Opinion

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Polyandry in nature: a global analysis

Michelle L. Taylor[1], **Tom A.R. Price**[2], **and Nina Wedell**[1]

[1] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Treliever Road, Penryn, TR10 9FE, UK
[2] Institute of Integrative Biology, Biosciences Building, Crown Street, University of Liverpool, Liverpool, L69 7ZB, UK

A popular notion in sexual selection is that females are polyandrous and their offspring are commonly sired by more than a single male. We now have large-scale evidence from natural populations to be able to verify this assumption. Although we concur that polyandry is a generally common and ubiquitous phenomenon, we emphasise that it remains variable. In particular, the persistence of single paternity, both within and between populations, requires more careful consideration. We also explore an intriguing relation of polyandry with latitude. Several recent large-scale analyses of the relations between key population fitness variables, such as heterozygosity, effective population size (N_e), and inbreeding coefficients, make it possible to examine the global effects of polyandry on population fitness for the first time.

Polyandry: past and present

The historical notion of monogamous females, pair-bonded with the same male for life, has been steadily eroded away over the past 40 years since the first review of sperm competition in insects [1–3]. Since then, ever-increasing numbers of studies have reported multiple paternity in natural litters, clutches, and broods, leading to the currently popular notion that females mating with multiple males, or polyandry (see Glossary), is a common and ubiquitous phenomenon in nature [4–7]. Theoretical developments have advanced our understanding of how the frequency of multiple mating might be explained, given other constraints on time, such as searching for mates [8], and identified potential social, ecological, and genetic factors selecting for polyandry [5,7,9–11]. Empiricists have responded by providing an equally impressive wealth of data to demonstrate these processes in action [5,12–14]. Polyandry not only is an undeniable staple of research into sexual selection, sex roles, and sexual conflict [4,15,16], but is also now regarded as a potent evolutionary force in population genetics [17,18], epidemiology [19], and conservation [20–23]. Clearly, we are at the point where the impact of polyandry is now being understood at multiple scales beyond the benefits and costs to individual females, to include the influence at population, landscape, and species scales. Given all this, it is perhaps surprising that we still lack a general overview of how frequently polyandry occurs in natural populations [24].

Measuring polyandry in nature

By far the most effective tool to date for examining polyandry in nature is microsatellite parentage analysis (Box 1). Microsatellites came to prominence after confirming widespread multiple paternity in bird broods, dispelling the idea that genetically monogamous pair bonds were common [13,25]. Gradually, as molecular libraries have been developed and expanded and statistical analyses improved, the techniques have been applied to an increasing diversity of species. However, although there are some reviews of multiple paternity in specific taxonomic groups [26–28], to date there has been no comprehensive review of the frequency and patterns of naturally occurring polyandry at a global scale. Such an overview can act as a

Glossary

Amplified fragment length polymorphism (AFLP): : an alternative method of parentage analysis that uses many loci at low levels of polymorphism to assign relatedness of individuals. Given that they are dominant markers, they do not distinguish between heterozygotes and homozygotes.
Climatic region: : we include large-scale geographic areas defined by abiotic variables, such as average annual temperature variation and precipitation: arid, Mediterranean, montane, temperate, tropical, and polar.
Cline: : a gradual change in gene frequencies or character states within a species across a geographic distribution.
Ecozone: : we include here major ecosystem divisions: marine, terrestrial, freshwater, and marine and freshwater amphibious areas, such as coastal zones and riverbanks.
Effective population size (: N: *e:):* : the number of individuals that would have the same magnitude of change in allele frequency as the real population [80].
Heterozygosity: : the proportion of a population that is heterozygous for one or more traits; this can give an indication of the overall genetic diversity in a population.
Heterozygosity-fitness correlations (HFC): : the relation between within-individual genetic diversity and genetic variation in characters closely related to fitness, such as life-history, morphological, or physiological traits. Populations suffering from inbreeding depression display positive HFCs and vice versa.
Inbreeding coefficient (f): : the probability of individuals sharing alleles by common descent; increases with the relatedness of mating individuals, such as full siblings.
Microsatellite: : sections of DNA comprising repeated two to six base-pair sequences; can be amplified by PCR and used to identify individual genotypes in a population.
Monandry: : females that mate with only one male per breeding cycle so that all offspring within a single clutch or litter are full siblings. Here, we use single paternity as an estimate of monandry and we use the two terms interchangeably.
Multilocus heterozygosity (MLH): : the average heterozygosity over all alleles used in a microsatellite paternity analysis.
Multiple paternity: : polyandry that results in offspring sired by more than one male. Often used as an alternative term for polyandry.
Polymerase chain reaction (PCR): : used for replicating selected sections of DNA to produce a large quantity for analysis.
Polyandry: : females that mate with multiple different males within a breeding cycle. Here, we use multiple paternity as an estimate of polyandry.
Single paternity: : all offspring in a brood being sired by one male.
Single nucleotide polymorphism (SNP): : an alternative method of parentage analysis that uses many loci of low levels of polymorphism. Although they are easier to sample per locus than microsatellites, the low levels of polymorphism make them less viable for statistical analysis of parentage unless coupled with genomic data.

Corresponding author: Wedell, N. (N.Wedell@exeter.ac.uk).

Keywords: polyandry; monandry; heterozygosity; population fitness; sperm competition; latitude.

0169-5347/

http://dx.doi.org/10.1016/j.tree.2014.04.005

Box 1. Microsatellites as the standard tool of polyandry

Several properties make microsatellites a significant improvement over traditional behavioural observations of mating behaviour in nature. As well as making multiple mating 'visible' to the observer, they translate mating behaviour into direct measures of fertilisation success, giving researchers an accurate representation of the frequency of success of polyandry. Methodologically, they are appealing because they are based on PCR-based assay techniques and interpreted with statistical methods based on simple rules of Mendelian inheritance [25]. However, less than ideal sampling can reduce the accuracy of the technique. Two key assets are sufficient sampling of adult candidate parents in a population and appropriate markers with a sufficient degree of polymorphism [25]. Failing this, an alternative is to sample many loci of lower variability across offspring, although this requires more extensive statistical testing [81,82]. We examined the efficacy of this approach in detecting levels of polyandry by recording the number of microsatellite loci used in each parentage analysis. We found a significant increase in the number of microsatellites used per analysis over the 16-year timespan of our data set (Pearson correlation $r = 0.258$, $P = 0.000$, $n = 203$), suggesting that there has been a general trend towards substituting field sampling for laboratory brute force. If this has served to improve the accuracy of multiple paternity, we would predict an increase in the number of true parents detected, resulting in an increase in the overall frequency of polyandry. We found that this is not the case, as rather than increase the frequency of polyandry, we found that greater numbers of microsatellites lowered the overall estimates of multiple paternity (Pearson correlations $r = -0.177$, $P = 0.01$, $n = 203$). If we hold with the assumption that more microsatellite loci in a study is equivalent to increasing the accuracy of the parentage analysis, then our data suggest that more recent estimates of polyandry are the most accurate and polyandry has declined over time. However, we found no significant evidence that polyandry has declined over time, although the relation does show a negative trend (Pearson correlation $r = -0.043$, $P = 0.547$, $n = 203$). Therefore, the alternative interpretation is that there has been no actual evolutionary change in polyandry and that simply applying a brute force approach in lieu of appropriate field sampling of candidate parents and high-quality markers might be a false economy.

benchmark comparative and diagnostic tool to identify research gaps, highlight patterns among species, confirm theoretical predictions, and even predict the outcome of specific evolutionary dynamics [24]. Therefore, we gathered available data from microsatellite paternity analysis in a wide diversity of species to present the first global overview of the frequency of polyandry as evidenced by multiple paternity in natural populations. We also explore the broad-scale patterns of polyandry in relation to environmental heterogeneity, and discuss the consequences for genetic diversity of populations.

The frequency of polyandry in nature

A common adage in many introductory texts to polyandry is that monandry is rare. We observed evidence of polyandry in every one of the 14 major taxonomic groups we investigated, from sea spiders to mammals. Furthermore, polyandry occurred in 89% of populations, providing the first demonstration that polyandry is both ubiquitous and common in nature. However, there are further important subdivisions afforded by our data set. For example, on average, polyandrous females accounted for just under half of the population (Figure 1) and, when we examined individual taxonomic groups, polyandry ranged from 0% to 100% in eight of 14 taxonomic categories (Figure 1). Clearly, multiple paternity is not expressed by all females in most species. The frequency of polyandrous females in a population can directly influence population viability and diversity via several processes, such as increasing N_e [18], controlling the spread of selfish genetic elements [29–31] and sexually transmitted infections [19]. Variability within and between populations in phenotypic plasticity of behaviour is a major topic of current interest, and the variation in polyandry shown here might represent evidence of how populations have responded to local environmental conditions, as well as the genetic history of individual populations [32]. Our review highlights groups that can be particularly fruitful study species in this respect. For example, insects are hailed as showing widespread polyandry and associated sperm competition because they can store sperm for extended periods of time [1,3], and with much empirical evidence for individual benefits of multiple mating [12]. However, we observed that polyandry also ranged from 0% to 100% in this taxonomic group. Other taxa highlight the potential for evolutionary divergence in polyandry between groups of species that have shared common ancestry or environments. If we compare the variability of polyandry in bony fishes (Osteichthyes) with cartilaginous fishes (Chondrichthyes), for example, we see that the distributions are different, being wide ranging in the former and bimodal in the latter (Figure 1). We note that our analysis does not control for several potentially confounding factors, including phylogeny, brood size, and sperm storage; hence, the patterns presented here will require further testing. Our data set also provides direct information on key groups that can be further used to investigate the extremes of polyandry or monandry in a population, because these represent populations exposed to circumstances that severely restrict or promote polyandrous behaviour. For example, population density can have a large role in the opportunity for females to remate, irrespective of any genetic tendencies, so that species or populations that display consistently high or low levels of polyandry might be symptomatic of other population-level processes. We note that the most common frequencies of multiple paternity in our data set were 0% (i.e., complete monandry) reported in 11% of all populations in the data set, and 100% (i.e., complete polyandry), which was reported in 12% of populations. This suggests that polyandry is more 'fixed' or constrained in some taxa, although the individual reasons for the variability in some, but not other populations are currently not clear.

Polyandry and ecology

Polyandry is common in nature, but is variable within and across species. One explanation is local ecology, which is well known to impact on mating systems through encounter rate, availability of breeding sites, and longevity [7]. For example, males that supply females with food during mating (nuptial gifts) might be unable to mate repeatedly when resources are scarce [33], thus preventing optimal rates of remating by females. Equally, the level of polyandry can impact on local ecology. For example, if the frequency of a sex ratio-distorting selfish gene is influenced by the level of polyandry [30,34], this could explain patterns of competitive ability between populations with different

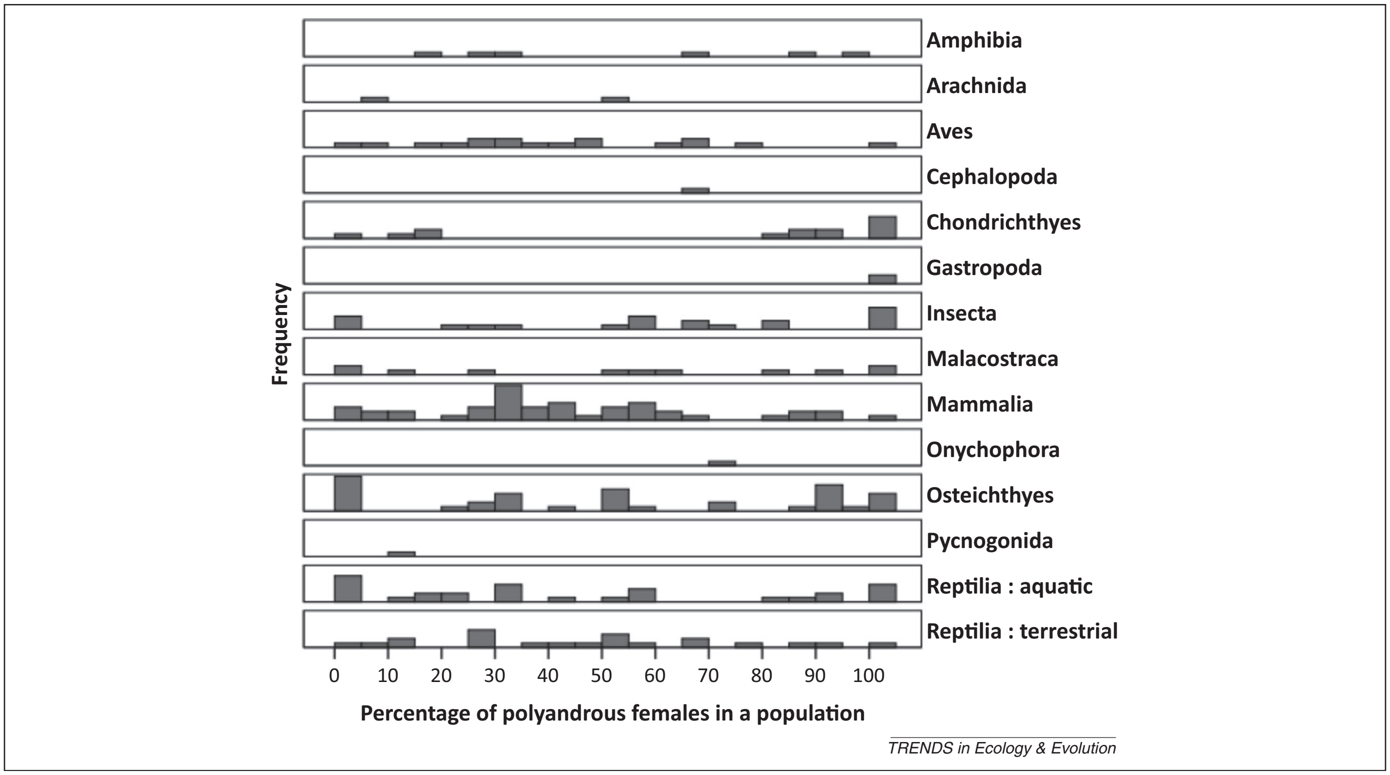

Figure 1. The frequency of polyandry by taxonomic class. To gather our data, we conducted a search on the Web of Science using the terms '*polyandry* microsatellites*' and '*multiple paternity* microsatellites*' across all available years. As well as selecting studies based on our focal aims (see below), we also omitted certain taxonomic groups that are known to have unusual or highly inflexible mating strategies (e.g., hermaphrodites, parasites, or social insects) that are deserving of their own review under these specific considerations. We focussed purely on the numbers of females within any one naturally occurring population that produced multiply sired litters, clutches, or broods of offspring within any one breeding cycle (polyandry). We did not include experimental studies, laboratory stocks, multiple clutches by the same females, or species where external fertilisation can obscure the link between polyandrous behaviour and multiply sired clutches. We also focussed on data from species where a measure of large-scale geographical variables could be deduced and a measure of the genetic diversity and accuracy of the paternity analysis could be gauged. We report here on polyandry in nature based on 203 population estimates from 150 studies that represent 160 species across 14 taxonomic groups. We observed a mean frequency of polyandry across all populations of 49%, standard error = 2.35, $n = 203$, suggesting that just under half of females in a population on average are polyandrous. Frequency of the y-axis is to a maximum of eight for each taxonomic group. Note that we did not control for potential confounding variables, such as phylogeny, clutch size, and sperm storage.

levels of polyandry, via altering population sex ratios. Although there are potentially vast numbers of two-way interactions between polyandry and ecology, current understanding remains limited to theory and case studies of particular species, and currently lacks broad generality. This problem could be satisfied by more large-scale analyses of the relation between polyandry and major ecological and/or environmental variables. Therefore, we explored polyandry in relation to four scales of environmental heterogeneity: latitude, climatic region, ecozone, and habitat. We found no relation with climatic region, ecozone, or habitat, suggesting that any interaction of polyandry with ecological or environmental factors is acting at a finer scale than our data can resolve. However, polyandry is more common in northern latitudes (Figure 2). Assuming this correlation is not artefactual, detecting it despite the enormous differences in ecology between the organisms in our data set suggests that the processes that create this correlation must be robust.

What can drive the increasing frequency of polyandry in the north? A suite of ecological variables tends to co-vary with latitude, including mean temperature, temperature range, and seasonality [35]. Biological factors that have well-established broad-scale relations with latitude include key life-history variables and processes such as body size, longevity, species diversity, speciation rate, and extinction rate [36–39]. Any of these variables might have a role in driving the differences in polyandry across the globe. For example, if females have higher longevity in the north, possibly due to colder temperatures, this might simply mean that they have more opportunities to remate. Alternatively, more variable environmental conditions at high latitudes might create a greater risk of a female failing to encounter males and suffering sperm limitation, driving females to mate whenever opportunities present themselves. These are just two examples of possible relations that demonstrate the impact of ecology on female fitness resulting in increased polyandry in the north.

Alternatively, it is possible that the correlation is due to higher-order effects, such as the increased persistence of polyandrous species in the north. For example, in the tropics where there are more species and niches are potentially more constricted, speciation rates might depend on evolving ecological divergence, so that subspecies that use the same niche as the parent species are driven extinct by competition. By contrast, in the north, there are fewer species, niches are broader, and competition is lower so that the speciation rate of a clade can be more dependent on the evolution of reproductive isolation than on ecological divergence [35,37]. If polyandry drives the evolution of rapid reproductive isolation, polyandrous clades can then become more common in the north. Unfortunately, theory

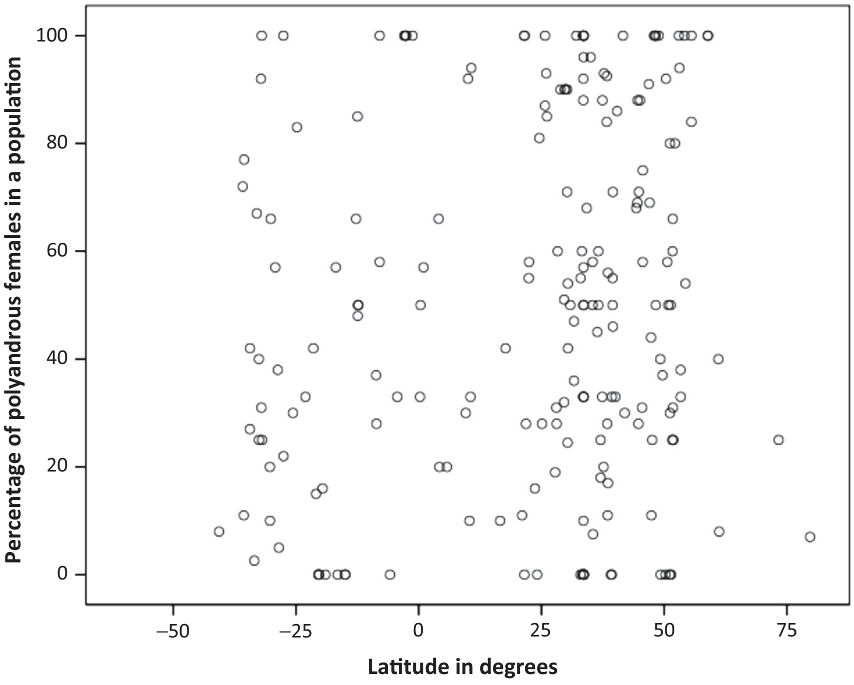

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Figure 2. Polyandry is positively correlated with latitude. This plot shows the raw polyandry data from all taxonomic groups, not controlling for phylogeny. Almost all taxonomic groups are represented at both northern and southern latitudes, with only ten of 203 data points from groups with restricted distributions. We observed that polyandry is weakly positively correlated with latitude: Pearson correlation $r = 0.147$, $P = 0.037$, $n = 203$. Polyandry did not have any relation with any other of our environmental scales: climatic region (Anova: $F_{5, 169} = 0.85$, $P = 0.52$); ecozone (Anova: $F_{4, 169} = 0.92$, $P = 0.45$); or habitat (Anova: $F_{23, 169} = 0.73$, $P = 0.81$). One possibility is that these data were assembled from availability, rather than purposefully selected to equally represent all categories of habitats, ecozone, or climatic regions, so that the lack of any large-scale relations is simply due to lack of statistical power. However, even when comparing groups of relatively robust statistical sizes, such as temperate and tropical climatic regions, there were no differences in the frequency of polyandry.

examining the interplay between polyandry and latitude, and the ecological factors that correlate with latitude, is scarce.

Ideally, this relation should be tested by comparison to within-species latitudinal differences in polyandry, or comparisons of closely related species that differ in distribution. Unfortunately, there have been few studies that examine this. However, there are some experimental demonstrations that polyandry varies with temperature [40–43]. One study on green-veined white butterflies (*Pieris napi*) found that northern populations were more monandrous, possibly due to monandrous females reproducing faster, which is a vital advantage where there are seasonal constraints on suitable breeding time [44]. Conversely, studies on two species of *Drosophila* showed higher levels of polyandry in northern populations, the reasons for which are still under investigation [34,45]. Further research on this topic, such as within and between species comparisons and broader reviews of taxonomic groups, will bring key factors influencing the relation between polyandry and ecology into clearer focus, as well as contribute more generally to the question of what factors drive the evolution of polyandry. Many of the ecological factors that correlate with latitude also correlate with altitude, providing an additional avenue of investigation into inter- and intraspecific variation in polyandry.

Polyandry and genetic quality

One of the explanations for polyandry is that females gain genetic benefits via their offspring [9,46]. Central to the current mechanisms proposed is genetic quality [47]. This includes specific alleles related to fitness-related traits, compatibility of male and female genotypes, and the survival and reproductive success of offspring [9,10,46–49]. An umbrella mechanism for these proposed benefits is selection for increased offspring heterozygosity, which was proposed as a general mechanism for mate choice and polyandry several decades ago but has received limited empirical testing compared with other suggested causes of polyandry [50,51]. ‘Polyandry for heterozygosity’ is appealing because it simultaneously satisfies both the underlying cause and solution to the issue of maintaining sufficient genetic variation under selection, without recourse to specific population processes that might not be widespread [50,52]. Heterozygosity itself is known to be associated with, for example, greater developmental stability, disease resistance, competitiveness, hatchability, and survivorship [14,50,51]. The relation between heterozygosity and fitness has also been formalised in heterozygosity–fitness correlations (HFCs), based on the assumption that heterozygosity, measured from multilocus microsatellite analysis [multilocus heterozygosity (MLH)] is positively or negatively correlated with variation in fitness-related traits [53]. Therefore, through this association, it might be possible to use MLH as a ‘catch all’ indication of the genetic benefits of polyandry in nature.

We observed that the frequency of polyandry was significantly associated with higher levels of heterozygosity (MLH) (Box 2). If we maintain the assumption that HFCs

Box 2. Polyandry and MLH as indicators of population fitness

Heterozygosity measured at multiple microsatellite loci (MLH) can be used to estimate the inbreeding coefficient *f*, either indirectly via a correlative approach or directly by reconstructing pedigrees of natural populations [83,84]. MLH-based measures of population fitness are more practical and accessible than assigning pedigrees directly from natural populations because they can be measured from microsatellite analysis of a random sample of individuals in a population (Box 1). This relation means that MLH can also be used as an indirect test of whether polyandry can confer genetic benefits via inbreeding avoidance. This form of genetic benefit has particularly acute consequences in small populations, or populations restricted in ways that make them vulnerable to inbreeding (e.g., populations with high natal philopatry) [51,85]. If polyandry can provide significant benefits via inbreeding avoidance, we should be able to detect its signature in nature via a positive relation with MLH. We observed a significant positive relation between polyandry and MLH in our data set (Figure I). Although further testing will be required to determine whether this relation is based specifically on inbreeding avoidance or other genetic benefits in individual populations, this is an intriguing global perspective of the effects of polyandry on population-level fitness.

Polyandry and N_e

A further prediction of the effects of polyandry on population fitness is that it increases the genetically effective size of a population by increasing the genetic variation represented in each generation [17,18]. This is of interest to population geneticists and conservation biologists, both of whom are primarily concerned with population viability over time [57]. Surprisingly, this hypothesis has received little empirical testing [18]. The key link between polyandry and N_e is heterozygosity (MLH). Our observation that polyandry is positively associated with heterozygosity provides the preliminary large-scale evidence that polyandry increases N_e, but requires further direct testing within populations.

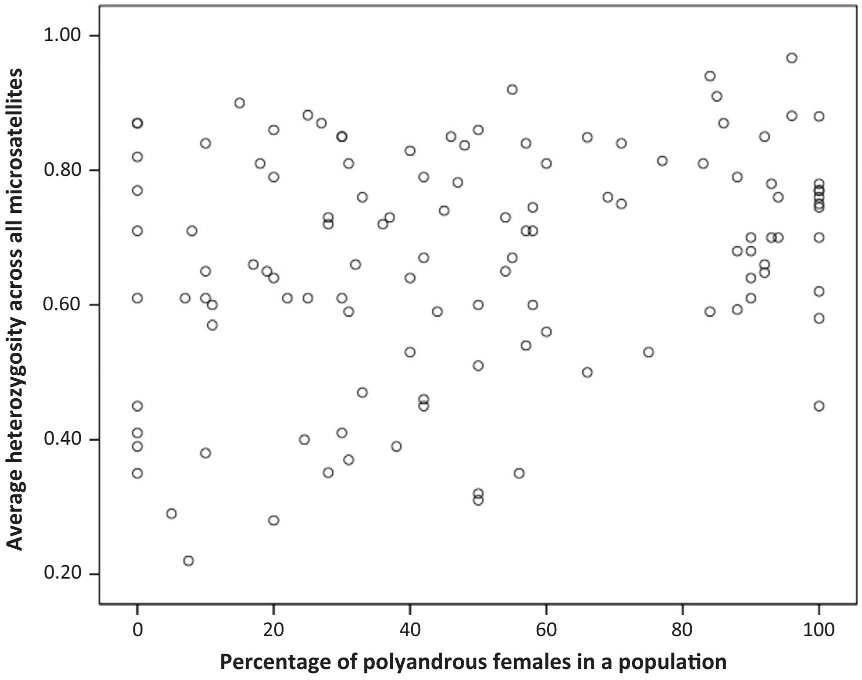

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Figure I. Polyandry and multilocus heterozygosity (MLH) are positively correlated. We recorded the average heterozygosity scored over the multiple loci used in each microsatellite analysis (MLH). MLH was available in all taxonomic groups except Cephalopoda and Onychophora. We observed that polyandry was positively associated with MLH (Pearson correlation $r = 0.274$, $P = 0.003$, $n = 118$). This was not due to an experimental artefact of the increasing use of microsatellite markers, because the relation between the number of microsatellite loci and MLH was negative (Pearson correlation $r = -0.314$, $P = 0.001$, $n = 118$).

can indicate selection on overall genetic quality, then this could represent the first large-scale corroboration of the 'Polyandry for heterozygosity' hypothesis. However, this result should be treated with caution because correlational data represent only a 'signature' effect and further empirical work must follow to examine the direction of causality. Although it is feasible that heterozygosity can indicate general genetic quality via HFCs, this is reliant on either linkage disequilibrium or linkage identity relations with physiological and morphological traits related to fitness, which might be far from a universal feature across species. A recent meta-analysis to establish whether this is indeed the case found that effect sizes for HFCs in fitness and nonfitness related traits are equivocal, so it remains possible, but debatable, whether MLH represents a general measure of genetic quality [53]. However, we note that our observation has a small to moderate effect size, which concurs with previous analyses that point to the generally small impact of genetic benefits in sexual selection [14,54–56].

Polyandry in the future: new directions and potential applications

Correlation versus causation

Polyandry has been posited as the cause and solution to key evolutionary puzzles, such as the maintenance of genetic diversity, the spread and control of sexually transmitted infections (STIs) and selfish genetic elements, and the long-term viability of populations. Yet, correlational data alone cannot support hypotheses about causality. Specific research gaps highlighted by our review include the direct relation between polyandry and N_e (Box 2), the strength of selection on heterozygosity via polyandry, and the prevalence of ecology-driven interactions, as hinted at by the latitudinal correlation. Insights such as these not only advance our theoretical understanding and move debates forward, but also have potentially practical applications.

Potential applications

Heterozygosity can provide offspring tolerance against unpredictable or unstable environments, preserving genetic variability and ensuring the future viability of otherwise vulnerable populations [17,18,57]. The positive relation between polyandry and heterozygosity presented here provides the potential for predicting how matings between individuals in managed populations can achieve desired levels of genetic diversity [23,58–60]. Our finding that polyandry is associated with higher heterozygosity might also be of concern to those managing invasive populations, because heterozygosity is known to benefit a range of traits, such as survivorship, longevity, and competitiveness, that could confer advantages to invasive or pest populations [61,62]. One potential application is in pest control programmes, such as the sterile insect technique (SIT). SIT relies on the ability of sterilised males to compete for matings against wild type males and deplete female reproductive success to zero [63–66]. However, it has an inherent weakness in polyandrous populations that are incompletely saturated with sterile males, because any remaining fertile females in a population represent strong selection for resistance to sterile males. It might be possible to utilise the relation between polyandry and heterozygosity to explore the likelihood of success in introducing SIT as a suitable pest control program and where it is likely to fail. The relation between polyandry and heterozygosity could be used to model the rates of evolved resistance in SIT populations [66,67]. The role of polyandry is also implicated in specific evolutionary conundrums, such as the spread and control of selfish genetic elements, and is a field currently gaining in popularity [29–31]. The insights into how polyandry interacts with other key measures of population fitness (Boxes 1 and 2) presented here can add a valuable perspective on these issues.

Explaining monandry

Finally, in exploring patterns of polyandry, we have also provided the mirror image large-scale patterns of monandry. On average, less than half of females per population were polyandrous, leaving most females showing single paternity. Explaining variation in monandry is not simply a matter of the flip side of polyandry because the causes and consequences of single paternity are not necessarily the opposite of those proposed for polyandry. There are two possible ways to consider the variation in monandry. One is that the costs of polyandry restrict its expression in various ways. For example, there is ample evidence from insects that the costs of excessive exposure to seminal fluid proteins transferred at mating can be significant and restrict the number of rematings that reap net benefits for females [68–70]. The recently expanding field of sexual conflict focusses directly on the costs of mating and how males and females evolve to win different battlegrounds involved in sexual decisions [16,71,72]. Other restrictions can arise via ecological variables that influence the availability of further mating opportunities (discussed above) and strong sperm precedence, all of which restrict the individual expression of otherwise polyandrous females. To take the example of strong sperm precedence, a female can mate several times with multiple males over a short time, setting up the ideal opportunity for sperm competition and the benefits of multiple mating. However, due to the extreme competitive ability of the last male to mate with her, the benefits of mating with all of the previous males are obscured, both from the experimenter and selection. Last male sperm precedence is a common feature of insect mating systems [1,3]. Key taxonomic groups, such as butterflies, that store spermatophores from each of the mating events in their lifetime are ideal organisms to examine the pattern of multiple mating in natural populations [73]. In addition, the extensive literature on sperm precedence patterns that provide values of P2 (a measure of the ratio of paternity secured by the second of two males to mate with a female) [3,73,74] provides an ideal resource to confirm whether this is a widespread explanation for monandry.

Alternatively, one might consider that monandry has its own benefits that are selected for in preference to polyandry. This distinction might appear subtle, but can be significant. If patterns of polyandry and monandry are genetically fixed, then we must assume that monandry has a genetic basis rather than being the phenotypic result of suppressed polyandry [75]. This can occur as an accidental consequence of unique systems of genetic architecture, such as chromosome inversions that preserve sections of genetic variation across generations [76–78]. One adaptive reason for remaining genetically ‘faithful’ is to conserve genetic diversity within desired parameters. This might occur, for example, in hybrid zones, or stressful environments where specific co-adapted gene complexes are beneficial [60]. One particularly intriguing idea is that monandry is an ancestral condition and a necessary precursor to the evolution of social or cooperative societies [79]. It might well be that, with further research, polyandry is proven to be the more prevalent mating behaviour, genetically and phenotypically, and that the volume of research dedicated to explaining it over the past four decades is well justified. However, our review of the patterns of polyandry shows that the frequency of monandry is not trivial, and that the causes and consequences warrant equivalent attention to that given to polyandry.

Concluding remarks

We began with a simple premise: is polyandry in nature as common as generally presumed? Although the answer is superficially yes, in the process of exploring the data we have uncovered several other patterns and associations that were previously either underappreciated or not directly of concern in the wider remit of explaining the evolutionary causes and consequences of polyandry. These include the extent and variation in monandry (single paternity), the relation of polyandry with ecology and latitude, the potential for heterozygosity (MLH) to function as a general indicator of genetic quality, and the potential for polyandry to function as an indicator of population fitness via its relation with heterozygosity. Although some of these relationships are preliminary insights and require further empirical testing to substantiate, the overall direction and scale of the relationships uncovered here should provide a suitable platform for the development of theoretical work as well as pointing researchers in the right direction to design suitable research agendas to explore more fully the questions and applications that we have highlighted.

Acknowledgements

This work was funded by a NERC grant to N.W., T.A.R.P., and G.D.D. Hurst (NE/I0277/11/1). The authors thank two anonymous reviewers for their insightful comments.

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