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Is meiosis a fundamental cause of inviability among sexual and asexual plants and animals?

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Differences in viability between asexually and sexually generated offspring strongly influence the selective advantage and therefore the prevalence of sexual reproduction (sex). However, no general principle predicts when sexual offspring will be more viable than asexual offspring. We hypothesize that when any kind of reproduction is based on a more complex cellular process, it will encompass more potential failure points, and therefore lower offspring viability. Asexual reproduction (asex) can be simpler than sex, when offspring are generated using only mitosis. However, when asex includes meiosis and meiotic restitution, gamete production is more complex than in sex. We test our hypothesis by comparing the viability of asexual and closely related sexual offspring across a wide range of plants and animals, and demonstrate that meiotic asex does result in lower viability than sex; without meiosis, asex is mechanistically simple and provides higher viability than sex. This phylogenetically robust pattern is supported in 42 of 44 comparisons drawn from diverse plants and animals, and is not explained by the other variables included in our model. Other mechanisms may impact viability, such as effects of reproductive mode on heterozygosity and subsequent viability, but we propose the complexity of cellular processes of reproduction, particularly meiosis, as a fundamental cause of early developmental failure and mortality. Meiosis, the leading cause of inviability in humans, emerges as a likely explanation of offspring inviability among diverse eukaryotes.

1. Introduction

The evolution of sexual reproduction (sex) is often understood through comparisons with asexual reproduction (asex) [1–5]. Whether natural selection favours sex depends in part on whether sex results in higher offspring viability, compared with asex, in the same or closely related populations. Sexually derived offspring suffer from inbreeding, outbreeding, recombination load [6] and interparental conflict [7], reducing viability. But the viability of asexual offspring is reduced by the relatively slow removal of deleterious mutations, inability to break up and form new allele combinations through mixis, homogeneous immune susceptibilities, reproductive systems evolved for sex and poorly optimized for asex, and an association with potentially deleterious polyploidy and hybridity [3,8]. Exceptions and counterexamples to most mechanisms causing viability differences are documented in the extensive literature on the evolution of sex. For example, hybridity can result in either higher viability through heterosis or lower viability through outbreeding depression [9]. No broadly applicable principle enables prediction or generalization about when sex or asex will result in greater viability.

We hypothesize that mechanistic complexities within the cellular processes of reproduction are a fundamental cause of developmental failure in eukaryotes, and therefore of viability differences between sexual and asexual offspring.

All eukaryotic sexual reproduction is based on meiosis, the highly conserved pattern of cell division used to produce haploid gametes. Meiosis requires chromosomal dynamics far more complex than the dynamics of mitosis, the basis of somatic cell division [10]. Meiosis includes all the basic mechanisms of mitosis (e.g. chromosomal replication and segregation), as well as additional mechanisms (e.g. pairing and recombination) [11], and has been described as 'the most complicated cellular process in eukaryotes' [12]. This complexity provides diverse opportunities for error [13]. For example, missing or extra chromosomes are found in 10–30% of human eggs, and derived chromosomal abnormalities caused by meiosis are the leading cause of human pregnancy loss [10,14]. Faults caused by meiosis are a documented cause of inviability in other, diverse taxa [15–17]. The hypothesis that meiotic asex results in lower viability than does mitotic asex [1] has never been tested in a formal comparative context, perhaps because few taxa employ both meiotic and mitotic asex.

However, numerous taxa employ both sex and one form of asex or the other. We test whether meiosis causes greater offspring inviability, compared with mitosis, by comparing each kind of asex with sex. Mitotic asex is the simplest way a eukaryote can produce an offspring. Sexual reproduction is more complicated, requiring both mitosis and meiosis. Meiotic asex is more complex than either mitotic asex or sex, requiring mitosis, meiosis and a mechanism of meiotic restitution [8,18] (i.e. meiosis normally renders the gamete haploid and so diploidy must be restored for most meiotically derived asexual offspring to be viable). Asex can therefore require cellular mechanisms that are either less or more complicated than sex. This observation, combined with our hypothesis that mechanistic complexity drives offspring inviability, leads to a simple model in which mitotic asex produces offspring that are more viable than closely related sexual offspring, while meiotic asex produces offspring that are less viable than their sexual kin.

To test this model, we compared the published viabilities of sexual and closely related asexual offspring across a wide range of plants and animals. Comparisons were drawn from published literature, and included eudicots, monocots, magnoliids, vertebrates, cnidarians, rotifers, platyhelminths and arthropods, including diverse insects (electronic supplementary material, S1). While sex and asex have been compared in many ways, including reproductive output [19], to the best of our knowledge, no prior compilation includes quantitative data on more than five contrasts of sexual versus asexual viabilities [5,20]. We compiled data on 44 viability contrasts that met our stringent criteria.

Our focus on a single variable across many taxa is unusual; research on viability contrasts between sexual and asexual offspring typically focus on particular cases in depth, and consider the evolutionary history, ploidy, ecology and population genetics of one or a few species. By targeting the cellular complexity of reproduction, we propose an organizing principle among the complex interacting mechanisms that influence viability, but risk losing the explanatory power of additional variables.

We therefore include in our analysis four additional variables that make clear predictions about which mode of reproduction should result in higher offspring viability. A recent transition to asex may lead to lower viability of asexual offspring because selection has had insufficient time to optimize the mechanisms of asex [21,22]. This was first documented by Stalker [23], who found that in an experimental asexual line of *Drosophila parthenogenetica*, asexual viability increased from 9 to 20% over the course of 30 generations. Similarly, in facultative asexual populations (those that engage in both sex and asex), selection for increased asexual viability may act less frequently than in exclusively asexual populations, and mechanisms that are used frequently for sex and infrequently for asex may favour sexual viability [3]. Moreover, whether asex arose in a lineage through hybridization can influence both the population genetics and the mechanisms of asexual reproduction, potentially altering offspring viability. Finally, parthenogenetic mechanisms of asex are mechanistically distinct from vegetative asexual reproduction. The relative heterozygosity of asexual versus sexual offspring, which can cause differences in viability, was not included in analyses because data are unavailable for most taxa. We therefore examined the power of a total of five variables (asex meiotic or mitotic, asex recent or not, asex facultative or not, asex of hybrid origin or not, and asex vegetative or not) to explain whether sex or asex achieves higher offspring viability.

2. Material and methods

(a) Identifying viability contrasts

To compare different modes of reproduction, we compiled a database of published contrasts between sexual and asexual offspring viabilities (electronic supplementary material S1) of plants and animals, classifying the asex in each case as either mitotic or meiotic. We defined sexual processes as those that involve the joining of the products of two meioses into an offspring, including self-fertilization, but excluding forms of automixis in which two products of the same meiosis recombine. To be included in our analysis, data had to meet a stringent set of inclusion criteria (electronic supplementary material S2). Briefly, we required that a single source provide quantitative viability data for closely related sexual and asexual offspring, along with methods and sample sizes on how those data were gathered, and that published conclusions exist as to whether the asex involves meiosis.

While many studies compare sexual and asexual reproduction in a wide variety of ways, most do not meet our criteria for inclusion. Most often, comparisons between sex and asex are not made in terms of offspring viability. Many that make viability contrasts obviously bias the comparison (e.g. [24]). Contrasts were included even if the primary source made no formal test of whether viabilities were significantly different, or declared the viability difference to be statistically insignificant, resulting in a more conservative test. Cases of haplodiploidy were excluded. If a source stated that one reproductive mode achieved higher viability but did not present data for both, or if data on meiosis in asex were not available, the case was not included in our analysis. Examples of excluded cases [24–30] are provided in electronic supplementary material S1, table S2.

We began by collecting contrasts referenced in books on the evolution of sex and asex [2,3,8,31], and by searching online bibliographic databases using a wide variety of relevant keywords. We expanded from this base by searching among references. Several additional plant contrasts were found using the COMPADRE database of plant demography [32]. However, because we needed to carefully evaluate whether each comparison met our criteria for inclusion, we took data solely from primary sources, never from secondary sources such as online databases or other compilations. In total, we read many thousands of titles, screened hundreds of papers for relevant data and examined roughly 300 papers in greater depth.

(b) Defining variables

Viability was most often defined in terms of proportion of eggs or seeds hatching or germinating, but survival through the first year or to adulthood was used for both sex and asex when this was the only available measure (as in vegetative reproduction). Measures used for each contrast are given in electronic supplementary material S1. Most comparisons in our database are from laboratory studies, but field studies were also used. Where viability was studied in multiple environments (e.g. across temperatures), we took the measure for each type of offspring in its optimal environment (i.e. the highest viability recorded for each type of reproduction). Where multiple closely related sexual or asexual populations were compared in a single study with no obvious pairing, we contrasted the mean of the sexual values to the mean of the values for each mode of asex. Cases were included when the sexual and asexual offspring were generated by the same population or same species, or when species were closely related (e.g. when one arose as an interspecific hybrid of the other), but not when data came from two distantly related species within the same large genus.

We divided asex into mitotic (without most aspects of meiosis) and meiotic (with a complete or nearly complete meiosis and mechanism of restitution). We followed published conclusions in categorizing parthenogenesis as mitotic or meiotic (electronic supplementary material S1), but acknowledge that parthenogenesis generally classified as mitotic may retain some simplified meiotic mechanism. Bulbils, shoots, buds and other forms of reproduction that do not involve a seed, egg or ovum were classified as vegetative; vegetative reproduction was assumed to be mitotic.

Low asexual viability is hypothesized to be associated with facultative asex (potentially diluting selection on asexual viability, and often tychoparthenogenetic [3]) and recently arisen asex (because there has been less time for selection to optimize asexual processes [21,22]). We therefore further classified each contrast as to whether the asex described is facultative and/or recently arisen. Asex was considered facultative if the same individual could reproduce both sexually and asexually, or produce a mix of daughters, some of whom would reproduce sexually and others asexually (as with monogonont rotifers [33]).

Published estimates of both mean generation times and dates of the origin of parthenogenesis are quite rough for most of the taxa in our dataset, often allowing for order of magnitude errors in estimates of generations since parthenogenesis arose. Given this numerical uncertainty, we treat recently arisen as a binary variable. Asex was considered recently arisen if the literature on that lineage estimates that asex arose within the last 10 000 generations (electronic supplementary material S1). This number was chosen because it yielded results consistent with most original sources' conclusions as to recentness. Other definitions of recent (e.g. at most tens of generations, or since the phylogenetic origination of the biological class) were also tested, but had no effect on our findings (analyses not shown).

Hybridity is often a key factor in the evolution of parthenogenesis. Taxa were classified as possessing asexual reproduction of hybrid origin according to the relevant literature. Where no relevant data were found, asex was assumed not recently arisen, not facultative and not of hybrid origin.

Several additional variables commonly discussed in the literature on the evolution of asex, including offspring genetic diversity and relative heterozygosity, taxon-specific differences in form and development between sexual and asexual offspring, and different mechanisms of meiotic restitution, were not included in our analysis either because data are not available for most taxa or because the variable is too complex to apply widely (e.g. most subclasses of meiotic parthenogenesis, which are defined according to variations in the order and fine mechanics of stages of meiosis and meiotic restitution, could be attributed to only one or two taxa in the dataset).

(c) Phylogenetic linear regression

Comparing viability measurements across disparate taxa, methodologies and experimenters requires care. Viability ratios, calculated as asexual viability over sexual viability within the same taxon, are directly comparable across taxa. For example, while it is difficult to interpret a comparison between hatching rates of *Daphnia* [34] in one study and survival to adulthood of *Hydra* buds [35] in another, it is informative to compare the hatching of sexually and asexually produced *Daphnia* eggs in the same study, and then the viability ratio for *Daphnia* to that of *Hydra*. Viability ratios were log transformed to provide a symmetrical contrast measure: the log of ratios 2 : 1 and 1 : 2 only differ by their sign (+1 and −1 with log in base 2), not by magnitude (2 versus 1/2). The log ratios were also more normally distributed within groups, satisfying an assumption made by our analysis.

To test the effect of five predictors (recent asex, facultative asex, meiotic asex, vegetative asex, hybrid origin asex) on log viability ratio, while accounting for the non-independence of the traits of related organisms, we performed phylogenetic linear regression. All five independent variables were included in a single initial model which was simplified using the phylostep function in *phylolm* 2.2 [36]. For each model considered, phylostep simultaneously estimates Pagel's λ and use this estimate of phylogenetic signal in a generalized least-squares model [37]. This analysis is similar to standard linear regression or multi-way ANOVA, except that the residual variation not explained by predictors is treated as being influenced by phylogenetic correlation across species. The level of that correlation is estimated from the data. The non-independence of related taxa is accounted for in calculating both the regression line and measurement of its significance. Unlike phylogenetic logistic regression (which uses a binary dependent variable), phylogenetic linear regression is robust to the risk of psuedoreplication brought about by relatively few transitions between states [38]. The function phylostep employs an Akaike information criterion-based algorithm (used here with default parameter values) to choose a set of variables that balance explanatory power with model simplicity [36,39].

As no existing phylogeny includes all of the taxa in figure 1, we assembled a composite tree drawing on multiple sources. Relationships among plants followed version 4 of the Angiosperm Phylogeny Group's classification [42]. Relationships among animals were based on multiple source for arthropods [43,44], vertebrates, particularly squamate reptiles [45], and the several metazoan phyla [46]. We computed branch lengths for the tree using the *compute.brlen* function in *ape* 3.1–4 [47] with default parameter values. Varying our assumptions about branch lengths had no effect on our conclusions.

3. Results

Forty-four viability contrasts (18 plants and 26 animals; figure 1) met our criteria for inclusion. While each contrast was based on data from an individual reference [7,9,23,33–35, 40,41,48–75] (see the electronic supplementary material, table S1 for details on each contrast), in many cases, additional sources were key to understanding the evolutionary history (e.g. the relatedness of the populations) and underlying biology (e.g. mechanism of asex) of each system [60,71,76–105].

Model selection resulted in a model with only two independent variables: meiotic asex and recent asex. Whether asex is meiotic or mitotic is a highly significant ($p < 0.0005$) predictor of whether asex achieves lower or higher viability than does sex. This result is not caused by phylogenetic correlations in trait values ($\lambda = 3.24 \times 10^{-7}$). Recent asex, despite its inclusion in the final model, is not significant ($p = 0.1$); we can reach no

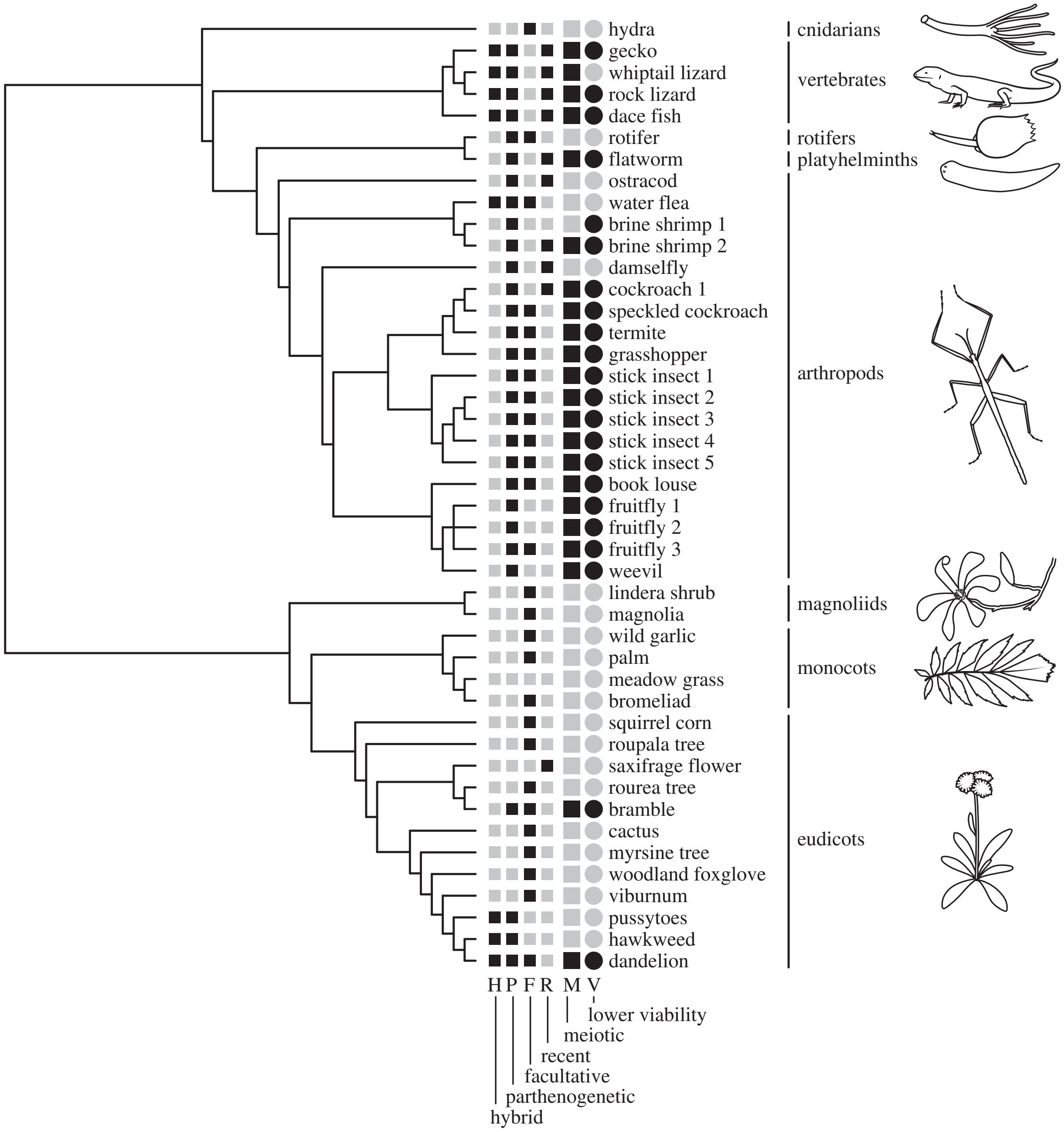

Figure 1. Phylogenetic distribution of traits. Whether asex results in lower viability (black circles) or higher viability (grey circles) than sex is compared with five explanatory variables. If asex is meiotic (black squares) rather than mitotic (grey squares), recently arisen (black squares) rather than ancient, facultative (black squares) rather than obligate, parthenogenetic (grey squares) rather than vegetative, and of known hybrid origin (black squares), the respective hypothesis predicts that asexual offspring will experience lower viability. Except in two cases ('whiptail lizard' and 'brine shrimp 1'), M correctly predicts V. This relationship is surprisingly consistent across tremendously divergent taxa, including budding *Hydra* [35] (Cnidaria), bulbil-producing *Allium* [40] (monocots), mitotic parthenogenetic damselflies [7] (Insecta) and meiotic parthenogens including brambles (eudicots) [41] and geckos [9] (Vertebrata). There is no significant correlation between V and any of the other predictors.

firm conclusion on its effect on viability. Facultative asex, hybridity and vegetative asex, when included in the model, are not significant predictors of viability ratios ($p > 0.1$).

Forty-two of the 44 viability contrasts support our thesis: when asex involves meiosis, sexual offspring are more viable than asexual offspring (figure 2). When asex does not involve meiosis, asexual offspring are more viable. We found only two counterexamples. Meiotic asexual whiptail lizards achieve a higher egg hatching rate (0.88) than do lizards from a similar sexual population (0.62). The authors of the study offer an explanation: this asexual population experiences 'widespread failure to complete meiosis' [68] and these failures are so severe as to terminate development, such that only successful meioses lead to egg formation. Sexual *Artemia salina* (syn. *A. tunisiana*) achieve higher cyst hatch rates (0.9) than do either meiotic (0.81) or mitotic (0.84) asexual *Artemia parthenogenetica* [49] (a polyphyletic grouping consisting of diverse parthenogenetic forms [97]), but how closely related the different *Artemia* populations are to each other is unclear [95,106].

4. Discussion

The data are surprisingly consistent with the hypothesis that meiosis is a fundamental driver of offspring inviability (figure 1). Mechanisms by which meiosis causes inviability are

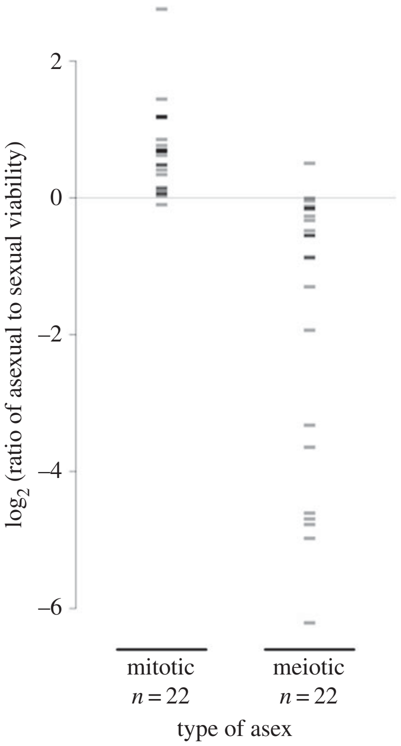

Figure 2. Viability ratios (viability of asexual offspring/viability of sexual offspring) by type of asex. Offspring viability is higher for asexual than sexual offspring (positive log viability ratios) for all but one contrast involving mitotic asex. Conversely, offspring viability is lower for meiotic asex than sex in all but one case. Points are semitransparent, with overplotting producing darker shades.

documented in a growing literature, and include aneuploidy [107–109], the loss of heterozygosity during asexual restitution [3,110] and the many regulatory checkpoints that abort development when meiosis deviates from its normal sequence [3,110]. Because meiosis can fail in multiple ways, the risk of failure compounds and is greater than the risk inherent in mitosis.

Other interpretations of the connection between reproductive mode and offspring viability require consideration. For example, reproductive mode can influence offspring heterozygosity. Some meiotic forms of asex reduce heterozygosity, while mitotic asex often does not [20]. If reproductive mode is closely correlated with offspring heterozygosity, the strong signal in our data could be one of differences in heterozygosity that result in viability differences. However, the few cases in which we found data to calculate both relative heterozygosity (of asexual offspring as compared to sexual offspring) and viability provide no obvious pattern. For instance, *Pycnoscelus* cockroaches [111] and *Ishnura* damselflies [7,93] have similar heterozygosity ratios (asexual/sexual offspring heterozygosity, 1.17 and 1.08, respectively) but divergent viability ratios (0.68 versus 1.09). More comparative data on meiotic mechanisms and relative heterozygosities are clearly needed. Sexual and asexual offspring may also diverge in other disparate aspects of morphology, development and ecology; we cannot preclude additional, as yet unidentified factors as involved in the obvious difference between mitotic and meiotic viability ratios (figure 2).

However, existing data are strongly consistent with a direct connection between meiosis and inviability. This connection would make coherent, and not negate, many other explanations for viability differences between sex and asex. For example, meiotic asex is more likely to lead to loss of heterozygosity than mitotic asex. Tychoparthenogens, organisms that reproduce asexually only rarely, are consistently meiotic and show very low asexual viability [3]. What seems to be a relationship between recently arisen asex and low viability may result from the fact that recently arisen asex is often meiotic. While meiosis itself is the best predictor of viability differences between sex and asex, in some cases, these associated factors, including offspring heterozygosity, may mediate that relationship and serve as a proximate cause of viability differences. Population genetic effects on viability (e.g. heterosis following from hybridity) probably interact with the effects of meiosis, and the two types of effects should not be considered alternatives to each other.

Until a comparative dataset supports an alternative mechanism, the simplest explanation for our findings is that meiosis causes developmental failures. 'The cost of meiosis' [31] is typically used to describe the fitness cost to each sexual female of passing only 50% of her genome to each daughter. But the phrase is a misnomer, because genomic dilution is a feature of many kinds of genetic outcrossing, even outcrossing that does not involve meiosis, as in fungal parasexuality, which involves only mitotic recombination [112]. Another phenomenon labelled as a 'cost of meiosis' is temporal: meiosis takes several times longer than mitosis, greatly slowing reproduction among short-lived organisms. This cost may explain why so many single-celled eukaryotes rarely engage in sex [113]. However, neither of these 'costs' is as general as the cost to viability, which appears to be imposed by meiosis itself.

If meiosis is so costly, why do some organisms continue to use meiosis as the basis for asexual reproduction? Meiosis may provide benefits, even in asex (e.g. by allowing a level of genetic diversity through occasional recombination in an otherwise clonal population [1]), and offspring viability is not the only fitness component with the potential to differ between reproductive modes. However, meiotic asex may also be maladaptive. In some obligate meiotic asexuals (e.g. parthenogenetic geckos [114]), the retention of meiosis is probably vestigial, inherited from sexual ancestors and not easily discarded despite its costs relative to mitotic asex. In facultative meiotic asexuals, including many insects and some plants, asex often relies on reproductive pathways that cannot be greatly altered without impeding sexual reproduction [3,22].

5. Conclusion

Evolutionary biologists have long noted an association between low offspring viability and asex [3,20,53], and have proposed this viability cost as offsetting costs of sex, particularly the genomic dilution resulting from mixis. The apparent correlation between asex and low offspring viability resulted from a focus on vertebrates and insects, which largely employ meiotic asex. Our broader dataset, with plants and mitotic asexual animals included, supported by many detailed previous studies of meiotic failures in numerous organisms (e.g. [15,17,68,108,115]), suggests that meiosis itself is a critical driver of early deaths, in both asex and sex. High mortality during the early stages of development, a phenomenon observed in most plants and animals [116], may be caused in part by the inherent complexity of eukaryotic development.

Data accessibility. All data used in our analysis are included in the electronic supplementary material S1.

Authors' contributions. D.A.L. theorized, collected data and drafted the text. K.Z. and A.P. contributed to finding and evaluating relevant comparisons, and refined both theory and manuscript. K.Z. conducted phylogenetic analyses.

Competing interests. We declare we have no competing interests.

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