1. Introduction

The term polyandry defines mating systems in which individual females mate with multiple males. Naturalists had long been aware that some species are overtly polyandrous. Aristotle [1] described how domestic hens often mate with multiple males. Darwin was clearly aware that in few species females form bonds with multiple partners simultaneously [2]. However, this mating system was considered quite rare, and the ecological and evolutionary significance of polyandry remained neglected for another century. This begun to change in the early 1970s when studies of insect reproductive behaviour inspired the first exploration of the consequences of polyandry. Parker [3] proposed that polyandry is widespread in some species of insects and—importantly—that it can generate competition between the sperm of different males for the fertilization of a set of ova, a process that became known as sperm competition. Childress & Hartl [4] presented evidence that polyandrous female fruit flies, Drosophila melanogaster, can bias sperm utilization and fertilization in favour of the ejaculates of certain males, a process they called sperm preference, which inspired ideas of cryptic female choice [5,6]. These early observations introduced the idea that polyandry might be more widespread than originally assumed, and that it may have drastic repercussions for the Darwinian fitness of males and females. The advent of molecular tools for parentage assignment combined with detailed behavioural studies has demonstrated that, in most sexually reproducing organisms, the sperm of different males have a non-zero probability of overlapping in time and space to fertilize the same set of ova. In fact, polyandry is emerging as an almost unavoidable consequence of sexual reproduction, from plants to primates.

Much of the early studies of polyandry focused on either the mechanisms mediating sperm competition and cryptic female choice (e.g. the role of sperm phenotype on paternity share), or on the evolution of male and female reproductive strategies, including male ejaculate expenditure and adaptive explanations of female polyandrous behaviours. However, the study of female polyandry has exploded over recent years, branching out by considering different ecological and evolutionary implications of this phenomenon and by using an increasingly multi-disciplinary approach. This more recent work is beginning to reveal that polyandry has ramifications—hitherto ignored—that far exceed the remits of sexual selection and sexual conflict, and have profound implications for a number of other fundamental evolutionary and ecological processes such as sex allocation, social networks, altruism and cooperation, sex-biased gene expression, selfish genetic elements (SGEs), sexually transmitted infections, population extinction and management. Up until now however, reviews of polyandry have been largely focused rather narrowly on the proximate mechanisms of sperm competition and cryptic female choice [6,7]. Very little has been done to cover the burgeoning development of studies considering the evolutionary ecology of polyandry in a wider, interdisciplinary context. The overarching goal of this Theme Issue is to integrate these recent empirical and theoretical developments to lay the foundations for an interdisciplinary, concept-based synthesis of polyandry.

2. Scope

The Theme Issue comprises 13 contributions, covering a wide range of inter-related issues linked to polyandry. We introduce them in the following sections...
grouped into four broad topics: (i) sexual selection, (ii) population structure, (iii) evolutionary conflicts and (iv) population fitness.

(a) Sexual selection: enduring paradigms and emerging complexities

The Theme Issue begins by considering the relationships between polyandry and sexual selection and sex roles. The intuition of polyandry has had a dramatic impact on our understanding of anisogamy, ‘sex roles’ and ultimately the operation of sexual selection.

Parker [8] had already identified, in sperm competition arising from polyandry, a necessary feature to explain the evolution and maintenance of anisogamy (see also reference [9], Bateman [10], and subsequently Trivers [11] considered anisogamy the original condition ultimately responsible for the evolution of sex-specific sexual selection, namely a positive gradient of the regression of reproductive success on mating success (Bateman gradient) that is typically steeper in males than in females. This has led to a Darwin–Bateman paradigm of ‘sex roles’, a cornerstone of sexual selection theory. Paradoxically, while polyandry has promoted anisogamy, it may also weaken sex differences in the Bateman gradient and challenge the Darwinian–Bateman paradigm. First, there is increasing evidence that some degree of polyandry might be adaptive in females, suggesting that the female Bateman gradient might be steeper than originally assumed. Second, polyandry might weaken the male Bateman gradient because mating is no longer guaranteed to fertilize a whole set of ova, and because sperm numbers become a limiting factor when males must invest large ejaculates in order to win sperm competition (or invest in defending paternity in other ways, e.g. mate guarding). Parker & Birkhead [12] present a historical perspective illustrating the development of the Darwin–Bateman paradigm, and review its relevance under the realization of widespread polyandry. The paper argues that polyandry has clearly nuanced and qualified the paradigm. However, the Darwin–Bateman paradigm remains a qualitatively valid principle and an important heuristic tool in sexual selection theory. An extensive review by Kvarnemo & Simmons [13] builds on this framework and discusses the way polyandry is changing the operation of sexual selection by generating post-mating variance in male paternity share (rather than mating success), and the consequences that this has for the way we measure sexual selection, and understand sex roles. This is followed up by a contribution in which Shuster et al. [14] develop a quantitative framework to measure the impact that polyandry has on the variance in reproductive success, and thus on the opportunity of sexual selection in a population. The approach proposed helps contextualize recent empirical demonstrations of the strong impact that polyandry can have on different episodes of sexual selection [15,16]. Another fundamental consequence of polyandry is that the operation of pre- and post-copulatory episodes of selection favours the evolution of alternative mating tactics. Neff & Svensson [17] provide a comprehensive review of male and female alternative mating tactics in polyandrous populations.

(b) Sexual networks and sex allocation in structured populations

The earlier-mentioned contributions consider fundamental aspects of sexual selection at population level. However, an emerging trend in the field is the realization that natural populations are often highly structured due to, for example, viscosity, and that this structure has important implications for the intensity of intra-sexual competition at the local and global scales, and thus for operation of sexual selection. Polyandry is a key modulator of these dynamics at local and global levels. McDonald et al. [18] integrate multi-level selection and network theory to develop a novel quantitative framework that measures sexual selection in polyandrous, structured populations. The authors demonstrate how at low-to-intermediate levels of polyandry consideration of local competition, derived from network information, makes a very big difference on estimates of sexual selection in a population. The issue of local versus global levels of sexual selection has been particularly well studied in two groups of organisms often neglected by sexual selection research, simultaneously hermaphrodic animals and flowering plants. In both groups, individuals can allocate simultaneously to male and female functions, so patterns of population viscosity and local competition also have profound consequences for sex allocation [19]. Schärer & Pen [20] consider this problem in hermaphrodites. The authors introduce the concept of local sperm competition, competition among genetically related sperm (typically from the same male), and show that when male allocation promotes local sperm competition (rather than global sperm competition driven by polyandry), allocation to sperm production is predicted to decline. Pannell & Labouche [21] discuss polyandry in seed plants, which they define as the competition for fertilization by pollen grains from multiple sporophytes within the stigma of another sporophyte. The review argues that this form of polyandry is likely to be the result of selection on plants to increase male outcross reproductive success. The authors point out that in animal-pollinated plants, local pollen competition can result in diminishing returns associated with investment in male function.

(c) Social conflicts: dynamic approaches, transcriptomics and eusociality

The realization of polyandry is also contributing to a much more dynamic view of social conflicts. The most obvious forms of conflict relevant to polyandry are conflicts arising among members of the same sex and between males and females over reproductive decisions.

On the one hand, polyandry creates potential for conflict over some reproductive decisions such as cryptic female choice and parental care. On the other hand, it may reduce potential for sexual conflict over other reproductive decisions such as mating rates by weakening the male and increasing the female Bateman gradient. Although the notion that polyandry creates potential for intra- and inter-sexual conflict is not new, studies of sexual conflict have up until recently ignored the diversity of proximate mechanisms through which mating and sperm competition can impact female fitness. These mechanisms can have fundamental repercussions for the fitness pay-offs of sexual rivals and sexual partners. For example, the gonadotropic effects of mating widespread in some taxa can create intra- and even inter-sexual mutualism with regard to mating decisions [22]. This indicates that the potential for conflict arising from polyandry can vary drastically with specific proximate mechanisms (e.g. nuptial gifts, inhibition of remating), over
specific reproductive decisions (e.g. female remating versus sperm utilization), and changes dynamically over evolutionary times. Alonso & Pizzari [23] present a theoretical framework to analyse the coevolutionary dynamics arising from different effects that mating can have on female fertility, fecundity and mortality. The study shows how selection on female propensity for polyandry is determined by the complex interactions of such effects. The level of polyandry will, in turn, determine selection on male investment in different ejaculates or mating traits that affect female fitness, thus exacerbating or relaxing polyandry. These theoretical results demonstrate that mating systems emerge from the intimate and dynamic inter-relationship between male traits affecting different female aspects of female fitness and female propensity to remate.

Ultimately, the social and physiological interactions between partners are mediated by the expression of suites of genes modulating reproductive allocation and responses. The sex-specific patterns of sexual selection caused by polyandry and the sex-specific role of such genes suggest that their expression should be strongly sexually dimorphic, and that when expressed in both sexes, their expression should be sexually antagonistic: beneficial in one sex but deleterious in the other, owing to divergent phenotypic optima of males and females, an evolutionary constraint known as ‘intra-locus conflict’ [24]. In their review, Mank et al. [25] explore the ways in which male and female transcriptomics and gene expression patterns are influenced by sexual conflict and sexual selection in polyandrous mating systems. There is evidence that selection generated by female multiple mating has had a major impact on the way genes are regulated and expressed [25]. This is particularly apparent for genes with sexually antagonistic effect. Recent transcriptomic advances have shown that many genes are differentially expressed in males and females, indicating sexual selection and sexual conflict are important in shaping overall patterns of gene expression. An effective way to generate sexual dimorphism and potentially to resolve or lessen the impact of sexually antagonistic alleles is to regulate their expression levels depending on whether they are present in males and females. For example, recent discoveries that many sex-linked genes are not dosage compensated in the heterogametic sex in some taxa [26,27] indicate that selection stemming from sexual conflict may be a potent force in promoting differential gene expression in the two sexes more generally [28]. Clearly, future advances in genomics will enable direct comparison of the pattern of gene expression in taxa with differing mating systems to unravel the mechanisms by which sexual dimorphism and potential resolution of loci with sexually antagonistic effect evolve.

A broader consequence of polyandry is that it breaks down genetic relatedness, with critical repercussions for inclusive fitness (indirect) pay-offs and the evolution of societies. Recent work has indicated that strict monogamy is a key original condition for the evolution of cooperation and eusociality. A review by Boomsma [29] tackles the evolutionary relationship between polyandry and social conflict. This contribution argues not only that polyandry prevents the evolution of eusociality, but that lifetime commitments (sexual and non-sexual) are the necessary condition for the evolution of higher levels of cooperation and organization at multiple biological levels.

(d) Populations: selfish genetic elements, sexually transmitted infections, viability and extinction

The final part of the Theme Issue is concerned with the consequences of polyandry for populations. Wedell [30] reviews recent work investigating the relationship between polyandry and SGEs or endosymbionts. SGEs often increase their spread at the expense of the fertilizing efficiency of a male carrier. These costs can severely impact on the fitness of a population. The review illustrates how one possible evolutionary response to combat the spread of SGEs is polyandry through which females can penalize the reproductive success of carrier males. Ashby & Gupta [31] focus on sexually transmitted infections (STIs). The authors present a new theoretical framework to study the way varying levels of polyandry can change the epidemiological dynamics of these infections. There is a clear parallel between the contributions by Wedell and by Asby & Gupta. The models presented by Ashby & Gupta on the epidemiological dynamics of STIs are mostly inspired by humans, but have direct relevance for the dynamics of endosymbionts causing reproductive failure in arthropods (analogous to STIs). The models of Ashby & Gupta show that heterogeneity in host sexual behaviour—specifically contact patterns—can have dramatic impacts on the infection rate and virulence of STIs. They show that STIs causing sterility rather than mortality can favour movement resulting in increased incidence of the disease. Similarly, movements (i.e. increased remating) of individuals owing to hatching failure (sterility) in insects may also favour the spread endosymbionts. Clearly, there is a direct link between the mating patterns and the dynamics and evolution of diseases. It is likely that this association is even more widespread and important in influencing the dynamic relationship between SGEs and mating strategies, by affecting the movement patterns and encounter rate of infected individuals harbouring SGEs [30]. Furthermore, we may also predict that mating systems dominated by a few individuals should in general be associated with lower than average infection levels and potentially also lower virulence levels. It will be interesting to examine whether this is the case in lekking mating systems or in species with stable dominance hierarchies.

Holman & Kokko [32] wrap up this issue with a very comprehensive review of the different pathways through which polyandry can drastically impact on the viability and extinction risk of a population by modulating inbreeding, effective population size and age structure in populations. The authors argue that the impact of polyandry (positive or negative) on population fitness might be difficult to evaluate when populations reproduce at a rate that exceeds the carrying capacity of the environment, but warn that such ecological masking may collapse under environmental perturbations (e.g. due to anthropogenic changes). The review presents a cogent argument that understanding and managing population trends hinges on a fuller understanding of the direct and indirect demographic consequences of polyandry.

3. Conclusive remarks and future directions

Collectively, the contributions of this Theme Issue demonstrate that polyandry is not only revolutionizing our understanding of sexual selection, but that it represents a
lens through which we can achieve a fuller understanding of a number of inter-related evolutionary and ecological processes. A number of general conclusions and promising avenues for future research emerge from across the individual contributions of the issue. Below, we highlight some of the most significant points:

— **Population viscosity.** A number of contributions of the present Theme Issue have emphasized the growing realization that population viscosity and population structure can drastically affect the evolutionary and ecological implications of polyandry, for example by modulating the intensity of local competition, kin selection, the epidemiology of STIs and inbreeding. In the future, it will be interesting to see how the advent of network tools to characterize sexual interactions will help us study the fine-grained structure of polyandry and its ecological and evolutionary significance.

— **Sexual conflict.** It is becoming clear that the original expectation that polyandry equates more intense sexual conflict is inadequately simplistic. While polyandry can certainly foster sexual conflict, potential for conflict is emerging as a highly dynamic property of individual reproductive decisions, which is contingent on specific physiological and behavioural mechanisms underpinning sexual interactions. A tighter synergy between proximate studies of such mechanisms and studies measuring their fitness consequences (both theoretical and empirical) should be particularly rewarding to understand the complex inter-sexual coevolutionary trajectories of polyandrous organisms.

— **Gene regulation and SGEs.** Recent findings show the SGE itself can also have sex-specific effects and function as a sexually antagonistic allele, in addition to directly affecting the level of gene expression in the two sexes [33]. This raises the exciting possibility that SGEs more generally are responsible for sex-specific gene regulation as they frequently target expression levels. As noted by Mank et al. [25], sex-specific gene regulation is the transcriptomic consequence of polyandry and sexual conflict. Future studies quantifying the impact of SGEs in more taxa are clearly needed to evaluate the role of SGEs both for variation in polyandry levels, but also for gene transcription patterns in the two sexes.

— **Population-level consequences.** The implications of polyandry have been largely studied in terms of individual fitness. However, as a number of contributions of the Theme Issue make clear, some of these mechanisms can lead to fundamental repercussions for the fitness and viability of a population as a whole. This suggests that in the future, patterns of polyandrous behaviour could be used as diagnostic and predictive tools to study, for example, the epidemiology of STIs, or the risk of extinction of a population.

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References

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