Sexual Dimorphism and Sexual Selection: A Unified Analysis[1]

Rough and Preliminary Draft

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Abstract: We develop a life history model with two sexes, and study the optimal energy allocation strategy of males and females. We join others in suggesting that the origin of sexual dimorphism and sexual selection is the difference between male and female reproduction costs. Due to this assumed cost difference, the resulting Bellman equations of gene dynamics in our two-sex life history model imply a large "energy surplus" on the part of males. This allows the male form to devote energy to the development of some male traits that help the males to compete for access to females. Eventually, this competition leads to the dimorphism of sex-specific traits. Using this life history model, we are able to explain many features of sexual dimorphism, as well as why males often transfer less to their offspring than do females, and why only females have menopause.

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1 Introduction

Over the past two decades a number of researchers (e.g. Bergstrom [1995], Rogers [1994], Robson and Kaplan [2003], Chu and Lee [2006, 2008]) have applied economic approaches to study various characteristics of species. A recent survey of such literature can be found in Cox (2007). A topic mentioned but not seriously studied in the economics literature is *sexual dimorphism*, a phenomenon that male and female adults possess significantly different biological traits, whereas the juveniles are much similar. In Cox (2007), some brief discussion and a classic article by Trivers (1972) were provided. A related area of discussion is sexual selection, where females choose their male mates according to some observed traits. In this paper we shall propose a unified economic theory that can explain most features we observe in sexual dimorphism and sexual selection.

1.1 Previous Literature

A brief introduction to the biological literature should be helpful to general readers. According to Maynard Smith (1991), there are two broad types of sexual interactions: *intrasexual* competition and *intersexual* selection. The latter involves both male traits and feale preferences; and the former does not consider the preference side of females, but emphasizes the male-male competition. It is well known from the research of evolution that sexual dimorphism is highly correlated with sexual competition, which refers to the competition (and the resulting equilibrium) of mating partners by organisms. In reality, this competition is usually between males.

For intrasexual competition, the classic article is a contribution by Trivers (1972). He argued that *relative parental investment* is the key to understand sexual competition. By parental investment, Trivers means “any investment by the parent in an individual offspring that *increases the offspring’s chance of surviving* (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring" (p.139). >From the italic we added and the discussion in his paper, we know that the resources Trivers refers to are mostly parental transfer after the offspring is born. But from the persepctive of life history, parental transfers are *endogenous* control variables chosen by organisms in their lifetime. We believe that sex dimorphism can be explained by more fundamental *exogenous* elements of species.

Other than Trivers (1972), Emlen and Oring (1977) emphasized the importance of operational sex ratio (OSR) on sexual selection, where the OSR is defined as the ratio of fertilizable females to active males. In practice, the OSR is evidently related to ecological, geographical, and spatial factors that may influence the environment of male-female interactions. In Kokko and Johnstone (2002), they considered the joint influence of parental investment, mortality, mate-encounter rate and OSR, and concluded that the importance of parental investment outweighs that of OSR. In this paper, we leave most environmental factors to the background, and concentrate on the role of parental investment.

In the analysis of sexual interaction, the literature is sometimes troubled by the *correlation* of dimorphic traits with other observations, and its interpretation. For instance, Leutenegger and Choverud (1982) found a correlation between sexual dimorphism and body size and provided some analysis; however, Gaulin and Sailer (1984) suggested a very different interpretation of the same correlation. Partly because of this difficulty of interpretation, we set up a *life history model* to analyze the problem of sexual dimorphism. In the framework of an optimal life history, species' traits such as body size and tooth size are control variables chosen by species, and the interpretation of implications follows naturally from the model. Basically, the only fundamentals in a life history model is the energy coefficients of various controls, and we shall interpret most observations by sex-specific differences based upon such fundamentals. For instance, we go beyond Trivers (1972) and differentiate after-birth parental transfers from fertility costs, which were both treated as investments by Trivers. As we mentioned, we believe that sex-specific fertility costs are fundamentals to the evolution, whereas parental transfers are something species choose in the process of evolution. Distinguishing such is important to the understanding of evolutionay dynamics. For example, our theory suggests that viviparous species are likely to have sexual dimorphism, for viviparous males and females have drastically different reproduction costs.

For intersexual selection, Zahavi (1975) argued that males may have some advantageous traits which are unobservable to females. In this case, males may use a seemingly useless trait (a handicap), such as the plumage of some birds, to signal his superior quality to females. However, Fisher (1958) and Lande and Arnold (1985) all pointed out that the evolution of such trait-preference may be selectively neutral. Using a simple 2-trait 2-allele model, Kirkpatrick (1982) showed that even the initial selective advantages of evolution are not necessary. This pretty much makes the evolutionay outcome of intersexual selection indeterminate. Later, Iwasa et al. (1991) showed that this neutrality result breaks down if there is a small cost of female searching. They also demonstrated that the handicap hypothesis is valid only if there exists a connection between male trait and viability parameters. Using our model we are able to provide a neat economic interpretation for this handicap hypothesis.

1.2 Contribution of this Paper

The existing literature explains various features of sexual dimorphism and sexual selection using different models, including quantitative genetics (Iwasa et al. [1991]), Malthusian competition (Hausken and Hirshleifer [2008]), and descriptive analysis (Trivers [1972]). In this paper, we propose a unified framework of two-sex life history along the lines of Stearns (1972) that can explain all related features comprehensively.

We suggest that the origin of sexual dimorphism and sexual selection proposed by (Darwin 1871) is the difference between male and female reproduction costs: the cost of producing sperms is trivial for males and that of producing eggs by females is significantly larger, not to mention the cost of pregnancy and delivery for many viviparous species. We study the optimal energy allocation strategy of male and female genes along a life history. Due to the cost difference of reproduction, the resulting Bellman equations of these genes imply a large “energy surplus" on the part of males. This leaves the male gene the room of a mutation, which commands a shift of such surplus energy to the growth of some male traits that help the males' sexual competition. The condition of a successful invasion of such a mutation can be derived.

Consider the scenario that many males compete to become an alpha male, who has the dominant privilege to mate. Since there is only a small chance to be an alpha male, ex ante each male child can be seen as a risky lottery: [having a small probability to mate many females and a large probabilty to mate none]. For female children, they almost surely can mate with the alpha male, and hence the correspondig lottery is a degenerated one. >From the parents' point of view, treating their children as assets of proliferating their genes, the parents actually have a (sex-specific) portfolio of children, some (males) are high-risk high-return, and some (females) are low-risk and low-return. We shall explain why this is an optimal design arising from a life history model.

The male competition leads to the growth of some male traits, end eventually to the phenomenon of sexual dimorphism. Using this two-sex life history model we are also able to explain, for instance, why for most species males provide less intergenerational transfers than females, and why menopause only happens to females. Thus, we elaborate the discussion of Trivers (1972), and extend it to many other sex-specific differences that have not been analyzed in the literature.

1.3 Paper Structure

The rest of this paper is arraned as follows. Section 2 introduces some preliminaries and notations for later analysis. Sections 3-4 present the model of life history and energy constraints, and derive the Bellman equation for maximizing fitness. We discuss intrasexual competition, and relate various phenomena of sexual dimorphism to the difference of distinct sex-specific reproduction costs. Section 5 explains the optimality of male-female “child fortfolio". The sixth and seventh sections are about differences in male-female transfers and menopause. Section 8 covers the discussion of intersexual selection. The final section summarizes and concludes.

2 Event Order and Preliminaries

Suppose individuals live two ages, 0 and 1. There are two sexes. Let $M_{a,t}$ be the value of a male gene at age-a and time-t, and $F_{a,t}$ be the value of a female gene at age-a and time-t. Let m (f) be the reproductive effort by males (females), and $p_{a,m}$ ($p_{a,f}$) be the survival probability for males (females) aged-a. In practical context, m refers to the male effort of producing sperms and successful insemination, and f refers to the female effort of successful pregnancy and delivering. In each age, energy is assumed to be allocated into four uses: maintenance, reproduction, somatic growth and parental downward transfers.

We shall consider a determinate growth path; that is, the species in question grows but does not give birth in age 0, and then are capable of giving birth but stops growing in age 1.[3] There is not much complication about the decision by the growing juvenile: the age-0 just allocate their energy between maintenance and growth; but the event order of age-1 needs to be specified.

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[3] It is well known from the literature that a determinate growth will appear in a model of optimal life history if a linear energy constraint is assumed. See e.g. Chu and Lee (2006) for details.

We assume that at the beginning of age-1, each adult first hunts or forages, and gets some energy for this age. Then, each adult faces a "lottery", which specifies a probability distribution of reproduction privileges (to be explained below). We allow natural selection to determine the lottery that has the best fitness in evolution. For instance, for males, monogamy and polygamy are two different marriage-fertility lotteries. When the random outcome of the lottery is realized, each adult allocates the available energy to maintenance, transfers and reproduction. The nature then determines whether the adult would survive, and only survived ones can reproduce. The above event order is to some extent arbitrary, but is something we must specify in this discrete-time model. However, none of our results will be affected qualitatively if this order is changed.

In this 2-sex model, individuals of opposite sexes have to put together their reproductive effort in order to give birth an offspring successfully. However, one sex has to be the one that bears the child, and we use to call it "female". There are two unique features associated with the female sex. First, as Trivers (1972 p. 138) pointed out, for almost all two-sex specieis (and especially evident for viviparous ones), the metabolic energy of reproduction is particularly large for females, but is very small for males. Second, the male's reproduction effort may spread among many females, whereas the female's effort determines her final births. The first property specifies a difference in energy coefficient associated with reproduction, and technically, as we shall see shortly, the second property suggests an aggregation constraint on male/female numbers.

An innovation of our model is to specify marriage-reproduction as a lottery; this turns out to be a convenient setup for analyzing sexual selection. Let $\{m_1, m_2, \cdots, m_i, \cdots,\}$ be a vector of possible reproductive numbers for a male, and $\{f_1, f_2, \cdots, f_j, \cdots\}$ be the vector for a female. We assume that each individual adult faces a lottery: for $i = 1, 2, \cdots$, males have q_i probability of realizing m_i; and for $j = 1, 2, \cdots$, females have r_j probability of realizing f_j. From now on, unless otherwise specified, i is the index used for males and j is the index used for females.

We can think of lions as an example. Male lions have to fight for the privilege to mate females. We imagine that the result of this fight is specified as a lottery. For instance, a male has q_i probability of winning the privilege of impregnating m_i times in his adult age. We want to show that the evolved lottery for males is: [winning a large m_k with very small q_k, and winning zero females with $1-q_k$ probability]. This is the typical case of male competition. On the other hand, we also want to show that evolution usually does not result in female lionesses fighting for their right of reproduction; for sure each female can mate a male lion king, whoever he is. This is indeed the case for many species.[4] However, ex ante we intentionally specify f as a lottery instead of a singleton, and we will prove that it is a fitness maximization design for the female's degenerated lottery; that is, reproducing f_k for sure ($r_k = 1$) for a particular k.

Of course, we know that a male lion's privilege to mate is not a pure lottery; it may be related to their strength and body size, and may also drive the evolution of male/female somatic capital investment. At the first stage, we leave aside the male's decision of somatic investment, and then in later sections we shall come back and discuss some related issues. For instance, does the emancipated male usually provide less downward transfers than females? And how does our model accomodate with the ecological and territorial arguments of Brown (1964)?

3 The Two-sex Bellman Equations

We shall first write down the Bellman's principle of optimality for genes that maximizes their fitness, and then explain its meaining. Following Chu and

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[4] Many examples can be found in Trivers (1972).

Lee (2006), we see that the Bellman equations for selfish genes look like

$$\begin{aligned}
F_{0,t} &= \max\Big\{p_{0,f}F_{1,t-1}\Big\} \qquad \textbf{(B)}\\
M_{0,t} &= \max\Big\{p_{0,m}M_{1,t-1}\Big\}\\
F_{1,t-1} &= \max\Big\{p_{1,f}\sum_j f_j r_j\Big(\frac{M_{0,t-1}}{4}+\frac{F_{0,t-1}}{4}\Big)\Big\}\\
M_{1,t-1} &= \max\Big\{p_{1,m}\sum_i m_i q_i\Big(\frac{M_{0,t-1}}{4}+\frac{F_{0,t-1}}{4}\Big)\Big\}
\end{aligned}$$

In the above expression, the fitness maximization is over age-specific controls including $(p_{a,m}, p_{a,f}, q_i, r_j),\ a = 0, 1$ and some others to be described shortly. We assume that m_i and f_j are specified over a wide enough range, and hence the choice of q_i and r_j are enough to characterize the specification of the reproduction-privilege lottery. Because the aggregate number of impreganancy made by males must be equal to the aggregate number of pregnancy, there is a constraint relation between r_j and q_i, which we shall explain soon.

3.1 Interpreting the Bellman Equations

The interpretation of the Bellman equations is as follows. For the age-0, they only grow but do not give birth, therefore their gene value hinges upon the event of successfully surviving to age 1 one period later. This explains the first two equations. For female genes at age 1, the specification of the $F_{1,t}$ equation is straightforward. If a female lioness has f_j pregnancy, we assume, as in Trivers (1972 p.140) that the probability of having a newborn of either sex is 1/2.[5] The values of male and female genes aged-0 in the next generation are denoted respectively $M_{0,t-1}$ and $F_{0,t-1}$. Becuase each birth only carries 1/2 of the original gene, we divide the $M_{0,t-1}$ and $F_{0,t-1}$ by 4 (1/2 of either sex, and 1/2 of gene from either the male or the female line) on

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[5] Our purpose is to find the optimal life history $(q_i, r_j, p_{a,s})$ and to discuss sexual dimorphism; we do not see the value of a digression to disproportionate birth sexes here.

the right hand side of the third equation. The event of facing f_j pregnancy has probability r_j, therefore we take expectation over such events. This explains the $F_{1,t-1}$ equation.

If a lioness faces an f_j outcome, as far as her gene succession is concerned, she will definitely reproduce f_j succession of her gene, regardless with whom she mates. But for a male gene, if he face a lottery (m_i, q_i), we know that this lottery will be feasible only if it is consistent with the capacity of female pregnancy. Specifically, the total number of effective impregnancy, which is $\sum_i m_i q_i$ times the number of age-1 males, must be equal to the total number of pregnancy, which is $\sum_j f_j r_j$ times the number of age-1 females. This aggregation constraint must be taken into account as we solve the Bellman equation listed above. Indeed, this is a fundamental difference between male and female reproduction. This character origins from the sole fact that the females is the sex that is pregnant and bears the child.

Replacing the controls by their optimum, we can iterate the Bellman equations to obtain the dynamic equations for $(M_{0,t}, F_{0,t})$, as in Chu and Lee (2006). The dimension of state variables can be further reduced, once we observe that we can define $x_t = (M_{0,t} + F_{0,t})/2$, and re-write everythig in x_t. It can be easily seen that the Bellman equations **(B)** now can be expressed compactly as

$$x_t = \frac{1}{4}\Big[p_{0,m}p_{1,m}(\sum_i m_i q_i) + p_{0,f}p_{1,f}(\sum_j f_j r_j)\Big]x_{t-1} \tag{1}$$

>From demography theory it is well known that as long as the controls $(q_i, r_j, p_{a,s})$ are time invariant, the dynamics of (1) will guarantee the convergence of x_t to a path of exponential growth rate, called the Euler-Lotka parameter. Suppose λ is the steady state growth rate of x_t. Then the above discussion suggests a **simple characterization of the Euler-Lotka parameter λ for the two-sex model:**

$$\lambda = \max \frac{1}{4}\Big[p_{0,m}p_{1,m}(\sum_i m_i q_i) + p_{0,f}p_{1,f}(\sum_j f_j r_j)\Big] \tag{2}$$

On the right hand side of (2), terms in the square parentheses are the expected lifetime reproduction of genes, just like the lifetime birth criterion adopted in many of the one-sex (female) models (see e.g. Sozou and Seymour [2003]).

3.2 Energy Constraints and Assumptions

In this simplified over-lapping generation structure, let us look at the energy constraint of the mature age. Let the unit cost of m and f be respectively c_m and c_f. Similarly, the unit cost of $p_{1,s}$ is assumed to be $b_{1,s}$. Then, if a male and a female realize event i and j from their respective lotteries, we have the following energy constraints:

$$\begin{aligned} b_{1,m}p_{1,m} + c_m m_i + T_m &\leq g(z_m) \\ b_{1,f}p_{1,f} + c_f f_j + T_f &\leq g(z_f), \end{aligned}$$

where T_s is the parental transfer to children provided by sex s, and z_f (z_m) is the total capital stock contributed by parents for females (males). If a child of sex s receives a tranafer intensity z_s, then we assume that the energy this child can generate as an adult is $g(z_s)$. In Trivers (1972), $c_f f_j$ and T_f are combined to be named the female *investment*, and similarly for males. Here we separate them and shall provide respective interpretations later.

For the time being, we skip the energy constraint of age-0; the juvenile's growing strategy will be more interesting as we introduce the sex-specific choice and evolution of z_s. For now we simply assume that T_s is a constant proportion of $g(z_s)$, and ignore it. We shall concentrate on the following question: how would the reproduction lottery evolve? Would evolution lead to a sexual competition scenario such that the male always faces a lottery “having a small probability of becoming a lion king and mate many, and a large probability of mating zero female lioness"? And would the female face a lottery of “having 100% probability of reproducing f^* offspring" (a degenerated lottery)? Note that equation (2) suggests that sexual dimorphism should be explained jointly: Despite that male and female genes dictate different *ex post* life history development pattern, *ex ante* they both carry 1/2 gene of their parent. Knowing that his or her offsrping will have 1/2 chance of becoming males or females, would a selfish *parent gene* prefer dimorphic lotteries for males and females?[6] If we can prove that the optimal lottery design for r_j and q_i are intrinsically dimorphic, then we can match our theoretical prediction with the practices we usually observe on species such as lions, baboons, etc.

4 Sex-dimorphic Mating Lotteries

We believe that the fundamentally intrinsic difference between males and females is the cost of giving birth. This is particularly evident for viviparous species. We shall relate most features associated with sex dimorphism to this intrinsic distinction.

Given that c_f is much laregr than c_m for most species, intuitively the optimal life history would imply a relatively small optimal f^*. If there is intrasexual competition, then it is perceived that having a female child is owning a low-return (small fertility f^*) and low risk (almost surely can be pregnant f^* times) asset, whereas having a male child is owning a high-risk (difficult to become a lion king) and high return (once being a king, can impregnate many times and spread the gene). Thus, the parent gene actually ownes a *sex-specific portfolio* from the children: the male gene is high-risk high-return, and the female gene is low-risk low-return. We wonder how evolution leads to this result.

Suupose $T_s = 0$ for the time being, as we said in the previous discussion, and we shall consider the scenario for any *given* z_s and juvenile survival probability $p_{0,s}$ $(s = m, f)$. As one can see, our conclusions still hold even if we consider z_s and $p_{0,s}$ as endogenous. When contingency i is realized

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[6] Biologically, we assume that genes that control traits are autosomal, and those control reproductive lotteries are haploid.

for a male, $p_{1,m}$ can be writen as $p_{1,m} = (g(z_m) - c_m m_i)/b_m$. Similarly, $p_{1,f}$ can be written as $p_{1,f} = (g(z_f) - c_f f_j)/b_f$ for a female facing contingency j. Substituting these into (2), we can rewrite the maximizing-fitness problem as solving

$$\begin{aligned} &\frac{p_{0,m}}{2}\Big(\max_q \sum_i [m_i(g(z_m) - c_m m_i)/b_m] q_i\Big) \qquad (3)\\ &+ \frac{p_{0,f}}{2}\Big(\max_r \sum_j [f_j(g(z_f) - c_f f_j)/b_f] r_j\Big). \end{aligned}$$

There is actually one more constraint for the male's maximization, which we shall soon add.

We first look at the female problem, because the male's choice does not affect its solution (with whomever she mates, her gene is passed on in each of her pregnancy). For the quardratic formula $f_j(g(z_f) - c_f f_j)$, there is an f_{j^*} that maximizes it. The optimal lottery for juveniles is certainly to make $r_{j^*} = 1$ and $r_j = 0$ for $j \neq j^*$. Thus, **each lioness should face a certain event of bearing $f^* \equiv f_{j^*}$ children; they should not face any uncertainty about their privilege to bear.** Considering the simplified approximation that f is a continuous variable, then the optimal f from the quardratic objective function can be written as

$$f^* = g(z_f)/(2c_f).$$

4.1 A Male-Female Interacting Constraint

Now we look at the male's choice. If the male portfolio dictates that each male has q_i probability of impregnating m_i times, then the constraint $N_{1,m}(\sum_i m_i q_i) = N_{1,f}(\sum_j f_j r_j)$ must hold, because the total numbers of pregnancy and impregnancy must be equal. Suppose on the optimal life history path, the male and female age-0 survival probabilities are about the same, so that given our assumption of equal proportion of male/female newborns, the age-1 male and female numbers, denoted respectively $N_{1,m}$ and

$N_{1,f}$, are about equal. Note that our result is independent of this assumption, and here we only simplify the presentation. Given that $N_{1,m} \approx N_{1,f}$, we see that **the design of male lottery must have an additional constraint**:[7]

$$\sum_i m_i q_i = \sum_j f_j r_j. \tag{4}$$

For the time being we ignore the constraint in (4), and see what the male's "ideal" solution is. If males are not constrained by (4), their optimal choice of m (when it can be chosen continuously) could be solved from the maximization problem in the first pair of square parentheses of (3). It is easy to see that under a continuous approximation,

$$m^* = g(z_m)/(2c_m).$$

Thus, without the constraint in (4), the male should also choose a degenerated lottery that assigns probability 1 to the point $m = m^*$, and probability zero to everywhere else. Suppose the adult male/female available energy does not differ much, so that the difference between $g(z_m)$ and $g(z_f)$ is not significant. Then, comparing $m^* = g(z_m)/(2c_m)$ with $f^* = g(z_f)/(2c_f)$, we see that m^* would be significantly larger than f^*, because c_m is significantly smaller than c_f.

Now we take into account the imposed constraint (4). When females choose $f = f^*$ for sure and males' choice of lotteries is constrained by (4), the ideal choice m^* is out of the question. From (4) the male has to choose q_i such that $\sum_i m_i q_i = f^*$. Because the objective function of males ($u(m) \equiv m[g(z_m) - c_m m]$) is concave in m, any spread lottery will be dominated by the one degenerated at its mean. Evidently the optimal strategy for males (maximizing $\sum_i u(m_i) q_i$ subject to $\sum_i m_i q_i = f^*$) is also to choose a degenerated lottery: assign probability 1 to $m = f^*$, and probability zero to

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[7] If the probabilities of surviving age-0 are different for different sexes so that $N_{1,m} \neq N_{1,f}$, then we should simply pre-multiply the right hand side of (4) by $p_{0,f}/p_{0,m}$.

everywhere else. The fact that f^* and m^* differ a lot indicates that males are very unhappy about this constraint (because $f^* << m^*$).[8] In view of Figure 1, we see that by choosing $m = f^*$, **males are very inefficient in using their energy, producing a $u(f^*)$ much lower than that of $u(m^*)$.**

insert Figure 1 about here.

4.2 The Male's Motivation for Competition

Feeling that his energy is used rather inefficiently, a male gene has much room for mutation options. Specifically, the male gene may shift some of his energy to somatic investment I which may improve the spread of his gene. The somatic investment may be enlarging canine teeth, improving muscle strength, or growing bigger antlers, etc. These investments increase the probability of his successful impregnancy either by being more attractive to females, or by fighting and driving away other competitors. Without such investments, the vector q for males is a purely exogenous random draw by Nature, while with such investments, the random draw will be affected by all competitors' efforts.

For demonstration purposes, we assume that females always live in a pack of size n, and that the lottery is specified as: having probability q of mating all n females of this pride, and probability $1 - q$ of mating none of them. In the latter case, we can think of it as a scenario that the male in question loses the competition and is driven away. Formally, for a male indexed k, let the probability of winning these n females be written as $q(I^k, I^{\sim k})$, where I^k is k's investment and $I^{\sim k}$ is the vector of investment of all other competitors. We shall consider a mutation of the male-k gene that increases I^k, and see if this will help k win over other genes. Recall from (3) that the male part's fitness index can be written as $\sum_i q_i m_i (g(z_m) - c_m m_i)/b_m$.

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[8] This is what Gaulin and Sailer (1984) called "sex differences in reproduction potentials."

Given our specification, that there is $q(I^k, I^{\sim k})$ probability of impregnating $m = nf^*$ times and $1 - q$ probability of having $m = 0$, the male's fitness index can be expressed as

$$\frac{[g(z_m) - I^k - c_m nf^*]}{b_{1,m}} \cdot q(I^k, I^{\sim k})nf^* + [1 - q(I^k, I^{\sim k})] \cdot 0 \tag{5}$$

First, we check whether a mutation of male investment could invade the original gene group without sexual competition. To simplify our discussion we shall consider the symmetric case. Suppose the original investment for all relevant males is the same, and is equal to I_0^k, which may well be zero. In such a symmetric equilibrium, each male is equally efficient in mate competition. Equation (4) in this case can be written as

$$q(I_0^k, I_0^k) \cdot nf^* + [1 - q(I_0^k, I_0^k)] \cdot 0 = f^*.$$

Also, since there are equal number of adult males and females by assumption, we know that $q(I^k, I^k) = 1/n$ must hold at any symmetric equilibrium. If male k now has a mutation and increases a little bit of his investment alone, while all other males have the same investment, the change of q can be written as[9]

$$\frac{\partial q(I^k, I^{\sim k})}{\partial I^k}\Big|_{I^k = I^{\sim k} = I_0^k} \equiv \phi(I_0^k) > 0.$$

We assume $\phi(I^k) > 0$ because more investment by k usually implies higher likelihood of winning the competition. We also assume that $\phi'^{k}) < 0$, meaning that the marginal return to investment decreases as I^k alone accumulates.

Noting that $q(I^k, I^k) = 1/n$, we see by differentiating (5) that whether the mutation will invade successfully depends on the sign of the following expression:

$$\Omega \equiv \frac{f^* n}{b_{1,m}}\Big[\frac{-1}{n} + [g(z_m) - c_m(nf^*) - I^k]\phi(I^k)\Big] \equiv \frac{f^* n}{b_{1,m}}\Big[\frac{-1}{n} + \Psi(I^k)\Big] \tag{6}$$

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[9] There is a bit of notation abuse here: $I^{\sim k}$ is a vector and I^k is a scalar. As we write $I^{\sim k} = I^k = I_0^k$, we actually mean that every element of $I^{\sim k}$ is equal to I_0^k.

where

$$\Psi(I^k) \equiv [g(z_m) - c_m(nf^*) - I^k]\phi(I^k).$$

As one can see from Figure 2, **if $\Psi(0) > 1/n$, meaning that the intercept of the Ψ curve is higher than $1/n$, then a mutation that commands a small investment $I^k > 0$ will invade the original gene group with $I^k = 0$ successfully**.[10] Since the offspring of this mutant has a larger fitness index, or a larger gene spread by (2), they will dominate and eventually drive away the original male genes. The new equilibrium will consist of all males with this positive I^k.

insert Figure 2 about here.

4.3 Relating Sexual Dimorphism to Reproduction Costs

Then we evaluate (6) at $I = I^k + \epsilon$ and see if a mutation that commands more investment will change the equilibrium once again. The conceptual experiment can be exercised on and on. Eventually, as one can see, the equilibrium I will be the intersection point A in Figure 2. Note that $f^* = g(z_f)/(2c_f)$, hence $c_m(nf^*) = ng(z_f)[c_m/2c_f]$. Thus,

$$\Psi(I^k) \equiv \left[g(z_m) - \frac{ng(z_f)c_m}{2c_f} - I^k\right]\phi(I^k).$$

Therefore, when c_m/c_f is smaller, Ψ is higher, implying a larger equilibrium I^* by Figure 2. Thus, **we directly relate the degree of male competition (I^*) in sexual selection to the difference in male/female reproduction costs**. This is intuitively appealing, for male species with smaller c_m/c_f can produce a relatively large m costlessly, and hence they

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[10] Intuitively, the tradeoff of increasing I is as follows: The reduction of p due to the increase of a unit of I is $1/b$; this term should be weighted by the original probability $q = 1/n$. The increase of a unit of I enhances the probability q by ϕ; this term should be weighted by the original $p = (g - c_m nf - I)/b$. Combining these two terms, we obtain equation (6).

feel particularly depressed by the constraint $\sum_i m_i q_i = f^*$. Their excess energy, therefore, is likely to be directed to investment on I^*.

Next, let us check how an interior-solution I^k is affected by the female pride size n. It is easy to see that

$$\frac{\partial \Omega}{\partial n} = \frac{f^*}{b_{1,m}}[g(z_m) - 2c_m(nf^*) - I^k]\phi(I^k).$$

In the above expression, terms in the square brackets are the first order condition of unconstrained male mating, when the male is choosing x to maximize $p_{1,m} \cdot x = (g(z_m) - c_m x - I^k) \cdot x / b_{1,m}$. As long as the female pride size n is not extremely large, when we substitute x in this first order condition by nf^*, $[g(z_m) - 2c_m n f^* - I^k]$ should be positive, and hence so is $\partial\Omega/\partial n$. Suppose the second order condition of an interior maximum holds. Then $\partial\Omega/\partial n > 0$ implies that the optimal I^k increases with n. Thus, with some abuse of language, we see that **there is a positive correlation between polygyny and the investment on traits which males use for competition**, whatever that trait is. Such male investment often causes a distinction of phenotypes between males and females. This is another way to describe what is found in the literature of Leutenegger and Cheverud (1982) and Gaulin and Sailer (1984) concerning the correlation between sexual competition and sexual dimorphism.

In the above analysis, we put most of our emphasis on the difference in reproduction costs. But what about the ecological and territorial costs emphasized by Brown (1964) and Emlen and Oring (1977)? In our setup, **these environmental factors are implicitly embodied in the** $q(I^k, I^{\sim k})$ **function**. For instance, in an environment where potential mates are not defendable, it is difficult for a strong male to maintain his control over females. In our model, this implies that ϕ is small, and hence a mutation of investing more I^k does not pay off well. Thus, sexual dimorphism along this direction cannot arise. For life history specification of genes, environmental factors are exogenous, but our model is consistent with the resource-environment argument of Brown, and Emlen and Oring.

Our theory is also consistent with models of intersexual selection with female preferences. Conceptually, **the q function in (5) may be determined by female preferences, and hence only investments that appeal to females can possibly have a rewarding ϕ**. As shown in the article of Kirkpatrick (1982), in a model with both male traits and female preferences, there are many possible equilibrium paths of sex selection, and this makes the analysis of sexual dimorphism even more difficult. We shall come back to this discussion later in section 8.

5 Is the Sex-specific Portfolio Efficient?

When a competition equilibrium A in Figure 2 is reached, each male devotes I^*; but since all individuals in the new symmetric equilibrium have the same I^*, the resulting probability of winning the mating privilege must still be $1/n$. Thus, what we observe is that the female chooses a degenerated lottery of $f = f^*$, whereas the male chooses a risky lottetry: $[m = nf^*$ with probability $1/n$ and $m = 0$ with probability $1 - (1/n)]$. Because realizing a small f^* is certain, the female strategy is low-risk and low-return. The male strategy on the other hand is high-risk and high-return, for nf^* is large and its realizing probability $(1/n)$ is small. Treating the male and female children as assets, we observe that a parent has a *portfolio* of some lotteries with high-risk high-return and some lotteries with low-risk low-return.

In Figure 3 we draw the utility (fitness index) for males. We see that, because the symmetric equilibrium $q(I^k, I^{\sim k})$ is always $1/n$, the final fitness index under competition (point B) is always lower than that of point C, which is the equilibrium if all males stick to the *certain* event of impregnating f^* times for sure. This is the case because the male's objective function $u(m) = m(g(z_m) - c_m m)$ is concave in m, and also because the somatic investment I is assumed to appear after the energy generation. If the somatic investment also increases z_m and hence helps the energy generation $[g(z_m)]$ of males, then it is possible that male competition may come up with a larger fitness index. We will come back to the discussion of endogenous z_s in the next section.

Now let us assume that $z_s,\ s = m, f$ is not changed as a result of changing I, and look at the possible inefficiency out of sexual selection. Maynard Smith (1958) remarked that "sexual selection will have evolutionary consequences only if those individuals which have characteristics which make them successful, in the competition for a mate, are also fitter than the average as parents". However, this remark has been revised by himself after the publication of the intersexual selection papers in the 1980s. In models of intersexual selection, if the mating preference of females is strong enough, evolution can even maintain a male trait that causes greatly reduced viability. Thus, male trait in a intersexual scenario may well be nonadaptive. In the following we show that this is also true even in our intrasexual competition model.

As one can see, when (6) is positive, the mutation of more trait investment will invade. However, all competition will end up with the same success probability $1/n$. Thus, as far as the final outcome is concerned, the new equilibrium is at point B of Figure 3, whereas the old one is at point C, which *always* has larger fitness index than B. Therefore, in a symmetric evolutionary equilibrium **the male competition is like a prisoners' dilemma game, in which a unilateral mutation of increasing I may be a dominant strategy, even though the degenerated monogamy strategy with $m = f^*$ actually provides more lifetime birth in the evolutionary equilibrium.** This is an inefficiency from intrasexual competition.

In Zahari (1975 p.211), the author pointed out the potential waste of peacock's tail in the context of *intersexual* selection. He suggested that this waste may be a necessary signal to inform the female of the male's quality. This is certainly a comparison of qeuilibria with and without beautiful tail plume. Along the same logic, if we compare the equilibrium with and without competition investment I, we suspect that the waste from intra-sexual male competition is in fact quite general. We do observe the useless tail plume of peacocks, but we never had the chance to observe the performance of a monogamous lion gene, which has already been driven away by evolution.

6 Why Do Males Transfer Less than Females?

Now we take into account the role of parental transfers, a variable we distinguish from the cost of fertility in section 1. This discussion is also related to the endogeneity of adult z_s, $s = m, f$, which were assumed as exogenous in previous analysis. In Trivers (1972), these two are treated jointly. When male (female) adults provide T_m (T_f) transfers to their children, from the energy budget constraint we see that the age-1 survival probability should be revised as $p_{1,m} = [g(z_m) - c_m m_i - T_m]/b_m$ for males and $p_{1,f} = [g(z_f) - c_f f_j - T_f]/b_f$ for females. From the previous discussion, we know that the female lottery still should be a degenerated one with $f^* = [g(z_f) - T_f]/(2c_f)$.

Parental transfers are taken as energy endowment by the juveniles aged-0. In general, such energy is used by the young for maintenance and somatic growth. To simplify the analysis, we assume that juvenile survival probability $p_{0,s}$ is mostly determined by parents' guarding and watching. Under this assumption, parental transfers are used all for in somatic growth z_s.

6.1 Transfers in Monogamy and Polygyny

We start our discussion with the monogamy case, where the male also chooses a certain $m = f^*$. The fitness function becomes

$$\lambda = \frac{p_{0,m}}{2} f^* [g(z_m) - c_m f^* - T_m]/b_m + \frac{p_{0,f}}{2} f^* [g(z_f) - c_f f^* - T_f]/b_f. \quad (7)$$

Suppose for simplicity that male and female juveniles share parental transfer equally.[11] Then, given that there are $p_{0,s}$ age-1 adults for sex s, the average energy shared by each of the f^* newborns would be

$$z_m = z_f = z_{\text{mono}} = \frac{p_{0,m}T_m + p_{0,f}T_f}{f^*}, \tag{8}$$

where the subscript "mono" indicates that this is the monogamy case. We can differentiate λ in (7) with respect to T_m and yield:

$$\frac{\partial \lambda}{\partial T_m} = \frac{-p_{0,m}f^*}{2b_m} + \frac{g'(z_{\text{mono}})f^*}{2}\Big[\frac{p_{0,m}}{b_m} + \frac{p_{0,f}}{b_f}\Big]\frac{dz_{\text{mono}}}{dT_m}. \tag{9}$$

When T_m is chosen optimally, (9) should be set to zero.

In the case of polygyny with male competition, we know from the previous discussion that the female still chooses f^* for sure, and leaving aside the consideration of cuckuldry and mating nomads, the male faces a randomized portfolio: either mating n females or mating none. The fitness index for a male indexed k then becomes

$$\lambda = \frac{p_{0,m}}{2}\Big\{(nf^*)\cdot p_{1,m}\Big\}q(I_m^k; I_m^{\sim k}) + \frac{p_{0,f}}{2}\Big\{f^*[g(z_f) - c_f f^* - T_f]\frac{1}{b_f}\Big\} \tag{10}$$

Since there are n females and one male in the pride, the corresponding formula for per-child transfer is

$$z_m = z_f = z_{\text{poly}} = \frac{p_{0,m}T_m + np_{0,f}T_f}{nf^*}, \tag{11}$$

where the subscript "poly" indicates that this is the polygyny case. Using the relation $p_{1,m} = [g(z_m) - c_m(nf^*) - I_m^k - T_m]/b_m$, we can differentiate λ in (10) and evaluate the result at a symmetric equilibrium with $q(I^k, I^k) = 1/n$. The result is:[12]

$$\frac{\partial \lambda}{\partial T_m} = \frac{-p_{0,m}f^*}{2b_m} + \frac{g'(z_{\text{poly}})f^*}{2}\Big[\frac{p_{0,m}}{b_m} + \frac{p_{0,f}}{b_f}\Big]\frac{dz_{\text{poly}}}{dT_m}. \tag{12}$$

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[11] This will be the scenario in the lion case, for instance, when the hunted food is left and shared by juvenile lions of both sexes freely, so that no juvenile of a particular sex has a systematic advantage of taking more food.

[12] Note that f^* is treated as given by the male gene, and hence it is not replaced by $f^* = [g(z_f) - T_f]/2c_f$ in the derivation. This means that the gene controlling f^* by females is haploid.

Again, when T_m is chosen optimally, (12) should be set to zero.

As one can see, ceteris peribus, the only difference between (9) and (12) is in the last term. Evidently, by (8) and (11),

$$\frac{dz_{\text{mono}}}{dT_m} = \frac{p_{0,m}}{f^*} > \frac{p_{0,m}}{nf^*} = \frac{dz_{\text{poly}}}{dT_m},$$

since $n > 1$. Thus, plugging the original optimal male transfer derived in the monogamy case, denoted T_m^{mono}, into formula (12), the result will be negative. This means that, other things being equal, when the male gene changes his mating lottery from a certain one to a randomized competitive one, he should also decrease his energy transfers to the young. If the optimal T derived from (12) (the polygyny scenario) is T_m^{poly}, then **we should have** $T_m^{poly} < T_m^{mono}$.

Put differently, **if a mutation that shifts the male energy from maintenance to growing canine tooth for competition in the polygyny scenario, then a co-evolution of decreasing male transfers to the young would also be selected**. The intuition for this co-evolution to be selected lies in the change of formula of z. When the formula of transfer changes from (8) to (11), the marginal contribution of male transfers are diluted. Originally in the case of monogamy, the male plays 1/2 of the role as a supporting parent. After a male takes over a big females pride, he then does not feel so important to contribute his energy as in the monogamy case, since there are n females doing the job. This dilution effect facilitates the appearance of selfish males.

In view of Figure 2, we can see another interesting phenomenon. First let us put in T_m and rewrite $-1/n + \Psi$ in (6) as

$$\frac{-1}{n} + [g(z_m) - c_m(nf^*) - I^k - T_m]\phi(I^k) \equiv \frac{-1}{n} + \Psi(I^k), \tag{6'}$$

We know from the formula of Ψ in (6) that when T_m decreases, the Ψ function increases. Figure 2 tells us that the resulting equilibrium I_m increases with the decrease in T_m. Thus, **the energy saved from reducing**

transfer by the male is indeed shifted to the increase of somatic investment to improve the winning probability q.

6.2 Transfers and the Risk of Cuckoldry

Now consider the case when the pride consists of other males. This will be the case when male competition can only generate an alpha male but he cannot drive away other males. Well-known examples include baboons, wolves, and sea lions. Then, the alpha male only has the priority privilege to mate, although he is never sure whether the pregnant female really carries his gene. In other words, we have paternal uncertainty, or the possibility of cuckoldry for the alpha male. Facing such a cuckoldry risk, how would the alpha male change his transfers?

Suppose each female still has a certain births, except that on average f^* of them are with the alpha male and f' of them are with other males. The female does not care because in either case the baby carries her gene. Since females try to maximize $f[g(z_f) - c_f f - T_f]$, her optimal fertility is $f^* + f' = [g(z_f) - T_f]/(2c_f)$. However, because only f^* births are from the alpha male, he still multiplies nf^* [instead of $n(f^* + f')$] in front of $p_{1,m}$ in (10). If the male loses the competition, there may be some small chance that he can mate other females as well. But we shall ignore this in our discussion of transfers, because the loser has even less incentive to make any transfer to the children, who are unlikely to be the outcome of his incidental sex.

In the transfer equation, the formula changes to

$$z_m = z_f = \frac{p_{0,m}T_m + np_{0,f}T_f}{n(f^* + f')}.$$

Using the above information, we see that the first order condition of T_m for the alpha male becomes

Evidently, the larger is f', the smaller is the first term on the left hand side of (12'), and the smaller is the optimal male transfer T_m. Thus, **paternal**

uncertainty, or the risk of cuckoldry reduces male transfers. This is consistent with the observation given by Trivers (1972 p. 146).

Again, the intuition behind this result is clear: Cuckoldry dilutes the probability that a particular child is the descendant of the alpha male, therefore reduces his incentive to transfer.

7 The Sex Asymmetry of Menopause

Very few species in the world have menopause. According to Carey and Gruenfelder (1997), only human beings, killer whales, and dolphins have adaptive menopause. In terms of life history, an adaptive menopause means that the species have an optimal life history path that corresponds to a corner solution of fertility in the female's old age. In the traditional evolutionary framework of maximizing gene proliferation, a species should not survive and waste resources if it cannot give birth. However, for species that have the practice of intergenerational transfers, even post-reproductive old age can still make contribution to gene proliferation as long as they provide net transfers to the young. Most researchers, for instance Hawkes et al. (1997), Carey and Gruenfelder (1997), and Chu and Lee (2008b), explain menopause as a special kind of division of labor between a grandmother and mothers, where the grandmother specializes in housework, food gathering, and baby caring, while the mothers do all these plus bearing children. However, all these papers implicitly consider a model of females, therefore leave aside the logical question why males never have menopause. In this section we shall provide an answer to this question.

To consider menopause in our framework, we must extend our model to two mature ages, so that a zero fertility choice in the old age is meaningful. However, with two mature ages, we have the possibility of a female aged 1 or 2 mating with a male aged 2 or 1, and also the possibility of marriages lasting 1 period or two periods. To avoid all these unnecessary complications, we make the following assumptions. We consider a polygamous species where the females living together have a size of n_1 age-1 adults and n_2 age-2 adults. Only males of age-1 can compete for the alpha place, and the probability of his winning is q_1. If a male wins, he will impregnate all females in his pride. He will be the alpha male for two consecutive periods if he survives well. When he dies, either at his age 1 or age 2, a new pride king arises out of a new round of competition. None of these assumptions are crucial to our results, but they significantly simplify our notations and presentation. As in our 2-age model of the previous sections, adult females also determine their optimal fertility independent of the male decision. We denote f_1 and f_2 these optimal decisions in females' age-1 and age-2 respectively.

Given the above assumptions, we can write down the following expanded Bellman equation for our 3-age setup; the interpretation is the same as in section 3, and is therefore omitted.

$$\begin{aligned}
F_{0,t} &= \max\Big\{p_{0,f}F_{1,t-1}\Big\}\\
M_{0,t} &= \max\Big\{p_{0,m}M_{1,t-1}\Big\}\\
F_{1,t} &= \max\Big\{p_{1,f}f_1\Big(\frac{M_{0,t}}{4}+\frac{F_{0,t}}{4}\Big)\Big\}+p_{1,f}F_{2,t-1}\\
M_{1,t} &= \max\Big\{p_{1,m}q_1(n_1f_1+n_2f_2)\Big(\frac{M_{0,t}}{4}+\frac{F_{0,t}}{4}\Big)\Big\}+p_{1,m}M_{2,t-1}\\
F_{2,t} &= \max\Big\{p_{2,f}f_2\Big(\frac{M_{0,t}}{4}+\frac{F_{0,t}}{4}\Big)\Big\}\\
M_{2,t} &= \max\Big\{p_{2,m}q_1(n_1f_1+n_2f_2)\Big(\frac{M_{0,t}}{4}+\frac{F_{0,t}}{4}\Big)\Big\}
\end{aligned}$$

Let the age of the alpha male be α. The energy budget constraint for this cooperative breeding pride is

$$\begin{aligned}
&n_1g_1(z_f)+n_2g_2(z_f)+p_{\alpha,m}g(z_m)\geq\\
&n_1(b_{1,f}p_{1,f}+c_ff_1+T_{1,f})+n_2(b_{2,f}p_{2,f}+c_ff_2+T_{2,f})\\
&+[b_{\alpha,m}p_{\alpha,m}+c_m(n_1f_1+n_2f_2)+T_{\alpha,m}+I_{\alpha,m}]. \qquad (13)
\end{aligned}$$

In the above expression, the left hand side adds up the energy output by all members in the pride. The first and second terms on the right hand side are the female's energy expense in her age-1 and age-2, and the third term is the energy expense of the alpha male. Other than this constraint, the somatic investment for each youth is determined by

$$z_f = z_m = z = \frac{n_1 T_{1,f} + n_2 T_{2,f} + T_{\alpha,m}}{n_1 f_1 + n_2 f_2} \qquad ((14))$$

The steady state of the pride can be solved from the above expressions, with the understanding that n_1 and n_2 being constant is valid only in a density-checked equilibrium. In a steady state equilibrium, the population age structure will appear, and the size of females aged a will be constrained by the environmental density. We do not want to go into details here, for that is not the purpose of our research. Here we want to study why males are less likely to have a menopause than males.

Chu and Lee (2008) showed that a key reason for menopause to appear is the division of labor between grandmothers and mothers. To specialize in child-caring, the grandmothers have to give up their hunting time, which in turn reduce their available energy. As the grandmothers move closer and closer to specialized child-caring, their energy constraint pushes toward a corner solution of their fertility, that uses much of their energy. This is how menopause arises. >From (13) and (14) **we can provide three reasons for males not to have menopause**:

- For females to have menopause, we have a life history choosing $f_2 = 0$, a particular corner solution. This would be a reasonable choice only if the opportunity cost of f_2 (which is c_f) is high, so that avoiding the age-2 birth saves much energy of potential mothers. But for males, since c_m is trivially small, it does not pay for males to avoid m_2. Even if males do have $m_2 = 0$, he cannot squeeze much energy out of it anyway. Thus, an efficient division of labor is unlikely to demand a corner solution of $m_2 = 0$ for old males.

- We see from Chu and Lee (2008b) that the division of labor is the key observation of menopausal species. However, we have shown in the previous sections that the alpha male has little incentive to transfer to children, due to the dilution effect in a cooperative breeding group. Even if the male does save some energy by choosing $m_2 = 0$, he is likely to move it to trait investment or body maintenance. Thus, because the males do not give away energy, it is difficult to form a division of labor with the males.

- In a polygyny pride, if the male aged 2 stops producing sperm, then all females in the pride are not able to reproduce offspring. Thus, it is logically inconsistent to have the alpha male to have $m_2 = 0$.

8 Inter-Sexual Selection

Our above analysis was restricted to the one-sided sexual competition of males, not the two-sided interaction of males and females, of which the literature describes as inter-sexual selection. The typical description on inter-sexual selection is that the male has a gene controling the size of some of their traits (such as plumage), and the female (such as a peacock) has a gene controling her preference for mating males having such sizable traits. The question is: if such traits appear to be useless or even harmful (e.g. the excessively large plumage of male peacocks), why and how would this trait-preference interaction arise from evolution?

There are two strands of theories that try to explain this evolution. The first was proposed by Fisher (1930) who suggests that the advantage of preferences lies in the choice of mates who will father *attractive* sons. If females on average prefer a particular male trait, then males having that trait will have a mating advantage. If this trait is heritable, then females would also prefer to mate with males with this trait. Fisher argued that this evolution may lead to a *runaway* process, leading to an inefficient trait size, such as the excessively large plumage of peacocks. However, as pointed out by Pomiankowski et al. (1991), this runaway argument is valid only when there is no cost associated with female preferences. If there is some cost (of say searching), no matter how small, Fisher's argument cannot go through.

The second hypothesis suggests that the benefit of female preferences hinges upon the improved survival of offspring. Zahari (1975) argued in his well-known “handicap" theory that the male trait provides the female with information about heritable male quality, very much like the idea of signaling in economics. Iwasa et al. (1991) showed that a correlation between male trait and viability is necessary to create an equilibrium with female preferences. With respect to this handicap theory, most existing literature uses quantitative genetic theories to present their arguments. In this section, we shall use our life history model to demonstrate this theory in a very neat way.

8.1 The Gene Dynamics

Consider a simplified life history with only one period of life, so that we can skip the age index associated with variables. The species in question has monogamous marriages, and each couple bears m children for sure. However, there is some probability that a male cannot find a female willing to mate him, and hence cannot give birth. Although mating models in general involve a distribution of male traits and a distribution of female preferences, as in the theory of quantitative genetics (see Iwasa (1991) p.1441), we consider an equilibrium with the species' population concentrated sharply around the population average, $(\bar{T}, \bar{S})$, where $\bar{T}$ is the average trait size, and $\bar{S}$ is the average search intensity. We assume away all other parameters in our previous discussion, except b, the efficiency parameter of maintaining survival. The smaller is b, the more viable an individual is.

After skipping the age subscript, we let M_t be the value of a male gene, and F_t be the value of a female gene at time t. Because growing traits and searching for preferred males both cost energy, M_t and F_t are both functions of male trait, female search, and the viability parameter b. Given that the average of T and S are $(\bar{T}, \bar{S})$, the dynamics of a male gene with T look like

$$M_{t+1}(T,b) = p_m(T,b) \cdot m \sum_{\tilde{s}} h_m(\tilde{S}|T;\bar{T},\bar{S}) \Big[\frac{1}{2}M_t(T,b) + \frac{1}{2}F_t(\tilde{S},b)\Big]$$

where p_m is the survival probability of males, which is a function of both trait size T and parameter b. For instance, the survival probability of a male peacock depends on the size of his plumage and his vigor. Term h_m is the male's probability of mating a female with search level $\tilde{S}$, given that the male trait is T, the male average is $\bar{T}$, and the female average is $\bar{S}$.

In an equilibrium with (T, S) nearly degenerated to the mean, $(\bar{T}, \bar{S})$, given that the mail itself has $\bar{T}$, the equation of male gene dynamics can be approximated as

$$M_{t+1}(\bar{T},\bar{S},b) = p_m(\bar{T},b) \cdot k_m(\bar{T},\bar{S}) \Big[\frac{1}{2}M_t(\bar{T},\bar{S},b) + \frac{1}{2}F_t(\bar{T},\bar{S},b)\Big],$$

with some function k_m. Similarly, the female gene dynamics can be written as

$$F_{t+1}(\bar{T},\bar{S},b) = p_f(\bar{S},b) \cdot k_f(\bar{T},\bar{S}) \Big[\frac{1}{2}M_t(\bar{T},\bar{S},b) + \frac{1}{2}F_t(\bar{T},\bar{S},b)\Big],$$

with some function k_f. Combining the above two equations, and let $x_t = (M_t + F_t)/2$ as before, we see that the intrinsic growth rate of the species is

$$\lambda(\bar{T},\bar{S};b) = [p_m(\bar{T},b)\bar{k}_m(\bar{T},\bar{S}) + p_f(\bar{S},b)k_f((\bar{T},\bar{S})]/2.(14)$$

Note that in a stationary state, $\lambda(\bar{T},\bar{S};b) = 1$, which implies an implicit function from (14):

$$b = b(\bar{T},\bar{S}).(15)$$

Equation (15) says that in any long run stationary equilibrium, there must be a relation between viability efficiency parameter b and $(\bar{T},\bar{S})$ under the force of selection. For instance, if a group of males have a large average male trait size, then this group must be efficient in the sense of having a smaller b. This implies that the relationship between b and $\bar{T}$ should be negative. Similarly, in a stationary equilibrium there must also be a negative relationship between b and $\bar{S}$.

8.2 The Trait-Search Interaction

Now we want to see how a mutation that changes trait size or search intensity can prevail. The optimal life history suggests it must be true that the trait and search reach their optimum. In the cass of an interior maximum, we must have from (14)

$$\frac{\partial\lambda(\bar{T},\bar{S};b)}{\partial\bar{T}} = 0 = \frac{\partial\lambda(\bar{T},\bar{S};b)}{\partial\bar{S}.}$$

On this optimal life history path, we should not observe “clumsy" plumages, that evidently hurt the males' intrinsic growth rate. The fact that we do observe clumsy plumages suggests $\partial\lambda(\bar{T},\bar{S};b)/\partial\bar{T} < 0$, meaning that the marginal impact of increasing plumage on fitness index ia already *negative.* The motivation of the discussion of sexual selection along the lines of Darwin and Fisher was indeed to explain why some evidently excessively large tails would appear.

Fisher's (1930) r̂unaway argument tries to link T with S: sexy males attract females, and hence females search for sexy males as mates. However, this only creates a secondary benefit of growing T, but does not justify the investment of S. In fact, if the benefit of search comes only through T, we have

$$\frac{\partial\lambda}{\partial S} = \Big(\frac{\partial\lambda}{\partial\bar{T}}\Big)\Big(\frac{\partial\bar{T}}{\partial\bar{S}}\Big).$$

When T is chosen optimally on a life history path, $\partial\psi/\partial\bar{T} = 0$, there is no independent benefit associated with S. Thus, if there is any cost associated with S, then the optimal search should be zero. As such, Maynard-Smith (1991) argued that the Fisher argument cannot justify a handicap phenomenon with positive search.

The handicap hypothesis suggests that natural selection must imply an association between viability coefficient b, trait size T and search intensity S. In our term, natural selection implies a relationship in (15). A handicap evolution is in fact a mutation of T in (14), *taking into account the stationary* *condition* (15). In a sense, this gene mutation is a very sophisticated one, which seems to be a Stackleberg leader, taking into concern the evolutionay response in (15), as the gene mutation changes the size of T. The first order condition of maximizing T now becomes:

$$\frac{\partial\lambda(\bar{T},\bar{S};b)}{\partial\bar{T}}=\frac{\partial\lambda}{\partial\bar{T}}+\frac{\partial\lambda}{\partial b}\frac{\partial b}{\partial\bar{T}}=0,(16)$$

where $\partial\lambda/\partial b$ is derived from (15). Since $\partial\lambda/\partial b$ is negative (smaller b means better efficiency) and $\partial b/\partial\bar{T}$ is also negative (larger-tail mails are more efficient ones), it implies that **on the optimal life history path,** $\partial\lambda/\partial\bar{T}$ **must be negative**. Indeed, this is our interpretation of “excessive" tail size: if you look at the marginal condition of tail *alone,* the tail seems to be over-sized. The large tail can be justified only when we take into account the viability-selection relation between b and T in (15).

Suppose a gene is indeed “sophisticated" and it does take into account the selection relationship in (15) as it considers a mutation. For a trait to appear excessively large to attract our attention, however, it must be the case that the organism can afford to spend much energy on T. We have shown in section 5 that since males' are constrained in reporduction and they spend very little energy on producing sperms, they are more likely than females to have extra energy for other uses. Indeed, in terms of Fisher (1930), the male traits sometimes appear to “run-away", whereas female traits never have show similar patterns. We believe that this is why we observe evidently large plumages on males birds, but almost never observe excessive search activities or traits of females. This kind of dimprphism still originates from the divergence of male-female reproduction costs.

9 Conclusion

In this paper, we provide a unified approach to explain sexual dimorphism, intrasexual competition, and intersexual selection in biology. In terms of analytical strucutre, we adopt a model of two-sex life history. Concerning the explanatory variable, we suggest that the difference in male-female costs of reproduction is the key. Using our model we are able to explain why males are motivated to grow canine teeth, why fathers provide less transfers to children, why there is a positive correlation between polygyny and sex-size dimorphism, how the environmental factors of sex competition enter our model, why males and females choose different mating lotteries, and why only females are likely to have menopause? Finally, we are able to explain the negative correlation between male traits and viability using our framework of optimal life history. The reason we observe excessively large organs in males, we believe, is also related to male's low reproduction costs.

There are of course observations different from our prediction. For instance, the hyena species has a matriarch instead of an alpha male, and the alpha male of wolves picks only one female to mate instead of many. Indeed, we believe the hyena and wolf cases indicate scenarios not covered by our model. For instance, wolves and African wild dogs are peck hunters, who need many agile individuals to join the hunt. Thus, they cannot have many pregnant females. In terms of our model, the energy-generating function g has to be specified differently. Hyenas have many predators such as lions, and they cannot provide effective protection for too many juveniles. This implies that one pregnant female would be enough. In either case, these examples fall into the broad-sense category of Emlen and Oring (1977) that some resources are “unfendable", and hence some sexual interaction phenomena do not arise. In fact, this is also why there is not much sexual dimorphism in such species.

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