POLYGYNOUS ANTS:
ECOLOGICAL REPERCUSSIONS OF A MULTI-QUEEN COLONY
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Abstract

Many recent studies of polygynous ants have focused on producing an ecological and reproductive cost-benefit analysis of polygynous systems in order to shed light on how or why it developed over the more common practice of monogyny. Polygyny, the practice of keeping multiple reproductive queens in one colony, has evolved in many ant species, some of which display both polygynous and monogynous strategies. These species are of special interest as they provide important insights into the evolution of this social structure and the ecological pressures that may have caused its development. The following work will outline how polygyny may benefit ants with differing life history and habits, the reproductive risks and benefits, and how morphology and ecological pressures have influenced the social structure of ants. (Hymenoptera: Formicidae)

Plant- Ants and Polygyny

Many ants have survived the various challenges of their environment by exploiting ecological niches and tying their survival strategy to another nearby species. The ant *Petalomyrmex phylax* displays an exclusive symbiotic relationship with the myrmecochorous plant, *Leonardoxa africana* ssp. *africana* (Dalecky et al., 2005). This symbiosis limits the ant’s dispersal to a narrow range where the plant can grow in the rainforest of Cameroon. This 250 x 80 km area contains a continuum of colonies ranging
from highly polygynous in the northern end to exclusively monogynous in the southern end. Each tree can be host to a single long-term colony, though several founding colonist queens may temporarily reside on the same tree until they are eliminated by competitors. After mating, queens are faced with the option to seek acceptance in natal nests which may result in rejection, lowered reproductive rates, and shorter lifespan. However, the initiation into a polygynous colony comes with the benefits of nest inheritance for offspring gynes, and the queen’s ability to avoid the incredibly difficult and vulnerable life stages that are associated with independently founding a new monogynous colony. Dalecky et al. (2005) assumed that the variability in colony social structure could best be explained by examining differences in tree quality and density, available nest sites, and nest turnover in each geographic area. To their surprise, they could find no ecological differences that would explain the variation among populations, which suggested that the key to development of polygyny in this species can be found in their colonization strategy. Polygyny results in an evolutionary trade-off between dispersal and colony longevity. By this logic, it would follow that ants in newer, less stable colonies would concentrate energy on dispersal methods as they slowly spread into the southern areas of the rainforest. Meanwhile, in the northern region, already established colonies had the ability to focus less on dispersal habits, and more on colony longevity. Such is the case with many invasive and plant-ant species.

The Mesoamerican acacia-ant is another prime example of how polygyny has evolved to help colonies protect food-rich bonanza resources for several generations (Kautz et al., 2009). *Pseudomyrmex* is a genus of ant that is now known to have one polygynous species *Pseudomyrmex peperi* living in the same geographic vicinity as their monogynous ancestors. When compared with other *Pseudomyrmex* species, *peperi* is a relatively poor colony founder as evidenced by its inability to dominate new ant-free hosts for longer than six months. Despite the significantly lower dispersal rates, *peperi* ants can maintain ownership of an established colony for over five years and typically aggregate into large, polydomous supercolonies (polydomous ants maintain several residences and allow for free flow between nests). Though each queen typically produces fewer offspring than their monogynous counterparts, the colony is highly invested in brood rearing, with 84% of the colony consisting of brood. In neighboring monogynous colonies, brood comprises only 60% of the colony, limiting the overall growth rate for these species. Supercolonies of the *peperi* species are thought to have developed from a single queen and successive
adoption of new queens within the family line, thus creating a large group of closely related kin that can extend the colony territory by budding.

**Invasive Ant Species**

Monogynous colonies tend toward independent colony foundation by a single vulnerable queen, while polygynous ants have adapted to colony stress by splitting colonies often enough to deal with catastrophic damage and an ever-growing population. Frequent movement is more common with polygynous ants, which can benefit invasive species like the polydomous Pharaoh ant, *Monomorium pharaonis* (Buczkowski & Bennett, 2009). This species solely inhabits urban areas and uses polygyny as a response to frequent environmental stress and nest disturbance. Because they exhibit a low worker to queen ratio of 12.86, the species can reproduce without mating flights and by way of budding. These ants display a high amount of control over caste partitioning in bud nests and tend to bud based on the intensity of nest disturbance, the amount of available nest sites, and a preferred minimum colony size. This high-risk strategy can have considerable payoffs in an urban setting.

The Pharaoh ant is just one example of many that shows how an effective dispersal and threat management system can give polygynous species a competitive edge in various environments. This is an important consideration when dealing with biological control agents and pest colonies within buildings. The odorous ant *Tapinoma sessile* is seasonally polydomous (Buczkowski & Bennett, 2008), highly polygynous, and capable of creating large supercolonies in urban environments. In natural environments, this species tends to form small, monodomous, single-queen colonies that are not particularly dominant over neighboring species (Buczkowski, 2010). This pattern of polydomy, polygyny, and frequent colony budding is common in invasive Argentine ants as well (Silverman & Brightwell, 2008). *Linepithema humile* is also a highly competitive and aggressive ant once introduced into urban areas. Because supercolonies often contain 16.3 queens for every 1000 workers and can stretch over large areas, treatment with insecticides and biological control agents can be problematic and ineffective. Invasive species often bud off into new colonies at the first sign of danger, isolating the newly relocated ants from mechanical disturbances and toxic baiting systems.
While this strategy may give invasive ant species the advantage over many insecticide control measures, it can be a hindrance for some species. The red imported fire ant (RIFA), known as *Solenopsis invicta*, was first introduced into the United States in the early 1900’s and was established for years before the first polygynous colonies were reported in the 1970’s (Lofgren & Williams, 1984). In 1973, researchers became interested in a microsporidian pathogen, *Thelohania solenopsae*, for its potential as a biological control agent (Oi, 2006). Because of the high nest densities, infection can be maintained for long periods of time before colony death. This allows for continued transmission of the pathogen to neighboring colonies. A study of pathogen infection rates in Florida pastures in 2004 showed that 83% of polygynous colonies were infected compared with 0% of monogynous colonies. While monogynous colonies can transmit the pathogen through colony raids or nuptial flights, infected colonies only survive for five months and infection rates among other monogynous colonies are not high. Because polygynous colonies habitually accept multiple queens into the nest, queen death is staggered and multiple generations can survive, keeping the colony alive and active for an average of eleven months, or in some cases, more than two years. This trend makes biological control of the predominantly monogynous fire ants in North America impractical. This is one case that further emphasizes how polygyny can significantly extend the lifespan of a colony under stressful conditions.

**Risks and Reproductive Consequences of Polygyny**

Many species of wood ants and slave-making ants have been known to kill queens of a foreign ant nest and take over the colony as the new queen (Czechowski & Radchenko, 2006). By masquerading as the original queen, heterospecific gynes can engage in a form of social parasitism and take advantage of local colony resources. This strategy may provide one alternative to independent colony foundation, but many queens instead chose to seek acceptance into foreign colonies by non-hostile means. Studies of colony aggression have shown that for *Formica truncorum*, *Formica exsecta*, and *Formica paralugubris*, virgin queens have a higher chance of acceptance in foreign and natal nests whereas for *Formica polyctena*, all older queens were accepted regardless of mating status or nest of origin (Holzer et al., 2008). Still, not all ant species are quick to accept social parasites into their society. *Pachycondyla*
luteipes colonies reject 70% of foreign queens while Leptothorax curvispinosus colonies reject all foreign queens.

In addition to initial danger, polygynous queens are faced with reproductive drawbacks and shorter lifespans. Holzer et al. (2008) reported that foreign queens accepted into Formica exsecta colonies contributed fewer offspring to the colony while queens in their natal nest produced 1.5 times the number of viable offspring in 80% of tested colonies. One theory that may explain the differences in offspring outputs is Hamilton’s theory of kin selection, where ant workers provide increased care for the brood of their maternal queen. Another idea that has yet to be confirmed is that variations in fecundity may be due to stress from settlement or inexplicit differences in treatment by resident workers. While the study could not produce evidence of nepotism among workers, it could not rule out the possibility that workers provided fewer resources to newly introduced queens, or that introduction itself did not directly affect queens in terms of fecundity.

Reproductive benefits of polygyny may also be limited by reproductive specialization (Kummerli & Keller, 2007). In colonies of Formica exsecta, 25% of queens in female-producing colonies specialized in reproduction of males compared with 79% of queens in male-producing colonies. Many species of ants show some amount of reproductive skew among ant classes including Solenopsis invicta, Formica sanguinea, Pheidole pallidula, Leptothorax acervorum, Linepithema humile, Leptothorax regulates, and Pachycondyla inversa. With S. invicta, a positive correlation was established between queen specialization and queen number, suggesting that some queens in polygynous colonies have a better chance of passing down their genetic material. Queens that produce more haploid males (containing 1 set of chromosomes passed down by the mother through an unfertilized egg) and diploid gynes (containing one set of chromosomes from each parent) are more likely to pass down their genetic lines than queens that specialize in non-reproductive female workers. Studies on the neotropical ant species Pachycondyla inversa show that polygynous colonies have dominant queens, that are mostly responsible for caring for the brood, as well as subordinate queens that forage outside the nest (Kellner et al., 2007). Differences in reproductive rate between subordinate and dominate queens decrease as colony size increases, but are still generally present. Because queens are usually unrelated and frequently mate with more than one male, these polygynous colonies can reap the benefits of genetic variation. This low level of relation
between nestmate workers raises the question of how polygynous colony members can recognize closely related foreign species from weakly related nestmates.

**Genetic Diversity**

Monogynous colonies with queens that mate only once or twice have a highly homogeneous genetic portrait and inbreeding is a risky reproductive habit for members of the order Hymenoptera (Breed, 2003). Polygynous colonies are prone to a higher amount of genetic variation because multiple queens increase variation along a number of different patrilines. To understand how nestmates can distinguish one another in the face of such variation, De Souza et al. (2006) studied two subspecies of leaf cutter ants, *Acromyrmex subterraneus molestans* and *Ac. Subterraneus subterraneus*, in both polygynous and monogynous colonies.

Hydrocarbons and chemical scents play an enormous role in kin recognition, and ants must standardize their cuticular hydrocarbons against those of their queen and nestmates to be considered part of the colony (de Souza et al., 2006). Physical separation results in incompatible scents in the species *Camponotus fellah*. There are two leading theories on how ants standardize their hydrocarbons to create a cohesive chemical cue throughout the nest. Based on studies with *Camponotus floridanus*, the queen was thought to be the source of chemical cues in the nest. However, later work based on biochemical information taken from *Cataglyphis niger* suggested that the queen was the center of chemical cues and that her interaction with workers causes her to usurp an average of the many different hydrocarbons in her environment. Despite the method of standardizing chemical scent, the important question was whether polygynous colonies could recognize foreign intruders within the nest. Ants could not discriminate between nestmates and non-nestmates of the same subspecies, but could discriminate outside of their subspecies, regardless of polygynous or monogynous status of the colony. Similar studies found that polygynous members of *Messor barbarous* and *Pseudomyrmex pallidus* were less aggressive than their monogynous counterparts when confronted by non-nestmates. These studies indicate that polygynous colonies have a decreased ability to distinguish nestmates from foreign workers, which may be a mechanism by which they can accept additional foreign queens. In some ants, such as the wood ant
species *Formica aquilonia*, *Formica polyctena*, and *Formica rufa*, distinguishable differences may be so diminished that telling species apart becomes a daunting challenge (Czechowski & Radchenko, 2006). Studies on these wood ants have shown that permanently mixed colonies of the three species exist. The colony under observation maintained a steady mixture of 75% *F. polyctena*, 22.5% *F. aquilonia*, and 2.5% *F. rufa* for a period of several years. The study did not determine whether the three species are able to distinguish each other using cuticular hydrocarbons or whether each species is simply more tolerant of the other species around them. Still, the mixed colony illustrates the broad range of aggression found within polygynous colonies towards foreign ant workers and queens.

**Morphology**

Ant dispersal strategies and colony founding patterns may provide another clue as to how polygyny has developed and become a successful survival strategy. Colonies of *Solenopsis invicta* typically produce three queen morphs that, initially may be indistinguishable, but develop into adult queens of significantly different sizes (Ross & Keller, 1995). Colonies were categorized either as monogynous M-types or polygynous P-types. Despite which colony young brood developed in, queens developing in M colonies became 48% heavier than queens developing in P colonies. In addition to M queens with high fat reserves and P queens with low fat reserves (no expression of the Pgm-3 gene), an intermediate type of queen existed, with 26% higher weight than P queens and homozygous expression of the Pgm-3a/a gene.

Because M-type queens had a higher percentage of body fat, chances of survival during independent colony foundation were understandably higher than those for the two other types. Alternatively, M-type queens and intermediate morphs were almost always destroyed when trying to lay eggs in a P-type colony. This evidence suggests colony structure is inherited by young queens and rigid social structures may be relatively hard to change without environmental pressure. In addition, colonies are generally more likely to develop a polygynous structure after many years of monogynous history. P-type colonies often outlive M-type colonies and can even replace them in the event of disease, catastrophe, or a changing environment.
Still, it is reasonable to wonder how intermediate queen morphs can hope to compete against their more extreme counterparts. Again, the answer lies within colony foundation strategies. Queens may found colonies independently without the help of workers (haplometrosis), found colonies with the help of another mated queen in the absence of workers (pleometrosis), or found colonies dependently with the help of several workers (Howard, 2006). Founding may also be claustral, where queens seal the nest to raise the first generation of workers using extensive fat-reserves, or semi-claustral, where queens forage for food in order to raise their brood. Polygynous colonies of *Temnothorax longispinosus* typically contain a larger proportion of small, low-fat, queens that are produced in lower numbers than monogynous colonies. Both large and small queen morphs can be found in either colony type, but the ratios of small to large morphs are not surprising (910 to 526 for polygynous colonies and 229 to 212 for monogynous). Monogynous colonies typically produce higher numbers of large queens, presumably because the mortality rate that accompanies dispersal and independent colony foundation is so high. These queen morphs can either have long wings and high fat content, making them most suitable for haplometrosis, or they can have slightly lower fat content, long wings, and large wing muscles that make them capable of independent or dependant colony foundation. The three distinct morphs explain why a colony typically maintains its monogynous or polygynous structure over long periods of time. However, should the need arise, existence of the third, low-fat, large-bodied morph gives colonies flexibility to change survival strategies.

While transitioning from monogyny to polygyny is the more common evolutionary pathway, there are some ant species that remain the exception to the rule. Several monogynous colonies have developed from polygynous ancestors in the genus *Cardiocondyla* and possibly even in *Cataglyphis* (Schrempf & Heinze, 2007). In semi-claustral monogynous colonies of *Cardiocondyla*, queens have developed only a slightly larger body form than their polygynous ancestors and have replaced most of their wing muscles with fat. They still maintain many telltale traits of a polygynous colony such as intranidal mating, dispersal on foot, and a high rate of production of female sexuals.
Conclusion

Polygyny has been thought to develop as an adaptation to nest site saturation, environmental disturbance, the presence of food-rich resources, overpopulation, cold climates, and habitat patchiness (Howard, 2006). In some cases, certain species have been known to develop into single-queen colonies after a long history of polygyny. This is a relatively rare phenomenon and generally polygyny has developed in many invasive species and even in small populations of plant-ants that were previously monogynous. Polygynous colonies gained the competitive edge in urban environments by creating long-lived, fast-growing colonies that spread quickly and can adapt easily to stress. Though polygyny does have some disadvantages in terms of dispersal and reproduction, the benefits are generally worth the risks. The existence of different queen morphs suggests that colony structure is fairly stable and often inherited. Still, intermediate morphs allow for plasticity of the colony structure in cases of environmental stress. Despite the fact that polygyny has not developed in most species of the order Hymenoptera, it has proven to be an advantageous strategy for many ant species attempting to exploit ecological niches.
References


