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The evolution of multiple mating

Costs and benefits of polyandry to females and of polygyny to males

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Polyandry is a paradox: why do females mate multiple times when a single ejaculate often provides enough sperm for lifetime egg production? Gowaty et al. addressed explanations for polyandry in *Drosophila pseudoobscura* from the perspective of hypotheses based on sex differences in costs of reproduction (CoR). Contrary to CoR, Gowaty et al. showed that (1) a single ejaculate was inadequate for lifetime egg production; (2) polyandry provided fitness benefits to females beyond provision of adequate sperm and (3) fitness benefits of polyandry were not offset by costs. Here, I discuss predictions of the ad hoc hypotheses of CoR and three alternative hypotheses to CoR to facilitate a discussion and further development of a strong inference approach to experiments on the adaptive significance of polyandry for females. Each of the hypotheses makes testable predictions; simultaneous tests of the predictions will provide a strong inference approach to understanding the adaptive significance of multiple mating. I describe a sex-symmetric experiment meant to evaluate variation in fitness among lifelong virgins (V); monogamous females and males with one copulation (M_{OC}); monogamous females and males with multiple copulations (M_{MC}); P_{AND} , polyandrous females; and P_{GYN} , polygynous males. Last, I recommend the study of many different species, while taking care in choice of study species and attention to the assumptions of specific hypotheses. I particularly urge the study of many more *Drosophila* species both in laboratory and the wild to understand the “nature of flies in nature,” where

opportunities and constraints mold evolutionary responses.

Multiple Mating in *Drosophila*

“Multiple mating” is mating with more than one potential mate, which potentially produces offspring of mixed parentage. Multiple mating is called “polyandry” when females do it and “polygyny” when males do it. In the vast majority of tested species, females mated in nature produce offspring sired by more than one male. Polyandry is common in wild *Drosophila*,^{1–17} but also in crickets,¹⁸ burying beetles¹⁹ and other insects,²⁰ as well as birds²¹ and mammals.^{22,23} Compared with birds, in which studies of hundreds of species in the wild demonstrate the ecological correlates of genetic polyandry, generalities about *Drosophila* polyandry come mostly from laboratory studies, and most generalities about *Drosophila* polyandry come from only two species, *D. melanogaster* and *D. pseudoobscura*, though this is changing as more behavioral and evolutionary ecologists²⁴ ask questions about non-model *Drosophila* and *Drosophila* species in nature. Despite enormous success in understanding the ecology of polyandry in birds and its costs and benefits to wild-living females, much less is known about proximate causation in birds than in *Drosophila*. Almost all we now know of polyandry’s proximate causes has come from *Drosophila*. A better understanding of the ultimate causes of polyandry in a variety of species of *Drosophila*, along with more studies of *Drosophila* in the wild, will close the

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intertwining linkages of proximate and ultimate causation in the paradoxes of polyandry—at least for *Drosophila*—and provide additional direction for studies of polyandry in other taxa.

In laboratory studies of multiple *Drosophila* species, females often readily mate with more than one male.^{15,17,25} Investigators often present experimental males to females sequentially rather than simultaneously, and this methodology has led to categorization of species as those with females re-mating at relatively fast vs. slow rates.¹⁷ There are very few fly species in which most females mate just once.^{17,26,27} In contrast, no studies of *Drosophila* from nature have demonstrated that specific males have sired offspring with more than one female, which might be explained by the methodological difficulty of assigning rather than rejecting paternity (assigning paternity is a problem not unique to *Drosophila*, but also in studies of other wild animals). In

the laboratory, male *Drosophila* multiple mating is much easier to observe, especially under experimental mating schemes with sequential presentations of females to subject males; and, in the laboratory, male multiple mating is common.¹³ Observations in some species suggest that female re-mating rate may be higher than male re-mating rate,²⁸ which may be associated with sex differences in development time, in turn affecting the operational sex ratio at eclosion sites where females often commence mating.¹⁷ Even Bateman's²⁹ classic laboratory experiment with *D. melanogaster* suggested on reflection^{30,31} and later re-analysis³² that most females re-mated more than once, sometimes as often as most males in the experimental trials. Thus, the widespread general expectation derived mostly from laboratory studies of *D. melanogaster* that male *Drosophila* always re-mate more often than females re-mate remains speculation.

In this paper, I describe conceptual and theoretical ideas (Table 1) that together allow a strong inference³³ approach to current investigations of the costs and benefits to polyandry in species from any taxa, concentrating on the implications in studies of *Drosophila*. The ideas that I consider here have implications for future investigations of the fitness consequences for both females and males of multiple mating, i.e., of genetic polyandry and genetic polygyny. I also suggest an experiment for the future (Table 2), from the perspective of a balanced approach³⁴ to the constraints and opportunities for males^{31,35} and females of multiple mating.

Polyandry Hypotheses

Hypotheses 1–5: Cost of reproduction. Anisogamy³⁶ and parental investment³⁷ theories are evolutionary explanations for fixed sex differences in pre-copulatory and copulatory mating behavior and physi-

Table 1. Comparison of fitness predictions for scenarios from cost of mating, compensation, demographic stochastic mating theory and the switch point theorem

| Polyandry hypotheses | Component of Fitness | | | | | |
|--|--|--|--|--|--|--|
| | Number of fertile eggs | Egg to adult survival† | Number adult offspring | Mother survival* | Adult offspring survival‡ | |
| | M _{OC} M _{MC} P _M | M _{OC} M _{MC} P _M | M _{OC} M _{MC} P _M | M _{OC} M _{MC} P _M | M _{OC} M _{MC} P _M | |
| 1 ¹ CoR: Guards against “sperm limitation” | M _{OC} < M _{MC} = P _M | No prediction | No prediction | No prediction | No prediction | |
| 2 ^{1,2} CoR: Decreases gamete incompatibilities | M _{OC} = M _{MC} < P _M | No prediction | No prediction | No prediction | No prediction | |
| 3 ¹ CoR: Enhances offspring health | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | No prediction | M _{OC} = M _{MC} < P _M | |
| 4 ¹ CoR: Enhances direct benefits to females | No prediction | No prediction | No prediction | M _{OC} ≤ M _{MC} ≤ P _M | No prediction | |
| 5 ^{1,2} CoR: Male coercion of remating by females | M _{OC} = M _{MC} = P _M | M _{OC} = M _{MC} = P _M | M _{OC} = M _{MC} = P _M | M _O ≥ M _{MC} ≥ P _M | M _{OC} = M _{MC} = P _M | |
| 6 ³ Compensation | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | M _O ≥ M _{MC} ≥ P _M | M _{OC} = M _{MC} < P _M | |
| 7 ⁴ Demographic stochastic mating theory | M _{OC} ≤ M _{MC} < P _M | No prediction | ≤ ≤ | No prediction | No prediction | |
| 8 ⁵ Switch Point Theorem | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} < P _M | M _{OC} = M _{MC} = P _M | M _{OC} = M _{MC} < P _M | |

Hypotheses for polyandry predict differences in components of fitness and the direction of effect comparing experimental treatments. The experimental treatments are (1) females with access to one randomly assigned male during only one day of their lives, i.e., monogamous females with one copulation MOC; (2) females with continuous access to a single randomly assigned male; i.e., monogamous females with multiple copulations MMC and (3) polyandrous females with access to a different randomly-assigned male (controlling for age and experience of males in MMC) on each day of the experiment; i.e., polyandrous females with multiple copulations, PMC. Read the entries thusly: MOC = MMC = PMC and so forth. *Mother survival is always expected to be lower for mothers with greater contact with conspecifics as required when females mate with more than one male, because of higher risk to pathogens and parasites, unless pathogen risk is offset by greater access to resources or other factors. †Offspring survival/per cohort is almost always expected to be higher under heterozygosity, particularly at immune coding loci, which in many ecological circumstances will be higher when mothers have broods sired by more than one male. ¹Assumes the cost of reproduction CoR organizes sex differences, and for species in which eggs are larger than sperm, assumes females are choosy about mating, but males indiscriminate; assumptions and predictions are sex-asymmetric, differing for males and females. ²CoR assumptions plus assume males are not just indiscriminate but coerce females into mating; and there are no additional benefits of multiple mating over single mating for females; asymmetric expectations for females and males. ³Compensation assumes that offspring viability determines mate preferences, constraints on mating with one's most preferred exist and that under constraints individuals will attempt to compensate for offspring viability deficits. ⁴Assumes demographic stochasticity affects opportunities for mating and all mating is “on encounter” (i.e., indiscriminate); symmetric expectations for females and males. ⁵Assumes individual time available for mating and the likelihood of fitness conferred or lost from a particular mating determine whether an individual “accepts” a potential mate on encounter (is “indiscriminate”) or “rejects” an encountered potential mate and waits for a partner with whom the individual will have higher fitness offspring (is “choosy”).

Table 2. The design of a sex-symmetric experiment to evaluate the costs and benefits of multiple mating

| Treatments (A through H) | | | | | | | | | |
|--------------------------|------|-----------------------------|------------------------------|-----------|-----------------------|-------------------------------------|-------------------------|--|--|
| Alone adults | | Monogamy varied copulations | | | | Multiple mating | | | |
| Female | Male | Single copulation | Many copulations | Life-time | Female | Male | | | |
| | | One-day exposure to partner | exposure to the same partner | | “Polyandry” | “Polygyny” | | | |
| | | | | | New virgin male daily | New sexually experienced male daily | New virgin female daily | *New sexually experienced female daily | |
| A | B | C | D | E | F | G | H | | |

With these treatments we will test the following predictions: (1) Assuming that the metabolic cost of producing eggs is greater than producing sperm, virgin females (A) die before virgin males (B). (2) Assuming that the cost to mating is greater in females than males, males live longer than females (D males > females). (3) Assuming that mating is costly, mated females die before virgin females (C females > A) and mated males die before virgin males (C males > B). (4) Assuming that female reproduction is limited by access to sperm, monogamous females who copulate once (C) lay fewer viable eggs than monogamous females who copulate repeatedly (D). (5) Assuming that polyandrous females have access to more variation in male haplotypes compared with monogamous females with constant access to males (D - while controlling variation in male age and experience), polyandrous females (F) have healthier offspring (% egg-to-adult-survival), more offspring who survive to eclosion and more adult offspring who survive longer. (6) Assuming that male quality varies with mating status, polyandrous females mated to a new virgin male every day (E) will lay more eggs than polyandrous females mated to sexually experienced males (F). (7) Assuming that multiple mating is associated with access to females with different alleles at immune coding loci, polygynous males (G) have healthier offspring than monogamous males - not controlling for female experience between treatments because males get a new virgin female everyday D males. (8) Assuming polygyny is costly for males, G and H males will die before D males. (9) Assuming that multiple mating is associated with access to more alleles at immune coding loci, polygynous males (H) have healthier offspring than monogamous males (D) while controlling between treatments for female age and mating experience, i.e., $D < H$. (10) Assuming pathogen risk is greater for polygynous than monogamous males, polygynous males (H) will die sooner than monogamous males (D) while controlling between treatments for female age and mating experience, i.e., $D > H$.

ology of males and females. Both anisogamy and parental investment assume that reproduction extracts predictable, deterministic costs that are greater in females than males, and thereby, in most species favoring choosy females and indiscriminate males. I call these arguments collectively “scenarios from the cost of reproduction” (CoR). CoR assumes the above selection arguments and predicts that selection acts differently on females and males such that male mating rate is much higher than female mating rate.

CoR arguments provide conceptual backing for Darwin’s³⁸ observations and Bateman’s²⁹ “principles” that (1) females are choosy and males indiscriminate about mating (2) which causes male variance in number of mates to be greater than female variance in number of mates so that (3) number of mates has a stronger effect on male reproductive success than female reproductive success.

Many investigators assume the veracity of the CoR arguments about choosy females and ardent males; yet very few experiments exist^{39,40} that were designed to test under experimentally controlled conditions for the existence and magnitude of sex differences in pre-mating behavior. Nor, are there studies that evaluate the many alternative hypotheses, for what is called “courtship” by males; “courtship”

could be attempts to persuade reluctant females to mate, or it could be, as it is in many bird and mammal species, a mechanistic way to coordinate male and female reproductive hormones; or it could be a type of communication serving collaborative functions between females and males both of whom have already indicated that the other is an acceptable mate. Instead of evaluating these alternatives, most investigators simply proclaim the generality of Darwin’s observations, Bateman’s conclusions⁴¹ and CoR’s predictions. Thus, they expect the optimal mating frequency for females to be once or always less than males, particularly in species in which females store sperm. Under CoR assumptions, it is unlikely that mating with more than one male increases female reproductive success. CoR scenarios predict that males provide to females in a single ejaculate enough sperm to fertilize their entire lifetime of egg production. And, under most characterizations of CoR assumptions, but not all,³⁵ whenever CoR is lower for males than females, males are predicted to be ardent and enthusiastic about mating, while females are predicted to be retiring, coy, relatively passive and choosy about mating.

Observations inconsistent with CoR. On the face of it, the very existence of polyandry rejects CoR. When there are

no survival differences between monogamous and polyandrous females, one must seek other explanations for sex differences in mating behavior. Yet, only a very few investigators have considered that non-confirmatory empirical observations are actually a challenge to CoR ideas. Confronted with empirical inconsistency, many investigators instead cast ad hoc hypotheses of, e.g., “requisite” sexual conflict from the “coy female, ardent male” imperative to explain contrary data. In addition to evidence inconsistent with CoR, many criticisms of the CoR assumptions exist: it is unsurprising that there are many ad hoc adjustments to the basic CoR assumptions.

There are five CoR polyandry hypotheses (Table 1) with predictions about the benefits and costs of polyandry. The predictions vary depending on additional assumptions about what fitness benefits to females, either direct or indirect, organize female choices of mates. For example, if female mate choice only guards against sperm limitations (hypothesis 1), such as insufficient or defective sperm or incompatibilities between gametes (hypothesis 2), the hypothesis predicts that the number of eggs laid is less for females who copulate one time rather than multiple times, independent of whether the multiple copulations are with the same male.

Discerning between hypothesis 1 and hypothesis 2 when there is empirical consistency with their predictions requires additional mechanistic studies to evaluate the cause(s) of variation in egg number.

If one assumes that females choose mates for enhanced offspring health benefits, (hypothesis 3) the CoR predicts higher number of eggs laid, higher egg to adult survival, more adult offspring, and healthier adult offspring for polyandrous than monogamous females, whether monogamous females mate more than once or not. The basic costs of egg production under CoR predict that polyandrous females die faster than monogamous females.

If one assumes that females choose mates for direct benefits (hypothesis 4), the CoR predicts no differences in number of eggs laid, in egg to adult survival, number of adult offspring, and survival of adult offspring for monogamous and polyandrous females. Hypothesis 4 does predict, however, a survival benefit for those females who mate more often, whether they are polyandrous or monogamous, copulating multiple times with the same male.

Hypothesis 5: Sexual conflict and polyandry. The ad hoc sexual conflict hypotheses often characterize female multiple mating as an interaction between two or several competing males inside the bodies of females where sperm battle, as though the females are jars. The inside-female mechanisms by which males may decrease the reproductive success of rivals sometimes extract costs to females,⁴² sometimes decreasing their survival probabilities and making tendencies for female re-mating to be inhibited.⁴³⁻⁴⁸ In this view, females are caught in the cross-fire of male rivals, so that the cause of female re-mating is only to reduce costs extracted from pre-mating chasing, so-called “courtship” harassment, or post-mating collateral cost, not to gain some intrinsic fitness rewards from the mating. The costs to females of post-copulatory sperm wars are through accessory peptides that increase female egg-laying and negatively affect females’ survival probabilities, which provides for some scenarios, the only selective force of female resistance,^{49,50} which as some have noted could indeed have huge

effects on the evolution of both female and male traits.

The “male coercion of females” sexual conflict hypothesis (hypothesis 5) predicts (Table 1) that egg-to-adult survival, number of adult offspring, and survival of adult offspring will be statistically similar whether females mate monogamously or polyandrously. Hypothesis 5 further predicts in most characterizations of the hypothesis that the more females mate the more likely they are to die.

Alternatives to CoR assumptions. It is also possible, but not yet experimentally investigated, that male mechanisms affecting females’ reproductive decisions are “nice” rather than “nasty”;⁴⁹ being things that may enhance, rather than decrease, female survival. This, according to the switch point theorem³⁴ (discussed below), would make females ever “choosier” and less likely to accept encountered potential mates in the future. And if there are independent benefits for females of multiple mating that drive their multiple mating in the first place, what might this mean to how we theorize the fitness dynamics of female polyandry? Positive effects on females may arise because competing rivals theoretically may also donate with their ejaculates nutritive or immune enhancing elements to females.^{51,52} And these, of course, may enhance female fitness directly.⁵² Negative effects of ejaculate donations on females are more commonly discussed; but the existence of negative effects does not mean that positive effects do not also occur, as they do.²⁷

Alternatives might start from the first principle: sex is a necessarily collaborative process between two individuals sharing gametes.^{49,53,54} Or, one might start with the idea that females have power too.^{49,55} Could it be that females who multiply mate in the first place organize and manipulate male contests for their own advantage?⁵⁶⁻⁵⁸ Why not imagine that females make the post-copulatory rules of the inside games through their physiological organization of the rules and their responses to males? Why not cast females not as umpires but players in their multi-way interactions with males? Indeed, why not hypothesize that females are “the architects of sperm competition,”⁵⁹ a reasonable alternative hypothesis, for

which supportive data exist.^{60,61} Why not imagine that the dynamic interactions and their outcomes between females and males lead sometimes to reversals of power between the sexes, and over time, to sex-symmetric power distributions?⁴⁹ Why not imagine a dance of symmetric jousting over the, only sometimes, competing, but often necessarily cooperative^{62,63} interests of females and males?

If no fitness rewards for females of multiple paternity exist, the problem of female multiple mating might indeed be entirely a problem of male-male competitive interactions: which male is the best competitor or which male extracts the least harm. However, if offspring viability (i.e., offspring health) matters to prospective parents, for example, alternative potential mates will often offer females a better or worse shot at healthy offspring.^{34,62,64} These alternatives have occasionally been tested,^{65,66} but seldom in the context of female lifespan variation,^{67,68} making it very hard to discern some selectively effective costs. Assuming that there exist fitness rewards for females of controlling their own reproductive decisions, male competitive interactions pre- or post-mating put females in exquisite binds in which the benefits and costs of polyandry are in dynamic tension, so that female resistance to male control attempts will evolve⁴⁹ in evolutionary time or be induced in ecological time.⁶⁹

Hypothesis 6: Compensation theory says multiple mating enhances offspring health with mutual benefits to both parents. If the pathogens and parasites of the offspring generation are different from those of the parental generation, as expected when pathogens and parasites evolve more rapidly than their hosts, the “Red Queen’s Challenge” to parents⁶² is how to produce the best immune systems in their offspring. Consideration of basic rules of inheritance of parental alleles means that in general parents will produce offspring with excellent immune function against the parent generation pathogens.⁶² What can parents do to increase the likelihood that offspring will have the rare alleles and rare phenotypes that will enhance their survival in the face of novel disease risks that arise in the offspring generation? One route would be mutual

mate choice, in which both females and males choose mates complementary (i.e., dissimilar) to themselves at immune coding loci.^{34,62,63} This option probably works for large, viscous populations with few social or ecological constraints on mate encounter; however, ecological and social impediments to free mate encounter are ubiquitous, probably vary by species, and suggest that most parents are making the best of a bad job, providing selection favoring variation in parental effects to increase the likelihood that offspring survive long enough to enter the ranks of breeders.

The compensation hypothesis (CH)⁶² (hypothesis 6) says that both female and male partners will be under selection waged via the success of other parents with healthier offspring to compensate for expected offspring viability deficits. In *D. pseudoobscura*, both females and males discriminate among potential mates,^{39,40} and when male or female choosers are in enforced experimental pairs with a potential mate they prefer compared with one they do not, the pair produce more adult offspring (but not more eggs) than when the chooser is with a potential mate they did not prefer.⁷⁰ These observations are inconsistent with the CoR prediction of indiscriminate male *D. pseudoobscura*, which have the smallest sperm of any known *Drosophila* species. More interestingly, as the CH predicted, females with males they did not prefer laid more eggs than females with males they did prefer. As a result, even though their offspring had lower egg-to-adult survival, some of the offspring survived to breeding age, keeping the lineage of compensating females alive. Laying more eggs to increase the likelihood that some survive to breed is a known compensatory mechanism, and may levy costs for both sexes of parent when environments are challenging.^{62,63} Similar compensatory mechanisms occur in several model vertebrate species as well as female *D. pseudoobscura*.⁶³ Likewise, CH predicts that polyandrous mating provides compensatory benefits to females mating under ecological or social constraints.⁶²

Many mechanisms of compensation are possible; some compensatory mechanisms are available for both females and males; others are sex specific. Elementary selection

logic suggests that both sexes might compensate in cooperative efforts to enhance the likelihood of survival of their offspring. In species like flies in which post-zygotic parental care is unlikely and unknown, there are nonetheless many options that individual parents might use facultatively or flexibly to enhance offspring survival. From the perspective of CH the remarkable observations of Markow and her collaborators of male elemental contributions to ovarioles,⁵² ejaculate-associated nutritive contributions to females and their offspring⁵¹ are particularly interesting. Could the long-tails of sperm in the giant sperm species sometimes be nutritive as well? Do males contribute more when they mate with females with whom they will produce less viable offspring? Are these mechanisms ones that could be flexibly upregulated in some matings but not others?⁵⁴ These questions about the options some males have to collaboratively attempt to enhance the reproductive performances of their mates or even the health of their mates are intriguing, and as far as I have been able to tell, uninvestigated in terms of their effects on fitness variation of parents. Perhaps this is not strange given the current hegemony of sexual conflict and sexual antagonism dominating discussions of the relationships between the sexes. Novel insights likely await newer investigations of the nature of these potentially collaborative interactions between males and females in species like flies that lack post-zygotic parental care.

If multiple mating is a mechanism of compensation for offspring viability deficits, the CH predicts (Table 1) egg to adult survival and adult offspring survival is greater in monogamous than polyandrous mating, but that the number of adult offspring for monogamous and polyandrous females is the same, and furthermore that polyandrous females die sooner than monogamous females, not just because of enhanced exposure to conspecifics, but because of the costs of compensation.

Hypothesis 7: Demographic stochastic mating theory predicts polyandry and polygyny are common in most species. In contrast to the intuitive scenarios above, the axiomatic mating theorem of Hubbell and Johnson⁷¹ proved theoretically that

multiple mating is common in both sexes. Assuming large population sizes, demographic stochasticity (by chance some individuals die or otherwise leave or enter populations), and no selection pressures against multiple mating, the analytical solution of demographic stochastic mating theory (DSMT) says that individual encounter probability (e) with potential mates, individual survival probability (s), and the time after mating to receptivity to remating (l) determine lifetime mating rates. Under the simplifying assumptions of DSMT, differences between individuals and the variance among individuals in their lifetime mating rates arise from differences in the time they have available for mating,⁶⁴ modulated in all individuals of either sex by s , e and l . Thus, multiple mating in either sex can evolve in the absence of fitness benefits for either sex. From the perspective of DSMT, female multiple mating is no more problematic than male multiple mating: “it’s all about time”⁶⁴ and the ecological and social constraints affecting individuals’ time available for mating and reproduction.

The DSMT (Hypothesis 7) predicts that there are no differences in egg to adult survival or in adult offspring survival between monogamous and polyandrous females (Table 1), and that the number of adult offspring is greater than or equal between monogamous and polyandrous females. Without additional assumptions DSMT makes no predictions about lifespan variation of monogamous and polyandrous females.

Hypothesis 8: The switch point theorem predicts that multiple mating by either sex is adaptive. The DSMT background certainties of probabilistic variation in e , s and l , which produces real-time changes in the time an individual has available for mating^{34,64,69,71} must also shape fitness enhancing mating decisions. For this to be so, females and males need to discern fitness costs and benefits of mating with this one or that one, given the unique demographic circumstances of each decision-making individual. If individuals discern fitness costs and benefits, the switch point theorem (SPT)³⁴ shows how adaptively flexible individuals evolve so as to maximize their fitness in contemporary time; trading off their time available

for mating with fitness, so that they sometimes accept and sometimes reject a mating opportunity. The SPT proved theoretically that males and females trade off time with fitness gains as they make “flexibly adaptive” decisions to accept or reject a mating.

If individuals make flexible reproductive decisions to accept or reject so as to optimize their fitness given specific demographic circumstances, as the SPT (Polyandry hypothesis 8) says, there will be differences in fitness outcomes among individuals, but these need not be, in nature, systematic benefits or costs to multiple mating relative to single mating by either sex (Table 2). More important, the SPT implies that there is no necessary sex differential cost of multiple mating over the cost of single mating for either sex (Table 2). That there is no further extracted cost in terms of survival of multiple mating for females is a unique prediction of the switch point theorem (Table 1).

Interpreting Results of Gowaty et al.

Gowaty et al. demonstrated that monogamously mated females with multiple copulations (M_{MC}) had more surviving offspring than monogamous females mated one time (M_{OC}), because single mated females ran out of sperm before they died or that sperm were otherwise inadequate. Compared with M_{MC} females, P_{MC} females with access to a new male every day, and who could have mated with each one and did mate with more than one male, had offspring with significantly higher egg-to-adult survival and significantly more offspring that survived to eclosion. Despite our a priori intuition that exposure to more conspecifics would decrease P_{MC} females’ health status and thus, their lifespan compared with M_{OC} and M_{MC} , there were no significant differences in lifespan among the three types of experimental females.

All females entered the experimental treatments at the same time. All females and males were virgin at the start of the experiment. We kept trial sets consisting of “paired” females who were M_{OC} , M_{MC} and P_{MC} together throughout the

experiment to control for bench effects. We controlled for the ages and prior experience of males interacting with M_{MC} and P_{MC} females by rotating the males in the P_{MC} treatments between other P_{MC} females. The study (Gowaty et al., 2010) was simple and tractable, but large and time consuming, with the oldest female dying at 138 d old, 131 d after the start of the experiment. We made the following conclusions: (1) polyandrous females produced offspring with higher probabilities of survival than that of offspring of monogamous females; and (2) polyandrous females did not die significantly faster than monogamous females. I considered the study important for two reasons. First, it solved the puzzle, “What do females want”—for *D. pseudoobscura*, at least. Because we eliminated the possibility of multiple-male pre-mating harassment of females, the conclusions were unambiguously associated with females’ mating with multiple, different males compared with one male. Second, it showed—to our surprise and for the first time in any *Drosophila* species—that exposure to and mating with more than one male was not costly to females.

Gowaty et al. did not dwell on the ramifications of the failure of our observations to match the predictions of the CoR and sexual conflict scenarios, nor its consistency with the predictions of compensation, DSMT or the SPT. The data provided no support for egg-laying prediction of hypothesis 1 about sperm limitation or hypothesis 2 about gamete incompatibilities. Our data are inconsistent with hypothesis 4 about direct benefits to females of multiple mating, and our data reject hypothesis 5 of male coercion of female remating. The data were inconsistent with the hypothesis 6, the CH, but CH advocates might argue that the comparison of costs and benefits of polyandry were an inadequate test of the underlying assumptions of the CH, and thus logically not a test of the compensation hypothesis. The data over all were consistent with hypothesis 7 DSMT, however, DSMT could not account for the enhancement of offspring viability via polyandrous mating—at least without an add-on ad hoc assumption. Overall, however, the data show explicitly that

polyandry benefited offspring health, consistent with hypothesis 3 about offspring viability and hypothesis 8, the SPT. This is not surprising as both of these ideas depend on an assumption of offspring viability as the main component of fitness organizing mating behavior; i.e., these two hypotheses are not alternatives and can be simultaneously so.

The discussion above stresses the significance of the assumptions of hypotheses. Clearly, in order to explore further the origins and benefits of multiple mating for females, our collective attention should be on the various assumptions of these hypotheses. Future strong inference crucial tests³³ of these hypotheses will depend upon the veracity of the assumptions of each hypothesis. Thus, surely it is the assumptions of the various hypotheses that future investigators should attend to.

Next Questions

Mechanism and strongly inferential tests of predictive theories of multiple mating in females and males. Gowaty et al. did not investigate the mechanistic bases for the study results, or whether pre-touching mate assessment or preferences predicted fitness; we asked no questions about mechanisms of sperm competition, physiological post-ejaculatory female resistance, variation in ejaculate secondary compounds and their possible negative or positive effects on females, zygotes and offspring were not part of our study. The study addressed only the “ultimate” questions of fitness variation of alternative mating scenarios, not the “proximate” mechanisms, except for the proximate “ecological” cause of availability to females of males who were potential mates (in two treatments females had access to only a single male and in the other multiple males). We necessarily left questions of proximate cause for others, not because we are uninterested. Simultaneous study of ultimate and proximate causes is an ideal, but constraints on funding and time seldom allow, perhaps never have allowed, simultaneous study of proximate and ultimate questions, particularly in demographic context.

Sexually symmetric tests of fitness payouts for multiple mating. Gowaty

et al. was necessarily silent about fitness costs and benefits for males, yet a symmetric study of female and male subjects would have been much more powerful in evaluating the intuitive CoR ideas, which “begin with sex differences to predict further sex differences.” However, my colleagues and I have a track-record of completed previous sex-symmetric studies using *D. pseudoobscura* showing the following: (1) both females and males make pre-mating assessments of potential mates.⁷⁰ (2) For individual males and females, pre-mating assessment (preference) behavior predicts reproductive success, including offspring health and the number of offspring that eclose.⁷⁰ (3) Lifespan variation for males whom females preferred or did not prefer and for females whom males preferred or did not prefer were statistically indistinguishable, consistent with the conclusion that there were not intrinsic “quality differences” between potential mates who were preferred or not preferred.⁷²

Gowaty et al. violated our tradition of sex-symmetric studies in our study of female, but not male, multiple mating. So, what would a simultaneous test (Table 2) of fitness costs and benefits for female and male subjects possibly tell us? Controlling for notorious “local bench,” diurnal and seasonal effects, simultaneous tests allow a fair comparison between the sexes. It would level the playing field by asking the same questions of males as we ask of females, in the same way, so that the experimentally manipulated constraints acting on our subjects, whether female or

male, would be the same. It would decrease the likelihood that subtle biasing factors associated with inevitable intuitions—about what males or females ought to do—from creeping in unnoticed. And, simultaneous testing of costs and benefits of male multiple mating would give our best chance of evaluating the effects of social and ecological constraints on individuals of either sex.

Next Steps: To Wild Nature

Connecting laboratory studies of fitness variation to real-world vagaries of the wild, where social opportunities and ecological constraints mold evolutionary response of *Drosophila* sex and evolution, is no easy task,²⁴ perhaps especially now that we know that developmental plasticity and epigenetic responses are so important to phenotypic evolution.⁷³ Arguing that laboratory experiments about fitness variation are beside the point misses the truth of what laboratory experiments are good for: namely they give us a precise understanding under specifically controlled conditions of how individual reproductive success and survival might vary, when many other confounding factors are removed. In the case of the polyandry experiment, we removed the confounding factors of pre-mating male-male competitive interactions, as well as overlooked, female-female competitive interactions, and potentially coercive inter-sexual interactions, such as multi-male harassment of females and mating pairs. In the idealized world, where these sorts of constraints were removed, we are able to make strong

conclusions about the fitness effects of different kinds of social exposures. Are these effects wiped out, one might ask, in the more realistic settings of nature, where hurricanes, predator risk and variation in food resources and mates might vary? Probably. But then we are left with only correlational explanations limited to variables we are able to measure and have measured in the wild. What we can hypothesize about such interesting phenomena as giant sperm, ejaculate-associated nutritional donations to females and offspring, ejaculate accessory proteins, or explanations for why within species some females lay more or fewer eggs than others are enriched with careful laboratory evaluations of many hypotheses, including particularly first principle, axiomatic, quantitative theory that most often yield highly vulnerable crucial predictions. Starting in the laboratory is probably a very good place to begin, but not a good place to end. Our knowledge about flies in nature would be enhanced with efforts to connect the intriguing results of lab experiments on social behavior—fitness⁷⁴ and mechanism—to what happens in the wild.

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