AD
 RRR FOR AD
 RRX FOR NW
 RRY REC ZE AD WBN
 RRY LAR ZE AD
 RXB FOR NW
 RXB FOR ZE
 RXY ABO AD
 RYG FOR NW
 RYG FOR AD
 RYY ABO AD
 WBG ABO ZE
 WBR FOR NW
 WBR ABO ZE
 WBN CAR ZE AD RRY
 WBN CLE AD
 WBX FOR ZE

WGR ABO ZE
 WGR REC JU ZE BBX
 WRG ABO AD
 WRX ABO ZE
 WRY FOR NW
 WRY ABO ZE
 WRY FOR ZE
 WNG ABO ZE
 WWR CLE AD
 WWR ABO ZE
 WWR TER JU ZE
 WWN ABO ZE
 WWY ABO ZE
 YBG ABO AD
 YBY FOR ZE
 YGR ABO JU
 YRB FOR NW
 YRX FOR ZE
 YRY ABO ZE
 YWB ABO AD
 YYR WAK ZE JU
 YYX FOR NW
 YYX ABO ZE
 YYX FOR ZE
 B4W5 ABO ZE
 B4W5 REC ZE JU Y=YRY
 G1R2 ABO ZE
 G=GG ABO ZE
 G=GG FOR ZE
 R1G4 CLE ZE
 R1Y2 ABO NW
 R=RB ABO ZE
 R=RB FOR NW
 R=RB FOR ZE
 R=RG ABO AD
 R=RY ABO ZE
 W1R2 ABO ZE
 W1R2 ABO AD
 Y1B2 ABO ZE
 Y4B5 ABO JU
 Y4B5 ABO ZE
 Y4B5 WAK ZE JU
 Y4B5 ABO AD
 Y4G5 ABO ZE
 Y=YX LAR ZE JU
 Y=YX REC ZE JU XXX
 Y=YY CLE ZE
 R=RWG ABO NW
 Y=YRY ABO JU
 Y=YRY CAR ZE JU B4W5

DATA FOR DAY 05P

R2 ABO AD
 R4 FOR WW
 W1 ABO ZE
 BBB FOR ZE
 BBR ABO AD
 BGX ABO ZE
 BYX ABO ZE
 BYY CAR ZE OL NBX
 GGR ABO ZE
 GGX EXC JU
 GGY FOR WW
 GRX FOR WW
 GXG FOR ZE
 GYY CDC ZE JU
 R14 EGG ZE JU
 RBX FOR ZE
 RGG EXC AD
 RRX ABO ZE
 RRY EXC ZE
 RXB ABO ZE
 NBX REC ZE OL BYY
 WGX CLE JU
 WRX ABO ZE
 WRY FOR ZE
 WYY FOR ZE
 YGR FOR JU
 YGY ABO ZE
 YRX ABO WW
 YRY ABO ZE
 YWB ABO AD
 YYX FOR ZE
 B4W5 CDC ZE JU
 R=RR ABO JU
 R=RX FOR WW
 RXGR ABO ZE
 W1R2 CLE ZE
 W=WY FOR ZE
 W=WY ABO JU
 WXYR ABO ZE
 Y1B2 TER ZE JU
 Y4B5 ABO ZE
 Y=YB COC ZE JU
 Y=YB REC ZE JU XXX
 Y=YW COC ZE JU
 Y=YW WAK JU ZE
 Y=YW EGG ZE JU
 Y=YX CLE WW
 Y=YY ABO ZE
 Y=YY CLE WW
 G=GYR ABO AD

DATA FOR DAY 06A

B2 ABO ZE
 B4 FOR WW
 R1 INS ZE
 R2 FOR WW
 W1 INS ZE
 W4 INS ZE
 BRG ABO WW
 BRX ABO WW
 BYY ABO OL
 GGY ABO AD
 GGY FOR WW
 RBR ABO OL
 RBY ABO ZE
 RGB ABO OL
 RGG ABO ZE
 WRY ABO ZE
 WWR ABO ZE
 WYY FOR WW
 Y14 INS ZE
 YBB ABO JU
 YGR FOR WW
 YRB ABO ZE
 YYB ABO ZE
 B4Y5 ABO WW
 B=BR INS ZE
 G1B2 INS ZE
 G=GB INS ZE
 R=RY ABO OL
 R=RY FOR OL
 R=RY LAR ZE OL
 RXYR ABO ZE
 Y1B2 INS ZE
 Y=YR ABO ZE
 Y=YX ABO ZE
 G=GYR INS ZE

DATA FOR DAY 07A

B2 INS DE	YBB ABO JU
B2 ABO DE	YBY FOR ZE
G4 ABO AD	YBY ABO DE
R4 FOR ZE	YGB ABO DE
W2 REC WW WW XXX	YGG FOR ZE
Y1 LAR WW AD	YGR FOR ZE
BBB FOR ZE	YGX ABO ZE
BBW ABO DE	YRX CLE ZE
BBX ABO DE	YRX ABO DE
BGB FOR JU	YRX TER ZE DE
BYX REC ZE DE X	YRY ABO ZE
GGR ABO ZE	YRY CLE ZE
GGX ABO ZE	YRY ABO DE
GRG FOR ZE	YXG FOR ZE
GRG ABO JU	YXY FOR WW
GRX COC WW ZE	YYB FOR ZE
GRX FOR DE	YYR ABO ZE
GRX ABO JU	B=BX ABO ZE
GXY ABO ZE	G1Y2 ABO ZE
GXY ABO DE	G=GB ABO ZE
GYG FOR DE	G=GR FOR DE
GYG COC AD ZE	G=GX ABO ZE
RBY FOR JU	R1Y2 ABO JU
RGB ABO ZE	R=RB ABO JU
RGR ABO AD	R=RB ABO ZE
RRG REC AD WW Y4B5	R=RR FOR WW
RRG ABO ZE	R=RW ABO WW
RRR FOR AD	R=RX FOR AD
RRX ABO ZE	RXGR ABO ZE
RRY LAR JU ZE	RXYR FOR ZE
RRY COC AD ZE	RXYR ABO DE
RXB CLE ZE	WXYR INS DE
RXG CLE ZE	Y1B2 ABO DE
RXY FOR WW	Y4B5 ABO ZE
RYX ABO ZE	Y4B5 CLE JU
RYY ABO ZE	Y=YB CLE ZE
WBG ABO ZE	Y=YG LAR WW ZE
WBR ABO ZE	Y=YR CLE ZE
WGR ABO AD	Y=YW ABO ZE
WGW ABO ZE	Y=YX ABO JU
WGX LAR AD ZE	G=GYR ABO ZE
WRR ABO DE	R=RWG ABO ZE
WRX INS DE	
WRX CLE ZE	
WRX ABO DE	
WRY FOR WW	
WRY ABO ZE	
WWG FOR ZE	
WWW ABO ZE	
WYY FOR ZE	
XRG ABO ZE	
Y14 CLE ZE	

DATA FOR DAY 07P

B2 ABO DE
 Y2 FOR JU
 BBX ABO DE
 BBX REC JU DE XXX
 BRG ABO AD
 BRV FOR ZE
 BWR ABO ZE
 GGR ABO ZE
 GRX REC ZE DE XXX
 GRX COC ZE DE
 GYG ABO ZE
 RRG ABO DE
 RRX CLE ZE
 W12 ABO ZE
 WBN CLE AD
 WGG EXC DE
 WRR ABO DE
 WWW EXC DE
 WNY ABO DE
 WYY FOR ZE
 XRG ABO DE
 YBB ABO AD
 YGB ABO DE
 YGG FOR ZE
 YRX REC ZE DE XXX
 YRY ABO DE
 YXG ABO JU
 YYR ABO DE
 YYR REC ZE DE YYG
 YYY ABO DE
 G=GW ABO AD
 R=RG ABO ZE
 R=RG CLE ZE
 R=RR ABO ZE
 RXYR ABO DE
 Y=YG ABO DE
 Y=YR ABO ZE

DATA FOR DAY 08A

B2 INS ZE
 B2 ABO DE
 B2 REC ZE DE RRX
 B4 FOR WW
 B4 ABO AD
 R1 INS ZE
 R4 INS ZE
 R4 ABO WW
 R4 FOR WW
 W1 INS ZE
 W2 INS ZE
 W4 INS ZE
 W4 ABO ZE
 W4 CLE JU
 W4 ABO AD
 Y1 ABO WW
 Y1 ABO ZE
 Y2 FOR WW
 Y2 ABO JU
 Y2 FOR JU
 Y4 INS ZE
 BBB INS ZE
 BBB ABO ZE
 BBW LAR ZE WW
 BGB ABO WW
 BGG INS ZE
 BGG REC ZE AD
 BGG REC ZE AD XXX
 BGG WAK ZE AD
 BGG REC ZE AD X
 BGG WAK AD ZE
 BGX CLE ZE ZE WRW
 BGX CLE ZE
 BRY INS ZE
 BRY ABO ZE
 BWG FOR WW
 BWG ABO JU
 BWG FOR JU
 BWR ABO ZE
 BWW ABO ZE
 BWW CLE ZE
 BWW ABO JU
 BWW CLE JU
 BYX ABO ZE
 GGR ABO ZE
 GGR FOR ZE
 GGX FOR ZE
 GGX CAR ZE JU Y4B5
 GGY FOR WW

GRG INS ZE
 GRG FOR ZE
 GRX ABO DE
 GRX ABO JU
 GXY ABO DE
 GXY ABO ZE
 GYG INS ZE
 GYG ABO ZE
 GYG LAR JU ZE
 GYG ABO DE
 GYY ABO JU
 GYY CAR JU ZE WBG
 GYY ABO ZE
 RBY INS ZE
 RGG ABO WW
 RGG FOR AD
 RRB INS ZE
 RRB ABO DE
 RRB ABO ZE
 RRG INS ZE
 RRG EXC ZE
 RRG CLE ZE
 RRG ABO DE
 RRX ABO DE
 RRX CAR ZE DE B2
 RRY ABO ZE
 RRY LAR WW ZE
 RRY CLE JU
 RRY TER JU ZE
 RRY CLE ZE
 RRY EXC ZE
 RXB INS ZE
 RXB ABO ZE
 RXB CLE ZE
 RXG LAR ZE AD
 RXY FOR AD
 RYX INS ZE
 RXY ABO ZE
 RYY ABO ZE
 W12 INS ZE
 WBG ABO JU
 WBG FOR WW
 WBG REC JU ZE GYY

WBR INS ZE
 WBR ABO ZE
 WBR ABO DE
 WBW ABO WN
 WBX ABO ZE
 WGG ABO DE
 WGG EXC DE
 WGR ABO JU
 WGR FOR WN
 WGX ABO JU
 WGX REC AD ZE B4G5
 WRW ABO ZE
 WRX ABO DE
 WRX ABO ZE
 WRX CLE ZE ZE W1R2
 WRX CLE ZE ZE WRW
 WRY INS ZE
 WRY ABO WN
 WRY CLE ZE ZE WRW
 WRY FOR WN
 WNG ABO ZE
 WNG FOR ZE
 WNW ABO DE
 WNY ABO ZE
 WYY INS ZE
 WYY ABO JU
 WYY ABO ZE
 XRG ABO DE
 XRG ABO ZE
 YBB ABO AD
 YBB FOR JU
 YBB CLE JU
 YGB ABO DE
 YGX INS ZE
 YGY INS ZE
 YGY FOR ZE
 YGY CLE WN
 YRB ABO ZE
 YRR INS ZE
 YRX LAR ZE DE
 YRY ABO DE
 YRY LAR ZE DE
 YWB ABO AD
 YXG ABO JU
 YXR FOR WN
 YXR ABO ZE
 YXY INS ZE
 YXY FOR ZE
 YYB FOR WN
 YYB FOR DE
 YYB CLE ZE

YYR ABO DE
 YYR ABO ZE
 YYR REC AD WN XXX
 YYR REC XE W=WB
 YYY ABO ZE
 B4G5 CAR AD ZE WGX
 B4W5 ABO JU
 B=BX INS ZE
 B=BX ABO JU
 B=BY ABO ZE
 B=BY CLE ZE
 G1B2 INS ZE
 G1Y2 ABO ZE
 G=GG INS ZE
 G=GG FOR ZE
 G=GR ABO DE
 G=GR ABO ZE
 G=GR TER ZE DE
 G=GW ABO AD
 G=GW ABO ZE
 G=GX INS ZE
 G=GX LAR WN ZE
 R1G2 CAR AD JU W=WG
 R1G2 ABO JU
 R=RB INS ZE
 R=RB ABO ZE
 R=RG ABO ZE
 R=RR INS ZE
 R=RW INS ZE
 R=RW EXC ZE
 R=RW ABO JU
 R=RX FOR WN
 RXBG ABO ZE
 RXGB ABO ZE
 RXGR INS ZE
 RXGY ABO ZE
 RXGY CLE ZE
 RXRG CLE ZE ZE WRW
 RXRY ABO JU
 W1R2 INS ZE
 W1R2 CLE ZE
 W1R2 EXC ZE
 W=WB ABO JU
 W=WB CAR ZE YYR
 W=WG ABO JU
 W=WG REC AD JU R1G2
 W=WG CLE JU
 W=WR INS ZE

X=XY INS ZE
 X=XY ABO ZE
 XXY ABO ZE
 XRG ABO ZE
 XXYR ABO DE
 Y102 CLE ZE
 Y102 CAR ZE JU Y485
 Y102 ABO JU
 Y104 INS ZE
 Y405 ABO ZE
 Y405 ABO JU
 Y405 REC ZE JU Y102
 Y485 LAR ZE JU
 Y405 REC ZE JU G6X
 Y=YB ABO ZE
 Y=YG ABO DE
 Y=YR INS ZE
 Y=YR EXC ZE
 Y=YR CLE JU
 Y=Y# ABO ZE
 Y=YX LAR JU ZE
 Y=YX ABO JU
 Y=YX FOR JU
 U=GYR INS ZE
 U=LYR ABO ZE
 U=CYR ABO JU
 R=RMG ABO ZE
 R=RMG CLE AD
 Y=YRY CLE ZE
 Y=YRY FOR WW