

## OFFSPRING QUALITY AND THE POLYGyny THRESHOLD: "THE SEXY SON HYPOTHESIS"

PATRICK J. WEATHERHEAD\* AND RALEIGH J. ROBERTSON

Department of Biology, Queen's University, Kingston, Ontario, Canada

The foundation for current theories on the evolution of mating systems was laid by Darwin (1871) in his elucidation of the process of sexual selection. Darwin introduced this concept to explain the evolution of characters that were not related to an individual's ability to survive in the environment (and in fact probably reduced this ability), but enhanced its ability to obtain mates. Implicit in this concept is that individuals of each sex differ from one another with respect to characteristics which affect the fitness they will confer on another individual if chosen as a mate. Consequently, selection pressures will exist that promote the development of techniques both for advertising superior characteristics and for distinguishing good characteristics from bad.

In his review of sexual selection and the role of parental investment, Trivers (1972) concludes that when the investment of each sex in its offspring is approximately equal, then sexual selection should affect both equally. However, when, for example, females invest more heavily than males, then competition among males to increase their frequency of mating will be high and, consequently, sexual selection among males will be strong. As Trivers (1972) points out, females initially have a much higher investment in terms of the energy supplied to each ovum relative to the very small amount of energy devoted by the male to each sperm. In highly polygynous mating systems the role played by the male in rearing young becomes extremely limited and thus the difference in the relative contributions of each sex increases. Consequently, in such systems sexual selection will act much more strongly on the male. A corollary to this is that selection will at the same time favor increased discrimination on the part of the female in her choice of a mate in order to protect her investment. A poor choice by the female has much greater repercussions on her fitness than a similar poor choice by a male has on his fitness (Orians 1969).

A model explaining the evolution of polygynous mating systems based on the importance of female choice is presented by Orians (1969) based on the work of Verner (1964) and Verner and Willson (1966). The foundation of the model rests on the definition of the polygyny threshold (Verner and Willson 1966) as the point at which the difference in quality of two males' territories is great enough that a female could rear as many young alone or with limited male assistance in the better territory

\* Present address: Department of Renewable Resources, Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec, H0A 1C0 Canada.

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as she could with full male assistance in the poor territory. Thus, polygyny is the consequence of major inequities in territory quality.

#### TESTS OF THE MODEL

As outlined by Orians (1969), there are two critical predictions that must be met for the model to be valid. The first requires that polygynously mated females rear as many offspring as those mated monogamously, while the second requires that harem size be positively correlated with territory quality. Evidence has been found that supports the first prediction (Willson 1966; Holm 1973; Price and Bock 1973), although Altman et al. (1977) have since shown that satisfaction or refutation of this prediction is not a valid test of the model. Altman et al. (1977) maintain that the second prediction does provide the basis for a valid test of the model. Weatherhead and Robertson (1977a) have presented evidence which contradicts this prediction.

The purpose of this paper is to expand the Orians-Verner model in order to accommodate those results which fit the current model, as well as those that do not. The direction for this expansion was suggested by McLaren (1967, 1972) and Bartholomew (1970), and requires that female choice be based not only on the quality of a male's territory but on the individual qualities of the male as well. (Although these two parameters have been recognized, the Orians-Verner model assumes that the two are functionally synonymous.) If the males with individual attributes most attractive to females are not necessarily those with the best quality territories, as Weatherhead and Robertson (1977b) have shown for redwinged blackbirds (*Agelaius phoeniceus*), then females mated with them may initially have relatively lower reproductive success than those nesting in the best quality territories. If the male offspring of these females inherit some of their father's attractive traits and in turn leave more offspring because they attract more females, then through these "sexy sons" (Verner, personal communication) their mothers will eventually leave more descendants. This is analogous to the "marginal male effect" described by Bartholomew (1970) for polygynous pinnepeds, whereby females risk higher pup mortality in order to breed with the best quality males. The problem with the Orians-Verner model is that, for the most part, reproductive success has been interpreted only as immediate success, when fitness is really a measure of an individual's ultimate contribution to the gene pool. A notable exception to this has been presented by Elliott (1975), although the model he develops does not seem generally applicable.

In order to incorporate the factor of ultimate success it is necessary to redefine the concept of the polygyny threshold in such a way that it includes the quality of a female's offspring, rather than just the quantity. Therefore, it must incorporate the situations covered by the existing definition where both initial and ultimate success of polygynously mated females are higher, and also situations in which only the latter is higher. The discussion will therefore focus on the conditions under which polygyny will be favored in spite of initial losses in reproductive output by polygynously mated females.

TABLE 1  
NO. OF DESCENDANTS PER FEMALE FROM MONOGAMOUS AND POLYGYNOUS MATING SYSTEMS

	Monogamous	Polygynous
$F_1$ .....	$1\sigma, 1\phi$	$x\sigma, x\phi$
$F_2$ .....	$1(2) + (1)(p)(2) + (1)(1-p)(2x)$ $= 2(1 + p + x - px)$	$x(k)(2x) + x(p)(2) + x(1-p)(2x)$ $= 2(kx^2 + px + x^2 - px^2)$

Let  $x$  represent the ratio of the number of young fledged per polygynously mated female to the number fledged per monogamously mated female. If  $k$  represents harem size, and it is assumed that males mate exactly as their father while females mate in relation to the proportion of monogamous ( $p$ ) and polygynous ( $1 - p$ ) males breeding, then several general equations may be formulated which can be used to determine the polygyny threshold. Assume the existence of a 1:1 sex ratio of the young fledged. Consider the case shown in table 1 where the mean number of fledglings per monogamous female is two. The offspring shown are the descendants per female from the two mating systems.

If a polygynously mated female is to realize an advantage after two generations then  $\frac{1}{2}F_{1P} + \frac{1}{4}F_{2P}$  must be greater than  $\frac{1}{2}F_{1M} + \frac{1}{4}F_{2M}$ , where  $M$  and  $P$  represent descendants of monogamous and polygynous females respectively, and the fractions by which the offspring in each generation are multiplied indicate the degree of relationship with the females being considered. This yields the inequality  $x + \frac{1}{2}kx^2 + \frac{1}{2}px + \frac{1}{2}x^2 - \frac{1}{2}px^2 > 1 + \frac{1}{2} + \frac{1}{2}p + \frac{1}{2}x - \frac{1}{2}px$ . Suppose that  $k = 2$  (i.e., bigamy) and  $p = \frac{1}{2}$ , then  $\frac{1}{2}F_{1P} + \frac{1}{4}F_{2P} > \frac{1}{2}F_{1M} + \frac{1}{4}F_{2M}$ , when  $x > 0.85$ . This means that for every offspring fledged by a monogamously mated female, a bigamously mated female must fledge more than 0.85 offspring to realize an advantage after two generations. It is interesting to note that, depending on the value of  $x$ , four different sets of selection pressures can result. If  $x$  is greater than one then bigamy will be favored for both sexes since both initial and second generation reproductive success will be higher for bigamously mated individuals. When  $x$  is less than one but greater than 0.85 bigamy will be favored for both sexes in spite of initial losses by the females. For  $x$  between 0.5 and 0.85 bigamy will be advantageous for males but not for females, and for values of  $x$  below 0.5 monogamy will be favored for both sexes.

It seems reasonable to expect that if a longer time were allowed for polygynous females to realize their advantage, the value of  $x$  could be reduced. As long as the difference between the number of descendants left by monogamously and polygynously mated females decreased each successive generation this condition will be met. Since this trend must begin in the second generation, the following inequality must hold;  $F_{2P} > F_{2M}$  or,  $2(kx^2 + px + x^2 - px^2) > 2(1 + p + x - px)$ . Again, consider the cases where  $k = 2$  and  $p = \frac{1}{2}$ . Then, the inequality holds for  $x > 0.77$ . When values of  $k$  greater than 2 are substituted into the inequality, the relationship of the polygyny threshold to harem size is obtained (see fig. 1). Before discussing the significance of this result it is necessary to examine the assumptions made in obtaining it and determine to what extent changes in them would alter the result.

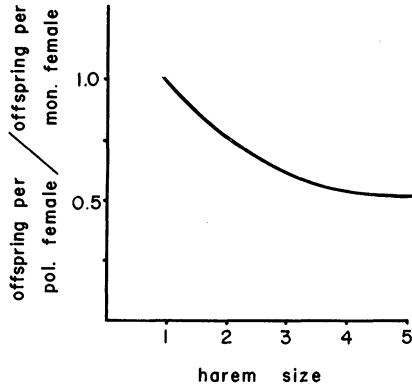


FIG. 1.—Minimum value for ratio of offspring per polygynous female to offspring per monogamous female for which polygyny is favored, in relation to harem size.

The assumption of an equal sex ratio of fledglings appears valid from the work of Orians (1961), Verner (1964), and Haigh (1968). However, assigning a value of  $\frac{1}{2}$  to  $p$  in the example given above would certainly not be valid if one considers the polygynous mating system at the time that it first evolved. At that time the proportion of monogamously mated individuals would essentially be one. Letting  $p = 1$  in the second model raises the polygyny threshold for bigamy from 0.77 to 0.78, and thus changes in the value of  $p$  have only limited effects on the polygyny threshold. In the models that were presented, heritability of polygynous traits in female offspring was considered to be zero, that is, they mated exactly in proportion to the number of monogamous and polygynous males available. If complete heritability is assumed such that females mate exactly as their mother did, then the value of  $x$  from the second model increases from 0.77 to 0.82, making bigamy slightly more favorable for females with randomly mating female descendants.

In both models it was assumed that males mated exactly as their fathers and it is this assumption that is critical in allowing a polygynously mated female to have an advantage in spite of initial reproductive losses. It is genetically unrealistic to assume that male offspring will be identical to their father with respect to their eventual mating success, although some environmental influence such as imprinting by male offspring on the behavioral patterns of their father could increase the degree of similarity between father and son. The rapidity with which the value of  $x$  approaches 1 as heritability is decreased from 100% to 0% is examined in the Appendix. These results indicate that for a given decrease in heritability there is a proportionately smaller decrease in  $x$ . It is noteworthy that as harem size becomes large very low heritability of male traits will still allow polygynous females a sizeable decrease in  $F_1$  reproductive success relative to monogamous females.

The final assumption to be considered is that which underlies the second model. In assuming that the selective advantage favoring polygyny could be realized at some time beyond the second generation, the polygyny threshold for bigamy was reduced from 0.85 to 0.77. Without a computer simulation of the mating system it is difficult to determine in which generation the advantage will be realized. Intuitively, however, it seems that the number of generations allowable for this to occur would be limited.

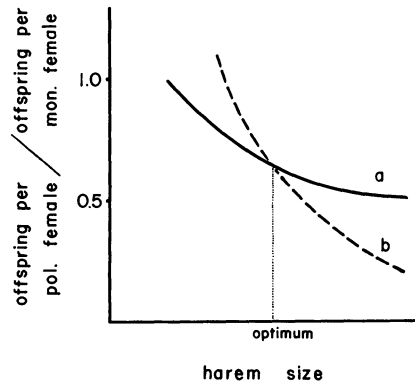


FIG. 2.—Optimum harem size determined from polygyny threshold (a) and ecological constraints (b).

As more generations are allowed for the selective advantage to be realized, the relationship of the initial female to those individuals becomes more distant and thus the possibility of interference by stochastic processes becomes greater. Therefore the actual values for the polygyny threshold probably lie somewhere between the values obtained using the two approaches that were presented. Because of the difficulty involved in determining what the actual values of  $x$  are, the lower limit for  $x$  will be used in further discussions. These are the values obtained by the second approach as shown in figure 1.

From the model that has been presented it has been shown that polygyny can be selectively favored for females in spite of initial losses in fitness. However, it was also shown that there is a limit to the magnitude of those losses, below which polygyny will not be selectively favored. The factor which will determine whether or not a species will be polygynous is the actual rate at which female reproductive success decreases with increased harem size; that is, the constraints imposed by the ecology of the species. This is best explained by figure 2. The solid line indicates the polygyny threshold determined by the model, while the broken line represents the ecological constraints. The point at which the two lines intersect represents the situation where the actual losses due to increased harem size equal the maximum allowable losses for polygyny to remain selectively advantageous. This point therefore represents the optimum harem size for females, since to the left of this point the male offspring will decrease in quality (with respect to the size of the harems they will obtain) and to the right of this point the initial losses by females will be too great to allow ultimate success to compensate for them.

Since monogamy is by far the most prevalent avian mating system (Lack 1968; Verner and Willson 1969), it must be assumed from the model that the ecological constraints resulting from males of monogamous species having more than one mate are great enough to intersect with the polygyny threshold line to the left of harem size 1.5. By determining why polygynous species are able to avoid this situation it may be possible to assess why monogamous species are unable to do so.

A study of the bobolink (*Dolichonyx oryzivorus*), which is polygynous to the degree of bigamy, revealed some interesting adaptations for polygyny (Martin 1974).

When a male bobolink is bigamously mated he restricts his aid in feeding nestlings to the nest of the primary female (i.e., the first female recruited). Secondary females have adapted to this loss of assistance by having a reduced clutch size, asynchronously hatching young and foraging behavior centered immediately around the nest. These adaptations allow them to fledge as many young as possible, although this number is below that fledged by primary females. From Martin's (1974) data in which primary females are treated as monogamous and secondary females as bigamous, the ratio of young fledged by secondary females to the number fledged by primary females was computed and a value of 0.66 was obtained. This is below the theoretical value of 0.77 obtained by the model that was presented. However, the value of  $x$  would be expected to be less than 0.77 since the number of offspring produced by bigamous males in this mating system is the sum of the offspring of a primary and secondary female rather than the sum of the offspring of two secondary females. These results show that one prerequisite for polygyny is either a high availability of the main food supply or else flexibility in the variety of food items taken. Without this, secondary females would be unable to raise a brood alone.

In a study of the Ipswich sparrow (*Passerculus sandwichensis princeps*) McLaren (1972) and Stobo and McLaren (1975) found another form of adaptation allowing for bigamous matings. Males recruited females at appropriate time intervals so that their nesting stages were asynchronous, and thus only one nest required the male's assistance at any given time. Verner (1963) found a similar recruitment pattern in long-billed marsh wrens (*Telmatodytes palustris*). This adaptation limits the number of females that a male can assist, and requires that eggs can be incubated without the aid of the male. The data from Stobo and McLaren's (1975) study were also used to compute the ratio of young fledged by bigamous and monogamous females. The value obtained was 0.84, which again corresponds well with the value predicted by the model. As with the bobolinks, the reduced success of bigamous females is again due primarily to poorer performance by the secondary female. In this case it is not due to lower nest productivity but to fewer nesting attempts.

Both studies indicate that secondary females tend to be younger than primary females, and it therefore becomes important to know to what degree reproductive performance is age related rather than a function of mating status. Our model has assumed equal performance of polygynously mated females regardless of recruitment order. Such an assumption is only valid if, by being a secondary mate in her first year of breeding, a female achieves a high probability of becoming a primary mate in subsequent years. If such were the case and females were able to breed for more than 2 yr, then the allowable losses as a secondary mate would be greater than that predicted by the model and would increase in proportion with the number of years a female could expect to breed as a primary mate. Martin's (1974) data suggest that for bobolinks this may be a valid hypothesis, while the data of Stobo and McLaren (1975) do not. Detailed information for a large number of individuals is not presented for either study, and to adequately test the hypothesis more data are required.

In general then, for species which are not nest-site limited, food availability appears to be the most important parameter for determining whether polygyny can evolve (Wittenberger 1976). If food is not limiting and low levels of polygyny evolve,

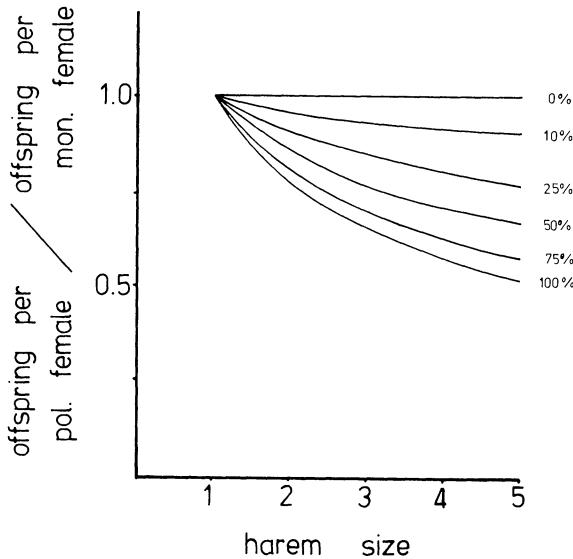


FIG. 3.—Minimum value for ratio of offspring per polygynous female to offspring per monogamous female for which polygyny is favored, in relation to harem size for different heritability values. Heritability (%) is shown to the right of each curve.

then the limit to the degree of polygyny will be determined by the extent by which males differ with respect to both individual and territorial qualities.

SUMMARY

An expansion of the Orians-Verner model for the evolution of polygyny has been made to explain evidence contradictory to that model. By separating the individual quality of the male from the quality of his territory and assuming that male offspring will at least in part inherit the individual qualities of their father, it was postulated that females mating with “attractive” males and suffering reduced reproductive success could ultimately gain an advantage through the success of their “sexy sons.”

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APPENDIX

The magnitude of allowable losses by polygynous females relative to harem size is shown for several values of heritability in figure 3. All computations are based on the second model and have employed the same assumptions. For heritability less than one a son’s success will fall between that of his father and the mean male success of the population. For example, with

75% heritability, the son's success will be  $(0.75) \times (\text{father's success}) + (0.25) \times (\text{mean male success})$ . Mean male success for the population will be  $p(2) + (1-p)(2kx)$ . Therefore, the  $F_2$  progeny for a monogamous female will equal  $(0.75)(2) + (0.25)(2p + 2kx - 2pkx) + p(2) + (1-p)(2x)$ . Similarly, the  $F_2$  progeny for a polygynous female will equal  $(0.75)(x) \times (2kx) + (0.25)(x)(2p + 2kx - 2pkx) + p(x)(2) + (1-p)(x)(2x)$ . The 75% heritability curve in figure 3 is then determined from the inequality  $F_{2P} > F_{2M}$  through substitution of different values of  $k$  and letting  $p = \frac{1}{2}$ . All other curves shown were derived in similar fashion using the heritability values indicated.

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