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## REPRODUCTIVE SUPPRESSION AMONG FEMALE MAMMALS: IMPLICATIONS FOR BIOMEDICINE AND SEXUAL SELECTION THEORY

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### ABSTRACT

*Female mammals experience a very high and often unappreciated rate of reproductive failure. Among human pregnancies alone, over 50 per cent fail between conception and parturition, and the majority of these failures are unexplained. These findings present important problems for evolutionary theory as well as for health care practices. This paper addresses these high rates of reproductive failure among mammals, by extending the work of a number of evolutionary biologists regarding the reproductive consequences of environmental adversity. The basic model upon which we elaborate, termed the Reproductive Suppression Model, argues that females can optimize their lifetime reproductive success by suppressing reproduction when future conditions for the survival of offspring are likely to be sufficiently better than present ones as to exceed the costs of the suppression itself. These costs are a function of reproductive time lost and the direct phenotypic effects of the suppression itself. To evaluate the benefits and costs of suppression, the following types of cues should be assessed: the female's physical and mental health, her stage of reproduction, the physical and genetic status of her offspring, and the external conditions at the time of birth.*

*We also examine various issues of social suppression, whereby the conditions for survival of offspring are a function of the reproduction and support of other group members. Under such conditions, some females may be able to improve current conditions for reproduction by suppressing the reproduction of others. Field data from our own work are presented, describing socially mediated reproductive competition among continuously breeding female yellow baboons and among female hoary marmots.*

*Social suppression in other mammals is also evaluated, including that in human beings, and we conclude with some implications of the Reproductive Suppression Model for sexual selection theory regarding female-female reproductive competition, as well as human health care.*

### INTRODUCTION

ONE OUT OF every two human pregnancies fails between conception and parturition (Shepard and Fantel, 1979). Comparable data exist for a variety of other mammals (Brambell, 1948; Wynne Edwards, 1962; Hendrickx and Nelson, 1971; Eleftheriou and Sprott, 1975; Assenmacher and Farner, 1978; Cohen, Malpas, and Klein, 1980). If we add neonatal mortality (1.3% of all human births: Health United

States, 1980), and the ovulations and conceptions that should occur but do not (a quantity that may be greater than all of the above combined: Carenza and Zichella, 1979), there is a much greater incidence of unsuccessful reproductive attempts in mammals than of successful ones. This is an important problem, both for evolutionary theory and also for health care practitioners. For example, in a well-known study predicting reproductive risks among women, Hobel, Youkeles, and Forsythe (1973) clas-

sified 18 per cent of their subjects as "high risk" on the basis of standard biomedical predictors—e. g., age, parity, past reproductive history, drug use, and diabetes. However, only 12 per cent of these subjects experienced complications, and a number of women predicted to be at low risk ended up having complications (see also Ratten, 1981).

Extra-biomedical factors have also recently been linked to poor reproductive outcomes. For humans, these factors include anxiety, depression, low self-esteem, poor coping skills, negative maternal desire, and a perceived lack of social support while undergoing stressful life events (Sturgis, 1962; Matsumoto, Igarishi, and Nagaoka, 1968; Grimm, 1962; Nuckolls, 1975; Laukaran and van den Berg, 1980; Carezza and Zichella, 1979). For other species, these fac-

tors include resource availability, social status, competition, persistent receipt of aggression, and experimentally induced stress (Table 1). Nevertheless, our ability to predict poor reproductive outcomes in humans, as well as in other mammals, remains embarrassingly low.

At least two reasons can be given for this. First, few scientists, if any, have attempted to consider both biomedical and other factors simultaneously, let alone identify the interactions that may occur between them. Second, as will be argued hereafter, the influence of these factors on reproductive outcomes should depend on their long-term and short-term temporal patterns. Yet such temporal patterns are commonly ignored.

In this review, we will expand upon existing evolutionary models linking the suppression of fecundity to increased lifetime repro-

TABLE 1

*Mechanisms of reproductive suppression among different species of mammals*

The progression from A to F represents suppression at later developmental stages; in all cases, such suppression seems to occur when conditions suggest that the caretakers cannot provide sufficient investment, or when direct competition between parents or young is extreme, or when both situations obtain.

Subject	Individuals Most Affected
<b>A. DELAY OF SEXUAL MATURATION</b>	
House mouse (1-3)*	Subordinates
Prairie deer mice (4)	Subordinates
Cactus mice (5)	Offspring—inhibited by mother
Mongolian gerbil (6)	Offspring—inhibited by mother
Microtine rodents (7)	Offspring—inhibited by littermates
Olympic and hoary marmots (8, 9)	All—correlated with high altitude environment
Myomorph rodents, macropod marsupials, and cervid artiodactyls (10)	Those food-stressed
Wildebeest (11)	Those at high densities
Elephants (12)	Those at high densities
Common marmoset (13)	Offspring—inhibited by mother
Rhesus monkey (14)	Subordinates
Humans (15)	Those with sufficient body fat
<b>B. INHIBITION OR DELAY OF SEXUAL RECEPTIVITY</b>	
House mouse (1)	Subordinates
Dwarf mongoose (16)	Subordinates
Wild dogs (17)	Subordinates
Wolves (18)	Subordinates
Common marmoset (13)	Offspring—inhibition by mother
Chimpanzee (19)	Sick or injured
<b>C. INHIBITION OR DELAY OF OVULATION</b>	
House mouse (3)	Subordinates—pheromonally induced
Swiss mice (20)	Those most severely crowded
Prairie deer mice (2)	Subordinates
Elephants (12)	Those nutritionally and socially stressed

TABLE 1 *Continued*  
*Mechanisms of reproductive suppression among different species of mammals*

The progression from A to F represents suppression at later developmental stages; in all cases, such suppression seems to occur when conditions suggest that the caretakers cannot provide sufficient investment, or when direct competition between parents or young is extreme, or when both situations obtain.

Subject	Individuals Most Affected
Gelada baboons (21)	Subordinates
Baboons ( <i>Papio</i> spp.) (22)	Subordinates—physically or psychologically stressed
Humans (23)	Those psychologically stressed
D. FAILURE OF IMPLANTATION	
(Difficult to measure; may have occurred in some of section C, above. Very high rates reported in humans in general (24, 26).	
Deer mice (25)	Those crowded
Humans (23)	Those physiologically and psychologically stressed
E. SPONTANEOUS ABORTION	
Marsupials (27)	Extreme environmental change
House mouse (1)	Subordinates
Rats (28)	Those psychologically stressed
African mole rat (29)	Those at high population densities
Dwarf mongoose (16)	Subordinates
Pigtail macaques (30)	Those psychologically stressed
Humans (31)	Those psychologically stressed
Humans (32)	Subordinates—low self-esteem; felt lack of control over self and environment; little support from others
Humans (33)	Those food-stressed
F. EARLY POST-PARTUM MORTALITY	
House mice (2, 34)	Subordinates and late bearers
Rats (28)	Those psychologically stressed
Rabbits (35)	Subordinates
Belding's ground squirrels (36)	Distant kin
Black-tailed prairie dogs (37)	Not stated: increase with size of coterie
Elephants (12)	Those physiologically, nutritionally, or socially stressed
Coke's hartebeest (38)	Females who fail to isolate themselves at parturition
Wild dogs (17)	Subordinates
Lions (39-41)	Late bearers and nomads
Langurs (42)	Subordinates
Pigtail macaques (30)	Those psychologically stressed
Chimpanzees (43)	Subordinates
Gorillas (44)	Subordinates
Humans (45)	Those psychologically stressed
Humans (46)	Subordinates (see E above)
Humans (47)	All castes marrying upward

\* Numbers in parentheses refer to references as follows: 1, Lloyd and Christian, 1969; 2, DeLong, 1978; 3, Bronson, 1979; 4, Terman, 1973; 5, Skryja, 1978; 6, Payman and Swanson, 1980; 7, Batzli et al., 1977; 8, Barash, 1974; 9, Holmes, 1979; 10, Sadleir, 1969a,b; 11, Watson, 1969; 12, Laws, 1969; 13, Eppele, 1975; Hearn, 1977; Kleiman, 1979; 14, Drickamer, 1974; 15, Frisch and McArthur, 1974; 16, Rood, 1978, 1980; 17, Frame et al., 1979; 18, D. Altmann, 1974; Raab, Woolpy and Ginsberg, 1967; Packard and Mech, 1980; 19, Van Lawick-Goodall, 1969; 20, Ryan and Schwartz, 1977; 21, Dunbar and Dunbar, 1977; 22, Rowell, 1970; Wasser, 1983; 23, Peyser et al., 1973; 24, Pullum and Williams, 1979; 25, Eleftheriou, Bronson and Zarrow, 1962; 26, Berndt and Barash, 1979; Shepard and Fantel, 1979; 27, Low, 1978; 28, Herrenkohl, 1979; 29, Jarvis, 1969; 30, Sackett et al., 1974; 31, Engstrom et al., 1964; 32, McDonald, 1965; Hetzel et al., 1961; Grimm, 1962; Nuckolls, 1975; 33, Frisch, 1978; 34, Sayler and Salmon, 1971; 35, Mykytowycz, 1973; Mykytowycz and Fullagar, 1973; 36, Sherman, 1981; 37, Hoogland, 1981; 38, Gosling, 1969; 39, Schaller, 1972; 40, Rudnai, 1973; 41, Bertram, 1975; 42, Hrdy, 1979; 43, Goodall, 1977; 44, Fossey, 1976; 45, Davids, DeVault and Talmedge, 1961; Davids and DeVault, 1962; 46, Grimm, 1961; Ferreira, 1965; Newton, 1968; 47, Dickemann, 1979.

ductive success (e. g., Hirshfield and Tinkle, 1975; Lack, 1968; Hamilton, 1966; Williams, 1966a, 1975; and Low, 1978), in order to account for these high rates of failure. The model we formulate is accordingly termed the Reproductive Suppression Model, and is based on the relationship of present to future reproductive conditions, as shown by temporal patterns in each individual's biomedical, psychological, and environmental conditions. Most significantly, we will extend the concepts linking reproductive effects and environmental adversity to include the individual's social environment as well.

The Reproductive Suppression Model should have important implications for health practitioners—improving their ability to predict and to prevent unsuccessful reproductive attempts among women—as well as for the general evolutionary theory of female-female reproductive competition.

#### THE REPRODUCTIVE SUPPRESSION MODEL

Fisher (1930) defined age-specific reproductive value,  $\Phi$ , as the mean amount of future reproductive success for individuals of a given age and sex. Williams (1966b) separated reproductive value into two components: that proportion allocated to reproduction at the present time,  $\phi$ , and that which remains following the current reproduction ( $\Phi - \phi$ ); the latter is termed the "residual reproductive value." Williams argued that for any reproductive attempt, selection should favor individuals who maximize their current probability of reproductive success with a minimal amount of effort and risk, and thereby maximize their residual reproductive value as well.

The Reproductive Suppression Model assumes that not all conditions are equally favorable for investment in reproduction. When future conditions may be expected to be better than present ones, individuals may be able to maximize their lifetime reproductive success ( $RS$ ) by suppressing their reproduction until that future time. If we elaborate on Williams's conception, this maximization should occur when the increment,  $a$ , to one's probability of reproductive success by reproducing at time 2 rather than at time 1 exceeds the cost,  $c$ , of suppression of the individual's residual reproductive value

( $RRV = \Phi - \phi$ ). In this formulation,  $RS2 = (1 + a)\phi$  and  $RS1 = \phi$ . The cost,  $c$ , is a function of reproductive time lost because of the delay itself, as well as any physiological costs of the suppression. The above conditions are stated more precisely in inequality [1].

$$(RS2 - RS1) > c(RRV) \quad [1]$$

This expression simplifies to  $a\phi > c(\Phi - \phi)$ .

Given the above, the reproductive suppression model predicts that variations in the suitability of conditions for reproduction should have led to the evolution of reproductive patterns among females that cause them to suppress reproduction whenever inequality [1] is expected to hold. Alternatively, when it does not—i. e., when conditions for reproduction are unlikely to improve, or are likely to get worse in the future—mature females are expected to reproduce even if present conditions seem poor. Of course, no conscious decision is necessarily implied in any of these cases; rather, females who experience such reproductive patterns, however acquired, should have a higher lifetime reproductive success than those who do not, and hence, if in some degree heritable, such patterns should have evolved.

Cues that may be used to predict conditions for reproductive success should include the female's physical and mental health, the physical and genetic status of her embryo or fetus, and the external conditions into which the female will give birth (e. g., the availability of resources, and the other environmental and psychological factors described above). Females are expected to attempt physiological termination of their reproduction as soon as the available cues suggest that the conditions of inequality [1] are satisfied. All else being equal, inequality [1] would be more readily satisfied early in a reproductive event than late. This is because, the earlier the loss, the lower will be the effect on the female's subsequent ability to reproduce (i. e., on her residual reproductive value), and hence the lower the value of  $c$  in inequality [1]. As a corollary of this, early terminations are physiologically easier to induce than later ones (Brambell, 1948; Matsumoto et al., 1968; Wilson, 1973;

Shepard and Fantel, 1979; Wasser, 1983; see also below).

We also point out, however, that it may be costly to suppress a reproduction that would otherwise have succeeded (perhaps analogous to a type I versus type II error in statistics). Hence, it becomes important that the cues used to assess the relative probability of offspring survivorship be both reliable and predictable. Since later cues are often more reliable than earlier ones, a trade-off occurs, whereby increasing uncertainty leads to suppression at progressively later stages of reproduction. It may also lead to "near-suppression," as in the production of premature or other low-birth-weight offspring. Similarly, one might also expect the production of less healthy offspring whenever conditions are such that filtering is relaxed—i. e., whenever the mother is less strongly selected to terminate parental investment earlier than she would otherwise (see also below).

We will review data on women and other female mammals that address these issues. We will also consider an underlying assumption of our model, namely, that a large proportion of losses will tend to be mediated by the mother, rather than by the developing embryo or fetus. (Exceptions should occur, however, when conditions result in intra-uterine competition, or when kin-selected effects on the embryo favor its self-destruction to the benefit of its present and future sibs, given that the embryo may have more information about its own status than the mother possesses.)

Finally, a female's expectation of reproductive success may be improved under some competitive conditions by manipulating the reproduction of other females of the population (e. g., through the induction of social stress). Under some conditions, therefore, females are also expected to attempt to suppress the reproduction of other females, rather than their own.

THE RELATIONSHIP OF PRESENT TO FUTURE  
CONDITIONS FOR OFFSPRING SURVIVAL:  
ILLUSTRATIVE EXAMPLES

Some of the clearest examples of reproductive deferral in response to a likely future improvement in reproductive conditions

come from the literature of population genetics and ecology. These include late versus early breeding in response to the growth pattern and age structure of the population (Fisher, 1930; Goodman, 1974; Schaffer, 1974; Pianka, 1976; Charlesworth, 1980); deferred fertility in response to seasonal changes in the availability of critical resources (Sadlier, 1969a,b; Assenmacher and Farner, 1978); sex-ratio adjustments in response to maternal condition relative to reproductive opportunities available to the offspring of each sex (Trivers and Willard, 1973); and sexual bimaturism (Geist, 1971; Estes, 1974; Wiley, 1974), whereby males become behaviorally mature later than females, apparently because intense male-male competition has favored their delayed entry into the world of reproductive competition.

Accumulating anthropological and demographic data on human beings also support the Reproductive Suppression Model. Traditional women of the hunter-gathering !Kung Bushmen of the Kalahari desert space their births 4 to 5 years apart (Howell, 1976). Yet females commence normal sexual activity long before their next conception, and infanticide as well as induced abortion appear to be rare (Lee, 1979, 1980). On the other hand, those !Kung women who shifted from their traditional lifestyle to a more sedentary one involving food production and storage showed a rapid decrease in birth spacing (Howell, 1976; Lee, 1972, 1980). These observations suggest that while traditional !Kung women may be physiologically capable of much more rapid reproductive rates, they typically experience reproductive deferral and, moreover, this deferral appears to be internally mediated.

Various explanations have been offered for the evolution of birth-spacing mechanisms among the !Kung. Thus, !Kung women walk long distances while gathering food, so it is energetically expensive if not impossible for them to carry more than one dependent offspring during such times. On the basis of this reasoning, Lee (1979) showed that it would be optimal for !Kung women to space their births an average of 4 to 5 years apart. Weiss (1976) has argued that birth spacing also may be advantageous

because weaning foods are limited in !Kung society so there is an advantage to prolonged lactation. Still others have argued that birth spacing may be due to food stress that prevents females from reaching a certain minimum nutritional level, necessary for pregnancy, within a period less than 4 to 5 years after giving birth. All of these explanations may be correct to some degree (Lee, 1980; Cohen, Malpas, and Klein, 1980). In any event, they are also consistent with expectations from the Reproductive Suppression Model—i.e., reproduction is suppressed until predictably better times.

Significantly, comparable shifts in birth-spacing appear also to have occurred among other traditional hunter-gatherers, such as the Inuit (Freeman, 1971). Cohen, Malpas, and Klein (1980), Hassan (1980), and Lee (1980) have argued, moreover, that similar spacing mechanisms operated historically among most human populations, a circumstance that would explain the increase in human population growth rates by two orders of magnitude that apparently occurred among hunter-gatherers 10,000 years ago, when human beings first began to produce and store food (Sussman, 1972).

Easterlin (1980) has also postulated mechanisms similar to those proposed by the Reproductive Suppression Model, in order to explain population growth rates in the United States today. Thus, he has explained the 20-year cycles seen in reproductive rates over the past 40 years as a function of simultaneous cycles in the quality of reproductive conditions. He assessed wages and competition in the job market in relation to those experienced by one's parents during the individual's childhood. When present conditions are perceived to be good, individuals marry and produce their first offspring relatively early, and this eventually results in a baby boom. The baby boom, in turn, floods the job market of the next generation, and so leads to conditions that are perceived to be poor for reproduction. Marriage and age at first reproduction are then delayed, and the cycle repeats itself (see also Becker, 1981).

The above observations, applying to humans, and their parallels among other animals suggest that reproductive suppression

mechanisms have been important in our evolutionary past and continue to be important today. This conclusion is critical to our later argument for the clinical implications of the Reproductive Suppression Model—i.e., improved abilities to predict and to prevent reproductive failure among women. However, these abilities will ultimately depend on whether we can determine the cues that are being used to assess reproductive conditions and, more important, the effects of temporal variations in their severity.

#### REPRODUCTIVE FILTERING, EARLY FETAL LOSS AND THE PREDICTABILITY OF CONDITIONS FOR THE SURVIVAL OF OFFSPRING: ILLUSTRATIVE EXAMPLES

Some of the best data regarding both temporal patterns of reproductive filtering and maternal, in contrast to embryonically mediated, loss come from the investigations of Brambell (1948). He sacrificed 3,000 wild-caught rabbits, under the assumption that prenatal mortality due to *maternal* failure would tend to fall on whole litters, whereas that due to *embryonic* failure would tend to fall on individual embryos. Rabbits are uniquely suited for such experiments because they are induced ovulators (ovulation therefore indicating that copulation has occurred). Moreover, their preimplantational losses of embryos, as well as losses of whole litters, can be assessed by counting the number of corpora lutea in comparison with the number of implantation sites in a given female. Finally, the temporal pattern of post-implantational embryonic loss can be determined by counting numbers of mummified embryos—these are resorbed rather than aborted in polytocous species unless the entire litter is lost.

As we can see from Table 2, the vast majority of loss of whole litters among Brambell's wild-caught rabbits occurred after implantation; most of these were lost prior to mid-pregnancy, between days 11 and 15 of gestation. On the other hand, most losses prior to implantation were of individual embryos. Interestingly, the proportion of ova lost, and the proportion of litters suffering loss, prior to implantation, increased with the number of eggs the female ovulated (Brambell, 1948). However, such

TABLE 2

*Percentage of ovulated ova that are lost prior to or following implantation*

Given in the form of whole litters or from surviving litters among wild-caught rabbits (adapted from Brambell, 1948).

Percentage of ova lost as whole litters			Percentage of ova lost from surviving litters			Overall
Pre-Implant.	Post-Implant.	Total	Pre-Implant.	Post-Implant.	Total	
1	34.7	35.7	7	0.6	7.6	43.4

\* All values given are minimums.

loss is less in animals that were above the mean body weight for the population. These observations suggest that the more eggs ovulated, relative to the condition of the mother, the less favorable the embryonic environment up to implantation. It also suggests that post-conception, pre-implantation filtering is occurring whereby only the strongest embryos implant. Post-implantation loss was also inversely related to female body weight. However, in contrast to the pre-implantation case, post-implantation loss was inversely related to the number of eggs implanted. Thus it appears that the "bad" eggs tend to be lost individually, prior to implantation. Post-implantation loss then becomes an inverse function of the number of presumably good eggs that the female has implanted, combined with the quality of the female's health and probably her external environment. The latter interpretation is further supported by the observations that dead embryos showed few visible abnormalities, and that most loss occurred over a short period of time—between days 11 and 15—a fact suggesting similar external causes.

Among humans, and in just about all other animals studied thus far, we find also that, as expected, reproductions are physiologically easiest to inhibit in the early stages. Thus, for example, temporary infertility is common among women, being caused even by small life changes. Moreover, the duration of infertility is directly proportional to the perceived severity of the stress (Rakoff, 1962; Piotrowski, 1962; Matsumoto et al., 1968; Fries, Nillius, and Peterson, 1974; Yaginuma, 1979). Once females conceive, the first trimester is by far the most vulnerable to loss from environmental stressors or teratogens. Moreover, in humans 50 to 60

percent of first trimester losses have been found to have structural and chromosomal abnormalities. The greater the anomaly, the earlier the loss (Wilson, 1973; Shepard and Fantel, 1979). Second and third trimester losses, on the other hand, are relatively low in frequency of chromosomal abnormalities because the grosser ones have already been filtered out. The majority of second and third trimester losses tend to be premature births, at least two-thirds of which are currently labeled idiopathic—i.e., are of unknown origin (Ratten, 1981). As Shepard and Fantel (1979) have emphasized, this pattern of loss among humans parallels that described by Brambell among rabbits and other mammals.

We emphasize, however, that for selection to favor early loss, the cues that reflect the conditions for reproductive success should be reliable. As stated earlier, the trade-off between the advantages of early embryonic or fetal losses when conditions are poor, and the disadvantages of premature termination before such cues or predictors are adequately reliable, should have a considerable influence on the timing of suppressions. Effects of this trade-off are probably best illustrated by making a comparison of reproductive patterns among marsupial and eutherian (placental) mammals.

The reproductive patterns of a number of marsupials (especially among the Macropodidae) appear to be well-suited to the unpredictable environments that characterize so much of their geographical range. In fact, Low (1978) has suggested that the primary factor that prevents placental mammals from excluding marsupials throughout their range is the unique ability of many marsupials to terminate reproduction at virtually any stage, with relatively low cost.



This adaptation includes facultative anestrus and facultative, as opposed to seasonal, embryonic diapause, which enable marsupials to reproduce rapidly as soon as conditions improve.

Marsupials also show a dramatically short, low-investment gestation and early lactation. These traits combine to favor easy, low-cost abandonment at relatively late stages of reproduction when poor conditions, such as high predation, occur suddenly. Finally, the short gestation of many marsupials does not interfere with the occurrence of other ovulations, as it does in placentals (i.e., current reproduction is relatively less likely to affect the subsequent ability to reproduce in marsupials than it is in placentals). This ability enables marsupials to breed again, or to implant a diapause embryo as soon as offspring survival conditions improve. The more unpredictable the cues, the more advantageous this "on-off" system of the marsupials.

Such a filtering system has an effect similar to that of asynchronous hatching in response to unpredictable environmental risks (Low, 1976; Clark and Wilson, 1981). Low's work has recently been criticized (Morton, Rescher, Thompson, and Braithwaite, 1982; Russell, 1982; but see Low and Wasser, in press).

#### RELIABLE CUES AND THEIR USE IN PREDICTING OUTCOMES

Given the importance of using reliable cues to predict temporal patterns of reproductive conditions, we can ask: what constitutes such cues and how can we take advantage of them to predict and prevent poor reproductive outcomes in human beings?

Natural selection should favor the use of any cues that reliably reflect temporal changes in an animal's reproductive condition. One such cue, for example, is age and its associated physical changes. All else being equal, future conditions for reproductive success that are a function of aging should tend to be better than present conditions ( $RS_2 > RS_1$ ) until females reach the age of their reproductive prime. (Note that genetic models of life-history tactics predict that this prime will be reached quickly fol-

lowing sexual maturation: Charlesworth, 1980.) Then, as females pass their prime, present conditions should tend to be better than future ones ( $RS_1 > RS_2$ ). In long-lived, highly social species such as human beings, in which offspring have the potential of benefiting from parental care throughout most of their reproductive lifetimes, but in which reproductive condition nonetheless continues to decline with age, females appear to reach a life stage such that the continued advantages (as well as the stresses) of providing adequate care to existing offspring has favored the evolution of menopause (see Williams, 1957; Hamilton, 1966; Alexander, 1974). A variety of predictions stem from this association between age and reproductive condition. First, reproductive deferral in response to externally imposed stressors should be most likely among very young females, because for them,  $RS_2 > RS_1$ . On the other hand, reproductive deferral should be least likely among premenopausal older females, because for them  $RS_1 > RS_2$ .

The data seem to support both of these predictions. Thus, for example, demonstrations of delayed sexual maturation in response to low body weight per unit of height (Frisch, 1978; Frisch and McArthur, 1974) have been much more convincing than attempts to demonstrate any ovulatory failure among mature women under such conditions (see review by Cohen, Malpas, and Klein 1980). Moreover, some of the highest rates of spontaneous abortion in technological societies occur among young, post-pubescent girls. Animal studies also concur, as best shown by Bronson's (1979) work on house mice (see also Table 1, part A). Male house mice secrete a pheromone in their urine that facilitates estrus and subsequent ovulation in females who immigrate into their territories. Adult females, on the other hand, secrete a pheromone that suppresses the facilitatory effect of the male's pheromone on other females. However, the inhibitory effect of the adult females is ineffective on other adult females; it suppresses only the male's facilitation of estrus among females who have just reached sexual maturity. (Just-matured female mice may also be less able to defend themselves against attacks by

adult females, and so may also gain by delaying their own reproduction.)

The available data on older women are quite limited, and contradictory. We would predict that older women should be more "tenacious" about retaining their fetuses, and yet, the overall tendency of women to abort increases with maternal age, presumably as one aspect of the female's declining reproductive potential with age. However, a possible result of this decline is to make older females at times relatively less likely to abort such a fetus when factors "independent" of the female's reproductive potential suggest that such a fetus has a reduced probability of survival. This is best illustrated by studies of Down's Syndrome by Erickson (1978) and Sved and Sandler (1981). These investigators have found that the high frequency of Down's syndrome (and of trisomy in general) in the children of older women is not simply due to a greater tendency for nondisjunction (i.e., abnormal chromosome segregation) to occur, but also to a decrease in the tendency of these older women to abort aneuploid fetuses (individuals abnormal in chromosome number). Thus, at least in these cases, older women seem less likely to defer their reproduction (as expected), presumably because for them  $RS2 < RS1$ .

Finally, Charlesworth (1977) used a model similar to ours to predict age-specific adjustments of the sex ratio among humans. Since male zygotes are known to have a higher probability of dying between conception and weaning, Charlesworth assumed that those women not using contraceptives who tend to produce a higher-than-average frequency of male zygotes should have a shorter than average interval between successive conceptions. Thus, he predicted that younger women should produce a higher frequency of males than do older women because older women, having a greater chance of becoming sterile or dying in the intervals between conceptions than young women, have a lower net ability to "compensate" for any deaths of offspring. Data on sex ratio at birth in human populations based on maternal age (Novitski and Kimball, 1958; Teitelbaum, 1972) are consistent with Charlesworth's prediction, and hence, with ours.

Most other cues (such as nutritional status, disease, and psychosocial stress) are likely to be less reliable long-term predictors of future reproductive success than age itself. Use of these cues may thus entail a somewhat different strategy. Since long-term past experience should often provide good prediction of the future, chronic temporal patterns in the degree and direction of these other cues may be important in predicting reproductive suppression as well. Some of the best illustrations of this come from comparisons of cases in which "stressors" (e.g., malnutrition or various diseases) are experienced chronically rather than acutely. In the chronic situation, long-term past experiences should make future conditions for reproductive success ( $RS2$ ) unlikely to be perceived as becoming better than those obtaining at present ( $RS1$ ; see inequality 1). Even though  $RS1$  may be low in absolute terms, the organism should be selected to evaluate its reproductive success in relative terms, so as to make the best of all available evolutionary "deals" for itself.

By contrast, individuals experiencing acutely worsened conditions should be more likely to perceive future conditions as probably better than those currently obtaining. Thus, such stress-related reproductive deferral would be expected to be much less dramatic when the stress is chronic than when it is acute. Relevant data on the reproductive consequences of malnutrition have been reported by Bongaarts (1980). He found that women in Third-World countries who suffered from chronic malnutrition did not have high rates of infertility and spontaneous abortion: The major effects on their reproduction occurred in the form of neonatal mortality and delayed sexual maturation. (Note: the above discussion of age-related effects also suggests why delayed sexual maturation might be expected here.) On the other hand, women suffering acute malnutrition, such as during the Dutch famine of World War II, had extremely high rates of infertility and spontaneous abortion (Stein and Susser, 1975). Thus, the findings are in agreement with the model.

Investigators have since gone back to evaluate the IQ's of children born during the Dutch famine, in the expectation that their

IQ's would be lower than those of children born prior to, or following, such severe malnutrition. However, this prediction was not confirmed (Stein, Susser, Saenger, and Marolla, 1975), a result suggesting that the suppression that did occur may have successfully "filtered out" those cases most likely to be affected by malnutrition. A similar case of reproductive filtering under stressful conditions was also reported by Avis Greene (pers. commun., cited in Bernds and Barash, 1979). She studied abortion rates of women in one Washington State prison, and not surprisingly found them to be extremely high. It was surprising, however, that of the 373 prison births that did occur, not a single one had any complication, although statistics for the U.S. population as a whole would have predicted 27. A reasonable explanation in this case is that under conditions of extreme stress, those cases least likely to succeed have been filtered out by reproductive suppression at some stage of gestation—presumably early (see also Shepard and Fantel, 1979, p. 240).

In conclusion, the high rates of reproductive failure among female mammals may at least in part result from an adaptive mechanism that avoids current reproduction when personal fitness would be best served by delaying reproduction until some future time.

Many clinical implications flow from this conclusion, the most important of which is an improved ability to predict and prevent poor reproductive outcomes among women in the future. These implications are further discussed at the end of this article. First, we must consider the role of social factors in affecting reproductive success, and the relevance of such factors for our model.

Studies of poor reproductive outcomes in women (e.g., Grimm, 1962; Sturgis, 1962; McDonald, 1965; Nuckolls, 1975; Carena and Zichella, 1979; Paykel, Emms, Fletcher, and Rassaby, 1980; Saksena and Srivastava, 1980) as well as in animals (see below, and Table 1) appear to be linked to social conditions. In addition, a very important social condition can be modified by manipulating the reproduction of other females, since the reproduction of other females itself constitutes a crucial part of the social environment of most female individ-

uals. Thus, the possibility of suppressing the reproduction of other individuals (or facilitating their suppression) adds a new dimension to the Reproductive Suppression Model.

#### SOCIAL SUPPRESSION

Social suppression occurs whenever reproduction is somehow inhibited by one's interactions with, and the reproductions of, other individuals. For a variety of reasons, social suppression provides some of the best and most interesting applications of the Reproductive Suppression Model. First, depending on the species' ecology and group structure, the relation of current to future conditions for reproduction may either be highly or poorly predictable early in a reproductive event. Situations of high predictability should result in suppression relatively early in a reproductive event, whenever socially dependent resources are scarce. This occurs, for example, among highly social species such as dwarf mongooses, wolves, and wild dogs, in which breeding resources are highly limiting and subordinate females sometimes defer reproduction indefinitely, with never-fulfilled "hopes" of becoming the dominant, breeding female in the future (Rood, 1978, 1981; Packard and Mech, 1980; Frame, Malcolm, Frame, and van Lawick, 1979; see also below).

By contrast, poor predictability should result in suppression at progressively later stages, as among elephant seals. Female elephant seals conceive their next year's offspring just after giving birth to their young of the year. They then leave the rookery, delay implantation by approximately four months, and then return to give birth and breed again one year later. Thus, competitive conditions during a specific birth, conditions that are a function of rookery density, cannot be predicted until the time of that birth. Under competitive circumstances, neonatal mortality is exceedingly high in this species, and results from exposure, injury, or starvation (Reiter, Panken, and Le Boeuf, 1981).

Whenever socially dependent conditions affect reproductive success, females may also be able to improve their current probability

of reproductive success by manipulating the timing and frequency of births among others in their own social group. The general tendency for reproductive suppression among females has almost certainly provided the preadaptation for females to influence one another's reproduction. Thus, as illustrated by the studies described below, suppressed females generally tend to be those whose social status makes them least able to fend for themselves in aggressive and other competitive interactions (see also Table 1). When competition is high, and particularly under persistent harassment by others, it should actually be beneficial for such females to suppress their own reproduction until less socially competitive times. At the same time, however, females may also benefit by suppressing the reproduction of others under such socially dependent conditions of resource availability. In fact, suppressing the reproduction of others should be the competitively favored mechanism (cf. Fox, 1975; Frame et al., 1979; Kleiman, 1979; Rood, 1978, 1980; see also Table 1) whenever it improves current conditions for reproductive success to a degree that exceeds the cost ( $c$ ) of suppressing others on one's residual reproductive value ( $c$  here is a function of the difficulty of suppressing others). These conditions are illustrated by inequality [2].

$$(RSw - RSw_0) > c(RRV) \quad [2]$$

where  $RSw_0 = \phi$ , the individual's reproductive success if it were not to attempt to suppress another individual; and  $Rsw$  is the individual's reproductive success if it were to suppress the reproduction of another individual.  $RSw$  is thus a function of the increment,  $a$ , to the individual's probability of reproductive success when the recipient's reproduction is suppressed, less the decrement,  $d$ , to that probability resulting from the risk of suppressing one's own reproduction while attempting to suppress that of the competition—i.e.,  $RSw = (1 + a - d)\phi$ . [The above inequality simplifies to  $(a - d)\phi > c(\phi - \phi)$ .]

Numerous studies have shown that socially-dependent conditions cause substantial variance in female reproductive success (see Lack, 1954, Wynne-Edwards,

1962, and Fox, 1975, for a variety of birds and mammals; Eleftheriou, Bronson, and Zarrow 1962, for deer mice; Lloyd and Christian, 1969, Sayler and Salmon, 1971, and DeLong, 1978, for house mice; Mykytowycz, 1973, and Mykytowycz and Fullagar, 1973, for rabbits; Sherman, 1981, for ground squirrels; Hoogland, 1981, for prairie dogs; Gosling, 1969, for Coke's hartebeest; Jarvis, 1969, 1981, for naked mole rats; Laws, 1969, for elephants; Schaller, 1972, Rudnai, 1973, and Bertram, 1975, for lions; Rood, 1978, 1980, for dwarf mongooses; Frame et al., 1979, for African wild dogs; Packard and Mech, 1980, for wolves; Reiter, Panken, and Le Beouf, 1981, for elephant seals; Fossey, 1976, for gorillas; Goodall, 1977, for chimpanzees; Dittus, 1979, and Silk et al., 1981, for macaques; Hrdy, 1979, for langurs; Kleiman, 1979, 1980, for common marmosets; Altmann, 1980, and Wasser, 1983, for baboons; Bongaarts, 1980, for humans). The occurrence of a large number of nondispersing infants born near the same date may also affect the age at which the infant reaches sexual maturity (e.g., Lloyd and Christian 1969, DeLong, 1978, and Bronson 1979, for house mice; Batzli, Getz and Hurley, 1977, for microtine rodents; Terman, 1973; Lombardi and Whitsett, 1980, for prairie deer mice; Laws, 1969, for elephants; Watson, 1969, for wildebeest; Drickamer, 1974, for macaques; Ahnlund, 1980, for badgers). This situation can affect the infant's relative lifetime reproductive success (Cole, 1954), and hence the inclusive fitness of its parents (Hamilton, 1964). Socially mediated reproductive suppression should be expected, and does occur, under such circumstances, as is illustrated in many of the citations above. Some illustrative examples from our own recent work, as well as from others, is given in more detail below.

#### REPRODUCTIVE INHIBITION IN YELLOW BABOONS (*Papio cynocephalus*)

In a study of yellow baboons at Mikumi National Park, in Tanzania, Wasser (1983) found that females frequently formed attack coalitions, whereby two or more females simultaneously attacked another female. The tendency of females to enter into attack

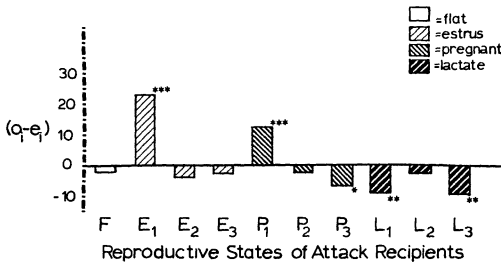


FIG. 1. COALITION ATTACKS RECEIVED BY FEMALE YELLOW BABOONS (*Papio cynocephalus*), AS A FUNCTION OF THEIR REPRODUCTIVE STATES

Data are presented as observed ( $o_i$ ) minus expected ( $e_i$ ).

The total number of attacks received by all adult females, from adult females,  $N_i = 83$ ;  $p_i$  = the proportion of females in the population that compose the  $i$ th reproductive state; thus the expected frequency ( $e_i$ ) is  $Np_i$ . \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.0001$  — binomial test. From Wasser, 1983.

coalitions was positively correlated with the number of females simultaneously in estrus. This, in turn, reflects the extent of clumped births likely to occur six months later, and presumably the degree of competition infants will face. Altmann (1980) found that infant mortality among yellow baboons at Amboselli (approximately 30% during each of the infant's first two years) was dependent on the number and relative ages of other infants simultaneously in their group, relative to the availability of easily obtained, eaten, and digested "weaning foods" (see also Dittus, 1979).

Wasser (1983) argued that the availability of paternal care (see Altmann, 1979; Parker, 1980) may be important to infant survival as well, since males with more than one offspring will have difficulty in surveying them simultaneously. These factors all suggest that the attack coalitions observed by Wasser may be attempts by attackers to manipulate the reproduction of the recipients in relation to themselves. A further analysis of these coalition attacks suggests that they do just that. The social stress that results from being attacked by a large number of adult females (or from having one's offspring so attacked), apparently serves to suppress the reproduction of the recipients (see also Gilman and Gilbert, 1946; De Vore, 1965; Rowell 1970; Sackett,

Holm and Landesman-Dwyer, 1975; Dunbar and Dunbar, 1977; Bowman, Dilley, and Keverne, 1978; Keverne, 1979; Wasser, 1983, for descriptions of actual suppressions that have been observed). Thus, those females harassed most were predicted to be in reproductive states that are most immediately involved in reproduction, as well as the most easily suppressed [this would have the respective effects of increasing the value of  $a$  while decreasing the value of  $d$  in inequality (2), as defined above].

Assuming that (A) suppression is physiologically easiest to induce early in a reproduction (Hendrickx and Nelson, 1971; Shepard and Fantel, 1979; Wilson, 1973); (B) cycling females approaching ovulation (in the follicular phase) are physiologically more susceptible to stress-induced delay or inhibition of their ovulations than are those at or past ovulation (Rowell, 1972; Matsu-moto et al. 1968); and (C) ovulating and newly lactating females tend to be buffered from attacks by their mates (Rowell, 1970; Hausfater, 1975; Altmann, 1980; Wasser, 1983), the following specific predictions were made: (1) cycling females approaching ovulation (estrus 1) should be attacked more frequently than females in any other reproductive state, and much more frequently than cycling females at estrus 2 or past ovulation (estrus 3 or flat); (2) females in the first trimester of pregnancy should be at-

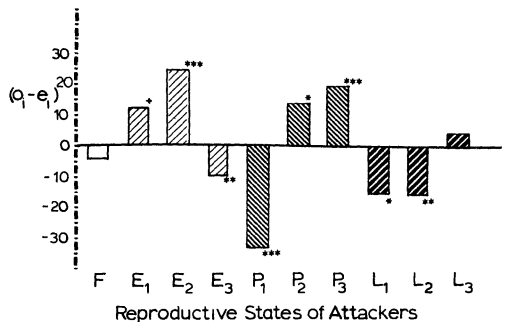


FIG. 2. COALITION ATTACKS GIVEN BY FEMALE YELLOW BABOONS, AS A FUNCTION OF THEIR REPRODUCTIVE STATES

Data are presented as observed minus expected.

$N = 360$ , the total number of coalition attacks given by females, summed across all adult females;  $p_i$  = same as in Fig. 1; the expected frequency is as in Fig. 1:  $e_i = Np_i$ . From Wasser, 1983.

tacked second most frequently, and the tendency for pregnant females to be attacked should then decline with succeeding stages or pregnancy.

For their part, females attacking others should also be in reproductive states most involved in reproduction as well, but also those most difficult to suppress (this would increase the value of  $a$  while decreasing the value of  $c$ , as defined above). Thus, subject to their availabilities, coalition attackers should most often be ovulating females (estrus 2) or females in their late trimester of pregnancy (pregnant 3), followed by females approaching ovulation (estrus 1) and females in their second trimester of pregnancy (pregnant 2). (Risk, as well as the demands of energy and time, are assumed to prevent lactating females from attacking others.) The Mikumi data support these predictions (Fig. 1 and 2).

The ranks of attackers and their recipients fit this pattern as well. Thus, recipients also tended to be low in rank (Fig. 3) and therefore easiest to stress, as well as those least able to fend for their young when competition is high. Attackers, on the other hand, tended to be primarily mid-ranking females (Fig. 4)—those who could benefit most from such behavior. Low-ranking females rarely attack others, as they are unlikely to win such encounters, and hence are unable to stress others adequately. High-ranking females also rarely attack others, apparently because their offspring already have a high probability of survival. Thus, to suppress the reproduction of other females would provide high-ranking females with few additional gains, except perhaps under extremely harsh conditions. Similar results were reported by Drickamer (1974), Hinde

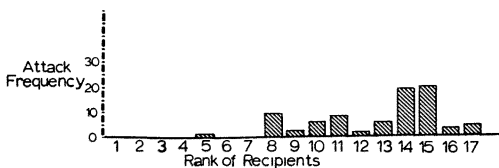


FIG. 3. COALITION ATTACKS RECEIVED BY FEMALE YELLOW BABOONS, AS A FUNCTION OF THE DOMINANCE RANK OF THE RECIPIENTS  $N = 83$ ; from Wasser, 1983.

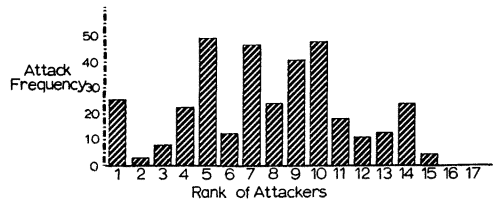


FIG. 4. COALITION ATTACKS GIVEN BY FEMALE YELLOW BABOONS, AS A FUNCTION OF THE DOMINANCE RANK OF THE ATTACKERS  $N = 360$ ; from Wasser, 1983.

(1974), Seyfarth (1976), Cheney (1977), Altmann (1980), and Dunbar (1980).

#### ANNUAL REPRODUCTIVE INHIBITION IN FEMALE HOARY MARMOTS (*Marmota caligata*)

Studies of hoary marmot behavior by one of us (DPB) during the past six years in the Washington Cascade Mountains have confirmed the occurrence of a biennial reproductive cycle (Barash, 1974; Holmes, 1979). Hoary marmots are typically found in either monogamous or bigamous social systems. Although biennial breeding is the rule, and no hoary marmot female has been observed to breed in successive years, additional years are occasionally skipped, so that some females miss two consecutive reproductive seasons.

Research on yellow-bellied marmots (*Marmota flaviventris*, Downhower and Armitage, 1971) has shown that polygynously mated females have a lower reproductive success, measured as number of yearlings dispersed, than do monogamously mated individuals. This finding suggests that female-female competition may mediate marmot reproductive success. Application of the Reproductive Suppression Model leads to the four following predictions. (1) Reproductive skipping (beyond the biennial norm) should be more pronounced among bigamously mated females, who have the opportunity or liability of competing with another female, than among monogamously mated females, who do not. (2) Reproductive skipping should be more frequent among bigamously mated females in cases where both females should otherwise be reproducing synchronously, than in cases in which the two females are already asynchronous. All else being equal,  $RS_2 > RS_1$  in the former

case, but equal in the latter case [see inequality (1)]. (3) When such reproductive skipping occurs, it should occur more frequently among subordinate than among dominant females, because  $RS_2 > RS_1$  for the subordinate but not for the dominant female; moreover, this difference could be further exaggerated by the relatively greater ability of dominants to decrease  $RS_1$ , relative to  $RS_2$  among their subordinates by means of aggression. In terms of inequality (2), this would increase  $RS_w$  relative to  $RS_{wo}$  for dominants by decreasing the value of  $d$ , as described above; at the same time, the value of  $c$  in inequality (2) should also be decreased. It follows (4) that asynchronous reproduction should be positively correlated with disparity in social dominance.

We have recorded nine cases of different females who skipped two consecutive years out of a total of 79 typical biennial breedings. Of these nine exceptional cases, eight were bigamously mated; the ninth was monogamously mated. Of the 79 biennial breedings observed, 56 were bigamously mated females and 23 were monogamously mated females. Bigamously mated females are significantly more likely than monogamously mated females to skip an additional year ( $p < .05$ , Fisher's exact test), and thereby prediction #1 is supported.

An alternative hypothesis, consistent with these findings, is that bigamous females are more likely to skip than monogamous females, because the former tend to occupy habitats lower in quality. This is unlikely, however, since forage quality is weakly correlated with marmot monogamy versus polygyny, at least among Olymptic marmots (Woods, 1973). The availability of hibernacula appears to be the primary determinant of monogamy versus polygyny among the hoary marmots (Holmes, 1979).

Another alternative hypothesis for prediction #1 is that female reproductive skipping is influenced by age and that monogamous females are likely to be a biased sample of the population's age distribution, either significantly older or younger than the mean. To test this hypothesis, we combine the years 1978, 1979, and 1980, and find the mean age for all adult marmot females (when such age was known) to be  $4.2 \pm 1.1$

years ( $n = 25$ ). For the bigamous females it was  $4.0 \pm 0.9$  years ( $n = 16$ ) and for the monogamous females it was  $4.3 \pm 1.3$  years ( $n = 9$ ). The difference is not significant, perhaps because of the small numbers of females in each class, but it seems unlikely that differences in reproductive skipping are due to differences in female age at monogamous versus bigamous sites. Furthermore, of the nine females that skipped an additional reproductive year, the age at skipping was known for six. Their mean age was  $4.1 \pm 1.4$  years, which is not distinguishable from the mean of the population as a whole.

Skipping females are also significantly more likely to be individuals who would otherwise be synchronous, rather than asynchronous, with the co-female ( $p < .05$ , by Fisher's exact test). Prediction #2 is thereby supported. In seven of the eight bigamously mated females who skipped an additional year, the skipping individual's co-female reproduced during that year. In only one case was the skipping female associated with another female who was in the nonbreeding year of her cycle. Moreover, during the six years for which data are available, bigamous hoary marmot females were more likely to be reproductively asynchronous rather than synchronous, with the co-female in their biennial cycles: there were 33 asynchronous breedings as opposed to 23 synchronous breedings. This disparity in itself suggests that there is an adaptive modification of female reproduction whereby competition between the offspring of different females is minimized by a reduction of the likelihood that both females reproduce during the same year.

Unfortunately, no data are available on the establishment of bigamous colonies. Thus, it remains to be determined whether the tendency of bigamous colonies to be occupied by asynchronous females is due to (1) the reproductive suppression of a newcomer or non-dispersing subadult by the prior resident, or (2) a greater propensity for nonbreeding females to be accepted by the breeding resident or to attempt to enter an existing colony, or (3) reproductive suppression of one of two founding females by the other. In any event, it seems evident that reproductive deferral (a step beyond asyn-

TABLE 3  
*Chase ratios for hoary marmots (Marmota caligata)*

The data indicate the proportions of chases initiated to total chases (initiated plus received) for bigamously mated females observed to skip an additional reproductive year, compared with similar proportions for their co-female who did not skip. (Calculated as proportions of chases per individual per 10 hours.)

A, one skipping and one non-skipping female, at each of four colonies; based on 247 observed hrs. B, these same individuals, one year prior to the skipping; based on 183 observed hrs.

A				
	Colony #1*	Colony #2*	Colony #3**	Colony #4 <sup>ns</sup>
Skipping female	$\frac{1.2}{4.1} = 0.29$	$\frac{0.9}{2.3} = 0.39$	$\frac{0.7}{3.6} = 0.19$	$\frac{0.5}{2.1} = 0.27$
Non-skipping female	$\frac{0.2}{0.4} = 0.5$	$\frac{1.1}{1.9} = 0.56$	$\frac{0.30}{0.61} = 0.49$	$\frac{0.9}{2.1} = 0.43$

B			
	Colony #1*	Colony #2*	Colony #3**
Skipping female	$\frac{0.71}{2.81} = 0.25$	$\frac{0.26}{0.85} = 0.30$	$\frac{0.15}{0.94} = 0.16$
Non-skipping female	$\frac{0.40}{0.89} = 0.45$	$\frac{1.3}{2.9} = 0.45$	$\frac{0.45}{0.71} = 0.63$

\* p < 0.05; \*\* p < 0.01; ns, not significant. All comparisons between skipping and non-skipping female within each colony.

chrony in overt non-reproduction) is correlated with reproduction by the co-resident female. (The data are insufficient to determine the possible role of kin effects in such suppression.)

If we consider only the seven bigamously mated females who skipped an additional year, prediction #3 suggests that these females should each be socially subordinate to their non-skipping co-resident female. Data on chases initiated and received during 247 hrs. of observation, using continuous sampling, are available for four colonies that contained skipping individuals. In three of the four colonies, the ratio of chases initiated to chases received was significantly lower for the skipping individual than for her non-skipping co-resident female. Whereas the fourth did not reach a significance level, the trend was in the predicted direction (Table 3A). Since pregnant marmots tend to be more aggressive than nonpregnant individuals, however, these data do not in themselves speak to the question of whether a low social status of the skipping individuals is a cause or an effect of their failure to reproduce. Accordingly, skipping and nonskipping co-resi-

dent females were compared for their ratio of chases during the year before the observed reproductive skip, i. e., at a time when both females were nonreproductive. Such data were available for three of the four cases (Table 3B). Each of the three females who skipped an additional reproductive year was significantly subordinate to her co-female during the previous year as well.

Prediction #4 was that among bigamous colonies, synchronous breeders should be closer in rank than asynchronous breeders. Data are available on the ratio of chases initiated to total chases (initiated plus received) for females at 7 synchronous colonies and at 8 synchronous colonies. Since reproduction influences dominance status, these comparisons used the dominance status of asynchronously breeding females calculated for each when she was breeding. Among the 7 synchronous colonies, the two females within each colony differed significantly in chase ratios (binomial test,  $p < .05$ ) in only one case. Among the 8 asynchronous colonies, the two females differed significantly in chase ratios 6 times (binomial test,  $p < .05$ ). Prediction #4 is therefore sup-



TABLE 4

*Partial reproductive inhibition among subordinate female hoary marmots*

Dominant and subordinate females are compared via the t-test.

	Adult females	Young per female*	Yearlings, per female*	Non-dispersing two-year-olds per female*
Dominant	14	4.3 (0.5)	2.7 (1.0)	0.9 (0.3)
Subordinate	12	2.2 (0.6)	0.5 (1.2)	0.2 (0.3)

Parentheses give standard deviation (SD).

\*  $p < 0.01$ .

ported by these findings: asynchronous breeders are significantly more likely to differ in dominance status than are synchronous breeders (Fisher's exact test,  $p < .05$ ), and this difference is in the expected direction.

Unlike primates, which typically have singleton births, marmots have litters as large as seven. The opportunity therefore also exists for subordinates to be partially suppressed in their reproduction relative to dominants, but nonetheless to reproduce (see also Brambell, 1948). Young marmots are first seen above ground at weaning. Adult females were identified as clearly subordinate to their co-resident adult female when their ratio of chases initiated to chases received was  $<0.5$ ; similarly, clearly dominant individuals had a chase ratio  $>2$ . Data are available for the number of young produced by 12 clearly subordinate females, and also for 14 females who were clearly dominant (Table 4; 316 observed hrs. of focal group, continuous sampling). Subordinate females produced significantly fewer young than did dominant females, and furthermore, this difference persisted in subsequent years, when their offspring became yearlings and eventually, two-year-olds. Although the possibility of female infanticide cannot be ruled out, no cases were observed of other adults entering the burrow of a recently post-partum female.

A nonexclusive alternative to our reproductive suppression hypothesis is that dominance status and reproductive success are both age-related, so that dominance and reproductive success are only incidentally correlated. This interpretation cannot be ruled

out; in fact, it is supported by the available data. Ages are known for 9 of the 12 clearly subordinate females who reproduced (mean =  $3.7 \pm 1.4$  years), and for 10 of the 14 clearly dominant females (mean =  $5.0 \pm .4$  years). The age difference between subordinate and dominant females here is significant (t-test,  $p < .05$ ). Thus, although skipping individuals appear to be no younger than the mean age for the population as a whole, older individuals are more likely to be dominant (see above). Among those individuals that do reproduce, however, dominant individuals have a higher reproductive success than do subordinates. The apparent role of age in mediating dominance status does not in any way contradict the point we are seeking to make. However, it would be profitable to disentangle these influences if we are able eventually to obtain a sufficient sample of young, dominant females and old, subordinate ones for statistical analysis. Until that time, we can nonetheless conclude that dominant females have a higher reproductive success than do subordinate females, regardless of the specific proximate mechanisms that lead to this difference.

In summary, hoary marmots reveal a syndrome of reproductive data suggesting that suppression of reproduction by females is an important aspect of their biology. Reproductive skipping is more pronounced in cases which would otherwise lead to synchronous breeding with the co-resident female; reproductive asynchrony correlates with disparity in social rank; and finally, subordinate females appear to leave fewer descendants than dominants, both because they are occasionally inhibited from reproducing at all

when co-resident females are doing so, and because when they do reproduce, they may nonetheless be partially suppressed.

SOME EXTREME EXAMPLES OF SOCIAL  
SUPPRESSION: REPRODUCTIVE DESPOTISM,  
RELATEDNESS, AND REPRODUCTIVE SUCCESS

We suggest the term "reproductive despotism" for cases in which only one female breeds in a social group of several adult females, each of whom helps care for the breeding female's young. Eusociality, as described for the social insects (Wilson, 1971), is an extreme case of this. Situations of reproductive despotism offer an intriguing problem for the Reproductive Suppression Model. Reproductive despotism has been reported in dwarf mongooses (Rood, 1978, 1980), wolves (Packard and Mech, 1980), wild dogs (Frame et al., 1979), tamarins (Kleiman, 1979), and most notably in the naked mole rat, which grades into eusociality whereby suppression is apparently irreversible (Jarvis, 1981). Not surprisingly, reproductive despotism tends to occur when the advantages to sociality are great but the resources per individual are severely limiting. Thus, with the exception of the naked mole rat, most cases of reproductive despotism occur among highly social, insectivorous or carnivorous mammals. According to Clutton-Brock and Harvey (1978), given equal group sizes, competition for food should be most extreme in such mammals. Naked mole rats, on the other hand, eat bulbs and roots, yet they show the most elaborate reproductive despotism known outside the eusocial insects (Jarvis, 1969, 1981). In fact, the natural history of the naked mole rats, who live totally underground and have an elaborate division of labor, largely parallels that of the termites (Jarvis, 1981). Like termites, mole rats also live under exceedingly high densities as colonies mature. It seems that the advantages of efficient division of labor, and hence of sociality, have partially resulted in the extreme reproductive despotism found among these peculiar mammals (see also below).

From the perspective of the successful, breeding female, we can readily see the

adaptive significance of combining reproductive suppression with "helping at the den." Given communal care, a female can increase its relative litter size without a proportional increase in its relative parental investment, and thereby dramatically increase its reproductive potential. But why should suppressed females continue to care for the breeding female's young, let alone show irreversible suppression at birth, or with advancing age, as in the naked mole rat?

As Hamilton (1964) has emphasized for the eusocial insects, relatedness can promote reproductive despotism in so far as helpers gain in inclusive fitness by helping their kin, especially those kin with the highest reproductive potential (Forsyth, 1980). This may be especially true for the apparently highly inbred naked mole rat and the termites as well, since their complex division of labor appears to improve the breeding female's productivity. Presumably, the increase in relatedness due to inbreeding and the complex division of labor have evolved together (Wasser, 1982).

Whenever inhibiting one's own reproduction improves the reproductive success of others, relatedness should also influence the effect of age, and hence of relative reproductive and competitive abilities, on reproductive suppression. In such cases, both young and very old females in groups of closely related females should be more likely to suppress their reproduction than females of these same ages in groups of distantly related females, because such suppression could, in the former case, augment their inclusive fitness. This would be particularly true when the other relatives are at their reproductive prime. As described earlier, a similar argument has been made by Williams (1957), by Hamilton (1966), and by Alexander (1974) for the evolution of menopause among humans. Inhibiting one's own reproduction could be of particular advantage to the reproduction of kin when the inhibited female provides alloparental care.

Relatedness is clearly much greater among the eusocial insects than among the diploid, outbred, communally breeding mammals. Among the latter, the acceptance of non-reproductive status appears, at least

at first glance, to be more of an evolutionary liability than such avowed "altruistic" acts as food-sharing (Yamada, 1963), defense (Kurland, 1977), or alarm-calling (Sherman, 1977). Moreover, non-kin who do not reproduce have also been reported to care communally for young animals. Among dwarf mongooses, immigrant (and apparently, unrelated) females occasionally provide more aid to the young of residents than is provided by any other female in the group (Rood, 1978).

One answer to this paradox appears to lie in the very high reproductive potential available to a formerly suppressed helping female, if she eventually achieves dominant breeding status [i. e.,  $RS_2 > RS_1$ ]. Moreover, up to a point, the more helpers, many of whom she has helped to rear, present when a female dwarf mongoose achieves this status, the higher will be her reproductive potential (Rood, 1978; see also Emlen, 1978; Wasser, 1982). Thus, future reproductive opportunities appear to be critical to the evolution of the reproductive despotism that is combined with communal care among pre-menopausal mammals, whatever the possible evolutionary role of kin selection. In fact, although a suppressed female wild dog will communally care for her sister's young, she will also emigrate to a new group as soon as one that lacks incumbent breeding females becomes available (Frame et al., 1979).

Similarly, it would be interesting to see whether female mole rats who become irreversible nonbreeders at birth have a lower reproductive value at birth, or are more closely related to the present breeding female, than are those who become irreversible nonbreeders at a later age. Finally, it is important to note that for species such as these, membership in a social group may often increase survivorship, as well as reduce the energy spent on maintenance, which may in itself preserve the animal's reproductive value until the opportunity to reproduce presents itself. Helping to rear the dominant female's young may be one way of ensuring such group membership.

#### SOCIAL SUPPRESSION AMONG HUMANS

As stated earlier, overwhelming evidence suggests that the low growth rate of tradi-

tional hunter-gatherer populations was not simply a result of high post-natal or pre-menopausal mortality, but was largely a result of elaborate birth-spacing mechanisms that limit the number of offspring born to a female. However, the social dynamics among the !Kung and other traditional hunter-gatherers suggest that reproductive suppression may be socially mediated among them as well.

Social suppression should be especially likely among the !Kung, since socially dependent needs for birth-spacing, such as the availability of weaning foods and other resources in relation to group size, could be partially alleviated by limiting the reproduction of others. Several lines of evidence suggest that social suppression does indeed exist among these seemingly "egalitarian" societies. First, data by Lee (1980) over the 10-year period from 1963-1973 for the still traditional !Kung of the Dobe area reveal considerable variance in reproductive success among females in their peak reproductive years. According to Lee, a production of two children per mother would have been optimal for these women over this 10-year period. Yet, out of 155 post-menarcheal pre-menopausal women from age 15 to 59, only 47 per cent gave birth to two or more offspring, and 41 per cent failed to give birth at all (see also Hassan, 1980; and Cohen, Malpas, and Klein, 1980). Second, conflicts among the !Kung are commonly triggered by an inequitable distribution of food. Although some conflicts escalate to physical combat, and may occasionally be fatal, the majority of conflicts are verbal ones. Interestingly, the most extreme forms of verbal arguments consist of sexual insulting, known as "za." "For females the most common za forms are du a !gum ('death on your vagina') and !gum/twisi = dinyazho ('long black labia'). . . . According to the !Kung, to be recipient of za in anger arouses intense feeling of dokum ('shame'), leading to suicide or assault" (Lee, 1979: p. 373), and often to a group split as well. Because of the importance of egalitarianism among the !Kung, it may be that socially mediated suppression among them serves more to prevent individuals from over-reproducing than to give particular individuals or groups of individuals an extreme reproductive advantage,

as appears to be the case in mammals such as baboons. The important point here is that socially mediated suppression may well occur among the !Kung, and that the proximal mechanisms for bringing this about are probably the induction of social shame and the consequential threat of a loss of social support.

The physiological effects of extended verbal arguments among the !Kung are unknown. However, among Western women, it is well known that lowered self-esteem and the lack of social support from family and friends are commonly associated with elevated rates of reproductive complications, including infertility, delay of ovulation, habitual spontaneous abortions, complications at and following parturition, abandonment, and even child abuse (Stott, 1958; Hetzel, Bruer, and Poidevin, 1961; Grimm, 1962; Sturgis, 1962; McDonald, 1965; Matsumoto et al., 1968; Fries et al., 1974; Nuckolls, 1975; Vaughn, Egeland, and Sroufe, 1979; Paykel et al., 1980; Saksena and Srivastava, 1980; Crockenberg, 1981). These socially mediated reproductive complications are especially prominent among women who are undergoing stressful life events. [Interestingly, Bresser (in Keverne, 1979; see also Bowman et al., 1978) notes that the physiological effects by which these processes are mediated appear to be quite similar to those experienced in other female mammals who are subjected to aggression by conspecifics.]

Reproductive suppression during stressful life events, when accompanied by a perceived loss of social support, should be expected to occur among humans, given our extreme degree of sociality, and our reliance upon social support as a resource in itself. Under such circumstances, conditions affecting the survival of offspring would indeed be poor. Moreover, recent sociobiological models (Wasser, 1982; Axelrod and Hamilton, 1981) have shown that social individuals have evolved to provide aid to others whenever they can themselves benefit by having these others around and in good health. Thus, the receipt of aid from others is an increasing function of the recipient's quality as a would-be associate to the donors. This being the case, low self-esteem—a perception that one's quality as an as-

sociate to others is low—when combined with a perceived lack of social support, should predictably have the observed devastating effects on reproductive outcomes among humans. Further investigation might focus on behavioral, as well as physiological, methods whereby individuals affect the self-esteem of others, as in the !Kung example.

#### IMPLICATIONS AND CONCLUSIONS

The Reproductive Suppression Model (*RSM*) is supported by the literature reviewed and data presented above. The pattern of reproductive failure among humans and other mammals seems to be based, to a large degree, on each female's perception of present, relative to future, conditions for reproductive success. This perception appears to result from each female's assessment of her own physical and mental health, the "quality" of her conceptus, and the harshness of her external environment. Given these conditions, the *RSM* has implications for health care practices and sexual selection theory.

#### HEALTH CARE PRACTICES

The Reproductive Suppression Model should help us better understand the relationship between temporal patterns in exposure to stress and the probability of reproductive failure as well as the likelihood of premature birth, low birth weight, or even physically anomalous offspring. Specifically, the relaxation of selection would predict the latter complications, whereas its stronger action would predict the former. Since reproductive suppression is often a response to cues in the external environment—particularly the social environment—individuals at risk could be treated by modifying their perceptions of these cues. In addition, of course, the cues themselves could be altered, whereas drug or other invasive therapies treat only the symptoms.

For this change of treatment to occur, however, we first need clinical investigations to evaluate the subjects' perception of the severity and likely change of both internal and external risk factors. The better we are at identifying women at risk, the more able we should be to help them. For example, psycho-social therapy for women predicted to be at high risk for poor outcomes could

focus on improving the subjects' perceptions of the quality of their present environment, their self-esteem, and hence their perception of how others view them, which should in turn improve perceptions of their likelihood of garnering support from others when needed (Wasser, 1982). Success in this endeavor should be strongly influenced by the subjects' previous experiences, and hence expectations. In short, given that individuals apparently manipulate—and are manipulated by—each other in their reproductive performance, there is every reason for confidence in our ability to effect such manipulations therapeutically.

Some pioneering clinicians have already applied supportive psycho-social therapy with considerable success in treating infertility (Sturgis, 1962), habitual spontaneous abortion (Grimm, 1962), and certain undesirable aspects of menopause (Ballinger, 1979). Nonetheless, many, if not most, medical treatments ignore root causes, and hence are only temporary palliatives at best.

Finally, our model questions the value of some medical treatments currently being used for women with reproductive complications that treat their end symptoms rather than the causes. This is especially true for some uses of fertility drugs. Among women who are infertile, between 5 per cent (Siebel and Taylor, 1982) and 80 per cent (Carenza and Zichella, 1979) owe this infertility to psychosocial stress. To treat such individuals with fertility drugs in order to induce ovulation may then place them at an even greater risk of later complications (see Jensen, 1982). At the very least, such treatment should include psychosocial therapy in the attempt to mitigate the patient's stresses. Moreover, the potentially detrimental effects of these fertility drugs is compounded by the fact that they may cause multiple ovulation. This is especially true for the human chorionic gonadotropin complex, and secondarily for clomid followed by bromocryptine (Kolata, 1978; Jensen, 1982). Such treatment may cause women to become pregnant with two or more children at a time when their bodies are telling them they shouldn't have even one.

We have examined over 1,000 studies evaluating the effects of fertility drugs and

we have yet to find a study that distinguishes between outcomes when the cause of infertility was psychosocial stress, or when it was some other, purely biomedical cause. Critical studies are needed before definite conclusions can be made here. In the meantime, we note that such drugs are still used with little or no consideration of the above concerns.

#### SEXUAL SELECTION AND FEMALE-FEMALE COMPETITION

The greater the parental investment (Trivers, 1972) contributed to a reproductive event, the more difficult it is to replace conceptions that eventually fail. This difficulty has in turn created a selection pressure for mechanisms that protect individuals from wasting investment on conceptions that are unlikely to succeed (Goodman, 1979). Since female mammals tend to contribute relatively large amounts of parental investment, such mechanisms are believed to be particularly important for female mammals. One such mechanism, commonly discussed in the sexual selection literature, is a cautious choice of mates (Williams, 1966a; Trivers, 1972). Two additional mechanisms have been discussed in this review. The first is suppression of one's own reproduction when future conditions for offspring survival are perceived as more likely to be favorable than present conditions by some critical degree [inequality (1)]. The second is to suppress the reproduction of other females in one's group, so as to improve one's present conditions for net reproductive success [inequality (2)]. Presence of the former mechanism probably provided a preadaptation for the latter one.

Intrasexual competition to increase the survivorship and reproductive success of offspring has only recently found its way into sexual selection theory (e. g., Wrangham, 1980; Hrdy, 1981; Wasser, 1983). Previous work has focused on competition that increases the quantity of conceptions rather than their quality. But competition to increase the quantity of conceptions should be particularly important for the sex that contributes the least amount of parental investment, usually the males (Bateman, 1948; Williams, 1966a; Trivers, 1972). However,

competition to increase the quality of conceptions should be particularly important for the sex that contributes the greatest parental investment, usually the females.

Although some investigators have recently begun to consider female-female competition (e. g., Frame et al., 1979; Packard and Mech, 1980; Rood, 1980; Wrangham, 1980; Hrdy, 1981; Reiter et al., 1981; Sherman, 1981; Silk et al., 1981; Dublin, 1983; Wasser, 1983), this issue has generally been neglected relative to its male-male counterpart. This neglect may be attributable, at least in part, to a male bias on the part of researchers. As a result (and in addition), accepted theory has not alerted us to its existence. Moreover, competition for conception number is generally much more conspicuous than competition for conception quality. The latter form of competition is especially inconspicuous because it tends to

be spread throughout the entire reproductive event, whereas competition for conception number tends to be concentrated around the time of mating.

In conclusion then, the Reproductive Suppressive Model appears to possess a variety of implications for health care practices as well as for sexual selection theory, especially in respect to female-female competition. The model alerts us to areas that have not been adequately considered in the past, and should help us to understand the existence and functioning of complex and important behavioral systems. The Reproductive Suppression Model also may help to provide a framework for health care practices, so as to predict and prevent reproductive complications that could otherwise severely affect both parents and offspring throughout their lives.

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