Syracuse University

SURFACE

Syracuse University Honors Program Capstone Projects

Spring 5-1-2007

Sexual Conflict Over Egg Allocation: A Dynamic Programming Approach to Modeling the Evolution of Male Harm and Female Resistance

David Kelley

Follow this and additional works at: https://surface.syr.edu/honors_capstone

Part of the Other Computer Engineering Commons

Introduction

Differential investment in gametes and an asymmetry in relatedness make sexual conflict a frequent outcome of sexual reproduction (Arnqvist and Rowe 2005; Parker 1979; Trivers 1972). Recent empirical studies have shown that sexual interactions can prove harmful to females (e.g., Blanckenhorn et al. 2002; Chapman et al. 1995; Crudgington and Siva-Jothy 2000; Morrow and Arnqvist 2003; Pitnick and GarcíaGonzález 2002). The adaptive significance of male traits that inflict harm on females has been a point of contention.

Harm to females may represent an unavoidable, negative pleiotropic consequence of a trait that otherwise benefits males (i.e., enhanced competitive fertilization success; Morrow et al. 2003; Parker 1979). Arnqvist and Rowe (2005) present a verbal model as to why this scenario presents the most likely general explanation for the origin and maintenance of harmful male traits. Alternatively, two theoretical models address mechanisms by which inflicting harm *per se* may be beneficial to males. The first model links an increase in male harm to a reduction in the probability of a female remating, and consequently a reduction in the risk of encountering sperm competition (Johnstone and Keller 2000). The second model contends that females respond to injury, and the concomitant reduction in survival prospects, by reallocating resources away from somatic maintenance (and future reproduction) and into current reproduction, thus siring more offspring with the harmful male (Lessells 1999, 2005; Michiels 1998).

Females of iterparous species are expected to evolve resource allocation

strategies that maximize their lifetime fitness (Roff 2002; Stearns 1992).

Resources must be allocated among growth, maintenance and reproduction, with

current reproductive effort influenced by the relative value of current reproduction

to future expectations of reproduction (Gadgil and Bossert 1970; Michod 1979;

Williams 1966). Selection to optimally allocate resources to reproductive effort

might result in a population of females with a progeny production schedule that is

either invariable across females or else varies with genetic quality but is otherwise

not adjustable (i.e. fixed clutch size). Alternatively, females may evolve a plastic

breeding schedule, where egg production varies both across females and among

clutches within females in a condition-dependent manner. One expected

consequence of such plasticity is the phenomenon of "terminal investment"

(Clutton-Brock 1984). When a female is in poor condition due to injury or aging

and her survival prospects are grim, her best strategy may be to increase her

investment in current reproduction. For example, females of both insect and bird

species have been demonstrated to increase egg production as a consequence of

pathogen or parasite infection (e.g., Bonneaud et al. 2004; Javois and Tammaru

2004; Polak and Starmer 1998; Shoemaker et al. 2006).

By providing the right amount of harm, a male may induce a terminal

response by his mate, manipulating her into siring more progeny with him then

she would otherwise do. In Lessells' (2005) model, females have limited

flexibility to respond to this form of manipulation. If male harm is significantly

damaging, female strategies that avoid manipulation will be selected strongly for.

Using dynamic programming, I explore how females optimize their lifetime egg

allocation, and how selection acts on males to exploit female offspring production. Initially, the model establishes the optimal egg laying behavior of females relative to their genetic condition, when females are free to choose mates, who will not inflict harm. Next, direct physical harm to females by their mates is introduced. The model explores under what conditions selection favors male harm as well as selective female responses to harm. Results are discussed with respect to the adaptive significance, prevalence and distribution of terminal investment by females.

Methods

Basic structure

The objective was to write a program to model the life history of a fertile female, allowing her to allocate resources and energy to different features of reproduction, particularly mate choice and offspring production. Females are modeled to have multiple discrete reproductive episodes during their lifetime. In essence, the model separates instances where a female has the opportunity to choose a mate and reproduce. Modeling reproductive episodes discretely significantly simplifies real life reproduction without much loss of generality as many species in nature will mate and reproduce in such a fashion. Parameters of the model can be varied to analyze how females adjust their reproductive strategies to maximize their fitness. In short, the model asks the question- given that females reproduce in discrete reproduction bouts, how should females allocate their resources between current and future reproduction to maximize

fitness?

Fundamentally, the model algorithm breaks the female's reproductive strategy into a sequence of decisions, e.g. whether to have another offspring in the current clutch or wait for the next clutch. Fitness is maximized by comparing the expected fitness of each specific choice at a decision point. Thus, a crucial element of the model is an accurate measure of female fitness. Since the model incorporates a female preference for male quality, simply counting the number of offspring is not enough. To also take into account the quality of those offspring, the number of grandchildren is the basis for the fitness metric.

Condition points and general costs

In order to simulate an individual's finite amount of energy and resources, each female is allotted "condition points" in the model. The number of condition points that the female begins with reflects her genetic condition, a measure of her predisposition for strong vitality, health, and ability to acquire resources from the environment. All actions for which the female must expend energy or resources subtract from her bank of condition points, which is scaled from 0-1000 where 0 is 100% certainty of death. The population of males and females is normally distributed around 800 points with a standard deviation of 75 points.

To allow females to express a preference for high quality males, the program models mate sampling using the "Best of N" strategy, in which females sample N males and choose the most fit of the males sampled (Janetos, 1980). Best of N is based on the assumptions that females are proactive in searching for

mates and can effectively discern the quality of a male. The cost of the female's search is modeled as being a near linear function of the number of males she samples, minimally influenced by an N^2 term, since each successive sampling costs the female time and energy. Though these assumptions may be simplifications of real world behavior, empirical evidence indicate that many species use a form of "Best of N" when searching for mates (e.g., Gibson, 1996; Trail and Adams, 1989; Uy et al., 2000).

At the beginning of each clutch, the female must determine how many males to sample by comparing her expected fitness for each possible choice of N. The model is only concerned with the genetic condition of the male, which can be treated as a random variable, with a normal distribution of mean 800 condition points and standard deviation 75. The maximum of N instances of this random variable is the genetic condition of the female's mate. The expected value of the genetic condition of the female's mate for different values of N follows, and is mainly what is used by the model.

Producing offspring also costs the female condition points. The cost of each successive offspring in a single reproductive episode is determined by a function of the number of offspring already produced during that episode. The function assumes that the cost of the first offspring in a clutch should be less then the next few to reflect shared resources of the mother in egg production, gestation and/or rearing. At some point the cost begins to accelerate upwards as the number of offspring that the female can produce is limited by her rearing ability and physiological constraints. The high cost of a large clutch gives the female reason

to eventually abstain and wait for a future clutch to continue reproducing. Since quantifying the cost of an offspring on such a scale is inevitably imprecise, simulations are run using two different offspring cost functions (Fig. 1).
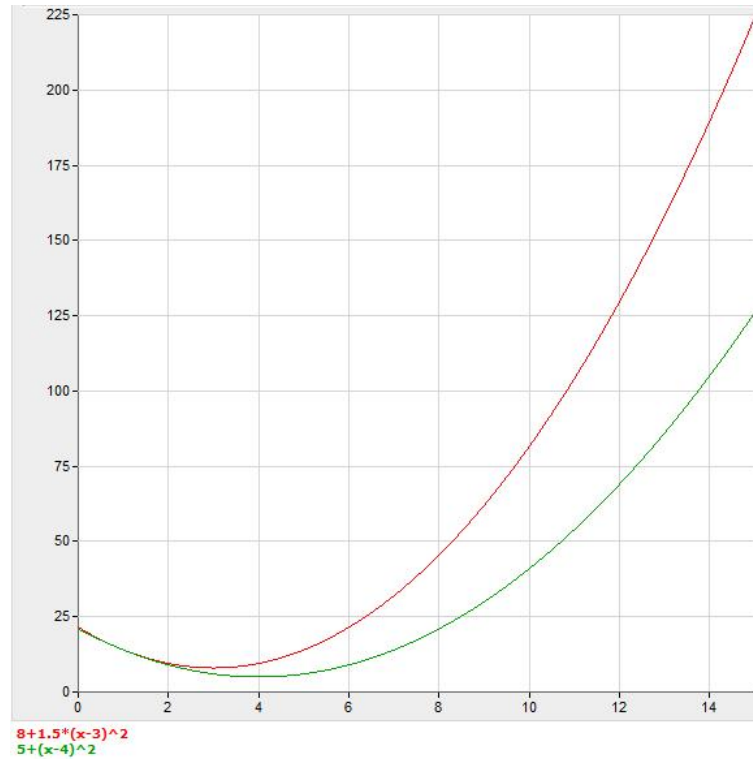

Figure 1: Two functions for the cost of an offspring- in red, (a) f(x)=8+1.5*(x-3)^2 and in green, (b) f(x)=5+(x-4)^2 where x is the number of offspring already in the current clutch.

Future expectation of survival

The probability of survival to future reproductive episodes is crucial in determining how the female should balance her allocation of resources between present and future reproduction. A function maps the female's current condition to a probability of surviving until the next reproductive episode. The value of an offspring in the next reproductive episode must be discounted by this factor to calculate the current expected value of that offspring. Survival probability is

given by a logistic function, or S-curve. A logistic function allows the female a high probability of survival during the early stages of her life, but has a significant drop off when condition becomes low. The model is run with three different functions to characterize a wide variety of living conditions (Fig. 2).
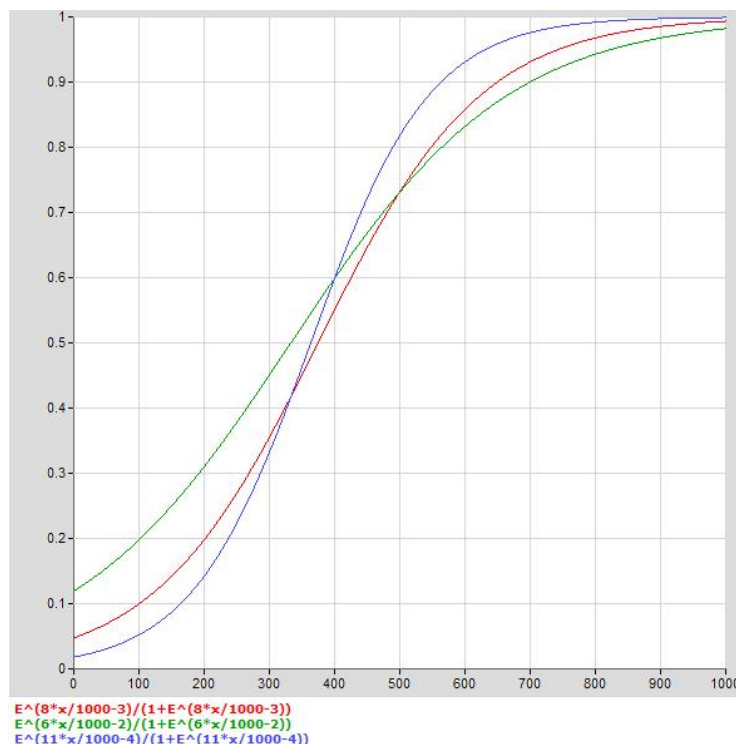

E^(8*x/1000-3)/(1+E^(8*x/1000-3))
E^(6*x/1000-2)/(1+E^(6*x/1000-2))
E^(11*x/1000-4)/(1+E^(11*x/1000-4))

Figure 2: Three functions for the survival probability- in red, (a) $f(x)=e^{(8x/1000-3)}/(1+e^{(8x/1000-3)})$, in green, (b) $f(x)=e^{(6x/1000-2)}/(1+e^{(6x/1000-2)})$ and in blue, (c) $f(x)=e^{(11x/1000-4)}/(1+e^{(11x/1000-4)})$ where x is the female's condition.

Dynamic programming algorithm

A close examination of the decisions a female must make leads to an algorithm for calculating a female's fitness and reproductive strategy. The problem of determining the optimal number of offspring to produce in a given clutch can be broken down into repeatedly determining whether to add one more offspring to the current clutch. The female will always produce a first offspring if

the cost can be afforded. The model then asks whether having a second, third, fourth, etc. is optimal. Eventually the answer will be no, and the female will have determined the size of her clutch and can move forward to the next episode.

The factors that determine whether or not the female should add another offspring are her current level of condition, the quality of her mate, and the number of offspring she has already produced in the current clutch. Let the term "situation" refer to a combination of specific values for these factors. Whether the female adds the offspring or not, her new situation can still be described by these three factors after a simple shift of the actual values. To determine whether the offspring is produced or not, the algorithm must compare the fitness values that describe each of the new situations. The set of situations that the female could be in is small enough that calculating a fitness value for each combination of these factors is feasible. Given a fitness value to describe every situation, the female's strategy can be extracted. The difficulty is that the fitness value for a given situation is highly dependent on fitness values for other situations, which are then dependent on even more situations.

To work around this difficulty, the algorithm exploits the property that condition can only decrease and that the fitness values for many very low condition situations do not depend on the fitness values for any other situations. These include trivial calculations such as whether the female has just enough condition left to produce one more offspring before 100% certainty of death. If fitness values for simple, low condition situations are determined first, calculations for more complex situations follow.

The algorithm uses dynamic programming to accomplish the goal of describing every situation with a fitness value. Dynamic programming finds the optimal solution to a problem in a bottom-up manner by beginning with trivial subproblems and using their solutions to obtain solutions to subproblems of increasing complexity, eventually reaching the solution of the original problem (Brassard 1996). Dynamic programming is especially efficient when the solutions of subproblems are needed many times because each subproblem solution is saved in a data structure so that the calculation only needs to be performed once. This property is the motivation for the implementation of dynamic programming in the model's algorithm. A fitness value for every situation can be calculated by presenting the algorithm with the problem of calculating the fitness of the female's initial situation, as each other situation becomes a subproblem.

Implementation

As previously mentioned, the algorithm first calculates the fitness for trivial situations that would occur late in the female's life. Fitness values are saved in a triple-scripted array with the three dimensions representing the combination of factors that make up the situation: number of offspring in the current clutch, current condition, and number of males sampled (to reflect the quality of her mate). If the subproblem has the female with no offspring in the current clutch and a zero for number of males sampled, then the female has not yet found a mate. Fitness values that would result from situations reflecting each

possible choice of N are examined and the maximum of these values is the solution to the subproblem. If the subproblem has the female with no offspring and a number of mates sampled greater than zero, then a mate has been chosen. If an offspring is affordable, the subproblem's solution is the sum of the value of that offspring and the fitness value describing the situation where she has had the offspring. If not, then she will never be able to afford an offspring and the fitness describing the situation is zero.

In all other situations, fitness is determined by the decision problem described above, where the female decides whether or not to produce one more offspring. If the female chooses not to produce another offspring, her fitness is determined by the situation where she has zero offspring in the current clutch, the same condition, and has not chosen the number of males to sample. This must be discounted by the probability that she survives to the next episode. The value to consider is:

$$A = S(C) * W(0, C, 0) \hspace{3cm} \text{Eq. 1}$$

Where A is the fitness value of abstaining, S(C) is the function that gives the probability of survival for a given condition, C is the current condition, and W is the array of fitness values with the three parameters, current number of offspring, current condition, and males sampled.

If the female chooses to reproduce, her fitness is determined by the sum of the contribution of the offspring to her fitness and the fitness for the situation where her number of offspring in the current clutch has been incremented by one, condition has been decremented by the cost of the offspring, and N is unchanged.

The value to consider is:

$$R = OF + W(F+1, C - T(F), N) \qquad \text{Eq. 2}$$

Where R is the fitness value of reproducing, OF is the contribution of this offspring to the female's fitness, F is the number of offspring in the current clutch, N is the number of males sampled, and T(F) is the function that gives the cost of the next offspring for a clutch of size F. The fitness value describing the female's current situation is the maximum of A and R.

By this procedure, a fitness value can be calculated for every situation. The array of these fitness values serves as an abstract description of the female's optimal reproductive strategy because her best action in any situation can be determined by comparing values in the array. For instance, to determine how many offspring the female should produce in her first reproductive episode, we can use the procedure outlined above and plug in values from the array. Again the decision is broken down into repeated simpler decisions of whether to add one more offspring, a question which is equivalent to asking whether R is greater than A. When A is greater than R, the female abstains to the next clutch, and the number of times the decision was repeated gives the number of offspring the female should produce in the clutch.

This procedure can be extended further to determine optimal decisions throughout the female's life. Starting the female at her initial level of condition and stepping through her decisions while carefully tracking her situation outputs an optimal path for the female's life. Potentially stochastic elements, such as the genetic condition of males that the female samples, can be made random and

changes in this optimal course can be observed as the female encounters different sets of situations.

However, a female's lifetime reproductive strategy may contain anomalies due to the accuracy with which the model allows her to make decisions. For example, her late life decisions may revolve around guaranteeing that she has the exact amount of condition she needs to produce a certain number of offspring in her last clutch. To introduce error into the female's foresight and smooth out the behavioral anomalies, the actual calculations examine a weighted average of the condition levels surrounding the situation she would find herself in after an action such as producing an offspring.

As a point of comparison for the strategies where females can facultatively allocate resources at each reproductive bout, the model has another mode where females cannot adapt their offspring production numbers to their situation and must produce a constant number of offspring every clutch. The algorithm is similar in this mode, except that the comparison of A and R is eliminated since the female cannot produce any more offspring than her quota nor can she abstain before her clutch size has reached it. To determine this quota of offspring that the female should produce at every clutch, the female's fitness is calculated for all possible values. The quota corresponding to the maximum fitness value is the female's optimal clutch size.

Value of offspring

The female's offspring are assumed to have a genetic condition equal to the average of the female and her mate's genetic conditions. Mapping the offspring's genetic condition to a value measuring the contribution of that offspring to the female's fitness is crucial to determining the optimal number of offspring for the female to have each clutch. To calculate a value for female offspring, the model uses the same algorithm described above from the offspring's perspective. For each value of genetic condition, the model runs the algorithm, simply substituting a one for the value of an offspring, which in effect, counts the number of expected grandchildren for the original female. The algorithm produces a fitness value for every potential level of genetic condition for female offspring. These values are then normalized to one by dividing each value by the population average.

Because the algorithm cannot quantify male fitness, a range of estimates are used to map a male offspring's genetic condition to a contribution to the female's fitness. Three factors contribute to how many grandchildren the female can expect her male offspring to sire: the expected number of opportunities to be sampled by a female, probability of selection in a competition with other males, and expected number of offspring a female would produce during a mating. Of these factors, the model can only easily obtain a measure of the male's probability of selection in a competition with other males. The mapping of the male's genetic condition to a contribution value starts with the probability that the male would be chosen over another random male and multiples it by a function of the male's

condition. Two different functions are used to add breadth (Fig. 3). Again the
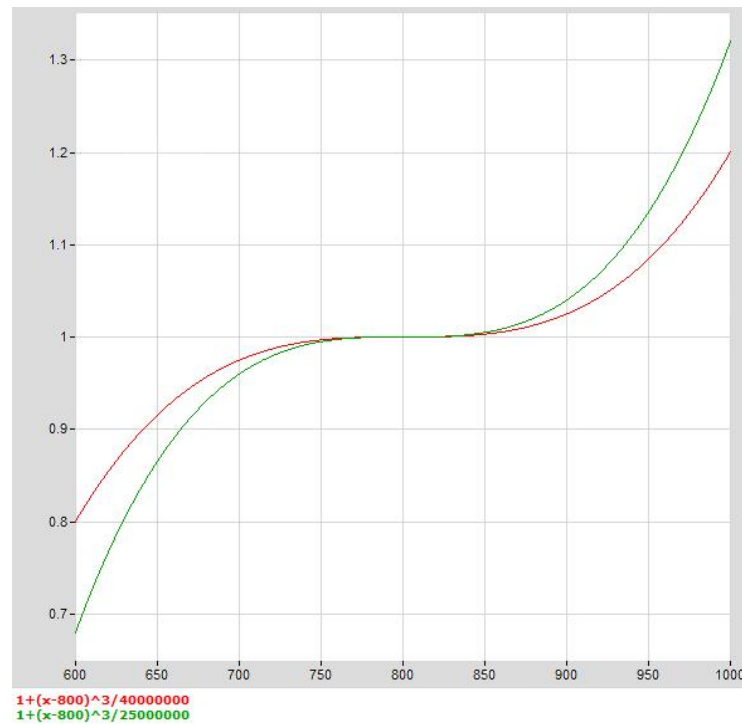
values are then normalized.

Figure 3: Two functions for the male offspring factor- in red, (a) $f(x)=1+(x-800)^3/4x10^7$ and in green,(b) $f(x)=1+(x-800)^3/2.5x10^7$ where x is the male offspring's condition.

Introduction of male harm

To explore how male harm influences female reproductive strategies, the

model has an option to give males the ability to harm their mates if doing so will

improve the male's fitness. Harm is implemented as a subtraction from the

female's current condition and represents any type of direct physical harm. When

the female first chooses a male to mate with, the algorithm compares the optimal

number of offspring for the female to produce if she begins the clutch at her

current level of condition with the optimal number of offspring for her to produce

if she begins the clutch at a number of lower levels of condition. If she will have

more offspring at a lower level of condition, the male can inflict enough harm so that she begins the clutch at the lower level of condition where she will produce more offspring.

However, there must be a limit to how much harm a male should be willing to inflict for each additional offspring. To explore this complex situation in depth, three different functions are used to map the number of condition points the male must subtract from the female to the number of offspring he must gain to be willing to inflict that much harm (Fig. 4). As the cost of inflicting harm decreases, the prevalence of male harm increases.
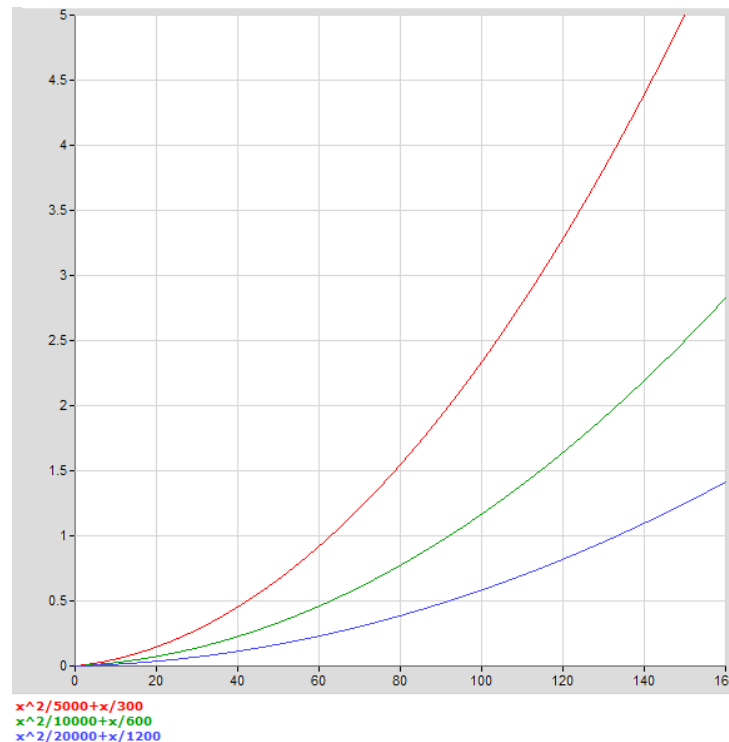

Figure 4: Three functions for the cost of male harm- in red, (a) f(x)=x²/5000+x/300, in green, (b) f(x)=x²/1000+x/600 and in blue, (c) f(x)=x²/2000+x/1200 where x is the condition points subtracted from the female and f(x) is the number of additional offspring the male would need to sire to be willing to inflict that level of harm.

With the introduction of male harm, two additional modes of the model arise. The first has males inflicting harm upon females that do not expect it. To analyze this scenario, females must make decisions based on a model without harm. The algorithm first runs the facultative mode in the absence of male harm to fill an array with fitness values for all situations. When a female must decide how to act, she compares the fitness values of what she expects the resulting situations to be from the array without harm. However, her choice is then examined in light of harmful males and the actual corresponding fitness value.

The second additional mode allows females to see that males are harmful. No further adjustments to the algorithm are necessary to accommodate this.

Data

Condition 650			Condition 725			Condition 800		
Fitness 12.59			Fitness 18.94			Fitness 27.26		
Clutch	N	Offspring	Clutch	N	Offspring	Clutch	N	Offspring
1	4.23	6	1	3	5	1	2.04	5
2	6.16	7	2	3.99	6	2	2.47	5
3	15.4	10	3	5.77	7	3	3.01	6
4	1	0.18	4	16	10	4	4.18	6.68
			5	1	0.23	5	9.24	10.9
						6	1	0.31

Condition 875			Condition 950		
Fitness 37.36			Fitness 48.58		
Clutch	N	Offspring	Clutch	N	Offspring
1	2	5	1	1.92	4.92
2	2	5	2	2	5
3	2	5	3	2	5
4	2.18	5.18	4	2	5
5	2.92	6.14	5	2	5
6	4.77	7.56	6	2.07	6
7	10.5	8.6	7	3.13	6.49
8	0.97	2.18	8	8.05	10.6
			9	3.71	1.75

Table 1: Typical output of the facultative mode of the model, where there is no male harm and clutch size can vary. The output includes a fitness value, the number of clutches, and N and offspring numbers for each clutch. There are 5 different levels of genetic condition using the (a) offspring cost function, (a) survival probability function, and (a) male offspring factor.
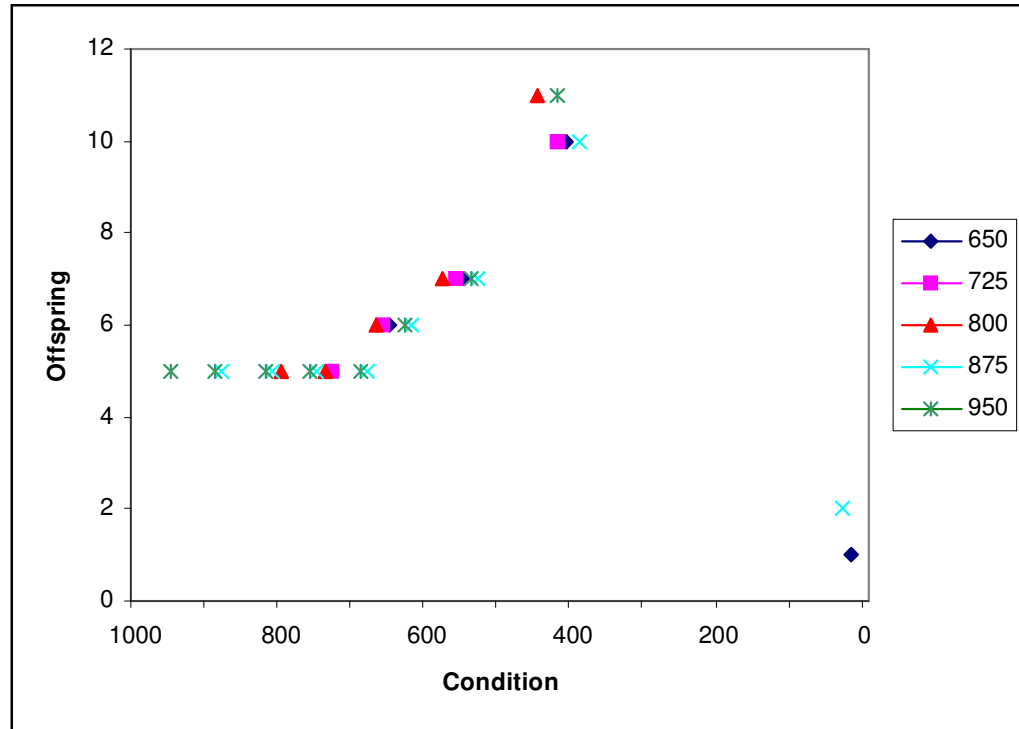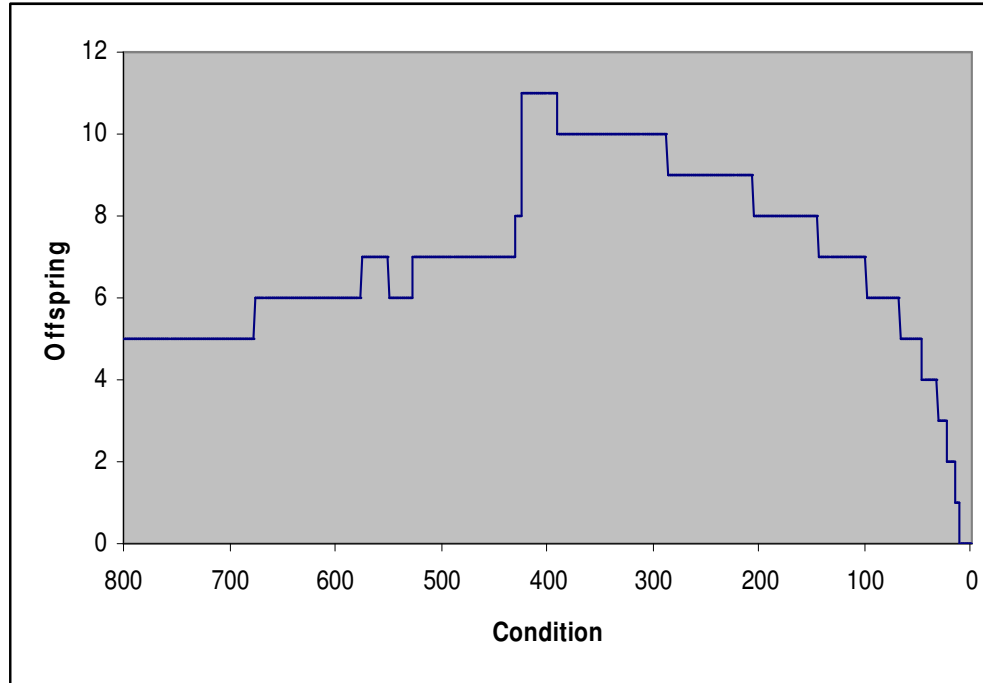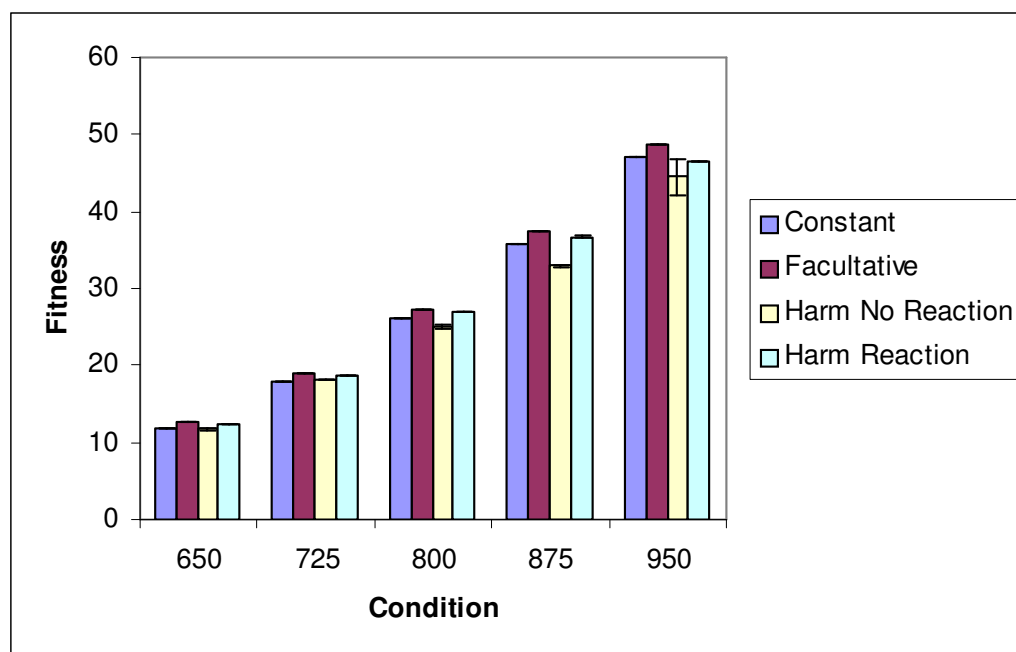
Figure 5: Number of offspring in each clutch plotted against the female's condition pre-clutch. There are 5 different levels of genetic condition using the (a) offspring cost function, (a) survival probability function, and (a) male offspring factor.

Figure 6: The number of offspring a female with genetic, condition 800 would have if she began a clutch at each level of condition using the (a) offspring cost function, (a) survival probability function, and (a) male offspring factor.

	Constant	Facultative	Harm No Reaction	Harm Reaction
650	11.920	12.600	11.717	12.443
725	17.946	18.937	18.184	18.778
800	26.149	27.245	25.059	26.880
875	35.850	37.395	32.944	36.706
950	47.165	48.599	44.450	46.536

Figure 7: Mean fitness values (± standard error) under the four different modes of the model for different levels of genetic condition using the (a) offspring cost function, (a) survival probability function, (a) male offspring factor, and (a) harm cost function. "Constant" refers to females that can only produce a fixed, constant number of offspring each clutch. "Facultative" refers to females that will adjust offspring production in the absence of male harm. "Harm No Reaction" refers to females that will adjust offspring production without expecting male harm, but do face male harm. "Harm Reaction" refers to females that will adjust offspring production, expecting that males will harm.

|	Constant	Facultative	Harm No Reaction	Harm Reaction
650	11.920	12.600	11.362	12.447
725	17.946	18.937	17.920	18.746
800	26.149	27.245	21.289	26.846
875	35.850	37.395	29.344	33.298
950	47.165	48.599	32.508	43.081
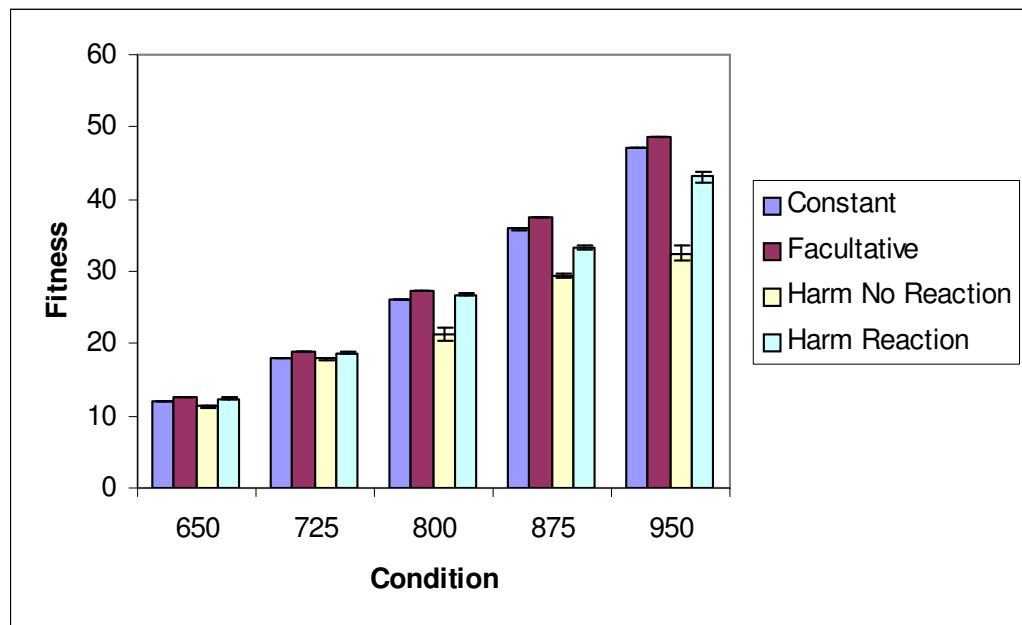
Figure 8: Mean fitness values (± standard error) under the four different modes of the model for different levels of genetic condition using the (a) offspring cost function, (a) survival probability function, (a) male offspring factor, and (b) harm cost function.

|	Constant	Facultative	Harm No Reaction	Harm Reaction
650	11.920	12.600	10.787	12.353
725	17.946	18.937	14.659	17.275
800	26.149	27.245	19.440	25.480
875	35.850	37.395	25.076	30.462
950	47.165	48.599	28.625	41.742
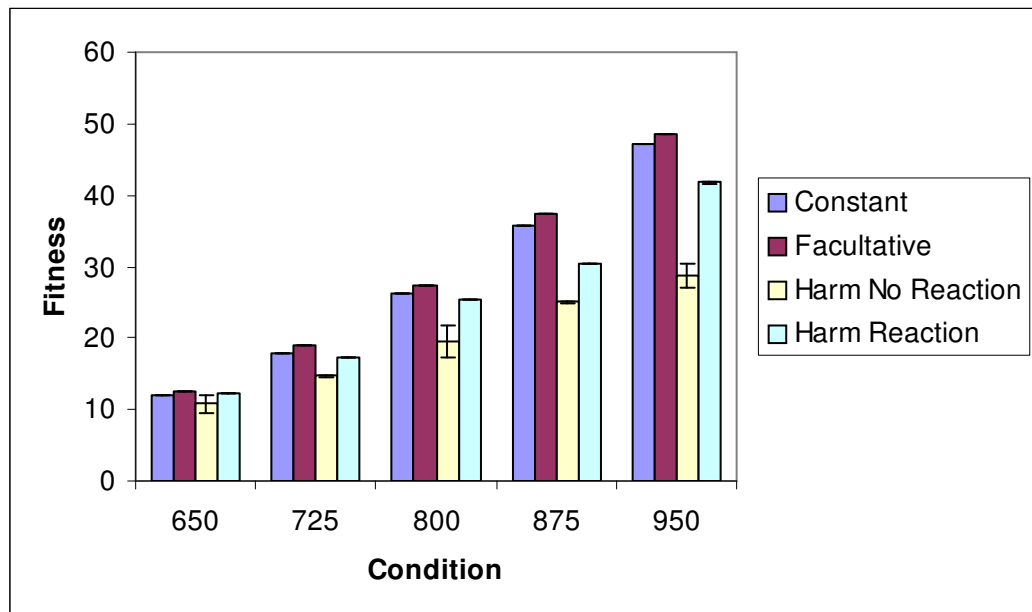
Figure 9: Mean fitness values (± standard error) under the four different modes of the model for different levels of genetic condition using the (a) offspring cost function, (a) survival probability function, (a) male offspring factor, and (c) harm cost function.
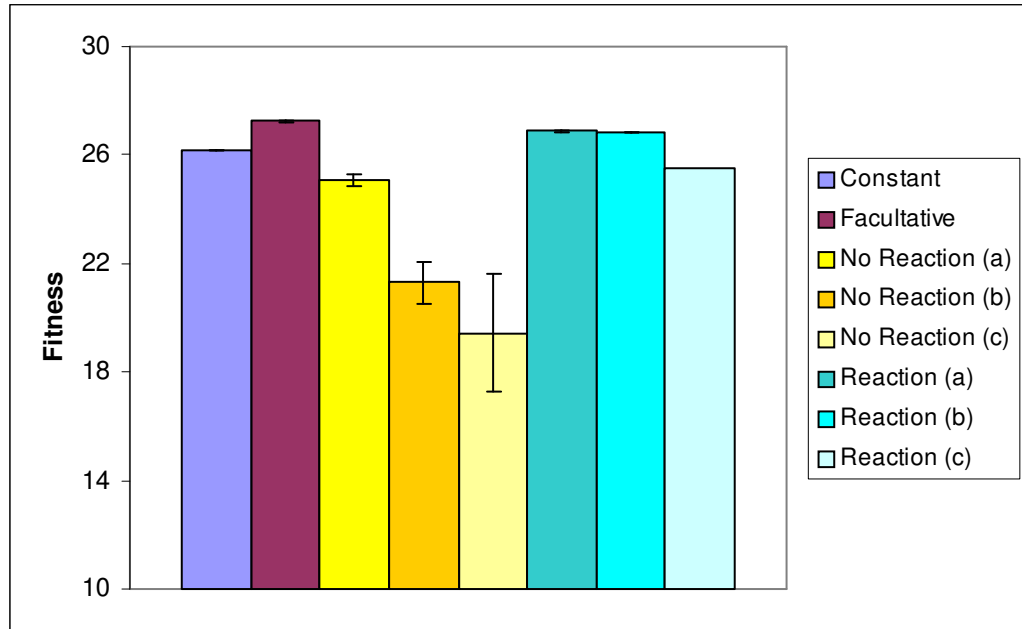
Figure 10: Mean fitness values (± standard error) at genetic condition 800 under the four different modes of the model, compared using the (a) offspring cost function, (a) survival probability function, (a) male offspring factor, and all three harm cost functions.

Results

Throughout all of the data shown, the (a) offspring cost function, (a) survival probability function, and (a) male offspring factor are used. However, all of the combinations of the functions produced qualitatively similar data.

The model consistently shows that when decreasing condition results in lower probabilities of survival, the optimal reproductive strategy includes pacing reproductive effort initially and then investing more heavily late in life (i.e. terminal investment). Table 1 demonstrates the large increase in preference and offspring production in the later clutches. For each condition, there is a final clutch where the female has a small number of offspring. Usually this reflects a situation in the model where the female has aimed to produce a high number of offspring in her final clutch to use up the last of her condition points, but has slightly miscalculated so that she has some left over for another offspring if she survives to the next clutch.

The data also shows that this terminal investment appears exploitable by males. Figure 5 shows that females of all genetic conditions will terminally invest at approximately the same point- around condition 400 under these parameters. Females in this state are most vulnerable to male manipulation via harm. In addition, the increase in offspring production can occur as a sudden spike as seen in (Fig. 6), presenting males with significant motivation to harm when a female's condition is just greater than the point of the spike.

When males are able to inflict calculated harm upon their mates, the female's fitness suffers significantly. Males are able to pinpoint conditions where females

will increase offspring production and inflict enough harm to reap the benefits. The effect of this harm can be seen in figures 7-10, and becomes more damaging to the female's fitness as the cost of inflicting harm decreases.

In the harm reaction mode, females will attempt to avoid beginning a clutch at certain conditions where they are more susceptible to heavy blows of harm. For example, in figure 6 we see that the difference between a female beginning at condition 435 and 420 is about four offspring. The female is clearly in danger of being harmed when close to this jump in offspring production. Suppose the female is at condition 500. If sampling 6 mates would have been optimal in the absence of harm, she could do so and begin her clutch at 470. However, she would be harmed 50 more points to bring her to 420. If she instead samples 16 mates, she will begin her clutch at 420 and the male will not benefit from harming. In the second case, the female gains the advantage of mating with a higher quality male on average, making the best of her bad situation. Figures 7-10 present the obvious result that females that expect harm will have greater fitness than those that do not.

Nevertheless, the fitness values that result from this strategy are exceeded in many cases by those for females that simply produce a fixed and constant number of offspring during each clutch. The data shows (Fig. 7-9) that as the female's genetic condition increases and the cost of inflicting harm decreases, producing a constant clutch size becomes a better strategy than attempting to avoid the harm in other ways. Even when the female's genetic condition is low and the cost of inflicting harm is high, the difference between the two strategies is small.

Discussion

Sexual conflict theory predicts that male harm to females only arise as a pleiotropic by-product of another adaptive function (e.g. sperm competitiveness; Arngqvist and Rowe 2005). This is because when males harm females they risk decreasing their own reproductive success. As such, any males bearing alleles that accomplish the competitive fertilization benefit without the incidental harm to mates will be at an advantage. Alternatively, males can directly inflict harm to females if this provides them with a direct advantage, and theoretical models have shown this to be possible (Johnstone and Keller 2000; Lessels 1999, 2005). However, the conditions under which direct male harm evolves may be restrictive or rare. Here the model examines the adaptive significance of harm under conditions of serial monogamy, but with no sperm competition, which is consistent with the results of Lessels (2005). The results indicate that males will evolve to harm their mates to take advantage of female terminal investment strategies. That is, if females facultatively adjust their investment in particular clutches based on their condition and invest more heavily when their condition is low, then males should harm females to reduce their condition and elicit a terminal investment response. This way, males sire more offspring than they would have if the female's condition had been higher.

These results lead to a unique conclusion of the model- that male harm should be exclusively or preferentially directed at older females and/or females in poor condition. Females offer the most significant benefit to male harm when they are near the brink of a terminal investment point and a male can push them

over the edge. In the model, healthy, young females are much less likely to respond to harm with an increase in reproductive effort. Currently, experiments have been conducted only with healthy, young females (e.g. Morrow et al. 2003, Rice 1996). Therefore, negative results from empirical studies may be an artifact of using young and healthy females.

In the face of male harm, the results indicate two evolutionarily adaptive responses by females. Recall that male harm in the model is adaptive and plastic, only occurring when the male perceives a benefit in increased egg production. First, females can behaviorally modify their egg production schedules and mate choice strategy in such a way that they (1) minimize the probability of remating at a time when they are most vulnerable to males exploiting their terminal investment response and (2) maximize the indirect benefits of mate choice in the face of inevitable direct costs. This is the result of the "harm reaction" mode of the model, where females were able to recoup a significant portion of the fitness that male harm had previously detracted. Second, females can forego the terminal investment response altogether, and in so doing, remove the opportunity for male exploitation. This is the "constant" mode of the model, where females were also able to achieve fitness levels slightly under a facultative egg production schedule in the absence of harm.

The first evolutionary response by females – sophisticated modulation of egg production to minimize the probability of male harm – seems a less likely evolutionary outcome than the second. Such modulation would require an honest and reliable signaling system and relies on males harming with complete

discretion and precision. That is, males and females would clearly decide how to maximize and reduce harm, and adjust their behavior accordingly. Alternatively, the strategy of simply forgoing the ability to facultatively adjust clutches for each mating bout allows females to avoid harm since the benefits of harm for males are no longer present. If true, then this model generates two predictions. First, if conflict between sexes is common so that terminal investment by females is vulnerable to male manipulation and the loss of terminal investment is an effective female response to such manipulation, then terminal investment by females should be uncommon. Although the phenomenon of terminal investment makes intuitive sense, examples from nature are relatively rare (e.g., Bonneaud et al., 2004; Clutton-Brock, 1984). This paucity in empirical data may be due to an insufficient number of studies searching for terminal investment in nature, or, as our model predicts, terminal investment being indeed uncommon because of sexual conflict. Second, terminal investment should occur at higher frequency among monogamous species, where male harm is never adaptive, than among polygamous species. In light of the model's results, future empirical work should test for patterns of female terminal investment and the intensity of sexual conflict.

References

Arnqvist, G., and L. Rowe. 2005. Sexual conflict. Princeton University Press, Princeton.

Blanckenhorn, W. U., D. J. Hosken, O. Y. Martin, C. Reim, Y. Teuschl, and P. I. Ward. 2002. The costs of copulating in the dung fly *Sepsis cynipsea*. Behavioral Ecology 13:353-358.

Bonneaud, C., J. Mazuc, O. Chastel, H. Westerdahl, and G. Sorci. 2004. Terminal investment induced by immune challenge and fitness traits associated with major histocompatibility complex in the house sparrow. Evolution 58:2823-2830.

Brassard, Gilles, and Paul Bratley. *Fundamentals of Algorithmics*. 1st ed. Englewood Cliffs: Prentice-Hall Inc., 1996. 259-266.

Chapman, T., L. F. Liddle, J. M. Kalb, M. F. Wolfner, and L. Partridge. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. Nature 373:241-244.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212-229.

Crudgington, H. S., and M. T. Siva-Jothy. 2000. Genital damage, kicking and early death. Nature 407:855-856.

Gadgil, M., and W. H. Bossert. 1970. The life historical consequences of natural selection. American Naturalist 104:1-24.

Gibson, R. 1996. Female choice in sage grouse: The roles of attraction and active comparison. Behavioral Ecology and Sociobiology 39:55-59.

Janetos, A. C. 1980. Strategies of Female Mate Choice - a Theoretical-Analysis. Behavioral Ecology and Sociobiology 7:107-112.

Javois, J., and T. Tammaru. 2004. Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. Animal Behavior 68:249-255.

Johnstone, R. A., and L. Keller. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. American Naturalist 156.

Lessells, C. M. 1999. Sexual conflict in animals. Pp. 75-99 *in* L. Keller, ed. Levels of selection in evolution. Princeton University Press, Princeton, N.J.

Lessells, C. M. 2005. Why are males bad for females? Models for the evolution of damaging male behavior. American Naturalist 165:S46-S63.

Michiels, N. K. 1998. Mating conflicts and sperm competition in simultaneous hermaphrodites. Pp. 219-255 *in* T. R. Birkhead and A. P. Møller, eds. Sperm competition and sexual selection. Academic Press, London.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. American Naturalist 113:531-550.

Morrow, E. H., and G. Arnqvist. 2003. Costly traumatic insemination and a female counter-adaptation in bed bugs. Proceedings of the Royal Society of London B: Biological Sciences 270:2377-2381.

Morrow, E. H., G. Arnqvist, and S. Pitnick. 2003. Adaptation versus pleiotropy: why do males harm their mates? Behavioral Ecology 14:802-806.

Parker, G. A. 1979. Sexual selection and sexual conflict. Pp. 123-166 *in* M. S.
Blum and N. A. Blum, eds. Sexual selection and reproductive competition
in insects. Academic Press, New York.

Pitnick, S., and F. García-González. 2002. Harm to females increases with male
body size in *Drosophila melanogaster*. Proceedings of the Royal Society
of London B: Biological Sciences 269:1821-1828.

Polak, M., and W. T. Starmer. 1998. Parisite-induced risk of mortality elevates
reproductive effort in male *Drosophila*. Proceedings of the Royal Society
of London B: Biological Sciences 265:2197-2201.

Rice WR, 1996. Sexually antagonistic male adaptation triggered by experimental
arrest of female evolution. Nature 381:232-234.

Roff, D. A. 2002. Life History Evolution. Sinauer, Sunderland, MA. Shoemaker,
K. L., N. M. Parsons, and S. A. Adamo. 2006. Egg-laying behaviour
following infection in the cricket *Gryllus texensis*. Canadian Journal of
Zoology 84:412-418.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press,
Oxford.

Trail, P. W., and E. S. Adams. 1989. Active mate choice at cock-of-the-rock leks:
tactics of sampling and comparison. Behavioral Ecology and Sociobiology
25:283-292.

Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 52-97 *in* B.
Campbell, ed. Sexual Selection and the Descent of Man. Aldine
Publishing Company, Chicago.

Uy, J. A. C., G. L. Patricelli, and G. Borgia. 2000. Dynamic mate-searching tactic
allows female satin bowerbirds Ptilonorhynchus violaceus to reduce
searching. Proceedings of the Royal Society of London Series B:
Biological Sciences 267:251-256.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University
Press, Princeton.