

copied with the changes at later ages impose a cost in efficiency at earlier ages.

The ability to cope with age-related environmental changes may arise through adaptation of fixed characteristics, such as the kinetic properties of an enzyme, or by conditional adjustments in traits as the environment changes. Conditional adjustments have the benefit of tracking environmental changes. But conditional adjustments also have the costs associated with the need for enhanced sensors of environmental change and enhanced regulatory controls to alter traits in response to the changed environment. Thus, the machinery of conditional adjustment probably also reduces efficiency at earlier ages compared with a simpler system designed with respect to the typical environment at early ages.

The topic leaves many open questions. Is regulatory control or genomic architecture in microbes partly designed to protect against competition from rogue mutant lineages? Do long-lived populations

have enhanced protections compared with short-lived populations? How much cost in terms of reduced short-term efficiency arises from protections against rogue lineages that arise later in the lifespan of populations? How much of regulatory design is influenced by age-related changes in microbial populations?

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Chemical Communication: A Jewel Sheds Light on Signal Evolution

When others show sexy tails or sing elaborate songs, many animals use the language of chemistry to attract potential mates. A study provides insights into the evolutionary conundrum of how new chemical signals can evolve in an established communication system.

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The chemical senses — smell and taste — have evolved in a wide range of organisms from bacteria to vertebrates and have enabled them to sense the surrounding environment and benefit from information carried by external chemical cues [1]. While organisms can perceive only a fraction of the chemical compounds present in their surroundings, they also contribute to the global olfactory cacophony by — intentionally or not — emitting molecules, such as waste products or biosynthetic

by-products [2]. Urine, for example, appears to be an endless source of chemical signals in mammals [3]. Chemical cues convey information to those who can detect them, which can have great fitness consequences for both the emitter and the receiver and can provide the bases for the evolution of communication systems [4]. In a recent study in *Nature*, Niehuis et al. [5] show how a new chemical cue evolved and was integrated into the communication system of the jewel wasp *Nasonia vitripennis*.

Sexual reproduction usually entails the encounter of the sexes, and the

use of sex pheromones — chemical signals that mediate interactions between individuals of the same species — is commonplace. Sex pheromones can be used to mediate attraction, to trigger sophisticated courtship displays and acceptance of the suitor or to repel competitors and incompatible mates. For example, the (Z7,Z11)-heptacosadiene produced by *Drosophila melanogaster* females acts as an aphrodisiac on conspecific males but deters males of other fruitfly species [6]. Accordingly, the emergence of new species is often accompanied by a divergence in the pheromones used by the forming species [7,8]. Since the first pheromone was identified in the silkworm *Bombyx mori* in 1959 [9], a tremendous diversity of chemical signals have been identified, many of them in insects. How the evolutionary diversification of sexual communication signals can take place poses a conundrum: normally, selections would act against senders

that send a deviant message or receivers that respond inappropriately, thus maintaining the integrity of signal and response and the coordination of the mate-recognition system [7,8,10].

Recently, molecular studies have demonstrated that a single amino acid change can produce a new pheromone blend or change the ligand specificity from one pheromone component to another in *Ostrinia* moths [11,12]. Also, Li *et al.* [13] described the parallel evolution of an odor biosynthesis pathway and odor-evoked behaviors mediated by an evolutionarily conserved chemosensory receptor. Studying acoustic communication, Shaw and Lesnick [14] reported the colocalization of the QTL underlying variation in song and song preference in *Laupala* crickets. So far, however, no such example is known from chemical communication systems, whereby a single locus would change both signal and response at the same time. Thus, either the signal or the response (receptor) has to change first, and the causal mutation has to escape negative selection to allow a matching change to eventually evolve. In their recent study, Niehuis and colleagues [5] shed light on how new signals might emerge and avoid being immediately selected against. Using the parasitoid wasps *Nasonia* they show that some males of a derived wasp species use a new component that makes their pheromone bouquet irresistible to females of the same species. However, females of related ancestral species seem to be either unable to smell the new male fragrance or they ignore it.

In *Nasonia*, females are guided to their mates by the pheromones males produce. All species use a blend of two molecules, here named RS and MQ (4(R), 5(S)-5-hydroxy-4-decanolide and 4-methylquinazoline, respectively), but in the cosmopolitan *N. vitripennis* males have added a third component to the mix, RR (4(R), 5(R)-5-hydroxy-4-decanolide). In their behavioral assay, the authors show that RR appears to be necessary in addition to RS and MQ to elicit robust attraction of *N. vitripennis* females, whereas females of the close relative *N. giraulti* could not care less: they are happy as long as RS and MQ are present but are neither attracted further nor repelled when

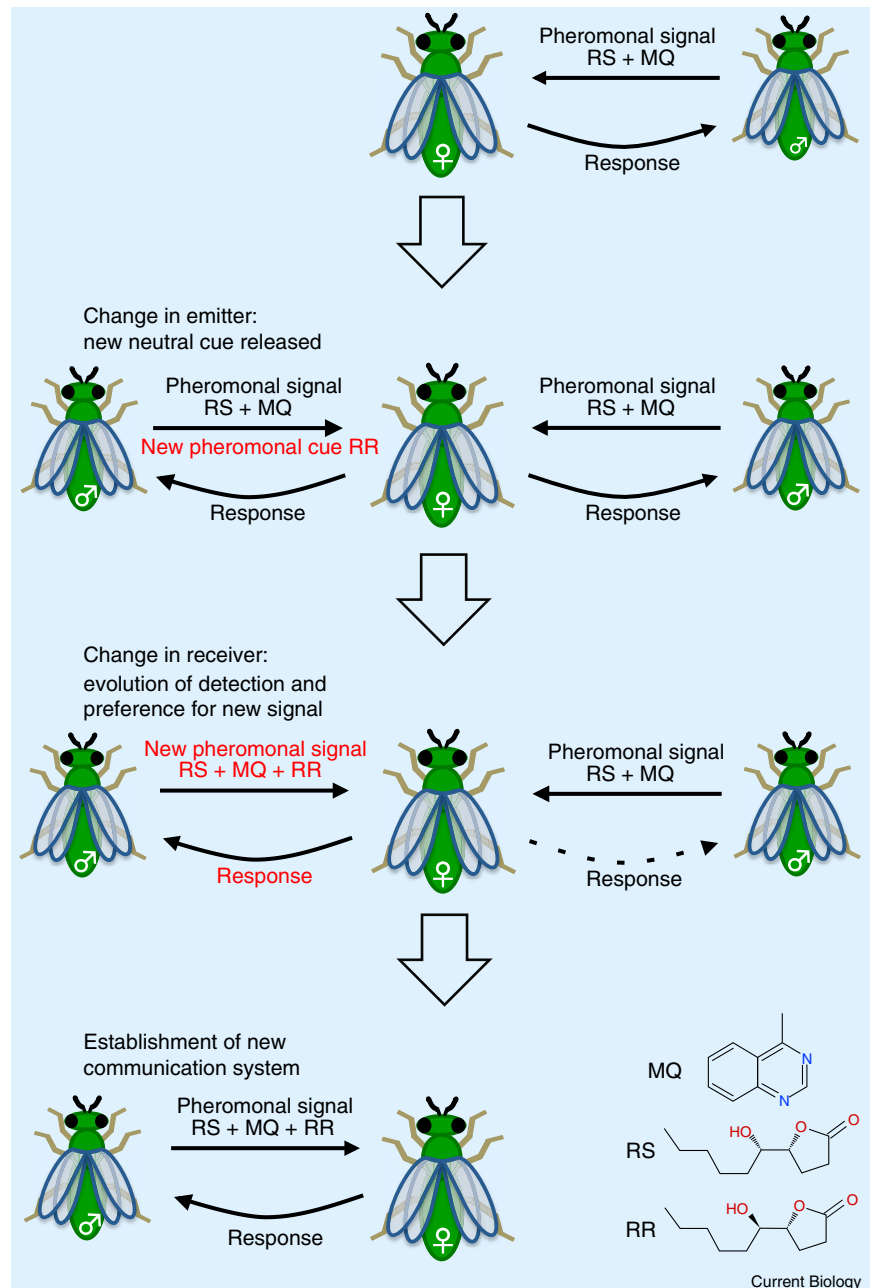


Figure 1. Evolution of a new pheromone communication system — a schematic view.

RR is found specifically in *Nasonia vitripennis* males. The ancestral species of *N. vitripennis* most certainly only used RS and MQ as its pheromone, not unlike contemporary *N. gaulti*, *N. oneida* and *N. longicornis*. Mutations affecting one or several biosynthetic enzymes lead to the production of RR in some males. These would be maintained in the population as the new cue is not eliciting any behavioral changes in females that can still rely on the presence of RS and MQ. Subsequently, a change in the receiver side would lead to emergence of a preference for male having RR in the blend, maybe because it provides a selective advantage. Consequently, males not producing RR would elicit gradually less response until the new communication system prevails.

RR is added. Based on a series of behavioral experiments, Niehuis *et al.* [5] bring convincing evidence that the ancestral state of *N. vitripennis* consisted of females just like *N. giraulti*: not selectively preferring

RR, but rather partial to it as a new cue and eventually allowing it to evolve as a new pheromone component (Figure 1). In other terms, the evolution of the preference did not predate the emergence of the new

trait as seen in many other biological systems [15].

But how do you make a new pheromone component when you are a jewel wasp? Well, after quick examination of the chemical structure, RR does not appear that different from RS. Indeed, the two molecules only differ by the stereochemistry of the hydroxyl group. Of course, whether it is S or R can make a big difference in the chemical love world of insects [16], but the two molecules may share a common biosynthetic pathway regardless. To unravel the pathway leading to the production of the novel pheromone compound, Niehuis and his colleagues [5] took advantage of the palette of tools that makes *Nasonia* an outstanding model to study the genetics of complex traits, including pheromone evolution [17,18]. The analysis of the offspring of interspecies crosses between *N. vitripennis* and *gaulti* allowed them to identify one quantitative trait locus explaining over 80% of the total variance in pheromone phenotype. Using fine-scale mapping and RNAi gene knockdown, they could narrow down the list of causative loci to a cluster of three genes encoding putative short-chain dehydrogenases. These enzymes catalyze the synthesis of RR using RS as substrate. Because the three genes are present in the *N. gaulti* genome and expressed in *N. gaulti* wasps, one may speculate that mutations affecting the substrate preference of the enzymes are responsible for the rise of a novel pheromone compound. Future functional characterization will certainly provide much-needed answers. Gene duplication followed by neo-functionalization of one or several of the paralogues combined is a possible mechanism that could have promoted the emergence of a new function in *N. vitripennis* [19]. This awaits further confirmation, but one thing is already certain: male wasps found a way to turn an old scent into an acclaimed perfume, which may represent a common strategy for modifying the qualitative properties of pheromones.

The study by Niehuis and coworkers [5] exemplifies how a new signal can be produced and recruited to serve in the communication channel of one species. However, we still know little

about the circumstances and evolutionary force that would favor the maintenance and fixation of a new signal, and nothing about the evolution of the matching changes that are necessary at the level of the receiver for the evolution of a new preference. There is a limit on what we can learn about evolutionary processes by mechanistic studies and phylogenetic reconstructions. Discussing the role of natural selection in speciation, Via [20] contrasted two approaches: using the *spyglass* the process is studied by attempting to look back to see the details of speciation from today's vantage point, whereas using the *magnifying glass* the mechanisms of reproductive isolation are studied in populations that are used as models of an early stage of speciation. Likewise, it may be necessary to study model communication systems that are polymorphic and potentially undergoing evolutionary changes currently. Pheromones, like other sensory signals, are integrated and processed to generate appropriate behavioral responses. Neither the receptors for RR and RS nor the neural circuitry transducing their effects are known; these fundamental pieces of information are necessary to deepen our understanding of the bases of pheromone signal evolution in the perspective of the receiver. How changes in sensory representation lead to modification in stereotyped decision-making awaits further study. The jewel wasps have not yet revealed all their secrets, but they are definitely exciting emerging models to study the evolution of pheromone communication aside from fruit flies and moths.

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