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ROLE OF ANTS IN PEST MANAGEMENT

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INTRODUCTION

Ants, with an estimated world population of 10^{15} adults (188), are most abundant in the tropics where in rain forests they may represent between one third and half of the insect biomass (32). About two hundred species of ants have been recorded in one locality in Papua New Guinea (187), and they also retain rich diversity in some tropical crops (76, 134). In general, ants are less common, with fewer species, outside the tropics (120, 187), but they may still be ecologically important, as in a European grassland where about 140 workers per m² consumed approximately 200 times their biomass annually (71). They are usually least common and diverse in disturbed arable habitats (120).

In view of their abundance, their stability as populations, and their feeding habits, ants have a major influence in many habitats (17, 30, 45, 59, 63, 118, 127, 188). As predators of pests, they may be useful in pest management, but such positive attributes must be weighed against possible disadvantages. Besides acting as biological-control agents, some ants are important in pollination, soil improvement, and nutrient cycling (45). In contrast, some feed on or disturb plants and may act as vectors of plant diseases, benefit

damaging Homoptera, and attack or irritate humans, domestic animals, and other beneficial organisms (162, 168). Virtually all species that prey on pests also possess some potential disadvantages.

This review briefly summarizes relevant aspects of ants' feeding habits and general ecology, followed by discussion of beneficial species and their attributes, and of how ecological conditions favoring their use can be manipulated for improved pest management.

FEEDING HABITS

Significance of Honeydew-Producing Homoptera

Predatory ants that are recognized as important in pest management are mostly omnivorous and rely also on plant foods. For example, a *Formica rufa* diet comprised 62% honeydew; 5% resin, fungi, carrion, and seeds; and 33% insect prey (179). In particular, ant-attended honeydew-producing Homoptera provide a dependable energy food supply needed for large stable populations of certain ants to maintain consistent protection of the plants on which they forage. The relationship confers mutual benefits to ants and Homoptera (175). Recent work (72) highlights the fact that particular Homoptera are essential for biological-control success. In contrast, predatory ant species that do not utilize Homoptera, such as the highly voracious army and driver ants, are raiders that only temporarily suppress most prey populations in a particular locality.

Ant-Prey Interrelationships

CHOICE OF PREY Predacious ants can be classified simply as specialists or generalists (187). Most so-called scavenger ant species prey on small organisms, including insect eggs. The specialists do not seem to be significant in biological control, though some must have an impact, for example, on certain pest termites. The generalist ant predators include those that are recognized as important in biological control, and some data are available on the range of prey species captured by these ant species (2, 7, 53, 95, 118, 128, 181). Larger ants tend to attack larger prey and may disregard, or not see, the smaller prey attacked by smaller ants (137, 174, 176). This relationship is no doubt related to the bioenergetics of costs and returns in prey capture and transport by different-sized ants. A hierarchy of ant influence on major insect groups has been suggested (76) but is not borne out by the evidence. For example, a single group such as the Lepidoptera varies widely from resistant to susceptible to predation, and other evidence refutes the hierarchy hypothesis (128).

Ants can repel other organisms, perhaps through chemical repellents (139, 167). Hostility does not always appear to be a key attribute because

Anoplolepis longipes can exclude some vertebrates and other large animals from its territory (52), unlike the much more aggressive Oecophylla species. Yet A. longipes does not attack many smaller organisms, including insect pests, that Oecophylla spp. kill (172). Dolichoderus thoracicus incidentally disturbs pests on which it does not prey (36, 72, 161).

PREY DEFENSE Many insects possess generalized defense mechanisms such as flight, jumping away, or dropping off the plant when threatened, but these may not be effective against ants that forage at different levels of the ecosystem (53). Size and other physical attributes aid in prey defense. For example, Formica and Camponotus spp. captured 56% of first-instar gypsy moth larvae, but this amount decreased to 4.8% as larvae grew (184). Larger larvae were attacked, but many escaped. Formica polyctena preys on larvae and adults of the Colorado potato beetle Leptinotarsa decemlineata, but the smaller Myrmica laevinodis does not. It is repelled by the beetle's chemical defenses, which the Formica species disregard (40). This observation raises the question of evolution of specific prey defense mechanisms against ants. Life in galls, mines, webbed leaves, or masses of spittle may have evolved partly as protection from ant predation (53), though leaf miners are heavily preyed on by some ants (25, 137). Potential prey may sequester ant-toxic compounds from larval host plants (12, 64), and the repugnatorial glands of some hemipteran predators protect them from Solenopsis invicta (125). Evolved protective mechanisms may include out-of-phase survival in ant-free space (53), which questions the suggestion (138) that insect herbivores find difficulty in countering ant predators. Although long stable evolutionary association in some natural habitats may favor development of some protective mechanisms against ants (53), this situation contrasts strikingly with that of most agricultural systems. Work comparable in detail to that of Heads & Lawton (53) still needs to be done in artificial habitats as a basis for improved use of predatory ants.

COMMUNITY AND POPULATION DYNAMICS

Majer (92) classified ants into status categories of dominant; subdominant, which can attain dominant status in the absence of dominant ants; and nondominant, which live within or between the territories of dominant ants. Dominant ants include species that are most conspicuously useful for biological control.

A dominant ant is numerically the most abundant ant species in its area of occupation from which it characteristically excludes all other dominant ant species, though this exclusion is not always clear cut (76, 132, 172, 177, 178). A single species may dominate a very large area; for example, A.

longipes had up to 300 queens/nest, a nest density of 700/ha, and a population sometimes exceeding 10 million/ha over 1250 ha in the Seychelles (51), and super-colonies of Formica yessensis in Japan comprised some 306 million workers and more than one million queens in 45,000 nests in a territory of 2.7 km² (55). Colonies of most dominant species occupy smaller areas, each forming part of a mosaic of interdigitating colonies of the same or other dominant species (84, 92, 94). In relatively stable habitats, such as in the soil of temperate grasslands, coexistence can be very stable (121, 122). Conditions are naturally less stable in the aerial environment, especially when simplified by agriculture in which useful indigenous ants such as Oecophylla and Dolichoderus spp. may become prey to invading, often exotic, species of Solenopsis, Anoplolepis, and Pheidole—"extirpators," to use Wilson's (188) terminology. In some circumstances, species can ebb and flow (48), though there is usually a notable hierarchy (13, 188). The manipulation of crop conditions to alter the rank order in favor of beneficial species and against harmful species is fundamental to the use of ants in pest management and is emphasized later in this review.

PREDATORY ANTS AS BIOLOGICAL-CONTROL AGENTS

Literature on beneficial and potentially beneficial predatory ants is available for the Old World (76) and for cocoa in the New World tropics (22). Gotwald (45) gives a few worldwide examples. Farmers were first to recognize the beneficial role of five species (16, 23, 60, 108, 113, 131). Published work has highlighted seven genera of dominant ant species—*Oecophylla, Dolichoderus, Anoplolepis, Wasmannia,* and *Azteca* in the tropics, *Solenopsis* in the tropics and subtropics, and *Formica* in temperate environments. This section includes case studies of the seven important genera and also discussion of the role of more inconspicuous ant species, especially as egg predators.

Oecophylla Species

Two humid-tropics species, *O. longinoda* in Africa and *O. smaragdina* in Asia and Australia, have biologies so similar that they can be treated as one. They are active throughout the year, and their distribution and abundance depends on evergreen trees and shrubs (15, 56, 173) with suitable leaves for silk-woven leaf nest construction. Individual colonies, which are mutually antagonistic, may cover up to 1600 m² and comprise approximately a million workers and brood (56, 57, 173). They are demarcated by no-ant boundaries where posturing, but rarely fighting, occurs (56, 57, 76, 173)

Colonies are monogynous (164, 173), and the queen is not replaceable

(164, 166). Monogyny is no doubt responsible for the outstanding colony organization of *Oecophylla* spp., which is based on pheromones providing "the most complex of such repertoires thus far discovered in ants" (58). Perhaps pheromones could be used to improve biological control by enhancing competitiveness against other ant species.

ROLE IN PEST MANAGEMENT A Chinese publication reputedly written in 304 AD states that "in the market the natives of Jiao-Zhi sell ants stored in bags of rush mats. The bags are all attached to twigs and leaves, which, with the ants inside the nests, are for sale. In the south, if the Gan trees (mandarin orange) do not have this kind of ant the fruits will all be damaged by many harmful insects and not a single fruit will be perfect" (60, 108). This, the earliest known example of biological control, is still practiced after 1700 years (190).

Oecophylla spp. workers attack many interfering animals, including humans, and kill a wide range of arthropods for food (173). They do not appear to perceive sessile animals such as the non-honeydew-producing Diaspididae, though they must recognize honeydew-producing Homoptera with which they are mutualistically associated (174, 175). This is also evident from their destruction of such Homoptera that exceed the honeydew requirements of the colony (174). *O. longinoda* workers do not attack very small insects such as parasites of their attended Homoptera, though some parasites are severely hampered (174). Predacious larvae of some Lepidoptera (173) and Coccinellidae (164) seem adapted to succeed within *O. longinoda* colonies.

No doubt the highly organized aggressive predatory behavior, combined with extensive foraging throughout the area occupied by a colony, explains the success of *Oecophylla* species in killing or driving away many pests or potential pests, notably Heteroptera and foliar-feeding Coleoptera. Table 1 lists localities where work on such predation has been done. Our recent observations that the ant can help protect cocoa against rodents and oil palm against some lepidopterous defoliators indicates that the potential of *Oecophylla* spp. has not been realized.

The effect of *Oecophylla* spp. against the Coreidae, *Amblypelta cocophaga* in the Solomon Islands, and *Pseudotheraptus wayi* and *Pseudotheraptus devastans* in Africa exemplifies the use of these ants in pest management. The pests cause identical damage to coconuts by feeding on female flowers and young nuts. Estimates of nut loss range from about 30–65% according to region (164; M. J. Way, unpublished data), to which should be added up to 50% yield loss from severely damaged nuts that survive to maturity (69). Locally, losses may be catastrophic, as indicated by a 10-fold yield increase after an experimental chemical treatment (171).

Coconut palms occupied by thriving colonies of Oecophylla species are

Ant species	Pest	Region	References
Coconuts		<u> </u>	
O. longinoda	Pseudotheraptus wayi	East Africa	164, 171
	Pseudotheraptus devastans	Ivory Coast	69
O. smaragdina	Amblypelta cocophaga	Solomon Islands	14, 119
	Axiagastus cambelli	Solomon Islands	79
		New Britain	6
		Papua New Guinea	112
	Brontispa longissima	Solomon Islands	144
	Promecotheca spp.	Papua New Guinea	107
Oil palm		•	
O. smaragdina Cocoa	Cremastopsyche pendula and others	Malaysia	G. F. Chung ^a
O. longinoda	Distantiella theobroma	West Africa	76, 99
	Crematogaster spp.	West Africa	149, 150
O. smaragdina	Helopeltis theobromae	Malaysia	177
	Amblypelta theobromae	Papua New Guinea	153
	Pseudodoniella laensis	Papua New Guinea	153
	Pantorhytes spp.	Papua New Guinea	135, 153
	Pantorhytes biplagiatus	Solomon Islands	143
	Rodents	Malaysia	M. J. Way ^b
Coffee		·	-
O. longinoda Citrus	Antestiopsis intricata	Ghana	76
O. smaragdina	<i>Tessaratoma papillosa</i> and other Heteroptera	China	60, 108
	Rhynchocoris humeralis	China	190
	Rhynchocoris serratus	Philippines	34
Eucalyptus			
O. smaragdina Mango	A. cocophaga	Solomon Islands	91
O. smaragdina Timber trees	Cryptorrhynchus gravis	Indonesia	170
0. longinoda	Scolytidae Platypodidae	Ghana	76

 Table 1 Reports of Oecophylla spp. as beneficial predators

^a Personal communication.

^b Personal observation.

completely, or almost completely, protected from damage by the pests, as is evident when O. longinoda is deliberately killed and when crops on occupied palms are compared with those on adjoining unoccupied ones (66, 172). Decreased damage and increased yields are associated with increasing O. smaragdina populations (143).

Unfortunately, relatively few coconut plantations in Africa and the Solomon Islands are well colonized by *Oecophylla* spp. because other useless dominant competing ant species have displaced them (119, 172). This observation stimulated work on causes of displacement and on how to enhance abundance of *Oecophylla* spp. (15, 48, 49, 143, 172). Investigators recognized that diversity in the form of appropriate shrub and ground vegetation benefits *O. longinoda* (173) and *O. smaragdina* (48). Interplanting with favored trees therefore benefits *Oecophylla* spp. both inherently and also indirectly by strengthening their ability to compete with other ant species (26, 143, 173). Promising results have been obtained with insecticides to control competing ants and so permit natural increase of *Oecophylla* spp. populations (26, 143, 163). The bait Amdro (hydramethylnon) has been particularly successful in selectively controlling *Pheidole megacephala* in East Africa (83) where it is the major competitor of *O. longinoda* (172).

Insecticides provide valuable components of well-established integrated pest management (IPM) in the Ivory Coast (26, 66–69) where they are used to control *P. devastans* and competing ants as a supplement to biological control by *O. longinoda*. Insecticide use on *O. longinoda*–unoccupied palms is based on treatment thresholds for the pest except where >60-70% of the palms are colonized by *O. longinoda*—a level at which damage becomes insignificant (66, 172). In the Ivory Coast, IPM practices also include artificial introductions of *O. longinoda* and encouragement of appropriate vegetation (26).

In conclusion, although intensive treatment with insecticides can directly control *P. wayi*, this causes outbreaks of Diaspididae, no doubt through destruction of their natural enemies (171). Moreover such treatments can only be justified for protecting accessible dwarf palms used for high-value seed. An average of one *P. wayi* or *A. cocophaga* per palm can cause very serious damage, putting a premium on intensive application of insecticides as well as precluding the use of conventional density-related natural enemies. Like any IPM system, the use of *Oecophylla* spp. requires organization (26). The aggressiveness of *Oecophylla* spp. is a constraint, a characteristic that has made *O. smaragdina* unacceptable to cocoa-plantation staff in Malaysia, despite its excellent control of the seriously damaging mirid *Helopeltis theobromae* (177).

Dolichoderus thoracicus

In parts of the humid Southeast Asian tropics, this ant nests in suitable crevices; very large populations can be found in the spadices of coconut palms (178), between appressed or folding leaves (72), and in insolated leaf litter on the ground (72, 178). Where nesting sites are small and unstable as in cocoa, the ant is benefited by artificial nests in the trees (72, 161). Suitable nesting sites are essential for the large populations of the ant needed to exert biological control (72, 178). D. thoracicus is polygynous, and a dense colony may cover an area of many hectares (178); sometimes colonies are relatively small

and separate as in a mixed cocoa-coconut plantation, where each radiates from a particular coconut palm. Here, inter-colony aggression occurs, but colonies seemingly anastomose as the ants become more abundant (178).

ROLE IN PEST MANAGEMENT In the early 1900s, cocoa planters in Indonesia observed that less mirid damage was associated with the presence of D. thoracicus on cocoa, so they introduced ants into new areas. Subsequent research improved these introductions (36, 131, 161), but interest declined during an era of insecticide overdependence, until the 1980s (5) when work also began in Malaysia (72, 177, 178).

D. thoracicus is not aggressive, and so it is not a nuisance to plantation staff. It deters other insects from places where it concentrates densely, as when attending Homoptera on cocca pods (72, 161). In Malaysia, it associates with the mealybug *Cataenococcus hispidus*, which does not appear to decrease yield (72).

D. thoracicus is particularly successful in protecting cocoa against the mirids *Helopeltis antonii* and *Helopeltis theivora* in Indonesia and *H. theobromae* in Malaysia, the feeding lesions of which kill and damage pods and young shoots. However, *D. thoracicus* is locally distributed and, even when present, may be insufficiently abundant to protect cocoa. Constraints include competition with other ants and insufficient nesting sites and honeydew-producing Homoptera, particularly in the wet season (5, 10, 37, 72, 161).

Recent establishments of D. thoracicus on cocoa (5, 72) have been made as follows: (a) ground treatment of the introduction area with an insecticide spray (Indonesia) or bait (Malaysia) to suppress antagonistic ants; (b) placement of bundles of coconut leaflets or polythene bags containing cocoa leaf litter as artificial nests in already heavily colonized areas and, when well colonized, removal to cocoa trees in the introduction area; (c) artificial colonization with mealybugs in the introduction area; (d) fresh introductions of D. thoracicus (Indonesia) or mealybugs (Malaysia) if needed; (e) leaving the proximal ends of harvested pods on the tree to conserve mealybugs (Indonesia); (f) maintenance of cocoa and coconut palm leaf litter to provide ground-nesting sites for the ants.

In conclusion, D. thoracicus is a valuable biological-control agent in its own right and also as part of an IPM program involving spot spraying of inadequately protected trees (5, 177). Use of other beneficial ants, notably O. smaragdina, could be integrated with that of D. thoracicus (178).

Formica rufa Group

Gosswald (43, 44) and others (2, 21, 47, 180, 183) have comprehensively covered the extensive literature on this complex of eight species. In their temperate forest environment, *Formica* spp. are inactive during winter; activ-

ity at other times depends on temperature. Subspecies may be either monogynous or polygynous (2), and colony boundaries are sometimes unclear and may only be apparent during reestablishment in spring (89). Colonies may be very large; for example, a single F. *lugubris* colony covered over 90 ha (19).

ROLE IN PEST MANAGEMENT The value of Formica spp. against defoliating outbreak pests in temperate forests has been recognized in Germany since the 19th century (41, 43, 44). Unlike the low-density endemic pests that can be controlled by Oecophylla spp. and D. thoracicus, the recognized pests controlled by Formica spp. are high-density epidemic species whose periodic rapid rise to abundance puts a premium on density-dependent predation. The ants' predatory potential is exemplified by an estimated eight million insects killed in a year by a medium-sized nest of F. polyctena (179) and some 14,000 tons of insects by the approximately one million ant nests of the F. rufa group in the Italian Alps (116). Consequently, damage around Formica spp. colonies may be minimal during outbreaks of defoliating caterpillars, the protection being inversely related to distance from the nest (2, 8, 9, 180, 182). In particular, "green islands" surround colonies of F. polyctena during outbreaks of the lepidopteran Panolis flammea; the ants disturb ovipositing adults, kill larvae on the trees and on the ground, and kill pupae beneath the soil (8, 9, 181). In fact, Formica spp. kill many different defoliating pests in European forests (2, 44, 114), from which tree growth may benefit (e.g. 186). F. polyctena and F. lugubris are particularly useful for artificial establishment in different climatic zones (21, 41, 116, 117). They are favored because they reach high population densities, are facultative predators active over a long season day and night at all levels of the forest, and are capable of killing both active and quiescent stages of different prey species, notably the caterpillar pests on which they concentrate during outbreaks. When prey is scarce, they maintain their large populations on the honeydew from attended Homoptera (175).

The large many-nest, polygynous ant colonies have been established artificially in many European plantations (30, 41, 42, 44, 47, 74, 117, 142, 157, 182), and *F. lugubris* has been successfully transferred to eastern Canada (31, 103). Recommendations for pest management include cultural practices that assist the ants (e.g. 44, 152, 189) and use in combination with microbial pesticides (117). The relative ease with which suitable *Formica* spp. can be established in temperate environments is probably associated with comparative lack of competition from other dominant ant species, in contrast to most tropical situations. Although *Formica* spp. kill very large numbers of pest insects during a pest outbreak, about 7% of prey may be beneficial species (8, 41), rising to approximately 15–20% in nonoutbreak situations

(2). The ants partly deterred Coccinellidae, yet when abundant, the latter could still eliminate populations of F. polyctena-attended aphids (179). Gridina (50) showed that a diverse but smaller community of other predators survived where F. polyctena was abundant. The role of these other beneficial species has not been determined. Though some prey importantly on the Homoptera that the ants attend (175), the ant protection enables some Homoptera, as on beech trees (Fagus), to reach damaging abundance (106).

In conclusion, although the use of the *Formica rufa* group may sometimes be undesirable, much evidence supports their role in usefully protecting trees from some damaging defoliating pests. Moreover, their stabilizing influence on pests and potential pests in forest ecosystems must be important and justifies further study.

Azteca Species

The value of these fiercely predacious tree-nesting New World tropical ants was recognized by the Kayapo Indians who used them against leaf-cutting ants in Brazil (22, 113). In Trinidad, *Azteca* sp.—occupied citrus trees are damaged much less by the leaf-cutting ant *Atta cephalotes* than unoccupied ones, and experimental destruction of *Azteca* sp. colonies led to *A. cephalotes* defoliation of 80% of the trees within two weeks (70). Many pest, or potential pest, species are excluded from the colony area of *Azteca* sp. (22, 62) through aggression and repellency (11, 139, 167). Although *Azteca* sp.—colonized cocoa had higher yields than adjoining uncolonized trees, and some growers continue to encourage *Azteca chartifex* by distributing nest fragments among their plantations, this traditional practice (156) is criticized because the discomfort the ants cause to people and damage by their attended Homoptera are said to outweigh the benefits the use of the ants confers (22). More thorough investigation of the role and use of *Azteca* spp. is needed (62, 77).

Wasmannia auropunctata

This ant is sometimes regarded as a pest in its native tropical America (160), and, as an introduced species, can greatly affect the indigenous insect community (20, 88). Its polygynous and apparently small but abundant colonies are associated with humid conditions in perennial, mostly tropical, environments (88). Two accidental introductions exemplify its role as a valuable, or potentially valuable, biological-control agent. In the Cameroons, local farmers establish nests in cocoa plantations, having recognized this ant's value against cocoa mirids (16). Appearing recently in the Solomon Islands, it controls a serious pest of coconuts, *Amblypelta cocophaga*, and is also displacing two other dominant pest ants, *Iridomyrmex cordatus* and *Pheidole megacephala*, which do not protect coconut palms from A. cocophaga (90). Even though W. auropunctata has a painful sting when severely disturbed, it

is remarkable that this very small, slow-moving ant can displace fiercely competitive species. Perhaps it uses a chemical repellent. In view of its potential importance for biological control in its indigenous (G. Pollard, personal communication) as well as some exotic environments, the ecology and impact of *W. auropunctata* should be studied in much greater detail.

Anoplolepis Species

Anoplolepis longipes probably originated in Africa but now occurs worldwide in the tropics where it forms super-colonies (51). It is a nuisance pest in homes and can kill or disturb domestic animals and harm plants directly and indirectly (52), but it is not conspicuously aggressive towards people and does not bite or sting. It has destroyed and displaced the beneficial O. longinoda from some habitats in East Africa (172) and is similarly recognized as a major constraint to establishment of D. thoracicus for control of cocoa capsids (72, 161), although A. longipes itself can provide some protection to cocoa (80). A. longipes usefully protects coconut palms from Amblypelta cocophaga in the Solomon Islands, in contrast to its ineffectiveness against the closely related and identically damaging P. wayi in East Africa (14, 48). Perhaps in the Solomon Islands, it depends more on prey for food (49). In Papua New Guinea, it is encouraged for control of Pantorhytes spp. (Coleoptera) on cocoa and because it displaces other ant species that can transmit Phytopthora spp. (102, 133, 140). It is also a valuable predator of Pseudodoniella laensis on cocoa (153) and is recommended in IPM programs (140). In the Seychelles, although condemned as a nuisance pest, it seems able to protect coconuts from the severely destructive Mellitomma insulate and Oryctes monoceros (81). The latter is presumably disturbed rather than killed, but this assumption should be investigated in view of the worldwide tropical importance of rhinoceros beetles.

Anoplolepis custodiens is largely limited to well-drained, usually sandy habitats with good insolation (172) and is considered a pest in South Africa because its attended Homoptera seriously damage crops such as citrus (148). In Tanzania, however, very dense populations can protect coconut palms from P. wayi (82) though populations with normal abundance do not (172). When the ant is very abundant, damage by its attended Homoptera might be unacceptable.

In conclusion, A. *longipes* has important biological-control attributes that can usefully be encouraged in places where it is clearly beneficial, although it sometimes needs to be controlled as a pest elsewhere.

Solenopsis Species

This genus includes three New World species of fire ant, S. geminata in the hotter climates, and S. invicta and S. richteri from subtropical South Amer-

ica, which have been introduced to the southern United States. The introduced species are opportunists that exploit and thrive in disturbed agricultural habitats (158, 169). At least 6000 rapidly growing colonies/ha, each sometimes comprising groups of queens, may be established on newly available land (99, 159), but ultimately only about 50–60 colonies mature (105). Normally only one queen survives in each mature colony of about 40,000 workers; and then the colony becomes territorial (159). Differences in colony organization pose economically important unanswered questions (158).

In the USA, the two introduced species are nuisance and public-health pests but are not regarded as major pests of crops (4, 84-86). Control measures have cost some \$200 million since 1957 (4, 84, 162). S. invicta is, however, a valuable predator (123), especially against some pests of sugar cane (1, 33, 123), cotton (27, 28, 65, 100, 101, 145, 151), and other crops (75, 123, 185) and some pests of veterinary importance (123). S. invicta may not harm other predacious insects in cotton fields (125, 147), and sometimes chemical control of the ant has made pests worse (1, 54, 87, 124). Current emphasis is therefore on preservation and enhancement, especially through cultural practices and selective use of chemicals in situations where the benefits of S. invicta outweigh its disadvantages (3, 65, 123, 146). Reagan (123) discusses opportunities for sugar cane pest management based on understanding interrelationships between the crop, its weeds, and predators, and other invertebrates. The indigenous S. geminata may also be a valuable predator, sometimes of weed seeds (18, 24, 61, 127, 136). That it can decrease Sitophilus sp. numbers by 98% on corn is striking evidence of its potential (127).

In conclusion, *Solenopsis* spp., particularly the introduced *S. invicta*, have undoubted biological-control attributes such that the ants need to be encouraged in localities where they do little or no harm.

Ants as Egg Predators

Good evidence shows that ants prey on eggs of pest species in many different countries and habitats (Table 2). For example, in Sri Lanka virtually 100% of eggs of *Opisina arenosella* were removed within 24 h by *Monomorium floricola* (176). *Solenopsis invicta* was part of a complex killing over 70% of eggs of *Heliothis virescens* in 24 h on cotton where ratios of predators to prey ranging from 2:1 to 200:1 seem able to prevent significant pest damage (100, 101). On sugar cane, over 90% of eggs and small larvae of *Castnia licus* (24) and 92% of eggs of *Eldana saccharina* (38) were killed by ants. *Pheidole* spp. are major predators in complexes that can kill over 95% of eggs of *Alabama argillacea* (46) and some 80% of *Diabrotica* spp. eggs in the soil (126). Certain cultural practices benefit predation, for example maintaining bare strips between rows of citrus (61) and some forms of intercropping (111). The

TION 7 STOPT	invide examples of predation by	ants on eggs or pest meetrs		
Country	Pest species	Crop host	Ant predators	Reference
Africa	Eldana saccharina	Sugar cane	Pheidole megacephala and others	35
Brazil	Alabama argillacea	Cotton	Pheidole sp. and others	46
Costa Kica Fiji	Diabrotica spp. Promecotheca cumingii	Several annual crops Coconut palm	S. geminata, Pheidole sp. Monomorium floricola	126 155
Ghana	Eldana saccharina	Sugar cane	Tetramorium bicarinatum, Camponotus sericeus, and	38
Guadeloupe, Martinique	Diaprepes abbreviatus	Citrus	Pheidole sp. and others	62
Kenya	Chilo partellus	Sorghum, Maize	Pheidole sp. and others	110
	Helicoverpa armigera	Smallholder crops	Pheidole sp., Camponotus sp., and others	H. van den Berg ^a
Malaysia	Helopeltis theobromae	Cocoa	Dolichoderus thoracicus	K. C. Khoo ^b
Panama	Castnia licus	Sugar cane	S. geminata and others	24
Peru .	Castnia daedalus	Oil palm	Odontomachus, Pheidole, and Iridomyrmer son	73
Portugal	Phoracantha semipunctata	Eucalyptus	I. humilis and others	M. J. Way ^b
Sri Lanka	Opisina arenosella	Coconut palm	M. floricola and others	176
Trinidad	Heteropsylla cubana	Leucaena spp.	Wasmannia auropunctata	G. Pollard ^a
USA	Anthonomus grandis	Cotton	S. invicta	28
	Helicoperva virescens	Cotton	S. invicta	100, 101
	Pseudoplusia includens	Soybean	S. geminata	109
	Anticarsia gemmatilis	Soybean	Pheidole morrisii and others	39
	Cacopsylla pyricola	Pear	Formica neoclara and others	115

Table 2 Worldwide examples of predation by ants on eggs of pest insects

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^a Personal communication. ^b Unpublished data.

significance of ant predation on eggs is evident from the conclusion that *Cactoblastis cactorum* inadequately controlled prickly pear in South Africa partly because ants killed up to 70% of its eggs, although this effect was harmful (129).

In conclusion, ants alone or as an important part of a predator complex (61, 101, 185) can cause very large mortalities of eggs and so can contribute importantly to natural control. More specific case studies are needed to assess the importance of such mortality, especially because increased egg mortality can sometimes be compensated for by decreased larval mortality (165; M. J. Way, unpublished data).

Role of Nondominant Ant Predators

Inadequate attention has been given to the many ant species that are relatively inconspicuous predators and/or scavengers of eggs (Table 2) and other life stages of pests. Many are categorized as sub- or nondominants (92) and are often relatively small, "passive aggressors" (78), some of which, as "in-sinuators" (188), can flourish even where other ants dominate. For example, these ants include species of *Monomorium, Technomyrmex,* and *Tetramorium* in the presence of *Oecophylla smaragdina* (176). Some are important predators of pests that the larger aggressive dominant ants do not attack (25, 130, 137, 154, 176, 181). Further understanding of their roles in pest dynamics and in pest management remains a challenge for the future.

PROMOTING USE OF ANTS IN PEST MANAGEMENT

Favorable Ant Qualities

Important attributes of useful ant species (30, 96, 97, 127) are listed by Risch & Carroll (127) as follows: (a) they are very responsive to prey density; (b) they can remain abundant even when prey is scarce because they can cannibalize their brood and, most importantly, use honeydew-producing Homoptera as a stable source of energy; (c) they can store food and hence continue to capture prey even if it is not immediately needed; (d) besides killing pests, they can deter many others including some too large to be successfully captured; (e) they can be managed to enhance their abundance, distribution, and contacts with prey.

Other useful criteria for ants as biological-control agents include broad habitat range and choice of species that are unlikely to be out-competed by other ants (96). Finnegan (30) lists desirable characteristics of certain *Formica* spp., some of which are relevant to other ants, including ability to hunt at different levels and to concentrate increasingly on a particular prey species as its population increases. Polygyny is a useful attribute because colony fragments can easily be transferred to establish new colonies. Many ant species

have insufficient desirable qualities so that they, like indigenous ants of Canadian forests, are not good for biological control (29).

Undoubtedly the most important attribute of useful or potentially useful predatory ants is stability as large populations, which together with efficient recruitment enables the ants to react quickly to surging numbers of a pest. Ants such as *Formica polyctena* can therefore cause direct density-dependent mortality, unlike the characteristically delayed action of nonsocial natural enemies. Another consequence of stability of large predatory ant populations is their unique ability, through efficient foraging, to protect plants from low-density pests. For example, *O. longinoda* protects all year against the correid *P. wayi*, which can cause catastrophic damage to coconut palms at densities of one to two individuals per coconut palm, a level at which conventional natural enemies are ineffective. Attended honeydew-producing Homoptera, besides ensuring local stability of large ant populations, can encourage foraging for prey on plants or in fields where they occur (104, 109), and in forests (30) where a ground-nesting ant may otherwise confine foraging to the forest floor (184).

Well-known mutualisms involve plants with specializations attractive to ants that in return protect the plants from herbivores (7, 63). Such attributes, however, are characteristic of plant species of little or no economic importance. Perhaps excluding extra-floral nectaries, coevolution does not seem to have led to such specializations in plants of notable economic importance.

Manipulations That Favor Ants in Pest Management

The proposal to protect, enhance, or introduce an ant for biological control can be rationalized by a sequence of decisions, just as for any control practice (133). Once it has been decided to make use of a particular ant, one must answer two main questions: first, how to suppress undesirable competing ants that otherwise displace the desired ant or keep it too scarce to be effective, and second, how to improve other favorable conditions. These requirements are interrelated; for example, other favorable conditions will naturally favor competitive ability. Suppression of competing ants is not always needed, for example in the use of *Formica* spp., which may have no significant competitors in their temperate forest environment, and of ants such as *S. invicta* that are invaders of open habitats.

Colonies of undesirable species can be killed or suppressed locally by insecticides but will usually become reestablished unless other conditions are created that inhibit reinvasion. Therefore, fundamental to use of an ant species in IPM is appropriate understanding of relevant aspects of its ecology and that of undesirable competing species.

SIGNIFICANCE OF THE CROPPING SYSTEM Illuminating evidence supports the importance of certain crop mixtures for encouraging beneficial ants.

Interplanted trees such as citrus and cloves strengthen the role of O. longinoda in control of coconut pests (173). This was also demonstrated with Q. smaragdina against Amblypelta cocophaga in the Solomon Islands (143). Similarly, coconut palms with underplanted cocoa are much less affected by Axiogastus cambelli (112) than are monocrop palms. Conversely, the palms benefit cocoa. Certain pests are worse under Leucaena shade than under coconuts including Pantorhytes szentivanyi, which is strongly associated negatively with coconuts and positively with Leucaena shade (135). Perhaps coconuts provide essential food and nesting sites for beneficial ants, as they do for D. thoracicus protecting cocoa from H. theobromae (178). Shading at different levels of vegetation may be important. For example, the beneficial ant Macromischoides aculeatus seems inherently to require a thick understory of a crop such as cocoa, whereas Oecophylla spp., if free from competition with other ants, can also flourish where there is relatively little shade (94). Appropriate coconut-cocoa planting regimes have been recommended for cocoa pest control (93).

Ground vegetation suppresses some deleterious competing ants; for example, Anoplolepis custodiens in East Africa depends on well-insolated soil for nesting and does not supplant O. longinoda in habitats where there is sufficient ground and shrub vegetation (172). There has been some controversy over the role of vegetation in relation to the control of A. cocophaga in the Solomon Islands (15, 48), but the conclusion must be that vegetation powerfully affects the outcome of competition between dominant ant species and that success in manipulating vegetation to favor beneficial species depends on understanding the quality of its diversity. Several studies help towards such understanding (18, 48, 49, 76, 96, 97, 127).

Ecological and applied ecological concepts (e.g. 98, 141) explain how exploiting species can dominate the unstable, less mature early stages of ecological succession and their arable crop equivalent, whereas differently adapted species require the stable environment of more mature climax perennial systems. As plantation systems mature, dominant ant species change correspondingly (92). Many invasive exploiting species, such as some Solenopsis spp., A. longipes, and Iridomyrmex humilis, are adapted to the more open, less mature stages of natural succession and to the arable crop equivalents of these stages (e.g. 158). S. geminata, for example, quickly invaded the open habitat of a cleared forest, but within a year decreased drastically as herb and tree vegetation became reestablished (18, 127). This species is favored by continuous mixed cropping cycles (136). In contrast, matureecosystem species such as D. thoracicus and Oecophylla spp. are no doubt denizens of natural forests (178). Habitats neither immature nor mature enough to favor one or another kind of ant seem highly unstable. For instance, in some semi-open cocoa-coconut plantations in Malaysia, four dominant

species, O. smaragdina, D. thoracicus, Crematogaster sp., and A. longipes, coexisted (177). All were relatively uncommon and all competed in cocoa tree canopies where up to three species were foraging sparsely on a tree with no obvious territorial distinctions except around each species' nests.

Crops are grown in a wide range of ecological conditions from very immature arable systems through more complex mixtures of arable crops, combinations of tree and arable crops, and trees in monocultures or complex combinations. The last most nearly approaches conditions in mature forests. At all levels, therefore, one should be able to manipulate conditions to favor a particular kind of ant, as is evident from recommendations to maintain strips of bare soil to favor the open habitat species S. geminata (75), or to keep vegetational diversification and shading to favor more closed-habitat species (26, 97, 172). The approach therefore is to simulate in agricultural systems the key elements of the equivalent natural ecosystem that benefit the chosen ant species. Carroll & Risch (18) studied and discussed aspects of this problem for ants in an arable agroecosystem, and Greenslade (48) did similar work in a perennial agroecosystem. In the arable cropping system, much may depend on the ability of the ant to reinvade newly cultivated land quickly, as can S. geminata, especially if refuges are provided by strip-cultivated or mixed-crop systems. In this respect, traditional slash and burn agriculture harms ants more than some continuous cropping systems (136). However, the "weed" species, S. invicta (158), seems able to reinvade very quickly a large simple cotton monoculture (145). In the perennial system, the encouragement of ants such as Oecophylla spp. depends primarily on creating conditions that are unfavorable for open-habitat, invasive species because otherwise the latter almost invariably seem to dominate.

So far, this section has contrasted the distinctive conditions favoring ants adapted to immature habitats with those adapted to more mature habitats. However, different species all adapted to the same habitat also compete. In a mature habitat, the outcome of competition between the adapted species may depend on availability of their favored niches in the three-dimensional mosaic (48, 76). Where the vegetation is relatively complex, as in a mixed plantation of tall trees, understory trees, and ground vegetation, ant species are horizontally segregated (48, 49, 187). However, with vegetational simplification of the lower-story vegetation, segregation changes to a more vertical arrangement such that species previously associated with lower stories begin to forage and even make subsidiary nests in upper stories, as do Pheidole spp., which then compete with and displace Oecophylla spp. from coconut palm crowns (172). Finally, even where there is horizontal segregation of lowerand upper-story ant species, dominants adapted to a particular story still compete, as in coconut palm crowns in the Solomon Islands (15, 48, 49). Here, Iridomyrmex cordatus has locally displaced O. smaragdina on palm

crowns, and a recently introduced ant, W. auropunctata, has begun to displace both O. smaragdina and I. cordatus (90). Reasons for the dominance hierarchy of such species are unknown.

CONCLUSIONS

The stability, social organization, and foraging behavior of some predatory ants enable them to react quickly to increasing prey density, and also make them uniquely able to protect crops from low-density pests. Such qualities require dependence on honeydew-producing Homoptera that may sometimes be made harmful by ant attendance. Cost-benefit judgments are therefore needed when such ants are to be used.

Predacious ants also affect other natural enemies, but less than might be expected, and may indeed benefit some. Ants tend to overlap the food niches of other predators and may force them into one competitive system. Whether overall biological control is benefited by such interactions is unknown. Work on the role of ants as part of overall natural-enemy complexes is needed. In addition, inadequate attention has been given to understanding ant-prey interactions. Research such as that done in some natural habitats needs to be undertaken in agroecosystems.

Behavioral attributes that enable one species, for example, a very small and apparently inoffensive species, to dominate over larger more aggressive species are not understood and need detailed investigation. Studies of this type should provide valuable clues to manipulating systems in favor of some beneficial species.

Biological-control attributes of many relatively inconspicuous nondominant ants have been inadequately studied. Some species may be valuable in their own right, but many also make a significant contribution to overall natural mortality, which needs to be understood much better than it is at present.

The results are promising from some ecological approaches to manipulating beneficial ants by cultural practices and habitat modification. More emphasis is needed on practical application, especially since some ants have sharply contrasting pest and beneficial attributes, e.g. *S. invicta*. Since eradication is impossible, the emphasis should be on enhancing their role in habitats where they are beneficial, while controlling them elsewhere. Such approaches need not be incompatible.

Although the introduction of exotic predatory ants for biological control is potentially hazardous, it should not be discounted. In this context, work is needed on some accidentally introduced species that have important biological-control attributes, e.g. *W. auropunctata*.

Finally, in some circumstances, ants are uniquely useful, as when they are the only alternative to intensive insecticide treatment, or where alternative practices are uneconomic or impracticable.

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