

SOCIAL ORGANIZATION, BREEDING BIOLOGY AND THE
PROCESS OF REPRODUCTIVE DIFFERENTIATION IN
OPHTHALMOPONE BERTHOUDI FOREL, A POMERINE ANT

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ABSTRACT

The queen caste has disappeared in the ponerine Ophthalmopone berthoudi and been replaced by breeding workers. Nests were excavated throughout the year, and large samples of ants were dissected. Sterile and fertile individuals all belong to the worker caste; there are no morphological differences between their reproductive organs, and they all possess a pygidial gland. The reproductive differentiation which occurs among the workers is controlled by insemination. Males disperse individually and copulation occurs inside foreign nests. Any worker that is below a certain age during the mating season may become mated, and this can result in a large number of breeding workers in nests that are visited by many males. Workers are short-lived and those whose period of sexual maturity does not coincide with the mating season remain sterile. During the rest of the year the proportion of breeding workers in the nests decreases through the emergence of new workers which remain unmated. As a consequence of this reproductive structure, the genetic relatedness between nestmates is expected to be very low.

Cooperative breeding is necessary because single breeding workers have a low rate of egg production. The interactions between breeding and sterile workers inside the nests show no evidence of distinctive "queen behaviour". There are no dominance hierarchies among the breeding workers, and all of them seem to lay eggs.

The activities of individually-marked ants were studied. Colonies consist of a variable number of distinct nests. Colony homogeneity results from the frequent transfers of adults and brood between nests, and there is a distinct colony identity. Colonies multiply by fission. Sterile workers exhibit a clear pattern of age polyethism: as they grow older they leave the confines of the nests and eventually become foragers. The selection pressures leading to the loss of the queen caste, the distinct ergatoid queen and breeding worker strategies, and the absence of a secondary egg-laying specialization in the worker caste are discussed.

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

Christian Paul Peeters

ERRATA

- 8:27 "Ferreira Brandao (1983)" should read "Brandao (1983)"
13:3 "were" should read "are"
13:8-11 "Active termite tunnels were intimately associated with the ant nests, and it is suggested that the ants take over abandoned parts of termite nests"
13:31- "A subjective impression was that foragers then spent more time away on single hunting expeditions, and that they returned with fewer termites"
36:23- add "The disappearance of marked ants reflected the death of the ants, as opposed to the loss of the marks"
42:10 "the main complex nests" should read "the main complex of nests"
51:14-17 These statements are based on data in Tables 6 and 7.
52:10-13 This statement is based mainly on data on nest (E), p.33
52:13-15 "The recruiters seem to behave in such a way as to enlarge the population of their own nests"
56:25-26 "... eg. underground invasion of Solenopsis and Dorylus"
59:28 add "The field observation that eviction was done by workers normally active above ground could merely reflect the fact that such workers are more likely to encounter interlopers first"

- 60:3 add "one test involving four ants was done, and there was distinct hostility between aliens"
- 62:10 delete "more"
- 63:14-17 "Thus the workers can only increase their personal *reproductive success* (as opposed to their inclusive fitness effect through aiding the queen) through the production of haploid eggs"
- 64:18 Odontomachus troglodytes (=haematodes auct.; Brown 1976)
- 66:20 "the length of the dorsal edge"
- 67:21 "There was no relationship" should read "There was no obvious relationship"
- 78:7 "nomenclatorial distinction" should read "distinction in nomenclature"
- 82:8-11 "In this species, the haploid eggs which develop into males are exclusively laid by the inseminated breeding workers; no others lay eggs"
- 84:18 "pupal emergence" should read "emergence from the pupa"
- 84:37- "...after the hardening of their exoskeletons has been completed. The occurrence of some sterile workers with..."
- 86:28-29 "The circumstantial evidence about adult longevity presented in the above paragraph supports the notion that the egg-layers in this species have a worker origin"
- 87:19-20 "As suggested in Chapter 5, each male may be capable of inseminating more than one worker, but a sufficient number of foreign males may not always reach certain nests"
- 88:18-20 "(as in the nests sampled in Table 16)" should read "(as in the nests sampled, see Table 16)"
- 92:15-17 "There are times of the year when few or no gamergates are present in the colonies (Table 14), and yet..."
- 97:30 "larval cuticle" should read "pupal cuticle"
- 98:8 "moved around the nest" should read "moved around nests"
- 104:17 "in a same nest" should read "in the same nest"

- 119:12 Pachycondyla (=Bothroponera) tesserinoda
121:7 "ethe" should read "the"
131:2 "temporal" should read "seasonal"
133:6 "accommodate"
138:30 "...the *only solution for survival*"
155:9 delete "Sonderdruck aus"

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



(Name of candidate)

30th day of April, 1984.

In memory of my Mother
Paulette Peeters
1930-1983

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TABLE OF CONTENTS

| | |
|-------------------------------------------------------------------------------------------------------------|-----|
| ABSTRACT | ii |
| DECLARATION | iii |
| DEDICATION | iv |
| ACKNOWLEDGMENTS | v |
| LIST OF TABLES | x |
| LIST OF FIGURES | xii |
| Chapters | |
| 1. INTRODUCTION : PONERINE REPRODUCTIVE STRATEGIES | 1 |
| 2. POLYDOMY AND COLONY FISSION IN <u>OPHTHALMOPONE BERTHOUDI</u> : SOCIAL ORGANIZATION WITH A DIFFERENCE | |
| 2.1. Introduction | 7 |
| 2.1.1. Selected literature survey | 7 |
| 2.1.2. Preview to <u>Ophthalmopone berthoudi</u> Forel | 9 |
| 2.2. Field methods | 9 |
| 2.3. Results - natural history | 12 |
| 2.3.1. Nest description | 13 |
| 2.3.2. Activity cycles | 13 |
| 2.3.3. Activities around the nest entrances | 15 |
| 2.3.4. Guests, intruders and enemies | 16 |
| 2.3.5. Foraging behaviour | 18 |
| 2.3.6. Adult and brood transfer | 20 |
| 2.4. Results - colony organization | 23 |
| 2.4.1. General features of colony organization | 23 |
| 2.4.2. Intensive study - colony one | 29 |
| 2.4.3. Intensive study - colony two | 31 |
| 2.4.4. Intensive study - colony three | 38 |
| 2.4.5. Intensive study - colony four | 42 |
| 2.4.6. Individual histories of selected individuals | 44 |
| 2.4.7. Colony identity | 45 |
| 2.5. Discussion | 48 |
| 2.5.1. Age polyethism | 48 |

| | |
|-----------------------------------------------------------------------------------|-----|
| 2.5.2. Recruitment between nests | 50 |
| 2.5.3. Polydomy and colony expansion | 55 |
| 2.5.4. Nestmate recognition | 58 |
| 2.5.5. Colony genesis | 60 |
| 3. MULTIPLE BREEDING WORKERS, INSEMINATION AND THE CONTROL OF REPRODUCTION | |
| 3.1. Introduction | 63 |
| 3.2. Methods | 65 |
| 3.2.1. Fieldwork | 65 |
| 3.2.2. Laboratory study | 66 |
| 3.3. Results | 67 |
| 3.3.1. Dynamics of brood production | 67 |
| 3.3.2. Characteristics of the egg-laying ants | 69 |
| 3.3.3. Reproductive structure of colonies | 78 |
| 3.4. Discussion | 80 |
| 3.4.1. Reproductive differentiation among workers | 80 |
| 3.4.2. Colony breeding patterns | 85 |
| 3.4.3. Ecological consequences of worker breeding | 88 |
| 3.4.4. Gamergates in the Ponerinae | 90 |
| 4. WITHIN-NEST INTERACTIONS BETWEEN BREEDING AND STERILE WORKERS | |
| 4.1. Introduction | 93 |
| 4.1.1. Selected literature survey | 93 |
| 4.1.2. Aims of this investigation | 95 |
| 4.2. Methodology | 96 |
| 4.3. Results | 97 |
| 4.3.1. Brood care | 97 |
| 4.3.2. Feeding and other "Innendienst" activities | 99 |
| 4.3.3. Organization of nest emigration | 99 |
| 4.3.4. Behaviour of breeding workers | 101 |
| 4.4. Discussion | 102 |
| 5. MALE BEHAVIOUR : COPULATION WITH WORKERS INSIDE FOREIGN NESTS | |
| 5.1. Introduction | 106 |
| 5.2. Methodology | 107 |

| | |
|-----------------------------------------------------------------|-----|
| 5.3. Results | 107 |
| 5.3.1. Dates of male activity | 107 |
| 5.3.2. Exit from home nest and dispersal | 108 |
| 5.3.3. Orientation to foreign nests | 109 |
| 5.3.4. Behaviour around foreign nests | 110 |
| 5.4. Discussion | 111 |
| | |
| 6. SEXUAL ATTRACTION AND THE PYGIDIAL GLAND | |
| 6.1. Introduction | 119 |
| 6.2. Materials and Methods | 120 |
| 6.3. Results | 121 |
| 6.4. Discussion | 121 |
| | |
| 7. GENERAL DISCUSSION : LOSS OF THE PONERINE QUEEN CASTE | |
| 7.1. Biology of <u>Ophthalmopone berthoudi</u> | 126 |
| 7.2. Why lose the queen caste? | 129 |
| 7.3. Ergatoids and breeding workers | 133 |
| 7.4. Transition from queenright to worker breeding system | 137 |
| 7.5. Why have queens not re-evolved? | 140 |
| | |
| APPENDIXES | 145 |
| LIST OF REFERENCES | 151 |

LIST OF TABLES

| | |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| 1. Size of the adult and brood populations of various colonies (34 nests), excavated at different times of the year | 14 |
| 2. Observations on ants marked after they were collected either inside the nests or when carried between nests | 24 |
| 3. Analysis of the activities performed by individual above ground workers over the various observation periods | 26 |
| 4. Fidelity of workers to particular carrying tasks over the various observation periods | 27 |
| 5. Activity of workers within polydomous colonies, showing the nests in which marked above ground workers were active | 29 |
| 6. Activities of marked workers during the days subsequent to their being carried to the new nest (E) | 34 |
| 7. Activities of marked workers during the two days subsequent to their being carried to the new nest (F) | 35 |
| 8. Ontogeny of individual workers' behaviour and movement within a complex of nests (colony two) over time | 37 |
| 9. Ontogeny of workers' behaviour and movement within a complex of nests (colony three) over time | 41 |
| 10. Activities of marked ants that were associated with the new nest (BY), colony four | 43 |
| 11. Stage of development and sex of the pupae in cocoons (n=588) collected in nests that were excavated at different times of the year in three successive years (1981-1983) | 68 |
| 12. Ovarian activity in breeding workers, samples of which were dissected in detail (i.e. the numbers of mature eggs were recorded) | 71 |
| 13. Rate of egg production in various isolated groups of ants | 72 |
| 14. Reproductive status of ants from a number of colonies | 76 |
| 15. Measurements (in mm) of the head and gaster of breeding and sterile workers | 77 |

| | |
|-----------------------------------------------------------------------------------------------------------------------------------------|-----|
| 16. Reproductive status (determined by dissection) of individuals from two nests excavated on 23.III.1982 (ie. after the mating season) | 80 |
| 17. Spatial distribution of the adult (n= 348) and brood populations within a nest excavated in October 1982 | 98 |
| 18. Size of the male population in nests excavated at various times of the year during the period January 1981 to March 1984. | 108 |

LIST OF FIGURES

| | |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| 1. A simple, hypothetical, branching phylogenetic diagram of the family Formicidae, showing the position of the Ponerinae within the poneroid complex (from Taylor 1978) | 2 |
| 2. Worker of <u>Ophthalmopone berthoudi</u> carrying a male between two nests | 21 |
| 3. Plan of colony one, indicating the location of the various nests | 30 |
| 4. Plan of colony two | 32 |
| 5. Plan of colony three | 39 |
| 6. Gas chromatograms of the mandibular gland secretions of three functional categories of workers of <u>Ophthalmopone berthoudi</u> (a) Innendienst workers, (b) foragers, (c) breeding workers | 54 |
| 7. Developed ovaries of a breeding worker of <u>Ophthalmopone berthoudi</u> | 70 |
| 8. Frequency distribution of the number of mature eggs found in the ovarioles of breeding workers (=gamergates) collected from five colonies | 73 |
| 9. Undeveloped ovaries of an unmated, sterile worker of <u>Ophthalmopone berthoudi</u> | 75 |
| 10. Frequency distribution of the percentages of gamergates in various nests collected at different times of the year | 79 |
| 11. Longitudinal section through the sixth and seventh abdominal tergites of a gamergate of <u>Ophthalmopone berthoudi</u> , showing the cells of the pygidial gland | 122 |
| 12. (a) Ergatoid queen and worker of <u>Leptogenys nitida</u> (b) Ovaries of inseminated ergatoid of <u>L. nitida</u> , showing two pairs of about 11 ovarioles, as well as the small size of the eggs | 135 |
| 13. Hypothetical scheme of evolutionary changes leading to the disappearance of winged queens | 138 |

CHAPTER ONE INTRODUCTION : PONERINE REPRODUCTIVE STRATEGIES

Queen differentiation is often thought to be fundamental to the maintenance of the Formicid organization. Various forms of social interplay between queens and workers usually control the phenomenon of worker sterility. Two theories have been elaborated to explain, in population genetics terms, the selective advantages of these interactions for the participants. Kin selection (Hamilton 1972) explains the altruism of sterile workers towards the queen as a means of maximizing their inclusive fitness, while parental manipulation (Alexander 1974, Michener and Brothers 1974) interprets the same phenomenon as a manifestation of queen control. Both these explanations have been framed in the context of a queen-based social organization.

There is a group of species in the phylogenetically-primitive ant sub-family Ponerinae where the eggs that develop into workers and males are laid by one or more worker-like individuals. As early as 1911, Emery speculated in his *Genera Insectorum* that the female of the ponerine Diacamma resembles the worker so closely as to be confused with it. Arnold (1915) suggested that, in species of the larger Ponerinae, "the functions of the female are usurped by one or more of the workers". In 1922, Wheeler and Chapman documented the mating of a worker with a male in Diacamma rugosum; externally the worker found in copula differed neither in size nor in structure from any of her sisters. The absence of a queen in the colonies of some Ponerinae contrasts sharply with the general Formicid pattern. A distinct female caste usually performs the reproductive function while the worker caste is sterile, or at the most produces trophic or male eggs (Wilson 1971). Loss of the queens is undoubtedly secondary in ants, but there is the possibility that worker reproduction stands as a viable eusocial alternative. The end of the queen's supremacy

as the diploid egg producer suggests that other mechanisms may be involved in the "dynamics of established eusociality" (Crozier 1982).

The sub-family Ponerinae is an ancient one, and some of its representatives are ancestral to four other sub-families in the poneroid complex of the family Formicidae (Figure 1). There are eight presently-recognized tribes in the Ponerinae, with the Amblyoponini forming the basal group of this assemblage. The Cerapachyini may link the ponerines to one of the doryline groups, and the Ectatommini are intermediate with the myrmicines (B. Bolton pers. comm.).

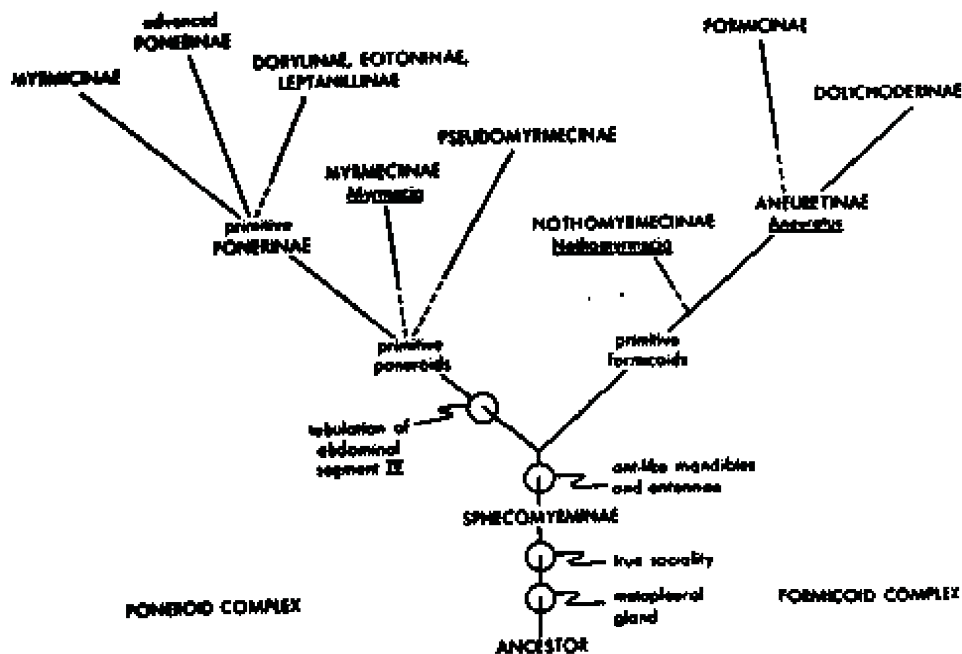


Figure 1 A simple, hypothetical, branching phylogenetic diagram of the family Formicidae, showing the position of the Ponerinae within the poneroid complex (from Taylor 1978).

The Ponerinae flourish chiefly in tropical regions, being poorly represented in the temperate zones; in southern Africa

they constitute about twenty percent of the known ant fauna (Arnold 1915). The extensive taxonomic differentiation exhibited by the members of this ancient sub-family led Wheeler (1910) to consider them as the surviving relicts of a great cosmopolitan and probably Mesozoic fauna. The behaviour of the Ponerinae presents a mingling of primitive and specialized features; among the former are the highly entomophagous habits of the adults, the feeding of the larvae with pieces of insect food, the retention of the cocoon, the ability of the callows to hatch unaided and the small size of the colonies (Wheeler 1910). Where winged females occur, the similarity of size between the latter and the workers (Haskins 1970) may indicate a low degree of fecundity.

Haskins (1970) has reviewed the reproductive biology of primitive ants (Myrmeciinae and Ponerinae) and explored the diversity in their patterns of breeding, dispersal and colony foundation. Many ponerines have typical queenright breeding systems, but in a number of genera the queens have lost their wings and become ergatogynes or ergatoids (i.e. intermediate in structure between queen and workers). In addition there is a group of species where no queens are distinguishable from the workers. Haskins and Whelden (1965) divided the Australian ponerine genus Rhytidoponera (tribe Ectatommini) into one group of species with typical winged queens, another group where such queens occur only occasionally, and a third group characterized by the absence of queens. Since there are no queen-worker intermediates (=ergatoids) in this genus, Haskins and Whelden suggested that in some species, the original queen caste may have disappeared entirely and one or more fertilized laying workers substituted as the functional reproductives. They did not indicate how such individuals could be differentiated from the sterile workers.

Despite Wheeler and Chapman's (1922) early work, the true worker nature of the functional egg-layers in some ponerines has repeatedly been misunderstood and confused with the ergatoid strategy. The common view was that there is still a distinct but cryptic reproductive caste in these queenless ponerines.

It was hinted (Haskins and Whelden 1965; Holidobler and Haskins 1977) that only a proportion of the Rhytidoponera "workers" possess functional spermathecae and can become inseminated by males. Haskins and Zahl (1971) suspected that the queen caste in Dinoponera "may be replaced by a reproductive form morphologically very similar if not identical to the worker but physiologically and structurally capable of fertilization and the production of worker brood". The literature abounds with inconsistencies, especially in Haskins' work. In 1965, Haskins and Whelden had pointed out that worker reproduction is a phenomenon distinct from the progressive reduction of the queen caste towards worker-like features (ie. the evolution of ergatoids). Yet Haskins (1970) explained the absence of morphologically distinct queens in terms of "... an almost complete convergence of the morphology of the two castes at worker level, save for the retention of functional spermathecae, and, possibly, of more fully developed ovarioles by the reproductives". The issue has also been obscured by the inappropriate use by some authors of the terms "ergatoid", "ergatogyne", "fertile brood female" and "gyne" when referring to what appear to be true breeding workers. Recently Ward (1981b, 1983) studied species in the Rhytidoponera impressa group and recognized that worker breeding is a distinct reproductive pattern. Ward also revealed an apparently stable intrapopulation dimorphism of colony structure involving single queens or multiple mated workers.

The major aspect of this study was to investigate whether the mated, laying "workers" are part of a distinct reproductive group or whether all workers have identical reproductive capabilities. If the egg-laying individuals have a true worker origin, how is their functional differentiation from sterile workers controlled? A comprehensive study of the different aspects of the biology of Ophthalmopone barthoudi Forel was attempted; this species had not previously been studied. The division of labour, breeding biology, male dispersal, pattern of colony foundation and the pheromonal basis of some of the interactions

between individuals were studied in order to resolve puzzles about the nature of the queenless social structure. The data obtained throw light on some major theoretical problems facing the student of hymenopteran eusociality.

Each chapter of this thesis deals with a roughly homogeneous body of evidence which was collected using a similar methodology. The subject matter of the various sections overlaps to a certain extent, and this necessitates extensive cross-referencing between chapters. Many chapters thus cannot easily be read in isolation. Chapter 2 examines the ecology and colony organization of this species in the field. A scarcity of life history details is often characteristic of social insect studies and this hinders the interpretation of evolutionary modifications at the level of the colony. The movement of workers between the nests of this polydomous species was studied in detail. The adaptive significance of a multi-nest colony structure, the pattern of age polyethism, the occurrence of colony fission, and nestmate recognition are all discussed. Chapter 3 concentrates on the reproductive biology. The novel approach here was to sample nests consistently throughout the year and look for temporal variations in the size of the contingent of egg-layers. With these data and others on the incidence of insemination, the mechanism of differentiation into fertile and sterile individuals is elucidated. Chapter 4 is a laboratory enquiry into the organization of within-nest activities, and especially into the interactions between sterile and breeding workers. The possibility that there is an inhibitory effect on oviposition among the reproductive ants was explored. This chapter also deals with the division of labour among the "Innendienst" workers, and with their care of the brood. Chapter 5 covers the behaviour of the males in the field. Chapter 6 deals with the issue of chemical communication, an important component of eusocial organization. An histological study determined that the pygidial gland, presumed to release sexual attractants, was present in all the workers. The origins of the "calling" behaviour of workers are discussed and this complements the data on mating behaviour in Chapter 5. Chapter 7 attempts to

synthesize the various facets of this study. The two major theories on the occurrence of worker sterility in Hymenoptera are examined in the light of this work. Original data from my work on other ponerine genera are presented in order to consider the range of reproductive adaptations. I also explore the concept of colony identity, the ecological conditions which led to the evolutionary loss of the queen caste, the ergatoid modification in queen morphology, the intermediate steps along the transition from queenright to worker reproductive colonies, the concomitant changes in male behaviour and mode of colony foundation, and the lack of secondary specialization in the group of egg-laying individuals.

Caryl P. Haskins has made a significant contribution to our knowledge of ponerine ants. He recognized that the primitive formicid fauna offers an outstanding opportunity for the study of social evolution.

There is today a rich assemblage of ancient forms, providing a living record of evolution, including near-facsimiles of types that were dominant on our planet sixty million years ago or more. In such "living fossils", we find in detail the specific evolution of many of the physiological and behavioral patterns that have cemented, reinforced, and perfected Formicid social life over the eons (Haskins 1970).

CHAPTER TWO POLYDROMY AND COLONY FISSION IN OPHTHALMOPONE
BERTHOUDI: SOCIAL ORGANIZATION WITH A DIFFERENCE

2.1. Introduction

2.1.1. Selected literature survey

The possession of distinct identities by separate colonies is an important characteristic of eusocial organization. The members of one colony are usually confined to a single nest. Different colonies are recognized by their mutual hostility, and this depends on the ability of nestmates to recognize each other instantly (Brian 1983). In a number of ant species however, several nests are connected with each other by frequent exchange of members with little exhibition of hostility (Yamauchi et al. 1981). The study of this polydomous organization ("unicolonial populations", Wilson 1971), which occurs exclusively in the Formicids, may reveal the nature of some of the mechanisms which are normally responsible for the maintenance of colony integrity. Polydromy is often associated with polygyny in each nest, colony multiplication by budding, reduced territorial behaviour and enlargement of colony size (Yamauchi et al. 1981). Most investigations of polydomous organization have relied on indirect methods in order to determine the movements of individuals between nests. Cherix et al. (1980) studied the organization of the nests in a population of Formica exsecta; since there are no above ground paths between the nests, they relied on the marked recapture of hundreds of ants, aggressivity tests involving ants from neighbouring or distant nests, and the measurement of density in different parts of the home range. Cherix and his co-workers found that exchanges of adults, brood and food were restricted to certain groups of nests, and that the polydomous and polygynous organization had not led to a reduction in the

distinctness of inter-colonial interactions.

Colonial organization in the social insects is based on the differentiation of nestmates into functional groups, and on division of labour based on these (Wilson 1971). Ant colonies seem to depend primarily on age polyethism and on environmentally controlled differences in growth and development to introduce behavioural variability into their populations (Sudd 1982). Investigations of division of labour are usually carried out in the laboratory. Oster and Wilson (1978) have outlined an approach to the study of the biological characteristics of caste systems. The activities occurring both outside and inside the nest are listed; if distinct physical groups or age classes of individuals can be distinguished, separate behavioural repertoires are compiled for each group. The relative frequencies of the acts can then be computed, and an ethogram is constructed. The latter incorporates the repertoires of different castes, the transition probabilities connecting individual acts and the time distributions spent in each act. A variety of approaches have been followed by different researchers however, and several aspects of polyethism have been studied. Miranda and Vinson (1981) observed a small sample of individually marked workers of Solenopsis invicta, and they determined the percentage of time spent by the marked ants in eight behaviours. Traniello (1978) studied worker profiles in the ponerine Amblyopone pallipes; he compiled individual ethograms with the frequency of each behavioural category relative to the total number of acts in a worker's repertoire. Ferreira Brandao (1983) followed changes in the frequencies of behavioural acts performed by queens and workers during the various phases of colony development in Odontomachus affinis. Porter and Jorgensen (1981) conducted a detailed field study of the "exterior workers" of Pogonomyrmex owyheei, where they investigated quantitatively worker role fidelity and population dynamics.

Fieldwork on a ponerine species with small colony units allows for a different approach to those normally used. Owing to the feasibility of individually-marking every ant that is active above ground, the roles of individuals over a number of

consecutive days can be monitored. This contrasts with the study of groups of ants (defined on the basis of age or behaviour), with its emphasis on random censusing and statistical inference. While this study does not investigate worker role fidelity in great detail, it provides descriptive information on the pattern of age polyethism and on the relationships between nests in a polydomous colony.

2.1.2. Preview to Ophthalmopone berthoudi Forel

Ophthalmopone berthoudi is known only from its workers and its males (Arnold 1915). The monomorphic workers are medium-sized (13 mm) with large bulging eyes. The genus belongs to the Tribe Ponerini (sub-tribe Poneriti), and its distribution is Ethiopian (Prinz 1975). There has been very little published work on Ophthalmopone, except for short references to its exclusively termitophagous diet. Columns of hunting ants have been observed in O. ilgi (Forel 1928), and it has been assumed that group-raiding behaviour occurs in the whole genus (Wheeler 1936).

Preliminary work revealed that adults of O. berthoudi are frequently carried from nest to nest. It was soon determined that a colony unit is made up of a number of nests, and that there are regular transfers of brood and nestmates between these. Thus the terms "colony" and "nest" are not used interchangeably in this work.

2.2. Field methods

This chapter deals with the behavioural work carried out in the field. The organization of the above ground activities in colonies of O. berthoudi was studied with a minimum of interference. At the end of most field visits nests were excavated and transferred to the laboratory (see Chapters 3 and

4). The ground in which the nests occurred was very hard and this necessitated strenuous digging with picks and shovels; the average depth of nest chambers was 30-50 cm. Fourteen trips were organized to Mkuzi Reserve during the period July 1980 to July 1983; this represents about 130 working days spent in the field.

Mkuzi Game Reserve (latitude 27°30' to 27°45' south, longitude 32°05' to 32°25' east) is situated on the coastal plain east of the Lebombo Mountains in north eastern Natal (South Africa) and is approximately 40km west of the coastline. The population of Ophthalmopone berthoudi which I studied (Gwambane area) occurred in an open woodland in which the grassland component has been reduced to a low level through heavy grazing pressure. The basal cover is low (grass component less than 1%) and the grasses are short (less than 20 cm), features which make this habitat particularly suitable for the behavioural observations of ground-dwelling ants.

The ponerine community at this site consisted of Plectroctena conjugata Santschi and P. mandibularis F. Smith (both predominantly millipede hunters), Pachycondyla sp. (soror-complex), P. krugeri Forel and Ophthalmopone berthoudi (all termite hunters).

These ponerine ants nest in the ground and thus their occurrence in this habitat can be partly attributed to the characteristics of the soil, which is a free-draining, red sandy clay loam. The surface is slightly capped and compacted and this, together with the sloping terrain, increases the run-off and decreases the infiltration. There are no sub-surface clay pans which would cause prolonged water-logging of the surface horizons.

Mkuzi is semi-arid (Goodman 1981), with a hot humid summer from mid-September to the end of March. The rainfall is highly seasonal, peaking in February and with the month of lowest rain occurring in June. The greatest variability in the mean monthly rainfall occurs during the dry winter months. The mean annual temperature is 23,2°C. The mean maximum temperature for the hottest month (January) is 32,5°C. Winters are warm with a

mean minimum for the coldest month (July) of 11,7°C; the absolute minimum for July is 5,5°C.

The initial step at each stage of the investigation was to colour mark individual ants. Ants were held with forceps and spots of paint were applied dorsally to five possible regions of the body (head, pronotum and mesonotum, first and second segments of the gaster). A choice of five colours (Humbrol enamel paint) was used to generate a large number of unique combinations. The marking procedure was not found to have any detrimental effects on the ants' behaviour, and the paint remained on the cuticle for a number of months.

Four different colonies were selected for intensive study. The component nests were located by following the transfers of adults and brood. Every ant coming in or out of the nests was collected, marked and released; some of the ants carried between nests were also marked. Exact details of date, nest and activity at the time of capture were kept for each individual. After a few days, having marked all the ants active above ground in one colony, further ants were collected from inside the nests by introducing a long grass stem in the entrances. Both marked and unmarked ants rushed out to attack this foreign object and the unmarked ants were painted.

The activities of individual ants were monitored for varying numbers of days, using a portable tape recorder. This was done during morning and afternoon observation sessions lasting up to 7 hours. The observations obtained do not represent a complete record of the activity in one colony. The entrances of each nest could not all be watched simultaneously because of the large areas covered by nest complexes. In some instances the data obtained (Appendix A) represent an exhaustive sample of the activities occurring in parts of the colony during a limited time period (eg. all the individuals entering and leaving a particular nest); at other times the sample was selective, covering particular events (eg. adult transfers) and interactions that were of interest. Only a description of the behavioural repertoire of the colony was aimed at. For the above reasons, the frequency of particular activities performed by individual

ants over a one-day period could not be determined; different ants were watched for varying amounts of time. Sampling intensities during the various field trips varied, and thus the data obtained from different colonies (Tables 2 to 5) must be compared with caution. The marked ants in some colonies were left in the field for a few months, so as to obtain data on the change in activities of individual workers over time, and the dynamics of nest and colony foundation.

A data storage programme written in Pascal was developed for interactive use on an Apple II microcomputer. The raw data from the tape transcripts was entered in code form; for each day's entry, repetitions and redundancies were eliminated, eg. when two similar activities were included for one ant, the one with the lower information content was discarded (Appendix A). All the records for each individual ant were then collated over the entire observation period (Appendix B). These data were visually examined in order to study the association between different activities, the extent of task fixation, the pattern of adult and brood transfers within nest complexes and the importance of this carrying behaviour. In the text the marked ants are identified with a colony prefix (eg. # for colony two, \$ for colony three, % for colony four) and an individual number. An observation period refers to a continuous number of days (ie. the duration of a field trip), while an observation session refers to a morning or an afternoon within the former.

2.3. Results - natural history

This section consists of a description of the above ground activities; the data are often based on the observation of individually-marked ants, and are seldom quantitative.

2.3.1. Nest description

The nest entrances were simple holes in the ground with little or no accumulation of soil near the periphery. They were usually located in open patches of ground or at the base of small bushes, away from the dense undergrowth below trees. Over forty nests were dug up; these consisted of a number of chambers and galleries with no distinct spatial arrangement, and seldom extended deeper than 50 cm. Active termite tunnels were intimately associated with the ant nests, and this together with other features indicated that the ants take over abandoned parts of termite nests. A few nests occurred in deserted Odontotermes chimneys.

Individual nests contained variable numbers of adults (mean= 186 \pm 151 s.d., range= 29-840, n=34) and brood (Table 1). The brood was generally found in the deeper chambers, though many cocoons were often found near the surface. There were from 2-7 nests in one colony, and these nests were separated by distances varying from 30 cm to 75 m. None of the nests were connected underground, even those with entrances very close to each other.

Four colonies had all their component nests excavated, and estimates of the total adult population are given below (mean is 517):

- (1) January 1981: 3 nests, 453 adults (84+142+227).
- (2) April 1981: 3 nests, 638 adults (445+75+318).
- (3) December 1981: 2 nests, 311 adults (261+50).
- (4) February 1982: 5 nests, 464 adults (168+124+72+80+20).

2.3.2. Activity cycles

The ants were observed outside their nests throughout the year. However the level of above ground activity decreased during the dry winter months; fewer observations were made during the study of colonies. Foragers then spent more time away on single hunting expeditions, and they returned with fewer

Table 1 Size of the adult and brood populations of various colonies (34 nests), excavated at different times of the year. The numbers in the last four columns refer to a particular nest except in those cases where an * is used, indicating a mean for that set of nests.

| Time of year | No. of colonies sampled | No. of nests excavated | Total numbers in each nest | | | |
|--------------|-------------------------|------------------------|----------------------------|----------|-----------|-----------|
| | | | workers | eggs | larvae | cocoons |
| January '81 | 2 | 4 | 149 * | 4 | 0 | 50 * |
| January '82 | 1 | 1 | 140 | 55 | 20 | 47 |
| January '83 | 2 | 3 | 116,121,222 | 23,40,7 | 16,34,50 | 17,13,74 |
| February '82 | 1 | 5 | 111 * | 47 * | 22 * | 26 * |
| March '82 | 1 | 2 | 77, 119 | 10,35 | 7,85 | 1,113 |
| April '81 | 1 | 3 | 75,318,445 | 0,50,437 | 0,50,109 | 33,43,226 |
| April '83 | 1 | 3 | 29,106,121 | 55,234,1 | 13,167,14 | 44,6,63 |
| July '81 | 5 | 5 | 351 * | 53 * | 4 * | 0 * |
| July '83 | 2 | 2 | 112,262 | 49,120 | 5,17 | 0,11 |
| October '81 | 2 | 2 | 81,190 | 7,10 | 2,60 | 71,91 |
| October '82 | 2 | 2 | 143,348 | 340,340 | 138,175 | 84,49 |
| December '81 | 1 | 2 | 50,261 | 0,155 | 6,141 | 0,106 |

not quantified

termites. This is probably linked to decreased termite availability; the dry soils and the low temperatures at night may reduce the nocturnal activity of the termites.

Daily patterns of activity varied during the year. The ants remained active outside the nests throughout the day during winter, but during the rest of the year the above ground activities stopped during the middle of the day. In summer foraging began around 04h30 and stopped as early as 09h00-10h00; it was seldom resumed before 17h00 and continued until sunset. This biphasic pattern appeared to be regulated by soil temperatures; when the ground surface became very hot, the ants stayed inside their nests where the rise in temperature was buffered by the soil layers (Appendix C). Workers returning to their nests towards the end of the period of activity climbed up into short grass or low vegetation. This seemed to be a thermal refuge from the hot ground, because the ants remained there for short periods before they ventured on the ground again and ran across to another plant. This pattern of activity was thus determined by particular environmental conditions; on cool, cloudy or rainy summer days foraging continued for longer periods and even for the whole day.

There were also patterns in termite activity which influenced the activities of foragers. The early hours of the morning were peak foraging times for the ants, because termites were still near the surface following their nocturnal forays. Later on in the day the termites retreated underground because of rising temperatures inside their soil galleries. On one night (20h40, April 1981) the ants were hunting termites that were active above ground very close to a nest entrance.

2.3.3. Activities around the nest entrances

Some excavation regularly occurred inside the nests because soil was brought to the surface and dropped in the vicinity (5 cm) of the entrances. This was most frequent after rain, and indeed seldom occurred during winter. Entrances of existing

nests were sometimes altered or changed, and occasionally entrance holes became filled up with mud during heavy rains. A number of workers often simultaneously excavated soil out of a nest.

Nest sanitation was another distinct activity, where workers came up to the surface and discarded empty cocoons and food remains. Dry pellets were carried for a certain distance (1-5 m) before being left on the ground; these pellets consisted of bits of hard termite exocuticle, jaws and limbs, which were densely packed into a distinctive rough-looking ball. There were also moist-looking, smaller pellets which were dropped closer to the entrances; these seemed to be the sucked-out remains of termites. The cleaning behaviour was distinctive because dry pellets were never discarded close to the nest entrances. Individual cleaners repeatedly dropped their pellets in the same place.

Dead or dying ants were dragged out of the nests and dropped a few metres away; this was rarely observed however. A few ants behaved idiosyncratically in that they brought flowers, sticks or leaves into the nests; these objects were later discarded by other workers. In addition, ants were observed to close up nest entrances on two occasions. In the one instance an ant did this for hours, picking up pebbles and pieces of ground litter from the vicinity and dropping them (even wedging them) in an entrance hole; that nest was still active however, and inhabitants coming in or out had to squeeze through the debris.

2.3.4. Guests, intruders and enemies

Isopods and thysanurans (were not identified further) were found in small numbers during the excavations of O. berthoudi nests.

Ectoparasitic mites were found on both the ants' bodies and on egg packets. Their numbers increased greatly after the ants had been kept in the laboratory. There were sometimes heavy

infestations of a fly larva during the winter months; these occurred in the moister regions of the ant nests. The behaviour of the adult flies was observed as they hopped behind foragers or other workers that were returning to their nests. The ants could become aware of this chasing and attempted to lose the flies. However flies did succeed in finding nests and were seen entering after the workers.

Other arthropods, such as mutillid females and small beetles, tried to enter the nests; they were seen to be repelled a few times, and once a mutillid was dragged out. There were no distinct soldiers, but ant workers sometimes actively guarded the nest entrances; they normally stood with their bodies half in the holes and their mandibles slightly opened, and would momentarily come out to challenge intruders. Myrmicine ants sometimes milled around the entrances in great numbers, scavenging on food remains; their entry into the nests was barred by the guards.

No natural instances of predation on O. berthoudi were recorded, but it is suspected that lizards feed on the ants. The ground woodpeckers which elsewhere feed on ground-dwelling ponerines do not occur in Mkuzi Reserve. A number of arthropods were observed to try to steal the termites brought by the foragers of this ant. Xeposis sp. beetles attempted to cause returning foragers to drop their food. One species of spider occasionally waited outside the nest entrances and jumped on the termites held in the ants' mandibles; they were seldom successful. Foragers also fell into ant lion pits; on most occasions they managed to get out but could lose their prey.

Although O. berthoudi and Pachycondyla krugeri (which also feed on termites) were generally active at different times of the day, a few interspecific interactions were observed around hunting grounds, and termites were stolen from O. berthoudi on one occasion. There were also interactions with formicine ants over food.

2.3.5. Foraging behaviour

Foraging originated from every nest and foragers always returned to their nest of origin in a colony. Foraging was accomplished by lone workers operating independently of their nestmates. This lack of cooperation between hunters was partly an effect of the absence of trail pheromones in this species. The distinctive trail-laying gait (where a part of the abdomen is dragged along the substrate) was never seen; the absence of continuous orientation trails on the ground was verified by disturbing the soil surface ahead of foragers and noting that they did not become disorientated. Some kind of discrete marking was observed however, the function of which is not completely understood. Workers stood momentarily still and rubbed the ventral tip of their gaster sideways over objects lying on the ground (eg. pebbles, dead leaves, sticks, fruit pods, dung pellets, ..); marking was never done directly onto the bare substrate. This behaviour was especially seen after rain (rain presumably removes old traces of chemical signals). Above ground workers often marked the vicinity of nests, and this may be involved in the close-range orientation to entrances; one day after a heavy downpour, returning workers had difficulty in locating entrance holes. Some foragers walked slowly away from their nests and regularly spotmarked along their route; when these were seen coming back with termites, they walked faster and did not mark. It was assumed that they were inexperienced or unfamiliar with a new area on their way out, and that they use the marks as personal orientation cues on the way back. The behaviour of workers from foreign colonies towards this secretion was not tested, but it is not thought to have a territorial function.

O. berthoudi was found to feed exclusively on termites. The foraging behaviour of termite species determined their availability to the ants. Three species that were conspicuous in the Gwambane area seemed to make up most of the ants' diet, with seasonal differences in the relative proportion of each.

Macrotermes natalensis and Odontotermes badius forage principally on wood-, grass- or leaf-litter on the surface, covering their food with a thin layer of soil and feeding beneath this protective cover (Longhurst et al. 1978). Lone foragers of Ophthalmopone that were searching in the appropriate terrain seemed to be attracted to the freshly-built soil sheetings of these termites. Once sites of activity had been located the foragers broke open the soil sheeting or looked for natural openings. Termites were captured one by one; the prey was held in the ants's mandibles, impaled on the sting and then flung underneath the body to the rear. Up to 15 termites were caught in this way, and the ants actually entered the soil covers at times. As the termites became sparse (they rapidly evacuated the area), the foragers gathered most of the semi-immobilized bodies and stung them once again. Using the front legs they then packed the paralyzed bodies between their mandibles and brought them back to the nest; up to ten termites could thus be retrieved. Hodotermes mossambicus are grass-harvesting, surface foraging termites which sporadically exit in small groups from underground galleries. The ants locate these visually; single termite workers were captured, immobilized with a sting and returned to the nest. Winged termite reproductives were caught following their nuptial flights. Odontotermes were sometimes captured in their own nests; this occurred when the ants entered their open chimneys and hunted the termites active on the inner lip. It was observed that the ants avoided the termite soldiers, though these were occasionally captured. Foragers were often found with missing limbs, and they presumably sustained such injuries during hunting.

The successful foragers only remained inside their nest for a short while before they reappeared and went back to the same food source (in Chapter 4 it is shown that they leave their prey near the entrance chambers). It was clear that recruitment never occurred, and individual foragers independently exploited a food source until it was exhausted. Instances of one ant following another (i.e. tandem running) were never observed. There appeared to be social facilitation within the nests whenever a

number of successful foragers returned to their nest; other ants were induced to go out and forage. The areas in which some marked foragers hunted were noted; it was determined that, on consecutive days, individuals generally returned to the same part of their colony's home range. Foragers did not always hunt around their particular nests; sometimes they were active at the opposite end of the colony's home range, eg. in colony three, ant \$271 hunted around nest (X) but brought its prey to (Z), 35 m away (Figure 5, p. 39); it did this on successive days. One ant walked 75 m away to forage, and then returned to its nest.

It was observed that various hunters consistently returned to the nests with termite loads of different sizes, and this may be partly related to individual experience. Workers involved in other nest activities also took part in foraging when the opportunity arose. A carrier ant involved in adult transfer between two distant nests came across a Hodotermes on its path. It captured it, turned back and brought it into its nest. A cleaner retrieved a termite which had been left in an ant lion pit. Excavators often retrieved paralyzed termites which had been dropped close to a nest entrance.

2.3.6. Adult and brood transfer

The transport of adult ants and brood between nests of the same colony was a frequent occurrence (Figure 2; males and workers were carried in the same way). When adults were carried this was preceded by a stereotyped interaction between the carrier ant and its recruit. These pairs of adults occasionally broke up above ground between nests, and the ants would then come together again; this provided the opportunity to observe the initiation of the carrying behaviour. The two ants faced each other head-on and there was vigorous antennation between them; stridulation was heard on a few occasions. One of the ants then lowered its head and pushed it underneath the other ant's mandibles; this sometimes gave the impression that the recruits led the interaction, but was more likely to be a submissive

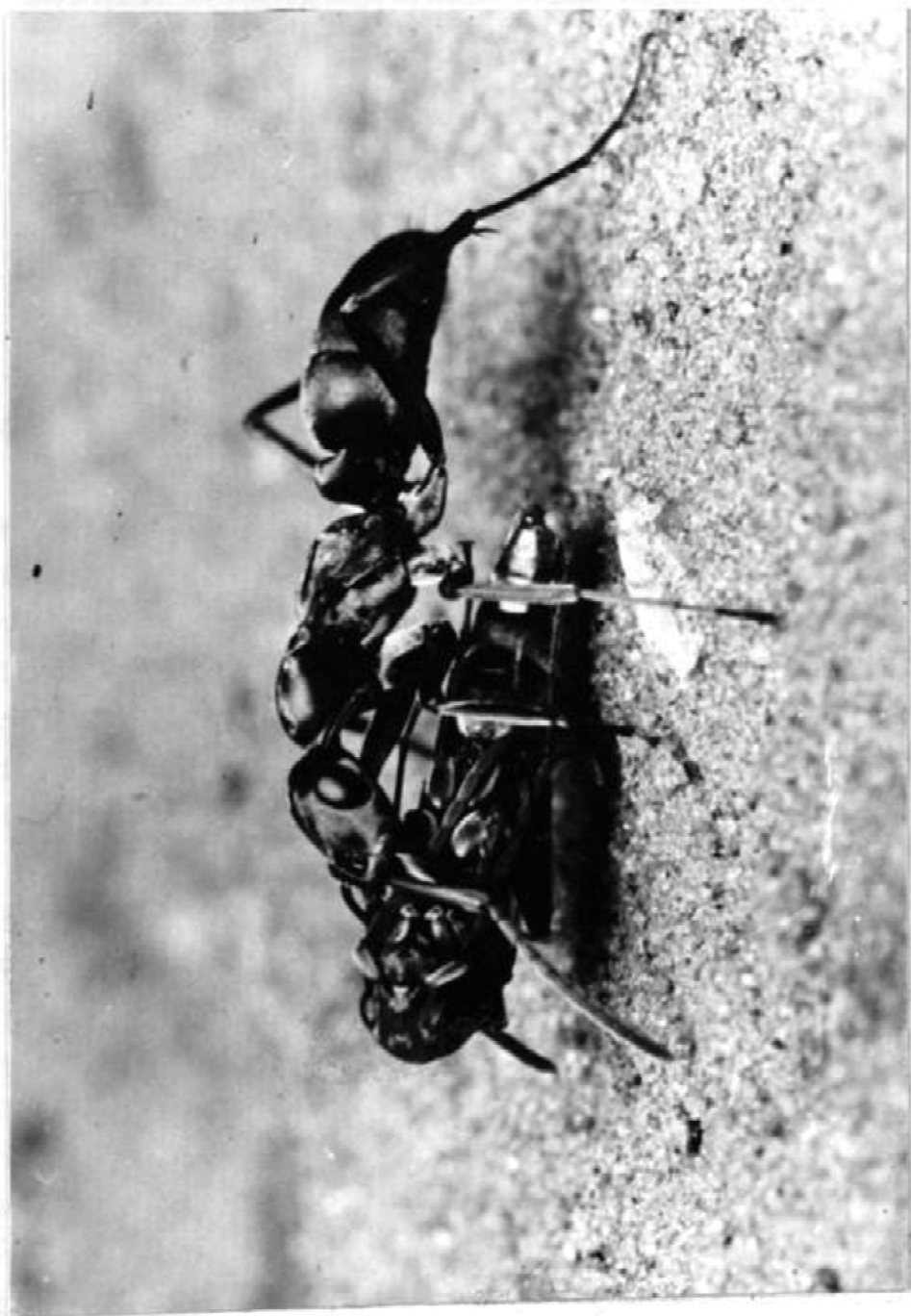


Figure 2 Worker of Ophthalmopone berthoudi carrying a male between two nests.

action. The carrier grasped the recruit's mandibles and lifted this ant slightly. The recruit responded by folding its legs and antennae close to its body, thus adopting a pupal posture. The carrier adjusted its grip around the pronotum and carried the adult head first. Adults were always carried in this conventional way, and the few exceptions to this often resulted in the pair breaking up above ground. Males were carried within the colony during the mating season.

Single cocoons, single larvae of all sizes and packets of 3-14 eggs were also carried between nests. The transfer of untanned cocoons (i.e. recently spun) was also observed. The inter-nest transport sometimes involved large numbers of brood; in 90 minutes I observed 41 cocoons being transferred between two nests that were 70 cm apart.

Different carrier ants active between the same nests seldom followed the same route, and indeed the paths were sometimes strikingly different; this again indicates that these ants do not rely on trails for navigation. Thus the nests of the polydomous colonies of O. berthoudi are not connected together by semi-permanent chemical trails. Observations of the same carrier ants over consecutive days revealed that they gradually took shorter routes.

The following observations complement the description of the carrying behaviour:

- (a) When a pair broke up outside the nests (often through my interference), the recruit behaved in one of two ways: it momentarily remained immobile on the ground in a crouched position, or it started walking as soon as it hit the ground. The carrier ant, which had initially run away, then proceeded to look for its recruit (the latter remaining fairly stationary). Once they were together again the recruit was picked up and the transfer continued normally (a carrier and its recruit never swapped roles). On a number of occasions the two ants did not find each other again. While the carriers were able to proceed on to their destination, the recruits could only walk back (with varying difficulty) to the nests from which they originated.
- (b) An adult pair was disturbed and the ants separated above

ground; as the carrier was searching for its marked recruit it met an unmarked ant, and there was a short interaction. The carrier left and soon found the marked recruit, which it picked up. In contrast, with two other pairs, carrying was readily initiated when the carrier from one was placed together with the recruit from the other. These data suggest that the carrier ants can recognize particular *individuals or categories of individuals*.

2.4. Results - colony organization

Intensive observations of four colonies containing large numbers of marked individuals provided valuable insights into the division of labour and the organization of colony activities over the nest complexes. *The general patterns common to all the colonies are first presented, followed by the individual histories for unique data.*

2.4.1. General features of colony organization

At any point in time, the adult members of a colony were divided into those ants confined to the inside of the nests and those active above ground. *Once all the workers outside the nests had been marked (during the first few days), a few more workers that were unmarked appeared above ground; it was assumed that these had previously been confined inside the nests.* The activities of the "Innendienst" ants (Wilson 1971) are described in Chapters 3 and 4. Various numbers of ants were collected inside the nests and marked (Table 2); these were small samples compared to the exhaustive samples of above ground workers. Many of these "inside" ants were not seen again during the rest of the observation periods; however on a number of occasions such ants were seen to be carried between nests (Table 2). *Similarly, some of the ants that were collected and marked as they were being carried within the colony, were not seen above*

Table 2 Observations on ants marked after they were collected either inside the nests or when carried between nests. Total number of ants marked is given to indicate that there were few individuals in these two categories, compared to the ants marked while active above ground. Colony codes are as follows: (1) colony one, January 1981; (2a) colony two, March 1981; (3a) colony three, October 1981; (3b) colony three, December 1981; (3c) colony three, January 1982.

| Colony studied | Total ants marked | Ants collected inside nests | | | | Ants collected when carried between nests | | |
|----------------|-------------------|-----------------------------|--------------------|------------------------------------------|---------------------------------|-------------------------------------------|--------------------|---------------------------------|
| | | no. marked | no. not seen again | no. seen only when carried between nests | no. seen only during next visit | no. marked | no. not seen again | no. seen only during next visit |
| (1) | 206 | 44 | 17 | 9 | - | 4 | 2 | - |
| (2a) | 214 | 42 | 18 | 4 | 6 | 19 | 11 | 7 |
| (3a) | 235 | 75 | 43 | 1 | 8 | 6 | 4 | 0 |
| (3b) | 114 | 9 | 5 | 1 | 0 | 5 | 5 | 3 |
| (3c) | 110 | 16 | 6 | 0 | - | 10 | 5 | - |

ground during the following days. The only further data (on nest occupancy) obtained on those ants resulted from sampling the populations inside the nests with a blade of grass.

The following above ground activities were distinguished during the observations (Appendix A): excavating, cleaning (=nest sanitation), carrying (eggs, larvae, cocoons, adults) and foraging. Many of the marked workers performed only one activity during the various observation sessions (Table 3). Other groups of individuals characteristically performed more than one activity during a single observation session, eg. instances of foraging interspersed with the discarding of pellets (cleaning). Certain combinations of above ground tasks were more common than others, eg. cleaning and foraging, carrying and foraging (Table 3). The same individuals seldom performed more than two different activities during an observation session. Some workers also changed activities from one day to the next. Many of the ants belonging to the large foraging groups seldom participated in other activities (Table 3); thus this class of workers exhibited a higher degree of task fixation than other groups (eg. cleaners).

The number of times on which an individual took part in a particular activity during an observation session (eg. one morning) was not determined; however visual examination of the raw data (from which Appendix A was generated) revealed that there were differences in the levels of activity exhibited by various ants. Some ants were observed repeatedly in contrast to others which were seldom seen (within samples of equal duration). Some ants only had one or two behavioural records over an entire observation period (examples are given in Appendix B). In addition, there were a number of workers present above ground that never took part in any definable activity (Table 3); the only data obtained on these ants were their entrances or exits from particular nests (ie. ABO in Appendices A and B). In the one colony a few foragers stopped being seen above ground, then after some days resumed their previous occupations.

Carrying was a conspicuous part of the colony's above ground activities. Carrier ants formed a distinct group of workers

Table 3 Analysis of the activities performed by individual above ground workers over the various observation periods. Where an individual performed more than one task, no indication is given as to the frequency of each. Associations of tasks other than those described below were rare or not observed. The relatively few ants that performed three or four activities were included in an appropriate category on the basis of an ascending order of priority of activities, i.e. excavator-cleaner-carrier-forager. Colony codes are as follows: (1) colony one, January 1961; (2a) colony two, March 1961; (2a) colony three, October 1961; (2b) colony three, December 1961; (2c) colony three, January 1962.

| Colony studied | Observation period (days) | Single activities | | | Combination of activities | | | | No. of workers with no known roles | |
|----------------|---------------------------|-------------------|--------------|--------------|---------------------------|-------------------------|---------------------------|---------------------------|------------------------------------|----|
| | | no. excavating | no. cleaning | no. carrying | no. foraging | no. cleaning & carrying | no. foraging & excavating | no. carrying & excavating | | |
| (1) | 9 | 3 | 4 | 16 | 38 | 2 | 1 | 0 | 11 | 24 |
| (2a) | 14 | 16 | 8 | 20 | 56 | 0 | 11 | 3 | 8 | 47 |
| (2b) | 13 | 3 | 15 | 13 | 40 | 13 | 19 | 5 | 21 | 31 |
| (2c) | 14 | 1 | 4 | 6 | 19 | 5 | 10 | 2 | 9 | 16 |

* an appreciable number of these also took part in cleaning (i.e. nest sanitation)

over the observation periods. The same individuals carried brood and adults interchangeably (Table 4). Individuals often selected one brood stage only (ie. larvae or cocoons) during single bouts of carrying; the transfer of egg packets was not a frequent occurrence. The transport of single termites between nests belonging to the same colonies often took place whenever Hodotermes mossambicus were hunted. This transfer of food was undertaken by the same individuals that carried adults and brood (Table 4); there were a few exceptions. Carrier ants were usually involved in transfers between two nests. They fetched a nestmate, a larva or a cocoon from nests in which they had previously been active (and they were thus familiar with it), and took them to the nests which they were presently inhabiting. In only a few cases did carrier ants visit three (or more) nests sequentially (see 2.4.6.).

Table 4 Fidelity of workers to particular carrying tasks over the various observation periods. Colony codes are as follows: (1) colony one, January 1981; (2a) colony two, March 1981; (3a) colony three, October 1981; (3c) colony three, January 1982.

| | Colonies studied | | | |
|------------------------------------------|------------------|------|------|------|
| | (1) | (2a) | (3a) | (3c) |
| No. of workers carrying adults only | 16 | 12 | 18 | 12 |
| No. of workers carrying brood only | 6 | 1 | 16 | 1 |
| No. of workers carrying adults and brood | 9 | 6 | 20 | 6 |
| No. of workers carrying termites ** | 1 | 5 | 11 | 3 |

** only some of these were seen also to carry adults or brood

At any point in time individual ants belonged to one particular nest within a colony; above ground workers performed their tasks from such a nest, and they presumably spent the nights there. Innendienst ants were normally confined inside their nests, except when they were transferred within colonies. When above ground workers were carried between nests their behaviour altered; they were observed to remain in the new nest and to continue with their previous activities. A few exceptions to this pattern are presented in 2.4.6. Some recently-transferred ants were occasionally observed to walk back to their nests of origin; either they had been active between the nests before, or they had learned the visual features of the route while being carried.

The majority of above ground ants were active in more than one nest over the time-span of an observation period (Table 5), and in many individual cases this was observed to result from being carried within the colony. Adult transfers occurred daily, and only a small fraction of these could be monitored in the colonies under study. There were many observations of single ants being transferred a number of times over an observation period. Some carrier ants were continuously active while others did it infrequently. Simultaneous two-way transfers (involving different carrier ants) between the same nests were occasionally observed. In addition to the carrier ants, another small group of workers was regularly active in two or more nests; such ants were often seen walking from one nest to another, but their purpose for doing so was not evident.

Carrier ants seemed to be capable of selecting between above ground and Innendienst workers (including callows). The samples examined were small however, and never more than three or four pairs with the same carrier were monitored over an observation session; in such cases they consistently carried adults who belonged to either of the above two groups. Carrier ants themselves were transported between nests, and they later similarly transferred between the same nests (there were exceptions, see 2.4.6.). Foragers were not often active in more than one nest, and this indicates that they were not carried

between nests as frequently as other classes of above ground workers.

Table 5 Activity of workers within polydomous colonies, showing the nests in which marked above ground workers were active. Results may vary between colonies because of varying incidences of nest foundation. Nest codes are as follows: (1) colony one, January 1981; (2a) colony two, March 1981; (3a) colony three, October 1981; (3c) colony three, January 1982.

| | Colonies studied | | | |
|---------------------------------------------|------------------|------|------|------|
| | (1) | (2a) | (3a) | (3c) |
| Observation period (days) | 9 | 14 | 13 | 14 |
| Total no. of nests in colony | 6 | 5 | 4 | 7 |
| No. of above ground workers observed ** | 107 | 163 | 169 | 73 |
| No. of workers active in only one nest | 34 | 71 | 45 | 34 |
| No. of workers active in two nests | 37 | 74 | 87 | 14 |
| No. of workers active in three nests | 21 | 15 | 33 | 11 |
| No. of workers active in four or more nests | 15 | 3 | 4 | 14 |

** only workers that were observed at least once after marking were included

2.4.2. Intensive study - colony one

This colony (Figure 3) was studied during a single visit (1st - 10th January 1981). Two hundred and six ants were marked. There were initially four nests in this colony, (AA), (AB), (AC),

▲ AA

▲ AC

▲ AB

● AD

▲ AE

● AF



0 1 2 3

METRES

Figure 3 Plan of colony one, indicating the location of the nests. Nests marked ▲ were active at the start of the observation period, while nests marked ● were subsequently established.

(AE); (AD) was started on day seven. Frequent transfer of adults (marked and unmarked) and brood occurred between these nests. The activity around nest (AE) was variable; on some days no ants were seen coming in or out. Transfers to a new nest (AF) started on day nine, mainly originating from (AB); however transfers away from (AF) were observed on the next day. On the last day of this visit, when all the nests were excavated, (AA), (AE), (AF) contained no adults or brood, evidence that the ants had emigrated. Of sixteen marked workers that were associated with (AF), only ten were found in other nests in the colony; it is not known where the missing ants were.

2.4.3. Intensive study - colony two

This complex of nests was observed on three separate occasions: 25th March-14th April 1981, 16th-18th May 1981, 2nd-5th July 1981.

Two hundred and fourteen ants were marked during the first study period. Initially the colony consisted of four nests: (A), (B) and (C) were grouped together (Figure 4), and (D) was 75 m away; this was the furthest distance recorded between the nests of a colony. There were frequent transfers of adults and larvae from (A),(B),(C) to (D), and carriers took 15- 17 minutes to walk the 75 m distance. Transfers also occurred between (A), (B) and (C). Nest (B) ceased to be active on 31/3. On 2/4 a new nest (E) was started and adults were carried to it from (D). On 4/4, transfers started from (D) to (A) and to (C), while transfers in the opposite direction were still common. Nest (F) was initiated on 6/4 with transfers from (A).

Thus two nests were initiated during this observation period, and the pattern of their establishment was studied almost from their inception. The identities of many of the ants carried there, and of those active around the entrance were recorded; since the nests were not monitored continuously, the record of the ants carried is incomplete.

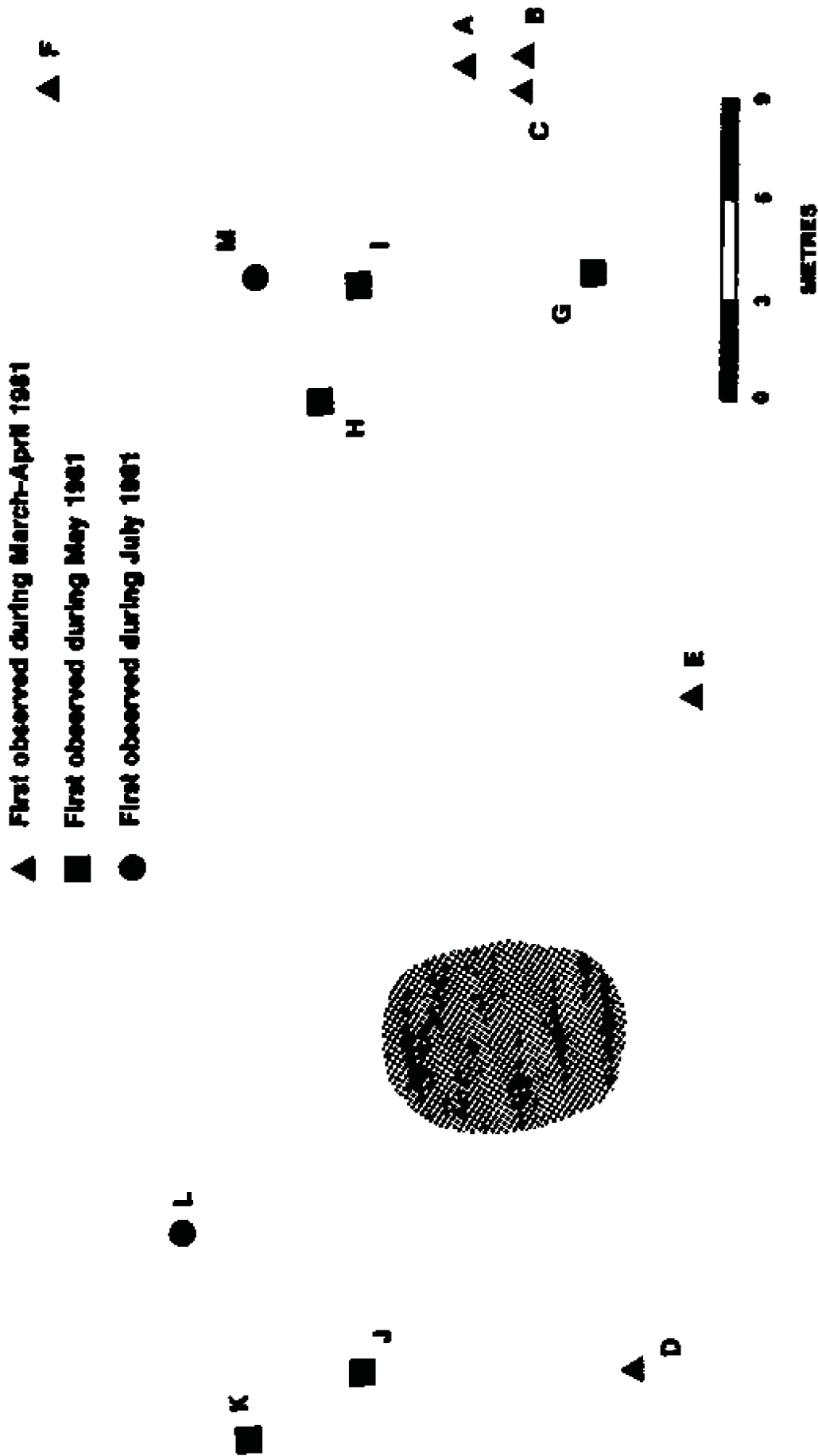


Figure 4 Plan of colony two. The nests were observed during different observation periods. (stipled area indicates a thicket)

Nest (E)

DAY ONE The occupation of this nest was started by ant #4, a carrier ant which had previously been transferring adults and larvae from (C) to (D) (Table 6). Six ants (5 marked, 1 unmarked) were seen to be carried to (E), and #4 was responsible for three of these transfers. Two of the other three carrier ants (#119, #168) were seen to have been transferred from (D) earlier on. Soon after being carried to (E), the ants (excepting the unmarked one) appeared in the entrance and came out to explore the immediate area. Some of them then proceeded with their former activities (eg. #168, #103), while others had different roles (eg. #20, #71) (Table 6). During the afternoon there was a sudden bout of excavating, with five workers rapidly becoming involved in this. Nine ants were recorded in this nest by the end of day one, and eight of these (all the marked ones) had been above ground workers while in nest (D).

DAY TWO Another six ants (all marked) became active around this nest, and all (except #112) had been above ground workers previously. The transfer of only two of these (#46, #7) was witnessed, and it is not known whether any unmarked ants were also transferred. Ant #7 however did not remain in this nest and resumed its previous occupation as a carrier between (D) and (C). More excavation took place, and three ants were observed to walk back to (D), ie. #4, #119, #46. Foraging was started by a worker which had been carrying adults on the previous day (#169).

DAY THREE The transfers of six adults were observed: #23, #26 as well as four unmarked ants; the five marked carrier ants involved were #4, #70, #169, #46, #7 (Table 6). Thus a minimum of 25 ants (20 marked, 5 unmarked) had moved to (E) by this stage. The first larva was transferred from (D) by #169; there was more foraging (#25), and a pellet of termite exocuticle was discarded by #26. An unmarked excavator was seen (this ant had not been active above ground in (D), or it would have been marked). The ant #4, which was involved in regular transfers to this nest, was itself carried away to (C) (this is not included in Table 6).

Table 6 Activities of marked workers during the days subsequent to their being carried to the new nest (E). Roles in the new nest were monitored from the time they appeared there. (Inst= confined inside nest, fe. Immediatent; exca=excavator; clea=cleaner; rec=adult carrier; lar-iarva carrier; for=forager; for=forager; wak=walking between nests; abo=unknown above ground activity). Upper case letters between brackets refer to nests, see Figure 4; when two nests are separated by a -, the direction of transfer was from the first to the second one.

| Ant | Activity in previous nest | Activity on day one | Activity on day two | Activity on day three | Activity on nest 4 days |
|------|---------------------------|---------------------|---------------------|-----------------------|-------------------------|
| #4 | rec (C)-(D) | (C), rec (D)-(E) | rec (D)-(E) | rec (D)-(E) | abo (E) |
| #70 | abo (D) | exca (E) | --- | rec (D)-(E) | --- |
| #119 | abo (D) | exca, rec (D)-(E) | wak (D)-(E) | rec (D)-(E) | --- |
| #169 | abo (D) | rec (D)-(E) | fora (E) | abo (D) | --- |
| #168 | rec (C)-(D) | rec (D)-(E) | --- | rec, lar (D)-(E) | --- |
| #20 | fora (D) | exca (E) | --- | --- | --- |
| #71 | fora (D) | exca (E) | --- | --- | --- |
| #103 | exca (D) | exca (E) | --- | --- | --- |
| #46 | fora (D) | --- | wak (E)-(D) | rec (D)-(E) | --- |
| #104 | exca (D) | --- | exca (E) | --- | --- |
| #112 | inst (D) | --- | exca (E) | --- | --- |
| #94 | clea, fora (D) | --- | abo (E) | --- | abo (D) |
| #3 | exca (D) | --- | exca (E) | --- | --- |
| #7 | rec (C)-(D) | --- | wak (E)-(C) | rec (D)-(C) | --- |
| #26 | abo (D) | --- | --- | clea (E) | --- |
| #16 | exca (D) | --- | --- | abo (E) | --- |
| #23 | abo (D) | --- | --- | exca (E) | --- |
| #25 | fora (D) | --- | --- | fora (E) | abo (E) |
| #90 | exca (D) | --- | --- | exca (E) | --- |
| #102 | exca (D) | --- | --- | exca (E) | --- |
| #128 | inst (D) | --- | --- | exca (E) | --- |
| #51 | abo (D) | --- | --- | --- | abo (E) |
| #65 | abo (D), (A) | --- | --- | --- | abo (E) |
| #157 | exca (D) | --- | --- | --- | abo (E) |
| #143 | abo (D) | --- | --- | --- | abo (E) |
| #141 | inst (D) | --- | --- | --- | inst (E) |

NEXT FOUR DAYS There was little activity on subsequent days, and no more transfers were observed. Ant #4 was back in this nest.

Nest (F)

DAY ONE No recruitment was witnessed on this day, but there were nine marked ants in this nest when observation started. Seven of these had been active above ground in nests (A) or (C), i.e. all except #84 and #148 (Table 7). Termites were transported from (A) to (F) by #96.

Table 7 Activities of marked workers during the two days subsequent to their being carried to the new nest (F).

(insi= confined inside nest, i.e. Innendienst; exca= excavator; clea= cleaner; rec= adult carrier; lar= larva carrier; coc= cocoon carrier; ter= termite carrier; fora= forager; abo= unknown above ground activity). Upper case letters between brackets refer to nests, see Figure 4 ; when two nests are separated by a -, the direction of transfer was from the first to the second nest.

| Ant | Occupation in previous nest | Occupation on day one | Occupation on day two |
|------|-----------------------------|-----------------------|-----------------------|
| #96 | fora (A),(C) | ter (A)-(F) | lar,coc (A)-(F) |
| #183 | fora (A) | abo (F) | coc (A)-(F) |
| #28 | rec (A) | abo (F) | --- |
| #76 | abo (C) | abo (F) | --- |
| #84 | insi (C) | insi (F) | --- |
| #161 | fora (A),(C) | abo (F) | --- |
| #173 | abo (A),(C) | abo (F) | --- |
| #136 | fora (A) | abo (F) | --- |
| #148 | carried (A)-(C) | abo (F) | --- |
| #156 | abo (A),(C) | --- | rec (A)-(F) |
| #48 | rec (A)-(C) | --- | coc (A)-(F) |
| #175 | fora (A) | --- | abo (F) |
| #87 | rec (C)-(D) | --- | rec (A)-(F) |
| #62 | rec (C)-(A) | --- | lar (A)-(F) |
| #174 | abo (C) | --- | abo (F) |
| #88 | abo (A),(C) | --- | abo (F) |
| #158 | fora (A) | --- | abo (F) |