

adaptation occurs even within strongly interacting, complex communities. These results demonstrate that multiple species interactions do not necessitate the diffusion of coevolutionary relationships. Emphasizing the value of this community perspective, Allen Herre (Smithsonian Tropical Research Institute, Balboa, Panama) and Richard Lenski both showed that an understanding of host–parasite specificity can aid in understanding mechanisms that promote community diversity. Integrating this community-level perspective with the mechanistic, model-oriented view of much host–parasite research will lead to a broader understanding of local adaptation in host–parasite interactions.

Acknowledgements

We thank Yannis Michalakis, Susan Mopper and John Thompson for comments on the manuscript.

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Establishing cryptic female choice in animals

In studies of paternity where females accept multiple mates, the explanatory mechanism responsible for variation in male reproductive success has generally been attributed to sperm competition. This is viewed as a process of competitive male–male interactions¹. This emphasis is partly because of the technical difficulties of demonstrating a role for females in sperm usage, which requires direct observation of sperm movement inside females. Current convention, however, relies on postfertilization protocols to measure paternity. This is unfortunate because copulatory and postcopulatory mechanisms of so-called 'cryptic female choice' – such as females selecting how many sperm from each male are initially stored, survive during storage or are lost during remating – may be equally important factors that bias reproductive success towards certain males². Although cryptic female choice has been extensively publicized, its importance is still debated^{3,4}.

Another reason for the emphasis on sperm competition is that there is arguably greater selection on males to ensure

fertilization than there is on females to use sperm differentially from mates⁵ (even though genetic benefits for offspring resulting from female mate choice are now widely accepted). Patterns of sperm usage are conventionally defined as the proportion of eggs fertilized by the second male when females are doubly mated (P_2). In support of selectional asymmetry, mathematical models that predict fertilization patterns based solely on rates and numbers of sperm transferred and displaced by males, without incorporating differential responses by females to individual males, have had considerable success in predicting P_2 in several species^{4,6,7}.

Qualitative arguments have been used to promote the view that females can influence the way in which a male's sperm is used². For example, analysis of the functional morphology of female reproductive tracts clearly shows that they have the potential to preferentially store, transport or extrude sperm from successive mates. Ultimately, however, experimental evidence is required to show that variation among females, or variation in their

responses to different classes of males, also accounts for variation in P_2 . If female traits account for variation in P_2 then they become available for sexual selection. It is these quantitative, statistical data that have been in short supply, with examples coming from studies across species or genetic strains rather than from within single populations (Box 1).

A recent study by Nina Wilson *et al.*⁸ provides compelling evidence that female bruchid beetles (*Callosobruchus maculatus*) influence P_2 values within a population. The experimental design used was similar to that of an earlier study on flour beetles (*Tribolium castaneum*), where a pair of males was mated to a series of females, with male mating order held constant⁹. By using several pairs, this approach allows for an estimate of the variation in P_2 attributable to differences among pairs of competing males. If variation among males is important, then a given pair of competing males should generate similar P_2 values when mated to each female. Statistically, this means that P_2 for male pairs is repeatable because there is greater variation among pairs than within them.

Wilson *et al.* perceptively extended this methodology by also allowing for an estimate of the variance in P_2 that could be attributed to female genotype. Their approach was as follows. Each replicate consisted of two unrelated males who were

both allowed to mate with each of three successive females. As in the earlier study, male mating order was held constant. Experiments were conducted separately on two populations of beetles: one originating from Niamey, Niger and the other from Brazil. In each replicate, the three females were either unrelated or were full sisters. When the females were unrelated, P_2 was marginally repeatable for male pairs from Niamey but not for those from Brazil. In contrast, P_2 repeatability was significant when females were full sisters. In both populations, mean repeatability was far higher for full-sister replicates, increasing from 0.55 to 0.90 and from 0.07 to 0.82, respectively. Reducing the genetic variability among females increased the repeatability of sperm precedence. Thus, the genotype of females affected the proportion of eggs fertilized by second males.

There are two explanations for this. First, there may be an interaction between male genotype and female genotype. A male who achieves high sperm precedence with one female genotype may not be able to achieve high sperm precedence with females of a different genotype. Second, some female genotypes may consistently generate higher P_2 values than others. Thus, variation in P_2 resulting from a female effect may swamp underlying repeatability because of differential competitiveness between two males. Either way, these initial results already hint at a strong female role in mediating sperm competition.

The second part of the experimental design clarified which of these two possibilities was more likely. In the Niamey population, different replicates of full sisters sometimes came from the same family. In total, eight groups of replicates of full-sisters were created. A comparison of P_2 across groups showed that repeatability was not significant when full sisters from the same family were mated to different pairs of males. Thus, there is no evidence that some female genotypes consistently generate high or low P_2 values. By elimination, this strengthens support for an interaction between male and female genotypes.

Finally, Wilson *et al.* created nine groups of replicates with Brazilian beetles, where the females were all full sisters and the paired males in each replicate had the same genetic relationships with one another. For example, in group 1 there were three replicates where the first male was always from family A, the second male was from family B and the females were all from family C. Under these conditions, P_2 was repeatable with greater variation among than within groups. Although this could be attributable to some male genotypes being consistently competitively superior to others, the initial finding that P_2

Box 1. Does female identity influence which sperm fertilize eggs?

Previous research has focused on biased fertilization by males from the same genetic strain as the female or by conspecifics over heterospecifics. In flour beetles (*Tribolium castaneum*), black strain males had lower P_2 (the proportion of eggs fertilized by the second male when females are doubly mated) values than wild-type males when they were the second mates of wild-type females, although both male types achieved similar values when mated to black strain females⁹. In the grasshoppers *Chorthippus parallelus* and *Podisma pedestris*, reciprocal crosses between two geographic races generated fewer hybrids than expected in one race of the former species and in both races of the latter^{12,13}. Similarly, in ground crickets (*Allonemobius* spp.), doubly mated females preferentially fertilized eggs with conspecific sperm, regardless of the order in which males were mated¹⁴. The most convincing evidence for a female role comes from new work on *Drosophila*¹⁵, where females of three species all preferentially use conspecific sperm. This conclusion was not confounded by differential mortality of hybrid and pure-bred offspring.

More importantly, it was also shown that P_2 values, which tend to be uniformly high for conspecific double-matings of both *Drosophila simulans* and *Drosophila mauritania*, are highly variable when two *D. mauritania* males mate with a *D. simulans* female. Interactions between the sperm of two conspecific males, therefore, depend on female-mediated processes, and consistently high P_2 values cannot be attributed solely to male sperm displacement or mechanical constraints on the manner of sperm storage by females.

shows low repeatability for a pair of males mating with females of varying genotypes argues against this conclusion. Overall, the best explanation for the combined results is that there are male–female interactions in which male fertilization success depends on female genotype.

Genetic incompatibility between mates provides one possible explanation for these results¹⁰. Repeatable P_2 values could be generated by nonrandom mortality of offspring without the need for consistent patterns of sperm precedence. Nonrandom offspring mortality will arise if some female–male genetic combinations lead to weak or inviable offspring. For example, high mortality of the first male's offspring, rather than low fertilization rates for first male sperm, could generate repeatable high P_2 values. Wilson *et al.*⁸ were, however, unable to find a positive relationship between P_2 and the pre-adult mortality of the offspring of the first male ($r=0.12$, $n=60$). In addition, P_2 was not related to the difference in pre-adult mortality before and after second matings (which controls for variation among females in baseline levels of offspring mortality). Finally, pre-adult offspring mortality for full sisters mated to the same male pairs was not repeatable, as would be expected if one male consistently fathered less-viable offspring. Widespread genetic incompatibility, therefore, seems unlikely, although it cannot be excluded.

At least ten proximate mechanisms² might explain how female bruchid beetles influence P_2 . These range from variation in the size and shape of female sperm storage organs to differential mortality of sperm inside the female reproductive tract resulting from gamete–somatic interactions and may even include biased use of stored sperm. It is often stated that knowledge of the exact proximate mechanisms responsible for sperm precedence patterns is required before we can demonstrate cryptic female choice¹¹. However, gaining this information is often beyond the capabilities

of current techniques. Processes inside females are likely to remain a 'black box' for some time, although following the fate of labeled sperm will go some way towards identifying possible mechanisms.

Nevertheless, studies that show genetic variability among females that affects P_2 provide powerful evidence that females can and do differentially influence male reproductive success during or following copulation. Any female trait, even seemingly 'passive' ones (such as differences in sperm leakage or spermathecae size) that lead to predictable patterns of sperm usage by different females can 'set the rules' under which males compete. These female traits then become available for sexual selection in the same way as conventional mechanisms of mate choice such as a mating preference for bigger males or being more strongly attracted to brighter colors. Evolution will only occur, however, if the female traits are heritable and if there are fitness benefits associated with different P_2 values.

Despite the success achieved in predicting P_2 in field crickets (*Gryllus bimaculatus*) and yellow dungflies (*Scatophaga stercoraria*) using mathematical models based only on variation among males, it would be useful to conduct similar breeding experiments in these and other species. Will the addition of female variability further extend our understanding and predictive powers? It also remains to be seen whether refined experimental designs can quantify the relative importance of male and female variability in predicting P_2 values. However, even if females account for little of the current variation in P_2 , directional selection on female traits that bias paternity (no matter how weakly) may still lead to dramatic changes in female reproductive biology over evolutionary time scales. Thus, when female genotype effects are demonstrated, establishing their heritability and consequences for female fitness is crucial in determining whether the underlying mechanisms of cryptic choice will evolve.

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Spiders hedge genetic bets

Males can increase their reproductive success by a combination of mating with many females and preventing the eggs of those females from being fertilized by other males¹. Indeed, an extraordinary diversity of mechanisms has evolved, in a broad range of taxa, enabling males to protect their sperm². In contrast, the reproductive success of females was thought to depend primarily on her choice of partner and the efficiency with which she invests resources into her offspring; any obvious benefit of polyandry arises through the paternal investment provided by the additional mating partners. Thus, there may be conflicts of interest between the sexes over the number of mating partners; the observed resolution of this conflict may be a compromise that minimizes the costs for both sexes, or it may favour one sex³.

It is evident that polyandry occurs in many species in which the male makes no contribution to either female fecundity or the care of the developing offspring². For these species, polyandry occurs either against the reproductive interests of the female or it provides some form of indirect or genetic benefits². For example, multiple mating may provide some insurance against the possibility that the first male is infertile; while plausible, this explanation seems to lack taxonomic generality⁴. Nevertheless, polyandrous females will produce clutches with greater genetic variation than monogamous females, which may reduce the variance in seasonal

reproductive success for species in variable environments. Finally, polyandry may provide the opportunity to exercise sequential female choice; in many species, females may not have the opportunity to assess a large sample of males before mating, and thus a mated female may encounter a male that is superior to her previous mating partner^{5,6}. Evidence of this benefit has been provided by studies of extra-pair copulations in birds⁷ and sperm manipulation in snakes⁸. Now, Paul Watson provides experimental evidence⁹ of the benefits of polyandry in the sierra dome spider *Neriene litigiosa* (Linyphiidae).

After reaching sexual maturity, male *N. litigiosa* cease building webs and search for females, who advertise their sexual receptivity with pheromones that are present on the web⁹. Males usually destroy the females' web before initiating courtship, thereby reducing the chances of other males locating the pair¹⁰. Like most other spiders, male *N. litigiosa* do not provide any paternal care of the offspring. In fact, the presence of males on her web results in a reduction to her foraging success as a result of web destruction and kleptoparasitism by the male¹¹. Thus, it appears that the only contribution of males to their offspring is genetic.

Although a single mating is sufficient to fertilize all of her eggs, females are polyandrous and 80–90% of the population will mate more than once¹². Females choose their first and second mates in different ways. The first male is the major sire, with

60–70% paternity of the clutch¹³, and is chosen after males have competed on her web¹⁴. Male size usually determines the outcome of these contests and thus females invariably mate with larger males. Later, she may mate with another male, whose paternity depends on his body size relative to that of her first mate. The second male can expect a paternity of more than 30% if he is larger than the first mate¹². The female's choice of sire seems to occur after mating¹², presumably by manipulation of the sperm and may be an example of cryptic female choice¹⁵. This result suggests that females hedge their genetic bets by mating more than once, thereby insuring against the possibility of an inferior male siring most of her offspring¹².

Verifying that genetic bet-hedging occurs in sierra dome spiders requires data demonstrating that (1) the preferred male trait is heritable; and (2) polyandry increases female reproductive success. Watson⁹ obtained these data by staging matings in the field and rearing the offspring under laboratory conditions. Virgin females were randomly assigned to monogamous or polyandrous mating treatments, and half of the females in each treatment were assigned a randomly chosen male as their first mate. This procedure increased the proportion of polyandrous females whose secondary mate was the larger potential sire of her offspring, and thus the opportunities within the sample for polyandry to provide fitness benefits.

The offspring of the monogamous and polyandrous females were then raised under laboratory conditions in order to monitor their growth and survival⁹. Moderate environmental stress was imposed on the developing spiderlings by restricting