Estimating genetic benefits of polyandry from experimental studies: a meta-analysis

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ABSTRACT

The consequences of polyandry for female fitness are controversial. Sexual conflict studies and a meta-analysis of mating rates in insects suggest that there is a longevity cost when females mate repeatedly. Even so, compensatory material benefits can elevate egg production and fertility, partly because polyandry ensures an adequate sperm supply. Polyandry can therefore confer direct benefits. The main controversy surrounds genetic benefits. The argument is analogous to that surrounding the evolution of conventional female mate choice, except that with polyandry it is post-copulatory mechanisms that might bias paternity towards males with higher breeding values for fitness. Recent meta-analyses of extra-pair copulations in birds have cast doubt on whether detectable genetic benefits exist. By contrast, another meta-analysis showed that polyandry elevates egg hatching success (possibly due to a fertilization bias towards sperm with paternal genes that elevate embryo survival) in insects. A detailed summary of whether polyandry elevates other components of offspring performance is lacking. Here we present a comprehensive meta-analysis of 232 effect sizes from 46 experimental studies. These experiments were specifically designed to try to quantify the potential genetic benefits of polyandry by controlling fully for the number of matings by females assigned to monandry and polyandry treatments. The bias-corrected 95% confidence intervals for egg hatching success ($d = -0.01$ to 0.61), clutch production ($d = 0.07$ to 0.45) and fertility ($d = 0.04$ to 0.40) all suggest that polyandry has a beneficial effect (although P values from parametric tests were marginally non-significant at $P = 0.075$, 0.052 and 0.058, respectively). Polyandry was not significantly beneficial for any single offspring performance trait (e.g. growth rate, survival, adult size), but the test power was low due to small sample sizes (suggesting that many more studies are still needed). We then calculated a composite effect size that provides an index of general offspring performance. Depending on the model assumptions, the mean effect of polyandry was either significantly positive or marginally non-significant. A possible role for publication bias is discussed. The magnitude of the reported potential genetic benefits ($d = 0.07$ to 0.19) are larger than those from two recent meta-analyses comparing offspring sired by social and extra-pair mates in birds ($d = 0.02$ to 0.04). This difference raises the intriguing possibility that cryptic, post-copulatory female choice might be more likely to generate 'good gene' or 'compatible gene' benefits than female choice of mates based on the expression of secondary sexual traits.

Key words: female choice, maternal effects, paternal effects, meta-analysis, multiple mating, paternity, polyandry, sexual selection, sperm competition.

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I. INTRODUCTION

(1) Overview

Much of modern sexual selection theory is still based on the premise that a male's reproductive rate is limited by access to females willing to mate, while a female's reproductive success is limited by access to material resources that can be converted into offspring, rather than by access to sperm (Trivers, 1972; but see Jennions & Kokko, 2010). This view has changed in recent years, however, as there is growing evidence that females can benefit from mating with several males over a single reproductive cycle (i.e. polyandry) (reviews: Jennions & Petrie, 2000; Tregenza & Wedell, 2000; Hosken & Stockley, 2003; Zeh & Zeh, 2003; Simmons, 2005; Kempenaers, 2007). On the other hand, there is good evidence that females incur significant costs when mating that include the loss of time and energy and an increased risk of predation, infection and/or injury that arise both from searching for a mate and the actual act of mating (e.g. Lima & Dill, 1990; Watson, Arnqvist & Stallmann, 1998; Crudgington & Siva-Jothy, 2000; Fedorka, Zuk & Mousseau, 2004; McNamara, Elgar & Jones, 2008). There is also evidence that males transfer accessory substances that facilitate their success in sperm competition but have toxic side-effects that reduce female lifespan (e.g. Wigby & Chapman, 2005). These costly aspects of polyandry have been the focus of many recent sexual conflict studies, where it is usually argued that polyandry arises as a by-product of an asymmetry in selection on mating rates between the sexes, whereby females sometimes benefit more by acquiescing to male mating attempts than resisting (review: Arnqvist & Kirkpatrick, 2005; for an interesting exception see Adler, 2010).

Despite the conflicting costs and benefits of polyandry, there is now overwhelming evidence from almost all taxa that females mate with several males within a given reproductive cycle (Birkhead & Møller, 1998; Birkhead, Hosken & Pitnick, 2009). Given the potential costs there is a need to quantify better any compensatory benefits to females that mate multiply. Indeed, there is growing evidence from both field studies (e.g. Madsen et al., 1992; Olsson et al., 1994; Rodriguez-Muñoz et al., 2010) and laboratory experiments (e.g. Olsson et al., 1996; Tregenza & Wedell, 1998, Fisher, Double & Moore, 2006b) that the number of mating partners sometimes predicts offspring performance. However, the extent to which these findings can be generalized remains uncertain and, despite many studies having been conducted, there is still little consensus. In this review we provide a brief background to the study of polyandry. We then present the results of a meta-analysis of a dataset that is deliberately confined to the most robust experimental design currently available to test whether polyandry is maintained because of genetic benefits that accrue to the offspring of polyandrous females.

(2) The benefits of polyandry

There are three main adaptive explanations for polyandry. The first two explanations are widely accepted and based on polyandry increasing a female's direct fitness (i.e. lifetime fecundity) due to either material benefits provided by males, or by reducing costs associated with sexual conflict over mating rates. The third explanation is that polyandry elevates mean offspring fitness through genetic benefits associated with biasing paternity towards males with certain genotypes. Despite much early enthusiasm, support for the importance of genetic benefits seems to have declined over the last decade (Hettyey et al., 2010). We will briefly discuss each of the three explanations, but it should be noted that they are not mutually exclusive (see Kokko, Jennions & Brooks, 2006 for the analogous situation of adaptive explanations for the evolution of female mating preferences).

First, there is evidence that natural selection favours polyandry because mating results in the transfer of, or access to, male resources that increase a female's lifetime fecundity. This direct benefit could be due to an increase in longevity and/or an increase in fecundity per breeding event. For example, in many insects males transfer nutrients to females such as nuptial gifts and stimulatory chemicals that increase short-term egg production (Eberhard, 1996). A meta-analysis of 122 experimental studies of 78 insect

species, where females were assigned to higher or lower mating rate treatments, found that, on average, females with a greater mating rate produced significantly more offspring. This result was due to a positive effect of mating rate on both egg production and fertility, which more than compensated for significantly reduced female longevity in species where males did not provide nuptial gifts (Arnqvist & Nilsson, 2000). A longevity cost of multiple mating has since been reported in several other studies (e.g. Kawagoe, Suzuki & Matsumoto, 2001; McNamara *et al.*, 2008), and might be a widespread phenomenon. Due to the design of the original studies, the difference in mating rate between treatments is associated with a difference in the number of actual or potential mates (i.e. females housed with several, only a few or a single male) so these findings are usually interpreted as evidence that polyandry is beneficial. The most likely proposed mechanism is that some male-derived ejaculatory substances are stimulants that elevate egg production or act as nutrients that can be converted into eggs. In principle, these material benefits could arise by mating repeatedly with the same male, or by mating with several different males, so that polyandry is simply a by-product of the same male not being available when a female is ready to re-mate (Fedorka & Mousseau, 2002). It is also widely argued that multiple mating ensures an adequate supply of sperm (review: Hasson & Stone, 2009). Sperm might be limited for some monogamous females if males occasionally fail to transfer viable sperm upon mating, are sterile, or because a single male can not transfer sufficient sperm during a mating bout (Parker & Pizzari, 2010). The latter explanation, however, tends to presuppose the existence of polyandry because the main cause of sperm limitation is usually sperm depletion and/or strategic ejaculation of smaller ejaculates when females have a high mating rate (Wedell, Gage & Parker, 2002; Parker & Pizzari, 2010).

There are other more specialised contexts in which multiple mating might provide a direct benefit and elevate offspring production. For example, polyandry in cooperatively breeding fairy wrens (*Malurus cyaneus*) could increase the total amount of male parental care received by a female and reduce her workload because several males potentially share paternity in a brood. This assistance could additionally allow a female to lay initially smaller eggs that are less costly to produce (e.g. Russell *et al.*, 2007) and/or increase her lifespan due to the known negative effects of elevated levels of parental care on mortality in passerines (Liker & Szekely, 2005). Similarly, in two other cooperatively breeding birds, the superb starling (*Lamprotornis superbus*) and the American crow (*Corvus brachyrhynchos*) females that mate with within-group, extra-pair males can increase the number of helpers at the nest (Rubenstein, 2007; Townsend, Clark & McGowan, 2010). In general, however, it should be noted that in socially monogamous passerines the bulk of evidence suggests that extra-pair mating (and the resultant increase in extra-pair young) imposes a direct cost because of a reduction in the level of male care provided by the cuckolded mate (Arnqvist & Kirkpatrick 2005; Albrecht, Kreisinger & Pialek,

2006). This decline in care is primarily attributed to a lower share of paternity decreasing the benefit of caring for males (review: Kokko & Jennions, 2008). By contrast, in mammals polyandry can obscure paternity and might decrease the risk of infanticide in species where several males interact socially with the same female (e.g. primates with multi-male groups, or rodents where several males' home ranges overlap those of a female) (Ebensperger & Blumstein, 2007). The first formal experimental evidence that polyandry reduces infanticide has recently come from a study of bank voles (*Myodes glareolus*) that manipulated the number of males in a social group with access to females and recorded the resultant levels of infanticide (Klemme & Ylönen, 2010).

A second adaptive explanation is that polyandry is a 'harm minimization' strategy that females employ to reduce costs incurred due to male harassment. Given the costs of mating, some researchers have argued that polyandry is primarily a male-driven process that arises from sexual conflict over mating rates (e.g. Thornhill & Alcock, 1983; Parker, 2006; Bilde *et al.*, 2009). Females only re-mate because the cost of resisting mating attempts is sometimes greater than the costs of an additional mating (Arnqvist & Rowe, 2005). Female acquiescence can lead to 'convenience polyandry' where it is less costly for a female to accept a mating than resist. If true, there is no prerequisite for polyandry to be beneficial in terms of fertility or fecundity in situations where females can control their access to males (or when researchers experimentally assign variable numbers of males to females). This explanation is associated with claims that sexual conflict, in the form of direct coercion of females to mate or seduction of females through sensory exploitation, is the driving force behind females mating at rates that are higher than the naturally selected female optimum (e.g. Arnqvist, Nilsson & Katvala, 2005). Strictly speaking, most studies do not discriminate between the relative effect of the number of mates and the number of matings, so repeated mating and multiple mating might be equally damaging. These costs include reduced longevity (Arnqvist & Nilsson, 2000), and less male parental care (Arnqvist & Kirkpatrick, 2005; but see Griffith, 2007). More importantly, this argument is bolstered by the perceived absence of evidence that polyandry elevates offspring fitness. This last point is crucial because it challenges the validity of the third adaptive explanation for polyandry.

The third explanation is that polyandry confers genetic benefits that elevate net offspring fitness so that polyandry is under indirect selection, all be it that this is a weak selective force (Kirkpatrick & Barton, 1997; but see Kokko *et al.*, 2006). The potential post-copulatory mechanisms leading to genetic benefits have been extensively reviewed by Jennions & Petrie (2000), Tregenza & Wedell (2000), Hosken & Stockley (2003), Zeh & Zeh (2003), Simmons (2005) and Kempenaers (2007). Genetic benefits could arise in two main ways. First, the production of a more genetically diverse set of offspring might elevate mean offspring fitness, even in the absence of any paternity-biasing mechanism. This benefit is most

likely to arise in species where half-siblings remain in contact after birth (see McLeod & Marshall, 2009). Eusocial insects have provided the strongest evidence for this benefit as more genetically diverse colonies have higher foraging rates, population growth and, ultimately, a greater reproductive output (e.g. Baer & Schmid-Hempel, 1999, 2001; Mattila & Seeley, 2007). These benefits could arise because there is a genetic basis to worker castes (e.g. Hughes *et al.*, 2003; Hughes & Boomsma, 2007; Jaffe *et al.*, 2007) such that colonies founded by polygamous queens are more efficient in their division of labour (review: Smith *et al.*, 2008; theoretical models: Gove *et al.*, 2009; Tarapore, Floreano & Keller, 2010). There is also good evidence that patrilines differ in their susceptibility to certain diseases, so that a more genetically diverse colony workforce reduces the spread of disease and/or parasites, and lowers the mean level of worker mortality (e.g. Baer & Schmid-Hempel, 2001, 2003; Hughes & Boomsma, 2004; Invernizzi, Penagaricano & Tomasco, 2009; reviews: Tarpy, 2003; Wilson-Rich *et al.*, 2009). Even if there is no change in mean mortality, polyandry could decrease the variance in the size of the workforce compared to that of colonies founded by monogamous females. Reduced variance is potentially important if there is a non-linear relationship between colony size and reproductive output, so that output decreases rapidly when colony size falls below a critical level (e.g. Tarpy & Page, 2002). If the relationship is linear, then reduced variance in colony size will not result in a difference in the mean output of a colony founded by a polyandrous female and a set of monandrous colonies sired by the same males (Yasui, 1997). Looking beyond eusocial insects, some researchers argue that polyandry will elevate geometric fitness by reducing variance in mean fitness over generations. This 'bet-hedging' effect is, however, very small in larger populations and unlikely to compensate for any direct costs of polyandry (Yasui, 1998).

A more widely invoked possibility is that polyandry provides an opportunity for females to use post-copulatory mate choice to bias paternity towards males that elevate offspring fitness. There has been much debate about the extent to which this process is driven by: (*i*) paternity biasing towards males with 'good genes' that have additive effects on fitness (e.g. Tomkins *et al.*, 2010), or (*ii*) non-additive genetic benefits due to 'genetic compatibility' associated with inbreeding avoidance or increasing heterozygosity at specific loci (reviews: Kempenaers, 2007; Neff & Pitcher, 2005, 2008). An attempt to clarify the terminology being used by quantitative geneticists and evolutionary ecologists was recently provided by Puurtinen, Ketola & Kotiaho (2009), who also presented evidence that the magnitude of 'compatible genes' effects is similar to that for 'good genes' effects for the traits usually measured to estimate offspring fitness (e.g. offspring survival or developmental rate). It should be noted, however, that they did not estimate the extent to which paternity is actually biased to promote each type of genetic benefit. They simply estimated the potential increase in fitness that could arise.

When assessing the strength of indirect selection on female traits (i.e. the propensity to mate polyandrously or express a mating preference) due to improved offspring performance, it is important not to focus too strongly on any single component of fitness such as, say, immune function or longevity (see Kokko *et al.*, 2006). The crucial question is whether mean offspring fitness is elevated. Net fitness will depend on a variety of positive and negative effects on offspring viability at different life-history stages, male attractiveness, sperm competitiveness, fecundity and fertility. There might even be sexually antagonistic genetic effects that make it difficult for females simultaneously to elevate the fitness of both sons and daughters (e.g. Fedorka & Mousseau, 2004; Brommer *et al.*, 2007; Foerster *et al.*, 2007; Hall *et al.*, 2010; reviews: Bonduriansky & Chenoweth, 2009; Connallon, Cox & Calsbeek, 2010). These sex-specific genetic effects could lead to strategic sex allocation based on the sire's identity towards the sex that benefits most (e.g. Calsbeek & Sinervo, 2004; Pryke & Griffith, 2009; Roulin *et al.*, 2010; Sato & Karino, 2010).

Finally, a fourth mechanism has recently been proposed to account for polyandry appearing to be beneficial (Simmons, 2005). The mean fitness of the offspring of polyandrous females might be increased through phenotypic interactions between maternal half-siblings. For example, some males might be better than others at siring offspring that produce signals that induce females to increase their investment into a brood, with the beneficial maternal effect shared by all the sires' offspring (e.g. a 'rescue effect' *sensu* Zeh & Zeh, 2006). Similarly, males might vary in the effect their ejaculates have on inducing females to invest into offspring and, again, the benefits of greater maternal investment are shared equally among all offspring (e.g. García-González & Simmons, 2007). The amount of maternal resources that offspring receive often has a large impact on their fitness (Sheldon, 2000). Although the basic idea is simple, the associated quantitative genetic terminology can be cumbersome. These patterns are designated as indirect genetic effects if the environment in which offspring develop is partly determined by parental genes (i.e. a paternal indirect genetic effect if sire genes vary in the effect they have on female investment into offspring). Of course, differential investment is a classic 'maternal effect', which can itself be a maternal indirect genetic effect if there are maternal genes that vary in their effect on the induced environment provided to offspring. The final piece of terminology needed is to note that these effects are attributed to 'interacting phenotypes' when the individuals in which the genetic effect is expressed (e.g. sire A) and the one whose phenotype changes as a consequence (e.g. offspring of sire B) are unrelated. It is worth noting that, in some respects, this mechanism could more simply be described as a benefit of greater genetic diversity that depends on siblings interacting (e.g. similar to the mechanism behind the lower rates of parasitism in mixed-paternity social insect colonies, but with the distinction that the process is driven by maternal investment).

To date, only two studies, involving a cricket (*Teleogryllus oceanicus*) (García-González & Simmons, 2007) and a

pseudoscorpion (*Cordylochernes scorpioides*) (Zeh & Zeh, 2006), have presented strong evidence that mean offspring fitness is elevated due to paternity and/or ejaculatory chemicals by some males increasing the fitness of other males' offspring. More generally, because polyandry provides females with the opportunity to engage in post-copulatory mate choice it might increase maternal investment into the offspring of preferred males (i.e. differential allocation; reviews: Sheldon, 2000; Ratikainen & Kokko, 2010). Such maternal effects could potentially inflate estimates of the genetic benefits of polyandry. If females are monitored over their lifetime, however, it is not immediately apparent why a process that depends on maternal effects would elevate the net fitness of polyandrous females' offspring. Differential allocation changes how resources are distributed among offspring and/or successive breeding attempts. It does not elevate the total amount of resources distributed, which raises the question as to whether polyandry is adaptive if maternal effects are the only reason for higher mean offspring fitness in a given brood. It is unlikely but might occur if a small increase in maternal investment has a disproportionately large, non-linear effect on the fitness of some male's offspring (e.g. the 'rescue effect' noted by Zeh & Zeh, 2006).

There is also a potential indirect genetic benefit if polyandry increases sons' fitness *via* maternal effects arising in the next generation when sons mate. If certain sires consistently induce greater maternal investment from females, and this ability is heritable their sons will benefit in the same way as if they inherited genes for, say, greater foraging efficiency (Sheldon, 2000). That is, they will induce their mates to invest more heavily in their own offspring (i.e. a polyandrous female's grandchildren). This type of indirect genetic effect is one of many mechanisms that have been proposed to maintain genetic variation in the benefits provided by females choosing mates with more elaborate sexual traits (modelled by Miller & Moore, 2007). By extension, the same benefits arise if polyandrous females can bias paternity/total offspring production towards males that are better at inducing greater maternal investment.

(3) Current controversy and empirical tests for genetic benefits

In many species, females gain no apparent direct benefits from mating but incur substantial costs when seeking additional mates (e.g. den Hollander & Gwynne, 2009; Suter *et al.*, 2009). In such cases it is common to invoke genetic benefits to explain polyandry. The logic underlying this approach is identical to that used to explain costly female mate choice for genetic benefits on leks. Both phenomena raise exactly the same problems. For example, the need to ensure that the observed changes in fitness are due to sire rather than maternal effects, failure to detect hidden material benefits of choice, and the issue of the maintenance of genetic variance in the benefits provided by males (reviews: Kokko *et al.*, 2006; Hettyey *et al.*, 2010). Experimental tests have

produced outcomes covering the full gamut of possibilities. Two examples are illustrative. In an experimental study of a marsupial (*Antechinus stuartii*) polyandry significantly elevated offspring survival, which is likely to be closely correlated with lifetime fitness (Fisher *et al.*, 2006a). Due to the breeding biology of *A. stuartii* this benefit is unlikely to be a result of maternal effects, as most females are semelparous and there is no opportunity for differential allocation. This study also directly showed that paternity was biased towards males that tended to increase offspring survival. By contrast, a recent study of the cow-pea weevil (*Callosbruchus maculatus*) found that paternity is biased towards males that lower females' lifetime reproductive output (Bilde *et al.*, 2009), partly because they have a negative effect on juvenile survival (Bilde *et al.*, 2008). These males also reduce the fecundity of their daughters. This result is readily explained by sexual conflict: males are always under selection to increase their share of paternity even if so doing is not in the female's best interest. The extent to which males that harm females succeed in overcoming female interests should influence the value of polyandry. If polyandry does not confer other benefits, then it is likely to be selected against. It is noteworthy that in *C. maculatus*, females can reduce the risk of dehydration by mating with males who transfer water in their ejaculates (Edvardsson, 2007; Ursprung, den Hollander & Gwynne, 2009), which could provide a direct benefit to polyandry.

Challenges to the view that polyandry and/or female mating preferences are maintained by genetic benefits come from both theoretical concerns and empirical evidence. The main theoretical issue is that indirect selection driven by additive genetic benefits is weak and is therefore unlikely to outweigh direct fitness costs associated with mating multiply (Curtsinger, 1991; Kirkpatrick & Barton, 1997; Cameron, Day & Rowe, 2003; but see Kokko *et al.*, 2006). Indirect selection is weak partly due to the low heritability of fitness. Although individual sexually selected traits might be heritable (Pomiankowski & Møller, 1995), and there is recent evidence for substantial additive genetic variation for individual components of fitness due to a mutational load of partly recessive deleterious mutations (e.g. Tomkins *et al.*, 2010), there might still be little or no additive genetic variation in the direction of sexual selection (i.e. for net fitness) (e.g. van Homrigh *et al.*, 2007; review: Walsh & Blows, 2009).

Individual empirical studies have produced evidence both for (e.g. Firman & Simmons, 2008b; Fisher *et al.*, 2006a; Head *et al.*, 2005) and against (e.g. Qvarnström, Brommer & Gustafsson, 2006; Bilde *et al.*, 2009; Maklakov & Arnqvist, 2009) the claim that genetic benefits of female choice/polyandry outweigh direct costs. In a previous meta-analysis, evidence was presented that there are small but significant benefits to female mate choice because of a correlation between male sexual trait expression and offspring survival (Møller & Alatalo, 1999). However, many of the studies included in this meta-analysis did not control fully for non-genetic paternal effects and other sources

of environmental variation (see Jennions, Møller & Petrie 2001), so it provided only circumstantial evidence for the necessary genetic correlation between preferred male traits and viability (which is assumed here to be a positive correlate of net fitness). Some individual studies do a reasonable job of controlling for maternal effects and the level of male parental care by comparing half-siblings reared under the same conditions, such as comparison of within-pair and extra-pair offspring in passerine birds (e.g. Sheldon *et al.*, 1997; Garvin *et al.*, 2006; Freeman-Gallant *et al.*, 2006), or *in vitro* fertilization of split broods by males that differ in sexual trait expression (e.g. Barber *et al.*, 2001), or by preferred and non-preferred males being assigned on a female-by-female basis (e.g. Agbali *et al.*, 2010). Ideally, fertilization *in vitro* is required to control for differential maternal allocation in response to male phenotype, such as the production of larger eggs (e.g. Evans *et al.*, 2010). Putting together the available evidence, two recent meta-analyses of extra-pair paternity in passerine birds have both concluded that there is no evidence for genetic benefits to polyandry (i.e. engaging in extra-pair copulations) (Arnqvist & Kirkpatrick, 2005; Akçay & Roughgarden, 2007; but see Griffith, 2007). By contrast, a meta-analysis of 29 effect sizes from studies of 12 insect species, which controlled for mating rate, showed a small but significant increase in egg hatching success for polyandrous females (Simmons, 2005). This beneficial effect could be due to genetic sire effects on early embryo survival, but it might also reflect sperm limitation if some males are sterile, have very low sperm counts or are generally poor at transferring sperm to females so that fertilization levels are lower for monogamous females (review: Hasson & Stone, 2009).

In their meta-analysis, Arnqvist & Nilsson (2000) found that an increase in the rate of offspring production led to higher lifetime reproductive success for polyandrous female insects despite a maternal longevity cost. They attributed this finding to direct benefits arising from sperm replenishment and/or stimulatory effects of mating on female physiology. The studies they analyzed did not, however, control for the effect of the number of mates. It is therefore impossible to use this meta-analysis to estimate the genetic and direct benefits of polyandry *per se*. To do so requires experimental manipulation of the number of mates while controlling for mating rate. It is necessary to standardise mating rate between monandry and different polyandry treatments to assess the potential genetic benefits of polyandry and to remove, or at least reduce, potentially confounding variation in material benefits and/or mating costs that might otherwise differ between females assigned to each mating treatment. This experimental approach was first used by Tregenza & Wedell (1998) and has since been adopted in many other studies. These experimental studies typically obtain several measures of female and offspring fitness including maternal fecundity and fertility, as well as offspring growth rate, development speed, size, survival and so on. There is, however, much variation among studies in the specific variables being measured. In general, we have little insight into which traits

are the best predictors of net offspring fitness. Aside from Simmons' (2005) initial review of hatching success effects in insects, a comprehensive meta-analysis of these experimental studies is currently lacking.

Here we provide a meta-analysis of all available data from experimental studies of polyandry across all taxa. We report the effect of polyandry for all fitness components measured allowing us to: (*a*) test whether the small but beneficial effect of polyandry on hatching success previously reported ($z_r = 0.192$, $P = 0.019$) by Simmons (2005) persists in an expanded dataset. (*b*) Determine whether a comparable beneficial effect of polyandry can be detected for other fitness components. (*c*) Test whether those offspring traits that are most likely to differ between mating treatment groups due to genetic effects (i.e. post-fertilization traits so that sperm supply effects can be excluded) are actually elevated by polyandry. (*d*) Test whether polyandry *per se* affects maternal longevity. Arnqvist & Nilsson (2000) have previously shown a detrimental effect of an elevated mating rate, but they did not test formally whether it was partly or entirely due to mating with several different males or just an effect of mating more often.

We have confined our meta-analysis to experimental tests designed to detect genetic benefits to polyandry while minimizing direct benefits. We do so because these experiments should provide the strongest evidence for/against genetic benefits. There are, of course, other lines of evidence for genetic benefits of polyandry from different types of studies that might also be amenable to future meta-analyses. These studies are described in greater detail in Section IV (see Table 6).

II. METHODS

(1) The use of meta-analysis

The published literature abounds with theoretical (Zeh & Zeh, 1997, 2003; Jennions & Petrie, 2000; Tregenza & Wedell, 2000; Hosken & Stockley, 2003; Simmons, 2005; Kempenaers, 2007; Hasson & Stone, 2009) and taxonomic reviews of polyandry (Arnqvist & Nilsson, 2000; Avise *et al.*, 2002; Griffith, Owens & Thuman, 2002; Westneat & Stewart, 2003; Uller & Olsson, 2008). We do not wish to add to this literature. Instead, we conducted a meta-analysis to determine whether the claims and summaries provided by these reviews are supported by a quantitative analysis of the available empirical studies. This should help researchers to decide where future research efforts might best be focussed (Borenstein *et al.*, 2009). More specifically, claims that polyandry generally improves offspring performance are unwarranted if they reflect the inflated influence of a few studies with very strong positive findings (e.g. Baer & Schmid-Hempel, 1999; Fisher *et al.*, 2006*a*). There is a wider concern that whenever studies measure several variables there could be a publication bias if traits that are significantly affected by an experimental treatment are preferentially reported ('selective

reporting'). There could also be a weaker publication bias in which significant results are more strongly emphasized in abstracts and discussion sections, or studies with one or more significant effects are more likely to be published in high impact journals (Leimu & Koricheva, 2005) ('dissemination bias') (review: Jennions *et al.*, 2011). Both forms of bias are a potential concern when evaluating polyandry studies as several different measures of offspring performance are often taken by researchers. Unlike narrative reviews, meta-analysis provides an objective method to summarise empirical studies to test whether the average effect of a treatment deviates from the null expectation (i.e. no benefit of polyandry). Meta-analysis can also identify which factors (e.g. taxonomic grouping, methodology) account for variation among studies in the effect of an experimental treatment; or whether the occurrence of 'conflicting' studies with significant and non-significant results could simply reflect sampling error because the true effect of a treatment is low so that Type II errors (failure to reject a false null hypothesis) will be common. Finally, and perhaps crucially in the light of our findings, because meta-analysis involves a systematic literature review it can identify gaps in the available data and point to areas where more research is required.

(2) Data compilation

We followed a rigorous search protocol that was designed to locate as many studies as possible but minimize sampling bias. First, in January 2010 we used the *Scopus* search engine (*www.scopus.com*) to compile a list of papers that cited Tregenza & Wedell (1998). This was the first polyandry study to use the controlled experimental design that is the focus of our meta-analysis. Second, we searched the published literature using *Scopus* for papers with "polyandry" OR "multipl* AND mat*" in the article's title, abstract or key words. These terms were selected to maximise the chance of locating relevant publications while keeping the number of papers to a manageable figure so that we could inspect each more closely to ensure it fulfilled our inclusion criteria. Third, we identified five influential taxon-specific reviews of polyandry: Arnqvist & Nilsson (2000) (insects); Avise *et al.* (2002) (fish); Griffith *et al.* (2002) (birds); Westneat & Stewart (2003) (birds); and Uller & Olsson (2008) (reptiles). We then scanned their reference lists to locate additional potentially relevant papers. The first and the second search method yielded 134 and 1019 papers respectively in April 2010. The combination of the three search methods yielded a total of 1280 unique papers (available on request from the authors as an Endnote Library).

To reduce the risk of assembling a biased dataset we did not haphazardly add papers that we encountered by chance. These are more likely to be drawn from higher impact journals that are more visible and might preferentially publish studies with significant results (Murtaugh, 2002). We also decided not to solicit unpublished datasets from colleagues (for justifications see Jennions *et al.*, 2011). To finalise the analysis we excluded several potentially usable papers published since January 2010 (e.g. Liu *et al.*, 2010; Kekäläinen *et al.*, 2010; Gowaty *et al.*, 2010).

To perform an initial cull of the 1280 papers we inspected titles, place of publication and, where possible, scanned the online abstract (see Côté *et al.*, 2011). We excluded publications that were obviously unsuitable, or highly unlikely to have used the required experimental design (see Section II.3). This left 108 potentially suitable papers. These were downloaded and read to see if they met our inclusion criteria.

(3) Inclusion criteria

We had three inclusion criteria: (1) does the study have an appropriate experimental design? (2) Is the study within the scope of our question? (3) Does the paper include extractable data? For Criterion 1 we required that females and males were randomly assigned to either a monandry or a polyandry treatment in an experiment in which the number of matings per female did not differ between the two treatments (e.g. a monogamous female mated with the same male four times and a polygamous female mated once each to four males or twice each to two males). We were interested in the genetic benefits of polyandry so studies that did not explicitly attempt to standardise the number of matings between the monandry and polyandry treatments were excluded. Full control of the number of matings is necessary to avoid potentially confounding effects of material benefits associated with copulation (e.g. transfer of nutrients) and/or harmful effects of additional matings on female fitness. Ideally, the exact number of matings was known because each mating was observed ('full control' studies). In some studies the number of matings was not directly counted so it was impossible to be certain that they were identical between the treatments. Nonetheless, equality in mating rate was assumed if general information on male and/or female post-mating refractory periods indicated that only a single mating was possible during the limited time in which a pair was housed together and the total time spent with males was equal across treatments. These studies were included in the dataset and treated as 'full control' studies. In other studies the number of matings was not directly counted, but a difference between the monandry and polyandry treatment in the total number of matings is unlikely because each female was confined with a single male for the same amount of time. We included these studies in our data set but conservatively coded them as 'partial control' of mating number. By contrast, we always excluded studies where polyandrous females were simultaneously exposed to all their prospective mates (e.g. female placed in a container with a single male or with four males and left for several days). We did so because male-male competition could affect the total number of matings, the ejaculate size per mating (Wedell *et al.*, 2002; Parker & Pizzari, 2010), and/or the intensity of male harassment of females.

For Criterion 2 we included any study that measured at least one component of offspring fitness. The offspring response variables measured were: initial size, development time, growth rate, juvenile survival, size at adulthood, various measures of offspring parasite load or prevalence, colony

performance in eusocial insects, and reproductive success (son's mating success or daughter's fecundity). In addition, we recorded the effect of polyandry on several direct measures of maternal fitness. These were: number of clutches, fecundity, proportion of eggs fertilized, hatching success and maternal longevity. Slightly different measures of the same general trait were assigned to common categories for analysis purposes (e.g. fecundity might have been measured over a lifetime or several weeks) (see supporting online information :Appendix S1 for details). Criterion 3 meant that we sometimes excluded a study with the appropriate experimental design (or one or more measures of fitness from such a study) because it was impossible to calculate the effect size and/or its variance. Exclusion was usually due to the absence of unambiguous information about sample sizes, the magnitude of the effect size or the direction of the effect. The latter two forms of missing data are more likely to be associated with non-significant results (e.g. Cassey *et al.*, 2004), so true effect sizes might be overestimated.

We have attempted to include the specific details of our approach so that the reader can decide for themselves whether it might bias our estimate of the true effect size. Despite our best efforts, we make no claim to have located all of the relevant literature, but we see no reason why our approach would yield an unrepresentative sample of the published experimental studies of polyandry.

(4) Meta-analysis statistical methods

The common effect size we calculated was Hedge's *d* [i.e. *J*-corrected Hedge's *g* sensu Rosenberg, Adams & Gurevitch (2000); but note that Cooper, Hedges & Valentine (2009) refer to the *J*-corrected effect as Hedge's *g*]. We preferentially calculated Hedge's *d* using the mean and a measure of variance (standard deviation or error) for each treatment derived from individual female values. Means and measures of variance were extracted from summary tables, the text or figures (using *Image J v. 1.43*). Where this approach was not possible, we converted test statistics (t, F or χ^2) or P values from tests of the main effect of the 'number of mates' treatment to Hedge's *d* using the software package *MetaWin* v. 2.0 (Rosenberg *et al.*, 2000). We then calculated the variance using the number of females per treatment as the sample size. In a few cases only the total sample size was provided. If so, we set the sample size as equal across treatments.

If there was more than one effect size per species, we calculated the species mean and its associated variance by pursuing a hierarchical approach to combining data (see Mengersen, Jennions & Schmid, 2011). First, within each study we calculated the mean effect and mean variance if the same set of individuals contributed two or more effects to the same focal trait (e.g. 'survival' measured as survival to day 50 and survival to adulthood). Second, if there was still more than one effect size per trait in a study (i.e. different sets of females used) we calculated the weighted mean for the study for that trait using a standard fixed-effects model. The variance of the mean of m effects (denoted X_i or X_j) each with

a variance of V_i or V_j and V_{ij} representing the covariance between X_i and X_j ($i \neq j$) and r_{ij} representing the correlation between X_i and X_j (only one combination of a given pair of effects is required) is:

$$V_{\text{mean}} = \left(\sum_{i=1}^{m} V_i + 2 \sum_{i,j} V_{ij} \right) / m^2$$

$$= \left(\sum_{i=1}^{m} V_i + 2 \sum_{i,j} (r_{ij} \sqrt{V_i} \sqrt{V_j}) \right) / m^2 \qquad (1)$$

(modified from Borenstein *et al.*, 2009, p. 228).

As the variance differed between effect-size estimates, we multiplied each V_i in the first sum by (W_i / W_{mean}) and each term in the second sum by $(W_{i*} W_j)/(W_{i*} W_j)_{\text{mean}}$ (i.e. to give greater weighting to effect estimates from traits with lower variances; $W_i = 1/V_i$; $W_{\text{mean}} = (\sum W_i)/m$). We set all $r_{ij} = 0$ if the effect sizes were calculated from fully independent sets of females within the study. If, however, the same individuals contributed to both effect sizes (i.e. because the same set of monogamous females was used to calculate effect sizes for two levels of polyandry treatment) we calculated r_{ij} as the proportion of individuals shared between the data sets used to estimate each effect size (see Borenstein *et al.*, 2009 p. 240). Third, we calculated the weighted mean and its variance across studies for each species using a standard fixed-effects model. Finally, we ran separate random-effects models in *Metawin 2.0* using species-level effects for each focal trait.

In addition to conducting separate analyses for each focal trait, we also calculated a composite effect size (Borenstein *et al.*, 2009; Mengersen *et al.*, 2011) for each species for post-fertilization offspring traits (e.g. growth rate, adult size) where difference in 'offspring performance' between monogamous and polyandrous females should reflect genetic sire effects (although differential maternal allocation can not be excluded). We also conducted a second, modified analysis in which we included data on hatching success from three studies (Marshall & Evans, 2007; McLeod & Marshall, 2009; Gershman, 2010) where hatching rates were only measured from eggs that had already been identified as fertilised (i.e. it was a measure of early embryo to hatchling survival). We excluded other hatching success effect sizes because they were potentially influenced by differences in initial fertilization success between treatments. We did not calculate a composite effect size for direct benefits because the traits in question (fecundity, fertility, number of clutches, hatching success and maternal longevity) have well-understood links with fitness so that they can be individually evaluated. The composite effect of 'offspring performance' was the weighted mean of the available effect sizes. To calculate its variance we used Equation 1. The correlation between the different trait measures is unknown and we therefore performed a sensitivity test by running two analyses. In one analysis we assumed the measures were uncorrelated ($r_{ij} = 0$) so that

each trait increased the precision of the estimate of the mean. In the other analysis we assumed that the measures were perfectly correlated ($r_{ij} = 1$) so that they did not increase the precision of the estimate, only the accuracy of the estimate of the mean (for justification of 'bracketing' see Borenstein *et al.*, 2009).

The null hypothesis for each analysis was that the mean effect size was zero. The effect sizes were always calculated such that a positive value implied greater fitness for polyandrous females (e.g. shorter development time, fewer parasites, larger size at adulthood, greater survival, greater maternal longevity). To test whether the mean effect size estimate differed from the null value, we used a *t*-test with N-1 degrees of freedom based on the parametric estimate of the standard error. However, due to small sample sizes per trait we place greater emphasis on whether or not the non-parametric, bias-corrected, bootstrapped 95% confidence intervals (calculated in *Metawin 2.0*) includes zero. In several cases the interval only just overlapped zero and we note cases where the overlap was less than 0.05 Hedge's *d* units. We also report the total heterogeneity (Q_T), assuming Q_T follows a χ^2 distribution with $d.f. = N-1$. We also tested (sample size permitting) whether effect sizes differed between insects and vertebrates using Q_b (formulae for Q_T and Q_b in Rosenberg *et al.*, 2000). Although we initially coded other potential moderator variables, sample sizes per group were too small to warrant analyses.

We used several methods to test the robustness of our effect-size estimates to publication bias (reviews: Jennions *et al.*, 2011; Møller & Jennions, 2001). First, we calculated the Spearman's correlation between standardized effect size and study sample size (denoted r_{bias}). This test has low statistical power when $N < 25$ (Begg & Mazumdar, 1994). Second, we used 'trim and fill' to calculate L, defined as the number of potentially 'missing' studies based on asymmetry of a plot of effect size *versus* sample size (i.e. funnel plot asymmetry) (see Duval & Tweedie, 2000). We then re-calculated the mean effect after including estimates for any 'missing' studies. Third, we calculated Rosenberg's fail-safe number. This is the number of additional studies taken from a distribution of studies centred on the null value with the same average sample size as the located studies that would be required so that the weighted mean from a fixed-effect model no longer differs from zero at $\alpha = 0.05$, based on a *t*-distribution (Rosenberg, 2005). Rosenberg's number is usually much smaller than the widely used Rosenthal fail-safe number (e.g. see Section III). Fourth, to test for temporal trends we calculated the Spearman's correlation between year of publication and effect size. We also conducted an analysis in which we weighted estimates by running a meta-regression in *Metawin 2.0* with year as the covariate. We report the *P* value from a randomization test for the slope of effect size on year and the direction of the slope. Not all tests were conducted for all focal traits because of sample size constraints for trim and fill tests, or because there was no need to calculate a fail-safe number given that the estimated effect was clearly non-significant.

III. RESULTS

(1) Single trait analyses

We extracted 232 effect sizes from 46 studies that met our inclusion criteria (Table 1). Of these studies, 39 had full and seven had partial control of the number of matings. There were effect sizes for 35 species with full control and five with partial control of mating number. Preliminary analyses showed that including the five species with only partial control did not markedly change estimates and confidence intervals for effect sizes when data were analysed at the species level. We therefore take a conservative approach and report only analyses based on effect sizes from studies with full control of the number of matings (analyses using all 40 species are presented as supporting online information in Appendix S2). In total we had 107 species-level effect sizes for 15 different focal traits. The sample size was, however, only greater than 10 for four traits.

The mean effect size, 95% confidence interval and the results of the test for heterogeneity among species are shown in Table 2. The main findings are summarised in Fig. 1. The non-parametric confidence intervals did not overlap zero suggesting that there is clearly a beneficial average effect of polyandry on fertility (mean $d = 0.19$) and the number of clutches produced (mean $d = 0.29$). The parametric *t*-tests showed that the estimates were only marginally non-significant for fertility ($P = 0.058$) and number of clutches ($P = 0.052$). There was also good evidence from confidence intervals which overlapped zero by less than 0.05 units (Fig. 1), that polyandry increases hatching success (mean $d = 0.27$), with a marginally non-significant *t*-test ($P = 0.075$). The 95% confidence interval also showed only a small (<0.07 units) overlap of zero for offspring survival and offspring size.

In contrast to polyandry's beneficial effects on these above traits there was evidence that it imposes a cost by reducing maternal longevity. The range of the 95% confidence intervals had an upper limit that was only 0.02 units greater than zero, although the *t*-test was non-significant ($P = 0.199$). There was little evidence that polyandry increased fecundity, and the sample size was sufficiently large ($N = 25$ species) to draw a fairly robust conclusion. For the other focal traits there was simply insufficient data to draw robust conclusions ($N \leq 6$ species). With the exception of hatching success ($P = 0.03$) there was no evidence for heterogeneity in effect sizes among species beyond that due to sampling error.

(2) A composite effect size for offspring performance

We had data for 20 species for the composite effect size which measured 'offspring performance' (Table 3). For the analysis excluding post-fertilization hatching success that treated each focal trait as an independent estimate there was a significantly beneficial effect of polyandry on offspring performance (mean $d = 0.19$, $N = 18$ species) based on

Table 1. Summary statistics and effect sizes for initial measures. See main text for the protocol used to obtain one effect size per trait per species

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment Mean	S.E. / S.D.	N	Polyandry treatment Mean	S.E. / S.D.	N	Test statistic	Effect size (Hedges' d)	Variance d	Study
Amphibia													
Crinia georgiana	Full	2	Size	115.54	6.80	8	123.69	6.27	8		0.417	0.255	Byrne & Roberts (2000)
		2	Size	109.54	6.41	8	115.66	7.24	6		0.319	0.295	Byrne & Roberts (2000)
		2	Size	47.33	1.44	7	50.18	1.57	6		0.693	0.328	Byrne & Roberts (2000)
		2	Size	49.46	1.54	6	49.98	1.69	5		0.126	0.367	Byrne & Roberts (2000)
		2	Development time	13.14	0.35	8	13.13	0.34	8		-0.010[a]	0.250	Byrne & Roberts (2000)
		2	Development time	13.21	0.35	8	13.33	0.40	6		0.114[a]	0.292	Byrne & Roberts (2000)
		2	Development time	43.23	2.13	7	41.71	2.32	6		-0.250[a]	0.312	Byrne & Roberts (2000)
		2	Development time	44.64	2.28	6	43.77	2.50	5		-0.142[a]	0.368	Byrne & Roberts (2000)
		2	Survival	84.96	7.19	8	80.91	7.16	8		-0.189	0.251	Byrne & Roberts (2000)
		2	Survival	53.34	7.28	8	52.70	8.26	6		-0.029	0.292	Byrne & Roberts (2000)
		2	Survival	42.17	8.52	7	28.70	9.31	6		-0.553	0.321	Byrne & Roberts (2000)
		2	Survival	28.08	9.15	6	40.80	10.02	5		0.519	0.379	Byrne & Roberts (2000)
Arachnida													
Cordylochernes scorpioides	Full	2	Fecundity	137	13	77	181	15	72		0.363	0.027	Newcomer *et al.* (1999)
		2	Clutches	2.31	0.20	68	3.15	0.21	69		0.492	0.030	Newcomer *et al.* (1999)
		2	Fertility			77			72	Fisher's test, $P = 0.371$	0.145[b]	0.027	Newcomer *et al.* (1999)
		2	Survival	0.24	0.03	68	0.36	0.04	69		0.407[a]	0.030	Newcomer *et al.* (1999)
Ascidiacea													
Pyura stolonifera	Full	5,6	Hatching	0.67	0.03	13	0.57	0.03	13		-0.856	0.168	Marshall & Evans (2007)
		5,6	Fertility	0.29	0.01	13	0.34	0.02	13		1.081	0.176	Marshall & Evans (2007)
Echinoidea													
Heliocidaris erythrogramma	Full	2	Fertility	0.54	0.03	10	0.62	0.04	10		0.702	0.212	Evans & Marshall (2005)
		2	Fertility	0.72	0.03	10	0.80	0.03	10		0.856	0.218	Evans & Marshall (2005)
Insecta													
Adalia bipunctata	Full	10	Fecundity	554.56	95.14	9	441.78	85.28	9		-0.396	0.227	Haddrill *et al.* (2007)
		10	Hatching	54.60	*23.40**	9	70.40	*6.50**	9		1.054	1.342	Haddrill *et al.* (2007)
Allonemobius socius	Full	4	Fecundity	102.00	13.35	24	63.60	6.52	24		-0.734	0.089	Fedorka & Mousseau (2002)
		4	Longevity	71.51	3.98	24	49.05	5.14	24		-0.981	0.093	Fedorka & Mousseau (2002)
		4	Hatching	0.19	0.04	24	0.55	0.06	24		1.418	0.104	Fedorka & Mousseau (2002)

Table 1. *(Cont.)*

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
	Full	4	Survival	0.18	0.04	24	0.30	0.05	24		0.514	0.086	Fedorka & Mousseau (2002)
		4	Fitness	0.86	0.29	24	1.94	0.50	24		0.531	0.086	Fedorka & Mousseau (2002)
Apis mellifera	Full	10	Parasites			14			14	Fisher's test, $P=1$	0.000[ab]	0.143	Seeley & Tarpy (2007)
		10	Parasites			14			14	$\chi^2=2.91$, $P=0.088$	−0.637[b]	0.150	Seeley & Tarpy (2007)
		10	Parasites			14			14	$\chi^2=5.40$, $P=0.0201$	−0.915[b]	0.158	Seeley & Tarpy (2007)
		10	Parasites			14			14	$t=2.45$, $P=0.0213$	−0.899[b]	0.157	Seeley & Tarpy (2007)
		15	Colony			14			14	$t=1.86$, $P=0.0639$	0.683[b]	0.151	Seeley & Tarpy (2007)
	Full	15	Colony			9			12	$F=25.76$, d.f. $=1,19$	2.172[b]	0.307	Mattila & Seeley (2007)
		15	Colony	240	109	9	384	240	12		0.207	0.196	Mattila & Seeley (2007)
		15	Colony	990	145	9	1390	120	12		0.906	0.214	Mattila & Seeley (2007)
		15	Colony	5300	2400	9	26700	1830	12		3.059	0.417	Mattila & Seeley (2007)
		15	Colony	0.09	0.01	9	0.30	0.05	12		1.513	0.249	Mattila & Seeley (2007)
Aquarius paludum	Full	2	Fecundity	90.60	4.40	13	89.70	4.40	10		−0.058	0.177	Ronkainen *et al.* (2010)
		2	Hatching	0.79	0.02	13	0.75	0.04	10		−0.472	0.182	Ronkainen *et al.* (2010)
		4	Fecundity	90.60	4.40	13	72.00	2.80	11		−1.352	0.206	Ronkainen *et al.* (2010)
		4	Hatching	0.79	0.02	13	0.67	0.03	11		−1.448	0.212	Ronkainen *et al.* (2010)
Bombus terrestris	Full	4	Parasites	2.40	0.05	12	1.08	0.04	7		−8.349[a]	2.061	Baer & Schmid-Hempel (1999)
		4	Parasites	1.38	0.33	12	0.03	0.02	7		−1.413[a]	0.279	Baer & Schmid-Hempel (1999)
		4	Parasites	0.68	0.08	12	0.55	0.09	7		−0.473[a]	0.232	Baer & Schmid-Hempel (1999)
		4	Parasites	0.13	0.04	12	0.02	0.01	7		−1.023[a]	0.254	Baer & Schmid-Hempel (1999)
		4	Parasites	0.97	0.09	12	0.67	0.12	7		−0.960[a]	0.250	Baer & Schmid-Hempel (1999)
		4	Parasites	2.50	0.26	12	1.71	0.36	7		−0.825[a]	0.244	Baer & Schmid-Hempel (1999)
		4	Colony	52.00	15.80	12	32.20	4.60	7		−0.424	0.231	Baer & Schmid-Hempel (1999)

Table 1. (Cont.)

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
		4	Fitness	23.65	3.18	12	46.94	10.24	7		1.212	0.265	Baer & Schmid-Hempel (1999)
	Full	2	Parasites	0.68	0.04	18	0.63	0.09	10		−0.228[a]	0.157	Baer & Schmid-Hempel (2001)
		2	Parasites	76.13	5.35	18	60.92	10.36	10		−0.555[a]	0.161	Baer & Schmid-Hempel (2001)
		2	Fitness	93.76	19.59	18	13.76	16.80	10		−1.048	0.175	Baer & Schmid-Hempel (2001)
		4	Parasites	0.68	0.04	18	0.55	0.05	17		−0.705[a]	0.122	Baer & Schmid-Hempel (2001)
		4	Parasites	76.13	5.35	18	48.05	5.85	17		−4.536[a]	0.408	Baer & Schmid-Hempel (2001)
		4	Fitness	93.76	19.59	18	88.16	24.08	10		−0.060	0.114	Baer & Schmid-Hempel (2001)
Cadra cautella	Full	2	Fecundity	71.40	11.40	15	83.40	9.00	15		0.294	0.135	McNamara *et al.* (2008)
		2	Fecundity	144.00	20.40	16	129.00	16.80	16		−0.196	0.126	McNamara *et al.* (2008)
		2	Fertility	0.54	0.39	15	0.67	0.25	15		0.100	0.134	McNamara *et al.* (2008)
		2	Fertility	0.55	0.37	16	0.60	0.40	16		0.032	0.125	McNamara *et al.* (2008)
		2	Longevity	5.36	0.33	15	5.14	0.27	15		−0.183	0.134	McNamara *et al.* (2008)
		2	Longevity	9.00	0.96	16	6.41	0.38	16		−0.865	0.137	McNamara *et al.* (2008)
Callosobruchus maculatus	Full	3	Fecundity			27			34	$F = 3.47$, d.f. = 1,58	0.474[b]	0.068	Eady *et al.* (2000)
		3	Survival			27			34	$F = 7.07$, d.f. = 1,58	−0.677[b]	0.070	Eady *et al.* (2000)
Chrysochus cobaltinus	Full	10	Fecundity	281.68	39.50	17	357.25	37.79	17		0.463	0.121	Schwartz & Peterson (2006)
		10	Clutches	0.94	0.07	17	1.02	0.06	17		0.267	0.119	Schwartz & Peterson (2006)
		10	Longevity	44.14	3.68	17	49.20	4.14	17		0.306	0.119	Schwartz & Peterson (2006)
Coelopa frigida	Full	4	Fecundity	94.85	6.23	57	109.77	7.27	57		0.290	0.036	Dunn *et al.* (2005)
		4	Clutches	2.15	0.12	57	2.37	0.14	57		0.219	0.035	Dunn *et al.* (2005)
		4	Fertility	29.25	2.50	57	28.83	2.44	57		−0.022	0.035	Dunn *et al.* (2005)
		4	Longevity	7.63	0.17	60	6.47	0.16	60		−0.901	0.037	Dunn *et al.* (2005)
		4	Survival	26.50	2.07	30	33.69	2.14	30		0.615	0.070	Dunn *et al.* (2005)
		4	Fitness	30.35	2.63	60	40.76	2.69	60		0.502	0.034	Dunn *et al.* (2005)
Cyrtodiopsis dalmanni	Full	3	Fecundity	3.01	0.23	45	2.59	0.26	42		−0.255	0.046	Baker *et al.* (2001)
		3	Hatching	61.90	5.00	40	73.40	4.00	32		0.406	0.057	Baker *et al.* (2001)

Table 1. *(Cont.)*

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment Mean	S.E. / S.D.	N	Polyandry treatment Mean	S.E. / S.D.	N	Test statistic	Effect size (Hedges' d)	Variance d	Study
Drosophila melanogaster	Partial	7	Fecundity	695	18	40	677	23	41	F = 0.42, d.f. = 1,76	−0.135	0.050	Brown et al. (2004)
		7	Hatching			40			41		−0.145[b]	0.051	Brown et al. (2004)
		7	Survival			40			41	F = 1.22, d.f. = 1,76	0.248[a,b]	0.052	Brown et al. (2004)
		7	Development time			40			41	F = 0.001, d.f. = 1,77	0.007[ab]	0.050	Brown et al. (2004)
Euborellia plebeja	Full	3	Fecundity	102.20	43.20	26	91.40	46.30	30		−0.237	0.072	Kamimura (2003)
		3	Fecundity	61.60	42.10	26	65.10	43.60	30		0.080	0.072	Kamimura (2003)
		3	Clutches	2.20	0.90	26	2.10	1.00	30		−0.103	0.072	Kamimura (2003)
		3	Fertility	57.50	29.10	26	68.60	29.10	30		0.376	0.073	Kamimura (2003)
Gryllodes sigillatus	Full	3	Fecundity	695.10	77.50	12	555.20	111.90	12		−0.405	0.170	Ivy & Sakaluk (2005)
		3	Longevity	41.50	3.01	12	45.58	5.03	12		0.274	0.168	Ivy & Sakaluk (2005)
		3	Hatching	0.97	0.01	12	0.94	0.02	12		−0.455	0.171	Ivy & Sakaluk (2005)
		3	Development time	67.17	1.28	12	66.25	1.26	12		−0.202[a]	0.168	Ivy & Sakaluk (2005)
		3	Adult size	172.20	7.20	12	193.40	7.00	12		0.832	0.181	Ivy & Sakaluk (2005)
		3	Adult size	212.50	6.20	12	234.60	10.50	12		0.714	0.177	Ivy & Sakaluk (2005)
		3	Survival	0.53	0.05	12	0.65	0.06	12		0.606	0.174	Ivy & Sakaluk (2005)
		5	Fecundity	752.20	115.90	12	810.30	109.20	12		0.144	0.167	Ivy & Sakaluk (2005)
		5	Longevity	49.42	4.38	12	51.00	5.53	12		0.088	0.167	Ivy & Sakaluk (2005)
		5	Hatching	0.98	0.01	12	0.97	0.01	12		−0.237	0.168	Ivy & Sakaluk (2005)
		5	Development time	68.17	1.39	12	69.13	1.62	12		0.177[a]	0.167	Ivy & Sakaluk (2005)
		5	Adult size	181.50	7.20	12	171.30	5.40	12		−0.447	0.171	Ivy & Sakaluk (2005)
		5	Adult size	216.30	8.80	12	228.70	8.00	12		0.411	0.170	Ivy & Sakaluk (2005)
		5	Survival	0.57	0.04	12	0.68	0.03	12		0.867	0.182	Ivy & Sakaluk (2005)
Gryllus bimaculatus	Full	2	Hatching	0.41	0.03	48	0.47	0.03	24		0.312	0.063	Tregenza & Wedell (1998)
		2	Survival	0.65	0.12	47	0.69	0.16	23		0.295	0.065	Tregenza & Wedell (1998)
		2	Adult size	6.71	0.53	47	6.78	0.55	23		0.129	0.065	Tregenza & Wedell (1998)
		2	Adult size	11.10	0.30	47	11.00	0.31	23		−0.326	0.066	Tregenza & Wedell (1998)

Table 1. (Cont.)

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
		2	Adult size	6.83	0.20	47	6.80	0.20	23		−0.148	0.065	Tregenza & Wedell (1998)
		2	Development time	39.40	3.94	47	39.00	3.43	23		−0.105[a]	0.065	Tregenza & Wedell (1998)
		4	Hatching	0.41	0.03	48	0.53	0.03	16		0.623	0.086	Tregenza & Wedell (1998)
		4	Survival	0.65	0.12	47	0.60	0.23	16		−0.320	0.085	Tregenza & Wedell (1998)
		4	Adult size	6.71	0.53	47	6.81	0.57	16		0.183	0.084	Tregenza & Wedell (1998)
		4	Adult size	11.10	0.30	47	11.10	0.28	16		0.000	0.084	Tregenza & Wedell (1998)
		4	Adult size	6.83	0.20	47	6.82	0.20	16		−0.049	0.084	Tregenza & Wedell (1998)
		4	Development time	39.40	3.94	47	40.40	4.22	16		0.246[a]	0.084	Tregenza & Wedell (1998)
Gryllus lineaticeps	Full	3	Fecundity	503.03	121.21	19	660.72	69.70	19		0.358	0.107	Wagner et al. (2001)
		3	Longevity	77.42	7.35	19	78.13	5.51	19		0.025	0.105	Wagner et al. (2001)
Gryllus vocalis	Full	5	Fecundity	440.41	35.62	40	566.45	49.32	25		0.533	0.067	Gershman (2010)
		5	Fertility	0.72	0.04	40	0.68	0.05	25		−0.142	0.065	Gershman (2010)
		5	Longevity	45.24	2.06	40	48.18	2.30	25		0.233	0.065	Gershman (2010)
		5	Hatching	0.88	0.05	40	0.84	0.03	25		−0.176	0.065	Gershman (2010)
		10	Fecundity	618.49	35.62	42	629.47	52.06	28		0.044	0.060	Gershman (2010)
		10	Fertility	0.75	0.03	42	0.68	0.03	28		−0.420	0.061	Gershman (2010)
		10	Longevity	49.24	2.41	42	46.59	1.71	28		−0.195	0.060	Gershman (2010)
		10	Hatching	0.87	0.03	42	0.88	0.03	28		0.111	0.060	Gershman (2010)
		15	Fecundity	604.80	43.84	47	703.43	43.84	27		0.353	0.059	Gershman (2010)
		15	Fertility	0.77	0.03	47	0.76	0.04	27		−0.069	0.058	Gershman (2010)
		15	Longevity	46.41	1.77	47	48.00	2.12	27		0.134	0.058	Gershman (2010)
		15	Hatching	0.87	0.04	47	0.86	0.02	27		−0.072	0.058	Gershman (2010)
Nicrophorus vespilloides	Full	2	Fecundity	54.17	4.08	42	51.07	4.73	42		−0.107	0.048	House et al. (2009)
		2	Fecundity	28.13	2.75	42	22.55	2.91	42		−0.301	0.048	House et al. (2009)
		2	Size	2.18	0.04	42	2.07	0.05	42		−0.371	0.048	House et al. (2009)
		3	Fecundity	58.25	5.22	42	50.09	4.24	41		−0.263	0.049	House et al. (2009)
		3	Fecundity	29.46	3.06	42	27.58	2.67	41		−0.101	0.048	House et al. (2009)
		3	Size	2.09	0.06	42	2.20	0.05	41		0.306	0.049	House et al. (2009)

Table 1. (Cont.)

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
Nysius huttoni	Full	2	Fecundity	377.39	152.17	45	362.17	133.91	45		−0.016	0.044	Wang & Davis (2006)
		2	Fertility	55.22	18.70	45	60.87	13.48	45		0.051	0.045	Wang & Davis (2006)
Panorpa cognata	Full	2	Fecundity	45.90	3.70	23	49.10	5.78	23		0.135	0.087	Engqvist (2006)
		2	Hatching	0.34	0.03	23	0.50	0.07	23		0.614	0.091	Engqvist (2006)
Phoracantha semipunctata	Partial	21	Fecundity	601.00	57.00	10	356.00	53.00	10		−0.135	0.245	Bybee et al. (2005)
		21	Clutches	12.30	1.40	10	7.50	1.50	10		−1.002	0.225	Bybee et al. (2005)
		21	Hatching	92.00	2.00	10	76	5	10		−1.273	0.241	Bybee et al. (2005)
		21	Development time	4.95	0.06	10	5.26	0.08	10		−1.328[a]	0.244	Bybee et al. (2005)
		21	Size	45.70	1.90	10	41.60	2.50	10		−0.559	0.208	Bybee et al. (2005)
Propylea dissecta	Full	5	Fecundity	455.00	26.36	10	516.20	23.57	10		2.344	0.337	Omkar & Mishra (2005)
		5	Hatching	83.13	2.07	10	88.81	3.29	10		1.979	0.298	Omkar & Mishra (2005)
		5	Development time	15.28	0.51	10	14.91	0.32	10		−0.834[a]	0.217	Omkar & Mishra (2005)
		5	Development time	14.18	0.26	10	14.05	0.28	10		−0.429[a]	0.205	Omkar & Mishra (2005)
		5	Development time	13.39	0.25	10	12.88	0.28	10		−1.846[a]	0.285	Omkar & Mishra (2005)
		5	Survival	87.65	3.29	10	89.71	1.51	10		0.770	0.215	Omkar & Mishra (2005)
		5	Survival	92.59	2.47	10	92.31	4.26	10		−0.075	0.200	Omkar & Mishra (2005)
		5	Survival	76.12	5.22	10	84.22	2.20	10		1.938	0.294	Omkar & Mishra (2005)
Rhizoglyphus robini	Partial	6	Fecundity	0.96	0.46	110	1.05	0.44	110		0.199	0.018	Konior et al. (2001)
		6	Offspring RS	0.93	0.03	110	1.15	0.03	110		0.674	0.019	Konior et al. (2001)
		6	Offspring RS	0.97	0.05	105	1.03	0.06	99		0.123	0.020	Konior et al. (2001)
		6	Survival	1.00	0.02	96	1.00	0.02	111		−0.029	0.019	Konior et al. (2001)
		6	Survival	0.99	0.03	105	1.01	0.03	109		0.095	0.019	Konior et al. (2001)
Scathophaga stercoraria	Full	2	Hatching	0.71	0.08	36	0.56	0.07	36		−0.350	0.056	Tregenza et al. (2003)
		2	Hatching	0.73	0.08	36	0.91	0.07	36		0.399	0.057	Tregenza et al. (2003)
		2	Hatching	0.80	0.08	36	0.73	0.08	36		−0.161	0.056	Tregenza et al. (2003)
Sphenarium purpurascens	Full	2	Fecundity	24.04	1.70	26	15.29	1.78	24		−0.991	0.090	Lugo-Olguin & Del Castillo (2007)
		2	Fecundity	95.52	7.11	26	65.70	7.42	24		−0.809	0.087	Lugo-Olguin & Del Castillo (2007)

Table 1. *(Cont.)*

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
Telegryllus commodus	Full	2	Hatching			80			40	0.054, S.E. = 0.097	0.505[b,c]	0.039	Jennions *et al.* (2007)
		2	Development time			75			39	4.2, S.E. = 1.4	0.279[a,b,c]	0.039	Jennions *et al.* (2007)
		2	Development time			75			39	2.7, S.E. = 1.3	0.193[a,b,c]	0.039	Jennions *et al.* (2007)
		2	Adult size			71			39	−7.9, S.E. = 13.9	−0.054[b,c]	0.040	Jennions *et al.* (2007)
		2	Adult size			72			39	−38.7, S.E. = 15.1	−0.242[b,c]	0.040	Jennions *et al.* (2007)
		2	Survival			75			39	−0.077, S.E. = 0.044	0.163[b,c]	0.039	Jennions *et al.* (2007)
		2	Survival			75			39	−0.067, S.E. = 0.048	0.130[b,c]	0.039	Jennions *et al.* (2007)
		3	Hatching			60			76	F = 1.322, d.f. = 1,129	0.197[b,c]	0.030	Jennions *et al.* (2007)
		4	Hatching			80			20	−0.027, S.E. = 0.129	−0.021[b,c]	0.063	Jennions *et al.* (2007)
		4	Development time			75			20	5.4, S.E. = 1.8	0.305[a,b,c]	0.064	Jennions *et al.* (2007)
		4	Development time			75			20	3.1, S.E. = 1.7	0.186[a,b,c]	0.064	Jennions *et al.* (2007)
		4	Adult size			71			20	−13.6, S.E. = 18.8	−0.075[b,c]	0.064	Jennions *et al.* (2007)
		4	Adult size			72			18	−31.6, S.E. = 19.9	−0.166[b,c]	0.070	Jennions *et al.* (2007)
		4	Survival			75			20	−0.071, S.E. = 0.047	0.154[b,c]	0.063	Jennions *et al.* (2007)
		4	Survival			75			20	−0.020, S.E. = 0.051	0.040[b,c]	0.063	Jennions *et al.* (2007)
Telegryllus oceanicus	Full	2	Hatching	0.48	0.02	34	0.55	0.02	64		0.474	0.046	Simmons (2001)
		2	Development time	76.90	1.60	34	76.60	1.80	59		−0.024[a]	0.046	Simmons (2001)
		2	Adult size	5.67	0.04	34	5.56	0.06	59		−0.277	0.047	Simmons (2001)
		2	Survival	0.28	0.02	34	0.27	0.03	59		−0.050	0.046	Simmons (2001)

Table 1. *(Cont.)*

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment Mean	S.E. / S.D.	N	Polyandry treatment Mean	S.E. / S.D.	N	Test statistic	Effect size (Hedges' d)	Variance d	Study
Tenebrio molitor	Full	4	Fecundity	65.20	5.50	43	85.40	5.50	43		0.555	0.048	Worden & Parker (2001)
		4	Fertility			43			43	Fisher's test, $P = 0.49$	0.146[b]	0.047	Worden & Parker (2001)
		4	Longevity	64.60	9.30	43	63.80	11.40	43		−0.012	0.047	Worden & Parker (2001)
Tribolium castaneum	Partial	3	Offspring RS	0.75	*0.3*	9	0.91	*0.14*	8		0.635	0.248	Bernasconi & Keller (2001)
		3	Offspring RS	53	*30*	9	41	22	8		−0.429	0.242	Bernasconi & Keller (2001)
		3	Offspring RS	0.78	*0.23*	9	0.96	*0.07*	8		0.978	0.264	Bernasconi & Keller (2001)
		3	Offspring RS	42	22	9	53	27	8		0.427	0.242	Bernasconi & Keller (2001)
		3	Offspring RS	0.65	*0.29*	10	0.69	*0.17*	8		0.156	0.226	Bernasconi & Keller (2001)
		3	Offspring RS	41	*24*	10	58	*16*	8		0.775	0.242	Bernasconi & Keller (2001)
		3	Offspring RS	0.47	*0.27*	9	0.59	*0.33*	8		0.380	0.240	Bernasconi & Keller (2001)
		3	Offspring RS	45	*29*	9	41	*20*	8		−0.151	0.237	Bernasconi & Keller (2001)
		3	Adult size	2.43	*0.12*	40	2.46	*0.12*	40		0.248	0.050	Bernasconi & Keller (2001)
		3	Adult size	2.16	*0.1*	40	2.14	*0.11*	40		−0.188	0.050	Bernasconi & Keller (2001)
Utetheisa ornatrix	Full	3	Fecundity	332.57	17.14	25	356.57	20.57	25		0.250	0.081	Bezzerides *et al.* (2008)
		3	Fertility	95.27	3.25	25	96.64	2.07	25		0.100	0.080	Bezzerides *et al.* (2008)
		3	Hatching	93.79	3.25	25	94.08	2.66	25		0.020	0.080	Bezzerides *et al.* (2008)
		3	Longevity	16.67	0.42	25	16.32	0.77	25		−0.111	0.080	Bezzerides *et al.* (2008)
Mammalia *Antechinus agilis*	Full	3	Fecundity	7.50	0.50	12	7.10	0.74	7	$t = 1.70$, d.f. $= 19$	−0.211	0.227	Fisher *et al.* (2006b)
		3	Size			12			7		0.772[b]	0.242	Fisher *et al.* (2006b)
		3	Growth	0.17	*0.03*	12	0.19	*0.01*	7		0.735	0.240	Fisher *et al.* (2006b)
Antechinus stuartii	Full	3	Fecundity			19			17	$\chi^2 = 8.0$, $P = 0.005$	1.017[b]	0.126	Fisher *et al.* (2006a)
		3	Fecundity			19			17	$Z = 2.1$, $P = 0.034$	0.719[b]	0.119	Fisher *et al.* (2006a)

Table 1. (Cont.)

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
		3	Fecundity	0.32	0.07	18	0.59	0.08	18		0.828	0.121	Fisher et al. (2006a)
		3	Growth	12.80	0.06	37	13.10	0.07	35		0.762	0.060	Fisher et al. (2006a)
		3	Survival	0.14	0.06	19	0.43	0.06	17		1.073	0.127	Fisher et al. (2006a)
		3	Survival	0.84	0.05	19	0.83	0.05	17		−0.046	0.112	Fisher et al. (2006a)
		3	Survival	0.70	0.10	18	0.94	0.04	18		0.739	0.119	Fisher et al. (2006a)
Clethrionomys glareolus	Full	2	Fecundity	5.10	1.30	30	4.30	1.40	30		−0.585	0.070	Klemme et al. (2008)
		2	Size	17.12	0.69	30	16.10	0.89	30		−0.233	0.067	Klemme et al. (2008)
		2	Size	20.14	0.62	30	19.80	0.96	30		−0.077	0.067	Klemme et al. (2008)
		2	Offspring RS			14			10	F = 4.52, d.f. = 1,17.5	0.911[b]	0.189	Klemme et al. (2008)
		2	Survival	0.46	0.10	30	0.61	0.11	30		0.260	0.067	Klemme et al. (2008)
		2	Survival	0.21	0.07	30	0.22	0.09	30		0.025	0.067	Klemme et al. (2008)
	Full	2	Fecundity	3.61	1.84	25	3.37	1.62	24		−0.137	0.082	Klemme et al. (2007)
		2	Fertility			30			29	Fisher's test, P = 0.546	0.153[b]	0.068	Klemme et al. (2007)
		2	Survival	3.86	2.16	24	3.37	2.30	20		−0.219	0.092	Klemme et al. (2007)
Mus musculus	Partial	3	Fecundity			23			24	F = 0.262 d.f. = 1,58	0.131[b]	0.067	Firman & Simmons (2008b)
		3	Development time			23			24	F = 0.102 d.f. = 1,45	−0.092[ab]	0.085	Firman & Simmons (2008b)
		3	Size			23			24	F = 2.587, d.f. = 1,41	0.482[b]	0.096	Firman & Simmons (2008b)
		3	Survival			23			24	F = 5.916, d.f. = 1,45	0.698[b]	0.090	Firman & Simmons (2008b)
		3	Survival			23			24	F = 0.483, d.f. = 1,58	0.177[b]	0.067	Firman & Simmons (2008b)
Pisces Poecilia reticulata	Full	2	Fecundity	8.52	0.74	31	8.26	0.64	35		−0.065	0.061	Evans & Kelley (2008)
		2	Size			31			35	F = 0.04, d.f. = 1,57.4	0.051[b]	0.067	Evans & Kelley (2008)
		2	Inter-individual distance			31			35	F = 3.69, d.f. = 1,48.8	−0.535[ab]	0.083	Evans & Kelley (2008)
		2	Shoaling time			31			35	F = 0.77, d.f. = 1,48.8	−0.125[b]	0.080	Evans & Kelley (2008)
	Partial	4	Size	6.73	0.13	10	7.12	0.09	10		1.057	0.228	Ojanguren et al. (2005)

Table 1. *(Cont.)*

Species	Mating control	Number of males in polyandry treatment	Trait	Monandry treatment			Polyandry treatment			Test statistic	Effect size (Hedges' d)	Variance d	Study
				Mean	S.E. / S.D.	N	Mean	S.E. / S.D.	N				
	Partial	4	Fecundity	5.10	0.61	38	8.8	1.2	38		0.624	0.055	Evans & Magurran (2000)
		4	Development time	44.10	2.60	38	35.4	2.22	38		−0.578[a]	0.055	Evans & Magurran (2000)
		4	Shoaling time	153.14	17.02	21	212.04	10.47	21		0.893	0.105	Evans & Magurran (2000)
		4	Capture time	4.94	0.63	21	6.7	0.63	21		0.600	0.100	Evans & Magurran (2000)
Polychaeta													
Galeolaria caespitosa	Full	3	Fertility			24			24	$F = 11.03$, d.f. = 1,9	1.831[b]	0.516	McLeod & Marshall (2009)
		3	Hatching			24			24	$F = 10.65$, d.f. = 1,6	2.007[b]	0.752	McLeod & Marshall (2009)
		3	Survival			24			24	$F = 6.56$, d.f. = 1,6	1.575[b]	0.655	McLeod & Marshall (2009)
	Full	3	Fertility	24.41	2.76	12	30.71	3.15	12		0.593	0.174	Marshall & Evans (2005)
		3	Fertility	86.62	2.36	12	93.31	2.36	12		0.789	0.180	Marshall & Evans (2005)
Reptilia													
Eublepharis macularius	Full	2	Clutches	1.40	0.36	16	2.04	0.48	17		0.361	0.123	LaDage *et al.* (2008)
		2	Fertility	1.79	0.61	16	3.12	0.77	17		0.455	0.125	LaDage *et al.* (2008)
		2	Size	2.46	0.65	16	3.12	0.63	17		0.250	0.122	LaDage *et al.* (2008)

[a]Effect size is usually polyandry - monandry but the sign was reversed for these cases because a smaller value of the trait being measured is presumed to elevate fitness.
[b]Effect size was calculated from the reported test statistic using standard formulae using the *Metawin 2.0* calculator.
[c]Effect size was calculated using estimated difference in means between control (= monandry) and polyandry treatments that correct for covariates and random effects in a linear mixed model. We converted the S.E. of the difference to a S.D. value using the standard formula.
*Standard deviations obtained from authors.
RS, reproductive success.

Table 2. Species-level analysis using only studies with full control of mating. Numbers in bold indicate a significant effect at $\alpha = 0.05$. Italics indicate a 95% CI that overlaps zero by less than 0.05 S.D. units. Q_T is total heterogeneity. The traits are arranged in order of decreasing sample size

Fitness trait	N (species)	Mean effect (d)	95% CI (bias corrected)	t	P	Q_T	P
Fecundity	25	0.076	−0.109 to 0.261	0.766	0.451	31.48	0.14
Hatching success	15	0.271	*−0.009 to 0.613*	1.93	0.075	**25.27**	**0.03**
Offspring survival	13	0.173	−0.068 to 0.439	1.296	0.219	13.28	0.35
Fertility	13	0.189	**0.043 to 0.397**	2.10	0.058	13.05	0.37
Maternal longevity	9	−0.229	*−0.554 to 0.022*	−1.402	0.199	7.71	0.46
Development time	6	−0.016	−0.151 to 0.190	−0.142	0.892	5.13	0.40
Clutches	5	0.286	**0.073 to 0.448**	2.745	0.052	3.69	0.45
Offspring size	5	0.034	−0.058 to 0.339	0.307	0.774	3.83	0.43
Adult size	4	−0.076	−0.227 to 0.160	−0.635	0.573	3.05	0.38
Fitness	3	0.365	*−0.003 to 0.531*	2.231	0.156	2.02	0.36
Colony	2	0.236	−0.424 to 0.807	0.384	0.766	1.00	0.32
Growth	2	0.756	**0.735 to 0.762**	3.459	0.179	0.00	0.96
Parasites	2	0.723	**0.390 to 0.946**	2.661	0.229	1.00	0.32
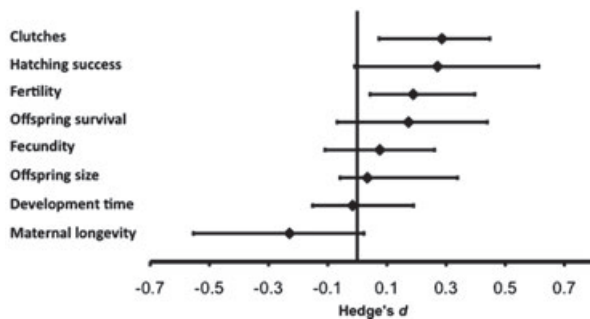
Fig. 1. Means (diamonds) and 95% confidence intervals (bias-corrected, bootstrapped using *MetaWin 2.0*, hence asymmetry is possible) for the eight traits where the minimum sample size was five species.

both the 95% confidence interval and the *t*-test of the mean effect ($P = 0.045$). The effect was marginally non-significant if we included post-fertilization hatching success (mean $d = 0.16$, $N = 20$ species, 95% CI: −0.01 to 0.35; *t*-test: $P = 0.073$). There was no significant difference in the

estimated mean effect size between insects and vertebrates ($Q_b = 0.65$, $P = 0.43$). The mean effect was smaller, and no longer significant, when we assumed that focal traits were correlated and/or excluded the two eusocial species. We ran analyses that excluded eusocial species because the most likely mechanism by which genetic benefits are derived (i.e. genetic diversity among workers) might differ from those in other species (i.e. additive or non-additive genetic benefits). That said, however, the 95% confidence intervals were still suggestive of a positive effect: the estimated mean effect ranged from $d = 0.071$ to 0.163 (Table 3).

(3) Publication bias

Publication bias tests have to be interpreted carefully because they offer only indirect evidence based on patterns in the data that could arise for other reasons. That noted, our analyses revealed that some of our findings should be viewed cautiously. The 'trim and fill' analysis suggests that if the asymmetry in funnel plots is due to publication bias, then the 'corrected' effect sizes and associated confidence intervals

Table 3. Species-level analysis of the composite trait of offspring performance. Data are based on studies with full control of mating and using only post-fertilization traits (i.e. due to genetic benefits or differential allocation; see main text for details). Numbers in bold indicate a significant effect at $\alpha = 0.05$. Italics indicate a 95% CI that overlaps zero by less than 0.05 S.D. units. Datasets vary in terms of whether it is assumed that traits measured in the same study are independent ($r = 0$) or fully dependent ($r = 1$), whether eusocial species are included and whether post-fertilization hatching success is included as a trait

Criteria	N (species)	Mean effect (d)	95% CI (bias corrected)	t	P	Q_T	P
All species ($r = 1$)	18	0.160	*−0.027 to 0.376*	1.557	0.119	18.57	0.35
All species ($r = 0$)	18	0.193	**0.018 to 0.373**	2.166	0.045	21.17	0.22
Excluding eusocial ($r = 1$)	16	0.120	−0.066 to 0.341	1.125	0.280	17.09	0.31
Excluding eusocial ($r = 0$)	16	0.163	*−0.047 to 0.364*	1.706	0.109	19.45	0.19
Including post-fertilization hatching success							
All species ($r = 1$)	20	0.112	−0.062 to 0.300	1.193	0.248	23.35	0.22
All species ($r = 0$)	20	0.164	*−0.008 to 0.348*	1.90	0.073	27.93	0.08
Excluding eusocial ($r = 1$)	18	0.071	−0.120 to 0.269	0.718	0.483	21.74	0.20
Excluding eusocial ($r = 0$)	18	0.133	−0.062 to 0.330	1.435	0.169	25.85	0.08

Table 4. Tests for publication bias for species-level analysis using only studies with full control of mating (see main text for details). Numbers in bold indicate a significant effect at $\alpha = 0.05$. Italics indicate a 95% CI that overlaps zero by less than 0.05 S.D. units

| | | | Trim & fill | | Fail-safe | | Year | | |
Fitness trait	N (species)	n_{bias} (P)	L	Corrected d (95% CI)	Rosenberg	Rosenthal	Weighted (slope; P)	Unweighted (r_s; P)	N
Fecundity	25	0.12 (0.58)	0	—	—	—	(−ve) 0.08	−0.308 (0.144)	24
Hatching success	15	−0.22 (0.44)	3	0.061 (−0.315 to 0.456)	20	74	**(−ve) 0.03**	−0.29 (0.292)	15
Offspring survival	13	−0.47 (0.11)	2	0.112 (−0.149 to 0.350)	—	—	**(+ve) 0.004**	**0.762 (0.004)**	12
Fertility	13	−0.80 (<0.01)	6	0.018 (−0.181 to 0.217)	0	32	(−ve) 0.27	−0.223 (0.487)	12
Maternal longevity	9	−0.07 (0.86)	0	*−0.229 (−0.554 to 0.022)*	7	17	(+ve) 0.39	0.152 (0.696)	9
Development time	6	−0.66 (0.16)	—	—	—	—	(−ve) 0.81	−0.174 (0.74)	6
Clutches	5	0.10 (0.87)	—	—	—	—	(−ve) 0.25	0 (1)	5
Offspring size	5	−0.70 (0.19)	—	—	—	—	(−ve) 0.21	−0.718 (0.172)	5
Adult size	4	−0.80 (0.20)	—	—	—	—	**(+ve) 0.006**	0 (1)	4

indicate an effect that is not significantly different from zero for fertility, hatching success and offspring survival. For individual traits, there were no clear temporal trends with a decrease in effect size over time for six of nine traits (Table 4). There was one significant decline with time (for hatching success), and two significant increases (for offspring survival and adult size). For the composite trait of 'offspring performance' there was a trend towards a positive relationship between effect size and year of publication. It was, however, only significant when we used weighted effect sizes and excluded post-fertilization hatching success from the composite measure (Table 5).

IV. DISCUSSION

Meta-analysis of the available data from experimental studies that controlled fully for the total number of matings per female showed that the effect on female fitness of mating with several males (polyandry), rather than repeatedly mating with the same male (monandry), is generally small. Even so, the limited available evidence indicates that there

is a trend for polyandry to be beneficial. These benefits can be divided into direct material gains (potentially driven by greater access to sperm) that increase total offspring production; and genetic benefits that improve offspring fitness either by biasing paternity towards certain males or, in the case of eusocial insects, by increasing genetic diversity within colonies.

(1) Direct benefits and a longevity cost

There was a significant direct benefit of polyandry based on effect-size estimates for two proxies for total offspring production: the number of clutches produced (95% CI: $d = 0.07$ to 0.45) and fertility (95% CI: $d = 0.04$ to 0.40) and a marginally non-significant benefit for hatching success (assuming, for now, that elevated hatching success is primarily due to a higher rate of egg fertilization due to a lower risk of sperm limitation) (95% CI: $d = -0.01$ to 0.61). In addition, while non-significant, the estimated mean effect for fecundity was positive (95% CI: $d = -0.11$ to 0.26). These positive effects of polyandry on offspring production were, however, countered by evidence that polyandry had a negative effect on maternal longevity (95% CI: $d = -0.55$ to 0.02).

Table 5. Tests for publication bias for species-level analysis using only studies with full control of mating for the composite trait of offspring performance. Numbers in bold indicate a significant effect at $\alpha = 0.05$. Italics indicate a 95% CI that overlaps zero by less than 0.05 S.D. units. Datasets vary in terms of whether it is assumed that traits measured in the same study are independent ($r = 0$) or fully dependent ($r = 1$), whether eusocial species are included and whether post-fertilization hatching success is included as a trait

| | | | Trim & fill | | Fail-safe | | Year | | |
Criteria	N (species)	n_{bias} (P)	L	Corrected d (95% CI)	Rosenberg	Rosenthal	Weighted P	Unweighted r_s (P)	N
All species ($r = 1$)	18	−0.37 (0.13)	3	0.100 (−0.099 to 0.279)	—	—	**(+ve) 0.027**	0.49 (0.057)	16
All species ($r = 0$)	18	**−0.47 (0.047)**	2	*0.153 (−0.034 to 0.331)*	26	94	**(+ve) 0.025**	0.37 (0.16)	16
Excluding eusocial ($r = 1$)	16	−0.44 (0.09)	2	0.072 (−0.119 to 0.290)	—	—	**(+ve) 0.027**	0.49 (0.057)	16
Excluding eusocial ($r = 0$)	16	−0.36 (0.18)	1	*0.146 (−0.045 to 0.372)*	—	—	**(+ve) 0.025**	0.37 (0.16)	16
Including post-fertilization hatching success									
All species ($r = 1$)	20	−0.42 (0.069)	2	0.074 (−0.112 to 0.240)	—	—	(+ve) 0.095	0.26 (0.30)	18
All species ($r = 0$)	20	−0.378 (0.101)	1	0.137 (−0.062 to 0.313)	19	75	(+ve) 0.08	0.14 (0.58)	18
Excluding eusocial ($r = 1$)	18	−0.41 (0.09)	1	0.051 (−0.166 to 0.259)	—	—	(+ve) 0.095	0.26 (0.30)	18
Excluding eusocial ($r = 0$)	18	−0.35 (0.16)	0	0.133 (−0.062 to 0.330)	—	—	(+ve) 0.08	0.14 (0.58)	18

Our results provide insights into two earlier meta-analyses of polyandry. First, Arnqvist & Nilsson (2000) reported that moderate levels of multiple mating increased fecundity and fertility (egg hatching success), but that very high levels of mating actually reduced egg production. In their analysis, however, there was no way to distinguish between the effects of mating rate and number of mates because many of the studies they used compared a group of females that were each provided with a single mating (or male) with a group of females that were allowed to mate multiply and/or had access to many males. Our meta-analysis only used studies that fully controlled for female mating rate. Jointly considering the two meta-analyses suggests that the increased egg production and fertility in studies where mating rate and number of mates co-vary could partly be due to an effect of the number of mating partners and not simply a higher mating rate. Similarly, Arnqvist & Nilsson (2000) reported a negative effect of mating rate/number of mates on maternal longevity, especially in species where there was no nuptial feeding. In our analysis, although a parametric test was not significant, inspection of the bootstrapped 95% confidence intervals strongly suggests that polyandry has a negative effect on maternal longevity. This cost of polyandry is an intriguing finding worthy of further investigation because it suggests that sexual conflict generates costs to females beyond those imposed by males inducing females to mate at a higher than optimal rate and/or direct effects of male harassment (e.g. den Hollander & Gwynne, 2009).

If there is a negative effect of polyandry on maternal longevity, one likely explanation is that males adjust their mating behaviour in response to information about a female's mating history so as to improve their fertilization success. This type of adjustment can result in 'collateral harm' to females (Morrow, Arnqvist & Pitnick, 2003; Lessells, 2006). For example, in the cricket *Teleogryllus oceanicus* males adjust the proportion of viable sperm in their ejaculate in response to cues about the level of sperm competition derived from cuticular hydrocarbons deposited by previous mates (Thomas & Simmons, 2007, 2009). Males might respond to elevated sperm competition by transferring greater amounts of toxic/harmful chemicals in their ejaculates to facilitate success under sperm competition (Chapman *et al.*, 2003) or engage in copulatory behaviour that is more likely to damage the female (e.g. Hotzy & Arnqvist, 2009). These harmful effects could account for an additional cost of polyandry on female longevity beyond that attributable to a higher mating rate (but for a counter-example see Reinhardt, Naylor & Siva-Jothy, 2009). Interestingly, in a leaf-cutter ant (*Atta colombica*), sperm storage by queens lowers immune function and the effect is greater when more males contribute to sperm storage (Baer, Armitage & Boomsma, 2006). In these ants, males transfer seminal chemicals that have substantial effects on sperm viability (den Boer, Boomsma & Baer, 2008). Wedell, Tregenza & Simmons (2008) also showed that receipt of multiple ejaculates reduces female lifespan in a bushcricket (*Requena verticalis*). Males can also increase their sperm competitiveness by secreting specific ejaculate substances that stimulate female oviposition (reviews: Gillott, 2003; Gwynne, 2008), which might account for the higher number of clutches produced by polyandrous females if such stimulants are more abundant in the presence of sperm competition (Schwartz & Peterson, 2006). An increased early reproductive rate promoted by polyandry could also contribute to reducing a female's lifespan due to the well-known life-history trade-off.

Second, a preliminary meta-analysis of controlled polyandry experiments detected a small but significant increase in egg hatching success for female insects mated to multiple males ($Z_r = 0.192 \approx d \approx 0.34$) (Simmons, 2005). This effect is only slightly larger than the estimate of $d = 0.27$ in our meta-analysis, although our result was marginally non-significant using a parametric *t*-test ($P = 0.075$). In our analysis, however, the strength of the effect varied significantly among species. In addition, the funnel plot was skewed, and if this is due to publication bias a revised estimate of the effect yields a far smaller, non-significant effect of $d = 0.06$. So, despite hatching success being the second most often measured trait in experimental polyandry studies (after fecundity), we still need additional studies to test whether polyandry has a genuinely beneficial effect on hatching success, as the current estimate is not robust to publication bias.

(2) Potential genetic benefits

For offspring performance measures that are usually attributed to genetic benefits (i.e. post-fertilization), the only individual trait that was even marginally significantly (based on 95% CI) elevated by polyandry was egg hatching success. Hatching success can be considered a measure of offspring performance if variation is primarily due to variation in embryo survival rather than the proportion of eggs fertilized. With the exception of three studies (Marshall & Evans, 2007; McLeod & Marshall, 2009; Gershman, 2010), however, the fertilization status of eggs used to measure hatching success was not reported. It is important to recognize that despite over a decade of experimental studies, sample sizes (especially at the species level) are very small for most traits so that the power to detect individually significant effects is low. It is therefore noteworthy that, using a 'vote counting' approach, the mean effect size was positive for seven of the nine offspring performance traits for which two or more species were examined (Table 2; to be conservative, we only used the mean effect for hatching success for the three studies that used fertilized eggs). Furthermore, there were two additional traits that were only examined in a single species where it is also possible to predict the direction of a beneficial change in trait value (see Table 1). Specifically, there was a positive effect of polyandry on the difficulty of capturing offspring (Evans & Magurran, 2000) and on offspring reproductive success (Klemme, Ylönen & Eccard, 2008). Taking these into account, the mean effect is positive for nine of 11 different offspring performance traits (binomial test, $P = 0.065$). Finally, in studies that partially controlled for mating number, there were positive

effects of polyandry on offspring reproductive success in two additional species (Konior, Radwan & Kolodziejczyk, 2001; Bernasconi & Keller, 2001), as well as on offspring longevity (Konior *et al.*, 2001). If these three effect sizes, and the additional trait of offspring reproductive success, are taken into account the mean effect is positive for 10 of 12 offspring performance traits (binomial test, $P = 0.039$). Unfortunately, these twelve measures of offspring traits are likely to be partially correlated within species so, given that some species contributed estimates for more than one trait, they are not fully independent estimates of net offspring fitness.

We therefore calculated a composite effect size for offspring performance (using only hatching success based on fertilised eggs) for each species. Although the use of composite effect sizes is not yet widespread in ecological and evolutionary meta-analyses, it is a worthwhile approach in cases where different measures are being used to estimate the same underlying trait (Borenstein *et al.*, 2009; Mengersen *et al.*, 2011). In the current example, the reason why researchers are measuring offspring growth rates, size at maturity, survival and so on, is clearly because they are assumed to be surrogate measures that can be used to infer the effect of polyandry on total offspring fitness. Ideally, we would like to weight each fitness component by its relative contribution to net fitness. This information is almost never available, however, so it is then justifiable to treat each trait as being equally likely to predict net fitness to look at the average effect across these traits. This approach has the benefit that it reduces the temptation for researchers to measure several traits (as is usually the case, see Table 1) and *post hoc* selectively emphasize those which differ between mating treatments. Using a composite effect size for 'offspring performance/fitness', we found that there was a small but significant (P ≈ 0.05 and 0.07 for data excluding and including post-fertilization hatching success, respectively) effect of polyandry on offspring performance ($d = 0.07$ and 0.19, respectively) when we included all species and assumed effect sizes were uncorrelated between traits (Table 3). The mean effect was no longer significant, however, if we excluded the two eusocial species.

In general, studies of polyandry in eusocial insects suggest that it has a positive effect on queen fitness (Oldroyd & Fewell, 2007). This fitness increase seems to be due to greater genetic diversity among colony workers reducing parasitism intensity and prevalence, even though a more diverse colony should be susceptible to a greater range of parasites (review: van Baalen & Beekman, 2006). The same benefits arise when colonies are founded by several queens, which also increases colony-level genetic diversity (e.g. Reber *et al.*, 2008; but see Castella, Christie & Chapuisat, 2010), suggesting that the fitness effects are due to increased genetic diversity. There is also growing evidence that genetic diversity is favoured because different genotypes specialize on different tasks, leading to more efficient division of labour in colonies founded by polyandrous queens (reviews: Oldroy & Fewell, 2007; Smith *et al.*, 2008). It should be noted, however,

that multiple paternity reduces worker relatedness, which is potentially damaging to colony performance, as kin-selected benefits are reduced when rearing half- rather than full siblings. Simultaneously, however, multiple paternity reduces queen-worker conflict over the optimal offspring sex ratio (Bourke & Franks, 1991). Unfortunately, the twin roles of polyandry and workers biasing the sex ratios of reproductives as forces driving the initial evolution of eusociality are often misunderstood (review: West & Gardner, 2010). Strict monandry means that the relatedness between parents and their siblings or offspring is identical so that selection for rearing siblings arises whenever other factors make it more efficient than rearing offspring (Boomsma, 2007, 2009).

The 'genetic diversity' explanation does not readily apply to non-eusocial species (but for a reassessment of this view see Mcleod & Marshall, 2009), where it is assumed that genetic benefits instead arise from offspring inheriting 'good genes' and/or 'compatible genes' that elevate individual fitness. Consequently, the composite effect size for offspring performance in species other than eusocial insects could be interpreted as providing little evidence that polyandry confers genetic benefits because it did not differ from zero using a parametric t-test, and (when including post-fertilization hatching success), nor did the 95% confidence intervals suggest a significant effect. In our view more studies are needed. However, it is reasonable to assume that if there is a genetic benefit to polyandry it is probably small (i.e. in the range of $d = 0.1$ to 0.2). This value is consistent with the general view from theory that the genetic benefits of mate choice are small due to the low heritability of fitness, an imperfect correlation between preferred male traits and a male's breeding value for fitness, and mistakes during mate choice (or failure fully to bias paternity towards the fittest male given polyandry) (e.g. Kirkpatrick & Barton, 1997; Cameron *et al.*, 2003). Even so, the effect-size estimates we obtained are still larger than those recently reported for the genetic benefits of polyandry in birds based on comparisons of within-pair and extra-pair offspring for a range of fitness components ($d ≈ 0.02$; Arnqvist & Kirkpatrick, 2005) and for maternal survival ($r = 0.02 ≈ d ≈ 0.04$) (Akçay & Roughgarden, 2007). It is unclear whether this difference between meta-analyses is due to a taxonomic effect (we did not locate any controlled polyandry experiments that used birds), the use of 'natural experiments' (e.g. comparison of within-and extra-pair young) rather than more tightly controlled laboratory experiments, other factors, or is simply due to sampling error. The difference does, however, caution against a blanket rejection of 'good genes' models of sexual selection based solely on studies of extra-pair paternity in birds.

The experimental studies we used are designed to minimise the extent to which factors other than the sires' relative genetic contributions generate differences in offspring fitness between mating treatments. Minimization is achieved by controlling for mating rate and, by extension, any material benefits transferred by males during mating. It is worth noting that even these well-designed experiments

are imperfect. There are several additional factors that could, in principle, differ between mating treatments and affect offspring performance. These effects could then be incorrectly interpreted as arising from females biasing paternity towards males that elevate offspring fitness through additive and/or non-additive genetic benefits. First, maternal effects might be partly responsible for differences between mating treatments (review: Simmons, 2005). The amount of resources that females allocate to reproduction can strongly influence offspring fitness (review: Qvarnstöm & Price, 2001). For example, a recent study suggests that a maternal effect driven by difference in the timing of fertilization and laying of eggs from extra-pair and within-pair males can fully account for the performance difference between within-pair and extra-pair offspring in blue tits (*Cyanistes caeruleus*) (Magrath *et al.*, 2009). In the experimental context, if females increase investment into broods when they have mated with several males, this investment could elevate offspring fitness. For example, a recent study where females were experimentally assigned sperm found that egg yolk reserves were higher for offspring from polyandrous matings with two males than for offspring from monogamous matings (Kekäläinen *et al.*, 2010). However, it is worthwhile asking why polyandry would favour increased maternal investment. If differential allocation is driven mainly by greater investment into offspring from males of higher genetic quality (Sheldon, 2000; Kotiaho *et al.*, 2003), it should only act to amplify pre-existing differences in offspring fitness.

Second, there could be indirect genetic effects due to interactions between paternal genes expressed in offspring (e.g. Zeh & Zeh, 2006) or *via* the production of seminal products that increase maternal investment (e.g. García-González & Simmons, 2007). For example, the presence of offspring from one male might increase total female investment into a brood and thereby elevate the fitness of all offspring, including those from another male that, if alone in the female, would invoke a smaller maternal investment. In an extreme example, it was shown that the presence of embryos sired by unrelated males reduced the risk of abortion of offspring sired by a brother (Zeh & Zeh, 2006; see also Teng & Kang, 2007). Paternal effects can also confound results when males have the potential to alter ejaculates (seminal fluids, sperm quantity/quality) in response to cues indicating greater sperm competition (i.e. other males have mated as occurs in polyandry treatments). Manipulation of ejaculates by males can be controlled for in some species where males produce ejaculates before being mated to a female (e.g. spermatophores in crickets, Jennions *et al.*, 2007) or by *in vitro* fertilization (e.g. Baer & Schmidt-Hempel, 2001; Marshall & Evans, 2007).

(3) Publication bias

We tested for publication bias at the species level for both individual traits (Table 4) and for a composite measure of offspring performance (Table 5). The results are mixed with respect to the possible effect of publication bias on our findings. Given small sample sizes even non-significant test results should be viewed with caution. Perhaps, the most important point comes from examination of the revised estimates of effect sizes following a 'trim and fill' based on a skew in the funnel plot of effect size on sample size. The revised effects are markedly smaller for hatching success, offspring survival and fertility, highlighting the sensitivity of the original estimates to a few studies with larger effect sizes (i.e. studies that are 'trimmed' and have counter-studies 'filled'). The revised effects are, however, only slightly smaller for the composite measure of 'offspring performance'. In terms of temporal effects, there were no general trends for effect sizes for individual traits to decrease over time (two increased significantly, one decreased significantly and six did not change significantly). There was a tendency for the composite measure of 'offspring performance' to increase with time. This was not significant if all studies were given equal weight, but was if the variance associated with each study's estimate is taken into account. For us, the main take-home message is that the only way to generate a robust estimate of the effect size for genetic benefits of polyandry is to perform further empirical studies.

(4) Other lines of evidence as to whether polyandry confers genetic benefits

Aside from the experimental studies we have analysed, there are at least seven other lines of evidence for genetic benefits to polyandry (Table 6). In principle, if a sufficient number of studies is available, each of these lines of evidence could form the subject of a meta-analysis.

First, there are observational studies showing that females that mate multiply produce more viable offspring, or more offspring (e.g. Olsson *et al.*, 1994; Rodgriguez-Muñoz *et al.*, 2010). These studies can only provide weak evidence for a direct benefit of polyandry, however, as a female's propensity (or likelihood) of mating multiply might be greater if she is in good condition and therefore more likely to produce high-performing offspring due to higher maternal investment or her offspring inheriting genes that improve performance.

Second, several studies have experimentally assigned females the same number of males, but in treatments where males differ in their relatedness to the females (e.g. two unrelated, two related or a related and unrelated male). This design tests whether polyandry allows females to bias paternity towards less closely related males to reduce inbreeding depression (for a theoretical model see Cornell & Tregenza, 2007). Inbreeding avoidance is often inferred if the offspring performance of females assigned a related and unrelated male is closer to that of females assigned two unrelated males than two related males (i.e. not simply the mean of the two male types) (e.g. Tregenza & Wedell, 2002; Pitcher, Rodd & Rowe, 2008); or in terms of the amounts of sperm stored from males that vary in their relatedness to the female (Welke & Schneider, 2009; Bretman, Newcombe & Tregenza, 2009). In some cases, the inbreeding-avoidance benefit of polyandry has been directly measured by determining paternity and testing whether it is biased against kin (e.g. Bretman, Wedell & Tregenza, 2004;

Table 6. The types of studies that are invoked as evidence for or against genetic benefits (GB) maintaining polyandry. The table highlights the experimental design, aims, predictions and limitations of each study type. Some examples of published studies that show evidence for or against genetic benefits based on offspring fitness are provided (i.e. $P < 0.05$ or >0.05 for tests of key prediction)[b]

Study type[a]	Design	Utility	Key predictions (P) and confounding issues (I)	Examples of studies with evidence[b]	
				For	Against
Experimentally controlled polyandry	Treatments: monandry and polyandry. Identical number of matings per female in each treatment. Females are randomly assigned males.	Removes most confounding direct benefits so that treatment differences are assumed to be due to genetic benefits (GB) (see text).	(P) Offspring of polyandrous females will show elevated fitness. In practice, only fitness components can be measured such as offspring viability or survival, or the mated females' fecundity (see text). (I) Predicted outcome might be due to differences in total ejaculate transferred to monogamous *versus* polyandrous females (Thomas & Simmons, 2007).	Meta-analysis conducted in this review	
Observational Studies	Phenotypic correlation between the number of matings by each female and her fecundity and/or offsprings' fitness. Matings are not controlled and the mating rate varies naturally between females.	Test for a relationship between a female's propensity to mate and offspring performance/fitness or maternal fecundity. Data more easily collected as no manipulations are performed. Can be applied to many taxa.	(P) Positive correlation between number of matings and number of offspring and/or offspring quality. (I) Assumes the relationship is causal. Also assumes that fecundity differences are due to early offspring mortality as opposed to low fertilization rate. Provides only weak evidence for GB, as certain females (e.g. those in good condition) might be more likely to remate *and* to produce higher quality offspring and/or offspring with lower early mortality.	Madsen *et al.* (1992); Olsson *et al.* (1994); Rodriguez-Muñoz *et al.* (2010)	Capula & Luiselli (1994)
Relatedness	Females in each treatment are assigned the same number of mates (usually two males). Comparison of females mated to: (a) only related males; (b) only unrelated males; (c) both types of males.	Test whether polyandrous females bias paternity to unrelated males to avoid the deleterious effects of inbreeding on offspring fitness.	(P) Paternity will be biased towards less closely related males to avoid inbreeding depression. Paternity is either directly measured, or the difference in fecundity or offspring performance between treatments (a) and (b) is used to infer the direction of paternity bias in (c). In some cases paternity tests are then used to directly quantify the degree of bias. (I) Assumes maternal fitness is always elevated by reducing inbreeding. In some cases this is incorrect (Kokko & Ots, 2005).	Tregenza & Wedell (2002); Bretman *et al.* (2004, 2009); Bilde *et al.* (2007); Firman & Simmons (2008*a*); Welke & Schneider (2009)	Jennions *et al.* (2004); Denk *et al.* (2005); Teng & Kang (2007); Evans *et al.* (2008); Pitcher *et al.* (2008)

Table 6. (Cont.)

Study type[a]	Design	Utility	Key predictions (P) and confounding issues (I)	Examples of studies with evidence[b]	
				For	Against
Half-siblings	Comparison of the performance of maternal half-siblings. Typically these are bird studies where there is a comparison between within-pair (WPY) and extra-pair young (EPY) that arise from extra-pair copulations (EPCs).	Tests whether offspring performance differs between EPY and WPY in the same brood/litter.	(P) EPY should perform better than WPY (ideally measured as fitness). (I) Assumes that any difference is due solely to effects of paternal genes (hence GB) rather than correlates of offspring type. For example, laying/hatching order might be associated with whether offspring are EPY or WPY and this might affect maternal provisioning (Magrath et al. 2009).	Richardson et al. (2005); Garvin et al. (2006); Whittingham & Dunn (2010); see also references 10–21 in Magrath et al. (2009)	Arnqvist & Kirkpatrick (2005); Akçay & Roughgarden (2007); Schmoll et al. (2009)
Genetic compatibility	Creating isogenic lines of known compatibility with each other. Allow females to mate multiply and test for a bias in paternity (either directly or using approach described above for Relatedness) or Mate females of known genotype to two or more males of known genotype. The fitness of the genotype combinations is either known, or it is assumed that increased heterozygosity elevates fitness. The experimental design controls for mating-order effects.	Estimates the extent to which females are biasing paternity toward more compatible genotypes	(P) Predicts paternity will be biased towards males with genotypes that elevate offspring fitness for the female in question. (I) Sometimes there is weak evidence for the assumption that a specific genotypic pairing will elevate net offspring fitness (e.g. greater heterozygosity at one or a few loci) (but see Pryke et al., 2010 for a clear exception).	Pryke et al. (2010)	Simmons (2001); Bilde et al. (2009)
Male attractiveness [sire effect on a major fitness component]	Females are mated to both an attractive and unattractive male and then tested for a paternity bias. [This design is also sometimes used to test for a paternity bias towards a male with a known greater beneficial effect on a measure of offspring performance (e.g. males that sire more viable offspring; García-González & Simmons, 2007)]	Polyandry promotes production of sexy sons favoured by pre- and/or post-copulatory selection.	(P) More attractive male should sire a higher proportion of offspring. The proximate mechanism biasing paternity could be cryptic female choice, or attractive males having more competitive ejaculates, or a combination of both mechanisms. (I) Assumes that genes enhancing male attractiveness are positively correlated with net offspring fitness. That is, they do not have a stronger negative effect of daughters' fitness (i.e. sexually antagonistic pleiotropy) and/or on sons' fitness because they are genetically correlated with other traits that reduce fitness under natural selection (i.e. selection outside the context of increasing male mating success).	Lewis & Austad (1994); Evans et al. (2003); Pilastro et al. (2004); Hosken et al. (2008); Polak & Simmons (2009) [Fisher et al. (2006a)]	Evans & Rutstein (2008) [García-González & Simmons (2007)]

Table 6. (*Cont.*)

Study type[a]	Design	Utility	Key predictions (P) and confounding issues (I)	Examples of studies with evidence[b]	
				For	Against
Selfish genetic elements	Experimental evolution in systems with selfish genetic elements (SGE) that decrease sperm production by carrier males. (*a*) Create populations with and without SGE and after several generations measure female re-mating rates between the two populations. (*b*) Create monandrous and polyandrous populations and measure change in the frequency of SGE changes after a number of generations	Tests (*a*) If presence of SGE influences evolution of female propensity to remate. or (*b*) If polyandry alters the frequency of selfish genetic elements in a population.	(P) (*a*) An increase in female mating rate in the presence of SGE thereby lowering frequency of SGE (*b*) That the frequency of SGE is lower in populations where females are polyandrous. These populations are thus less likely to go extinct. (I) Results are due to a combination of the direct benefits of avoiding sperm limitation and indirect GB of offspring inheriting non-SGE genes.	(*a*) Price *et al.* (2008) (*b*) Price *et al.* (2010)	

[a]Caveat: in general, studies assume that genetic benefits are due to inheritance of paternal genes or interactions between maternal and paternal genes/genomes within individual offspring. Each study type implicitly assumes that results are not due to other uncontrolled factors such as biased maternal investment (Magrath *et al.*, 2009), direct paternal investment in offspring, or interactions between half-siblings that elevate net fitness (e.g. rescue effect: Zeh & Zeh, 2006).

[b]We urge caution in interpreting the evidence based on the listed studies. They are not a systematic set of all available studies. In addition, a simple 'vote counting' of studies that do/do not report a significant effect can lead to erroneous conclusions (Borenstein *et al.*, 2009).

Denk *et al.*, 2005; Simmons *et al.*, 2006; Evans *et al.*, 2008; Firman & Simmons, 2008*a*). These 'polyandry as inbreeding avoidance' studies have produced results both for (e.g. Tregenza & Wedell, 2002; Bretman *et al.*, 2004, 2009; Bilde, Maklakov & Schilling, 2007; Firman & Simmons, 2008*a*; Welke & Schneider, 2009) and against (e.g. Jennions *et al.*, 2004; Denk *et al.*, 2005; Teng & Kang, 2007; Evans *et al.*, 2008; Pitcher *et al.*, 2008) the claim that polyandry reduces inbreeding. There is probably a sufficiently large number of these studies now available to conduct a meta-analysis. One weakness of these studies is that related and unrelated males might produce different-sized ejaculates due to sexual conflict over fertilization rates; or that kin selection can favour a female mating with a relative if his reproductive success is otherwise likely to be low, and the effects of inbreeding on offspring fitness are not high enough to ameliorate the kin-selected gains females obtain from inbreeding (Kokko & Ots, 2005).

Third, researchers have compared the performance of maternal half-siblings, most notably between within- and extra-pair offspring in passerine birds (reviews: Arnqvist & Kirkpatrick, 2005; Akçay & Roughgarden, 2007; for more recent studies see references in Magrath *et al.*, 2009, and Whittingham & Dunn, 2010) and in flies (Long, Pischedda, & Rice, 2010). As noted, despite some studies showing beneficial effects, the general trend appears to be that extra-pair copulations in passerines do not elevate offspring fitness. It is also noteworthy that, despite the apparent 'control', maternal effects could still arise if laying order and paternity co-vary (e.g. Magrath *et al.*, 2009). A slightly different line of evidence comes from studies showing that extra-pair copulations lead to offspring with greater heterozygosity (e.g. Foerster *et al.*, 2003; Fossøy, Johnsen & Lifjeld, 2008). If heterozygosity elevates fitness (review: Chapman *et al.*, 2009), then this non-additive genetic benefit might favour polyandry in some birds and mammals (e.g. Cohas *et al.*, 2008).

The beneficial effect of greater heterozygosity/within-individual genetic diversity is of special interest to those studying major histocompatibility complex (MHC) genes (review: Spurglin & Richardson, 2010). For example, there is evidence from Seychelles warblers (*Acrocephalus sechellensis*) that extra-pair fertilizations elevate the MHC diversity of offspring of females paired to males with low MHC diversity (Richardson *et al.*, 2005). In the field, higher MHC diversity is positively correlated with greater juvenile survival and a longer lifespan (Brouwer *et al.*, 2010). The later study highlights the importance of directly comparing within- and extra-pair young from the same brood. In an analysis which pooled offspring across broods (because 80% of pairs lay only one egg), there was no difference in performance between within- and extra-pair young. This occurs because pairs that produce extra-pair offspring are a non-random subset of the population (i.e. the males have low MHC diversity) and the genetic benefit of extra-pair paternity is to elevate offspring MHC diversity to the population mean (i.e. comparable to that of the average within-pair offspring) (Brouwer *et al.*,

2010). This is an important point because it raises the wider issue that the benefits of polyandry might vary among females (e.g. vary with female age: Whittingham & Dunn, 2010).

Fourth, there are several experimental study designs that reduce the likelihood of conflating maternal and paternal genetic effects (see Simmons, 2005). There are now many quantitative genetic studies using, for example, diallelic crosses between inbred lines (e.g. Ivy, 2007; Dowling, Nystrand & Simmons, 2010), crossed breeding designs (North Carolina II) (e.g. Evans, García-González & Marshall, 2007) and full-sib/half sib studies (e.g. García-González & Simmons, 2005) to estimate the extent to which females could benefit from biasing paternity. These studies often emphasize the relative importance of additive and non-additive genetic variation among males in the benefits they might provide to polyandrous females. It is, of course, ultimately still necessary to test whether females actually bias paternity towards males that elevate offspring fitness. In a few studies, polyandrous females have been assigned matings with two or more males with specific genotypes that have known effects on offspring fitness to test whether paternity is biased towards males that elevate fitness. For example, a study of *C. maculatus* used a series of isogenic genotypes that differed in their genetic complementarity to each other. When females were allowed to mate with two males with different genotypes there was a significant paternity bias towards males that lowered offspring fitness (measured as daughter's fecundity) (Bilde *et al.*, 2009). This result is again a reminder that sexual conflict over fertilization could reduce or even eliminate genetic benefits to polyandry. By contrast, in Gouldian finches (*Erythura gouldiae*) there is a colour polymorphism with a well-understood genetic basis and major genetic incompatibility between red- and black-headed morphs that results in 60% greater egg-maturity mortality compared to offspring produced by parents of the same head colour (Pryke & Griffith, 2009). Females paired with an opposite- or same-coloured head morph were equally likely to engage in extra-pair copulations. However, post-copulatory mechanisms exist which bias fertilization towards more compatible males of the same head colour (Pryke, Rollins & Griffith, 2010).

Fifth, several studies have tested whether more attractive males gain a higher share of paternity (e.g. Lewis & Austad, 1994; Evans *et al.*, 2003; Pilastro *et al.*, 2004; Hosken *et al.*, 2008; Evans & Rutstein, 2008), or if there is a link between sexual trait expression and sperm competitiveness (e.g. Polak & Simmons, 2009). Sperm competitiveness is based on share of paternity and could be driven by both male effects (e.g. greater sperm production or production of faster swimming sperm) and cryptic female choice. Positive findings suggest that polyandry could lead to the production of sons favoured by pre-copulatory and post-copulatory sexual selection as predicted by 'sexy sperm' and 'good sperm' models (review: Evans & Simmons, 2008). This process requires, however, that male ejaculatory traits are heritable, and that any increased success of sons is not ameliorated by sexually antagonistic genes that lower daughters' fitness (e.g. Foerster *et al.*, 2007; for a recent theoretical model see Connallon, 2010).

Ideally, studies are required that show a positive genetic correlation between sperm competitiveness (i.e. the ability to gain paternity given polyandry) and major fitness components (such as male mating success), or preferably net fitness. Some studies have shown a positive genetic correlation with attractiveness (e.g. Hosken *et al.*, 2008), others that there might be a negative genetic correlation between traits favoured by pre-copulatory and post-copulatory sexual selection (e.g. Simmons & Emlen, 2006; Evans, 2010), and still others have found no detectable additive genetic variation for sperm competitiveness (e.g. Dowling *et al.*, 2010). More generally, while individual sperm traits show reasonable heritability, net sperm competitiveness tends to show low heritability (review: Simmons & Moore, 2009), possibly due to strong maternal effects that could be genetic (see references in Dowling *et al.*, 2010). The lack of heritability echoes the equivalent findings for sexual traits under pre-copulatory sexual selection, which tend to be heritable even though 'attractiveness' *per se* is often not (review: Walsh & Blows, 2009).

Sixth, in studies very similar to those described above, researchers have tested whether males that carry genes that elevate a major component of offspring fitness (of which 'attractiveness' is only one example) gain a higher share of paternity. For example, García-González & Simmons (2007) tested whether male crickets that have a more beneficial effect on offspring viability (based on offspring performance when males mated with a monandrous female) gain more paternity. No such bias was reported. By contrast, a paternity bias towards males that elevate offspring fitness was reported for the small marsupial *Antechinus stuartii* (Fisher *et al.*, 2006*a*).

Finally, a range of 'one-off' studies have taken advantage of specific phenomena that point to some potential genetic benefits of polyandry. For example, it has been suggested that polyandry reduces the likelihood of offspring inheriting selfish genetic elements that reduce mean offspring fitness. Two recent studies provided support for this claim and show that polyandry reduces the rate of inheritance of a sex ratio distorter in *Drosophila pseudoobscura* (Price *et al.*, 2008; Price, Hurst & Wedell, 2010). A similar argument has been made for inheritance of the extra-nuclear genome of intra-cellular parasites such as *Wolbachia* (de Crespigny, Hurst & Wedell, 2008). Another example of a 'one-off' study is testing for cryptic male choice in the form of differential ejaculation that might lead to greater paternity for males with genotypes that elevate offspring fitness. For example, male jungle fowl (*Gallus gallus*) transfer relatively more sperm to females with MHC genotypes that complement their own genotype, leading to the production of more immunocompetent offspring (Gillingham *et al.*, 2009). This strategic ejaculation could make polyandry beneficial if females can not directly assess a male MHC genotype (although this would require an asymmetry in discriminatory ability between the sexes).

V. CONCLUSIONS

(1) There is only weak evidence for genetic benefits to polyandry. The strongest evidence is that polyandry increases egg hatching success, but the effect is only marginally significant. Future studies should measure the hatching success of fertilized eggs to clarify the extent to which polyandry may affect early embryo survival *versus* egg fertilization rates. The two strongest effect sizes for direct benefits of polyandry were for greater fertility and a higher rate of clutch production. Again, however, the effects were only marginally significant.

(2) Experimental polyandry studies should strive to record lifetime reproductive output rather than shorter term measures (see supporting online information Appendix S1). It is possible that polyandry stimulates females to produce offspring more rapidly (e.g. shorter inter-brood interval, hence more clutches) without affecting lifetime output. *A priori*, it is hard to envisage how polyandry (i.e. controlled for mating rate) could increase lifetime reproductive output (aside from sperm limitation effects).

(3) Ideally, offspring fitness should be measured as lifetime reproductive success (Kokko *et al.*, 2006). Only one study that fulfilled our inclusion criteria measured offspring reproductive success (Klemme *et al.*, 2008). Examining the effect of polyandry on the fertilization success of sons is particularly important because there is uncertainty about the extent to which sperm competitiveness is heritable (review: Evans & Simmons, 2008). Evidence for a general lack of heritability in the direction of selection once multivariate selection is accounted for (review: Walsh & Blows, 2009) strongly cautions against over-reliance on the use of single trait measures of offspring fitness.

(4) Many researchers now use quantitative genetic designs to estimate the extent of additive and non-additive genetic variation in different fitness components (references in Dowling *et al.*, 2010). These studies identify potential genetic benefits, but they are no substitute for controlled experiments of the type analysed here, that test directly whether polyandry elevates offspring fitness.

(5) Experimental studies testing for biased paternity in species where males of known genotypes that have large effects on offspring fitness for females of known genotype might offer a rare, but potentially powerful demonstration of the genetic benefits of polyandry (e.g. Pryke *et al.*, 2010; studies of animals of known *MHC* genotype). This is because these are species in which selection on females to bias paternity is likely to be unusually strong.

(6) Over a decade ago, Tregenza & Wedell (1998) provided an excellent experimental design to study the genetic benefits of polyandry. It promoted much research, as we located 39–46 usable studies. Even so, there is still surprisingly little information available to test whether polyandry confers genetic benefits. This is due to fairly few species being studied and different traits being measured in different studies. We encourage researchers to conduct additional studies and to measure as many traits as possible. Otherwise we are left with the current set of inconclusive results that are, at best, only weakly suggestive of genetic benefits.

(7) Although not always described as such, studying the genetic benefits of polyandry is the exact post-copulatory equivalent of testing 'good gene' or 'compatible gene' models for the evolution of female choice. The same problems of imperfect choice and low heritability of fitness (if benefits are additive) apply in both cases. It would therefore be interesting to conduct an equivalent meta-analysis to the current one that quantifies the genetic benefits when females are experimentally assigned preferred and non-preferred males. One could then test formally whether the estimated genetic benefits differ between the two types of studies. This meta-analysis would test directly the provocative suggestion of Zeh & Zeh (1997) that egg-sperm interactions and cryptic female choice allow for more precise identification of genetically compatible males than is possible during pre-copulatory mate choice.

VI. ACKNOWLEDGEMENTS

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Further details about effect sizes presented in Table 1.

Appendix S2. Species-level analysis using studies with full and partial control of mating.

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