
Exotic Ants

Biology, Impact, and Control of Introduced Species

EDITED BY

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1994

Westview Press

BOULDER • SAN FRANCISCO • OXFORD

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Characteristics of Tramp Species

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Introduction

There are a number of economically important ant species, the most significant of which are certainly the fire ants (Adams 1986, Lofgren 1986) and the leaf cutter ants (Cherrett 1986, Fowler et al. 1986), all limited to the American continents. Because of the damage they do to the environment and crop production, and the danger they pose to human health, these ants certainly warrant the term "pest ants". Among pest ants, attention in the last few years has focused on several species that exhibit a group of characters that has led to the term "tramp species". According to Hölldobler and Wilson (1990, p. 215), tramp species have the following characteristics: they are polygynous, unicolonial, they reproduce by budding, are largely dispersed throughout the world by human commerce and live in close association with humans. In this review the definition of tramp species is refined in light of recent work on three main species: the Pharaoh ant, *Monomorium pharaonis*, the Argentine ant, *Linepithema humile*, formerly *Iridomyrmex humilis*, and the little fire ant, *Wasmannia auropunctata*. Other less well-known species will be briefly discussed in order to better understand the strategies adopted by the principal pest species.

The Human Environment

Linepithema humile: since its description from the Buenos Aires area in 1868, this dolichoderine has spread throughout the world touching all the continents: the southern USA, starting with Louisiana, Mississippi, Alabama and California around 1891 (Newell and Barber 1913), South Africa in 1908 (Skaife 1955), Europe about 1904-1905 (Chopard 1921),

Australia in 1939, without sparing islands like Madeira or Hawaii (Wilson and Taylor 1967). Each time human commerce was the cause of introduction. In France it was apparently introduced with tropical plants (orchids and ferns) imported from South America to green houses in the Côte d'Azur. In South Africa it is suspected that trade with Argentina involving animal forage during the Boer War was responsible for the introduction. In Polynesia it followed the movement of troops during the second world war. Everywhere this species has invaded, it lives in close association with human habitations. For example, in the Languedoc-Roussillon region of France it is found in seaside resorts (Port-Leucate and La Grande Molte), but it is totally absent from the beaches that separate these resorts (Passera, unpublished). It appears to prefer areas modified or disturbed by human activity, such as cultivated fields, landscaped areas, garbage dumps, plaster rubble and dwellings.

Monomorium pharaonis: this cosmopolitan species probably originate from primary virgin forest of the Ethiopian zone (Bernard 1968). It is found in all tropical regions where it inhabits both natural outdoor situations and the inside of buildings (Wilson and Taylor 1967). This species has colonized temperate regions throughout the entire world, where it almost always lives inside houses. In Europe, for example, it is found especially in northern countries (Great Britain, Denmark, Belgium, Switzerland, Germany, Czechoslovakia, etc.) or in southern countries in which the altitude exceeds 1000 m, such as the principality of Andorra (Eichler 1978, Edwards 1986). Curiously, it seems less common in southern Europe because in 1976 it was not yet reported from Greece or Spain (Eichler 1976). Even though buildings are heated for a longer period each year in northern Europe and in countries with harsh climates like Andorra, perhaps *M. pharaonis* finds the short winter season in southern Europe unfavorable, because buildings are not heated as well as in northern Europe. It generally inhabits only the best-heated buildings: hospitals, houses with children, retirement homes, etc. Only exceptionally does it seem able to complete its lifecycle outdoors, e.g., in garbage dumps that generate heat (Kohn and Vlcek 1984). The Pharaoh ant is also found on the American continent (USA and Canada), Africa (Guinea), Asia (Japan) and in Australia. Like the Argentine ant, there is no doubt that it has spread through human commerce; we have found it in Toulouse in the packing carton of an electron microscope originating from Japan. At least two other species of *Monomorium*, *M. floricola* from Asia (Emery 1921) and *M. destructor* from Africa, which have pantropical distributions (Wilson and Taylor 1967), could also be considered tramp species.

Wasmannia auropunctata: this species originated from tropical America. It has colonized Central America, South America (Kempf 1972), North America (Florida and Canada) (Ayre 1977), Cameroon in Africa (Bruneau de Miré 1969), numerous islands in the Caribbean, New Caledonia, Wallis and Futuna Islands and the Galapagos Islands (Silberglied 1972; Ulloa-Chacon 1990). It prefers cultivated areas (citrus orchards, coffee fields, cacao plantations) and also buildings where it forages on various food sources (Smith 1965).

Other species: based only on the criterion of dispersal by human commerce, Wilson and Taylor (1967) counted 37 species of tramp ants in Polynesia. Several of these don't appear to merit the title of tramp species because they don't satisfy all of the conditions considered here (in particular, the absence of nuptial flight, intranidal mating and colony reproduction by budding). Others, *Tetramorium caespitum* or *Solenopsis geminata*, warrant special mention.

Cardiocondyla: *C. emeryi* and *C. nuda* originate from Africa and are found throughout the tropics (Wilson and Taylor 1967). *C. nuda* occurs in Malaysia, Oceania, India, Madagascar, northern Africa, Egypt, Cyprus, Australia and Polynesia (Bernard 1956). *C. emeryi* is known to occur in the Antilles, Madeira, Syria, Congo, Sudan and Madagascar (Bernard 1956), and South Africa where it causes damage in citrus orchards (Samways 1990). *C. wroughtoni* originates from tropical Asia and is known throughout the tropics (Wilson and Taylor 1967, Reimer et al. 1990) but is also found in Florida (Stuart et al. 1987), Japan (Kinomura and Yamauchi 1987) and Israel (Lupo and Galil 1985).

Pheidole megacephala: this species probably originates from Africa and has conquered almost all of the humid tropics (Wilson and Taylor 1967). It is an important pest in South America (Fowler et al. 1990). In South Africa it is a big problem in buildings (Prins et al. 1990). In Hawaii it tends scale insects on coffee (Reimer et al. 1990). In Morocco it inhabits the sidewalks of cities (Bernard 1968). In Europe it is found in heated greenhouses (Bernard 1968).

Paratrechina longicornis: this "crazy ant" is abundant in pantropical cities. It probably originates from the old world tropics (Wilson and Taylor 1967), but now occurs in Polynesia (Wilson and Taylor 1967, Reimer et al. 1990), the southern USA (Smith 1965, Trager 1984), in Cameroon (Dejean, personal communication), Brazil (Banks and Williams 1989) and South Africa (Prins et al. 1990). Depending on the climate, it lives outdoors or in heated apartments. In Europe, *P. longicornis* is found in greenhouses (Bernard 1968).

Anoplolepis longipes: this "crazy ant" originating from Africa (Wilson and Taylor 1967) has invaded the old world tropics: Polynesia (Wilson and Taylor 1967), New Guinea (Baker 1976), several islands in the

Indian Ocean including Zanzibar, Mauritius, Reunion and the Seychelles (Haines and Haines, 1978a), Malaysia (Fiedler 1989), Sri Lanka, Myanmar (Burma), India (Veeresh 1990) and South Africa (Prins et al. 1990). *A. longipes* prefers cultivated fields (sugar cane, cacao, coffee), orchards (mangos, citrus) and dwellings.

Tapinoma: *T. melanocephalum* is a small species with a black head whose origin is not precisely known (Wilson and Taylor 1967). It is largely distributed in the tropics and subtropics of the world, where it occurs in association with humans (Smith 1965). It can be found in heated locations in northern regions such as Canada (Ayre 1977) and Germany (Steinbrink 1987). It is very common in the southern USA, Central America and South America (Kempf 1972; Nickerson and Bloomcamp 1988; Fowler et al. 1990; Harada 1990).

Lasius neglectus: this species is provisionally included in this list because it is perhaps the most recent member of the tramp ants. At present it has only been found in the city of Budapest. It nests in human structures and also in the soil (Van Loon et al. 1990). It is of unknown origin, but it is certain that it was accidentally imported by humans (Van Loon et al. 1990). Its status as a true tramp ant will be determined later by seeing if its distribution is linked to human activity.

Migration

The attraction of tramp ants to unstable and perturbed environments linked to human activity explains their strong tendency to move. As noted by Wilson (1971, p. 311), species observed in captivity exhibit a permanent nervousness. At the least disturbance (shock, vibration, manipulation of the nest, lighting, etc.) workers of *L. humile* pick up larvae and attempt to flee. In a natural setting, colonies of the Argentine ant relocate in response to changes in weather and/or human activity. This phenomenon was noted by Newell and Barber (1913) and Markin (1968) in the USA. In France, it has been well-studied by Benois (1973) on the Côte d'Azur, and we have verified this at Port-Leucate in the Roussillon near Perpignan. At the onset of winter, several colonies fuse to form large concentrations of ants that collect in places with southern exposure, including the base of walls, tree roots and the edges of sidewalks. In the spring the colonies split and seek out areas that are more shaded and humid. The spring and summer colonies are extremely mobile and react immediately to physical disturbance (trash disposal, gardening, etc.), to changes in weather conditions (increase or decrease in humidity) or to dietary modifications (exhaustion or discovery of a food source).

M. pharaonis, which habitually nests in buildings, also readily undergoes migrations in response to over-population or changes in nest site (Peacock et al. 1955a, Edwards 1986).

In Colombia and in the Galapagos, *W. auropunctata* prefers leaf litter, an unstable habitat that favors frequent migrations (Ulloa-Chacon 1990). In Israel *C. wroughtoni* was introduced inside figs of *Ficus sycomorus*, where it utilizes a cavity only 5 to 8 mm in diameter. It is also found in insect galls (Lupo and Galil 1985). Such habitats are very short lived requiring their occupants to change nest sites frequently.

The readiness with which *A. longipes* migrates has been noted by Baker (1976) who was able to trap entire colonies by placing bamboo stems in infested cacao plantations which were then rapidly colonized.

T. melanocephalum, which frequently nests in unstable and temporary habitats (plant stems, clumps of dried grass, debris), rapidly changes nest sites when conditions become unfavorable (Nickerson and Bloomcamp 1988).

Unicoloniality

According to Wilson (1971), unicolonial species are characterized by the absence of aggressive behavior between individuals from different nests occurring in one area. It is this absence of aggressivity that is responsible for the exchange of individuals between the different nests. These societies are called "open" in the sense of Le Masne (1952), as opposed to the "closed" societies that are typical of multicolonial species.

Unicoloniality is well-established in *L. humile*. As early as 1913, Newell and Barber remarked that even though colonies of this species are very intolerant toward other species, there is no antagonism between different colonies. In fact, in a heavily infested area it is impossible to distinguish among colonies, because all appear to belong to a single and enormous colony. This phenomenon was confirmed by Markin (1968) in California. It is identical in France: the site of Port-Leucate constitutes an immense society occupying some 700 by 300 meters. It is even possible to mix individuals from sites separated by distances of several hundred kilometers (Bonavita-Cougourdan 1988; Passera and Aron, unpublished data). This does not mean that there is an absence of colony recognition. Kaufmann and Passera (1991) showed that workers spend more time examining non-nestmate conspecifics coming from distant colonies. The absence of aggression applies equally well to mated queens. By contrast, males are attacked and killed when they are introduced into a queenright colony even though they are perfectly accepted in colonies that are deprived of a queen (Kaufmann

and Passera 1991). This indicates that the openness of unicolonial societies has certain limits.

The different nests of the polydomous societies of the Pharaoh ant are open and individuals can be exchanged without aggression (Peacock et al. 1950, Edwards 1986, Berndt and Eichler 1987). Nevertheless, just as in the Argentine ant, certain individuals such as queens, can be attacked depending on their physiological condition (Petersen-Braun 1982).

W. auropunctata exhibits no aggressivity toward conspecifics: colonies collected in the field can be mixed without any problem in the laboratory (Clark et al. 1982, Ulloa-Chacon 1990). Observed seasonal variation in the composition of natural colonies, moreover, shows colony fusions alternate with colony divisions.

Less is known about other tramp species, but it seems they show the same tendency. For example, colonies of *T. melanocephalum* show no signs of aggression when mixed (Smith 1965) or when individuals are exchanged along foraging trails (Oster and Wilson 1978). In a same way in *A. longipes* individuals from different nests do not exhibit aggression towards each other (Haines and Haines 1978b).

Interspecific Aggression

The absence of intraspecific aggression seems to go along with strong interspecific aggressivity. Because tramp species are most often imported, they collide with native species that they must drive off. This is certainly the case with *P. megacephala* (Haskins and Haskins 1965, Fowler 1988). Undoubtedly the best known example is that of the Argentine ant. Several authors have studied the decline of native species in communities colonized by *L. humile* in Australia (Pasfield 1968) and in California (Erickson 1971, Tremper 1976). On the coastline of Languedoc-Roussillon in France, the Argentine ant has eliminated all the local species, in particular, *Tetramorium* spp. and *Tapinoma erraticum*, which are dominant in this area. Only a few colonies of *Plagiolepis pygmaea* and *Diplorhoptrum fugax* persist (Passera 1977, unpublished data). The more thorough study of Ward (1987) was conducted in different natural habitats in the Sacramento valley in California. This author found that even though *L. humile* alters the ant fauna in every locality, (16 of 27 species disappeared from the areas colonized by *L. humile*), there were differences among the species in the degree affected. Epigaeic species were more affected than hypogaeic species; less obvious species, like *Stenamma diecki* or *S. californicum* that forage in the soil and in the litter, are very resistant. Even among the epigaeic species, the extent of the effect depends on whether the species has a biology

similar to that of the Argentine ant: *Liometopum occidentale* and *Tapinoma sessile*, which are dominant and opportunistic species that forage under the same conditions as *L. humile* are eliminated, whereas *Prenolepis imparis*, which forages at lower temperatures, remain present.

Strong competition can occur between two tramp species. This situation has been well-studied in Bermuda by Crowell (1968), Haskins and Haskins (1965), Fluker and Beardsley (1970) and Lieberburg et al. (1975). *P. megacephala* became established first around 1902 in displacing the other species present. At the time of the arrival of *L. humile* around 1953, it had conquered the whole island. The introduction of *L. humile* was followed by intense competition between these two tramp species, and about 1975 the Argentine ant seemed on track to eliminate its rival. However, the latest observation of Haskins and Haskins (1988) lead one to think that the situation is reaching an equilibrium, because *P. megacephala* had retaken several areas.

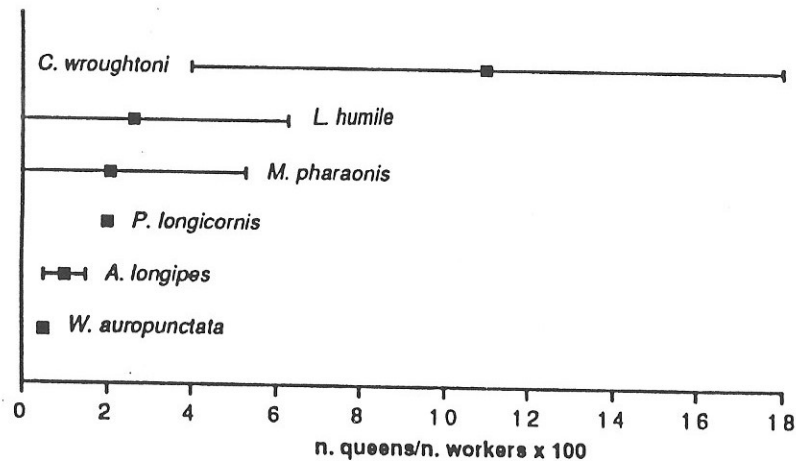
W. auropunctata also exhibits a remarkable level of aggression. Several studies have tracked its spread and its effects on the local ant fauna following its colonization of the Galapagos Islands (Silberglied 1972; Clark et al. 1982). Lubin (1984) estimates that only four of 29 species belonging to the genera *Solenopsis*, *Hypoponera* and *Strumigenys* (the last two genera are subterranean) are able to persist in its presence.

The recent introduction of *Lasius neglectus* into central Budapest has resulted in a reduction of the local ant fauna (Van Loon et al. 1990); in a period of 15 years, 17 local species disappeared or almost disappeared.

Polygyny

Tramp species are characterized by true polygyny, i.e., nestmate queens show no signs of hostility toward one another that could be construed as dominance. For example, in *L. humile*, although there is strong variation in individual oviposition rates, there is no clear dominance hierarchy (Keller 1988). The number of resident queens is high, although it is difficult to quantify due to the absence of clear boundaries between colonies. Another reason queen number is difficult to quantify is the fact that there is often seasonal variation linked to the production of new queens. In *L. humile*, queen number varies with season from 0.1 to 1.6 queens per 100 workers (Keller et al. 1989). Because the number of workers is often enormous, the number of queens can be immeasurable. Thus Horton (1918) estimated collecting 1,307,222 queens in one year in a 10-hectare orchard (6.3 queens per 100 workers). In *M. pharaonis*, Peacock et al. (1955b) studied colonies by

FIGURE 3.1. Average number of queens per 100 workers for several tramp species. The extreme values are represented by a bar. Data are from studies referenced in the text.



trapping in buildings and found from 0.8 to 5.3 queens per 100 workers, and they found a maximum of 110 queens in a single nest. Sequential trapping over a year by Bellevoeye (1889) yielded 1,360,000 workers and 1,809 queens (or 0.13 queens per 100 workers). In *W. auropunctata*, Ulloa-Chacon (1990) found a mean of 1 to 13 queens per nest. The nests of this species range from small, containing only a few hundred workers, to very large with thousands of workers. Baker (1976) counted a few dozen queens and 10- to 20,000 workers in colonies of *A. longipes* in wet tropical forests and Haines and Haines (1978b) found up to 300 queens per nest in the Seychelles. *P. longicornis* nests contain about 2000 workers and 40 queens (Mallis 1982). The largest proportion of queens seems to be found in *C. wroughtoni*, which forms colonies containing up to 18 queens and a few dozen workers (Kinomura and Yamauchi 1987). In Figure 3.1 all these data have been converted to number of queens per 100 workers. The relationship is evidently highly variable, ranging from 0.1 to 11 but often surpasses 1.

Mating and Budding

These are undoubtedly the most important characters because, they are responsible for the unique dispersal of these species. A number of tramp ants, in which sexuals are normally winged, seem to have lost the

capacity to undergo mating flights. Mating occurs inside the nest, and colony reproduction occurs via budding, i.e., departure on foot of workers and mated queens which will establish a new nest several meters away. This form of spread is slow and thorough and favors strong linkage among the different nests, but it does not allow colonization of distant areas. Long distance dispersal occurs only by passive transport, either natural (nests of the Argentine ant are transported along the Mississippi by pieces of driftwood; Newell and Barber 1913) or artificially by human commerce.

In this regard, the behavior of the Argentine ant is well-known: winged queens have not been observed to participate in nuptial flights by a number of authors (Skaife 1955, Markin 1970a, Benoist 1973, Giraud 1982, Bartels 1983, Keller and Passera 1988) or only under exceptional conditions by others (Newell and Barber 1913; Passera and Vargo, unpublished data). By contrast, there are numerous accounts of males flying short distances, especially at dusk (Newell and Barber 1913; Skaife 1955; McCluskey 1963; Benoist 1973; Giraud 1982; Bartels 1983; Keller, Passera and Vargo, unpublished data). Mating takes place in the nest, with the young virgin queens being inseminated either by foreign or nestmate males.

M. pharaonis behaves in a very similar manner; there is no nuptial flight and mating takes place in the nest (Peacock et al. 1950, Petersen and Buschinger 1971a, Edwards 1986, Berndt and Eichler 1987). Peacock et al. (1955a) studied colony reproduction under both natural and laboratory conditions. The smallest observed colony possessed one dealate queen, 35 workers and brood of all ages. Using traps these authors obtained colonies, the smallest of which contained three dealate queens, 150 workers and brood of all ages. Finally in the laboratory, these authors did not succeed in initiating new colonies by independent colony founding, not even by pleometrosis, although they succeeded in starting a new colony by isolating a single queen, several dozen workers and brood. However, Petersen and Buschinger (1971b) succeeded in starting new colonies beginning with a young queen in isolation with brood, and even partially succeeded in initiating independent colony founding by a single queen in isolation (a few workers were produced but the colony died a short time after). It is clear that throughout the world, new colonies of *M. pharaonis* originate from budding of larger colony fragments: Peacock et al. (1955b) demonstrated this experimentally by observing that a colony divided up into several fragments when small nests were connected to the principal nest.

In *W. auropunctata*, Ulloa-Chacon and Cherix (1989) observed mating inside laboratory nests, and, based on the behavioral repertoire of this species, it seems that nuptial flights are absent (Lubin 1984).

Independent colony founding by young queens is not possible, supporting the hypothesis that budding is the main mode of colony founding (Ulloa-Chacon 1990).

The observations of Van Loon et al. (1990) regarding *L. neglectus* are similar; no nuptial flight has been seen in the city of Budapest since the appearance of this new species and it seems that mating occurs in the nest followed by budding.

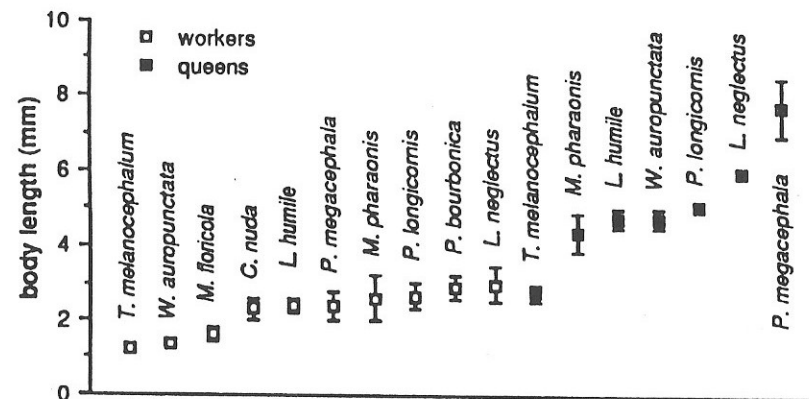
The other tramp ants are less well-studied. *M. floricola* must reproduce by budding with intranidal mating, because the queens are wingless (Smith 1965). The observations of Trager (1984) on *P. longicornis* are also worth mentioning. Males exit and assemble at nest entrances. Females then leave the nests and are undoubtedly inseminated on the ground near the nest entrance. In any case, Trager concludes that there is no nuptial flight. Given these conditions, colony reproduction can only occur via budding. In other species, the occurrence of a nuptial flight is possible, but intranidal mating has been observed, and it is not known what proportion of females fly or mate in the nest. This is the case with *C. wroughtoni*. Both winged and wingless males are found in this species, and both mate inside the nest with young winged females (Kinomura and Yamauchi 1987, Stuart 1990). Budding is undoubtedly the normal mode of colony reproduction, because attempts at haplometrosis fail (Stuart 1990). Nevertheless, it is possible in the laboratory to rear colonies successfully from groups of females (Stuart 1990). The biology of *A. longipes* is poorly understood; alates are able to fly but they were never definitely seen engaged in a nuptial flight so Haines and Haines (1978b) estimate that sexuals mate in the nest thus spread by budding. This is also the opinion of Veeresh (1990). Moreover, the number of dealate queens increases after sexuals eclose (Baker 1976).

Information is even more sketchy or non-existent for other species. It is not known whether mating flights occur in *T. melanocephalum* (Harada 1990), but it is known that new colonies are formed by budding (Smith 1965). Mating flights of *P. megacephala* have been seen in Hawaii (Wilson and Taylor 1967), but colony reproduction occurs via budding (Hölldobler and Wilson 1990). Trager (1984) observed sexuals of *P. bourbonica* flying, but the mode of colony foundation is not known.

Size and Monomorphism

Tramp ants are always very small in size; the smallest seems to be *T. melanocephalum* (worker length < 1.5 mm), *W. auropunctata* and *M. floricola* (worker length < 2 mm). All other species are smaller than 3.5 mm (Figure 3.2). The queens of course, are larger, but only rarely exceed

FIGURE 3.2. Mean body length of workers and queens of some tramp species. The extreme values are represented by a bar. Data are from studies referenced in the text and from personal measurements.



6 mm in length in *L. neglectus* and *P. megacephala*. All species, with the notable exception of *P. megacephala*, have monomorphic workers.

Lifespan of Queens

In general, queens of polygynous species are shorter lived than queens of monogynous species (Keller and Passera 1990). In the case of tramp ants, their lifespan can be extremely short. The record may belong to *T. melanocephalum*, in which, according to Harada (1990), queens live only a few weeks. The lifespan of queens of *M. pharaonis* has been well-studied; it does not surpass 29 weeks according to Petersen-Braun (1975), 38 weeks according to Edwards (1987), 39 weeks according to Peacock and Baxter (1950), 49 weeks according to Kretzschmar (1973). It is therefore considerably less than 12 months, but a few individuals may live a little longer than a year (Edwards 1986).

In *L. humile* the potential lifespan of queens is greater, but 90% of them are executed by their own workers in April or May. Since they eclose in June of the previous year, the effective lifespan is less than a year (Keller and Passera 1990).

The lifespan of queens of *W. auropunctata* is similar, because it barely exceeds a year: 11 to 14 months (Ulloa-Chacon and Cherix 1989, Ulloa-Chacon 1990). Information on queen lifespan is lacking for other species.

A short queen life may seem disadvantageous, but it is compensated for by the large capacity of tramp species to produce and rear new queens. In the Pharaoh ant new queens can be produced all year long; it

is only necessary to isolate a few dozen workers with a little brood in order to rear sexuals no matter what the season (Peacock et al. 1955a; Petersen-Braun 1975; Edwards 1986, 1987). The Argentine ant is almost as plastic. Although sexuals are naturally produced in springtime and it seems advantageous to produce sexuals seasonally, small queenless colony fragments in the laboratory almost always yield sexuals no matter what season the colonies are collected (Passera et al. 1988a, Vargo and Passera 1992). Ulloa-Chacon (1990) investigated for a period of 16 months the nest contents of *W. auropunctata* in Colombia. Except for December, winged female sexuals were present throughout the year. Trager (1984) reports that *P. longicornis* is capable of rearing sexuals throughout the year in warm regions, but it is limited to the period from May to September in cooler climates. In the Seychelles sexuals of *A. longipes* occurred throughout the year (Haines and Haines 1978b). It is evident that tramp species often succeed in adjusting to seasonal cycles.

Worker Sterility

Worker sterility may be a common character among tramp ants. This has been verified for *L. humile* by several authors (Markin 1970b, Benois 1973, Bartels 1983, Giraud 1983, Keller 1985, Passera et al. 1988b). This fact is equally well-established for *M. pharaonis*; Edwards (1986) and Berndt and Eichler (1987), among others, have established that the workers are sterile. Studies of *W. auropunctata* suggest a similar situation (Clark et al. 1982, Ulloa-Chacon and Cherix 1988); the latter authors reared queenless colonies for 80 days without observing oviposition. In *P. longicornis*. Aron and Passera (unpublished data) have held workers queenless for several weeks without seeing eggs appear.

Data are lacking for other species. One can speculate that workers of *P. megacephala* are sterile, because workers of this genus are reported not to lay eggs (Choe 1988). It will be interesting to study the situation in *L. neglectus*, because it belongs to a genus in which worker egg-laying is common (Choe 1988).

Discussion

Of the nine characteristics reviewed, the most exclusive may be the strong relationship tying tramp species to humans, whether it be for nest sites or long distance transport. A number of other ant species also exhibit an anthropophilic tendency (Bernard 1958, 1974; Smith 1965; Kondoh 1976; Pisarski 1982; Prins et al. 1990; Thompson 1990), but only

tramp species are truly domestic since they follow humans in their movements. This anthropophilic tendency is accompanied by frequent nest changes. Nesting in the human environment implies utilization of very unstable habitats subject to frequent changes due to human activity, requiring tramp species to migrate often. Migration is by no means a unique attribute of tramp species. Nomadism is well-known in army ants in which it is linked to foraging for prey (Gotwald 1982). Changing of nests can also be provoked by intra- or interspecific competition, as in several species of *Pogonomyrmex* (Hölldobler 1976). Finally it may be linked, as in tramp species, to environmental instability. This is the case in *Leptothorax rugulatus* (Möglich 1978).

Small size and monomorphism (with the exception of *P. megacephala*) are characteristics that tramp species share with many other species. This goes for worker sterility, because it is known that the worker caste is sterile in entire genera, e.g., *Tetramorium*, *Pheidole* and *Solenopsis* (Fletcher and Ross 1985).

Three other characteristics that seem well-established for tramp species (unicolonality, polygyny and colony reproduction by budding) are found to different degrees in other species and, in particular, in polydomous ants, which can form supercolonies containing many nests often occupying large areas.

Unicolonality and its attendant properties, the absence of aggression and of clear nest boundaries, allow workers to be exchanged. This has been found in several species that form polycalic colonies, such as *Tapinoma sessile* (Smith 1928), or supercolonies, such as *Formica yessensis* (Ito and Imamura 1974), *F. lugubris* (Cherix 1980), *F. truncorum* (Rosengren et al. 1985), *Lasius sakagamii* (Yamauchi et al. 1981) and *Pseudomyrmex venefica* (Janzen 1973). The absence of aggression in these polycalic species is limited to members of the supercolony, whereas in tramp species (at least in *L. humile*) the tolerance seems to extend beyond the limits of a single habitat.

The degree of polygyny is often very great in tramp species, but it is not necessarily larger than in polydomous species; there may be more than 200 dealate queens in a single nest of *F. yessensis* (Ito 1973), 1,080,000 for the entire supercolony (Higashi et Yamauchi 1979), and up to 3000 to 5000 dealate queens per nest in *Formica polycytena* (Gösswald 1951, Lange 1956). On the contrary, it should be noted that there can be species that are both polydomous and monogynous, e.g., *Oecophylla longinoda* (Hölldobler 1979) and *Paratrechina flavipes* (Ichinose 1986), although tramp species are always polygynous.

Queen longevity seems to be characteristically short in tramp species. This particularity may be without equal in polydomous ants, but it needs to be confirmed by studying more species. It is the same for the

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readiness with which new queens are reared in tramp species. In polydomous species, like most ants, production of sexuals is seasonal and occurs in strict accordance with climatic and social factors (Brian 1980).

Colony founding by budding is a general tendency of polydomous species, e.g., *T. sessile* (Smith 1928, Kanno 1959), *F. yessensis* (Ito 1973; Higashi 1976, 1983), *F. polycytena* (Mabelis 1979), *F. lugubris* (Cherix 1981), *L. sakagamii* (Yamauchi et al. 1981) and *Polyrhachis dives* (Yamauchi et al. 1987). Initiation of new colonies by budding is facilitated by the existence of intranidal mating, which can occur together with nuptial flight, as in *T. sessile* (Smith 1928, Kanno 1959), *F. yessensis* (Ito 1973, Higashi 1983) and *F. lugubris* (Fortelius et al. 1990) or without nuptial flight, as in *L. sakagamii* (Yamauchi et al. 1981).

Thus tramp species are very similar to polydomous ants with which they share in common certain attributes (unicolonality, colony reproduction by budding, and, significantly, reduced nuptial flight), although these attributes are more strongly expressed in tramp species. To these characteristics of polydomous species, tramp species add their privileged relationship with the human environment assuring their ecological success.

In conclusion, the following definition of tramp ants is proposed: tramp ants are ant species with small, sterile workers, widely distributed throughout the world by human commerce, living in close association with humans. Tramp ants are polygynous, unicolonial and exhibit a reduction or the absence of nuptial flight leading to colony reproduction by budding.

Acknowledgments

This study was supported by a grant from the CNRS (URA 664) and the "European Network of Research Laboratories grant N° 418 210 57". I am very grateful to E. L. Vargo and J. P. Lachaud for reviewing the manuscript and respectively for assistance with the English version and the Spanish summary.

Resumen

En este trabajo, tratamos de esclarecer las características comunes de las "hormigas vagabundas". Para llegar a este objetivo, utilizamos lo que se conoce de las tres especies vagabundas las más estudiadas (*Linepithema humile* [= *Iridomyrmex humilis*], *Monomorium pharaonis* y *Wasmannia auropunctata*) en conjunto con los datos relacionados a otras especies vagabundas menos conocidas de los géneros *Cardiocondyla*, *Paratrechina*, *Pheidole* y *Anoplolepis*. Así, nueve caracteres son revisados.

Aparte de las fuertes relaciones trabadas con el Hombre para su diseminación, los demás caracteres se encuentran compartidos con otras hormigas. Sin embargo, es con las especies polidomas que las semejanzas parecen las más fuertes: unicolonialidad, poliginia, fundación de las colonias por estacas y tendencia al apareamiento dentro del nido se encuentran en los dos grupos no obstante es en las especies vagabundas que estas estrategias están mejor realizadas. A fin de cuentas, las especies vagabundas se pueden definir como especies de pequeño tamaño con obreras estériles, ampliamente distribuidas en el mundo por intermedio del comercio humano, y viviendo en asociación estrecha con el Hombre; estas especies son poliginias, unicoloniales y presentan una ausencia o una reducción del vuelo nupcial lo que conduce a una reproducción de las colonias por estacas.

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