= Worker policing =

Worker policing is a behavior seen in colonies of social hymenopterans (ants , bees , and wasps) whereby worker females eat or remove eggs that have been laid by other workers rather than those laid by a queen . Worker policing ensures that the offspring of the queen will predominate in the group . In certain species of bees , ants and wasps , workers or the queen may also act aggressively towards fertile workers . Worker policing has been suggested as a form of coercion to promote the evolution of altruistic behavior in eusocial insect societies .

Proposed mechanisms for the recognition of worker @-@ laid eggs or active reproductive workers include marker hydrocarbons on the surface of queen @-@ laid eggs , cuticle hydrocarbons on reproductive workers , and recognition of nest @-@ mates . In rare cases , worker @-@ laid eggs carry mimicked queen hydrocarbons and escape policing , a condition known as the anarchic syndrome .

Not all forms of policing require the presence of a queen ; it also occurs in a few species of ants which establish a dominance hierarchy of reproductive female workers , where top @-@ ranking individuals reproduce .

= = Evolutionary basis = =

In many social insect communities , sex is determined through haplodiploidy . Haploid male drones develop from unfertilized eggs while diploid females develop from fertilized eggs . Queens of a colony may mate with one or several drones . On average , a queen shares half of her genes with her sons , but only shares a quarter of her genes with the sons of fertile female workers . Therefore , it is in the queen 's best interests to have her own sons raised , and not the sons of workers . Workers can reproduce in many ants , bees , and wasps because male offspring come from unfertilized eggs .

By contrast , the worker shares half of her genes with her sons and only a quarter with her brothers . Furthermore , the workers in colonies with a single once @-@ mated queen are related to their nephews by three eighths , higher than they are related to brothers . This results in a conflict where the queen and worker females are at odds over the proportion of male offspring they contribute , since each side tries to maximize its reproductive fitness . Queens favor production of their own sons while workers favor production of their own sons , and do not stop their sisters from laying because of the favorable relatedness to nephews .

Worker policing occurs when worker bees in the colony are genetically more closely related to the queen than the reproductive female . In many instances , the eggs of the female worker are eaten , or she is repeatedly attacked by other workers . This mechanism of egg removal ensures that the queen 's sons predominate .

Experiments confirming the role of kin selection in worker policing demonstrate the effects of multiple matings , which can lead to lower average relatedness between workers . Queens of the social wasp Dolichovespula saxonica mate singly or multiply . Researchers who study these wasps have observed a strong positive correlation between worker relatedness and male production . After controlling for the absolute number of eggs laid , these scientists conclude that the queen 's multiple matings favor mutual worker policing .

Although early theories of worker policing focused on the kin selection component , evidence from honey bees suggests that altruism is sometimes enforced . Fewer workers reproduce as policing effectiveness rises , and policing effectiveness decreases with increasing relatedness except in colonies with no queen . This suggests that worker policing is a social sanction imposed on selfish individuals .

= = Proposed mechanisms for kin recognition = =

Mechanisms suggested for egg discrimination in worker policing include queen hydrocarbons , fertile worker hydrocarbons , and nestmate recognition .

= = = Queen hydrocarbons = = =

A study on the carpenter ant Camponotus floridanus found a special surface hydrocarbon on queen @-@ laid eggs . Workers in the colony with the queen 's eggs refrained from egg @-@ laying , whereas other groups that did not have queen @-@ laid eggs showed worker reproduction . Thus , the hydrocarbon could act as a signal to alert workers to halt reproduction . More generally , however , the authors concluded that the hydrocarbons were a fertility signal . It is still unknown as to how the decision to restrain reproduction occurs or what minimum threshold of fertility in the queen is needed to reduce worker reproduction .

= = = Fertile worker hydrocarbons = = =

The study of cuticle hydrocarbons has also been applied to the reproductive workers . In some colonies of the ponerine ant Platythyrea punctata , the presence of CHCs in new reproductive workers triggered aggressive behavior from the rest of the colony , often between new and old reproductive workers . Specifically , the old reproductive workers rubbed a marker hydrocarbon on the antennae of the new females , identifying them as rivals and targets for aggression .

= = = Nestmate recognition = = =

In contrast to the other ant species , worker policing in the ant Formica fusca appears to incorporate nestmate recognition in addition to the queen hydrocarbons . Workers displayed higher levels of aggression toward non @-@ nest mates and also removed some queen @-@ laid eggs . Thus , queen hydrocarbons were not the only contributor to discrimination of the eggs .

= = Examples from social Hymenoptera = =

Worker policing has evolved convergently in several social insect species . The following cases are examples :

= = = Bees = = =

One of the first examples of worker policing to be discovered was in the honey bee , Apis mellifera . Worker policing is prevalent in most honey bee colonies , and worker reproduction is minimal (0 @.@ 12 %) in this species . Worker policing occurs via egg @-@ eating (oophagy) in Apis mellifera colonies . In many of these hives , the activation of ovaries in fertile females is diminished , suggesting that there are disincentives to laying eggs .

Workers in colonies of the Asian honey bee , Apis florea , are also reported to engage in oophagy . Using microsatellite analysis , researchers concluded that no mature drones had non @-@ queen alleles in the colonies they investigated . Thus , even though workers had activated ovaries and were capable of laying eggs , worker policing ensured the functional sterility of otherwise fertile workers .

A higher percentage of female workers of the bee species Apis cerana are reported to activate their ovaries than those of Apis mellifera or Apis florea . When queens were removed , up to 40 % of the workers activated their ovaries in subsequent days . However , policing workers continued to eat the worker @-@ laid eggs , suggesting that the mechanism of policing in this species does not involve direct intervention from the queen .

The observation that all these Apis species engage in polyandry has led researchers to conclude that worker policing is plesiomorphic for the Apis genus .

Worker policing also occurs in the primitively eusocial bumblebees such as Bombus terrestris .

= = = Ants = = =

In colonies of the ponerine ant , Pachycondyla inversa , workers eat the eggs of fertile female workers and display aggressive behavior towards egg @-@ laying females .

In colonies of the ant Gnamptogenys menadensis , workers will sometimes mate and lay eggs while others remain as virgins to lay trophic eggs that are consumed as nourishment . In a display of policing , workers can immobilize female reproductive workers by biting their limbs ; it is reported that 50 % of the victims die from this treatment . The attacking workers may also drag offending workers outside the colony . Since workers can lay both male and female eggs , worker policing could be favored since the cost to the community is large .

The ant species Aphaenogaster smythiesi japonica also display evidence of policing . When researchers separated and then reunited workers from colonies that did or did not have queens , workers from the queen @-@ containing colonies attacked the workers with activated ovaries from the queenless colonies .

= = = Wasps = = =

The tree wasp Dolichovespula sylvestris also displays worker policing . Both egg @-@ eating and aggression are reported in these wasp communities , and the queen also engages in the policing process . Similar behavior has been observed in the closely related species Dolichovespula media .

In colonies of the paper wasp , Polistes chinensis antennalis , workers can lay up to a quarter of the male eggs in the colony . The number of eggs that survived to hatching , however , was minimal compared to the number produced by the queen . Analysis of the microsatellite markers showed that both queens and workers contributed to policing of worker and queen @-@ laid eggs even in monogynous and monandrous colonies .

The common wasp , Vespula vulgaris , engages in worker policing , and it is known that a significant number of workers have active ovaries . However , studies by researchers have suggested that relatedness may not be the key factor in the development of worker policing . Rather , it is hypothesized that worker policing has been selected due to conflict suppression in the colony .

In a test of worker policing , researchers examined the removal of worker @-@ laid eggs in Vespula rufa , a wasp that has low paternity . Under the testing conditions , worker policing was not as efficient , and some of the drones appeared to be from worker @-@ laid eggs .

The European Hornet , Vespa crabro , was previously thought to be under reproductive pheromone control by the queen , thus explaining why the other females didn 't reproduce , even though they were capable of doing so . Experiments by Foster showed that the workers were instead regulating sterility in each other , thus instead exhibiting worker policing . While each worker is capable of reproducing , the colony as a whole is more efficient and organized if the workers allow only the queen to lay larvae .

Synoeca cyanea also engage in worker policing during times when queen repopulation is not needed . They will prevent females from laying eggs through aggressive behavior and egg @-@ eating .

= = Exceptions = =

= = = Anarchic syndrome = = =

Very rarely , female worker bees lay eggs that escape worker policing , in a process known as the anarchic syndrome . Female reproductive workers in these colonies activate their ovaries even in the presence of a queen . The worker eggs are allowed as they mimic queen hydrocarbons . Thus , female workers can maximize their reproductive fitness at the expense of the colony . Anarchic syndrome is an example of selection working in opposite directions at individual and group levels .

= = = Selfish worker policing = = =

Temnothorax unifasciatus , a myrmicinid ant , has been shown not to have collective worker policing . However , when a queen is removed , a rank order for reproduction appears , where top ranking reproductives display aggression towards lower @-@ order female workers . Thus , reductions in egg laying are created by dominance hierarchies . Individuals do not act in benefit of the colony , instead opting to increase their own fitness by laying their eggs and reducing the contributions of opponents .

This type of policy is common in Dolichovespula norwegica wasps where despite being more related to other workers ? sons , worker @-@ laid eggs were consumed by other workers .

= = = Worker policing without genetic conflict = = =

In the thelytokous ant Platythyrea punctata , colonies are clonal ; therefore , workers are all equally related genetically , and worker policing is not expected as there is no genetic conflict . However , one would expect severe effects on the condition of the colony if reproductive workers were left unchecked . For example , more time spent on individual reproduction would be predicted to detract from care of the queen 's offspring . In studies of these ants , workers did actually display worker policing , as evidenced by increased aggression towards reproductive workers . Worker policing here is favored for group efficiency .