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Digest: Evolution and maintenance of androdioecy in a haplodiploid insect*

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The coexistence of hermaphrodites and males (androdioecy) is rare in both plants and animals and has hitherto remained unknown in insects. Mongue et al. report a new case of androdioecy in the invasive haplodiploid insect *Icerya purchasi*, in which hermaphrodites can only self-fertilize, but occasionally mate with males. Revealingly, *I. purchasi* shares several features with other androdioecious species such as the consequences of evolution from separate sexes, low outcrossing rates, and its colonizing habit.

Digest

Both plants and animals have diverse reproductive systems, but whereas most plants are hermaphroditic, animals typically have separate sexes. Interestingly, the intermediate state androdioecy, where males and hermaphrodites coexist, is equally rare and understudied in both kingdoms (Pannell 2002; Weeks et al. 2006). Mongue et al. (2021) have now discovered androdioecy in a worldwide invasive pest, the scale insect *Icerya purchasi*. To determine whether males participate in reproduction, and thus outcrossing, the authors assessed genetic variation among populations (F_{ST} and population structure), outbreeding (F_{IS} and selfing rate), and genotyped outbred individuals. They found very low genetic variation and population structure in 12 microsatellites in 295 individuals distributed worldwide, with 90% of the samples carrying either one of two closely related haplotypes. They also found high but variable homozygosity, in line with a high but not maximal selfing rate (82%). As hermaphrodites very likely only self-fertilize, this suggests that males occasionally participate in reproduction and hence that this haplodiploid species is functionally androdioecious (Mongue et al. 2021).

Androdioecy in *I. purchasi* appears to have evolved from gonochory (separate sexes), with females acquiring a male function. In this sense, *I. purchasi* is similar to most cases of androdioecy studied to date, in which androdioecy is derived from separate sexes rather than from hermaphroditism (Pannell 2002; Weeks 2012). It conforms with theory suggesting that males are unlikely to evolve among hermaphrodites, especially when the hermaphrodites are partially selfing (Charlesworth 1984). Because in *I. purchasi* females evolved into hermaphrodites, only males possess a penis-like structure capable of transferring sperm to another individual, as is the case for androdioecious animals evolved from gonochory (Weeks et al. 2006). Thus, hermaphrodites can only self-fertilize. This male siring advantage, although not as extreme, is also found in plants: in one wind-pollinated androdioecious plant, for example, males disperse their pollen from inflorescence stalks held above the plants. Hermaphrodites lack such stalks and as a result have reduced siring success through outcrossing (Eppley and Pannell 2007).

Importantly, because hermaphrodites of *I. purchasi* cannot mate with one another, males provide the only avenue for any outcrossing in its populations. This scenario is similar to that found in the androdioecious crustacean *Eulimnadia texana* and the nematode *Caenorhabditis elegans*. Mongue et al. (2021) show that, as in these other animals, outcrossing with males in *I. purchasi* is rare. Indeed, as they point out, hermaphrodites from *E. texana* and *C. elegans* have evolved behaviors to avoid cross-mating. Even if selfing allows the purging of inbreeding depression, in the

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long term a complete lack of outcrossing and genetic recombination will tend ultimately to condemn species to extinction. Could it be that hermaphrodites of *I. purchasi* have evolved a strategy of predominant selfing due to advantages stemming from enhanced gene transmission (Fisher 1941), but that males have been maintained in part because of lineage-level selection to maintain outcrossing (Pannell 2009, c.f. Goldberg et al. 2010)?

Another factor that could influence the maintenance versus elimination of males comes from haplodiploidy in *I. purchasi*. Hermaphrodites are diploid female-like individuals that carry within their reproductive system haploid tissue producing male gametes. One hypothesis is that hermaphrodites' male-germ tissue originates directly from a male and is inherited in a clonal fashion (Royer 1975; alternatively, this tissue may be of diploid origin). In this case, new alleles emerging in this male-germ tissue would be transmitted to all offspring produced by selfing and be quickly exposed to selection as homozygous in the following generations. Paradoxically, this male-inherited tissue could thus ease the purging of inbreeding depression, to the benefit of hermaphrodites, reducing the short-term advantages of outcrossing. Investigating inbreeding depression and selfing mechanisms in this species will help clarify the implications of males for the evolution of genetic load in populations of *I. purchasi*.

Finally, it is also significant that *I. purchasi* is an invasive species: a successful colonizer is precisely the sort of species in which we should expect to find a new case of androdioecy. Apart from the unusual and fascinating case of androdioecy in several species in the olives family, in which males are maintained by an unusual linkage between self-incompatibility and female sterility (Saumitou-Laprade et al. 2010), androdioecy tends to occur in species in which colonization probably plays a role in their persistence. In these species, self-fertile hermaphroditism probably evolved via the modification of females in response to selection for reproductive assurance during colonization bouts. Populations are thus easily established by self-fertilizing hermaphrodites, but the high siring prowess of males allows them to invade populations as migrants. In addition to the long-term implications of male maintenance for the genetic integrity of its populations, androdioecy in *I. purchasi* thus conforms to models of metapopulation dynamics or range expansions in which combined and separate sexes, respectively, are selected at different points in a cycle of population establishment and turnover (Pannell 2002).

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