onto the snow in vast numbers as snow fleas. Extreme cold tolerance always involves supercooling with the accumulation of cryoprotective substances.

Oxygen requirements of Collembola also vary enormously. The greatest tolerances discovered are in the Antarctic *Cryptopygus antarcticus,* which has a 30% survival rate after 30 days in pure nitrogen atmosphere. In many Collembola, respiration when submerged is via air films surrounding the animals as a result of their hydrophobic cuticle, but this apparently not necessary in all forms. In many forms the eggs are more resistant to immersion than in other stages.

Collembola, even in uniform soils, are never randomly distributed, but show strong clumping because of pheromones or local food abundance or simply as a result of limited dispersion after founding events and subsequent population growth.

Competition between Collembola species in cultures has in at least a few instances shown that there is no evidence for competitive exclusion, even under long-term clearly competitive conditions. In addition it has been shown that interactions between two species can be either positive or negative depending upon the nature of the interaction (airborne allomones, substrate-transmitted allomones, or direct contact.

While most soil- and litter-inhabiting Collembola feed primarily on decaying vegetation and fungi (and appear to be general feeders), experimental studies have shown that, given a choice, they may be very selective as to both the decay state and nature of the vegetation and the species of fungi. A number of Collembola are occasionally or primarily (and in a few species exclusively) carnivores, different species feeding on a variety of organisms, ranging from rotifers to other Collembola. Probably the most commonly eaten prey is nematodes. Vegetation-inhabiting Collembola eat primarily unicellular algae, pollen, and soft parts of vegetation and fungal spores. Many Collembola are coprophagic, feeding largely on arthropod feces. Some littoral species appear to feed largely on diatoms or unicellular algae, and forms with piercing–sucking mouthparts feed largely on fungal hyphae juices. Thus their primary role in the environment is that of reducer; however, another major role is that of prey. The ability to jump is the major defense mechanism of Collembola; however, many Poduromorpha, particularly those with the furcula short or absent, have body fluids that are repellent to predators, and they may release these by reflex bleeding when attacked. Most carnivorous soil organisms feed on Collembola, and many beetles, ants, and wasps are specialized for feeding on them.

HUMAN INTERACTIONS

Collembola rarely interact overtly with humans. There are few agricultural pests and, except for the introduced Lucerne flea *(Sminthurus viridis)* in Australia, which is a pest in pastures and horticultural crops, these are of little economic importance. There are no parasitic Collembola and they are not known to transmit any diseases. Mass emergences occur and may cause a temporary problem with household infestation but they are generally short lived there. The true household Collembola are unobtrusive and generally overlooked. Collembola play an important role in the development and maintenance of healthy soils, but this is not generally understood. Here they are usually abundant and may reach densities up to a trillion per square meter.

See Also the Following Articles

Amber • Arthropoda • Diplura • Protura

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Colonies

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Some species of insects spend much or all of their life living in organized social groups called colonies. Insect colonies have long fascinated biologists because they resemble superorganisms. Although insect societies are composed of distinct individuals, they possess group organization and coherence. Colonies exhibit emergent developmental properties, which are characteristics that cannot be explained or predicted by examining the behavior of their component parts. Insect colonies can serve as useful models of biological processes that occur in other complex living systems. One powerful analogy has been to compare the initiation, growth, and reproduction of an insect colony to the process of development of multicellular organisms.

Like individual plants and animals, insect colonies are initiated by propagules that are produced by parents (mother colonies); they then grow, reproduce, and often decline in old age. However, a wide array of developmental patterns have evolved in insect societies. Some of this variation can be explained by abiotic factors, such as the climate that prevails in the geographic range of a given species. Seasonality of temperature, daylength, and rainfall appear to have far-reaching effects on colony development. Climatic variables are not the whole story, however, since a diversity of colony cycles can be found among closely related species that live in the same area. Pressure from natural enemies, such as predators and parasites, as well as pressure from social competitors, has shaped the evolution of colony development.

MODES OF FOUNDATION: INDEPENDENT, SWARMING, AND BUDDING

Parent Colony Investment Decisions

SIZE VERSUS NUMBER OF PROPAGULES Insect colonies vary widely in the amount of investment they make in each of their offspring colonies. At the low end are independently founded colonies, wherein single inseminated females (such as eusocial thrips and aphids and some Hymenoptera) initiate new colonies alone. In these species, the colony passes through a solitary phase. Examples of independent founders include sweat bees (Halictidae), bumble bees *(Bombus),* several genera of paper wasps [most Vespinae (hornets and yellowjackets), *Parapolybia,* some *Ropalidia, Mischocyttarus,* and *Polistes*], and many ants (Formicidae). In some species, the lone foundress may be later joined by one or more conspecific cofoundresses. In other species, cofoundresses are not tolerated. In many termites, the smallest possible social group founds the new colony: a single reproductive male–female pair. At the other extreme, the relatively large colonies of some species issue discrete colony-founding swarms. Swarms are made up of reproductives and workers that migrate to a new nest site as a coordinated unit. Swarms often include a sizeable portion of the worker force, and they represent a large investment. Swarm-founding lineages include honey bees *(Apis),* swarm-founding wasps (tribe Epiponini), and army ants *(Eciton).*

There is an inherent trade-off between the size of the offspring colony propagule and the number of propagules that a given parent colony can produce. Large propagules are logically restricted to species with large colony sizes, but not all large-colony species reproduce by swarming or budding. *Vespula* paper wasps, higher termites (Termitidae), and leafcutter ants *(Atta)* achieve mature colony sizes of thousands or millions of adults, yet reproduce by issuing solitary dispersing reproductives. Production of new colonies by swarms has evolved independently in bees (honey and stingless bees), paper wasps (Neotropical *Epiponini,* some *Ropalidia, Provespa,* and *Polybioides*), and ants (*Eciton* army ants). Some species of ants produce new colonies by budding, wherein portions of the colony that occupy discrete nests gradually reduce interchange of members and eventually become independent.

SURVIVAL OF PROPAGULES: PREDATORS AND ENVIRONMENTAL EFFECTS One important set of selective pressures that may explain variation in propagule size is negative biotic interactions. These can take the form of predation, attack by other natural enemies such as parasites, and conflict with conspecific competitors. Larger incipient colonies result from swarming and budding. These larger groups possess a defensive worker force and are more likely to resist destruction or consumption by enemies.

Abiotic challenges may also select for larger numbers of participants during incipient colony formation. Larger social groups may be better able to resist desiccation and temperature fluctuations, especially when they nest in enclosed spaces. Interesting in this regard are ant colonies that exhibit seasonal polydomy. Polydomy occurs when a single colony occupies several distinct nest cavities or structures. *Leptothorax* ants nest in small cavities in the leaf litter, such as hollow twigs. The colonies of some *Leptothorax* species divide themselves among several nests in summer when milder weather prevails, later coalescing into a single nest cavity as winter approaches.

Independent Foundation and Options for Social Cooperation

TO JOIN OR NOT TO JOIN In some species of independent-founding eusocial Hymenoptera, reproductives have the option of joining an already-initiated nest as a cofoundress, rather than starting one of their own. The degree of division of reproductive rights among the cofoundresses can be analyzed as a type of social contract. Often, the cooperating females are closely related. Differences in social status and reproductive capacity may be influenced by the degree of genetic relatedness among the cofoundresses. Dominant females can attempt to monopolize reproduction, or they can share a portion of reproduction as an incentive to stay and help on the part of subordinates. Kin selection theory predicts that the incipient society should be more equitable if the social partners are less closely related, since a greater incentive to help is required of nonrelatives. Cooperative colony founding may also represent a form of bet hedging and may be favored irrespective of genetic relatedness. If lone nest founders have little chance of succeeding, then cooperating can be favored by all individuals, even in the face of complete reproductive division of labor. In some cases, such as bull-horn *Acacia*-inhabiting *Pseudomyrmex* ants, female reproductives of different species may occupy a young plant, even though only one colony will eventually emerge to monopolize the tree.

USURPATION AND SOCIAL PRASITISM Another option for reproductives of some species is to steal or usurp a young colony from a conspecific or from another species. Social parasitism occurs when an invading reproductive uses the workers of a nest she did not construct to rear her reproductive offspring. A range of degrees of integration of social parasites into their host colonies can be observed in a diversity of insect lineages. Good examples occur in yellowjacket wasps (Vespinae), European *Polistes* paper wasps, bumble bees and their *Psythris* parasites, and ants. In the simplest cases, queens attack conspecific colonies and kill the resident reproductive, taking over the worker force. Simple heterospecific parasitism is similar to conspecific takeovers, in that the invading queen kills the resident queen. Often, females of socially parasitic species exhibit adaptations to improve their chances of winning queen vs queen combat, such as enlarged heads and mandibles. Parasitic species are often incapable of producing workers of their own, so the colony switches to producing new parasite reproductives after a takeover. In some species of ants, the socially parasitic queens are better integrated into the host society (e.g., *Teleutomyrmex* invading *Tetramorium* colonies). The parasitic queens coexist with the host queen and allow her to continue to produce a worker force, while the parasites produce reproductive offspring.

Social Groups as Founding Units

DIVISION OF LABOR When new colonies are founded by swarms or by buds, a worker force is always present. One potential advantage to this strategy is the increased efficiency of the colony resulting from division of tasks among the group members. An important form of division of labor, which swarm-founders generally exploit, is the removal of the reproductives from the need to perform such risky and expensive tasks as food collection and nest defense. Division of labor is often weaker in independently founded colonies and is absent by definition for solitary foundresses.

DEFENCE A group of workers can protect incipient colonies from natural enemies. New nests that are left unattended when solitary foundresses leave to forage are often attacked by parasites and predators. Survival of colony propagules increases dramatically with group size, particularly in areas where negative biotic pressures are most intense. Several studies of independent-founding paper wasps (*Polistes* and *Mischocyttarus* spp.) have shown that young colonies with cofoundresses fare dramatically better than singly founded nests.

THE NEED FOR COMMUNICAITON A special challenge facing swarm-founding species, and perhaps to a lesser extent budding species, is the need to coordinate movement from the parent nest to the offspring nest site. Special communicative mechanisms are used, such as the dance language in honey bees (*Apis* spp.), and trail pheromones in stingless bees and epiponine wasps. The need to evolve communicative mechanisms may constrain the evolution of swarming as a mode of colony foundation.

COLONY GROWTH

Social insects provide interesting and accessible models for testing life history theory because workers are roughly equivalent to the soma or body of a metazoan organism, while the reproductives can be treated as the germ or reproductive line. This analogy becomes weaker when the workers have some opportunity for direct reproduction. Nonetheless, insect colonies often develop in ways that suggest a trade-off between growth (i.e., worker production) and reproduction [i.e., production of gynes (new queens) and males].

One important decision that colonies make is the size at which to reproduce. This varies widely among even closely related species. For example, average size for mature colonies varies over at least five orders of magnitude among eusocial paper wasps (Vespidae).

Another important concern is the timing of reproduction. In some species, colonies exhibit a big-bang pattern of reproduction. The worker population of the nest increases as the growing season progresses, often exponentially. At some critical point in development the colony ceases to produce workers, switching entirely to the production of gynes and/or males. Colony decline or senescence follows reproduction. Temperate bumble bees and yellowjackets often approximate a big-bang approach to reproduction, and their life cycles resemble those of annual plants. Other species produce workers and reproductives simultaneously. In the extreme case, some males and gynes may emerge among the earliest offspring from the nest. For example, some Neotropical paper wasps (*Mischocyttarus* spp.) exhibit a great deal of overlap of worker and reproductive production. Swarm-founding species frequently undergo several bouts of reproduction, issuing reproductive swarms sequentially over a long period without undergoing parent colony decline.

For eusocial Hymenoptera, production of male offspring is potentially costly to the colony, and selection for labor efficiency may act to delay male production. Male Hymenoptera rarely work for their colonies and are often thought to represent a drain on colony resources. This cost does not accrue to termites, both sexes of which participate fully as workers.

REPRODUCTION

Timing and Synchrony

In seasonal habitats, the proper conditions for nest foundation can be constrained to a narrow window of time. This can select for a high degree of synchrony among colonies in a population in the timing of release of reproductives. In some species, reproductive offspring that depart from their natal nest must mate and either overwinter or initiate a new nest or perish. This pattern is apparently common to many ants and termites. In other species, reproductive females (honey bees, some bumble bees) and males (other bumble bees, some tropical *Mischocyttarus* wasps) can leave to find mates, but then return to the natal nest.

Sex Ratios and Sex Allocation

Beyond the germ line vs soma distinction, investment in the different sexes is an important consideration facing many insect societies. This is especially important for eusocial Hymenoptera, the males of which perform little or no labor for their colonies to offset their production and maintenance. Sex allocation theory, which attempts to predict the optimal investment an organism should make in the proportion of male compared to female offspring, has been applied to ant colonies. There is some evidence to suggest that, as predicted, colonies alter their relative amount of investment in males and gynes, depending on such environmental conditions as food availability.

COLONY SENESCENCE

Seasonal Effects versus Programmed Senescence

Colonies of many temperate eusocial insects are annual and appear to exhibit a programmed decline and senescence. Colony decline appears to be related to queen longevity and queen condition. For example, late-season colony breakdown appears to follow a decline in the queen's ability to suppress worker reproduction or the queen's death, in temperate bumble bees, *Polistes* paper wasps, and yellowjackets. The queen is not the whole story, however. Queens lost early in the season can be replaced or supplanted by reproducing workers without colony decline. The larger worker forces that are present late in colony development may be harder for the queens or their replacements to suppress. However, closely related species in less seasonal habitats do not exhibit time- or stage-determined colony decline. The plasticity of colony development exhibited in subtropical and tropical habitats by temperate invaders, such as German yellowjackets *(Vespula germanica),* may provide valuable insights into the factors that cause colony decline. German yellowjacket colonies in invaded sites (e.g., Hawaii and New Zealand) can be polygynous, accepting new queens into established nests, and are often perennial. These colonies can grow to much larger sizes than occur in temperate habitats, and the invading populations have become serious pests.

Can Colonies be Immortal?

When abiotic forces do not terminate colonies, their longevity can be determined by the longevity of the reproductives. Queens and nests of *Atta* leafcutter ants may survive a decade or more in the wild. If colonies can replace dying queens, there is no inherent limit on colony longevity. The polygyne (multiple queen) of the imported fire ants *Solenopsis invicta* in the United States is an example of a species that accepts new, young queens into active nests. In thes case, colonies may not senesce, and the observed upper limit on colony longevity will be set by the background rate of colony mortality. In other words, the chance of colony termination may be independent of colony age. Particularly interesting in this regard are some unicolonial invasive ant species, such as the Argentine ant, *Linepithema humile.* In habitats outside their native South American range, such as the western United States, these ants fail to show internest aggression. Colony boundaries are fluid, and workers, brood, and reproductives are freely exchanged among nests. The entire population, which at present extends over a range greater than 1000 km in length, functions as a single colony. Colony longevity therefore equals the time to population extinction, and these may prove to be the longest lived insect colonies.

See Also the Following Articles

Ants • Apis Species • Division of Labor • Recruitment Communication • Sociality

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Colorado Potato Beetle

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The Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), is the most devastating, defoliating, insect pest of potato *(Solanum tuberosum).* Uncontrolled, it is capable of causing complete crop failure. The potato beetle is important because of the damage it causes to potato and some related crops, as well as its extraordinary ability to evolve resistance to insecticides used in its control.

GEOGRAPHICAL SPREAD AND HOST RANGE

The Colorado potato beetle is native to Mexico. It was first recorded in the United States in 1811, feeding on a native plant, buffalo bur *(Solanum rostratum)* near the Iowa/Nebraska border. It was first reported as a pest on potato in Nebraska in 1859. The expansion of its host range to include potato allowed the beetle to spread rapidly eastward, moving among farm and garden plantings of potato. By 1874, it had expanded its geographic range to the East Coast of the United States. The potato beetle now occurs in North America throughout Mexico, the United States, and Canada, except