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Perspectives

A crazy ants' crazy form of reproduction: Causes and consequences

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1. The yellow crazy ant

The yellow crazy ant, or the long-legged ant, *Anoplolepis gracilipes* (formerly *Anoplolepis longipes*) – named so for its meandering movements when disturbed, possibly owing to its long legs and antennae – is globally widespread and currently classified as one of '100 of the world's worst invasive species' (Lowe *et al.* 2000). This status is assigned to species that are non-native in a region and cause significant negative ecological and/or socioeconomic impacts, including declines in native biodiversity, changes in native ecosystem structure and function, and the breakdown of native biogeographic realms. Possibly, the most devastating and multipronged impacts of *A. gracilipes* have been observed on island ecosystems, such as on Christmas Island in the Indian Ocean, where it impacted the entire island ecosystem by reducing arthropod, reptile, bird, and mammalian diversity on the forest floor and canopy, causing an 'invasional meltdown' (O'Dowd *et al.* 2003).

While trade, transport, and tourism in the Anthropocene have acted as facilitators of species movements, a non-native species has to fend for itself on foreign shores. It faces several barriers that adversely impact its survival and reproduction, causing the transported population to decline. Only a fraction of the non-native or alien species can find mates in new environments, escape genetic bottlenecks created by smaller founder populations, avoid new negative interactions such as predation, competition, and parasitism, and foster positive interactions such as mutualisms in the new environment. A non-native or alien species that can achieve this feat, establishes successfully breeding populations, first expanding its population size, and then its population range, spreading in the new environment. Such success in the new environment requires a suite of behavioural, morphological, physiological and life-history traits related to behavioural aggressivity, generalist feeding habits, high dispersal abilities, and unusual reproductive strategies. To quite a large extent, the invasion success of *A. gracilipes* can be attributed to all of the above traits. It is behaviourally aggressive, is generalist with polygynous colonies, forms supercolonies with hundreds of thousands of individuals per colony (Abbott 2005) and has a bizarre reproductive strategy, as has been recently discovered (figure 1) that perhaps also contributes to its status as a formidable invader.

2. The unusual reproductive system of the crazy ant

Hugo Darras of the University of Mainz in Germany and his colleagues have recently discovered a hitherto wholly unknown form of reproduction in the yellow crazy ant *Anoplolepis gracilipes* – males are obligate chimaeras containing a mixture of haploid cells of two

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Figure 1. A portion of a nest of the yellow crazy ant *Anoplolepis gracilipes* (the inset shows a few workers) (photographed in the Wayanad district of Kerala, India, by Dr. Thresiamma Varghese).

genetic lineages, while workers have diploid cells with chromosomes of both lineages, and queens are diploid with two sets of chromosomes of only one of the lineages (Darras *et al.* 2023) – can anything be more bizarre?

Thus, reproduction in the crazy ant appears to violate several well-established principles of sexual reproduction. Indeed, it is the violation of Mendel's laws of inheritance noticed in previous studies (Drescher *et al.* 2007; Gruber *et al.* 2013) that prompted the present authors to undertake this new investigation. When Darras and colleagues genotyped queens and workers from different locations using microsatellites, they found that even more established norms of reproduction were violated. Queens and workers had an unexpectedly high genetic distance of 0.37, with many loci present in one caste and not the other. Workers had a very high level of heterozygosity of 99%, while the queens had only a modest level of 12%. All this suggests that the population contains two different genetic lineages that have been unable to replace each other and that the queens are diploid individuals of a single lineage, while workers are diploid individuals with genomes from both lineages.

A focus on the males made the story even more complicated. Genotyping the males, they found that while some males belonged to one lineage and some to the other, 65% of the males had genomes from both lineages. These males could be diploid, of course, as male diploidy is seen infrequently due to the peculiar mode of sex determination in the Hymenoptera, but the diploid males are sterile. However, the authors used flow cytometry to show that all male nuclei had only half the DNA content of the females, suggesting males with both genomes were chimaeras with their cells containing separate nuclei from the two lineages.

From these multiple unusual findings, the authors reconstruct the most plausible mode of reproduction in the crazy ant that seemingly accounts for all their crazy findings. They label the genetic lineage in the queens as 'R' (for reproductive) and the other lineage seen only in the workers and males as 'W'. Since queens are expected to be RR, the only eggs available for fertilisation would be R. But sperm should be either R or W since both genetic lineages persist in the population (assuming the workers do not reproduce). Thus, when an R sperm fertilises an R egg, the two parental nuclei fuse (a process called syngamy) and the resulting diploid RR zygote develops into a queen. If a W sperm fertilises an R egg, however, there are two outcomes. One outcome is that syngamy takes place, and the resulting diploid RW zygote develops into a worker. The other outcome is that the two parental nuclei do not fuse, and the resulting chimaeric zygote develops into a male with both R and W nuclei in its cells. It should not go unnoticed that the crazy ant violates another general principle that caste differentiation into queens and workers is based on environment, not genes. It must be said, however, that there are a growing number of examples of the role of genetics in caste determination in social insects (Schwander *et al.* 2010).

If this model of the crazy ant reproduction is correct, then there arises a paradox: How does the W lineage persist? It should disappear because it only ends up in the sterile workers, and that is a dead end because workers do not reproduce. The W lineage is at a great disadvantage compared to the R lineage because R, being only in the reproductive queens, passes on to the next generation. It is only the males that can resolve this paradox.

The authors argue that the resolution of this paradox is made possible due to two consequences of the presence of the W genome. One is that in the presence of W, syngamy somehow fails to occur in some of the zygotes of the RW genotype, and so these zygotes develop into reproductive males, as we have already seen. This results in at least some copies of the W genome in the reproductive pool. There is a second consequence of the presence of the W genome that results in the W genome remaining in circulation even more than it might have been with just the first consequence. When the zygotes containing two separate nuclei of R and W lineages divide, they result in some daughter cells with only the R nucleus and others with only the W nucleus. This should normally be a random process with equal numbers of R and W cells. But in the presence of the W genome, the balance somehow appears to tilt, resulting in unequal numbers of R and W cells, conferring an evolutionary advantage to the W genome. Using a competitive PCR assay, Darras and colleagues showed that W is found in the sperm more often than R, while R is more common in somatic tissues. They found that 77% of the somatic cells were R, whereas only 35% of the sperm cells were R. In many males, the competitive advantage of W was even greater—43% of the males had 100% W sperm, whereas only 26% of the males had 100% R sperm.

As Darras *et al.* argue, the novel mode of reproduction in the crazy ant that they have discovered points to a competition between the genetic lineages R and W. R seems to be winning because only RR zygotes develop into queens, whereas with even one copy of W, the RW zygotes develop into sterile workers. Thus, W cannot transmit to the next generation through the male line. Besides, if RR queens produced haploid males parthenogenetically, and workers remained sterile, as is the norm in most social Hymenoptera, W would be doomed. Yet, W persists by skewing some of the RW zygotes into male development and also rescues them from sterility (which is normally the fate of diploid males) by inhibiting syngamy and making the males chimaeric. It further promotes its transmission to the next generation by preferentially transferring to the germ line and relegating R more to the soma.

In summary (box 1):

R oocytes + R sperm (with syngamy) = diploid RR queens

R oocytes + W sperm (with syngamy) = diploid RW workers

R oocytes + W sperm (without syngamy) = chimeric R+W males

Box 1. Overview of the crazy ant's mode of reproduction.

Thus, we seem to have a reasonable model of reproduction in the crazy ant, however novel and bizarre. Furthermore, that intragenomic conflict leads to such a peculiar form of reproduction seems to be a reasonable argument. This knowledge and interpretation open up myriad other questions concerning both the biology and ecology of the crazy ant and the possible molecular mechanisms of the multiple ways in which established norms of reproduction are violated. Why do only the RR zygotes develop into queens? Why not the RW? How does the W genome channel some RW zygotes into male development? Why not all of them or more of them? How does the W genome prevent syngamy? How is the meiotic drive achieved to overrepresent the W genome in the sperm? Is underrepresentation in the somatic cells necessary for overrepresentation in the sperm? Understanding such molecular mechanisms that permit violation of reproductive norms will be sure to enrich our understanding of cell and molecular biology. Perhaps our understanding of diseases such as cancer and our ability to prevent or treat them are being severely handicapped by our assumption that cells and biomolecules strictly obey the simplified picture presented in our textbooks. Understanding out-of-the-ordinary, non-model systems such as the crazy ant should unleash our powers of imagination about what might be going wrong in the diseased state.

Then, there are unanswered evolutionary questions. Do RR queens prefer to mate with R or W males or utilise stored sperm of the R or W kind? If they mate with R males, they will make queens but no workers. If they mate with W males, they will make workers and males, but the males will suppress the R genome in the next generation. Why can't the RR queens produce R males parthenogenetically as in other species, or do they also do that? How do these possibilities play out in their attempt to achieve an optimal sex ratio and an optimal number of workers? Answers to such questions will likely shake up more textbook knowledge, but eventually make our theoretical understanding of evolutionary principles more robust.

This discovery of such an unusual reproductive system also raises two fundamental questions. How does such a bizarre form of reproduction arise in the first place, and what does it mean for the biology of the species? We may have some clues on both counts, but there is clearly a promising line of research ahead. We discuss below the possible causes and consequences of the crazy form of reproduction of the yellow crazy ant.

3. Evolutionary origins

Some clues about the evolutionary origin of the crazy ant's most unusual form of reproduction may be buried in the facts that the crazy ant belongs to the order Hymenoptera, and that it is a social insect. Hymenopterans already have an unusual mode of reproduction. Females lay unfertilised eggs to produce haploid sons and fertilised eggs to produce diploid daughters. Thus, the haploid males produce sperm that are clones, leading to unusual asymmetries in genetic relatedness. Females are related to their full sisters by 0.75 and to their brothers by 0.25, both deviating from the 0.5 expected in diploid organisms. Moreover, males have neither sons nor fathers. Such oddities in kinship are among the factors that have promoted extreme levels of cooperation and altruism in some Hymenoptera, namely ants, bees, and wasps (Hamilton 1964a, b; Wilson 1971; Gadagkar 1997; Hölldobler and Wilson 2009). Oddly enough, the same kinship oddities seem to make social insects perhaps the best examples of intragenomic conflict (Queller 2003; Burt and Trivers 2006; Pegoraro *et al.* 2017; Matsuura 2020; Oldroyd and Yagound 2021).

4. Conflict and cooperation

Natural selection, by definition, involves competition between alternative phenotypes in 'the struggle for life', to use Darwin's phrase. Such competition or conflict can occur between different species, populations of the same species, individuals of a species, cells inside an individual's body, and even between chromosomes, genes, or pieces of DNA inside the cell. Not surprisingly, competition and conflict have been the major focus of many evolutionary biologists.

On the other hand, we also see spectacular forms of cooperation and collaboration within and between individual bodies and even between different species. Unless some 30,000 genes work in concert in the 'parliament of genes', to use a phrase coined by Egbert Leigh, our bodies would not be able to function with the remarkable precision and efficiency that they do (Leigh 1971; Scott and West 2019). However, neither would we have food to eat if flowering plants and honey bees had not made a mutualistic pact to trade pollen and nectar for pollination services, to take just one example (Bronstein 2015).

Often, those who study competition and conflict are, however, different from those who focus on cooperation and mutualism. A false dichotomy between cooperation and conflict is sometimes articulated, suggesting that some evolutionary biologists are unnecessarily obsessed with conflict and ignore the myriad examples of cooperation. It is easy to spin a moral angle to these seemingly alternate choices as topics of study. In *Evolution by association,* Jan Sapp recounts the history of the many twists and turns in the real and perceived obsessions with conflict and cooperation (Sapp 1994). However, a closer inspection makes it clear that cooperation and conflict are closely intertwined and that organisms always have to balance these two seemingly opposing forces. Considering various levels of biological organisation, from genes to ecosystems, it is often the case that conflict at lower levels can lead to and may be essential for cooperation at higher levels (Gadagkar 1997). There is also a growing appreciation of how conflict at lower levels (e.g., genes) is managed and prevented from wrecking the smooth functioning at the higher levels (e.g., individuals) (Burt and Trivers 2006; Scott and West 2019). The gene's eye-view perspective shows how the tendency of individuals to cooperate and even altruistically sacrifice themselves to help each other may be driven by the conflict between their 'selfish' genes (Williams 1966; Dawkins 1976; Burt and Trivers 2006; Ågren 2021).

5. Intragenomic conflict

Intragenomic conflict can lead to bizarre manifestations in the genetics and reproductive biology of organisms, most notably a non-Mendelian pattern of inheritance. Genes that distort Mendelian transmission and enhance their own transmission to future generations relative to the alternative allele are said to possess 'drive', or more specifically 'meiotic drive' (Sandler and Novitski

1957). Drive can be achieved in many ways, although not all of them may qualify for the strict definition suggested by Sandler and Novitski (1957).

One way is to replicate faster than the alternative allele. Transposable elements employ a clever way of overapplication; they make copies of themselves and jump to different parts of the genome and even between individuals of the same and other species. First discovered by Barbara McClintock in maize, and since discovered and studied in many species of prokaryotes and eukaryotes, they have been implicated in health and disease and genome function and evolution (Burt and Trivers 2006; Bourque *et al.* 2018).

Another way is to interfere with the transmission of the alternative allele or even to kill it. B chromosomes are masters at this strategy. In the parasitoid wasp *Nasonia vitripennis*, for example, some strains carry a selfish B chromosome in the male lines. Upon reaching the fertilised egg along with the rest of the chromosomes of the male, it inactivates all the male-derived chromosomes except itself. The fertilised egg, which now has only the haploid functional complement of chromosomes from the female and the B chromosome from the male, develops into a male (as is the norm in all Hymenoptera; see below), allowing the B chromosome to transmit to the next generation (apparently it cannot do so through the female line). Indeed, the B chromosome of *N. vitripennis*, also called PSR (paternal sex ratio), has been dubbed the 'most selfish genetic element known' and 'ultra-destructive' (Werren *et al.* 1987; Nur *et al.* 1988; Burt and Trivers 2006).

A third way to achieve drive is exclusively available when genes pass through the female line. During spermatogenesis, males undergo meiosis to produce four viable, haploid spermatocytes. On the other hand, for reasons that we do not understand, female meiosis results in only one viable, haploid oocyte and three inviable polar bodies, one at the end of each of the two meiotic divisions. When all is fair, any gene (allele) or chromosome has only a 50% chance of ending up in the viable oocyte, thus passing on to future generations. Here is an opportunity to cheat and get into the oocyte, more often than the alternative allele or chromosome, a phenomenon appropriately called 'gonotaxis' (Burt and Trivers 2006; Searle and de Villena 2022). Many genetic elements have exploited this opportunity, including the W genome of the yellow crazy ant, as we have seen above.

Perhaps the best-known example is the case of chromosome 10 in maize which comes in a standard and knobbed version. The knobbed version transmits to the oocyte more often than the standard version. Such drive is made possible by knobs on the chromosome that function as additional 'neocentromeres', which also attach to the spindle facilitating their movement to the periphery of the meiotic arena and preferential transmission to the oocyte. It is fascinating that while one copy of each of the standard and knobbed chromatids goes to each of the four products of the second meiotic division (because the cells containing the knobbed chromatids are in the periphery, and only one of the cells in the periphery become the viable oocyte), the knobbed chromosome has an advantage. One knobbed chromatid does end up in the polar body and the other in the oocyte, while both normal chromatids end up in the polar bodies. The knobbed chromosomes have no advantage (drive) in males as all four products of meiosis become viable sperm (Burt and Trivers 2006).

6. Male chimaerism

An equally remarkable feature of the bizarre reproductive system of the yellow crazy ant is that the males are chimaeras of haploid cells belonging to two different genetic lineages. It would be most interesting to know if such male chimaerism has any consequence for the biology of the species. Males are effectively haploid as each of their cells is haploid with a single copy of the genome of one of the genetic lines. However, the two genetic lines are differently represented in the sperm produced by the male because the W is overrepresented compared to the R. Nevertheless, it is not evident if and how this will alter the genetic relatedness in the colonies of this species with possible downstream effects on the evolution of cooperation. Could there be other consequences?

The paradox of chimaerism is that it is extremely rare but very widely known, at least in popular culture. The 'original' chimaera in Greek mythology was a fire-breathing combination of a lion, goat and snake. *Narasimha*, the man-lion, is a revered incarnation of lord Vishnu in Indian mythology. Numerous fanciful stories of the good and evil superhuman powers of such chimaeras abound in the popular cultures of many countries. In real life, chimaeras, defined as individuals with cells of different genotypes, are occasionally observed in humans and other animals and are likely to be accidents of development. They sometimes arise from the accidental cross-connections between the blood vessels of fraternal twin embryos or by the accidental fusion of multiple gametes (Yu *et al.* 2002). When cells are similarly exchanged between male and female embryos, it leads to a condition called 'freemartinism', resulting in infertile embryos with the XX/XY genotype. Freemartins have been observed in cattle and less frequently in humans (Szczerbal *et al.* 2022).

There are, however at least two examples of obligate chimaerism. One is the case of germline chimaerism observed in the marmoset *Callithrix kuhlii*, formed by the placental chorionic fusion and exchange of cell lines between fraternal twin siblings. This case is interesting because chimaerism is not restricted to blood cells but is also present in many somatic tissues and, most interestingly, in the germ line too. The latter means that individual marmosets can transmit alleles derived from their siblings to future generations. This has fascinating sociobiological implications for the evolution of relatedness-based parental care and sibling rivalry (Ross *et al.* 2007).

The case of some deep-sea anglerfishes is equally interesting. Here, dwarf males permanently attach themselves to conspecific females, presumably to overcome the difficulties of finding a mate, which must be severe in the deep sea. The attachment is not just permanent, but it also involves the fusion of the male and female tissue sufficiently for them to have a common, shared circulatory system. This should normally result in histocompatibility-based tissue rejection by the bodies of both parties, but that does not happen. The remarkable reason for this seems to be that the anglerfishes have modified their immune system to be able to tolerate the foreign tissue. How then do they deal with other parasites and infections is not clear. The advantage of such a system for finding mates for sexual reproduction is obvious, and indeed, it must be so great as to result in somehow downgrading their immune systems. Anglerfish chimaerism is necessitated by their unusual reproductive strategy that may be highly advantageous in the deep-sea environment (Isakov 2022).

Neither the marmoset chimaerism nor the anglerfish chimaerism help us to speculate on the consequences of male chimaerism in the yellow crazy ant. But it does appear that the chimaerism of the yellow crazy ant is more advanced because all males have cells from two different lineages throughout their bodies. One possibility is that such chimaerism is the inevitable result of intra-genomic conflict. In that case, does the ant pay a price? Only more studies of the biology of the species can tell.

Moreover, burning questions remain about how syngamy is prevented and how males with two genomes throughout their bodies develop into males. Yet another complication created by the unusual reproductive system of the yellow crazy ant is that the W genome transmits from one generation to the next only through the male line. Thus, there is no scope for any recombination events. The lack of recombination in the W genome must have consequences for the accumulation of mutations and its rate of evolution. These are all most interesting topics for future study.

7. Ecological consequences

As we have seen, the haplodiploid sex-determination system in hymenopterans opens up the possibility of the evolution of very unusual reproductive strategies. The complex and fascinating reproductive system in *A. gracilipes* is only the latest discovery in the burgeoning line-up of similar unusual reproductive systems being discovered in ants. For example, hybrid interlineage genomes and double clonal reproduction have been found in invasive ants such as *Wasmannia auropunctata* (Fournier *et al.* 2005), *Vollenhovia emeryi* (Okhawara *et al.* 2006; Kobayashi *et al.* 2008), *Paratrechina longicornis* (Pearcy *et al.* 2011), and *Cardiocondyla kagutsuchi* (Okita and Tsuchida 2016). As the mechanisms behind such reproductive strategies get unravelled, they reveal new questions related to their consequences. For example, why do many invasive ants display unusual reproductive strategies? Are the unusual reproductive strategies discovered in many invasive ants a cause for their invasion success or, instead, an effect resulting from a frantic race for survival in a new environment? Do such unusual reproductive strategies impact the bearer of these traits by conferring better adaptability, productivity, and spread in new environments?

It is becoming increasingly evident that such unorthodox reproductive strategies in some ants could at least partially explain their success as global invaders (Kronauer 2023). The reproductive system in *A. gracilipes* described above can help surpass several reproductive barriers posed in the new environment. For example, a single mated queen, even without her retinue of workers, has all the available genetic raw material and information available to establish a new colony. The segregation of queen and male gene pools as two distinct lineages and the production of workers as hybrids of these two segregated lineages may help the species to achieve a golden mean of benefits associated with asexual and sexual reproduction without the associated costs. On the one hand, the progeny of a single invading queen can still undergo sib-mating without suffering inbreeding depression and can escape the mate-related component of Allee effects wherein small populations might result in mate scarcity that eventually may lead to negative per capita growth rate and even population crashes (Foucaud *et al.* 2010; Mesgaren *et al.* 2016). Avoiding Allee effects operating on small populations allows the invasive species to establish itself in the new environment. On the other hand, the availability of a hybrid worker lineage can help maintain genetic diversity within the colony, allowing the species to escape founder effects due to low genetic diversity typically associated with founding populations. In a polygynous species like *A. gracilipes* that forms supercolonies in the invaded environments, the worker lineage may carry a broad range of alleles, depending on the parent lineage, creating an ideal situation for the operation of social heterois (mutualistic benefits from genetic diversity at a single locus across individuals within that group) boosting colony fitness via more efficient division of labour, better adaptability to the new environmental conditions, occupation of new ecological niches, and higher resistance to pathogens and diseases (Burke and Arnold 2001; Nonacs and Kapheim 2007).

8. Closing comments

The reproductive system of the yellow crazy ant is crazy indeed! The discovery of such an unusual system of reproduction raises many questions about how such a system evolved and what it means for the biology and ecology of the species, and indeed, for the species with which it interacts. What may be less obvious is that this study demonstrates the close connection between basic research and its consequences for applied research. The basic aspects related to the behaviour, population, reproduction, and evolutionary trajectory of a species almost always have strong implications within an applied context, as seen clearly in the case of the crazy ant's invasion potential. As ecology expands its ambit, compartmentalisations such as 'basic ecology' and 'applied ecology' may become inevitable and may even be used to demarcate selective funding for research. However, such artificial compartments created for the convenience of managing research can often become stumbling blocks in fully comprehending the manifold ecological factors operating on a species. These artificial compartments create information islands, distanced intellectually by blurred connections, often becoming invisible in time. It is essential to utilise multiple vantage points to create interconnections to gain a holistic understanding of any species.

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Author contributions

RG conceptualised the article and all authors wrote parts of the first draft and edited and approved the final version.

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