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FEMALE CHOICE AND EXTRA-PAIR COPULATIONS

By

Christopher David Wilson

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ABSTRACT

FEMALE CHOICE AND EXTRA-PAIR COPULATIONS

By

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The discovery that social monogamy does not always lead to genetic monogamy has forced us to reassess our understanding of sexual selection. Comprehension of the factors that are important in causing the inconsistencies between the social and sexual relationship is essential if we are to understand the evolution of mating systems. Empirical work on this subject has been largely focused on avian species and much data has been accumulated that demonstrates the considerable variation in levels of sexual infidelity within and between socially monogamous species. It has been reasoned that the motivation behind these extra-pair copulations (EPCs) is the acquisition of indirect good genes benefits, so within such a framework, a probability model of female choice at the point of EPCs is presented. The model takes the assumption that the female appraises the genetic quality of her partner in relation to the genetic quality of the population of potential males (probably at the point of initial mate choice) and along with benefit-cost information, resolves whether or not to make a cuckold of her partner. The model allows us to quantify the indirect benefits and costs of EPCs to females from observational data, and results in an explanation for the variation in the frequency of extra-pair copulations, with population levels of variation for fitness related genes being the important factor.

To Doreen and Ernie

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INTRODUCTION

Content with Hermia! No; I do repent
The tedious minutes I with her have spent.
Not Hermia but Helena I love:
Who will not change a raven for a dove?
The will of man is by his reason sway'd;
And reason says you are the worthier maid.

A Midsummer Night's Dream. Act II, Scene 2.

In his writings on sexual selection, Darwin did not consider why females should copulate with more than one male, since he believed that females were strictly monogamous. We are now familiar with the various mating systems that are present in different species, these being traditionally described as being the result of the spatial and temporal distribution of resources. However, if we are to take this definition, the mating systems themselves determine only the social bond and not the sexual relationship of individuals. If individuals are constrained in their mate choice by the mating system, they will attempt to improve this situation through sperm competition, and it is sperm competition that dictates many aspects of the sexual relationship above that of the social. Sperm competition as a field of study is concerned with processes on a number of levels, from the physiological processes in the female reproductive tract, to the subject of this work: explanations for extra-pair copulations.

Extra-pair copulations (or EPCs) are a prevalent behaviour in avian breeding systems. This discovery has revolutionized our understanding of sexual selection, since until the recent application of genetic markers, 90% of bird species were categorized as monogamous. We are now more than aware that social monogamy does not always lead to genetic monogamy.

We therefore not only have situations of female choice at the time of mating, but also a second round of active female selection, the difference in propensity to participate in the latter being predisposed by the quality of male attained during the original mating. The original mate choice, and therefore the degree of inclination to participate in EPCs, may be a function of the original female mating order[8] (be it controlled by the time of arrival on the breeding territories or the physical ability to initiate reproduction[6]) and consequently the quality of the female, i.e. both male and female quality control the predisposition to take part in EPCs.

There are a number of possible benefits of EPCs to females ranging from the direct and non-genetic (such as insurance against sterile mates or increased parental care) to the indirect and genetic (such as good genes or increased genetic diversity). However, if females are participating in EPCs for apparently non-genetic benefits (because future matings are necessary to ensure reproductive success) genetic differences between males will be the factor that prompted the EPC in the first instance. That is, multiple mating for purely non-genetic benefits is unlikely as it invariable leads to the possibility of genetic benefits as well[20]. Intraspecific analyses of the patterns of extra-pair behaviour have suggested that the main benefit females gain from extra-pair matings is an improvement in the genetic quality of their offspring, i.e. indirect good genes benefits[17, 28].

There is also great variation in frequency of extra-pair paternity (EPP) both at the species level and the population level (natural populations vary in the level of EPP from

0% to more than 75%[27]) and understanding this variation will provide us with an opportunity to understand which factors are important in promoting polygamy.

Females usually participate in extra-pair copulations more readily with males that are of high quality. This preference for quality has been shown to operate on the age[1, 2, 3, 4], the dominance rank[5], health[6], and the degree of expression of secondary sexual characteristics[7, 8, 9, 10, 11, 17] of the males concerned, these factors being indicators of the potential genetic quality and sex appeal of the offspring. Furthermore, there is much evidence that suggests that a female's desire to participate in EPCs, along with their choice of EPC partner, is a function of the difference in quality between her original mate and the EPC male[11]; the practice of females performing EPCs with males that are more attractive in terms of their secondary sexual characteristics than their partners being the most obvious example.

The male quality evidence is usually interpreted in the following way. Paired females actively accept or reject individual extra-pair solicitations (or decide whether or not to solicit themselves) depending on the difference in quality of her mate and the extra-pair male, i.e. if the extra-pair male is of sufficiently greater quality than her partner she will accept the EPC, if he is not sufficiently superior, she will reject. We may assume that the degree of expression of a secondary sexual characteristic is equivalent to quality, specifically genetic quality, since other female choice criteria associated with original mate choice, such as ability to provide parental care or territory quality, rarely apply to EPCs[6].

If we are to think of the female behaviour in terms of adopting a particular strategy, then for the above behaviour we would have something along the lines of 'only have extra-pair copulations with males of sufficiently greater quality than my own partner.' The data which has been interpreted as supporting this idea shows an expected distribution of EPC male quality, but a significant portion of this lies below the level of quality of the original mate, i.e. a notable number of EPCs take place with males of poorer quality than the mate; contradictory to the suggested strategy[14, 15, 16, 17] .In order to explain these EPCs with poorer quality males, along with providing us with an alternative explanation of why females mated to relatively poor quality males have a higher propensity to engage in EPCs, the following is presented.

I propose a model in which females are not selective of individual extra-pair males. Depending on the quality of their current partner in relation to the rest of the population of potential male mates, they adopt a strategy of 'accept EPCs' or 'reject EPCs' (or again, decide whether or not to solicit themselves), regardless of the quality of the specific individual EPC males. This assumption requires some clarification, since if females are able to assess male quality, then why are they not selective of the individual extra-pair male? There are a number of advantages that arise from making the decision to accept or reject prior to the EPC proposition, especially if active solicitation on the part of the female is involved, which is often the case. These advantages regard not incurring certain costs that may arise if the female puts herself in the position of assessing individual extra-pair male quality. Parker[21] suggested that when the duration of copulation is short (as it is in birds) it might be less costly for females to accept an EPC rather than wasting time avoiding or rejecting persistent non-mates. If the female has decided on a strategy already, she will not find herself in this position and therefore incur neither cost. Furthermore, she is much less likely to be subject to a forced EPC in which she might get injured or her eggs damaged that may occur if the female assesses an individual male and then rejects. Further, she avoids increased predation risks and harassment from males that may reduce her foraging efficiency. The assumption that such a strategy is employed seems highly justified.

It will be shown that this approach allows us to begin quantifying the relative power of the costs and benefits of extra-pair copulations, through translating EPC and male quality data back to marginal benefit: cost ratios, and predictions regarding levels of polygamy may be made by working in the opposite fashion. With the intention of simplifying matters, the strategy of only accept EPCs from superior males shall be referred to as Hermia, while the strategy that I propose involving assessing the quality of the population of available males shall be referred to as Helena. The two are young women involved in the love triangle in A Midsummer's Night's Dream, rather fitting for a study on cheating and extra-pair antics.

The study proceeds by comparing the two strategies in terms of the expected proportions of EPCs that will be with superior males. The intention here is to show that Helena, even with what may be seen as looser selection criteria still achieves a comparable proportion of EPCs with superior males.

The next section of this work essentially examines the variation in extra-pair copulation frequencies (data here is usually obtained from extra-pair offspring data since EPCs are notoriously difficult to observe in the field) both within and between species.

Previous studies that have addressed this question have come up with a variety of origins for the variation, based around such factors as local breeding density[18] and the degree of breeding synchrony[19]. Since these possible explanations are controversial, with no clear support, I have focused my attention on the degree of variation in male fitness-related traits (as a correlate of total genetic variation) within the population. By applying the Helena strategy to populations with differing variations it is shown that one should expect EPC frequencies to be greater in populations containing more variation. This is quite logical since if one takes female choice of fitness related traits to be a general explanation for the occurrence of extra-pair paternity, then it follows that one would expect that more females would seek to modify the paternity of their clutch when there are greater differences between the genetic quality of potential fathers. The effect of population size on the whole equation is also examined.

Helena Derived

When should females adopt strategies of 'accept' and when should they adopt strategies of 'reject'?

Let p = the proportion of males in the population of potential mates that are of higher quality than her partner.

So $(1-p)$ = the proportion of males of lesser quality

We need to know the relative fitness of the two strategies:

1) The fitness of 'reject'.

Just has the basic fitness of 1, which arises solely from interactions with her partner.

2) The fitness of 'accept'.

Has the same basic fitness of 1 from copulations with her partner.

Add to this the benefit b when EPCs are performed with superior males, occurring at frequency p.

Subtract the cost c when EPCs are performed with inferior males, occurring at frequency $1-p$.

Giving the fitness of 'accept' to be $1+bp-c(1-p)$

So the relative fitness of the two strategies is: $\frac{1+bp-c(1-p)}{1}$

So if $bp-c(1-p)>0$ then the strategy of 'accept' should be adopted.

$$bp - c(1-p) > 0 \text{ translates to } p > \frac{c}{b+c}$$

So females should choose the strategy of 'accept' extra-pair copulations (or again, decide to actively solicit EPCs themselves) if the proportion of males in the population better than their own is greater than $p > \frac{c}{b+c}$. This is Helena.

It is important to remember that b and c are not the benefits and costs of a single EPC, but simply the benefits of copulating with a superior male, and the costs of copulating with an inferior male, both with respect to the quality of the original partner.

If we assume a normal distribution of male quality in the population, then the females mated to each individual male have the p-variables indicated:

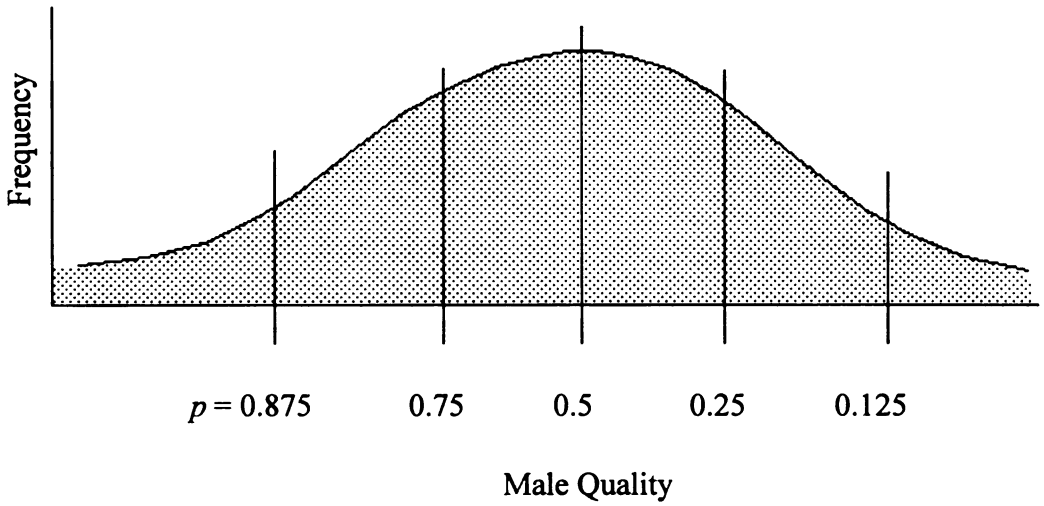

Figure 1. Proportions of males superior to the female's attending male for females mated to males of differing genetic quality.

But not only are the p-variables different for each individual female, the values of b and c are also, since if a female has a p-variable of 0.125, she will obviously not benefit from an extra-pair copulation with a superior male as much as a female with $p = 0.875$. It is the differences between b and c (or the ratios of b/c) that are crucial in determining which strategies are adopted, these required ratios being easily calculated as follows:

If $p = 0.25$ (i.e. the female's partner is better than 0.75 of the population) then for 'accept' to be adopted then $0.25 > \frac{c}{b+c}$, which translates to $b > 3c$, i.e. the benefits must be at least three times as great as the costs.

If $p = 0.5$, then $0.5 > \frac{c}{b+c}$, giving $b > c$.

And if $p = 0.75$, then $0.75 > \frac{c}{b+c}$, giving $b > c/3$, i.e. the benefit of an EPC with a superior male need only be a third as much as the cost of copulating with an inferior male. This is perfectly logical since when $p = 0.75$, on average three out of four interactions will be with superior males, i.e. p may not only be seen as proportion of superior males in the population, but also as the probability of accepting an EPC from a superior male, given that a strategy of accept has been adopted. For example, arbitrarily, if $p = 0.75$, $b = 5$ and $c = 16$ ($\frac{c}{b+c} = 0.76$) then 'reject' should be adopted, however if $p = 0.75$, $b = 5$ and $c = 14$ ($\frac{c}{b+c} = 0.73$) then 'accept' should be adopted. If the latter turns out to be the case, then the probability of that EPC being with a superior male is 0.75.

Helena, the p-Variable and Benefit-Cost Ratios

Figure 2 shows the minimum benefit: cost ratios required for a strategy of 'accept' to be adopted.

If the benefit-cost ratio is greater than that given by the Helena Curve for any given p-variable, then a strategy of accept should be adopted, and below the line; reject. It is now theoretically possible to determine *p* for each female; observe whether or not females perform EPCs for any given value of *p*; then tracking back (using the $p > \frac{c}{b+c}$ equation and fig. 2) to find the relative values of *b* and *c*.

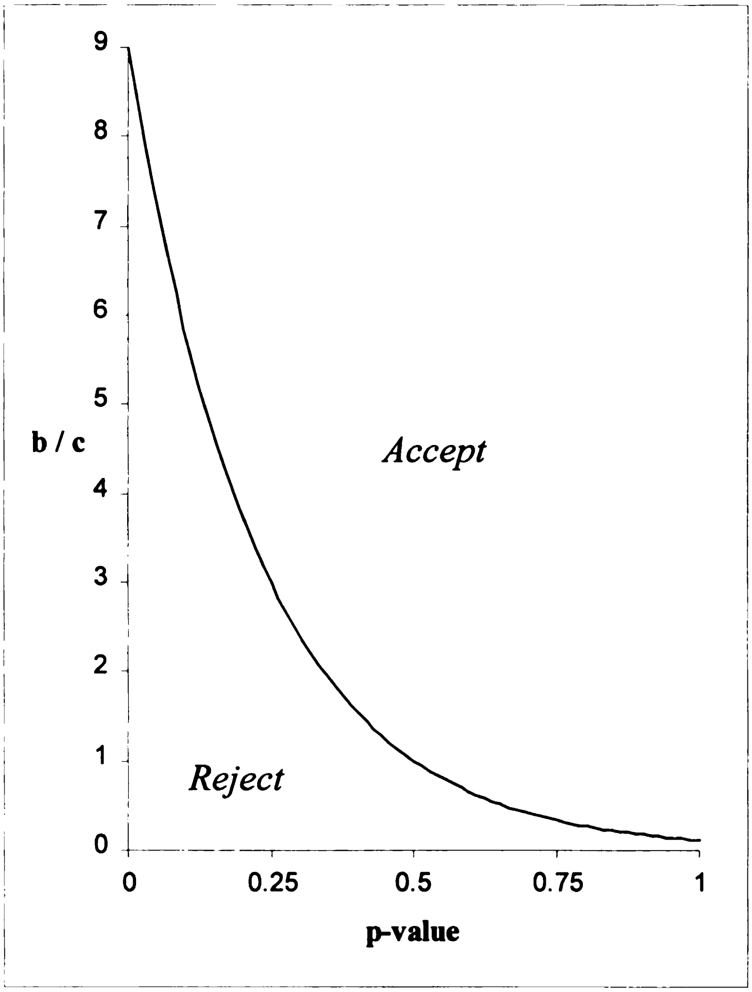

Figure 2. The minimum benefit-cost ratios required for a strategy of accept to be adopted.

For example, suppose the following data from a group of 7 females:

Table 1. Hypothetical field observations of EPC behaviour from a subset of a population.

p - variable	Accept or Reject EPCs
0.9	Accept
0.75	Accept
0.67	Accept
0.5	Accept
0.33	Accept
0.25	Reject
0.1	Reject

From the change from accept to reject between p-variables of 0.33 and 0.25, and from looking back to $\frac{c}{b+c}$ and fig. 2, it can be seen that these represent ${}^{b}\!/_{c}$ ratios of 2 and 3 respectively. One *cannot* assume from this data that for *all* females, the benefits of copulating with a superior male are between 2 and 3 times as great as the costs of copulating with an inferior male, since as stated above, b and c values are different for each p-variable. We can only deduce a relationship between b and c for each individual:

Table 2. The relationship between the benefits and costs of EPC behaviour for the subset of individuals.

p - variable	Accept or Reject EPCs	Relationship between b and c
0.9	Accept	$b > c/9$
0.75	Accept	$b > c/3$
0.67	Accept	$b > c/2$
0.5	Accept	$b > c$
0.33	Accept	$b > 2c$
0.25	Reject	$b < 3c$
0.1	Reject	$b < 9c$

We can now go on to plot this information onto figure 2, in order to show in which portions of the graph our population lies (shown by the 'Accept' and 'Reject' regions below).

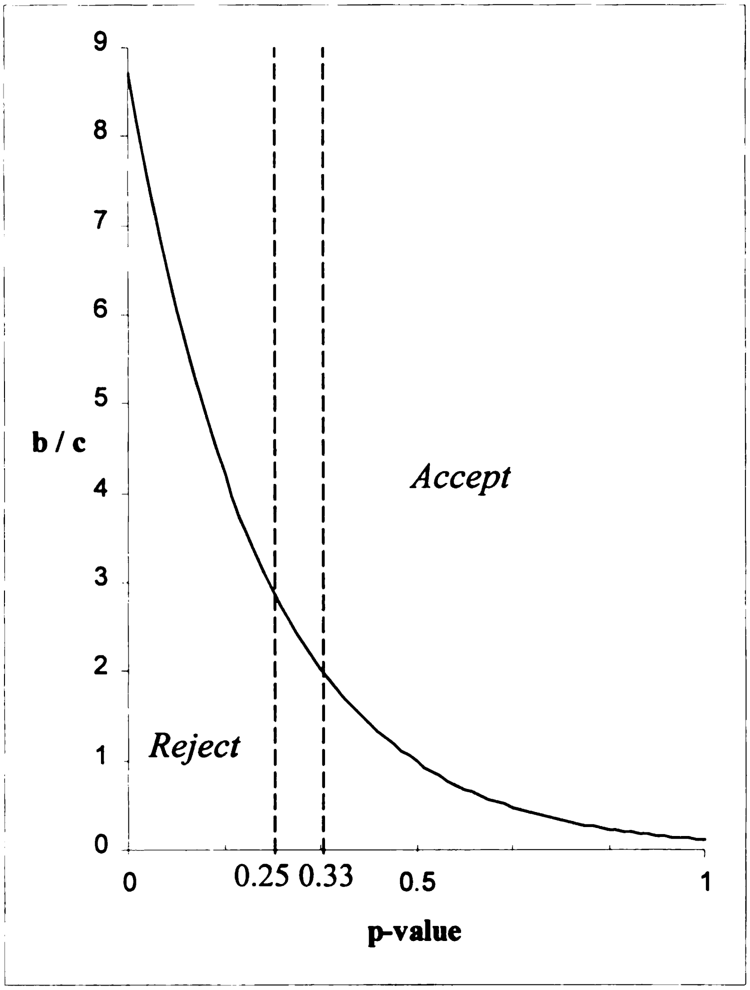

Figure 3. Hypothetical field observations applied to the minimum benefit-cost curve.

No conclusions may be drawn concerning the area between $p=0.25$ and $p=0.33$, since we have no data from within this transitional area.

It is important to note that this graph only represents one moment in time. Both the costs and benefits of the EPCs are transient quantities, liable to change at any time due to a number of factors, such as changes in the male population structure, the time in the breeding season or even participation in an EPC. This point also influences one of the predictions of the original proposition:

Since females are choosing strategies of 'accept' or 'reject' even before being confronted by a prospective EPC male, one would expect them to either reject all solicitations or accept the first that comes along,

I.e. (where R = reject and A = accept)

Either R, R, R, R
Or A, A, A, A
But not R, R, R, A

But since b and c may change, and performing an EPC is one factor that may change these quantities, we may get A, R, R, R.

As a consequence, interesting insights into the factors that mediate such sexual behaviours may be gained from observing a change in strategy. For example, instead of interpreting the behaviour of rejecting a number of EPC propositions and then accepting one as being characteristic of a female only wishing to copulate with a male of preferred quality, rather we may investigate the factor that have caused a change in the cost: benefit ratio to now make EPCs preferable.

One of the predications of the model outlined above is that the predisposition of a species or population to engage in EPCs will depend upon the degree of variation in perceivable male quality. The important determinants of EPC behaviour are not only those factors that affect the relationship of *b* and *c*, but also those that control *p* and the female's interpretation of *p*. It is therefore reasonable to presume that the a larger distribution of male quality (i.e. of greater variance) will lead to a higher frequency of EPCs, since with a reduction in male quality variance we have a resultant drop in the possible values of *b* and *c*, and a corresponding drop in the female's ability to assess graduations in *p*. This prediction is examined later in this work.

The Strategies Compared

The Hermia strategy (only accept EPCs from superior males) predicts that all EPCs that are observed will be with males superior to the female's current partner (assuming perfect discrimination on behalf of the female). Will Helena result in some EPCs being with inferior males (as is often the case in the data) and will the proportions of EPCs with superior males be comparable between the two strategies?

1) Hermia.

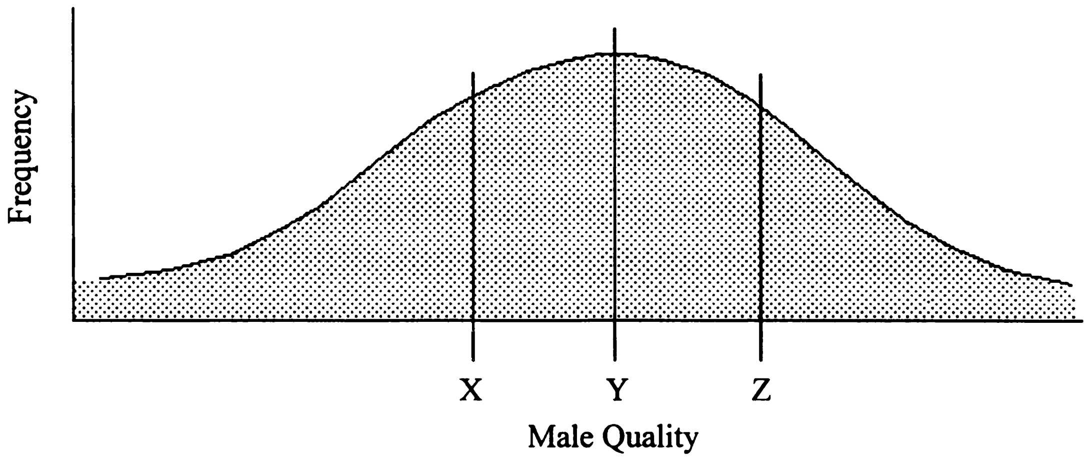

Figure 4. A Gaussian distribution of male quality and the Hermia strategy.

I.e. A female mated to male Y will accept an EPC from Z, but not with X. So 100% of EPCs will be with superior males. It is important to remember that we are only concerned with EPCs in which the females choose (i.e. Accept or Reject, or actively seek) and not forced EPCs.

2) Helena.

Take 10 females mated to 10 males, with male quality distributed as follows:

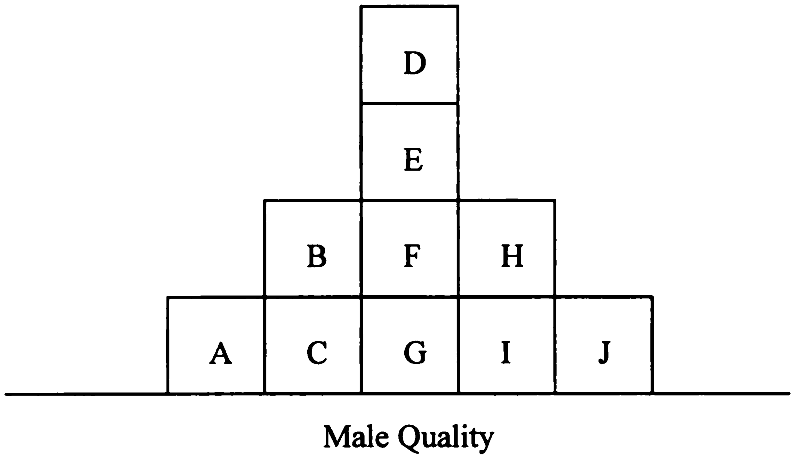

Figure 5. Discrete distribution of male quality in a population of ten males mated to ten females.

The p-variables (proportion of males in the population superior to their own mate) will be as follows:

A: $p = 1$

B & C: $p = \frac{7}{9}$

D, E, F & G: $p = \frac{3}{9}$

H & I: $p = \frac{1}{9}$

J: $p = 0$

Let us make the assertion that:

Moving up one place gives a benefit of one, up two gives two and so on. Similarly, moving down one place has a cost of one, down two gives a cost of two, and so on. For example, if a female mated to B accepts an EPC with H, she will receive a benefit of 2. For the purposes of this example, there are no costs or benefits associated with accepting an EPC from a male of equal quality to their own.

We can now calculate the average benefit and cost to each female of accepting an EPC:

For A: Benefit: $\frac{((2\times1)+(4\times2)+(2\times3)+(1\times4))}{9}=2.22$

Cost: 0

For B & C: Benefit: $\frac{((4\times1)+(2\times2)+(1\times3))}{7}=1.57$

Cost: $(1\times1)=1$

For D, E, F & G: Benefit: $\frac{((2\times1)+(1\times2))}{3}=1.33$

Cost: $\frac{((2\times1)+(1\times2))}{3}=1.33$

For H & I: Benefit: $(1\times1)=1$

Cost: $\frac{((4\times1)+(2\times2)+(1\times3))}{7}=1.57$

For J: Benefit = 0

$\text{Cost} = \frac{((2\times1)+(4\times2)+(2\times3)+(1\times4))}{9}=2.22$

Now putting these values in to the equation 'Accept if $p > \frac{c}{b+c}$':

For A: $1 > \frac{0}{(2.22+0)}$ Therefore Accept

For B & C: $7/9 > \frac{1}{(1.57+1)}$ Therefore Accept

For D, E, F & G: $3/9 < \frac{1.33}{(1.33+1.33)}$ Therefore Reject

For H & I: $1/9 < \frac{1.57}{(1+1.57)}$ Therefore Reject

For J: $0 < \frac{2.22}{(0+2.22)}$ Therefore Reject

So with Helena, the only females that should accept EPCs are those mated to A, B and C, whilst with Hermia, all females except that which is mated to male J will potentially participate in EPCs. The word 'potentially' is important here, since although 9 out of 10 Hermia females could plausibly partake in such behaviour, the likelihood that they would do so depends on the quality of the male encountered, since not all encounters will be with superior males. We can calculate the probability of any individual EPC proposition being accepted by simply totaling the fraction of superior males for each female and dividing by the total number of females:

$$\frac{1}{10}\left(1+\left(\frac{7}{9}\right)+\left(\frac{7}{9}\right)+\left(\frac{3}{9}\right)+\left(\frac{3}{9}\right)+\left(\frac{3}{9}\right)+\left(\frac{3}{9}\right)+\left(\frac{1}{9}\right)+\left(\frac{1}{9}\right)\right)=0.411$$

Since this prerequisite of higher quality does not apply to the Helena females, then for them the probability of any EPC proposition being accepted is simply the fraction of females that fall into the accept category, i.e. 3 out of 10.

It is also interesting to compare the two strategies in relation to the fraction of EPCs that are with inferior and superior males. For Helena, 100% of A's EPCs will be with superior males, and 8 from 9 (88.9%) of B and C's will be with equal or superior males. So any single EPC observation will have a probability of $\frac{(1+0.889+0.889)}{3} = 0.926$ of being with an equal or superior male, and 1 minus this number (7.4%) will be with inferior males. Needless to say that with Hermia, all EPCs will be with superior males.

All this is shown with greater clarity in Table 3 below.

Table 3. Comparisons of predicted EPC activity under strategies of Hermia and Helena in populations of ten couples.

	Hermia	Helena
Number of females.	10	10
Number of females potentially participating in EPCs.	9	3
Probability of any EPC proposition being accepted.	0.411	0.3
Probability of any one of the EPCs being with an equal or superior male.	1	0.926
Probability of any one of the EPCs being with an inferior male.	0	0.074

So what insights may be gained from this? First of all, with Helena we can expect some EPCs to occur with males of lesser quality than the attending male, which as mentioned above, is in line with most published data. We may also test empirically the difference in the probability that any EPC proposition in the population will be accepted (in this case: Hermia 0.411, Helena 0.3). Further modelling would need to be performed to assess how these figures vary over different population sizes and different levels of genetic variation (see later), but it appears possible that once a predictor of this factor had been developed, one could distinguish between Hermia and Helena in the field.

EPCs and Genetic Variation

Let us now examine the relationship between EPC frequencies and genetic variation that I mentioned briefly on page 16.

The model outlined above assumes that females are able to assess the quality of their partner with respect to that of the other males in the population and make their decision to accept or reject EPCs based on this assessment along with the average benefit gained from an EPC with a superior male and the average cost of an EPC with an inferior male. As a consequence, the number of females participating in EPCs will be a function of the amount of variation in male quality, since more females will have the propensity to engage in EPCs when there are greater differences in the quality of potential fathers. The connection between the variation in male quality and genetic variation is made by assuming that total genetic variation is positively correlated with the additive genetic variation of the fitness-related traits[22].

Below (figure 6) we have three populations, each consisting of nineteen females mated to nineteen males, with male quality distributed as indicated.

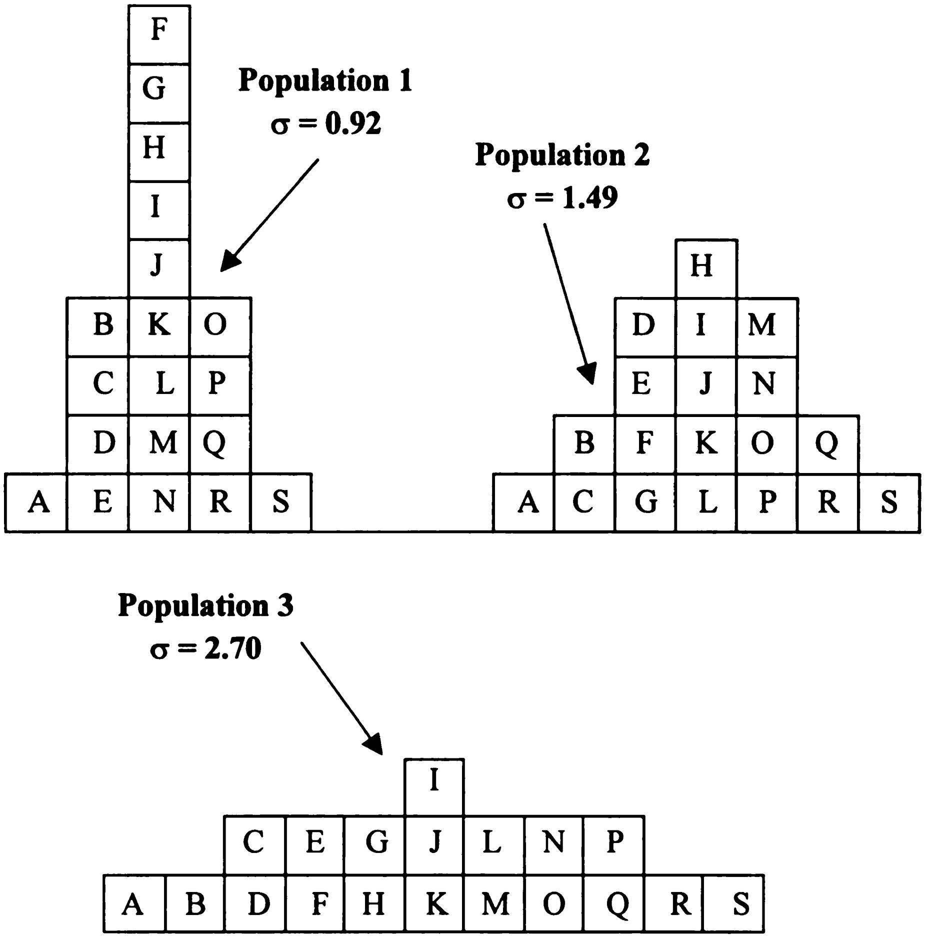

Figure 6. Three discrete populations with differing levels of male genetic variation.

To keep things simple, let us take the same cost-benefit payoff system as we did previously, i.e. moving up one place gives a benefit of one, up two gives two and so on. Similarly, moving down one place has a cost of one, down two gives a cost of two, and so on. The actual cost-benefit payoff system that we choose to use is unimportant; varying it in terms of making the costs or benefits more or less important with relation to the other will only increase or dampen the resulting trends. Under this scenario, the average benefits and costs to each female of participating in an EPC can be calculated, as is shown in table 4.

Table 4. Average benefits and costs of participating in EPCs for each female in three populations with different levels of genetic variation.

	Population 1		Population 2		Population 3	
Female	Benefit	Cost	Benefit	Cost	Benefit	Cost
A	$\frac{4+18+12+4}{18}=2.11$ 2.11	0	$\frac{2+8+15+16+10+6}{18}=3.17$ 3.17	0	$\frac{1+4+6+8+15+12+14+16+9+10}{18}=5.27$ 5.27	0
B	$\frac{9+8+3}{14}=1.43$ 1.43	1	$\frac{4+10+12+8+5}{16}=2.44$ 2.44	1	$\frac{2+4+6+12+10+12+14+8+9}{17}4.53$ 4.53	1
C	1.43	1	2.44	1	$\frac{2+4+9+8+10+12+7+8}{15}=4$ 4	$\frac{1+2}{2}=1.5$ 1.5
D	1.43	1	$\frac{5+8+6+4}{12}=1.92$ 1.92	$\frac{2+2}{3}=1.33$ 1.33	4	1.5
E	1.43	1	1.92	1.33	$\frac{2+6+6+8+10+6+7}{13}=3.46$ 3.46	$\frac{2+2+3}{4}+1.75$ 1.75
F	$\frac{4+2}{5}=1.2$ 1.2	1.2	1.92	1.33	3.46	1.75
G	1.2	1.2	1.92	1.33	$\frac{3+4+6+8+5+6}{11}=2.91$ 2.91	$\frac{2+4+3+4}{6}=2.16$ 2.16
H	1.2	1.2	$\frac{4+4+3}{7}=1.57$ 1.57	1.57	2.91	2.16
I	1.2	1.2	1.57	1.57	$\frac{2+4+6+4+5}{8}=2.63$ 2.63	2.63
J	1.2	1.2	1.57	1.57	2.63	2.63
K	1.2	1.2	1.57	1.57	2.63	2.63
L	1.2	1.2	1.57	1.57	2.16	2.91
M	1.2	1.2	1.33	1.92	2.16	2.91
N	1.2	1.2	1.33	1.92	1.75	3.46
O	1	1.43	1.33	1.92	1.75	3.46
P	1	1.43	1.33	1.92	1.5	4
Q	1	1.43	1	2.44	1.5	4
R	1	1.43	1	2.44	1	4.53
S	0	2.11	0	3.17	0	5.27

The p-variables can then be calculated as before, and by applying these, along with the benefits and costs to our original $p > \frac{c}{b+c}$ equation, we get table 5. Only the females up to and including the first to reject are shown, since all females mated to higher quality males will reject also. The females participating in EPCs are shown more clearly in the shaded regions in figure 7.

Table 5. Predicted number of females that would accept or reject EPCs in three populations with different levels of genetic variation.

Population 1			
Females	$p > \frac{c}{b+c}$?	**Accept or Reject?**	**Total**
A	$1 > \frac{0}{2.11+0}$	Accept	**5 Accept**
B, C, D & E	$0.77 > \frac{1}{1.43+1}$	Accept	
F, G, H, I, J, K, L, M & N	$0.277 < \frac{1.2}{1.2+1.2}$	Reject	
Population 2			
A	$1 > \frac{0}{3.17+0}$	Accept	**7 Accept**
B, C	$0.89 > \frac{1}{2.44+1}$	Accept	
D, E, F & G	$0.67 > \frac{1.33}{1.92+1.33}$	Accept	
H, I, J, K & L	$0.39 < \frac{1.57}{1.57+1.57}$	Reject	
Population 3			
A	$1 > \frac{0}{5.27+0}$	Accept	**8 Accept**
B	$0.94 > \frac{1}{4.53+1}$	Accept	
C & D	$0.83 > \frac{1.5}{4+1.5}$	Accept	
E & F	$0.72 > \frac{1.75}{3.46+1.75}$	Accept	
G & H	$0.61 > \frac{2.16}{2.91+2.16}$	Accept	
I, J & K	$0.44 < \frac{2.63}{2.63+2.63}$	Reject	

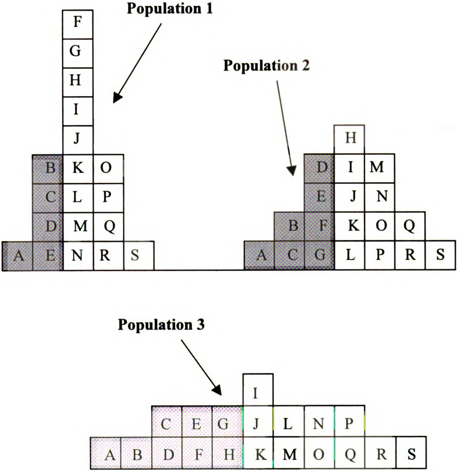

Figure 7. The females that have the propensity to engage in EPCs in three populations of differing levels of male genetic quality.

So one factor that appears to be important in determining levels of EPP are the population levels of variation for fitness related genes, so it appears possible to use these measures of variation to predict levels of polygamy. This idea is beginning to gain increasing support from the literature; a study by Pertie et. al.[23] has found differences in the proportion of extra-pair young were significantly positively correlated with the proportion of polymorphic loci, whilst another by Griffith[24] has compared island populations with those on the mainland and found that island populations are indeed characterized by low levels of EPP.

In addition, the probability that any of the EPCs are with an equal or superior male also varies between the three populations. These probabilities are as follows:

Table 6. The probabilities that any accepted EPC will be with a male equal or superior to the female's attending male, in three populations of differing genetic variation.

Population 1	$\dfrac{1+4\left({}^{17}\!/_{18}\right)}{5} = 0.956$
Population 2	$\dfrac{1+2\left({}^{17}\!/_{18}\right)+4\left({}^{15}\!/_{18}\right)}{7} = 0.889$
Population 3	$\dfrac{1+\left({}^{17}\!/_{18}\right)+2\left({}^{16}\!/_{18}\right)+2\left({}^{14}\!/_{18}\right)+2\left({}^{12}\!/_{18}\right)}{8} = 0.826$

So as variation in male genetic quality increases, the probability that any extra-pair copulation is with an equal or superior male decreases. One more testable prediction.

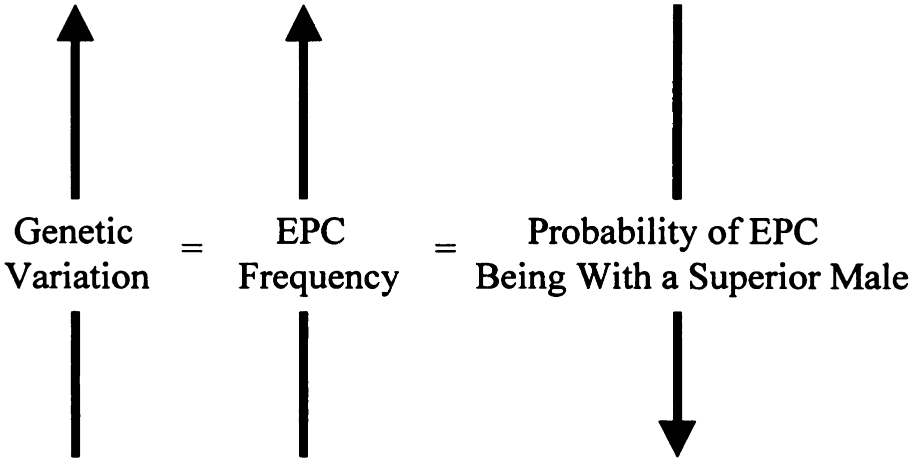

Figure 8. As additive genetic variation in the population of males increases, the frequency of females participating in EPCs also increases, yet the probability that any one of these EPCs is with a male superior in quality to her partner decreases.

EPCs, Genetic Variation and Population Size

We now have a clear relationship between the number of females in a population that will potentially participate in EPCs and the amount of additive genetic variation in the population, so let us now examine how this relationship varies with regard to the population size.

Four conceptual populations of differing sizes were set up, containing 11, 21, 31 and 41 mated couples, i.e. 22, 42, 62 and 82 individuals in total. The variation in male quality was assumed to follow as close to a normal distribution as was possible. You may recall from the three populations examined above that in the case of symmetrical distribution of quality, the model predicted that all females mated to males to the left of the median bar would potentially participate in EPCs, and all those on and to the right of the median bar fell into our reject category. This statement, although true in this case, only applies to this specific benefit-cost scenario. If one refers back to figure 2 and the calculations that surround it, we can see that when $b = c$ (i.e. $b/c = 1$, the cost-benefit ratio used in this analysis) then the p-variable that we find on the accept / reject crossover line is 0.5. Since the median bar in this inquiry is representative of $p = 0.5$ one would therefore expect (strongly, because within the confines of this model and its cost-benefit payoff system, no other result is possible) that those females that are unfortunate enough to have males that fall shy of this condition (left of the median bar, and $p > 0.5$) to slide into the accept category, whilst the males of high quality (right of the median bar, and $p < 0.5$) avoid the embarrassment of cuckoldry.

Taking this, we can now vary the number of females participating in EPCs by simply varying the size of the median bar, and then calculating the variation in the population. The size of the median bar is calculated by simply subtracting $2 \times$ the number of females participating in EPCs from the population size. The measure of variation used was the standard deviation. How this relates to the ratio of polymorphic loci or gene diversity measure is another question, but since all three attempt to measure essentially the same thing, the standard deviation will suffice. An example of how the variation measures were calculated is shown below.

In this example (figure 9), $n = 11$ (the number of couples) and e represents the number of females participating in EPCs.

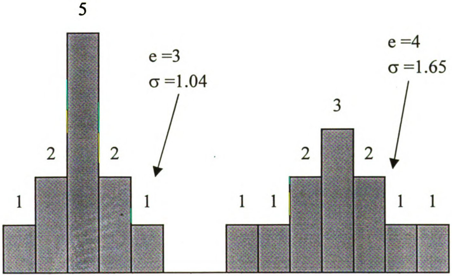

Figure 9. Example of distributions used to calculate required levels of variation.

This process was repeated for each number of females that would potentially participate in EPCs (i.e. up to $\frac{n-1}{2}$, re. Left of the median bar statement above) for each of the four population sizes. The results are shown in Figure 10 below, in terms of an estimate of the variation required in a population for one to observe x-number of females participating in EPCs. The data has been significantly smoothed since each distribution (such as those above) could have been set up in a number of different ways (e.g. for the set on the left consider 3-5-3 instead of 1-2-5-2-1), besides, we are only concerned with relatively general trends. Once again, n refers to the number of couples (or males, or females). Despite the fact that in my calculations the number of females participating in EPCs was the dependent variable, the axes could be switched to represent the actual order of biological dependency.

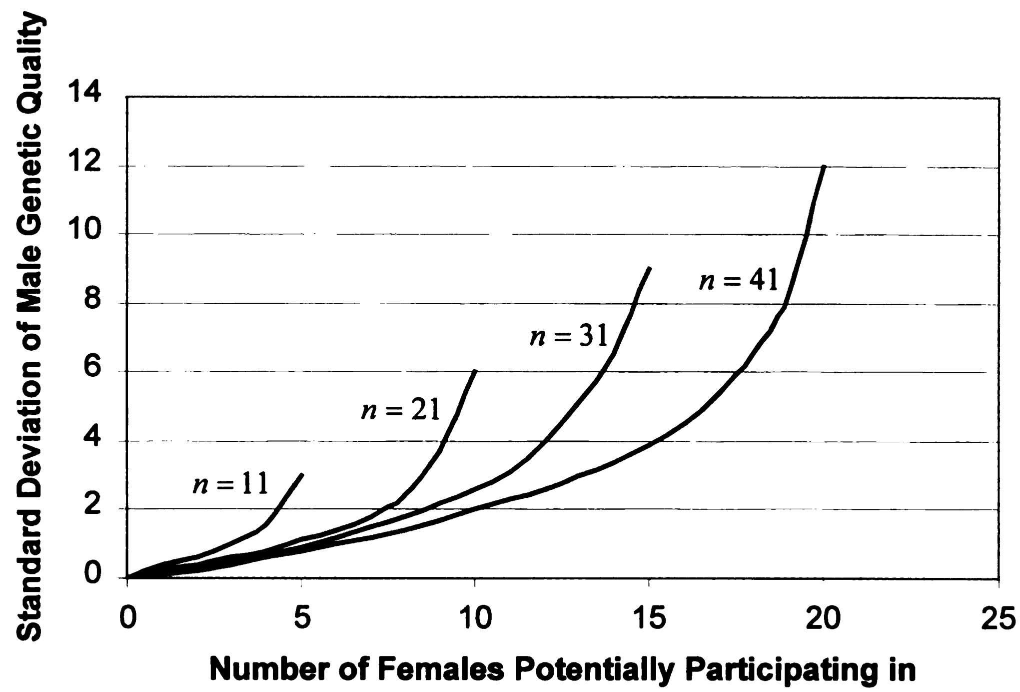

Figure 10. The genetic variation required for x-number of EPCs decreases with increasing population size.

The trend is self-evident. At larger population sizes, the genetic variation required for a fixed number of females to have the potential to participate in EPCs decreases. Looking at it another way, a fixed level of variation will result in a greater number of females inclined to partake in EPCs in larger populations. What observations would authenticate such a prediction? Proportionally higher EPC frequencies at higher population sizes.

A Note on Inbreeding Depression

With the present model, we so far have increasing EPC frequencies with increasing male genetic variation, a trend that may be attributed to the increase in the probability of an EPC resulting in a step up the good genes ladder, and is one that rings true with the published data on the subject[22, 23, 24]. We must now consider the other potential indirect genetic benefit to the female of participating in EPCs, that being increasing the genetic variation of her offspring. If females were participating in EPCs to reduce the risk of inbreeding then one might expect an EPC frequency - genetic variation trend contrary to that expected under a good genes strategy since the risk of inbreeding will decrease with increasing genetic variation. That is, one would expect higher frequencies of EPCs in populations with low genetic variation, rather than the opposite as Helena predicts. However, it is difficult to see the significance of such a prediction since as mentioned above, not only does the published data, however limited, support the good genes trend, but also the occurrence of inbreeding depression has been observed so rarely in wild bird populations (Donald Beaver; personal communication) that the strength of selection against it is unlikely to be particularly strong. It has also been pointed out that competition between unrelated individuals within broods would probably negate any advantages that may ensue from increased diversity[12, 25].

If increasing offspring variation were the sole motivation behind EPCs, then we would see drastically different selection criteria by the females when choosing EPC males than with the strategies discussed above. As is shown below, one would expect there to be no female preference for EPC-male quality, since as is with recombination itself, any initial reduction in offspring mean fitness would theoretically be offset by the greater variation within the brood.

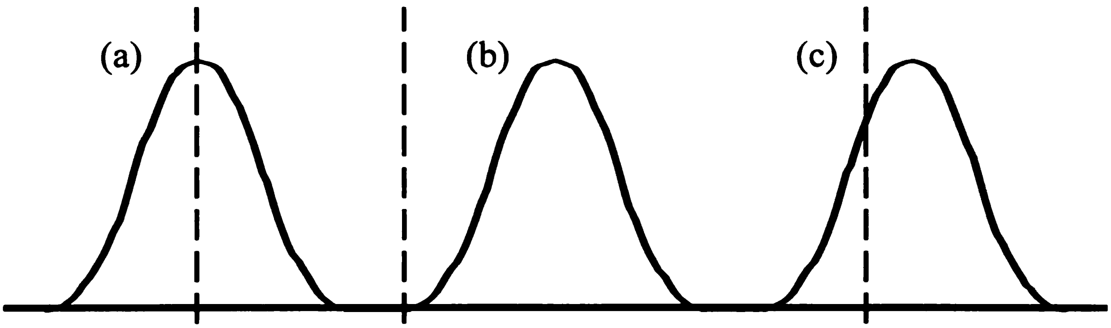

Figure 11. Distributions reflecting the quality of potential EPC-males with respect to the quality of the current partner (dashed line). (a) Increasing the genetic variation of the offspring; any EPC male will do just fine. (b) "Hermia"; only superior males are considered. (c) "Helena"; most EPCs are with superior males.

Finally, it is often found that the distribution of extra-pair offspring between broods is skewed, with most broods having either all or no offspring fathered by an extra-pair male[26], thereby negating the EPC's genetic variation benefit. Be sure to note that this reasoning does not necessarily apply to the male's motivation for engaging in EPCs, but his concerns are outside the realms of this piece of work (although having more offspring sounds like a pretty safe bet).

These arguments are probably sufficient to excuse me from attempting to squeeze genetic variation benefits into my model of female choice, but I shall mention one more reason for their exclusion. If inbreeding depression countermeasures were allowed entry then one would be pushed to justify leaving out the myriad of other potential costs and benefits of EPCs that one sees in the literature from time to time. As with the avoidance of inbreeding depression, these direct factors (such as guarding against defects from prolonged sperm storage or the avoidance of rejection costs, see reference 6 for a comprehensive list) only apply, if at all, to certain species, populations or even individuals, and so have no real place in a general model of choice behaviour. One is therefore forced to return to the one thread that runs throughout all female birds' attitudes towards extra-pair copulations, that being the genetic quality of their offspring.

Some Conclusions

- Helena appears to be a viable alternative strategy to Hermia and allows us to begin quantifying the indirect genetic benefits of EPCs to females.

- Helena predicts that a small number of EPCs will take place with males that inferior in quality to the female's attending male, in line with the literature.

- If we are to assume that females' motivation to participate in EPCs is to increase the genetic quality of their offspring, then we can expect higher levels of EPP with higher population levels of variation for fitness related genes.

- Helena predicts that he variation required for a fixed number of EPCs decreases with increasing population size.

Some Future Directions

- To develop a more general predictor of levels of EPCs and EPP to allow distinction between Hermia and Helena in the field.
- To model Helena analytically to avoid the constraints and lack of clarity that arises from the probability approach with discrete populations.
- To develop field studies to test the various predictions of Helena.

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