Journal of Animal Ecology (1983), **52,** 349–355

ASSEMBLY OF MANGROVE ANT COMMUNITIES: COLONIZATION ABILITIES

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SUMMARY

(1) Characteristics of the biology of mangrove ants which affect colonizing ability are discussed.

(2) Studies of the comparative social behaviour of mangrove ants showed that *Xenomyrmex floridanus* Emery invests relatively much more in the production of new workers than other mangrove ants, thus increasing colonizing ability.

(3) Two species, *Crematogaster ashmeadi* Mayr and *X. floridanus* have a large queen–worker size ratio. A large ratio allows the queen to produce more workers in the claustral stage of colony founding.

(4) Two species, *Zacryptocerus varians* (F. Smith) and *Camponotus* (*Colobopsis*) sp., have a distinct major worker caste. Ergonomic theory suggests that species with more complicated caste structure will have reduced colonizing ability.

(5) *Pseudomyrmex elongatus* Mayr places its nests in the periphery of mangrove trees. Because this will reduce the frequency with which aggressive species are encountered, it has an advantage in colonizing ability.

(6) By the characteristics considered, mangrove ants, in order of colonizing ability are: *X. floridanus*, *C. ashmeadi*, *P. elongatus*, *Z. varians* and *Colobopsis*.

INTRODUCTION

In ecological communities interactions between species will determine which species can coexist. If interactions between species are unimportant (Rathcke 1976) any combination of species from the same habitat is possible. If there are competitive interactions between species (as in mangrove ants, Cole 1983) some combinations of species may not be stable. Perfect knowledge of the kinds of interaction (or lack of interaction) between species cannot provide a complete picture of the pattern of coexistence for any group of species. The relative dispersal and colonizing abilities of a group of species determine the frequency with which various species combinations appear and thus the importance of competitive or other interactions.

I have examined the aggressive interactions between mangrove ants and demonstrated that the patterns of interaction are consistent with the patterns of geographical distribution (Cole 1983). There are questions concerning the species that are not answered by a knowledge of competitive interactions. *Pseudomyrmex elongatus* is much more common and found on a wider range of island sizes than *Zacryptocerus varians* although the two species are nearly identical from a competitive standpoint. One would predict that *P. elongatus* has an advantage in colonizing ability compared to *Z. varians*. *Xenomyrmex floridanus* is capable of preventing the invasion of *Crematogaster ashmeadi* only when it

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possesses a vast numerical advantage. This means that *X. floridanus* must colonize empty islands before *C. ashmeadi* has an opportunity to do so. One would predict that *X. floridanus* has an advantage in colonizing ability compared to *C. ashmeadi.*

Any characteristic of the biology of the ants that either (i) increases the rate of colony growth or the speed of colony founding, or (ii) decreases the frequency and risk of interaction with other species will increase the colonizing ability of the species. I shall examine the investment in producing workers, relative worker and queen size, caste composition and nest site placement, four characteristics that affect the relative colonizing ability of these ants.

MATERIALS AND METHODS

Colonies of the mangrove dwellings ants, *Crematogaster ashmeadi, Xenomyrmex floridanus, Pseudomyrmex elongatus, Zacryptocerus varians* and *Camponotus* (*Colobopsis*) sp. were collected from red mangroves in the Florida Keys. Colonies were maintained in glass tubes for observation as described in Cole (1980). All behavioural acts taking place within the nest were recorded. Observations were continued until an estimated sample coverage of 0·9995 or better was achieved (Fagen & Goldman 1977). Such a sample coverage indicates that observation of an additional 10 000 behavioural acts would produce approximately five behavioural acts that do not belong to categories already observed. This sample coverage has been found to be sufficient to allow accurate estimates of the size of the complete behavioural repertoire for an ant species (Wilson & Fagen 1974; Cole 1980).

The relative investment in worker production and worker maintenance is fairly insensitive to observational conditions. Replicate observations of *Z. varians* (Wilson 1976; Cole 1980) have shown that differences in observer and observational conditions have minor effects. However, to obviate potential confounding effects all species were kept in similar culture conditions. Size measurements on ants were made of the length of the body or the head width across the eyes with an eyepiece reticle.

The position of nests within a mangrove island was assigned to one of four regions. Region I is the volume encompassed by the stilt roots. Region II is the relatively open central area of a mangrove tree. This volume has an abundance of dead branches and includes the main trunks of the tree. Region III is the more distal shell of the highly ramified dead branches. Region IV is the outermost shell of the tree in which the foliage occurs. In the transition between regions two and three, classification of twigs into one or the other of the regions was occasionally difficult and admittedly arbitrary. However, the vast majority of nests could be assigned unequivocally to one of the four regions.

RESULTS

A total of 16 831 behavioural acts were observed in the five species of ants. The frequency of each behavioural category for the five major species of mangrove ants is shown in Table 2. The fraction of the behavioural acts that involve feeding larval ants and feeding workers is shown in Table 1. Categories of behaviour that involve larval feeding include: feeding insect remains to larvae, feeding trophic eggs to larvae, feeding infrabuccal pellets to larvae and regurgitating liquid food to larvae. Categories of behaviour that involve feeding of workers include: feeding on insect remains, eating an egg or larva, feeding on infrabuccal pellets, engaging in liquid food regurgitation with other workers.

Table 1. The frequency with which a category of behaviour was observed in mangrove ants. The estimated sample coverage is given for the *C. ashmeadi*, *P. elongatus* and the minor worker caste of *Z. varians* and *Colobopsis*. By method of Fagen & Goldman (1977) the estimated sample coverage for *X. floridanus* would be 1·0

Behavioural category	*C*	*X*	*Ps*	*mZ*	*MZ*	*mCo*	*MCo*
Total acts	4004	3418	3713	3303	25	1911	457
Estimated sample coverage	0·9998	–	0·9995	0·9995	–	0·9995	–
Self-grooming	0·3729	0·3376	0·5252	0·3250	0·56	0·3804	0·317
Antennal tipping	0·0040	0·0149	0·0024	0·0234	0	·0016	0
Extrude anal tube and/or sting	0·0452	0	0	0	0	0	0
Flick gaster	0·0080	0	0	0	0	0	0
Lick wall of nest	0·0017	0·0433	0·0062	0·0100	0	0·0120	0
Transport dead nestmate	0·0002	0	0·0005	0	0	0	0
Stridulate	0	0	0·0032	0	0	0	0
Drag minor worker	0·0030	0	0·0030	0	0	0	0·002
Drag major worker	–	–	–	0	0	0·0010	0
Drag queen	0	0	0·0003	0	0	0·0021	0·002
Allogroom minor worker	0·0627	0·1161	0·0436	0·550	0	0·0345	0·011
Allogroom major worker	–	–	–	0·0027	0	0·0094	0
Allogroom queen	0·0130	0·0056	0	0·0039	0	0·0078	0·015
Carry insect remains	0·0165	0·0255	0·0145	0	0	0·0031	0
Lay trophic egg	0·0020	0	0	0·0009	0	0	0
Carry infrabuccal pellet	0	0	0	0·0006	0	0·0010	0
Carry solid remains	0	0	0	0·0006	0	0·0010	0
Brood care:							
Carry egg(s)	0·0275	0·0029	0·0016	0·0125	0	0·0115	0·004
Lick egg(s)	0·0052	0·0076	0·0011	0·0067	0	0·0178	0
Carry larva(e)	0·0827	0·0892	0·0329	0·0477	0	0·0340	0·020
Lick larva(e)	0·1216	0·1445	0·1163	0·1388	0	0·0900	0·061
Assist larval ecdysis	0	0·0006	0·0005	0·0009	0	0	0
Meconium removal	0	0·0015	0·0011	0	0	0·0005	0·002
Carry pupa(e)	0·0027	0·0050	0	0·0030	0	0·0010	0
Lick pupa(e)	0·0125	0·0135	0·0124	0·0118	0	0·0105	0·006
Assist eclosion to adult	0·0012	0·0029	0	0	0	0	0
Feed insect remains to larvae	0	0·0793	0·0100	0	0	0	0
Feed egg to larvae	0·0052	0	0	0·0018	0	0	0
Feed infrabuccal pellet to larvae	0	0	0·0167	0·0070	0	0·0078	0
Abdominal trophallaxis							
Receive or solicit from minor	0	0	0	0·0410	0	0	0
Receive or solicit from major	0	0	0	0·0043	0	0	0
Receive or solicit from queen	0	0	0	0·0018	0	0	0
Regurgitate:							
With larvae	0·0827	0·0518	0·0385	0·0653	0	0·0597	0·009
With minor worker	0·0587	0·0462	0·1602	0·2072	0·44	0·1669	0·471
With major worker	–	–	–	0·0033	0	0·1125	0·066
With queen	0·0040	0·009	0·005	0·0024	0	0·0021	0
Feed on insect remains	0·0412	0·0094	0·005	0·0012	0	0·0141	0·011
Feed on larvae	0·0042	0·0018	0	0·0009	0	0·0010	0
Feed on egg	0·0030	0	0	0·0003	0	0	0
Feed on infrabuccal pellet	0	0	0	0·0106	0	0·0068	0·002
Share infrabuccal pellet	0	0	0	0·0015	0	0·0010	0
Feed on solid remains	0	0	0	0·0009	0	0·0010	0
Feed egg to queen	0·0007	0	0	0	0	0	0

TABLE 2. The summed fraction of the behavioural repertoire of mangrove ants involving larval feeding, feeding of adult worker ants and the ratio of these two quantities

	Larval feeding	Worker feeding	Larval feeding / Worker feeding
X. floridanus	0·13	0·06	2·28
C. ashmeadi	0·09	0·11	0·82
P. elongatus	0·07	0·16	0·41
Z. varians	0·07	0·23	0·33
Colobopsis	0·07	0·30	0·22

The fraction of behavioural acts involved in feeding of workers is significantly different between all species at least at the 5% level (percentage test). The fraction of behavioural acts involved in feeding of larvae for *X. floridanus* and *C. ashmeadi* are also significantly different from one another and the other species at least at the 5% level. Food collected by the foraging workers of the colony can be allocated either to the maintenance of existing workers or to production of new workers. The relative investment in production of new workers as opposed to maintenance of existing workers can be estimated by the ratio of the amount of larval feeding to the amount of worker feeding (Table 2). *X. floridanus* has a much greater relative investment in larval feeding than any of the other species including *C. ashmeadi*, the other Primary species (Cole 1983). The relative investment in larval feeding by *Colobopsis* is an order of magnitude smaller than that of *X. floridanus*.

The relative sizes of the queen and workers of the species of mangrove ants are shown in Fig. 1. For *Z. varians* and *Colobopsis*, which have a distinct major worker caste, the size ratio compares the queen and the minor worker. Minor workers were used as the basis of comparison due to the fact that minor workers are the caste that is produced in the initial stages of colony founding. This size ratio is large and comparable in *C. ashmeadi* and *X. floridanus*. *Z. varians* and *Colobopsis* have intermediate queen–worker size ratios while there is very little size dimorphism between the reproductive and worker caste of *P. elongatus*.

Three of the species of mangrove ants, *C. ashmeadi*, *X. floridanus* and *P. elongatus* have a monomorphic caste structure. There is one size of worker with very little variability in

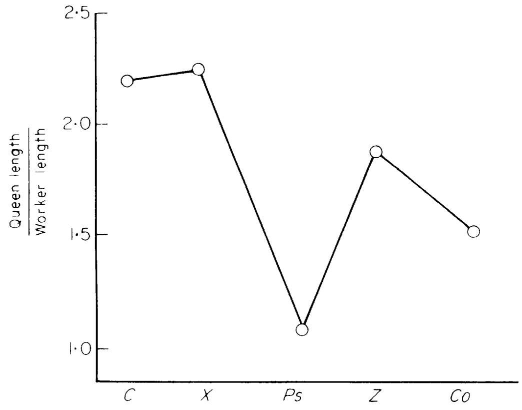

FIG. 1. The ratio of the body length of the queen to the length of the worker. *C* = *C. ashmeadi*; *X* = *X. floridanus*; *Ps* = *P. elongatus*; *Z* = *Z. varians*; *Co* = *Colobopsis*. The species are ordered along the abscissa by the Minimum Size Requirement (Cole 1983) of the species.

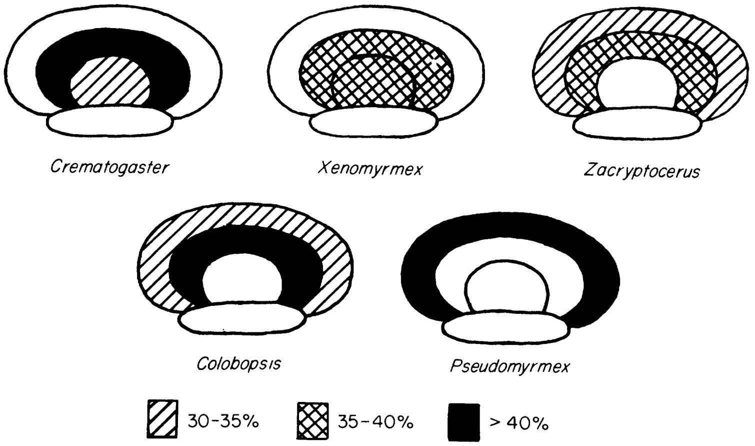

FIG. 2. The placement of nests on a mangrove tree. The lower section of the diagram of the mangrove tree is region I. Regions II, III and IV are progressively more distal. The degree of shading indicates the percentage of the nests of that species which are found in a given region. Unshaded areas indicate regions occupied by fewer than 30% of the nests of a species. The number of nests of each species is: *C. ashmeadi*, 176; *X. floridanus*, 90; *P. elongatus*, 91; *Z. varians*, 115; *Colobopsis*, 27.

size. The coefficient of variation of the head width across the eyes varies from 3% to 4%. The remaining two species, *Z. varians* and *Colobopsis*, have a dimorphic caste structure. There is a minor worker caste and a morphologically distinct major worker caste; there are no intermediates. The size difference between the major and minor workers of *Z. varians* is greater than in *Colobopsis*. The major worker of *Z. varians* is behaviourally more specialized than the major worker caste of *Colobopsis* (Cole 1980). In accord with current ergonomic theory (Oster & Wilson 1978) the major worker of *Colobopsis* is relatively more abundant than the major worker of *Z. varians*. The lesser abundance of the major worker of *Z. varians* is countered by the greater size difference between major and minor workers with the result that the coefficient of variation of head width for *Z. varians* (12%) and *Colobopsis* (14%) is comparable.

The position of 499 twigs used as nests by the five species was assigned to one of the four regions described above. The pattern of nest site placement is shown in Fig. 2. *C. ashmeadi* and *X. floridanus* show a central placement of nest sites. *Z. varians* and *Colobopsis* are found more distally on a mangrove island. Nests of these two species are found most frequently in regions III and IV. *P. elongatus* places its nests peripherally on mangrove islands, almost exclusively in region IV.

DISCUSSION

A relatively high investment in larval feeding, large queen–worker size ratio, monomorphic caste structure and peripheral nest placement all contribute to increased colonizing ability in mangrove ants. A relatively large investment in larval feeding may increase the rate of colony growth. Peripheral nest placement decreases the frequency of encounter between aggressive Primary species and Secondary species. A large queen–worker size ratio and monomorphic caste structure contribute both to rapid colony founding and to reducing the risk of interactions with other species.

Rapid growth rate is one of the most important characteristics of a successfully colonizing species (Lewontin 1965; MacArthur & Wilson 1967; Richter-Dyn & Goel 1972). Investment in larval feeding on an absolute scale varies over a factor of about two, while investment in worker feeding varies over a factor of about five. Variability in the relative investment in larval feeding indicates a redirection of colony resources towards worker production and away from worker maintenance.

The relative investment in larval feeding is one measure of reproductive effort (Gadgil & Solbrig 1972; Abrahamson & Gadgil 1973). It is important to remember that production of new workers is not equivalent to production of the sexual forms and is thus more perfectly analogous to growth versus maintenance in plants. Major differences in relative investment such as between *X. floridanus* and *C. ashmeadi* or between the Primary species and the Secondary species reflect major differences in the pattern of energy allocation to colony growth versus colony maintenance. Assessed by this criterion alone, *X. floridanus* has an advantage in colonizing ability followed by *C. ashmeadi*, *P. elongatus*, *Z. varians* and *Colobopsis*.

Raising the first brood is the critical first stage of colonization by an ant. In higher ants the queen, after the mating flight, raises the first brood 'claustrally,' i.e. without foraging outside the nest. Metabolism of stored fat and flight muscles must provide the energy to produce the first foraging members of the colony.

The larger the size of the queen in relation to the workers the more workers that can be produced without depleting the energy reserves of the queen. In extreme cases, in which the queen is actually smaller than the worker, colony founding is usually by temporary social parasitism (Wilson 1971). Increasing the number of workers that can be produced in the first brood increases colonizing ability due to two effects. First, the growth rate of the colony is increased. Second, the loss of a worker during aggressive interactions with other species is not as significant. By this criterion *C. ashmeadi* and *X. floridanus* have an advantage in colonizing ability followed by *Z. varians*, *Colobopsis* and *P. elongatus*.

Oster & Wilson (1978) drew a dichotomy between high-risk species of social insects and low-risk species. A high-risk species trades a high risk of failure for a high payoff. They suggest that there may be a relation between monomorphic caste structure and high-risk species. This parallels the suggestion that those species adapted to marginal or unstable habitats tend to be better colonists (MacArthur & Wilson 1967). Good colonists should be high-risk species and will tend to have a monomorphic caste structure.

Colobopsis and *Z. varians* produce specialized castes that function in colony defence and little else (Cole 1980). Major workers are not produced during the early stages of colony founding (Wilson 1971). Thus during the period that the colony is at its most vulnerable, there is no defensive caste. By the criterion of caste structure, *Z. varians* and *Colobopsis* should have reduced colonizing ability compared to *C. ashmeadi*, *X. floridanus* or *P. elongatus*.

The placement of nests illustrates three patterns among mangrove ants. The two Primary species place their nests centrally within the tree. Central nest placement will minimize the distance that foragers must travel if they are moving over the entire island. Whether this is an adaptation or a fortuity is unknown. Peripheral nest placement minimizes the encounters between *P. elongatus* and *C. ashmeadi* or *X. floridanus*. This is important due to the aggressive response of the Primary species to *P. elongatus*. If an island is only marginally large enough to permit coexistence between a Primary species and Secondary species, *P. elongatus* will have an advantage in colonizing ability over *Z. varians* or *Colobopsis*.

There is no a priori reason to attribute greater significance to one of the characteristics of a good colonist. Several conclusions can be drawn, however. Although *X. floridanus* and *C. ashmeadi* are similar in most characteristics related to colonizing ability, *X. floridanus* clearly invests relatively much more in larval feeding than *C. ashmeadi*. This commitment to rapid colony growth may provide *X. floridanus* with an advantage in colonizing ability that is necessary to allow persistence with *C. ashmeadi* in a patchy environment.

The relative colonizing abilities of *P. elongatus* and *Z. varians* are somewhat more subject to interpretation. The high queen–worker size ratio gives *Z. varians* an advantage in colonizing ability. On the other hand, *P. elongatus* has a monomorphic caste system. The decisive factor may be the peripheral nest placement of *P. elongatus*. By most criteria the colonizing ability of *Colobopsis* is less than that of any other species. Although *Colobopsis* has competitive abilities comparable to the other Secondary species it is by far the least abundant of the ant species of small mangrove islands.

ACKNOWLEDGMENTS

I thank E. O. Wilson for many helpful suggestions, Henry Horn and Bob May stimulated useful discussion. Douglas Green, Cathy Bristow, Diane Wiernasz, Tony Janetos, David Duffy, David Tonkyn, Kathy Schneider and Rich Kiltie provided invaluable aid.

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(*Received 28 July 1981*)