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NEWS AND VIEWS

PERSPECTIVE

Two lineages that need each other

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In ants as in bees, a diploid female is either a reproductive or worker. In honeybees, female larvae fed a high protein substance known as 'royal jelly' become reproductives, while those not fed the necessary nutrients become workers (Linksvayer *et al.* 2011). Feeding experiments in ants suggested that like honeybees, the fate of a diploid female egg is usually determined as a larva by food supply (Brian 1951). It was thus unexpected to discover about 15 years ago (Volny & Gordon 2002; Cahan & Keller 2003), using microsatellite markers, that in some populations in the harvester ant genus *Pogonomyrmex*, there is an association between genotype and reproductive status. There are two interdependent lineages. Matings between a reproductive and a male of the same lineage produce daughter reproductives, while matings between a female reproductive and a male of the other lineage produce daughter workers (Fig. 1). The haploid males are produced from unfertilized eggs. The two lineages need each other because a colony cannot produce offspring colonies without reproductives, and it cannot raise and maintain reproductives without workers. In this issue of Molecular Ecology, Romiguier *et al.* use RNA sequencing to demonstrate a similar system in *Messor*, another harvester ant genus.

The dependent-lineage system raises intriguing evolutionary questions. One is how this process is related to hybridization. The first, and original sense of 'hybridogenesis', described in frogs, is a hemiclonal mode of sex determination that produces two distinct sympatric genomes. In ants, however, diploids are female, and the developmental fate of a diploid egg is not due purely to genetic factors. In *Pogonomyrmex* populations with the dependent-lineage system, mated queens produce worker and reproductive eggs in the ratio in which they mated with the same and other lineages (Schwander *et al.* 2006). But colonies do not produce adult reproductives until the colony has reached a mature size, at about 5 years in *P. barbatus* (Gordon 1995). Thus, the decision whether to produce reproductives is in part made by workers, who apparently eat the reproductive eggs while the colony is small and young. It is possible that the process that leads to the development of reproductives requires some kind of special feeding from the workers, as in honeybees and other species of ants. All of this contributes to the determination of the reproductive status of females.

'Hybridogenesis' in ants sometimes refers to the hypothesis that the dependent-lineage system is the result of hybridization between related sympatric species. This hypothesis for *Pogonomyrmex* harvester ants is controversial and has not been supported by phylogenetic evidence (Anderson *et al.* 2008; Sirviö *et al.* 2011; Mott *et al.* 2015). It seems that there may have been hybridization in the past, but not in the present, and that even within populations, different systems for producing workers and reproductives may be at work. When we have a broader set of examples of species with dependent-lineage systems, it will be interesting to consider whether the origins of such systems are in fact related to hybridization among related species.

Another use of 'hybrid' is that workers are produced by two independent lineages. They are 'hybrids' in the sense that they are the product of two lineages without gene flow between them. But those two lineages are both contributing to the production of colonies, with parent colonies of the same species, in a single species that cannot persist without both lineages. Thus, in the dependent-lineage system, female reproductives and workers are not hybrids in the usual sense of having parents that come from different species that can each reproduce independently.

The dependent-lineage system also raises interesting ecological questions. In dependent-lineage systems, a queen must mate more than once, because a queen must mate with at least one male of each lineage to produce a viable colony with both reproductives and workers. This means, as Romiguier *et al.* point out, that species with the dependent-lineage system are likely to be among the thousands of ant species with large, population-wide mating aggregations.

Are there other ecological factors associated with dependent-lineage mating systems? This study by Romiguier *et al.*, using RNA sequencing, and the recent study by Norman *et al.* (2016), now demonstrate a dependent-lineage mating system in a second genus of seed-eating ants. An intriguing feature of the dependent-lineage system in *Pogonomyrmex* harvester ants is that the ratio of colonies of the two lineages (colonies with a founding queen of a particular lineage) tends to be strongly asymmetrical. For the same reasons that sex ratios ought to be 1:1 – the two lineages need each other – so should the lineage ratios, but they are not. In a long-term study of a *Pogonomyrmex* population, with a persistently asymmetrical ratio of colonies of the two lineages, we found no ecological differences between colonies of the two lineages in survival, mortality, nest mound size or foraging behaviour (Gordon *et al.* 2013). This suggests that the dependent-lineage system may be tenuously maintained, not by

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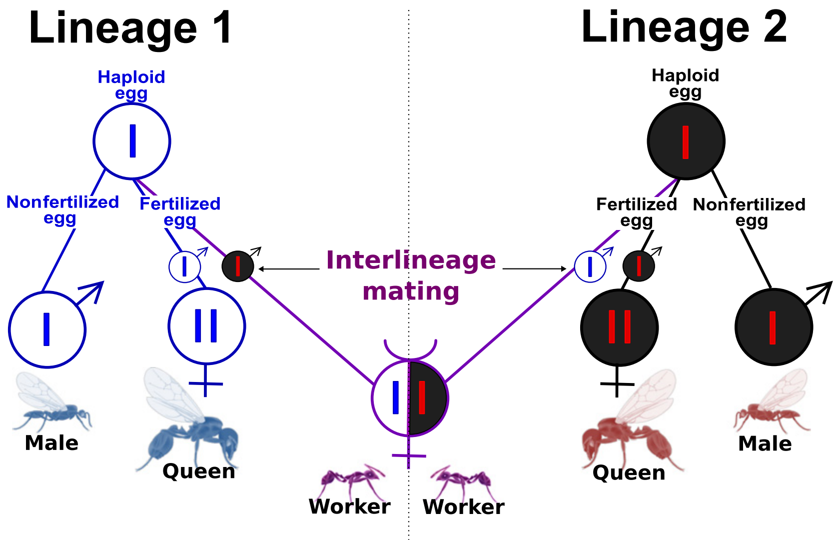

Fig. 1 The dependent-lineage system in harvester ants. Matings between a reproductive and a male of the same lineage produce daughter reproductives, while matings between a female reproductive and a male of the other lineage produce daughter workers.

ecological forces, but merely by differences between lineages in male production.

The two harvester ant genera in which such systems have been discovered, *Messor* and *Pogonomyrmex*, are within the same subfamily. But this may be a coincidence. It appears that two-lineage systems are widespread among the more than 14 000 species and about 20 subfamilies of ants (Norman *et al*. 2016). It seems likely that the more we look for these systems in other genera and subfamilies, the more we will find them. The methods introduced by Romiguier *et al*., using high-throughput sequencing, will contribute greatly to this effort. Until we investigate the ants more broadly, it is difficult to interpret the significance of the discovery of similar systems in two harvester ant genera.

An intriguing question is why it is apparently so easy for such diverse systems to evolve in ants. In the *Pogonomyrmex* system, for the males of one lineage, matings with the other lineage are a dead end, because their offspring are sterile workers. Yet each lineage needs the other, as a colony cannot raise reproductives without workers. One feature of the *Messor* system suggested here is that there may be occasional gene flow across lineages, if workers can produce males carrying alleles from both lineages; this may also occur in *Pogonomyrmex*, although population genetic data show this has not happened recently (Curry *et al*. 2010). How exactly such gene flow would contribute to the progeny of those males remains an open question. The genetic systems of ants, like everything else about them, are likely to be extremely diverse.

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