One mother for two species via obligate cross-species cloning in ants

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Living organisms are assumed to produce same-species offspring[1,2]. Here, we report a shift from this norm in *Messor ibericus*, an ant that lays individuals from two distinct species. In this life cycle, females must clone males of another species because they require their sperm to produce the worker caste. As a result, males from the same mother exhibit distinct genomes and morphologies, as they belong to species that diverged over 5 million years ago. The evolutionary history of this system appears as sexual parasitism[3] that evolved into a natural case of cross-species cloning[4,5], resulting in the maintenance of a male-only lineage cloned through distinct species' ova. We term females exhibiting this reproductive mode as xenoparous, meaning they give birth to other species as part of their life cycle.

Although clonality is the most straightforward mode of reproduction, most animal species take a more complex route[6]. In sexual species, for instance, reproduction requires the interaction of males and females, which typically means that two different morphs have to be produced[7]. Such complexity is further amplified in some species, in which females produce distinct morphs depending on seasonal conditions, population density or social caste[8–11]. Even in these extreme cases, a seemingly universal constraint persists: regardless of their morphological variation, phenotypes produced by a female invariably belong to the same species. Here, we report that this rule has been transgressed by *Messor ibericus* ants, with females producing individuals from two different species.

Previous studies on *Messor* genus ants have reported conflicting results, suggesting widespread hybridizations between species that rarely co-occur in Europe[12,13]. Here, a combination of field work, population genomic analyses and laboratory experiments provide the resolution of this paradox: females of one of the species (*M. ibericus*) clone males of the other (*Messor structor*), as they need their sperm to produce the worker caste. We discuss the evolutionary history of this natural case of cross-species cloning, which suggests a domestication-like process for exploiting another species' gametes.

Queens depend on another species' sperm

Population genetic analyses revealed that *M. ibericus* queens are unable to produce workers without mating with males of another species. To reach this conclusion, we analysed genome-wide data in 390 individuals (Supplementary Table 1) from five European species of the *Messor* genus (phylogenetic tree in Fig. 1a and Extended Data Figs. 1 and 2). In ants, workers and queens of the same species are diploid individuals expected to be genetically similar[14]. Our data showed that this is not the case in one out of the five species analysed. In *M. ibericus*, all worker genomes ($n = 164$) featured a 15 times higher heterozygosity than their queens or queens and workers of the four other species ($n = 127$; average of 0.797 versus 0.047 on 43,084 polymorphic sites, two-sided Wilcoxon rank-sum test $P < 2.2 \times 10^{-16}$; Fig. 1a). Such high heterozygosity levels suggest that *M. ibericus* workers are hybrids. We confirmed this hypothesis by conducting an analysis specifically designed to detect first-generation hybrids[15], which identified all *M. ibericus* workers as such (Methods and Supplementary Table 1). With the exception of one *Messor ponticus* worker, queens and individuals of the other four species were identified as non-hybrids (Supplementary Table 1).

To identify the maternal origin of hybrid workers, we conducted a phylogenetic analysis on the maternally inherited mitochondrial genome. The resulting tree suggests an *M. ibericus* maternal ancestry, as all hybrid workers share the mitochondrial genome of *M. ibericus* sexual individuals (Extended Data Fig. 2). To identify the paternal species, we conducted a phylogenetic analysis of nuclear DNA after separating the maternal and paternal alleles of the hybrid genomes (Methods). The resulting phylogenetic tree showed that hybrid workers have an *M. structor* paternal ancestry, as all paternal alleles ($n = 164$) formed a well-supported clade with individuals of this species (Extended Data Fig. 3). Finally, a population structure analysis[16] on 5,856 genes (44,191 variants) revealed that workers in *M. ibericus* colonies had virtually equal population ancestry proportions from *M. ibericus* and *M. structor* (averaging 0.49 and 0.51, respectively; Fig. 1 and Supplementary Table 1), which confirms further that they are first-generation hybrids.

These results imply that *M. ibericus* depends on hybridization for worker production, as already observed in cases of sperm parasitism[17], in which queens exploit sperm from another lineage or species to produce workers[12,18–21]. Here, *M. ibericus* queens strictly depend on males of *M. structor*, which is a well-differentiated, non-sister

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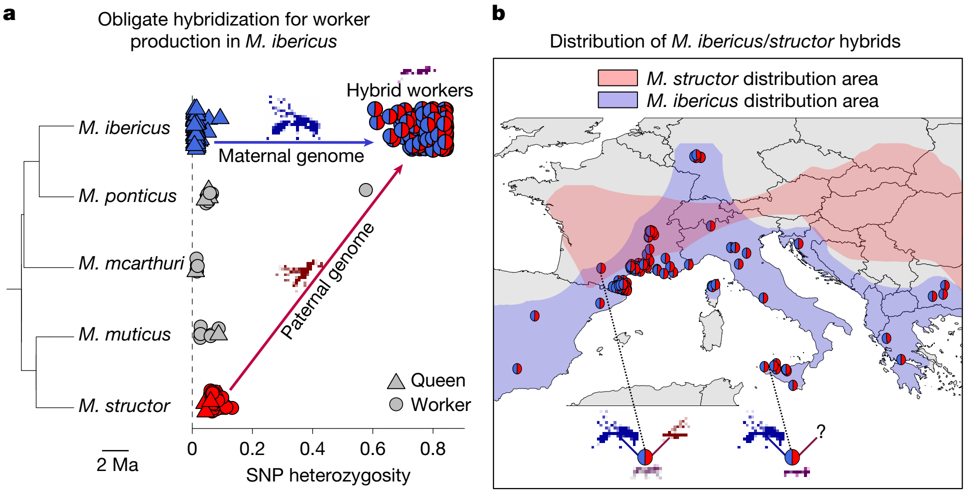

Fig. 1 | Obligate hybridization for worker production expands beyond parental species' range. a, Proportion of heterozygous positions on the total number of polymorphic sites (SNPs, $n = 43{,}084$) for queens and workers of *M. ibericus* ($n = 220$), *M. ponticus* ($n = 12$), *Messor mcarthuri* ($n = 6$), *Messor muticus* ($n = 8$) and *M. structor* ($n = 45$). Species individuals are arranged vertically according to their phylogenetic relationships (tree was built from one representative individual of each species; Extended Data Fig. 1). Each hybrid worker from *M. ibericus* colonies ($n = 164$) displays a pie chart representing its respective population ancestry proportion estimated from the fastStructure software[16], with blue and red representing, respectively, *M. ibericus* (maternal) and *M. structor* (paternal) genome proportions. Average hybrid worker heterozygosity ($n = 164$) is significantly higher than average heterozygosity of *M. structor* queens or queens and workers of the four other species ($n = 127$; average of 0.797 versus 0.047, two-sided Wilcoxon rank-sum test, $P < 2.2 \times 10^{-16}$). **b**, Map representing the distribution of sequenced hybrid workers ($n = 164$). The distribution areas of each parental species have been estimated from our sampling and reports from the literature[13,23]. Hybrid workers localized in areas where both parental species co-occur are highlighted by a picture representing an *M. ibericus* queen (blue) with an *M. structor* male (red). Hybrid workers localized in areas without the paternal species are highlighted with the same picture but with a question mark instead of the father. SNP, single nucleotide polymorphism.

species (Fig. 1a). This finding is particularly surprising because these two species do not share the exact same distribution area[22,23]. This paradox is clearly illustrated by hybrid workers being found across Southern Europe in spite of the total absence of their paternal species (Fig. 1b; 69 Mediterranean populations with confirmed *M. ibericus* but no *M. structor* colonies found). As even more compelling evidence, first-generation hybrid workers from the Italian island of Sicily are found more than a thousand kilometres away from the closest known occurrence of their paternal species. This raises the question of how queens can hybridize in such an isolated area (Fig. 1b). To solve this conundrum, we examined males from *M. ibericus* colonies more closely.

Queens produce males from two species

Morphological and molecular analyses showed that *M. ibericus* queens lay the *M. structor* males they require for worker production. By sampling 132 males from 26 *M. ibericus* colonies, we observed a sharp morphological dimorphism: 44% of sampled males displayed a dense pilosity (Fig. 2a), whereas the other 56% were nearly hairless (Fig. 2b). By conducting phylogenetic analyses including 62 hairy versus 24 hairless male nuclear genomes, we showed that the two morphs perfectly correspond to two different species (Extended Data Fig. 2). Whereas all hairy males group with *M. ibericus*, all hairless ones group with *M. structor*, which are two non-sister species that we estimated to have split more than 5 million years ago (Ma) (Methods, Fig. 2c and Extended Data Figs. 1 and 4). Multiple lines of evidence point to the production of males of both species by *M. ibericus* queens.

First, *M. structor* males share the same mitochondria as their *M. ibericus* nestmates, pointing to common *M. ibericus* mothers for the whole colony ($n = 24$; Fig. 2, Extended Data Fig. 2 and Supplementary Table 1). This nuclear–mitochondrial genome mismatch is unique to males found in *M. ibericus* colonies, as it has not been observed in any other *M. structor* individual when found in their own species colonies ($n = 53$; Extended Data Fig. 2 and Supplementary Table 1).

Second, genotyping 286 eggs or larvae from 5 *M. ibericus* laboratory colonies showed that 11.5% exclusively contained *M. structor* nuclear genome (Supplementary Note 1, Supplementary Table 2 and Supplementary Figs. 1 and 2). To confirm that such *M. structor* eggs were laid by *M. ibericus* queens and not workers, we isolated 16 queens and genotyped their newly produced eggs after 24 h. Again, we found that 9% of these eggs exclusively contained *M. structor* DNA (Supplementary Note 1, Supplementary Fig. 3 and Supplementary Table 3), which was not the case for broods produced by workers (see Supplementary Note 2 for details).

Third, beyond genetic evidence, direct observations confirmed the emergence of adult males of both species from a single queen colony. We monitored a laboratory colony headed by a single *M. ibericus* queen for 18 months, checking broods weekly. Among seven eggs that developed into reproductive adults, two were identified as *M. structor* (hairless) males, and three as *M. ibericus* (hairy) males. Genomic analyses confirmed their morphological identification, with their whole nuclear genome matching solely either *M. ibericus* or *M. structor* (individuals ORT3M1 to ORT5M5; Extended Data Fig. 1 and Supplementary Table 1). Despite those *M. structor* births, we confirmed that the whole genome of the mother queen solely matches *M. ibericus* (ORT3Q1; Extended Data Fig. 1 and Supplementary Table 1). Other adult male emergences of both species (one of each) have been observed in another laboratory colony after 19 months of brood monitoring (Extended Data Fig. 5 for a picture of live individuals).

Whereas male Hymenoptera typically inherit their nuclear genome from their mother through unfertilized eggs[24], our results demonstrate that *M. ibericus* queens can produce males without transmitting their nuclear genome. This observation points to androgenesis (that is, male clonality), whereby a male provides the sole source of nuclear genetic material for the embryo[25]. Embryos devoid of maternal DNA have been observed in other groups, with the fertilization of non-nucleate ovules[26] or the elimination of the maternal genome after fertilization[27]. In ants, both should spontaneously lead to males genetically identical to the sperm, as males are typically produced from haploid embryos through

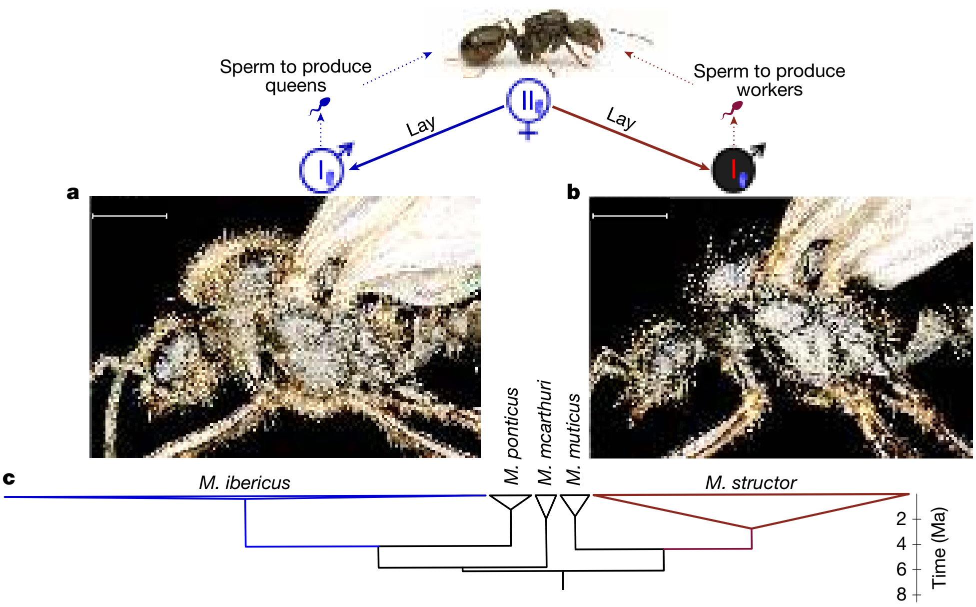

Fig. 2 | *M. ibericus* queens lay males from two different species. *M. ibericus* queens lay males belonging to different species that differ morphologically (symbolized by male symbols in blue and red for *M. ibericus* an *M. structor*, respectively) and genetically. *M. ibericus* and *M. structor* males produce sperm for producing either new queens or workers, respectively. All share the same mitochondria (corresponding to the *M. ibericus* mitochondria, depicted here in blue; Extended Data Fig. 2). **a**, *M. ibericus* male photo (hairy). **b**, *M. structor* male photo (hairless). **c**, Phylogenetic tree of 223 non-hybrid individuals. Based on 5,656 nuclear genes (2,780,573 bp) and simplified from Extended Data Fig. 1. All represented nodes have maximal bootstrap support (100). Triangle widths are relative to the number of individuals. Branch lengths are relative to divergence time estimated from Fig. 1 and Extended Data Fig. 4 (see Methods for details). Scale bars, 1 mm. Credit: The top picture of an ant is adapted with permission from a photo from Flickr (https://www.flickr.com) taken by M. Kukla. bp, base pairs.

haplodiploidy[24]. At the intraspecific level, several cases of ants cloning males from their own species' sperm have been observed[28–31]. Here, our results imply that this phenomenon has crossed species barriers, with male cloning from allospecific sperm stored in the spermatheca. Consistent with this explanation, *M. ibericus* queens are polyandrous and mate with both species' males, as we retrieved sperm of both *M. ibericus* and *M. structor* when sequencing the spermatheca content of a queen that gave birth to both species (ORT3QS1 in Supplementary Table 1 and Extended Data Fig. 3; see also the BAN1QS spermatheca, which again contains spermatozoa of both species).

Maintenance of a clonal lineage of males

The combination of obligate hybridization for worker production (Fig. 1) and cross-species cloning (Fig. 2) points to the following scenario: *M. ibericus* queens first stored sperm from another species, then began to clone males from this sperm. This pathway is consistent with the widespread observation of facultative or obligate sperm parasitism[17], a well-described phenomenon in which queens use sperm from a co-occurring lineage or species to produce their workers[15,18–21,28–30,32]. This strategy may have been selected either to benefit from potential worker hybrid vigour[17] or to prevent queen-only production due to the fixation of a caste-biasing genotype[18,32]. In the ancestral state of this scenario, *M. ibericus* exploits sperm from co-occurring *M. structor* colonies (Fig. 3a), as has been observed in other *Messor* species[12,33]. In the derived state, *M. ibericus* queens directly produce the species they depend on, resulting in a clonal lineage of *M. structor* males they maintain in their colonies (Fig. 3b).

To confirm the advent of such a clonal lineage of males, we examined the two primary subdivisions of the *M. structor* nuclear phylogeny (Fig. 3c). As expected, one subdivision corresponds to a clonal lineage, consisting exclusively of nearly identical *M. structor* males, all found within *M. ibericus* colonies and carrying *M. ibericus* mitochondria ($n = 24$; Fig. 3b,c and Extended Data Fig. 1). By contrast, we retrieved a 'wild-type' lineage, which grouped all *M. structor* castes when found in their own species' colonies ($n = 53$; Fig. 3a,c and Extended Data Fig. 1). To further confirm our scenario, we tracked the exact parental origin of each hybrid worker ($n = 164$; Methods). Consistent with occurrences of both the ancestral and derived states (Fig. 3a,b), we found that the paternal genome can belong to either the 'wild-type' or 'clonal' lineage (Fig. 3c and Extended Data Fig. 3). Although most hybrid workers were fathered by clonal males (144 out of 164), the fact that some (20 out of 164) were fathered by wild-type males confirms the recent occurrence of our ancestral state hypothesis (Fig. 3a). Consistent with our scenario, ancestral state cases were restricted to a limited geographical area where both species still co-occur (for example, eastern France; Fig. 1b, Extended Data Fig. 3 and Supplementary Table 1). By contrast, derived state cases were widespread across Europe, as maintaining a clonal lineage of males is likely to have allowed rapid expansion of *M. ibericus* beyond the natural range of *M. structor* (for example, Mediterranean Europe; Fig. 1b). This pathway seems analogous to domestication[34], as *M. ibericus* co-opted *M. structor* males into its life cycle, maintaining them as a clonal lineage rather than exploiting them from the wild.

Supporting this view, the clonal lineage exhibited extremely low genetic diversity with high genetic load compared with the wild-type lineage (average synonymous nucleotide diversity π_s of 0.00027 versus 0.0014, average ratio of non-synonymous to synonymous nucleotide diversity π_n/π_s of 0.43 versus 0.21; Supplementary Table 4). This pattern is typically observed in clonal species[35,36], after rapid range expansions[37,38] or in domesticated lineages maintained by humans[39,40]. Interestingly, clonal males also differ morphologically: in a similar way that they differ from their *M. ibericus* nestmates (Fig. 2), they also seemed hairless compared with their wild-type counterparts (Fig. 3d,e). More generally, this clonal morph differs on several other criteria, standing out as the most divergent compared with the wild-type and *M. ibericus* males (Supplementary Note 3 for details and Supplementary Figs. 4–6), akin to the morphological divergence of domesticated species compared with their wild relatives[41]. Such a stark morphological

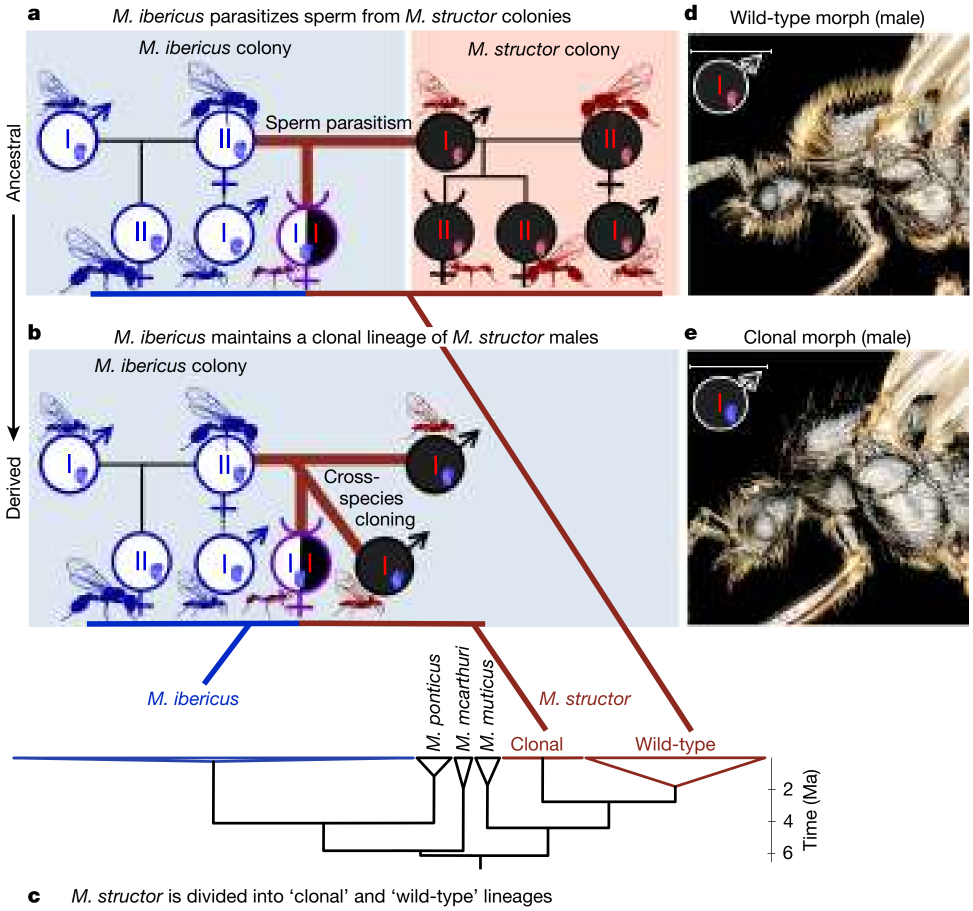

Fig. 3 | Evolution of obligate cross-species cloning from sperm parasitism is reflected by different genetic and morphological lineages within *M. structor*. **a**, Ancestral state of the *M. ibericus* reproductive system; $n = 20$ colonies deduced to correspond to this state have been sampled (Supplementary Table 1). **b**, Derived state of the *M. ibericus* reproductive system; $n = 130$ colonies deduced to correspond to this state have been sampled (Supplementary Table 1). Note that *M. structor* males have an *M. ibericus* mitochondrial genome, which is indicated with a red chromosome and a blue mitochondrion. **c**, Phylogenetic tree simplified from Extended Data Fig. 1 (as in Fig. 2c). Links to **a** and **b** are based on Extended Data Fig. 3, in which hybrid workers have been separated into paternal and maternal genomes. *M. structor* 'clonal' lineage stands for a clade composed of males from *M. ibericus* nests and the paternal genome of their worker daughters (derived state). *M. structor* 'wild-type' lineage stands for a clade composed of all castes from normal *M. structor* nests and the paternal genome of some hybrid workers found in *M. ibericus* co-occurring nests (ancestral state). **d**, Photo of *M. structor* males from *M. structor* colonies (hairy). **e**, Photo of *M. structor* males from *M. ibericus* colonies (hairless). Scale bars, 1 mm.

difference does not necessarily result from a selection process. Instead, this difference may have been randomly retained from ancestral polymorphism, or may be due to incompatibilities between the nuclear and mitochondrial genomes of the two species (Fig. 3b) or plasticity due to different rearing conditions when born and kept within *M. ibericus* nests.

To assess whether clonal males can escape their 'domesticated' situation by mating with their wild female counterparts, we conducted a detailed analysis on 45 *M. structor* genomes to detect potential hybrids (Supplementary Note 4). Our findings confirmed that such events are at present non-existent or extremely rare, as we did not identify any hybrid between clonal and wild-type lineages (Supplementary Fig. 7). Similarly to typical cases of domestication, this raises the question of whether recent genetic isolation from wild populations warrants a different species classification[42]. Further analyses therefore support the idea that clonal males still belong to *M. structor*, as phylogenetic conflict (Supplementary Fig. 8a), population genetic structure (Supplementary Fig. 8b), species delimitation inferences (Supplementary Fig. 8c,d), low F_{st} fixation index (Supplementary Fig. 9), low genetic divergence (Supplementary Fig. 10a) and high historical gene flow (Supplementary Fig. 10b) are all consistent to support clonal and wild-type lineages as part of the same species (see Supplementary Note 4 for details). Taken together, these results further support the idea that clonal males should be characterized as a domesticated lineage of *M. structor*. All in all, this means that *M. ibericus* females interact with up to three males that are morphologically and genetically distinct (*M. ibericus*, 'domesticated' *M. structor* and 'wild' *M. structor* males; Extended Data Fig. 6), laying two of them (Fig. 2) and mating with the three (Fig. 3).

Discussion

To our knowledge, females needing to clone members of another species have not previously been observed. Although cross-species cloning has been reported in hermaphrodite conifers and clams[25], these are instances of male parasites occasionally using other species' eggs. In such cases, producing males of another species is not in the interest of females, as they are incidental victims of parasitism. This contrasts with the system reported here, for which producing another species' male is not an accident, but a female life cycle requirement. We suggest defining such females as xenoparous, meaning they need to produce individuals of another species as part of their life cycle. This shows the evolution of xenoparity (xeno-, meaning 'foreign, strange, different', and -parity, meaning 'produce, bring forth, give birth'), which is the need to propagate another species' genome by means of its own eggs.

Transition towards xenoparity seems to result from sexual evolution along a parasitism–mutualism continuum. Similar to several other harvester ant species, *M. ibericus* first transitioned into obligate sperm parasitism[12,17] (Fig. 3a), a situation in which they lost the ability to produce workers by themselves due to epistatic incompatibilities[18,43] or selfish caste-biasing genotypes[32]. Although not the most straightforward path towards xenoparity, this situation might have evolved towards reciprocal sperm parasitism, a form of sperm mutualism seen in other harvester ants in which two lineages depend on each other's sperm for worker production[12,18,21]. Whether it be in the case of simple or reciprocal parasitism, dependence on males from another species is sub-optimal for queens, as it requires them to mate with two different male partners and restricts their colonies to the geographic range of their host. By producing the required species' males in their own colonies (Fig. 3b), *M. ibericus* has gained a clear advantage, as it maintains obligate hybridization while minimizing the inherent constraints (Extended Data Fig. 7). Investigating the male cloning mechanism will help to determine whether this developmental innovation is analogous to male parasitism[25] or unique to the *M. ibericus* reproductive system.

While trapped in the life cycle of a species exploiting their sperm, clonal males propagate their genome through the reproductive efforts and parental care of *M. ibericus*. In a sense, clonal males can be viewed as a perfected form of male parasites, as they are essential to their female hosts but reproduce at the expense of their ova. By depending on each other's gametes, both species have intertwined their life cycles, evolving from sexual parasitism[3] to sexual co-dependency (Extended Data Fig. 8). In spite of this, females seem to control the terms of the relationship, as our data on brood genotyping suggest that they impose the timing of male eggs' development and maturity (Supplementary Note 1). Such a situation seems akin to a sexual domestication, as *M. ibericus* controls the reproduction of a species it first exploited from the wild.

Although matching all criteria of domestication[34], the relationship we describe is both more intimate and integrated than the most remarkable examples known so far, from human-driven domestication[40] to lichen symbiosis[44]. Contrary to such examples, both partners are obligate mating partners, as the domesticating species is directly cloning the domesticated one by means of its own egg cytoplasms. Such replication of an alien genome within one's own cytoplasm echoes the endosymbiotic domestication of organelles (for example, mitochondria) within eukaryotic cells[45,46]. Clonal males may thus be regarded as organelles at the superorganism level[47,48], resulting from the integration of this alien genome into a colony that directly replicates it. This leads to colonies producing the greatest diversity of individuals, differing in terms of sexes, castes and species, each with a dedicated role within a cohesive reproductive unit. Besides revealing a reproductive mode under which one species needs to clone another, such a 'two-species superorganism' challenges the usual boundaries of individuality. Major evolutionary transition in individuality occurs when distinct entities evolve into an integrated, higher-level unit[49–51]. As two species have become sexually interdependent in such an integrated entity, evolution towards xenoparity exemplifies how such transitions can occur through a sexual domestication process.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-025-09425-w.

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