

Dispatches

Social Evolution: The Smell of Cheating

Coercion is a powerful means to enforce altruism and promote social cohesion in animal groups, but it requires the reliable identification of selfish individuals. Experiments in a desert ant provide the first direct proof that a single cuticular hydrocarbon elicits the policing of reproductive workers by other colony members.

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Cooperation is tightly linked to communication and discrimination across all levels of biological organization [1]. Cooperative systems are always at risk of being invaded by selfish elements that profit from cooperation without paying the costs, so-called ‘cheaters’; the maintenance of cooperation, therefore, requires mechanisms to discriminate against such cheaters. There is an arms race: co-operators are selected to signal their status, whereas cheaters should hide their identity to escape detection. This dynamic game has attracted much attention, and understanding how cooperation evolved and which mechanisms stabilize cooperation remains one of the major goals of evolutionary biologists [2–4].

In eusocial ants, bees and wasps, where workers do not usually reproduce, social coercion of selfish workers by peers — a process called ‘worker policing’ — has long been known to promote social harmony. However, the precise cues used to identify cheaters have proved difficult to identify [5,6]. In a recent paper in *Current Biology* [7], experiments in the desert ant *Aphaenogaster cockerelli* showed that a simple hydrocarbon triggers the aggression of egg-laying workers by other workers [7]. Reproductive *Aphaenogaster* workers are policed because they apparently cannot mask a queen’s perfume associated with fertility [7,8].

Insect societies are characterized by reproductive altruism: workers usually forego direct reproduction and collectively take care of all other tasks, such as brood care, foraging and colony defence [9]. The evolution of worker altruism is primarily driven by kin selection — workers care for related individuals and by so doing indirectly transmit copies of their genes to the

next generation [10]. However, workers are not clones, and the relatedness that underlies kin selection is generally too low to completely erase potential conflicts and promote voluntary self-restraint. Recent theoretical and empirical studies have therefore emphasized that the high level of altruism observed in social insect colonies is supported by robust discrimination mechanisms against selfish individuals [11,12].

One such discrimination mechanism is worker policing [5]. Workers of social Hymenoptera — ants, bees and wasps — are generally unable to mate and produce diploid offspring, but in many species they have retained the ability to lay haploid eggs that will develop into males, and they indeed often produce a large number of males when their colony becomes queenless [13]. In contrast, worker-produced males are rare or absent in colonies that have a queen; there is increasing evidence that this pattern is due to the fact that workers collectively prevent each other from reproducing in queenright conditions [5,6]. They can do this by two main means: first, by destroying eggs laid by other workers, and second by attacking workers that become fertile, so that these workers might be killed, driven out of the nest, kept away from the brood pile, or possibly forced to regress their ovaries so that their reproduction is curtailed.

The ultimate factors driving the evolution of worker policing have been the matter of some debate, because relatedness and productivity jointly set the balance for policing [6,14]. Overall, worker policing should evolve when workers’ reproduction decreases the average inclusive fitness of workers, which is expected when workers are more related to brothers than to nephews, or when worker reproduction has a negative

impact on colony productivity. Productivity costs are likely because egg-laying workers may not work as efficiently as non-reproductive ones and competition among workers may decrease colony efficiency.

How do workers detect queen presence and identify reproductive workers? Increasing evidence points to a role for cuticular hydrocarbons [15]. Cuticular hydrocarbons are complex mixtures of compounds on the insect cuticle that contain primarily alkanes and alkenes and show qualitative and quantitative variation between individuals. Cuticular hydrocarbons have multiple roles: they provide resistance to desiccation and are major cues permitting the discrimination of nestmates from foreigners.

Many recent studies in ants suggest that cuticular hydrocarbons have the double function of signalling queen fertility and protecting queen-laid eggs from policing [1,15–17]. Worker-laid and queen-laid eggs show distinct hydrocarbon profiles in several ant species [15]. Moreover, in *Camponotus floridanus* worker-laid eggs that had been experimentally treated with a queen cuticular extract had a reduced risk of getting destroyed by workers [16]. However, unequivocal direct proof that one or more specific hydrocarbon compounds trigger worker policing was still missing.

The new work by Smith, Hölldobler and Liebig [7] now provides strong direct evidence that a single hydrocarbon elicits the policing of reproductive workers by other colony members in an ant species [7]. *A. cockerelli* is a slim, long-legged desert ant that forms colonies containing one queen and many morphologically distinct workers. On their cuticle, *Aphaenogaster* queens have high quantities of straight-chained alkanes (tri-, tetra-, penta- and hexacosane) that are absent on non-reproductive workers, but appear on reproductive workers [7,8]. Workers isolated in queenless colony fragments produce

male-destined eggs that are not policed by other workers and that show cuticular hydrocarbon profiles very similar to that of queen-laid eggs, with the characteristic queen-like alkanes [8]. Reproductive workers are attacked by other workers when returned to queenright fragments, and in other ant species such aggression inhibits ovarian development and egg-laying.

Smith and colleagues added synthetic pentacosane, one of the straight chained alkanes typical of the queen profile, onto the cuticle of non-reproductive workers [7]. When they returned pentacosane-marked workers to queenright colony fragments, they became targeted aggressively by other workers (Figure 1). In contrast, pentacosane-marked workers returned to queenless colony fragments were not attacked, as expected if aggression is due to policing, which should not occur in the absence of the queen. Controls in which workers were treated with hexane solvent or with another straight-chained alkane (nonacosane) that is present on both queens and non-reproductive workers further confirmed that aggression was specifically elicited by pentacosane.

These elegant experiments demonstrate that pentacosane reveals the reproductive status of workers, and thus allows detection and coercion of cheaters. Reproductive workers should try to avoid coercion, so why do they express this queen-like smell? The authors suggest that egg-laying workers are bound to reveal their status because they cannot decouple the signal on their eggs and on themselves. They need to produce the fertility cues that are typical of queens, because other workers would presumably recognize and destroy worker-laid eggs without such cues. However, producing hydrocarbons without showing them up on the cuticle might be impossible, because hydrocarbons are synthesized by specialized glandular cells spread in the body cavity and transported by the hemolymph to other body parts, including the cuticle and ovaries. Workers might thus be physiologically constrained to reveal their reproductive status.

The suggestion that *A. cockerelli* workers would police eggs without the queen-specific alkanes remains speculative, but is consistent with studies of other ant species that have

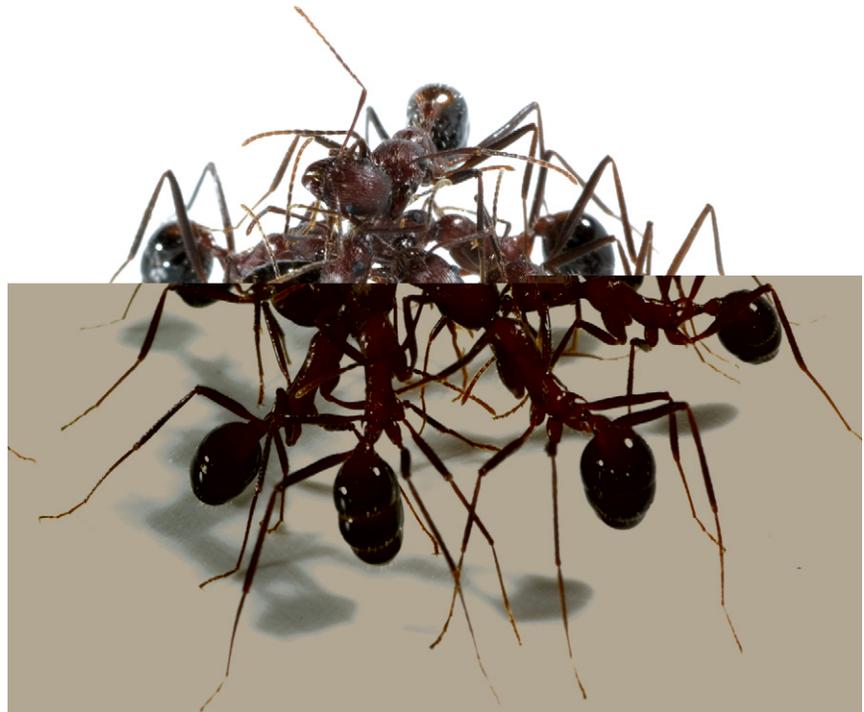


Figure 1. Ant policing.

Workers of the ant *A. cockerelli* attack a nestmate that has become reproductive. Photograph by Adrian A. Smith.

shown that workers police eggs whose hydrocarbon profiles differ from those of queen-laid eggs [15–17]. Direct tests of this hypothesis are difficult to perform in *A. cockerelli*. They would require manipulation of the hydrocarbon profile of viable eggs and examination of whether this treatment triggers egg destruction by other workers. Like the workers they study, the researchers are constrained in the ways they can manipulate chemical cues: it appears to be difficult to remove specific chemical compounds that are present on the surface of eggs without interfering with nestmate discrimination or egg viability.

Reproduction affects the composition of cuticular hydrocarbons in many species of insects, including ants, bees and wasps [15]. There is also increasing evidence that other individuals can sense these changes and react accordingly. Whether queen-specific compounds are signals that have evolved because they benefit queens and non-reproductive workers or cues linked to fertility for primary reasons other than signalling remains an open question. In both cases the compounds have to reliably reveal the reproductive potential of an individual. This raises the interesting question of

what maintains the so-called ‘honesty’ of the signal or reliability of the informative cues. Generally, honest signals are associated with conflict-free situations, condition-dependent production costs, or constraints [18]. The studies by Smith and colleagues [7,8] suggest that the combined constraints set by social coercion and physiology of hydrocarbon production maintain the signal’s honesty. The fact that fertility-revealing hydrocarbons appear to vary across the social insects further suggests that they might be evolved signals, rather than mere cues [8,15,17]. However, to fully demonstrate that specific hydrocarbons are honest signals of fertility will require more studies on the expression and evolution of genes regulating hydrocarbon synthesis, as well as on hydrocarbons’ function in producers and mode of action in receivers.

The studies by Smith and colleagues [7,8] point at a simple mechanism to stabilize cooperation: workers cannot lay eggs that smell like queen eggs without revealing their reproductive status, and this triggers aggression by other workers. The conditions for stable cheater detection appear simple: a signal that permits queen-laid

eggs to be distinguished and that obligatorily shows up on the cuticle of the individual producing it. Reproductive workers are trapped because they necessarily show both queen's and worker's compounds. More generally, physiological or genetic constraints that prevent the uncoupling of traits involved in dual functions may suffice to stabilize reproductive cooperation in many biological systems [19].

References

1. D'Ettorre, P., and Hughes, D.P., eds. (2008). *Sociobiology of Communication* (Oxford: Oxford University Press).
2. Lehmann, L., and Keller, L. (2006). The evolution of cooperation and altruism - a general framework and a classification of models. *J. Evol. Biol.* 19, 1365–1376.
3. Pennisi, E. (2005). How did cooperative behavior evolve. *Science* 309, 93–93.
4. Bshary, R., and Bergmueller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* 21, 405–420.
5. Ratnieks, F.L.W., Foster, K.R., and Wenseleers, T. (2006). Conflict resolution in insect societies. *Annu. Rev. Entomol.* 51, 581–608.
6. Wenseleers, T., and Ratnieks, F.L.W. (2006). Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory. *Am. Nat.* 168, E163–E179.
7. Smith, A.A., Hölldobler, B., and Liebig, J. (2009). Cuticular hydrocarbons reliably identify cheaters and allow enforcement of altruism in a social insect. *Curr. Biol.* 19, 78–81.
8. Smith, A.A., Hölldobler, B., and Liebig, J. (2008). Hydrocarbon signals explain the pattern of worker and egg policing in the ant *Aphaenogaster cockerelli*. *J. Chem. Ecol.* 34, 1275–1282.
9. Wilson, E.O. (1971). *The Insect Societies* (Cambridge, MA: Harvard University Press).
10. Hamilton, W.D. (1964). The genetical evolution of social behaviour. *J. Theor. Biol.* 7, 1–52.
11. Wenseleers, T., and Ratnieks, F.L.W. (2006). Enforced altruism in insect societies. *Nature* 444, 50.
12. Ratnieks, F.L.W., and Wenseleers, T. (2008). Altruism in insect societies and beyond: voluntary or enforced? *Trends Ecol. Evol.* 23, 45–52.
13. Bourke, A.F.G. (1988). Worker reproduction in the higher eusocial Hymenoptera. *Quart. Rev. Biol.* 63, 291–311.
14. Hammond, R.L., and Keller, L. (2004). Conflict over male parentage in social insects. *PLoS Biol.* 2, 1472–1482.
15. Monnin, T. (2006). Chemical recognition of reproductive status in social insects. *Ann. Zool. Fenn.* 515–530.
16. Endler, A., Liebig, J., Schmitt, T., Parker, J.E., Jones, G.R., Schreier, P., and Hölldobler, B. (2004). Surface hydrocarbons of queen eggs regulate worker reproduction in a social insect. *Proc. Natl. Acad. Sci. USA* 101, 2945–2950.
17. D'Ettorre, P., Heinze, J., and Ratnieks, F.L.W. (2004). Worker policing by egg eating in the ponerine ant *Pachycondyla inversa*. *Proc. R. Soc. Lond. B* 271, 1427–1434.
18. Maynard Smith, J., and Harper, D. (2003). *Animal Signals* (Oxford: Oxford University Press).
19. Foster, K.R., Shaulsky, G., Strassmann, J.E., Queller, D.C., and Thompson, C.R.L. (2004). Pleiotropy as a mechanism to stabilize cooperation. *Nature* 431, 693–696.

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Speech Perception: Motoric Contributions versus the Motor Theory

Recent studies indicate that the motor cortex is involved not only in the production of speech, but also in its perception. These studies have sparked a renewed interest in gesture-based theories of speech perception.

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Recognizing speech is a deceptively difficult problem, as anyone who has ever shouted down the phone at a computerized speech recognition system will attest. Every consonant and vowel sound is influenced by the sounds around it, which affect the raw acoustic signal — the vibrations in the air — making it more difficult to isolate and identify an individual sound. This phenomenon is called *co-articulation*, and it presents a fundamental challenge to theories of phonetic categorization. Consider, for example, the sound of the letter 'd': depending on the context, the sound can have very different acoustic profiles (Figure 1). Although listeners identify all of these disparate acoustic patterns as members of the same phonetic category, there is no single acoustic cue that reliably defines the category

/d/. Instead, what all of these examples of 'd' share is the fact that when they are generated, the tongue is always placed at the roof of the mouth. This observation led Liberman and colleagues [1] to suggest that the perception and production of speech are intimately linked, such that the motor commands used to generate speech sounds are directly involved in perceptual categorization [1]. According to Liberman's motor theory of speech perception, the necessary and sufficient features for recognizing speech are not acoustic at all, but rather are motoric — it is the articulatory gesture that forms the basic unit of speech perception [2].

Liberman's motor theory went further, however, and posited a special processing mechanism dedicated to speech perception: in this view, categorical perception of speech sounds is not accomplished by general mechanisms of audition, but instead

relies entirely on a speech-specific module responsible for detecting the intended gestures of the speaker. The speech module was suggested to be separate from the auditory system, with a distinct, innately specified neural instantiation. On the basis of these strong claims, the motor theory made a number of controversial predictions. First, speech and nonspeech sounds should be perceived and categorized in fundamentally different ways. Further, because other species do not possess the necessary specialized processing mechanism, categorical perception of speech sounds should be unique to humans. Subsequent research, however, has offered persuasive evidence against these predictions: perceptual phenomena once believed to be speech-specific have since been demonstrated using nonspeech stimuli; and categorical perception of speech sounds has been shown in a wide range of non-human animal species [3,4]. The evidence against motor theory led to the development of alternative theories of speech perception in which phonetic categorization is based on the integration of information from multiple sensory cues, without reference to the motor commands responsible for speech production [5,6].

The discovery of mirror neurons in the 1990s, however, rekindled interest