Model Systems, Taxonomic Bias, and Sexual Selection: Beyond *Drosophila*

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Abstract

Although model systems are useful in entomology, allowing generalizations based on a few well-known species, they also have drawbacks. It can be difficult to know how far to generalize from information in a few species: Are all flies like *Drosophila*? The use of model systems is particularly problematic in studying sexual selection, where variability among taxa is key to the evolution of different behaviors. A bias toward the use of a few insect species, particularly from the genus *Drosophila*, is evident in the sexual selection and sexual conflict literature over the past several decades, although the diversity of study organisms has increased more recently. As the number of model systems used to study sexual conflict increased, support for the idea that sexual interactions resulted in harm to females decreased. Future work should choose model systems thoughtfully, combining well-known species with those that can add to the variation that allows us to make more meaningful generalizations.

INTRODUCTION

Model system: a species used as an exemplar of general principles

Sexual selection: differential reproduction based on differences in the ability to acquire mates

Sexual conflict: the potentially antagonistic interactions that occur when males and females have different fitness optima in reproduction

Most fields of biology use model systems to formulate and test hypotheses. As Kunkel (42) put it, "We are unlikely to ever know everything about every organism. Therefore, we should agree on some convenient organism(s) to study in great depth, so that we can use the experience of the past (in that organism) to build on in the future. This will lead to a body of knowledge in that 'model system' that allows us to design appropriate studies of nonmodel systems to answer important questions about their biology."

Model organisms such as zebrafish, laboratory rodents, and a variety of primates have helped biomedical and other life science researchers establish basic principles of fields such as systematics, evolution, physiology, genetics, and behavior. Insects, of course, have provided some of the most productive model systems: *Tribolium* flour beetles; the honey bee, *Apis mellifera*; and perhaps most notably flies from the genus *Drosophila*, especially *D. melanogaster*.

Model systems have many advantages. They facilitate research because the basic methodology for husbandry and other techniques has been developed by previous workers using the same system. Model species are usually easy to rear, observe, or otherwise experimentally manipulate. They therefore allow knowledge to be built up rapidly and efficiently, because confounding factors are known and thus can be controlled in subsequent experiments. New approaches in genomics, now far easier to adopt than ever before, have been a particular boon to the use of model species, because they add comprehensive knowledge of genetic details to already-existing databases. Scientists can now capitalize on natural-history observations of previously obscure animals and use them to examine the genetic basis for differences in behavior, as was recently accomplished using oldfield mice (*Peromyscus polionotus*) (87). Oldfield mice are not, of course, traditional model systems, but they provide a much better window into the operation of selection on behavior in nature than the more conventional laboratory mice (*Mus musculus*). Nonetheless, an editorial in *Nature* accompanying the report on the research warned, "If every interesting animal becomes fair game, there is a risk that behavioral genetics will be fragmented" (22).

Although scientists have been quick to extoll the virtues of model systems in insects as well as other taxa, critiques of their use have been much less common. Model systems are of particular use when an entire field is based on the derivation of general principles that transcend the details of an individual species' natural history. *Drosophila* is thus ideal for inferring how traits are inherited. Similarly, although some animal psychologists objected (9), the early-twentieth-century focus by comparative psychologists on laboratory rats (*Rattus norvegicus*) and pigeons (*Columba livia*) was useful for developing a general theory of mind that could eventually be applied to all other animals, including humans.

In other fields, however, the ability to generalize is not always so useful, or at least not so much of an end in itself, and this means that model systems can be problematic. Many aspects of ecology and evolutionary biology, for example, are explicitly concerned with how individual differences lead to species competition or coexistence, or with the ways in which variation can influence the speciation process. The same problem—how to perpetuate one's genes via sexual competition—turns out to have a multitude of solutions, and the diversity is instructive.

The study of sexual selection is a particularly good illustration of the perils of model systems in ecological and evolutionary studies. Bateman's principle, the idea that males continue to benefit from increasing numbers of mates, whereas female reproductive success plateaus after just a few matings, was developed from observations of *Drosophila* (7). *Drosophila* has also been instrumental in developing ideas about sexual conflict and the evolution of sexually antagonistic traits such as toxic accessory gland fluids (13, 39). As discussed below, dung flies (*Scathophaga* spp.) helped establish the application of game theory to the evolution of alternative reproductive strategies

and sperm competition (60). Other insect groups used in multiple studies on sexual selection and reproductive behavior include crickets (Gryllidae and Tettigoniidae), flour beetles (*Tribolium* spp.), and seed beetles (*Callosobruchus* spp.).

Although it is indisputable that these key species have advanced our understanding of the evolution of male-female interactions, the heavy reliance on a few model insect species has also had drawbacks. First, how far can we generalize across taxa? Taxonomic bias has become a concern in conservation, where researchers fear that efforts to preserve biodiversity have been unduly influenced by an emphasis on so-called charismatic megafauna (6, 15). Insects and other invertebrates are characteristically underrepresented in the conservation literature relative to their abundance (15). The animal migration literature has also been criticized for its disproportionate emphasis on birds and mammals, despite the large numbers of fish, insects, and other invertebrates that migrate (8).

In a related concern, researchers working on less conventional or popular study systems may be further handicapped by reviewers' and editors' reluctance to publish their findings, a result of so-called taxonomic chauvinism (11). A recent survey of parental care literature, for example, found that birds and mammals were disproportionately represented compared with both other vertebrate taxa, such as fishes, and invertebrates (80). Even though some groups are less convenient to study, they may provide important insights (64), and the title of a 2009 article goes so far as to suggest "Taxonomic Chauvinism Threatens the Future of Entomology" (44).

Whether or not we accept such a dramatic risk to the field, focus on a single representative species can cause us to ignore very real diversity, diversity that is key to a truly explanatory theory such as sexual selection. Do all insects show the same limitations on mating rate as *Drosophila*? How might mode of metamorphosis, or the use of visual versus acoustic signaling, influence mate searching, mate choice, or sperm competition? Is the cost of multiple mating comparable across species? If not, we may be overlooking crucial contributions to our understanding of the role of reproductive competition in shaping insect evolution. Given the extraordinary species richness demonstrated by insects, the revelation of taxonomic bias is particularly egregious.

Second, and perhaps more troubling, model systems can fuel confirmation bias, the tendency to see what we expect to see and pay attention only to findings that confirm what we already believe to be true. In this vein, emphasis on *Drosophila* flies as exemplars of sexual conflict may have inadvertently canalized our thinking. *Drosophila* males transfer seminal fluid proteins that reduce the longevity and fitness of the female but deter her from mating with subsequent males, which is advantageous to the first male to mate. This striking example of sexually antagonistic evolution has prompted numerous studies on sexual conflict, with the underlying assumption that mating is harmful to females. But few researchers have considered the generality of the findings; how many insects possess such toxic ejaculates? And if they do not, what is the implication for sexual conflict and how widespread is sexual antagonism expected to be? We highlight work below that suggests that *Drosophila* seminal fluid composition may in fact be very different from the norm. Are our biases and tendency to use model systems preventing us from making other such discoveries, some of which might alter our basic understanding of sexual selection?

In this review, we examine the ways in which a few well-studied species have dominated the sexual selection literature, and the benefits as well as unforeseen costs of such an emphasis. First, we trace the history of two key model insect species used in sexual selection studies. Then, we survey the literature, assessing the use of model systems in studies on sexual selection and sexual conflict. Finally, we advocate a more deliberate approach to the choice of study organisms, with a diversity of models from which to derive theory.

Sperm competition: competitive process between the sperm of different males inside the reproductive tract of a female

Taxonomic bias: a tendency to overuse certain taxa in research because of availability, attractiveness, or other reasons extraneous to the scientific goal

HISTORY: *DROSOPHILA* AS THE ARCHETYPE INSECT

In his compelling book *Lords of the Fly: Drosophila Genetics and the Experimental Life*, Robert Kohler (41) suggests that well-entrenched experimental organisms such as *Drosophila* have themselves become a part of technology. Like laboratory rats or mice, the flies have been designed for a particular use and thus are more than simply representative organisms—they are tools. *Drosophila* flies were initially brought into the laboratory for use in the pioneering genetic studies of the early twentieth century, although Kohler suggests that the choice of the flies was one of convenience rather than scientific judgment: *Drosophila* "was brought indoors because its habits and seasonal cycle were well-suited to the needs and seasons of academic life" (41, p. 20). Several biologists, most famously Thomas Hunt Morgan (41), began to use *Drosophila* for cytology and studies on evolution in the early 1900s and found that the flies lent themselves to use in both the research laboratory and the classroom, thriving despite frequent mistreatment and neglect by student research assistants. A fly culture could follow an academic schedule, going relatively dormant during holidays and being renewed when classes resumed. *Drosophila* flies were also cheap and easy to obtain, and because they were viewed as pests, "they entered the laboratory through the back door, as a kind of poor relation to established domesticated creatures" (41, p. 29).

Interestingly, at one point crickets were considered as an alternative to *Drosophila*, with the entomologist and geneticist Frank Lutz urging their use to his colleagues at Cold Spring Harbor (41). At least some of the scientists at the time expressed a preference for organisms that could more easily be studied both in the laboratory and the field. Although he experimented with amphibians, fish, and mollusks, Morgan (41) soon established a burgeoning research program at Columbia University using *Drosophila*. He was interested mainly in mutations, as part of a focus on speciation and its mechanisms, and Morgan, Lutz, and their coworkers (41) developed experimental designs both to breed flies with mutations such as curled-wing or dwarf and to capitalize on those mutations once they occurred. The flies became, in Kohler's words, "a breeder reactor" (41), producing thousands of spontaneous mutants that were used to understand the mechanisms of inheritance and development, as well as to construct the first genetic maps of chromosomes. The stocks could be exchanged among scientists relatively easily, further facilitating research across laboratories.

And in those formative years, *Drosophila* was virtually synonymous with *D. melanogaster*. Although a few of the early evolutionary biologists explored other species, including *D. pseudoobscura* and *D. simulans*, *D. melanogaster* reigned supreme. Again, this concentration on a single model species arose partly out of convenience—*D. melanogaster* tolerates a wide variety of environmental conditions and feeds on easy-to-obtain nutrients—but also because it had already become established as the standard, creating a kind of self-fulfilling process.

By the middle of the twentieth century, the iron grip of *D. melanogaster* had eased somewhat, with eminent evolutionary geneticist Theodosius Dobzhansky pioneering the use of *D. pseudoobscura* in his studies on geographic variation in chromosomes and hybrid sterility (19, 20). This work also brought the study of fruit flies back into the field and paved the way for later work on other *Drosophila* species. Though some of these, including *D. bifurca* and *D. simulans*, became subjects in sexual selection research, the entire *Drosophila* machinery was developed for use in genetics. If we were starting out from first principles, and asking for an ideal model insect to use for studies of behavior, or sexual selection, fruit flies would arguably not have been a first choice, and perhaps not even in the running. The small size that makes them good subjects for genetic manipulation also makes the flies difficult to observe, and their behaviors are often subtle. Flies also lack the conspicuous secondary sexual characteristics of many other insect species.

Scatophaga stercoraria   *Drosophila melanogaster*

Figure 1

(*a*) A female yellow dung fly, *Scatophaga stercoraria*, deposits her eggs into the dung while guarded by her mate. The yellow dung fly has become a model species for research on both pre- and postcopulatory sexual selection (photo by David Evans, reproduced from Wikimedia Commons under the Creative Commons Attribution-Share Alike 2.0 Generic license). (*b*) A male fruit fly, *Drosophila melanogaster*. This fly is probably the most widely utilized model system in biology. It was Bateman's (7) model for his early exploration of sexual selection, and the discovery of sexually antagonistic coevolution (65) generated a surge in research on sexual conflict (photo by André Karwath, reproduced from Wikimedia Commons under the Creative Commons Attribution-Share Alike 2.5 Generic license).

SEXUAL SELECTION, SPERM COMPETITION, AND THE YELLOW DUNG FLY, *SCATOPHAGA STERCORARIA*

As a graduate student in the mid-1960s, Geoff Parker (59) set himself the task of showing how the evolution of male mating behavior could be explained by sexual selection acting on individual fitness, at a time not only when evolutionary thinking was dominated by group selection, but the concept of sexual selection had been largely abandoned (69). To achieve his goal, Parker studied the behavior and ecology of the yellow dung fly, *Scatophaga stercoraria*, not because it was then a model system but because it exhibited many of the characteristics he sought to explain (**Figure 1***a*). As its name suggests, the life history of this fly revolves around animal droppings, which provide a source of both larval and adult nutrition (52–55). Females are attracted to fresh droppings, where they deposit their eggs. They arrive downwind of the droppings, alighting on the grass upwind and walking back to the dung surface to lay their eggs. Males, often in considerable numbers, search the dung surface and the surrounding grass for arriving females. There is no courtship; the male simply seizes the female and copulates with her for an average of 35 min. The male then remains mounted on the female for a further 16 min while she lays her eggs in the dung, and then he abandons her in search of a new female. Parker recognized that many aspects of the mating behavior of this fly were overtly male driven, thereby making *S. stercoraria* a good model for analyzing sexual selection acting on male behavior.

Parker reasoned that sexual selection should favor any behavior that maximized fitness gain over a male's life span. Under the assumption that time is equivalent to eggs fertilized, he asked how competition for access to females might influence male searching behavior, why copulation takes so long, and why males remain with females after copulation is over (52–55). From his meticulous observations of the arrival of males and females and their rates of encounter, Parker showed that the distribution of search times at the dropping yielded equivalent fitness returns in

terms of eggs gained per minute. He also showed that the number of searching males tracked the number of arriving females, such that more males searched on the upwind side of the dropping, where the arrival rate of females was highest (53). Later, by including variation in competitive abilities among individuals, he showed how larger males should monopolize the locations where the input of females was greatest, leading to a nonrandom distribution of phenotypes on and around the dropping (49, 63, 67). These findings from the yellow dung fly contributed greatly to the development of the general concept of ideal free distribution and provided firm evidence of the importance of sexual selection in the evolution of male mate-searching behavior (57).

Parker (54) observed that mate-searching males frequently encounter ovipositing pairs. The mounted male's immediate response is to push the female into the dung surface with his forelegs while raising the midlegs to fend off the mate-searching male. Should the searching male gain contact with the female, intense struggles ensue during which the searching male attempts to take over the female. If successful, the new male copulates with the female before allowing her to continue ovipositing. Larger males are generally more successful in takeover attempts (66). Parker's (56) detailed observations of dung fly struggles led him to consider contest theory more generally, the importance of resource holding potential, and other asymmetries that determined fight outcome, and marked the beginnings of his contributions, along with those of John Maynard Smith (47), to the development of evolutionarily stable strategy theory, which has been so influential in behavioral and evolutionary ecology.

The finding that males would take over and mate with ovipositing females suggested that these females must have considerable reproductive value, even though they have already mated. Parker (52) used the sterile-male technique, then popular for the control of insect pests, to quantify male fitness gain when copulating with already-mated females. Thus, he mated a female with two males, one of which had been rendered sterile, and assigned paternity to each male on the basis of the proportion of eggs that hatched. He found that male fitness returns increased with diminishing returns during copulation and that the last male to mate sired 80% of the female's clutch (52). Postcopulatory mate guarding by males made immediate sense in light of sperm displacement; males that remained with and defended their mates during oviposition would achieve greater fitness returns than males that immediately abandoned their mates after copulation because of the high probability that these females would be discovered and mated by other searching males (55). Parker & Stuart (62) reasoned that a male should copulate until the fitness returns with his current mate fall below that which could be obtained from copulating with a new female, given the costs associated with searching for a new female. Based on his empirical estimation that finding a new female would take an average of 156 min, the predicted optimal copula duration was close to the copulation duration found in natural populations of these flies (62). Using dung flies as a model system, Parker thus derived, coincident with Charnov (14), the influential and generally applicable marginal value theorem for resource exploitation.

From the insights gained with the yellow dung fly system, Parker (51) collected data from the literature on the incidence of multiple mating by female insects and the patterns of paternity following multiple matings, concluding that sperm displacement was a common phenomenon, as were adaptations for its avoidance, in the form of mating plugs, prolonged copulations, mate guarding, and the avoidance of takeovers. In so doing, he used the insects to show how sexual selection via male competition continues after copulation in the form of sperm competition. Evolutionary biologists were quick to recognize that sperm competition was a pervasive force, driving the evolution of reproductive behavior, physiology, and morphology across animal taxa (77). Although Parker was explicit in his statement that females cannot be regarded as inert environments in and around which adaptations to sperm competition evolve, the study of postcopulatory sexual selection was focused for many years on male adaptation. Could yellow dung

flies have played a part in deflecting attention away from the study of female adaptations, given the overt male competition that this model system presents? Many researchers suggested that female influences could be important (68, 75). Regardless, it was not until the mid-1990s that the importance of cryptic female choice—the role females play in determining paternity—became widely recognized (21).

Given the importance of the yellow dung fly as a model system in sexual selection research, it is reasonable to suggest that it could tell us much about cryptic female choice. Females actively transfer sperm from the bursa copulatrix, where they are delivered by the male, into the spermathecae, where they are housed before being used for fertilization (40, 72). Accounting for female effects on sperm transport and storage greatly increases the accuracy in predicted optimal copulation duration (61, 72). But could females selectively store and use sperm from preferred males? The fact that females have multiple sperm storage organs suggested that they might be able to store sperm from different males separately, allowing them to choose among potential sires (37, 85, 86). After much effort, however, and some remarkable advances in our abilities to identify sperm from different males in different spermathecae using molecular techniques, there is no evidence to suggest that female dung flies exercise cryptic female choice (10, 16, 17).

Does this mean that cryptic female choice is not generally important? The answer to that question is a definite no. Rather, yellow dung flies are simply not the best model system with which to seek evidence for it. Because males displace 80% of the sperm stored by females from previous matings (69, 72), the opportunities for females to choose sperm are greatly reduced. A more appropriate model system with which to study cryptic female choice would be a species in which sperm displacement by males does not occur, in which females have access to sperm from multiple males, and in which there is a subsequently large variance in paternity (69, 73). Indeed, in another model system utilized in sexual selection research, gryllid crickets, females bias the storage and utilization of sperm on the basis of a variety of male traits, including relatedness and attractiveness (12, 35, 70, 82).

SEXUAL CONFLICT AND THE FRUIT FLY, *DROSOPHILA MELANOGASTER*

Parker's observations of dung fly struggles at their oviposition sites led him to the conclusion that male adaptations to sperm competition may not be in the best interests of the female. Takeover attempts can be lengthy and the female can be seriously harmed by struggling males or even drowned in the dung (58). Thus, stimulated by the notion of sexual conflict between the evolutionary interests of males and females, Parker (58) developed a series of theoretical models in which he revealed the evolutionary potential of sexual conflict for the evolution of anisogamy through to the evolution of mating decisions, identifying circumstances in which sexual conflict can generate evolutionary chases or antagonistic coevolution between male and female reproductive traits. However, this important conceptual advance went unnoticed for 15 years, as evidenced by the absence of citations. The paper was a purely theoretical contribution, with no data to demonstrate sexual conflict in action. Alexander & Borgia (1) also suggested that, for insects in general, behavior advantageous to males is likely in conflict with the best interests of the female. But only when sexual conflict was demonstrated in the model system *D. melanogaster* did researchers pay attention and recognize sexual conflict as an important force in evolution (65).

The reproductive behavior of *D. melanogaster* is very different from that of *S. stercoraria* (**Figure 1b**). Males search for females on and around decaying fruit, to which they are attracted to lay their eggs. On encountering a female, the male begins courting, delivering a series of

Cryptic female choice: female-controlled biased paternity that occurs after copulation

Anisogamy: the occurrence of different-sized gametes

complex sexual stimuli in olfactory, auditory, tactile, and visual modalities (18, 26). Females exert strong mating preferences that impose sexual selection on males (90). Copulation lasts for approximately 20 min. As for yellow dung flies, the last male fruit fly to copulate gains the majority of fertilizations (33). However, unlike dung flies, copula duration has no relationship with paternity, although it does influence whether the female remates (32). Copulations exceeding 8 min are sufficient to switch off female receptivity to further mating, negating any necessity for males to physically guard their females after mating (32, 33). Research with *D. melanogaster* has revealed that males transfer a cocktail of seminal fluid proteins that serve to mobilize and displace sperm from the female sperm storage organ, the seminal receptacle (36, 46). Moreover, the compound *sex peptide* is responsible for the loss of sexual receptivity of females following mating and for an increased rate of offspring production (91). Whereas *sex peptide* benefits male fitness through its effects on the avoidance of sperm competition from rival males and the elevated rate of reproduction by females (29), it is costly for females, reducing their life span (13, 88).

The negative consequences of *sex peptide* for female fitness make *D. melanogaster* an excellent model system for the study of sexual conflict. Thus, by experimentally preventing females from coevolving with males, Rice (65) documented a rapid evolution among males to the static female phenotype. By preventing females from contributing to the gene pool as selection on males continued, Rice (65) isolated the effects of such selection. After numerous generations in the laboratory, male fitness was enhanced, whereas female mortality was increased, by increased toxicity of seminal fluid. This clever experiment generated a flood of studies on sexual conflict. In *D. melanogaster* these studies are largely supportive of the idea that conflicts of interest between the sexes culminate in harm to the female (see below). Thus, reproductive proteins from the female reproductive tract have been found that interact with those of seminal fluid (92), and *Drosophila* seminal fluid proteins have undergone rapid and divergent evolution characteristic of the evolutionary chases anticipated by Parker (58).

The seminal fluid of *Drosophila* contains more than 100 different proteins, many of which bear the signature of strong positive selection (28, 34). The sexual selection literature often claims that it is well known that mating or seminal fluids are generally bad for females, supported by citations to studies on *Drosophila* (for numerous examples, see the references provided in the data set of the **Supplemental Material**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). But can we generalize across species on the basis of this single model system? We argue that we cannot. All insects do not behave the same way as *Drosophila*; the occurrence of mating at the same site as oviposition constrains female ability to both choose and reject mates, which might favor male benefits in such cases. In many other species, however, including many orthopterans and coleopterans, males signal from sedentary sites and females approach males for mating in situations removed from oviposition. Under such circumstances, males do not have the same opportunities to control female behavior.

In contrast to the findings in *D. melanogaster*, a wealth of literature exists on the fitness benefits for females associated with male seminal fluids in insects (summarized in 69). Furthermore, multiple mating by females is frequently found to increase female fitness, rather than to reduce it (5, 76). In some species of crickets (30, 31), beetles (23, 24) and butterflies (48, 89), seminal fluid products can enhance female fecundity and/or survival through their nutritive and/or hydration effects (83). Moreover, the promotion of sperm competition by females can generate significant genetic benefits via good-sperm and sexy-sperm processes (25, 71). Even in the closely related *D. simulans*, multiple mating by females has been shown to increase rather than decrease female fitness (81).

In this regard, it is worth returning to Parker's (58) original models. He found that evolutionarily stable resolutions to sexual conflict could be achieved in which either sex wins, depending

on starting conditions and selection intensities, and evolutionary chases are avoided. Empirical evidence from crickets (31) shows that although seminal fluids may reduce life span, the benefits derived from them can outweigh these costs, eliminating the evolutionary conflict over mating frequency. Finally, proteomic and genomic studies on the seminal fluid proteins of other insect species are beginning to appear. In some species of *Heliconius* butterflies 51 seminal fluid proteins have been identified (84), in several species of field and ground crickets just 30 have been found (3, 74), and in *Tribolium castaneum* beetles the number of proteins in the seminal fluid is just 14 (79). The simpler protein composition of seminal fluid in these taxa relative to that of *Drosophila* suggests that the various groups may not be subject to the same levels of sexual conflict (74). We believe that an increased taxonomic breadth in the study of insect seminal fluid biochemistry will reveal that the generalizations concerning seminal fluid toxicity—and sexual conflict itself—that are drawn from the *Drosophila* model system are unfounded.

QUANTIFICATION OF MODEL SYSTEM USE IN SEXUAL SELECTION AND SEXUAL CONFLICT RESEARCH

A Literature Survey

To obtain an overview of the use of model systems in sexual selection and sexual conflict research, we conducted a literature survey using Web of Science (Thomson Reuters). The protocol that we employed to investigate taxonomic affinity did not rely on using keywords for subject organisms because we found in preliminary trials that these keywords themselves may be a source of bias. Thus, we inspected the studies individually, which meant that sample size was sacrificed for the sake of accuracy. Full details about the methodology followed in our survey can be found in the section Literature Survey. Full Methods of the **Supplemental Material**. Briefly, the search string that we used was "sexual selection OR sexual conflict" in the Topic, and refined by source title (14 leading journals in four disciplines: Evolutionary Biology, Genetics and Heredity, Biology and Multidisciplinary Sciences, and Behavior). To allow the inspection of temporal trends, our search focused on three periods: publication years 1989–1990, years 1999–2000, and years 2009–2010.

The search returned 1,565 studies. We screened each of these studies to determine (*a*) whether it addressed sexual selection directly; (*b*) whether it was strictly empirical (see Literature Survey. Full Methods of the **Supplemental Material** for details); (*c*) whether the study dealt explicitly (i.e., acknowledged by the authors) with any aspect of sexual conflict or sexually antagonistic selection; (*d*) whether the study provided support for sexual conflict, that is, for the existence of traits that increase the reproductive success of one sex at a cost to members of the other sex (see Literature Survey. Full Methods of the **Supplemental Material** for further details); and (*d*) the organism(s) used in the study. After excluding those studies not dealing directly with sexual selection or that did not meet the requirement of empirical study, our sample consisted of 1,029 empirical articles on sexual selection. Of these, 24 articles were ambiguous with regard to whether they dealt with sexual conflict, whereas 152 empirical studies on sexual selection explicitly addressed aspects related to sexual conflict. The data set can be found in the section Literature Survey. Full Methods of the **Supplemental Material**.

Taxonomic Bias in Sexual Selection Research

Sexual selection research has become increasingly popular over the past three decades (**Supplemental Figure 1a,b**). Similarly, sexual conflict publications have increased in numbers and relative frequency, particularly during the late 1990s (see **Supplemental Figure 1a,b**).
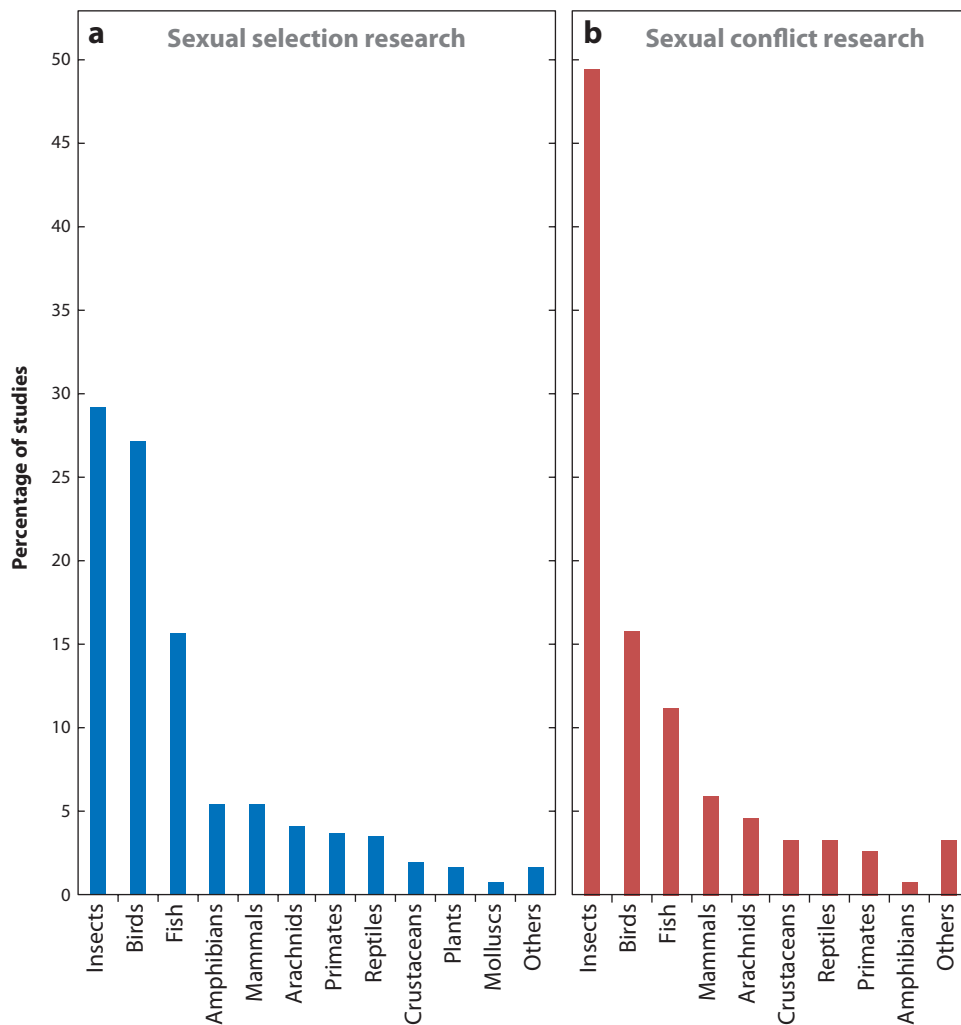
Figure 2

Distribution of model systems in (*a*) sexual selection research (*n* = 1,029 empirical articles on sexual selection) and (*b*) sexual conflict research (*n* = 152 empirical articles on sexual conflict).

Sexual selection studies focus predominantly on insects (29%) and birds (27%), followed by fish (16%) and to a lesser extent by other groups such as amphibians, primates, nonprimate mammals, arachnids, and reptiles (**Figure 2***a*). Temporal trends across the past three decades show a steady increase in the diversity of higher-order taxa studied, as well as a higher proportional use of insects and fish (**Supplemental Figure 2**).

Sexual selection research is diverse overall. Approximately 580 different species distributed in more than 425 genera were used in our sample of 1,029 empirical articles on sexual selection. The number of taxa used has increased over the past three decades (**Supplemental Figure 3**). However, despite this profusion of model organisms, the most frequently used 25 species and most frequently used 25 genera account for nearly 30% and 40% of the studies, respectively (**Supplemental Table 1**). Notably, studies on *Drosophila* dominate generally, composing over 8%

Supplemental Material

Table 1 Most common arthropod model systems (species and genera) used in sexual selection research[a]

Most common species	Percentage of articles[b]	Most common genera	Percentage of articles[b]
Drosophila melanogaster	10.5	Drosophila	23.1
Callosobruchus maculatus	3.0	Gryllus	3.9
Teleogryllus oceanicus	2.5	Teleogryllus	3.6
Drosophila pseudoobscura	1.9	Callosobruchus	3.3
Drosophila simulans	1.9	Schizocosa	2.5
Achroia grisella	1.7	Onthophagus	2.2
Drosophila serrata	1.7	Pieris	2.2
Gryllus integer	1.7	Calopteryx	1.9
Aquarius remigis	1.4	Achroia	1.7
Gryllodes sigillatus	1.4	Aquarius	1.7
Onthophagus taurus	1.4	Teleopsis	1.7
Pararge aegeria	1.4	Gryllodes	1.4
Teleopsis dalmanni	1.4	Heliconius	1.4
Drosophila mojavensis	1.1	Laupala	1.4
Forficula auricularia	1.1	Pararge	1.4
Pieris napi	1.1	Argiope	1.1
Scathophaga stercoraria	1.1	Forficula	1.1
Sepsis cynipsea	1.1	Scathophaga	1.1
Teleogryllus commodus	1.1	Sepsis	1.1
Acheta domesticus	0.8	Acheta	0.8
Calopteryx splendens	0.8	Cimex	0.8
Cimex lectularius	0.8	Coelopa	0.8
Drosophila bunnanda	0.8	Gerris	0.8
Drosophila montana	0.8	Gnatocerus	0.8
Gnatocerus cornutus	0.8	Hetaerina	0.8
Heliconius spp.	0.8	Hygrolycosa	0.8
Hygrolycosa rubrofasciata	0.8	Ischnura	0.8
Kawanaphila nartee	0.8	Kawanaphila	0.8
Latrodectus hasselti	0.8	Latrodectus	0.8
Onthophagus sagittarius	0.8	Nasonia	0.8
Schizocosa ocreata	0.8	Panorpa	0.8
Tribolium castaneum	0.8	Tribolium	0.8
Utetheisa ornatrix	0.8	Uca	0.8
		Utetheisa	0.8

[a]As estimated in our literature survey.

[b]Percentage of articles using each taxon ($n = 363$ empirical sexual selection studies using arthropods).

of all studies. Taxonomic bias is also patent in studies on arthropods ($n = 364$ studies in our survey): Two hundred fifteen different species in 153 genera were the subject of research, but the most frequent 25 species and most frequent 25 genera account for more 40% and 60% of the studies, respectively (**Table 1**). In this case, the relative frequency of studies on *Drosophila* is approximately 23%.

Table 2 Most common arthropod model systems (species and genera) used in sexual conflict research[a]

Most common species	Percentage of articles[b]	Most common genera	Percentage of articles[b]
Drosophila melanogaster	14.9	*Drosophila*	27.6
Callosobruchus maculatus	9.2	*Callosobruchus*	10.3
Aquarius remigis	4.6	*Aquarius*	5.7
Drosophila pseudoobscura	4.6	*Argiope*	3.4
Gryllodes sigillatus	3.4	*Gryllodes*	3.4
Cimex lectularius	2.3	*Gryllus*	3.4
Ischnura senegalensis	2.3	*Ischnura*	3.4
Nehalennia irene	2.3	*Cimex*	2.3
Pieris napi	2.3	*Coelopa*	2.3
		Nehalennia	2.3
		Pieris	2.3
		Teleogryllus	2.3
		Thermosphaeroma	2.3

[a]As estimated in our literature survey.
[b]Percentage of articles using each taxon ($n = 87$ empirical articles on arthropods dealing explicitly with sexual conflict).

Taxonomic Bias in Sexual Conflict Research

The analysis of taxonomic use in sexual conflict research shows similar patterns, but the existence of taxonomic bias is even more apparent. In this case, insects are clearly the preferred model system, with a frequency of 50%, followed by birds and fish (**Figure 2b**). The relative frequency of insect use has increased markedly during the past decade, and the field has become more taxonomically diverse over time in the number of species used (**Supplemental Figure 3b**) or higher-order taxa (**Supplemental Figure 4**).

Overall, 121 species in 102 genera were the subject organisms in the 152 empirical sexual conflict studies in our sample. Nonetheless, the most frequent five species and genera are represented in over 21% and 29% of the studies, respectively (**Supplemental Table 2**), with *Drosophila* at the top followed by *Callosobruchus* beetles and *Aquarius* water striders. One-fourth of current sexual conflict research is conducted on these three model organisms alone (see **Supplemental Figure 5** for temporal trends and the shift point observed one decade ago). The bias in the use of these three models is of course more severe when analyzing sexual conflict studies on arthropods ($n = 87$ studies; 63 species distributed in 45 genera): The relative frequency of studies on *Drosophila*, *Callosobruchus*, and *Aquarius* is 28%, 10%, and 6%, respectively (**Table 2**).

Arthropods in general, and insects in particular, offer a bewildering array of diversity in almost every aspect of biology, including life histories and mating systems. This implies that more choices exist for models among insects than in other groups (e.g., birds), which further underscores the paucity of insect model systems.

Truth Lies in Diversity

Our data illustrate an interesting pattern that encapsulates an important message; the rate of support for sexual conflict shows a declining trend over time, and this decrease in support is associated with an increase in the diversity of model systems used in sexual conflict research

Supplemental Material
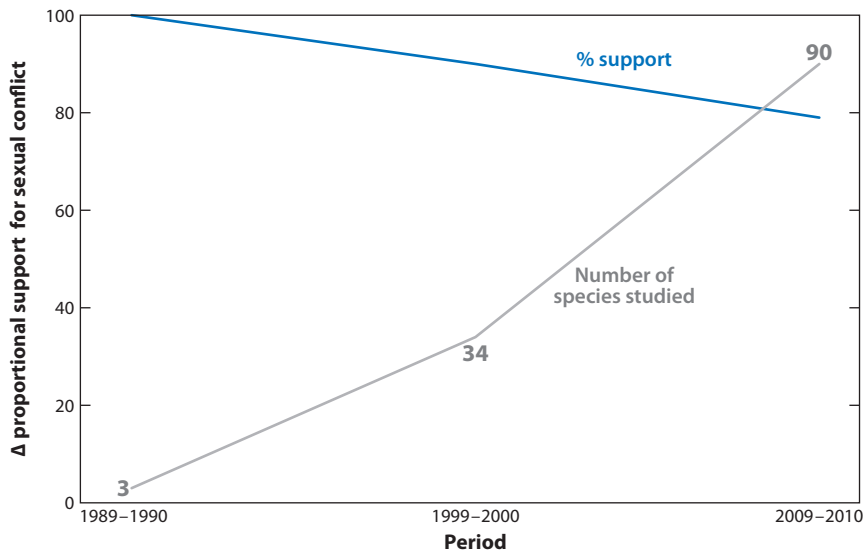
Figure 3

Change in proportional support for sexual conflict across the three periods (sample size: 3, 29, and 100 studies, respectively) and diversity of model systems (number of different species) per period in studies on sexual conflict. Numbers above the gray line indicate the number of different species in each period. Sexual conflict was not explicitly supported or unsupported in 20 studies (see the data set provided in the **Supplemental Material**); thus, those studies were excluded from these calculations.

(**Figure 3**). The survey indicates that taxonomic bias is rampant in sexual selection research despite sexual selection research using a wide array of taxa as study subjects. We believe that increasing the diversity of subject organisms will advance the field. Several species, typically *D. melanogaster*, *Callosobruchus maculatus*, *Aquarius remigis*, *D. pseudoobscura*, and a few others (see first rows of **Table 2**), tend to be frequently studied in sexual conflict investigations. These species are those that exhibit more or less intense sexual conflict. The questions therefore are, Can we generalize from just a few species? Can we answer whether sexual conflict prevails in sexual interactions across taxa from focusing on just a few species? Broadening the diversity of model systems used in sexual conflict (and sexual selection) research, as well as avoiding publication bias and acknowledging confirmation bias, is overdue.

FUTURE ROLE OF MODEL INSECT SYSTEMS

Several authors predict that the classic biological model animals (*M. musculus*, *D. melanogaster*, *Caenorhabditis elegans*) will not only continue their dominance in biological research, but will become even more dominant (27, 78). For some fields in biology (genetics or developmental biology) this may be justified, as the focus of analysis is to identify mechanisms. The detailed mechanistic knowledge allows technological breakthroughs that can then spread through the research community (27).

Encouragement to embrace the classic model organisms in behavioral and evolutionary research, however, is contentious (43, 50). On the one hand, classic model organisms, such as *Drosophila*, can provide powerful mechanistic explanations for broad evolutionary ideas. For example, the interaction of sperm from two males within the female duct has recently been visualized in *D. melanogaster* (46) but remains elusive in most other animals (38). On the other hand, as noted

above, evolutionary and behavioral research is concerned with quantifying inter- and intraspecific variation. This clearly motivates the establishment of new model systems to generate a broader understanding of the natural world and its processes, a view that is also held in some reductionist fields (27, 45). More fundamentally, however, is whether theory stands up to rigorous testing across multiple taxa, necessitating the establishment of a broader set of study organisms.

Choice of Future Model Organisms in Sexual Selection

The informative nature of many established model organisms has often not been evident in the wild and has been discovered only after intensive research (4). Traits of suitable model systems for research in sexual selection include small size and short generation time, suitability for study in the wild, well-described phylogeny, and tractability for experiments (2). Moreover, the previously prohibitive costs of detailed genetic and genomic information are no longer an impediment to establishing a usable new model system (45). Many insect species satisfy these criteria for model species. Future models should be chosen on the basis of the question at hand. Parker chose dung flies to study male competition because they exhibited the behaviors he sought to explain. Subject species should not be chosen simply because they are already model systems.

CONCLUSIONS

Despite the undeniable progress some fields have made by focusing exclusively on a limited set of model species, we argue that now is the time to strongly push the diversification of study systems, and our literature review is already indicating this trend. This is particularly important in evolutionary biology, with its inherent interest in variation. All species have their idiosyncrasies and classic model species are no exception. The verification of theory or broad trends will come from embracing, not reducing, diversity. We eagerly anticipate the discovery and description of novel systems that will challenge our thinking.

SUMMARY POINTS

1. Although model systems can be extremely useful in entomology, they can also unnecessarily canalize thinking about a topic, so that the system becomes not merely representative of a set of biological principles, but emblematic so that variation is less recognized as important.

2. This drawback of model systems is particularly problematic in ecological and evolutionary studies, where variability among individuals and across taxa is often critical to developing meaningful theories.

3. The classic insect model system, *D. melanogaster*, was chosen for a number of somewhat idiosyncratic reasons, including its compatibility with an academic calendar, and it was selected primarily for use as a genetic model. In other fields of biology, however, such as sexual selection, the behavior of *Drosophila* is not representative of the majority of insects.

4. Different species may be good models for some concepts but not others. For example, yellow dung flies were key in the development of theory about sexual conflict and sperm competition but are less well-suited to the examination of the potential for cryptic female choice.

5. A literature survey reveals that taxonomic bias is rampant in sexual selection research on insects and is particularly severe in sexual conflict research, with approximately 25% of studies conducted on *Drosophila*, *Callosobruchus*, and *Aquarius*. Studies using these systems tended to find support for the idea that sexual interactions result in harm to the female.

6. The rate of support for the notion of sexual conflict as necessarily showing harm to females shows a declining trend over time, and this decrease in support is associated with an increase in the diversity of model systems used in sexual conflict research.

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7. Examines the limits on mating frequency for males and females, demonstrating that male reproductive success continues to climb with successive matings, whereas females do not gain by having multiple mates.

9. Bemoans the tendency for his colleagues to focus on only a few species, particularly laboratory rodents, in their research.

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