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# Model Systems in Behavioral Ecology

Integrating  
Conceptual,  
Theoretical, and  
Empirical Approaches

Edited by Lee Alan  
Dugatkin

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## Genetic Consequences of Sexual Selection in Stalk-Eyed Flies

Gerald S. Wilkinson

My interest in using stalk-eyed flies, family Diopsidae, to study the genetic consequences of sexual selection developed while I was a postdoctoral fellow at the University of Edinburgh in 1984. I began postdoctoral work on *Drosophila melanogaster* at the University of Sussex in the laboratory of Brian Charlesworth, an eminent evolutionary geneticist. Partway through my twelve-month fellowship, he moved to the University of Chicago so I asked Linda Partridge, who had recently been conducting studies of life history evolution with *Drosophila*, if I could spend the remainder of my fellowship time in her lab in Edinburgh. She graciously agreed.

I went to England without any prior lab experience studying flies. In fact, I began graduate studies as a committed field biologist. After taking a two-month course in tropical ecology sponsored by the Organization for Tropical Studies in 1978, I initiated a five-year project on the social behavior of the common vampire bat, *Desmodus rotundus*. During this time I lived in Costa Rica for three years and gathered evidence that female vampire bats reciprocally exchange blood when a group member has failed to feed successfully during the night (Wilkinson 1984). Although females are sometimes related to the recipient of these blood meals (Wilkinson 1985), the primary benefit of reciprocal food sharing lies in increasing individual survivorship of group mates (Wilkinson 1988). While I enjoyed studying vampire bats, I realized that inferring causation can be difficult when the results consist of correlations from observational field studies. I also realized that much of the relevant theory underlying the evolution of social behavior is based on genetic models, the results of which are often taken for granted without ever questioning the underlying assumptions. I decided, therefore, to pursue postdoctoral work that would give me experience designing and conducting experiments aimed at testing assumptions or predictions of genetic models. I reasoned that together with my thesis work on vampire bats, these experiences would allow me to pursue and advise a wide range of field and laboratory studies in behavioral ecology when I eventually obtained a faculty position.

The fly experiments I conducted in Scotland were motivated by two theoretical papers that had recently been published on sexual selection and the evolution of female choice. In 1981 Russell Lande had published a quantitative genetic model (Lande 1981) which made the startling prediction that a

line of equilibrium is expected because sexual selection by female choice for a male ornament will eventually be opposed by natural selection against the trait. In the absence of direct selection on females, an infinite combination of selection pressures can result in equilibrium, hence the line. Under some genetic conditions, for example, when the genetic regression between the trait and preference is particularly high, the male trait and female preference will increase at geometric rates and produce what Fisher (1958) called "run-away" sexual selection. In 1982 Mark Kirkpatrick published qualitatively similar results using a two-locus, haploid genetic model that had first been explored by O'Donald (O'Donald 1962, 1980). These models substantiated Fisher's insights and not only motivated my work, but also inspired many other theoretical and empirical studies (see Andersson 1994 for review).

My experiments with *D. melanogaster* were designed to test the equilibrium assumption, that is, that some male traits are constantly under equal but opposing forces of natural and sexual selection. I reasoned that if you prevent flies from competing for or choosing their mates by pairing randomly chosen males with females, then sexual selection would be eliminated, but natural selection would still occur. Consequently, by comparing populations of flies that had either been allowed to mate in large cage populations or were pair-mated I could measure the intensity of natural selection in the absence of sexual selection. Because previous work had indicated that body size influenced mating success (Ewing 1961; Partridge & Farquar 1983), I measured the length of the thorax to determine if selection was occurring. In replicated experiments I found consistent evidence for sexual selection on thorax length in males (Wilkinson 1987). Large body size increases development time and exposes larvae longer to inhospitable media (Botella et al. 1985). Thus, natural selection apparently favors smaller bodied males while sexual selection favors larger bodied males. After observing matings and conducting female choice experiments I concluded that much of what I had observed was consistent with larger males outrunning smaller males for access to receptive females (Partridge et al. 1987), rather than females choosing to mate with larger males. I began, therefore, looking for an alternative system more appropriate for testing female choice models of sexual selection.

### Model System Discovery

Even though I had only been working with flies for less than a year, I was already convinced that an insect would be preferable for further study. Flies seemed particularly attractive because generation times are short and captive breeding is often simple and inexpensive. When I first saw a picture of a diopsid stalk-eyed fly (Burkhardt & de la Motte 1983), I immediately knew I had found the perfect system. In contrast to *Drosophila*, where few mor-

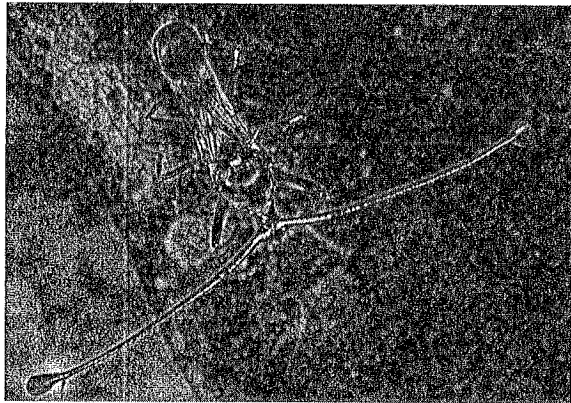


Figure 5.1. Male *Teleopsis belzebuth* from Brunei. Photograph by Mark Moffett.

phological characters exhibit sexual dimorphism, in many species of diopsids (Burkhardt & de la Motte 1985) males have dramatically longer eye stalks than females (Fig. 5.1). Furthermore, Dietrich Burkhardt at the University of Regensburg had been successful at breeding several species. One day at lunch in Edinburgh I mentioned my growing interest in diopsids to Arthur Ewing, a faculty member who studied courtship song in *Drosophila*. Arthur proceeded to describe stalk-eyed flies he had seen at a fishing camp on the side of Mount Kenya during a recent holiday. Within a month I had booked a cheap flight from London to Nairobi. The day after I arrived, just as he had described, I found stalk-eyed flies in abundance along several streams in the forests on Mount Kenya (Fig. 5.2). During two weeks at the site, I failed to observe any matings probably because it was the dry season and because I failed to go out and observe the flies at dawn. I did, however, manage to bring some back to Scotland and discover that they could be bred in the lab.

My fellowship ended in Scotland soon thereafter and I moved to the University of Colorado to begin a second postdoctoral fellowship. Even though I had received funding to study behavior genetics in mice, I hoped I could also begin developing methods for culturing stalk-eyed flies. Unfortunately, I was unable to obtain permission to import diopsids into Colorado. The species I had collected from Kenya fed on decaying plant material, but at least one diopsid species is a minor pest of maize (Tan 1967). The number one export crop in Colorado is corn, so the state entomologist decided it was not worth risking the importation of any diopsid. Therefore, I had to wait until I joined



Figure 5.2. Nocturnal aggregation of *Di- asemopsis collaris* from Thego National Forest, Kenya.

the faculty at the University of Maryland in 1987 before I could return to Africa and collect more flies to establish my own breeding colony.

After several more years of experimentation, a postdoctoral associate, Paul Reillo, and I developed methods for breeding flies consistently and in quantity. We also traveled to Southeast Asia and collected several species that had been studied by Burghardt and his associates. The Southeast Asian diopsids proved to be much easier to breed than any of the African species and in several cases exhibited dramatic differences in sexual dimorphism for eye span. I chose the most reliable breeder, *Cyrtodiopsis dalmanni*, to use in an artificial selection study designed to test several key assumptions of the sexual selection models. This decision turned out to be fortuitous, because these experiments led to unforeseen discoveries, as I describe below, that have fostered new theoretical work.

### Genetic Correlation between Trait and Preference?

A central prediction shared by all coevolutionary models of sexual selection by female choice, that is, Fisherian runaway (Kirkpatrick 1982; Lande 1981) and good genes (Iwasa et al. 1991; Pomiankowski 1988), is that a genetic correlation, if the model is based on quantitative traits, or linkage disequilibrium, if the model is based on single-locus traits, should develop between the male trait and the female preference. Most models of sexual selection by female choice assume that autosomal genes affect female mating behavior and are physically separate from autosomal genes influencing the male trait. A genetic correlation develops because of nonrandom mating and is neces-

sary for the evolution of the female preference when it is not under direct selection. Thus, finding evidence for a genetic correlation between a male trait and a female mating preference is a testable prediction of these models.

Genetic correlations can be estimated in two ways: family comparisons, or artificial selection. Family comparisons are used to estimate causal components of variance either from an analysis of variance among full or half-siblings, in which sire and dam are random effects, or a regression analysis of offspring on parents (Falconer 1981). For example, if a male trait correlates with his daughter's preference, a genetic correlation can be inferred. Family comparisons are attractive because they provide estimates in one generation and, therefore, may be less influenced by adaptation to a laboratory environment. However, considerable statistical error is associated with these estimates (Klein 1974). Consequently, unless the correlation is high, very large sample sizes (often two hundred or more families) are required to demonstrate that a correlation differs from zero. Because coevolutionary models of sexual selection could operate even when the genetic correlation between trait and preference is very small, I decided to use artificial selection rather than a family comparison. I also thought that selected lines might be useful for future studies because they would provide a replicable source of individuals that differ genetically for a sexually selected trait.

Before embarking on any artificial selection study several questions must be answered. What trait should be selected? How many animals should be bred in each line? How many replicate lines should be maintained? I used my burgeoning experience with stalk-eyed flies to answer each of these questions. Direct evidence for a genetic correlation would be obtained if female preferences changed as a consequence of selecting on a male trait or vice versa. Thus, either male eye span or female preference could be chosen for selection. At the time I began this study we had not found a reliable method for scoring female preferences. We attempted to replicate experiments (Burkhardt & de la Motte 1988) where model males were glued to strings and female preferences were scored as female approaches to models with surgically lengthened or shortened stalks. However, we were unable to obtain repeatable preferences using this method, so I decided to select for male eye span rather than female preference. Because eye span correlates phenotypically with body size (Burkhardt & de la Motte 1985), I was concerned that selecting only on eye span would simply create large or small flies. Therefore, I decided to select on the ratio of eye span to body length in males. By temporarily immobilizing flies with CO<sub>2</sub> under a microscope, we could quickly measure adult flies from digitized images with a computer program.

The time needed for measuring and the space available for breeding effectively dictated the total number of flies we could breed and select each generation. When we began this experiment I estimated we could process about 500 flies every 8 weeks. To find evidence for a correlation I needed to select

for both increased and decreased eye span. Replicate lines are essential to distinguish effects of selection from genetic drift, and control lines are needed to assess unexplained environmental variation shared each generation by all lines. Given these constraints, I opted to measure 50 males and choose 10 for breeding each generation in each of 6 lines. These males were mated to 25 randomly chosen females in 2 control lines, 2 lines selected for long relative eye span, and 2 lines selected for short relative eye span. Because I only exerted selection on males, net selection on autosomal genes was one-half that experienced by males, that is, 40 percent. Assuming a normal distribution of trait values, truncation selection of 40 percent corresponds to an overall selection intensity of 0.7 standard deviation units each generation (Falconer 1981). This intensity of net selection is about double what we measured in the field, as the covariance between the number of females roosting at night with a male and his relative eye span divided by the standard deviation in male relative eye span (Wilkinson & Reillo 1994).

I quickly discovered that selection on relative eye span in males was having the desired effect of changing eye span but not body length. Because eye span in females was also exhibiting change, I knew that a genetic correlation between the sexes existed for eye span. Under an assumption of equal heritabilities for eye span in each sex, I estimated the between-sex correlation for relative eye span to be  $0.39 \pm 0.07$  (Wilkinson 1993). Selecting on the ratio of eye span to body length also caused the slope of the phenotypic regression between eye span and body length to change (Wilkinson 1993). Thus, by selecting on the ratio of eye span to body length we had changed allometric relationships between eye span and body length in a way that mirrored the differences between species (Burkhardt & de la Motte 1985; Baker & Wilkinson, in press). These results demonstrated that allometric relationships can be molded by selection and do not act as constraints on evolutionary change, *contra* Gould (1989).

Although I was eager to know if morphological change in males was accompanied by behavioral change in females, I waited for 2 years (13 generations) before testing female mating preferences. By waiting I figured I would be more likely to detect change if the genetic correlation between trait and preference was small. For example, after 10 generations of selection with intensity of 0.66 (Wilkinson 1993), heritabilities of 0.35, and a genetic correlation of 0.1, a female preference should have changed by 0.5 standard deviation units.

To score female preference I put two males on opposite sides of a transparent perforated partition in a small cage. I used selected-line males that were matched for body length but differed in eye span by 15 percent. Several females were then introduced and allowed to explore the cage. Because the holes in the partition were greater in diameter than female eye span but smaller than male eye span, females could pass unimpeded to either side of the cage while males were restricted to one side. Initially, we scored female

preference as the proportion of five nights a female spent on the same side of a partition as a male (Wilkinson & Reillo 1994), because most matings in the wild occur in aggregations (Lorch et al. 1993). In subsequent experiments (Wilkinson et al. 1998a) we measured preference as the proportion of copulations by a female with each male over a ten-day period. The repeatability, which sets an upper limit to the heritability for a trait, of the preference was 0.4 and 0.3 for *C. whitei* and *C. dalmanni*, respectively, the two closely related sexually dimorphic species.

As predicted by coevolutionary models of sexual selection, we found evidence for a genetic correlation between a female's mating preference and male eye span (Wilkinson & Reillo 1994). Females from lines with decreased eye span preferred to mate with males that had shorter eye stalks while females from lines with increased eye span preferred to mate with males that had longer eye stalks. Contrary to prediction, however, females from lines with increased eye span did not differ in their preferences from outbred, unselected females. A possible explanation for this apparent contradiction is that we only provided a single choice to females, that is, a 15 percent difference between two males. Subsequent experiments, where we systematically varied the difference between two males, indicate that *C. dalmanni* and *C. whitei* females can detect a difference in eye span of 7 percent, and exhibit increasingly strong preferences as the eye span difference between males increases (Wilkinson et al. 1998a). Thus, perhaps we would have detected a difference between unselected and selected line females if we had offered them a series of males that differed progressively in eye span. Nevertheless, this result remains one of a handful of examples in which a genetic correlation between a female mating preference and a male trait has been documented (Bakker 1993; Houde 1994).

### Good Genes for Viability?

Distinguishing between the Fisher process and good genes models of sexual selection has proven difficult. Most studies that have claimed to have demonstrated one process over the other have focused on finding evidence for a correlation between a male ornament and offspring survival. Several recent studies on birds (Hasselquist et al. 1996; Møller 1994; Norris 1993; Petrie 1994; Sheldon et al. 1997) have found such a relationship. However, offspring survival is only one component of fitness, so even when a positive correlation is detected, the possibility remains that there are trade-offs which would cause other fitness components to covary negatively with male ornaments (Boake 1986). Nevertheless, my initial approach to this problem was to determine if the genes that influence eye span are linked to genes that influence offspring survival from egg to eclosion as an adult *C. dalmanni*.

I used the lines selected for long and short eye span after twenty genera-

tions of selection to test for differences in egg hatchability, development time, and pupal eclosion success. To minimize any confounding effects of inbreeding that might differ between lines, I crossed the replicate lines before quantifying these fitness components. I decided to cross flies from each line to flies from one of the control lines to test genes with known effects on eye span in similar genetic backgrounds. In retrospect, this crossing scheme had the undesirable effect of decreasing any potential difference between the lines. A better method for these experiments would have been to cross the replicates within each selection treatment. Nevertheless, this experiment produced significant and informative results. In addition, I scored survival of twenty adult flies from each selected line after seventeen generations of selection. I did not use line crosses for scoring adult survival because the time associated with such work was prohibitive. Flies routinely survive more than six months.

The fitness component analysis revealed that changing eye span influenced both development and survival (Fig. 5.3). No difference between the lines was found in the proportion of eggs that successfully developed into pupae ( $\chi^2 = 2.5$ , 2 df,  $P = 0.29$ ) after being transferred from agar in groups of 50 to 50 ml of food. On average, about 30 percent of eggs hatched in each treatment (Fig. 5.3a). In contrast, development time at 25°C differed significantly between lines ( $F_{1,625} = 71.4$ ,  $P < 0.0001$ ) as well as between males and females ( $F_{1,625} = 71.4$ ,  $P < 0.0001$ ). Post hoc tests revealed that flies carrying genes for long eye span took longer to develop than either control-line flies or flies carrying genes for short eye span (Fig. 5.3b). In most flies, rapid development is assumed to be under strong directional selection because larvae are usually more vulnerable than pupae or adults. In addition, pupal eclosion success differed between lines ( $\chi^2 = 32.7$ , 2 df,  $P < 0.0001$ ). Flies carrying genes for long eye span did not eclose as successfully as control-line flies or as flies carrying genes for short eye span (Fig. 5.3c). Finally, mean age of death differed between lines (repeated measures ANOVA,  $F_{1,58} = 4.02$ ,  $P = 0.023$ ). Short eye span—line flies did not survive as long as control-line flies or flies carrying genes for long eye span (Fig. 35.d). Thus, longer eye span increased larval mortality while shorter eye span increased adult mortality.

While these results obviously depend on captive rearing conditions, it seems likely that development rate and pupal eclosion success would exhibit similar, if not more extreme, differences in the wild since these measurements reflect developmental processes. We know that there are more than six thousand neurons that run the length of the eyestalks in these flies (Burkhardt & de la Motte 1983; Seitz & Burkhardt 1974) and that during the development of the eye-antenna imaginal disc the stalks are present before any neurons have begun to project from either the eye bulb into the brain or vice versa (Buschbeck & Hoy 1998). Consequently, it seems likely that increasing eye stalk length could create developmental problems that would

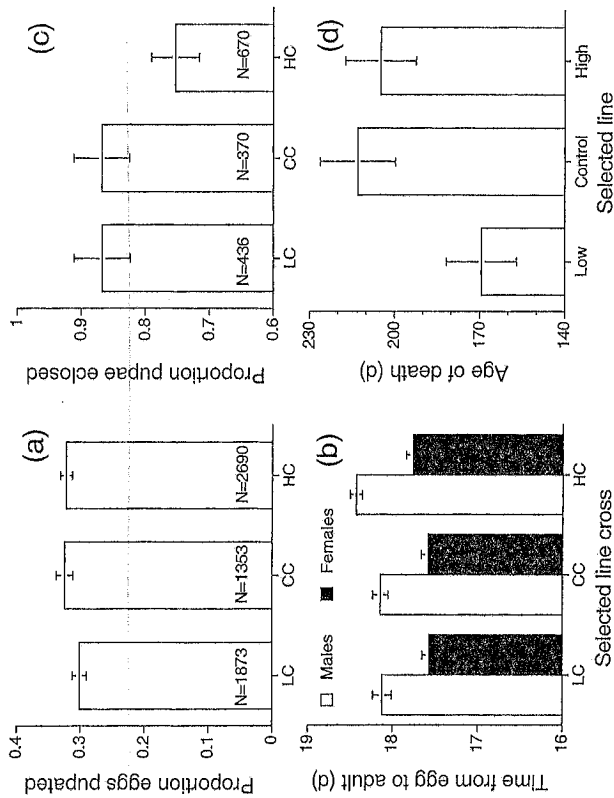


Figure 5.3. Effect of genes for increased or decreased eye span on fitness components in *Cyrtodiopsis dalmanni*: (a) egg eclosion and larval survival, (b) development time, (c) pupal eclosion success, and (d) adult survival. In a–c, flies from lines selected for decreased (L) or increased (H) eye span were mated to control line flies after twenty generations of selection. In d, selected line flies were used after seventeen generations of selection. See text for methods.

increase mortality during metamorphosis. Thus, in contrast to a conventional good genes process, increasing eye span does not appear to improve offspring viability, at least under laboratory conditions. Nevertheless, we discovered that a good genes process can operate by a mechanism quite different from anything previously imagined.

### Selfish Genes and Sexual Selection

As part of a series of experiments designed to determine the magnitude of change in genetic variation and covariation for morphological traits that have or have not been under sexual selection (Pomiankowski & Møller 1995; Rowe & Houle 1996), we conducted large-scale half-sib breeding studies of 6 species of stalk-eyed flies (Wilkinson & Taper 1999) and of the replicate lines selected for long and short eye span after 22 generations of selection. In these experiments one male was mated to 6 or more females. Our goal was to measure 2 male and 2 female offspring from each of 4 females mated to one male and then replicate this mating scheme to create 100 half-sib

families for each line and species. Such large samples are necessary to determine if genetic variation or covariation differs between populations (Shaw 1991). As we began this work I instructed my research assistant, Lili Crymes, to count the number of males and females produced by each female because I thought progeny sex ratios might provide information about differential mortality between the lines. To my surprise, Lili told me that she was collecting more males than females from the lines selected for long eye span and more females than males from the lines selected for short eye span. This observation, in combination with results that we were obtaining at the same time regarding sex chromosome meiotic drive (Presgraves et al. 1997), made me realize that we had inadvertently stumbled upon a novel mechanism for sexual selection: perhaps females choose males that alter their progeny sex ratio and thereby increase their production of grandchildren. Understanding how this mechanism might operate requires an understanding of meiotic drive.

Sex chromosome meiotic drive is used to describe cases where one of the sex chromosomes is transmitted to more than half of the gametes. The most common mechanism for such non-Mendelian inheritance involves differential development and survival of X-bearing sperm relative to Y-bearing sperm. Sex chromosome meiotic drive can lead to the production of all female progeny by male carriers in species with male heterogamety. X chromosome meiotic drive has now been documented in twenty-one different species of *Drosophila* (Jaenike 1996, 1999; Lyttle 1991) and has also been reported to occur in a number of other fly species, as well as in some mammals and fishes (Hurst et al. 1996). Previously reported cases in butterflies appear to be due to cytoplasmic agents that kill males (Jiggins et al. 1999). Y chromosome drive is much less common than X chromosome drive, perhaps because it can rapidly cause population extinction (Hamilton 1967), and has only been reported in some mosquitoes (Wood & Newton 1991). A driving X chromosome,  $X^d$ , is a selfish genetic element that can spread itself at the expense of genes on the Y chromosome and the autosomes. Autosomal genes do not benefit from the presence of  $X^d$  because half of the time they occur in Y-bearing sperm, which are destroyed. For this reason, genetic modifiers on autosomes, as well as on Y chromosomes, are favored by selection if they ameliorate or suppress the effects of drive. Because sex chromosome drive can cause population extinction if one sex is lost, either selection against  $X^d$ , genetic suppression, or both must occur to maintain sex chromosome meiotic drive in a population (Hamilton 1967).

Very soon after we first brought the two sexually dimorphic Southeast Asian species, *C. dalmanni* and *C. whitei*, into the lab we discovered that some males produced strongly female-biased sex ratios and that this sex ratio bias was caused by an X-linked factor. However, it took several more years of experiments to show that the mechanism of sex ratio change is caused by improper elongation of the heads of some sperm, and that other



genetic factors on the Y chromosome and on the autosomes act to suppress this X-linked drive (Presgraves et al. 1997). Evidence for Y-linked or autosomal suppression of X chromosome drive has been found in *D. mediopunctata* (Carvalho & Klaczko 1993; Carvalho & Klaczko 1994), *D. subobscura* (Hauschteck-Jungen 1990), *D. affinis* (Voelker 1972), *D. simulans* (Cazemajor et al. 1997), *D. paramelanica* (Stalker 1961), and *D. quinaria* (Jaenike 1999). In some of our crosses we even found sex ratios of males that were carrying  $X^d$  to exhibit male bias, that is, up to 75 percent of the progeny of such males were sons. This observation is unique among sex chromosome drive systems, but it potentially explains the sex ratio changes that we observed among the selected lines. Apparently, by increasing eye span we also increased the frequency of genetic modifiers that counter the effect of drive and cause the production of male-biased offspring (Wilkinson et al. 1998b).

These observations led us to propose that sex chromosome meiotic drive could provide a novel mechanism for maintaining genetic variation in fitness that can be exploited by choosy females (Wilkinson et al. 1998b). The basic idea is that sex chromosome meiotic drive will cause the population sex ratio to deviate from 1:1. If the drive polymorphism is maintained by selection (Curtisinger 1980), then the sex ratio will equilibrate and remain constant at some proportion of males below 50 percent. In the two sexually dimorphic *Cyrtodiopsis* species the proportion of males carrying the driving X chromosome in wild populations is 17 to 30 percent (Wilkinson et al. 1998b). Consequently, females that preferentially mate with males that either produce unbiased or male-biased sex ratios will leave more grandchildren (Fisher 1958). The feasibility of this scenario is bolstered by experiments with *D. mediopunctata*, which have shown that sex chromosome meiotic drive can maintain heritable variation in the sex ratio (Varandas et al. 1997). While this proposal has generated interest (Hurst & Pomiankowski 1998), it has also been met with skepticism (Reinhold et al. 1999). However, a recent population genetic model (Lande & Wilkinson 1999) confirms that meiotic drive can enhance the evolution of female preference for a male ornament.

This conclusion comes from comparing the evolution of female choice for ornamental males in the presence and absence of meiotic drive. To keep the model as simple as possible, we assume that a sex-limited male ornament is influenced by an X-linked locus while female choice for ornamented males is determined by an autosomal locus. In the absence of meiotic drive and without natural selection on either the ornament or preference, the introduction of choice and ornament alleles at low frequencies into a population leads to evolution of the male trait, but no correlated change in the female preference. If selection maintains a stable polymorphism for  $X^d$  and the male ornament is enhanced by an allele on the nondriving X chromosome, then evolution of the male trait occurs more rapidly and is accompanied by evolution of the female preference due to sex ratio selection. In a population with

a female-biased sex ratio, females that mate with nondriving males produce more grandchildren than average because sons contribute a higher proportion of autosomal genes to the next generation than daughters. However, in the absence of recombination on the X chromosome, female choice sexual selection will eventually eliminate  $X^d$  from the population. On the other hand, if recombination is rare, that is, occurs at rates comparable to what has been observed among paracentric inversions (Powell 1992), such as are often associated with sex chromosome meiotic drive, then trait and preference can coevolve until a recombination event moves the ornament allele from the nondriving X to  $X^d$ . At that point, further evolution of the preference ceases and the drive frequency returns to its equilibrium value. If a new mutation influencing eye span arises on the nondriving X, then further evolution of the trait and preference can occur. Thus, meiotic drive can catalyze the evolution of female preferences.

This model makes the prediction that the X chromosome should contribute disproportionately to the expression of the male ornament. Recent evidence indicates that the X chromosome does exert considerable influence on male eye span (Wolfenbarger & Wilkinson 2000). Reciprocal crosses between the lines selected for long and short eye span after thirty-two generations of selection show that the X chromosome explains  $25 \pm 6$  percent of the difference between the parental lines in relative male eye span. Measurement of the X chromosome from metaphase chromosome preparations indicates that the X comprises only 7 percent of the genome in males (Wolfenbarger & Wilkinson 2000). Additional work is in progress to determine if autosomal or Y-linked genes also contribute to eye span variation.

A second prediction made by the meiotic drive sexual selection model is that selection should act against the drive chromosome in order for it to persist as a stable polymorphism in the population. We are currently investigating if males or females carrying the drive chromosome differ in fertility or survival in comparison to individuals that carry the nondriving chromosome. We have preliminary evidence that  $X^dY$  males that carry the drive chromosome do not fertilize as many eggs as XY males (Fry & Wilkinson, in preparation). Similar results have been reported for *Drosophila pseudoobscura* (Wu 1983) and *D. quinaria* (Jaenike 1996). By using *C. whitei* males that differ in body color, we have been able to score sperm precedence of females mated on successive days and have found that  $X^dY$  males fertilize only about 5 percent of female eggs, independent of the order of mating. In previous work we found that the precedence of sperm from the second male to mate with a female, that is, P2, averages 0.5 as long as males mate with females after an hour or more (Lorch et al. 1993). Thus, these results suggest that either  $X^d$ -carrying sperm are competitively inferior to X- and Y-carrying sperm, or that females somehow preferentially use X- and Y-bearing sperm, rather than  $X^d$ -bearing sperm, for fertilization. We are in the process of designing studies to investigate these fascinating alternatives.

### Evolution of Exaggerated Eye Stalks

A resurgence of interest in the pattern (Harvey & Pagel 1991), rather than the process, of evolution has, I believe, led behavioral ecologists to more closely examine the role of evolutionary history in explaining species-level variation than has been characteristic of the field over the past twenty years. With regard to sexual selection, a number of investigators (Burley 1985; Endler & McClellan 1988; Ryan et al. 1990) have suggested that female preferences may arise through preexisting biases that influence behaviors in other contexts. If males evolve traits to exploit sensory biases of females, then the evolution of female preferences should be decoupled from, rather than coevolve with, the evolution of male ornaments. Thus, if one reconstructs the evolutionary history of a preference and an ornament in a group of organisms, the sensory exploitation expectation is that the female preference should have evolved earlier in the lineage than the male ornament (Basolo 1990, 1995).

A somewhat different idea, termed chase-away sexual selection (Holland & Rice 1998), has recently been proposed and yields a similar prediction. In a number of species (Partridge & Hurst 1998) evidence now indicates that conflict occurs between the sexes over many aspects of the mating process. For example, in some cases the process of mating can be detrimental to female survival due to the transfer of male proteins (Chapman et al. 1995; Holland & Rice 1999), which presumably are produced to augment competition with other males' sperm. Thus, females might be expected to evolve resistance to male courtship, which should then favor the evolution of more elaborate male display in order to overcome female resistance. Female preferences must, therefore, precede the evolution of male ornaments for this process to occur.

We have considered these non-coevolutionary alternatives for eye span exaggeration by developing a phylogenetic hypothesis for thirty-three species of diopsid flies using three mitochondrial and three nuclear genes (Baker et al. 2000) and then examining the behavior of a few closely related species. By giving females two males with different eye spans and observing which males mate, we measured female preference as the proportion of matings that occur with the male exhibiting the longer eye span. This work shows that a female preference for long eye stalks does not exist in the sexually monomorphic Southeast Asian species, *Cyrtodiopsis quinqueguttata* or *Teleopsis quadriguttata*, which lie basal to the two sexually dimorphic *Cyrtodiopsis* species (Wilkinson et al. 1998a). Thus, the phylogenetic evidence is consistent with the artificial selection studies in supporting coevolution between the male trait and female preference.

Our work still begs the question of which came first—the ornament or the preference. For now, this question remains unanswered. However, the ab-

sence of a preference as well as no evidence for sex chromosome meiotic drive in the sexually monomorphic congener (Wilkinson et al. 1998b), is consistent with the meiotic drive system arising prior to the evolution of female preferences. We have also found evidence for sex chromosome meiotic drive in an African species with sexually dimorphic eye span in another genus (Lande & Wilkinson 1999). Thus, the tantalizing possibility that eye span exaggeration indicates sex chromosome behavior in other lineages of flies cannot be ruled out. For meiotic drive to be more than a curiosity, though, one would expect to find cases of sex-linked inheritance of sexually dimorphic traits in other groups of organisms. Interestingly, such a pattern has recently been reported (Reinhold 1998). Furthermore, a number of poeciliid fish that exhibit female choice for male ornaments or body size also display sex-linked inheritance of these traits, that is, guppies, *Poecilia reticulata* (Houde 1992); platyfish, *Xiphophorus maculatus* (Kallman & Borowski 1977); sailfin mollies, *X. latipinna* (Ptacek & Travis 1997; Travis 1994); and pygmy swordtails, *X. nigrensis* (Zimmerer & Kallman 1989). In at least one case, the guppy, there is also evidence that sex chromosome meiotic drive occurs (Farr 1981).

Unfortunately, obtaining evidence for the presence or absence of sex chromosome meiotic drive can be complicated by the existence of genetic suppressors. *Drosophila simulans* provides an instructive example. Sex chromosome meiotic drive was recently discovered (Mercot et al. 1995) in this cosmopolitan, well-studied species when flies from Tunisia were crossed with flies from the Seychelles. The F1 males produced highly distorted sex ratios because they lacked the appropriate genetic modifiers that suppress drive. Subsequent study has revealed that X<sup>d</sup> chromosomes occur at frequencies up to 60 percent in populations throughout the world (Atlan et al. 1997). Thus, considerable work is required to test for the presence of sex chromosome meiotic drive in other species.

Before concluding, I must acknowledge that my focus on female choice has ignored the very important role eye stalks likely play in resolving contests among diopsids, as well as among other flies with head projections (Grimaldi & Fenster 1989; Wilkinson & Dodson 1997). Examination of male fighting among *Cyrtodiopsis* species has shown that sexually dimorphic flies use eye span to resolve contests while sexually monomorphic species do not (Panhuis & Wilkinson 1999). Because eye span correlates highly with body size and, therefore, provides an honest indicator of larval condition (David et al. 1998; Wilkinson & Taper 1999), males, as well as females, should be expected to use eye span for assessment. We have found strong evidence indicating that eye stalks play important roles for both male contest resolution and female mate choice, as expected if eye stalks function as both ornaments and assessment signals (Berglund et al. 1996). However, additional work is needed to determine if both mechanisms of sexual selection are involved in the evolution of sexual dimorphism in other lineages in this



family as well as in other families of flies in which males exhibit eye stalks (Wilkinson & Dodson 1997).

### Conclusions

I believe my research on stalk-eyed flies illustrates some of the benefits associated with trying to test key assumptions or predictions from currently controversial theories using an appropriate animal model. After some perseverance, we discovered that stalk-eyed flies are easier to rear and study in the lab than almost any other appropriate vertebrate or invertebrate species, with the notable exception of some *Drosophila* species. While sophisticated genetic experiments are not easily conducted with stalk-eyed flies, they are arguably better for studying sexual selection than most *Drosophila* because the male ornament and female behavior are easy to quantify, can be changed readily by selection in the lab and field, and exhibit extraordinary variation among related species.

On the other hand, our discovery of sex chromosome meiotic drive and its relationship to sexual selection provides a valuable lesson for how scientific advances are made. While we now have theoretical confirmation that biased sex chromosome transmission can influence sexual selection, no one conceived of this possibility before we initiated our work. While serendipity may be unpredictable, it is possible to remain open to alternative interpretations as well as refrain from becoming too invested in any single hypothesis under study. One of the best pieces of advice my own advisor gave me was never to ignore "cheap" data. Such philosophy encourages data collection that may seem tangential to the purpose of a current study, but could inform future work.

Testing model assumptions and predictions is a necessary part of science. However, most major advances in behavioral ecology, as well as in other fields of science, have not been made this way. Rather, discovery of unexpected behavioral patterns or associations, such as that between haploidy and reproductive altruism, has led to the development of an explanation for those patterns, that is, kin selection (Hamilton 1964). Thus, future advances in the field will depend on discovering behavioral patterns that fail to conform to conventional theories. My best advice, therefore, is to be alert for the unexpected. Such discoveries may well turn out to be more important than any preconceived ideas under examination.

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