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To have and not to have sex: when multiple evolutions of conditional use of sex
elegantly solve the question in the ant genus *Cataglyphis*

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Organisms use an amazingly large diversity of mechanisms to pass on their genes to the next generation. Sex is ancestral in eukaryotes, where it remains the most widespread way of reproduction. By combining one's genes with those of a partner, sex entails a dilution of one's genes at each generation. Evolution has been particularly creative in devising mechanisms allowing females to avoid this dilution, from classical parthenogenesis to the elimination of male genes after fertilization (Bell, 1982). Moreover, the term parthenogenesis include various forms. Parthenogenesis can be used for female (thelytoky) or male (arrhenotoky) production and it can be associated with different cytological mechanisms, from strict clonality to meiotic division with the fusion of two of the four products of meiosis to restore diploidy (Suomalainen, Saura, & Lokki, 1987). Understanding the evolution of these diverse reproductive systems remains one of the most exciting and longstanding questions in evolutionary biology. By characterizing the reproductive systems of 11 species from the thermophilic ant genus *Cataglyphis*, in this issue of *Molecular Ecology*, Kuhn, Darras, Paknia, & Aron (2020) show the high lability of parthenogenesis, with multiple independent evolution of facultative thelytoky from sexual ancestors. The diversity of life history traits and social characteristics of this genus (e.g. mode of colony foundation, female polyandry) provides a unique and exciting opportunity to investigate the social and environmental factors driving the evolution of reproductive systems in social Hymenoptera.

Since the first discovery of a peculiar mode of reproduction combining sex and thelytoky in the ant *Cataglyphis piliscapa* (formerly *C. cursor*), where the queen produces workers sexually but most new queens by thelytoky (Pearcy, Aron, Doums, & Keller, 2004), the democratisation of genetic analysis has led to the discovery of tens of other species using thelytoky. The recurrent evolution of thelytoky in hymenopterans may be facilitated by the release from constraints on the cytological mechanisms allowing the production of offspring from unfertilized eggs because they use parthenogenesis for producing haploid males (Rabeling & Kronauer, 2013). Eusociality could also be a positive driver of thelytoky as the occurrence of two female castes, workers and queens, offers the opportunity to conditionally use sex according to the caste being produced. All species with conditional sex use thelytoky for producing queens and sexual reproduction for producing workers (Goudie & Oldroyd, 2018). This combines the benefits of a higher transmission of genes by asexual reproduction with those of a genetically diverse sexually-produced worker force. In some species with conditional sex, the queen mates with males that are all from the same genetic lineage and that is distinct from the queen's, leading to the sexual production of highly heterozygous interlineage hybrid workers (social hybridogenesis). To date, the genus *Cataglyphis* is the only one known to harbour species using the three types of reproduction, i.e. classic

haplodiploidy and conditional sex with or without social hybridogenesis (Aron, Mardulyn, & Leniaud, 2016) (Figure 1).

By sampling 11 *Cataglyphis* species mainly from the northern range of the group distribution, Kuhn, Darras, Paknia, & Aron (2020) nicely complete the picture of the distribution of thelytoky in this group (figure 1). Their investigation rests on an impressive sample of 211 colonies (9-37 colonies per species) and the analysis of 349 mother and 159 daughter queens and 1,172 workers (about 6 per colony). They indirectly determined father genotypes via the spermathecal content of the mother queen and the comparison of mother queen and worker genotypes. Out of nine species for which they were able to characterize the reproductive system, they discovered six species using conditional sex, five of which used social hybridogenesis, raising the percentage of *Cataglyphis* species using conditional sex to nearly 50% (Figure 1). Using a phylogenetic approach based on a Bayesian consensus tree, built on seven nuclear loci and one mitochondrial locus, they confirmed that the ancestor of *Cataglyphis* had a classical haplodiploid reproductive system, and that both conditional sex with and without social hybridogenesis evolved independently many times (up to five times within the *altisquamis* species group). This highlights the evolutionary lability of thelytokous reproduction. Their results even suggest that speciation occurred in social hybridogenetic species, which is an exciting prospect as speciation of parthenogenetic species is considered to be very rare (Bell, 1982). How the divergent lineages of social hybridogenetic species evolved in the first place and could even give rise to new species remains a puzzling question that would merit further investigation. Precise assessment of gene flow among lineages using high-throughput sequencing would likely be useful in this respect.

Strategies that combine sexual and asexual reproductions get the best of both, by keeping the genetic advantages of occasional sex while paying lowered costs of sex (D'Souza & Michiels, 2010). This applies to conditional sex as expressed in *Cataglyphis* and other ants, where the queen maximizes gene transmission while ensuring genetic diversity within and among offspring. However, if thelytoky is a labile trait that does not suffer strong evolutionary constraints, as Kuhn, Darras, Paknia, & Aron (2020) showed, why then is conditional sex not more common? One element of answer is that workers have ovaries in most ant species, so that the evolution of thelytoky by the queen may entail its use by workers and result in heightened reproductive conflicts between the queen and workers (Goudie & Oldroyd, 2018). Multiple mating by the queen, by reducing worker-worker relatedness, limits reproductive conflicts since, collectively, workers should prefer rearing new queens thelytokously produced by the mother queens (worker-queen relatedness: $r = 0.5$) rather than by workers (worker-worker relatedness: $r < 0.5$ for

polyandry > 2). The assumed ancestral origin of polyandry in *Cataglyphis* (Aron, Mardulyn, & Leniaud, 2016) might thus have facilitated the recurrent emergence of conditional sex in this genus. As proposed by Kuhn, Darras, Paknia, & Aron (2020), conflicts may also be prevented under social hybridogenesis if interlineage workers suffer from hybrid sterility, as seems to be the case. Another potential obstacle for the evolution of thelytoky is linked to its cytological mechanism. Meiotic thelytoky with central fusion, as observed in *Cataglyphis*, increases homozygosity for loci located far from the centromeres while keeping high heterozygosity in loci close to the centromeres, thereby resulting in heterogeneous level of inbreeding throughout the genome. While the consequences of inbreeding are well known in sexual and selfing species (Charlesworth & Willis, 2009), their extent in the context of meiotic thelytoky with central fusion is not clear and would merit further empirical and theoretical studies. Last but not least, sexual conflicts may constrain the evolution of conditional sex because males are still required for mating but they received no fitness returns when new queens are produced by thelytoky of the queen. Strong selective pressures may thus favour mechanisms that allow males to transmit their genes such as occasional parthenogenetic production of males and new queens by workers (arrhenotoky and thelytoky, respectively), and occasional sexual production of new queens by the mother queen.

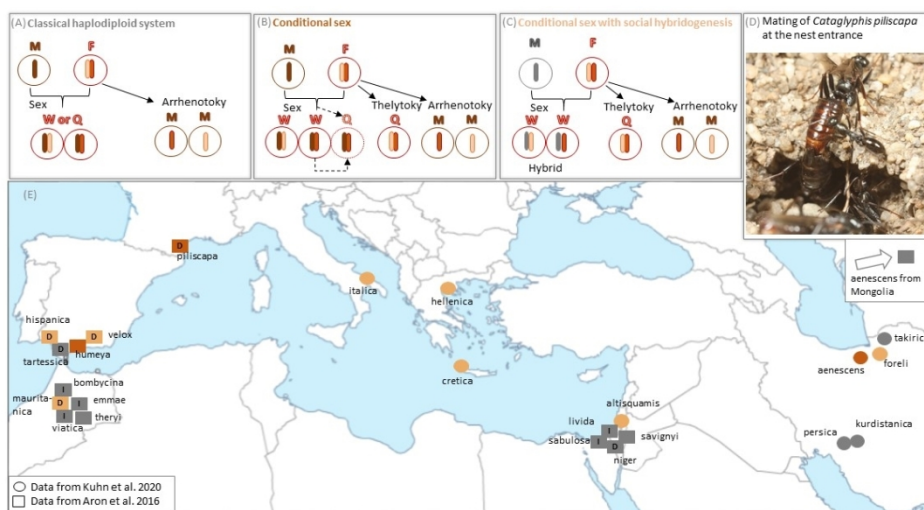
The diversity of reproductive systems uncovered in *Cataglyphis* by Kuhn, Darras, Paknia, & Aron (2020) paves the way for investigating the social and environmental factors favouring the evolution of thelytoky. Two main modes of colony foundation occur in ants and both can be found in *Cataglyphis*: independent colony foundation where the queen founds the new colony alone, after dispersal by flight, and dependent colony foundation where the queen founds the new colony with the help of a worker force, so that selection never acts on the queen alone. So far, when the mode of colony foundation is known, thelytoky has only been observed in species with dependent colony foundation ($n = 4$), in contrast with sexually reproducing species that use either dependent or independent colony foundation ($n = 7$) (Figure 1). By avoiding strong selection on the queen during colony foundation, dependent colony foundation could favour the evolution of thelytoky by reducing the potential costs of inbreeding and of producing genetically similar queens. More studies are needed to confirm this association. A second testable hypothesis is that sex tends to be favoured under stressful environments and/or with high biotic interactions (Bell, 1982). In *C. velox* social hybridogenetic populations are found in arid lowlands that are the typical habitat of these thermophilic ants, whereas mountainous regions may be less favourable and harbour sexual populations (Darras, Kuhn, & Aron, 2019). Interestingly, in their study, Kuhn, Darras, Paknia, & Aron (2020) found a large frequency of thelytoky in species from the Northern parts of the

distribution of the genus (Figure 1). Whether this is due to phylogenetic constraints or environmental factors still remain an open question that could be tackled in future works thanks to the high evolutionary lability of thelytoky in this group.

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Figure 1: the three reproductive systems found in *Cataglyphis* and their distribution. (A) Under the classical haplodiploid system, females (workers and new queens) are produced sexually and males are produced by arrhenotokous parthenogenesis. In many species, workers can produce males (not shown), usually after queen death. (B) Under conditional sex, workers are produced sexually, and both males and new queens are produced parthenogenetically. In some cases, new queens can be produced sexually either directly by the mother queen or by thelytokous reproduction of workers (dotted queen and lines). (C) Under conditional sex with social hybridogenesis, the queen mates with males that are all from the same genetic lineage and that is distinct from the queen's and uses sex for producing hybrid workers and parthenogenesis for producing new queens and males. (D) A queen of *C. piliscapa* re-entering her nest while dragging a male *in copula*. Only the rear of the queen's abdomen is visible in the gallery, with the male clawing to the outside soil. (E) Distribution of the three reproductive systems (haplodiploid in grey, conditional sex in orange, and conditional sex with hybridogenesis in beige). When known, the modalities of colony foundation are given ((I) for independent colony foundation and (D) for dependent colony foundation). Conditional sex (with or without social hybridogenesis) seems more prevalent in species from the Northern area and associated with dependent colony foundation. Data are based on Kuhn, Darras, Paknia, & Aron (2020) (circle) and Aron, Mardulyn, & Leniaud (2016) (square) and on the original papers cited in them.



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