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Parental Investment and Sexual Selection

Introduction

Charles Darwin's (1871) treatment of the topic of sexual selection was sometimes confused because he lacked a general framework within which to relate the variables he perceived to be important: sex-linked inheritance, sex ratio at conception, differential mortality, parental care, and the form of the breeding system (monogamy, polygyny, polyandry, or promiscuity). This confusion permitted others to attempt to show that Darwin's terminology was imprecise, that he misinterpreted the function of some structures, and that the influence of sexual selection was greatly overrated. Huxley (1938), for example, dismisses the importance of female choice without evidence or theoretical argument, and he doubts the prevalence of adaptations in males that decrease their chances of surviving but are selected because they lead to high reproductive success. Some important advances, however, have been achieved since Darwin's work. The genetics of sex has now been clarified, and Fisher (1958) has produced a model to explain sex ratios at conception, a model recently extended to include special mechanisms that operate under inbreeding (Hamilton 1967). Data from the laboratory and the field have confirmed that females are capable of very subtle choices (for example, Petit & Ehrman 1969), and Bateman (1948) has suggested a general basis for female choice and male-male competition, and he has produced precise data on one species to support his argument.

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This paper presents a general framework within which to con sexual selection. In it I attempt to define and interrelate the key varia No attempt is made to review the large, scattered literature relevai sexual selection. Instead, arguments are presented on how one r *expect* natural selection to act on the sexes, and some data are prese to support these arguments.

Variance in Reproductive Success

Darwin defined sexual selection as (1) competition within one se members of the opposite sex and (2) differential choice by members of sex for members of the opposite sex, and he pointed out that this us meant males competing with each other for females and females cho some males rather than others. To study these phenomena one need curate data on differential reproductive success analysed by sex. Acc data on female reproductive success are available for many species, similar data on males are very difficult to gather, even in those species tend toward monogamy. The human species illustrates this point. In society it is relatively easy to assign accurately the children to their bi ical mothers, but an element of uncertainty attaches to the assignme children to their biological fathers. For example, Henry Harpending (sonal communication) has gathered biochemical data on the Kal Bushmen showing that about two per cent of the children in that so do not belong to the father to whom they are commonly attributed. on the human species are, of course, much more detailed than similar on other species.

To gather precise data on both sexes Bateman (1948) studied a s species, *Drosophila melanogaster*, under laboratory conditions. By a chromosomally marked individual in competition with individuals l ing different markers, and by searching for the markers in the offsprin was able to measure the reproductive success of each individual, wh female or male. His method consisted of introducing five adult mal five adult female virgins, so that each female had a choice of five n and each male competed with four other males.

Data from numerous competition experiments with *Drosophila* reve three important sexual differences: (1) Male reproductive success v much more widely than female reproductive success. Only four per of the females failed to produce any surviving offspring, while 21 per of the males so failed. Some males, on the other hand, were phenome successful, producing nearly three times as many offspring as the most cessful female. (2) Female reproductive success did not appear to be ited by ability to attract males. The four per cent who failed to cop were apparently courted as vigorously as those who did copulate. On other hand, male reproductive success was severely limited by abilit attract or arouse females. The 21 per cent who failed to reproduce showed no disinterest in trying to copulate, only an inability to be accepted. (3) A female's reproductive success did not increase much, if any, after the first copulation and not at all after the second; most females were uninterested in copulating more than once or twice. As shown by genetic markers in the offspring, males showed an almost linear increase in reproductive success with increased copulations. (A corollary of this finding is that males tended not to mate with the same female twice.) Although these results were obtained in the laboratory, they may apply with even greater force to the wild, where males are not limited to five females and where females have a wider range of males from which to choose.

Bateman argued that his results could be explained by reference to the energy investment of each sex in their sex cells. Since male *Drosophila* invest very little metabolic energy in the production of a given sex cell, whereas females invest considerable energy, a male's reproductive success is not limited by his ability to produce sex cells but by his ability to fertilize eggs with these cells. A female's reproductive success is not limited by her ability to have her eggs fertilized but by her ability to produce eggs. Since in almost all animal and plant species the male produces sex cells that are tiny by comparison to the female's sex cells, Bateman (1948) argued that his results should apply very widely, that is, to "all but a few very primitive organisms, and those in which monogamy combined with a sex ratio of unity eliminated all intra-sexual selection."

Good field data on reproductive success are difficult to find, but what data exist, in conjunction with the assumption that male reproductive success varies as a function of the number of copulations,[1] support the contention that in all species, except those mentioned below in which male parental care may be a limiting resource for females, male reproductive success varies more than female reproductive success. This is supported, for example, by data from dragonflies (Jacobs 1955), baboons (DeVore 1965), common frogs (Savage 1961), prairie chickens (Robel 1966), sage grouse (Scott 1942), black grouse (Koivisto 1965), elephant seals (LeBoeuf & Peterson, 1969), dung flies (Parker 1970a) and some anoline lizards (Rand 1967 and Trivers, in preparation, discussed below.) Circumstantial evidence exists for other lizards (for example, Blair 1960, Harris 1964) and for many mammals (see Eisenberg 1965). In monogamous species, male reproductive success would be expected to vary as female reproductive success, but there is always the possibility of adultery and differential female mortality (discussed below) and these factors should increase the

1. Selection should favor males producing such an abundance of sperm that they fertilize all a female's available eggs with a single copulation. Futhermore, to decrease competition among offspring, natural selection may favor females who prefer single paternity for each batch of eggs (see Hamilton 1964). The tendency for females to copulate only once or twice per batch of eggs is supported by data for many species (see, for example, Bateman 1948, Savage 1961, Burns 1968 but see also Parker 1970b).

variance of male reproductive success without significantly altering of the female.

Relative Parental Investment

Bateman's argument can be stated in a more precise and general f such that the breeding system (for example, monogamy) as well as adult sex ratio become functions of a single variable controlling sexual lection. I first define parental investment as *any investment by the pa in an individual offspring that increases the offspring's chance of survi (and hence reproductive success) at the cost of the parent's ability tc vest in other offspring.* So defined, parental investment includes the m bolic investment in the primary sex cells but refers to any investment (: as feeding or guarding the young) that benefits the young. It does noi clude effort expended in finding a member of the opposite sex or in sul ing members of one's own sex in order to mate with a member of the posite sex, since such effort (except in special cases) does not affect survival chances of the resulting offspring and is therefore not *pare* investment.

Each offspring can be viewed as an investment independent of other spring, increasing investment in one offspring tending to decrease in ment in others. I measure the size of a parental investment by referenc its negative effect on the parent's ability to invest in other offspring: a l parental investment is one that strongly decreases the parent's abilit produce other offspring. There is no necessary correlation between the of parental investment in an offspring and its benefit for the young. Ind one can show that during a breeding season the benefit from a g parental investment must decrease at some point or else species would tend to produce any fixed number of offspring per season. Decrease ir productive success resulting from the negative effect of parental in ment on *nonparental* forms of reproductive effort (such as sexual com tion for mates) is excluded from the measurement of parental investr In effect, then, I am here considering reproductive success as if the relevant variable were parental investment.

For a given reproductive season one can define the total parental in ment of an individual as the sum of its investments in each of its offsp produced during that season, and one assumes that natural selections favored the total parental investment that leads to maximum net re ductive success. Dividing the total parental investment by the numbe individuals produced by the parent gives the typical parental investr by an individual per offspring. Bateman's argument can now be refor lated as follows. Since the total number of offspring produced by one of a sexually reproducing species must equal the total number prod by the other (and assuming the sexes differ in no other way than in

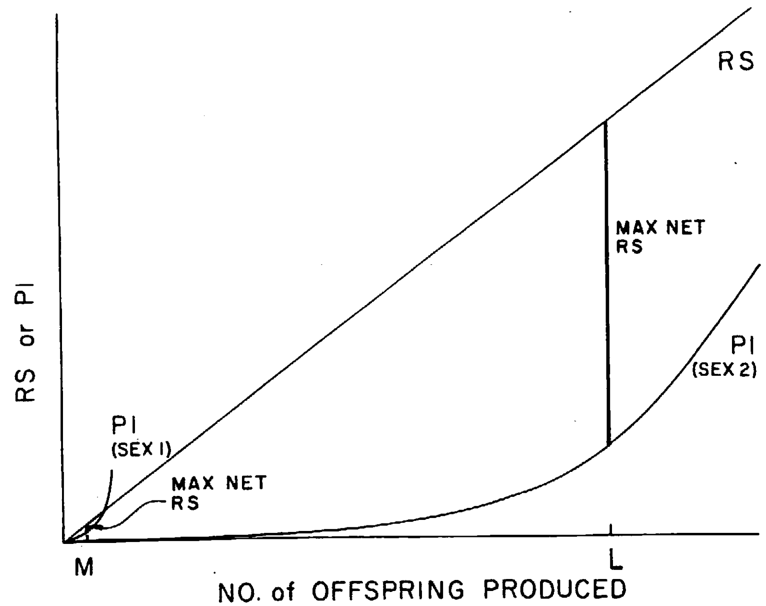

Figure 7.1. Reproductive success (RS) *and decrease in future reproductive success resulting from parental investment* (PI) *are graphed as functions of the number of offspring produced by individuals of the two sexes. At* M *and* L *the net reproductive success reaches a maximum for sex 1 and sex 2 respectively. Sex 2 is limited by sex 1 (see text). The shape of the* PI *curves need not be specified exactly.*

typical parental investment per offspring)[2] then the sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex. Individuals of the sex investing less will compete among themselves to breed with members of the sex investing more, since an individual of the former can increase its reproductive success by investing successively in the offspring of several members of the limiting sex. By assuming a simple relationship between degree of parental investment and number of offspring produced, the argument can be presented graphically (Figure 7.1). The potential for sexual competition in the sex investing less can be measured by calculating the ratio of the number of offspring that sex optimally produces (as a function of parental invest-

2. In particular, I assume an approximately 50/50 sex ratio at conception (Fisher 1958) and no differential mortality by sex, because I later derive differential mortality as a function of reproductive strategies determined by sexual selection. (Differential maturation, which affects the adult sex ratio, can also be treated as a function of sexual selection.) For most species the disparity in parental investment between the sexes is so great that the assumptions here can be greatly relaxed.

ment alone, assuming the opposite sex's investment fixed at its op value) to the number of offspring the limiting sex optimally proc (L/M in Figure 7.1).

What governs the operation of sexual selection is the relative par investment of the sexes in their offspring. Competition for mates us characterizes males because males usually invest almost nothing in offspring. Where male parental investment per offspring is comparable ı male investment one would expect male and female reproductive su to vary in similar ways and for female choice to be no more discrimin than male choice (except as noted below). Where male parenta vestment strongly exceeds that of the female (regardless of which se vests more in the sex cells) one would expect females to compete aı themselves for males and for males to be selective about whom they a as a mate.

Note that it may not be possible for an individual of one sex to inv only part of the offspring of an individual of the opposite sex. When a invests less per typical offspring than does a female but more than one what she invests (or vice-versa) then selection may not favor male co tition to pair with more than one female, if the offspring of the secon male cannot be parcelled out to more than one male. If the net repr tive success for a male investing in the offspring of one female is l than that gained from investing in the offspring of two females, the male will be selected to invest in the offspring of only one female. argument is graphed in Figure 7.2 and may be important to understa differential mortality in monogamous birds, as discussed below.

Fisher's (1958) sex ratio model compares the parental expenditure defined) in male offspring with that in female offspring and suggests e and time as measures of expenditure. Restatements of Fisher's model example, Kolman 1960, Willson & Pianka 1963, T. Emlen 1968, V 1965, Leigh 1970) employ either the undefined term, parental expend or the term energy investment. In either case the key concept is imp and the relevant one is parental investment, as defined above. Energ vestment may often be a good approximation of parental investment it is clearly sometimes a poor one. An individual defending its brood a predator may expend very little energy in the process but suffer a chance of mortality; such behavior should be measured as a large in ment, not a small one as suggested by the energy involved.

Parental Investment Patterns

Species can be classified according to the relative parental invest of the sexes in their young. In the vast majority of species, the male's contribution to the survival of his offspring is his sex cells. In these sp female contribution clearly exceeds male and by a large ratio.

A male may invest in his offspring in several ways. He may provid

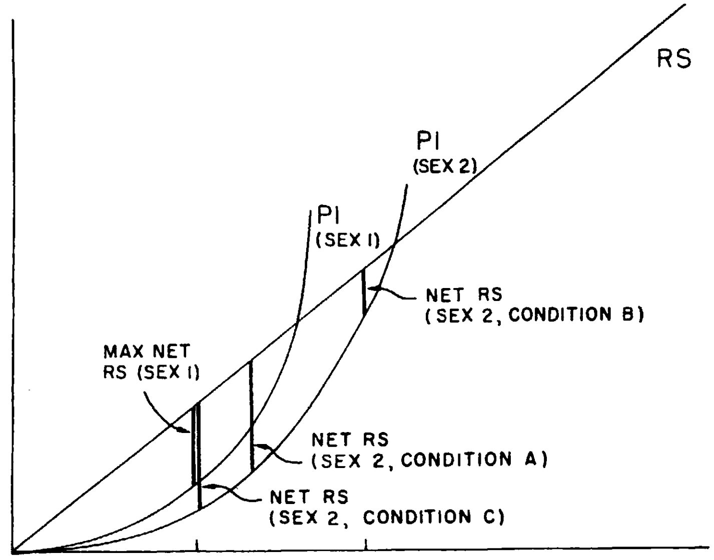

Figure 7.2. RS *and* PI *as functions of the number of offspring produced for two sexes. Sex 2 invests per typical offspring more than half of what sex 1 invests. Condition A: maximum net* RS *for a member of sex 2 assuming he can invest in any number of offspring between* N *and* 2N. *Condition B: net* RS *assuming member of sex 2 invests in* 2N *offspring. Condition C: net* RS *assuming member of sex 2 invests in* N *offspring. If member of sex 2 must invest in an integral multiple of* N *offspring, natural selection favors condition C.*

mate with food as in baloon flies (Kessel 1955) and some other insects (Engelmann 1970), some spiders, and some birds (for example, Calder 1967, Royama 1966, Stokes & Williams, 1971). He may find and defend a good place for the female to feed, lay eggs or raise young, as in many birds. He may build a nest to receive the eggs, as in some fish (for example, Morris 1952). He may help the female lay the eggs, as in some parasitic birds (Lack 1968). The male may also defend the female. He may brood the eggs, as in some birds, fish, frogs, and salamanders. He may help feed the young, protect them, provide opportunities for learning, and so on, as in wolves and many monogamous birds. Finally, he may provide an indirect group benefit to the young (such as protection), as in many primates. All of these forms of male parental investment tend to decrease the disparity in investment between male and female resulting from the initial disparity in size of sex cells.

To test the importance of relative parental investment in controlling sexual selection one should search for species showing greater male than

female parental investment (see Williams 1966, pp. 185–186). The candidates include the Phalaropidae and the polyandrous bird specie: viewed by Lack (1968). In these species, a female's parental investı ends when she lays her eggs; the male alone broods the eggs and care: the young after hatching. No one has attempted to assess relative par investment in these species, but they are striking in showing very male parental investment correlating with strong sex role reversal: fen tend to be more brightly colored, more aggressive and larger than males, and tend to court them and fight over them. In the phalaropes ı is no evidence that the females lay multiple broods (Höhn 1967, J 1969), but in some polyandrous species females apparently go from to male laying successive broods (for example, Beebe 1925; see also O 1969). In these species the female may be limited by her ability to in males to care for her broods, and female reproductive success may more than male. Likewise, high male parental investment in pipefish seahorses (syngnathidae) correlates with female courtship and b coloration (Fiedler 1954), and female reproductive success may be lin by male parental investment. Field data for other groups are so scanty it is not possible to say whether there are any instances of sex role rev among them, but available data for some dendrobatid frogs suggest at the possibility. In these species, the male carries one or more young oı back for an unknown length of time (for example, Eaton 1941). Fen tend to be more brightly colored than males (rare in frogs) and in at one species, *Dendrobates aurata,* several females have been seen pursı and possibly courting, single males (Dunn 1941). In this species the carries only one young on his back, until the tadpole is quite large, bu males have been found with as many as six large eggs inside, and it is sible that females compete with each other for the backs of males. T are other frog families that show male parental care, but even less is kr of their social behavior.

In most monogamous birds male and female parental investmeı probably comparable. For some species there is evidence that the mal vests somewhat less than the female. Kluijver (1933, cited in Coulson 1 has shown that the male starling (*Sturnus vulgaris*) incubates the egg: and feeds the young less often than the female, and similar data are a able for other passerines (Verner & Willson, 1969). The fact that in r species males are facultative polygynists (von Haartman 1969) sug that even when monogamous the males invest less in the young than females. Because sex role reversal, correlating with evidence of grı male than female parental investment, is so rare in birds and becau: certain theoretical considerations discussed below, I tentatively cla most monogamous bird species as showing somewhat greater female male investment in the young.

A more precise classification of animals, and particularly of siı species would be useful for the formulation and testing of more hypotheses. Groups of birds would be ideal to classify in this way, because slight differences in relative parental investment may produce large differences in social behavior, sexual dimorphism and mortality rates by sex. It would be interesting to compare human societies that differ in relative parental investment and in the details of the form of the parental investment, but the specification of parental investment is complicated by the fact that humans often invest in kin other than their children. A wealthy man supporting brothers and sisters (and their children) can be viewed functionally as a polygynist if the contributions to his fitness made by kin are devalued appropriately by their degree of relationship to him (see Hamilton 1964). There is good evidence that premarital sexual permissiveness affecting females in human societies relates to the form of parental investment in a way that would, under normal conditions, tend to maximize female reproductive success (Goethals 1971).

The Evolution of Investment Patterns

The parental investment pattern that today governs the operation of sexual selection apparently resulted from an evolutionarily very early differentiation into relatively immobile sex cells (eggs) fertilized by mobile ones (spermatozoa). An undifferentiated system of sex cells seems highly unstable: competition to fertilize other sex cells should rapidly favor mobility in some sex cells, which in turn sets up selection pressures for immobility in the others. In any case, once the differentiation took place, sexual selection acting on spermatozoa favored mobility at the expense of investment (in the form of cytoplasm). This meant that as long as the spermatozoa of different males competed directly to fertilize eggs (as in oysters) natural selection favoring increased parental investment could act only on the female. Once females were able to control which male fertilized their eggs, female choice or mortality selection on the young could act to favor some new form of male investment in addition to spermatozoa. But there exist strong selection pressures against this. Since the female already invests more than the male, breeding failure for lack of an additional investment selects more strongly against her than against the male. In that sense, her initial very great investment commits her to additional investment more than the male's initial slight investment commits him. Furthermore, male-male competition will tend to operate against male parental investment, in that any male investment in one female's young should decrease the male's chances of inseminating other females. Sexual selection, then, is both controlled by the parental investment pattern and a force that tends to mold that pattern.

The conditions under which selection favors male parental investment have not been specified for any group of animals. Except for the case of polygyny in birds, the role of female choice has not been explored; instead,

it is commonly assumed that, whenever two individuals can raise mor dividuals together than one alone could, natural selection will favor parental investment (Lack 1968, p. 149), an assumption that overlook effects of both male-male competition and female choice.

INITIAL PARENTAL INVESTMENT

An important consequence of the early evolutionary differentation o sex cells and subsequent sperm competition is that male sex cells re tiny compared to female sex cells, even when selection has favored a male parental investment that equals or exceeds the female investr The male's initial parental investment, that is, his investment at the ment of fertilization, is much smaller than the female's, even if through parental care, he invests as much or more. Parental investme the young can be viewed as a sequence of discrete investments by each The relative investment may change as a function of time and eacl may be more or less free to terminate its investment at any time. In th man species, for example, a copulation costing the male virtually no may trigger a nine-month investment by the female that is not trivial lowed, if she wishes, by a fifteen-year investment in the offspring th considerable. Although the male may often contribute parental care d this period, he need not necessarily do so. After a nine-month pregn a female is more or less free to terminate her investment at any mo but doing so wastes her investment up until then. Given the initia balance in investment the male may maximize his chances of leaving viving offspring by copulating and abandoning many females, som whom, alone or with the aid of others, will raise his offspring. In sp where there has been strong selection for male parental care, it is likely that a mixed strategy will be the optimal male course—to h single female raise young, while not passing up opportunities to mate other females whom he will not aid.

In many birds, males defend a territory which the female also use feeding prior to egg laying, but the cost of this investment by the m difficult to evaluate. In some species, as outlined above, the male may vision the female before she has produced the young, but this provisi is usually small compared to the cost of the eggs. In any case, the cost copulation itself is always trivial to the male, and in theory the male not invest anything else in order to copulate. If there is any chance th male can raise the young, either alone or with the help of others, it be to the male's advantage to copulate with her. By this reasoning would expect males of monogamous species to retain some psychol traits consistent with promiscuous habits. A male would be selected t ferentiate between a female he will only impregnate and a female whom he will also raise young. Toward the former he should be eager for sex and less discriminating in choice of sex partner than the female toward him, but toward the latter he should be about as discriminating as she toward him.

If males within a relatively monogamous species are, in fact, adapted to pursue a mixed strategy, the optimal is likely to differ for different males. I know of no attempt to document this possibility in humans, but psychology might well benefit from attempting to view human sexual plasticity as an adaptation to permit the individual to choose the mixed strategy best suited to local conditions and his own attributes. Elder (1969) shows that steady dating and sexual activity (coitus and petting) in adolescent human females correlate inversely with a tendency to marry up the socioeconomic scale as adults. Since females physically attractive as adolescents tend to marry up, it is possible that females adjust their reproductive strategies in adolescence to their own assets.

Desertion and Cuckoldry

There are a number of interesting consequences of the fact that the male and female of a monogamous couple invest parental care in their offspring at different rates. These can be studied by graphing and comparing the cumulative investment of each parent in their offspring, and this is done for two individuals of a hypothetical bird species in Figure 7.3. I have graphed no parental investment by the female in her young before copulation, even though she may be producing the eggs before then, because it is not until the act of copulation that she commits the eggs to a given male's genes. In effect, then, I have graphed the parental investment of each individual in the other individual's offspring. After copulation, this is the same as graphing investment in their own offspring, assuming, as I do here, that the male and female copulate with each other and each other only.

To discuss the problems that confront paired individuals ostensibly cooperating in a joint parental effort, I choose the language of strategy and decision, as if each individual contemplated in strategic terms the decisions it ought to make at each instant in order to maximize its reproductive success. This language is chosen purely for convenience to explore the adaptations one might expect natural selection to favor.

At any point in time the individual whose cumulative investment is exceeded by his partner's is theoretically tempted to desert, especially if the disparity is large. This temptation occurs because the deserter loses less than his partner if no offspring are raised and the partner would therefore be more strongly selected to stay with the young. Any success of the partner will, of course, benefit the deserter. In Figure 7.3, for example, desertion by the male right after copulation will cost him very little, if no offspring are raised, while the chances of the female raising some young alone may be great enough to make the desertion worthwhile. Other factors are

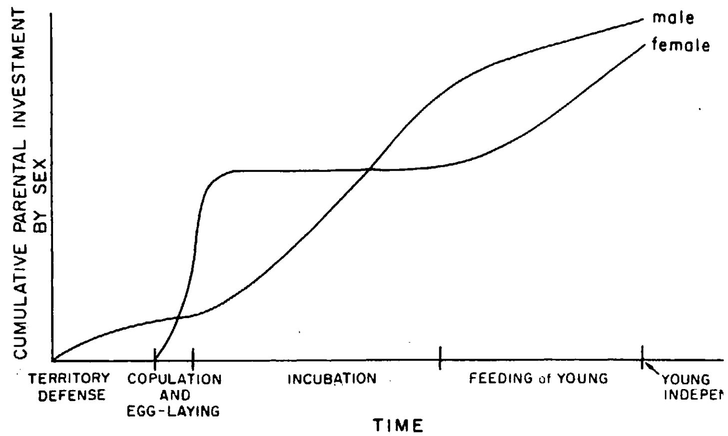

Figure 7.3. Hypothetical cumulative parental investment of a male and ... *male bird in their offspring as a function of time.* Territory def... *Male defends area for feeding and nest building.* Copulation ... egg-laying: *Female commits her eggs to male who commits hi*... *fended nest to the female.* Incubation: *Male incubates eggs* ... *female does nothing relevant to offspring.* Feeding of young: ... *parent feeds young but female does so at a more rapid rate.*

important in determining the adaptiveness of abandonment, factors ... as the opportunities outside the pair for breeding and the expected sl... of the deserter's investment curve if he does not desert. If the male's in... ment curve does not rise much after copulation, then the female's cha... of raising the young alone will be greater and the time wasted by the ... investing moderately in his offspring may be better spent starting a ... brood.

What are the possible responses of the deserted individual? If the ... is deserted before copulation, he has no choice but to attempt to start ... process over again with a new female; whatever he has invested in tha... male is lost. If either partner is deserted after copulation, it has t... choices. (1) It can desert the eggs (or eat them) and attempt to b... again with another mate, losing thereby all (or part of) the initial in... ment. (2) It can attempt to raise the young on its own, at the risk of ... exertion and failure. Or, (3) it can attempt to induce another partne... help it raise the young. The third alternative, if successful, is the ... adaptive for it, but this requires deceiving another organism into d... something contrary to its own interests, and adaptations should evolv... guard individuals from such tasks. It is difficult to see how a male coul... successful in deceiving a new female, but if a female acts quickly, ... might fool a male. As time goes on (for example, once the eggs are l...

it is unlikely that a male could easily be fooled. The female could thus be programmed to try the third strategy first, and if it failed, to revert to the first or second. The male deserter gains most if the female succeeds in the third strategy, nothing if she chooses the first strategy, and possibly an intermediate value if she chooses the second strategy.

If neither partner deserts at the beginning, then as time goes on, each invests more and more in the young. This trend has several consequences. On the one hand, the partner of a deserter is more capable of finishing the task alone and natural selection should favor its being more predisposed to try, because it has more to lose. On the other hand, the deserter has more to lose if the partner fails and less to gain if the partner succeeds. The balance between these opposing factors should depend on the exact form of the cumulative investment curves as well as the opportunities for further breeding outside the pair.

There is another effect with time of the increasing investment by both parents in the offspring. As the investments increase, natural selection may favor *either* partner deserting even if one has invested more in the young than the other. This is because the desertion may put the deserted partner in a cruel bind: he has invested so much that he loses considerably if he also deserts the young, even though, which should make no difference to him, the partner would lose even more. The possibility of such binds can be illustrated by an analogous situation described by Rowley (1965). Two neighboring pairs of wrens happened to fledge their young simultaneously and could not tell their young apart, so both pairs fed all six young indiscriminately, until one pair "deserted" to raise another brood, leaving their neighbors to feed all six young, which they did, even though this meant they were, in effect, being taken advantage of.

Birds should show adaptations to avoid being deserted. Females, in particular, should be able to guard against males who will only copulate and not invest subsequent parental effort. An instance of such an adaptation may be found in the red-necked phalarope, *Phalaropus lobatus.* In phalaropes the male incubates the eggs alone and alone cares for the young after hatching (Höhn 1967, Johns 1969), so that a graph of cumulative parental investment would show an intitial large female investment which then remains the same through time, whereas the initial male investment is nil and increases steadily, probably to surpass the female investment. Only the female is vulnerable to being deserted and this right after copulation, since any later desertion by the male costs him his investment in incubation, the young being almost certain to perish. Tinbergen (1935) observed a female vigorously courting a male and then flying away as soon as he responded to the courtship by attempting to copulate. This coy performance was repeated numerous times for several days. Tinbergen attributed it to the "waxing and waning of an instinct," but the behavior may have been a test

of the male's willingness to brood the female's eggs. The male under ol vation was, in fact, already brooding eggs and was courted when hc the eggs to feed on a nearby pond. In order to view a complete egg-la sequence, Tinbergen destroyed the clutch the male was brooding. W a half day the female permitted the male sexual access, and he su quently brooded her eggs. The important point is that the female c apparently tell the difference between a free and an encumbered male, she withheld sex from the latter. Courtship alternating with flight ma the test that reveals the male's true attachments: the test can show, foı ample, whether he is free to follow the female.

It is likely that many adaptations exist in monogamous species to g against desertion, but despite evidence that desertion can be com (Rowley 1965) no one has attempted to analyze courtship with this da in mind. Von Haartman (1969) has reviewed some evidence for ad tions of females to avoid being mated to a polygynous male, and beir mated is sometimes exactly equivalent to being deserted by the male Haartman, 1951).

External fertilization requires a synchrony of behavior such that male can usually be certain he is not attempting to fertilize previ fertilized eggs. With the evolution of internal fertilization the male ca be so certain. For many species (for example, most mammals), the dis tion is not important because the male loses so little by attempting to f ize previously fertilized eggs. Where male parental care is involved, ever, the male runs the risk of being cuckolded, of raising another n offspring. For Figure 7.1 it was assumed that the pair copulated with other and each other only, but the male can usually not be sure that is the case and what is graphed in such a situation is the male's invest in the *female's* offspring. Adaptations should evolve to help guarantee the female's offspring are also his own, but these can partly be coun by the evolution of more sophisticated cuckolds.

One way a male can protect himself is to ensure that other males their distance. That some territorial aggression of monogamous male is devoted to protecting the sanctity of the pair bond seems certain, an man male aggression toward real or suspected adulterers is often ext Lee (1969), for example, has shown that, when the cause is known major cause of fatal Bushman fights is adultery or suspected adultery. In limited data on other hunter-gathering groups (including Eskimos Australian aborigines) indicate that, while fighting is relatively rar that organized intergroup aggression is infrequent), the "murder rate" be relatively high. On examination, the murderer and his victim are us a husband and his wife's real or suspected lover. In pigeons (*Col livia*) a new male arriving alone at a nocturnal roosting place in the attacked day after day by one or more resident males. As soon as the male appears with a mate, the two are treated much more casually (Trivers, unpublished data), suggesting that an unpaired male is more threatening than a paired one.

I have argued above that a female deserted immediately after copulation may be adapted to try to induce another male to help raise her young. This factor implies adaptations on the part of the male to avoid such a fate. A simple method is to avoid mating with a female on first encounter, sequester her instead and mate with her only after a passage of time that reasonably excludes her prior impregnation by another male. Certainly males guard their females from other males, and there is a striking difference between the lack of preliminaries in promiscuous birds (Scott 1942, Kruijt & Hogan 1967) and the sometimes long lag between pair bonding and copulation in monogamous birds (Nevo 1956), a lag which usually seems to serve other functions as well.

Biologists have interpreted courtship in a limited way. Courtship is seen as allowing the individual to choose the correct species and sex, to overcome antagonistic urges and to arouse one's partner (Bastock 1967). The above analysis suggests that courtship should also be interpreted in terms of the need to guard oneself from the several possibilities of maltreatment at the hands of one's mate.

Differential Mortality and the Sex Ratio

Of special interest in understanding the effects of sexual selection are accurate data on differential mortality of the sexes, especially of immature individuals. Such data are, however, among the most difficult to gather, and the published data, although important, are scanty (for example, Emlen 1940, Hays 1947, Chapman, Casida, & Cote 1938, Robinette et al. 1957, Coulson 1960, Potts 1969, Darley 1971, Myers & Krebs 1971). As a substitute one can make use of data on sex ratios within given age classes or for all age classes taken together. By assuming that the sex ratio at conception (or, less precisely, at birth) is almost exactly 50/50, significant deviations from this ratio for any age class or for all taken together should imply differential mortality. Where data exist for the sex ratio at birth and where the sex ratio for the entire local population is unbalanced, the sex ratio at birth is usually about 50/50 (see above references, Selander 1965, Lack 1954). Furthermore, Fisher (1958) has shown, and others refined (Leigh 1970), that parents should invest roughly equal energy in each sex. Since parents usually invest roughly equal energy in each individual of each sex, natural selection, in the absence of unusual circumstances (see Hamilton 1967), should favor approximately a 50/50 sex ratio at conception.

It is difficult to determine accurately the sex ratio for any species. T most serious source of bias is that males and females often make the selves differentially available to the observer. For example, in small ma mals sexual selection seems to have favored male attributes, such as h mobility, that tend to result in their differential capture (Beer, Frenzel, MacLeod 1958; Myers & Krebs, 1971). If one views one's capture te niques as randomly sampling the existing population, one will concl that males are more numerous. If one views one's capture techniques randomly sampling the effects of mortality on the population, then c will conclude that males are more prone to mortality (they are captu more often) and therefore are less numerous. Neither assumption is lik to be true, but authors routinely choose the former. Furthermore, it is of not appreciated what a large sample is required in order to show sign cant deviations from a 50/50 ratio. A sample of 400 animals showin 44/56 sex ratio, for example, does not deviate significantly from a 50/ ratio. (Nor, although this is almost never pointed out, does it differ sign cantly from a 38/62 ratio.)

Mayr (1939) has pointed out that there are numerous deviations fr a 50/50 sex ratio in birds and I believe it is likely that, if data w sufficiently precise, most species of vertebrates would show a signific deviation from a 50/50 sex ratio. Males and females differ in numer characteristics relevant to their different reproductive strategies and th characters are unlikely to have equivalent effects on survival. Since it not advantageous for the adults of each sex to have available the sa number of adults of the opposite sex, there will be no automatic select agent for keeping deviations from a 50/50 ratio small.

A review of the useful literature on sex ratios suggests that (except birds) when the sex ratio is unbalanced it is usually unbalanced by th being more females than males. Put another way, males apparently h a tendency to suffer higher mortality rates than females. This is true those dragonflies for which there are data (Corbet, Longfield, & Mo 1960), for the house fly (Rockstein 1959), for most fish (Beverton & H 1959), for several lizards (Tinkle 1967, Harris 1964, Hirth 1963, B 1960, Trivers, discussed below) and for many mammals (Bouliere & V schuren 1960, Cowan 1950, Eisenberg 1965, Robinette et al. 1957, B Frenzel, & MacLeod 1958, Stephens 1952, Tyndale-Biscoe & Smith, 19 Myers & Krebs, 1971, Wood 1970). Hamilton (1948) and Lack (19 have reviewed studies on other animals suggesting a similar trend. M (1939) points out that where the sex ratio can be shown to be unbalan in monogamous birds there are usually fewer females, but in polygynous promiscuous birds there are fewer males. Data since his paper confirm finding. This result is particularly interesting since in all other groups which males tend to be less numerous monogamy is rare or nonexistent.

THE CHROMOSOMAL HYPOTHESIS

There is a tendency among biologists studying social behavior to regard the adult sex ratio as an independent variable to which the species reacts with appropriate adaptations. Lack (1968) often interprets social behavior as an adaptation in part to an unbalanced (or balanced) sex ratio, and Verner (1964) has summarized other instances of this tendency. The only mechanism that will generate differential mortality independent of sexual differences clearly related to parental investment and sexual selection is the chromosomal mechanism, applied especially to humans and other mammals: the unguarded X chromosome of the male is presumed to predispose him to higher mortality. This mechanism is inadequate as an explanation of differential mortality for three reasons.

1. The distribution of differential mortality by sex is not predicted by a knowledge of the distribution of sex determining mechanisms. Both sexes of fish are usually homogametic, yet males suffer higher mortality. Female birds are heterogametic but suffer higher mortality only in monogamous species. Homogametic male meal moths are outsurvived by their heterogametic female counterparts under laboratory conditions (Hamilton & Johansson 1965).

2. Theoretical predictions of the degree of differential mortality expected by males due to their unguarded X chromosome are far lower than those observed in such mammals as dogs, cattle and humans (Ludwig & Boost 1951). It is possible to imagine natural selection favoring the heterogametic sex determining mechanism if the associated differential mortality is slight and balanced by some advantage in differentiation or in the homogametic sex, but a large mortality associated with heterogamy should be counteracted by a tendency toward both sexes becoming homogametic.

3. Careful data for humans demonstrate that castrate males (who remain of course heterogametic) strongly outsurvive a control group of males similar in all other respects and the earlier in life the castration, the greater the increase in survival. (Hamilton & Mestler 1969). The same is true of domestic cats (Hamilton, Hamilton & Mestler 1969), but not of a species (meal moths) for which there is no evidence that the gonads are implicated in sexual differentiation (Hamilton & Johansson 1965).

An Adaptive Model of Differential Mortality

To interpret the meaning of balanced or unbalanced sex ratios one needs a comprehensive framework within which to view life historical phenomena. Gadgil & Bossert (1970) have presented a model for the adaptive interpretation of differences between species' life histories; for example, in the age of first breeding and in the growth and survival curves. Although they did not apply this model to sexual differences in these parameters,

their model is precisely suited for such differences. One can, in effect, the sexes as if they were different species, the opposite sex being a resc relevant to producing maximum surviving offspring. Put this way, fe "species" usually differ from male species in that females compete an themselves for such resources as food but not for members of the opp sex, whereas males ultimately compete only for members of the opp sex, all other forms of competition being important only insofar as the fect this ultimate competition.

To analyze differential mortality by sex one needs to correlate diff reproductive strategies with mortality, that is, one must show how a g reproductive strategy entails a given risk of mortality. One can do thi graphing reproductive success (RS) for the first breeding season as a f tion of reproductive effort expended during that season, and by grap the diminution in future reproductive success (D) in units of first bree season reproductive success. (Gadgil and Bossert show that the repro tive value of a given effort declines with age, hence the need to co future reproductive success to comparable units.) For simplicity I as that the diminution, D, results entirely from mortality between the first second breeding seasons. The diminution could result from mortality later year (induced by reproductive effort in the first breeding se which would not change the form of the analysis, or it could result fron creased ability to breed in the second (or still later) breeding se which sometimes occurs but which is probably minor compared tc diminution due to mortality, and which does not change the analys long as one assumes that males and females do not differ appreciably i extent to which they suffer this form of diminution.

Natural selection favors an individual expending in the first bre season the reproductive effort (RE) that results in a maximum net r ductive success (RS—D). The value of D at this RE gives the degree c pected mortality between the first and second breeding seasons Figures 7.4 and 7.5). Differences between the sexes in D will give th pected differential mortality. The same analysis can be applied to th breeding season to predict mortality between it and the nth + 1 bre season. Likewise, by a trivial modification, the analysis can be used to erate differences in juvenile mortality: let D represent the diminutic chances of surviving to the first breeding season as a function of RE a breeding. Seen this way, one is measuring the cost in survival of dev ing during the juvenile period attributes relevant to adult reprodu success.

SPECIES WITH LITTLE OR NO MALE PARENTAL INVESTMENT

In Figure 7.4, I have graphed RS and D as functions of reproductive in the first breeding season for females of a hypothetical species in v males invest very little parental care. The RS function is given a sigmoidal shape for the following reasons. I assume that at low values of RE, RS increases only very gradually because some investment is necessary just to initiate reproduction (for example, enlarging the reproductive organs). RS then increases more rapidly as a function of RE but without achieving a very steep slope. RS finally levels off at high values of RE because of increased inefficiencies there (for example, inefficiencies in foraging; see Schoener 1971). I have graphed the value, f, at which net reproductive success for the female reaches a maximum. Technically, due to competition, the shape of the RS function for any given female will depend partly on the reproductive effort devoted by other females; the graph therefore assumes that other females tend to invest near the optimal value, f, but an important feature of a female's RS is that it is *not* strongly dependent on the RE devoted by other females: the curve would not greatly differ if all other females invested much more or less. I have graphed D as a linear function of RE. So doing amounts to a definition of reproductive effort, that is, a given increment in reproductive effort during the first breeding season can be detected as a proportionately increased chance of dying be-

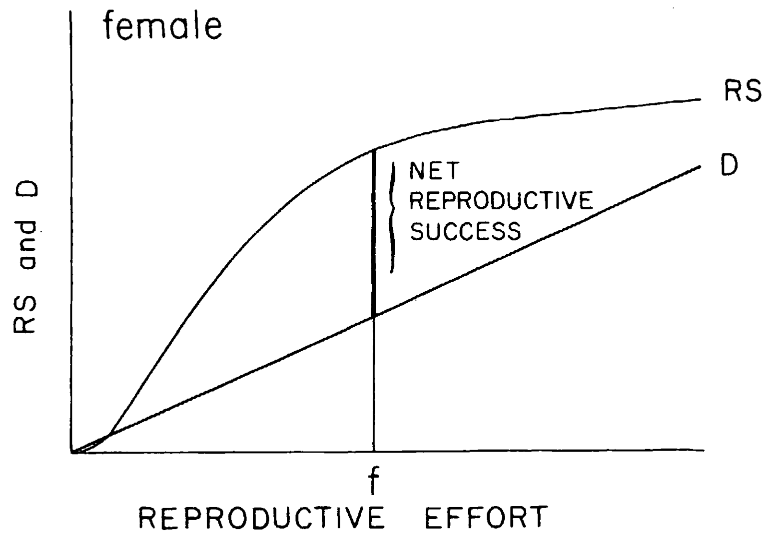

Figure 7.4. Female reproductive success during the first breeding season (RS) *and diminution of future reproductive success* (D) *as functions of reproductive effort during first breeding.* D *is measured in units of first breeding (see text). At* f *the net reproductive success reaches a maximum. Species is one in which there is very little male parental investment.*

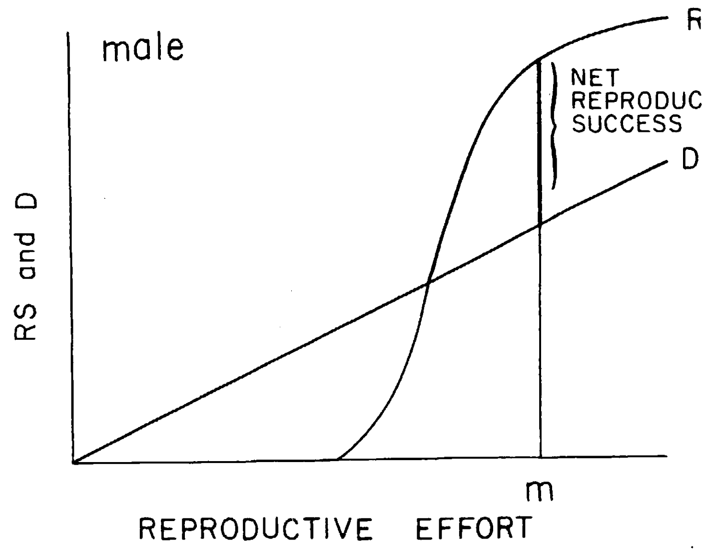

Figure 7.5. Same as Figure 7.4 except that it is drawn for the male instead female. At m *the net reproductive success reaches a maximun*

tween the first and second breeding seasons. Note that reproductive for the female is essentially synonymous with parental investment.

Male RS differs from female RS in two important ways, both of stem from sexual selection. (1) A male's RS is highly dependent on th of other males. When other males invest heavily, an individual mal usually not outcompete them unless he invests as much or more. A siderable investment that is slightly below that of other males may in zero RS. (2) A male's RS is potentially very high, much higher thai of a conspecific female, but only if he outcompetes other males. should exist some factor or set of factors (such as size, aggressiveness bility) that correlates with high male RS. The effect of competitio tween males for females is selection for increased male RE, and this tion will continue until greater male than female RE is selected as long higher associated D is offset by the potentially very high RS. This ment is graphed in Figure 7.5, where the steep slope of RS reflects the interaction between one male's RS and the RE of the other males. that the argument here depends on the existence of a set of factors lated with high male reproductive success. If these factors exist, n selection will predispose the male to higher mortality rates than the fe Where a male can achieve very high RS in a breeding season (as in breeding seals, Bartholemew 1970), differential mortality will be respondingly high.

SPECIES WITH APPRECIABLE MALE PARENTAL INVESTMENT

The analysis here applies to species in which males invest less parental care than, but probably more than one-half, what females invest. I assume that most monogamous birds are so characterized, and I have listed reasons and some data above supporting this assumption. The reasons can be summarized by saying that because of their initial large investment, females appear to be caught in a situation in which they are unable to force greater parental investment out of the males and would be strongly selected against if they unilaterally reduced their own parental investment.

Functions relating RS to parental investment are graphed for males and females in Figures 7.6 and 7.7, assuming for each sex that the opposite sex shows the parental investment that results for it in a maximum net reproductive success. The female curve is given a sigmoidal shape for the reasons that apply to Figure 7.4; in birds the female's initial investment in the eggs will go for nothing if more is not invested in brooding the eggs and feeding the young, while beyond a certain high RE further increments do not greatly affect RS. Assuming the female invests the value, f, male RS will vary as a function of male parental investment in a way similar to female RS, except the function will be displaced to the left (Figure 7.7) and some RS will be lost due to the effects of the cuckoldry graphed in Figure 7.8.

Because males invest in parental care more than one-half what females

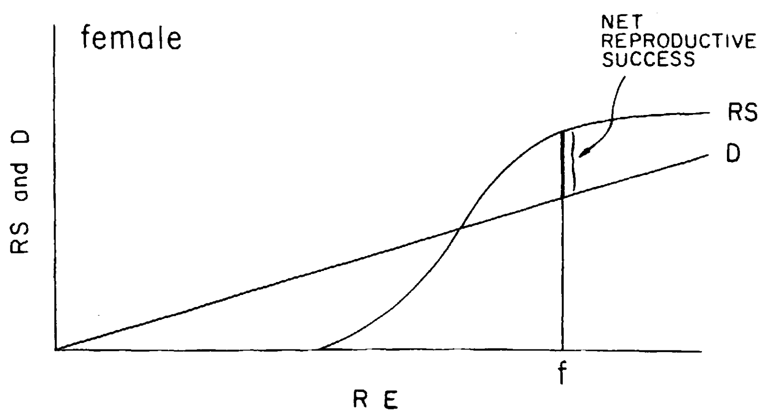

Figure 7.6. Female reproductive success and diminution in future reproductive success as functions of reproductive effort (RE) assuming male reproductive effort of m_1. *Species is a hypothetical monogamous bird in which males invest somewhat less than females in parental care (see Figure 7.7 and 7.8).*

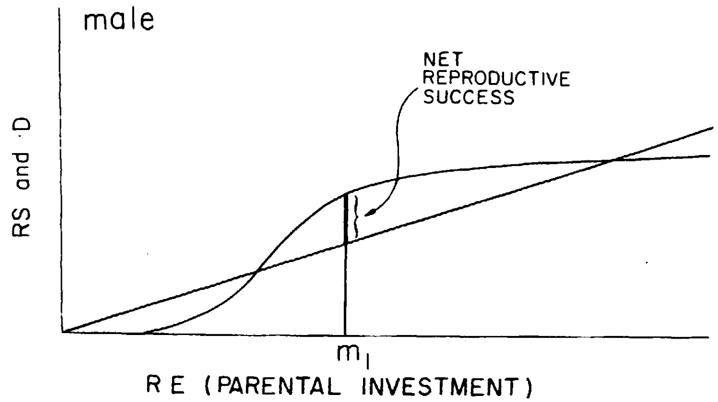

Figure 7.7. Male reproductive success and diminution in future reprodu success as functions of reproductive effort, assuming female re ductive effort of f. *Species is same as in Figure 7.6. Reprodu effort of male is invested as parental care in one female's offsp Net reproductive success is a maximum at* m_1.

invest and because the offspring of a given female tend to be insemin by a single male, selection does not favor males competing with each c to invest in the offspring of more than one female. Rather, sexual selec only operates on the male to inseminate females whose offspring he not raise, especially if another male will raise them instead. Since selec presumably does not strongly favor female adultery and may oppose it for example, detection leads to desertion by the mate), the opportur for cuckoldry are limited: high investment in promiscuous activity bring only limited RS. This argument is graphed in Figure 7.8. The dicted differential mortality by sex can be had by comparing D (f) D ($m_1 + m_2$).

It may seem ironic, but in moving from a promiscuous to a monogar life, that is, in moving toward *greater* parental investment in his young male tends to *increase* his chances of surviving relative to the female. tendency occurs because the increased parental investment dispropor ately decreases the male's RE invested in male-male competition to ins nate females.

Note that in both cases above differential mortality tends to be self-l ing. By altering the ratio of possible sexual partners to sexual compet differential mortality sets up forces that tend to keep the differential ; tality low. In species showing little male parental investment differe male mortality increases the average number of females available for t males who survive. Other things being equal, this increase tends to r it more difficult for the most successful males to maintain their relative

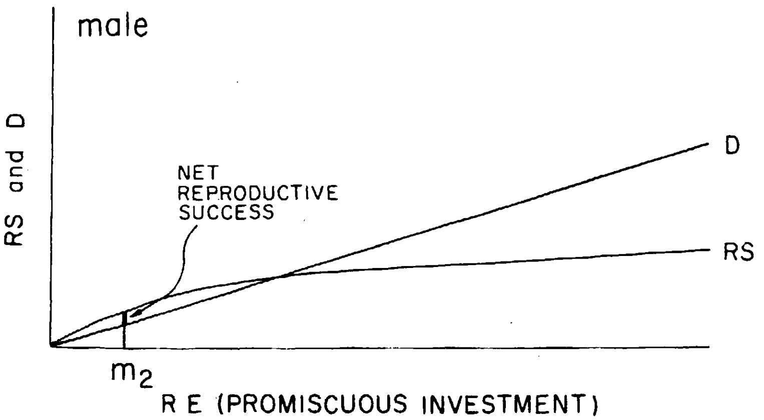

Figure 7.8. Male reproductive success and diminution of future reproductive success as a function of reproductive effort solely devoted to promiscuous behavior. Net reproductive success at m_2 is a maximum. Same species as in Figures 7.6 and 7.7.

vantage. In monogamous birds differential female mortality induces competition among males to secure at least one mate, thereby tending to increase male mortality. Such competition presumably also increases the variance in male reproductive success above the sexual differential expected from cuckoldry.

SPECIES WITH GREATER MALE THAN FEMALE PARENTAL INVESTMENT

Since the above arguments were made with reference to relative parental investment and not sex, they apply to species in which males invest more parental effort than females, except that there is never apt to be a female advantage to cuckolding other females, and this advantage is always alive with males. Where females invest more than one-half what males invest, one would predict differential female mortality. Where females invest less than one-half what males invest, one would predict competition, and a resulting differential female mortality.

Male–Male Competition

Competition between males does not necessarily end with the release of sperm. Even in species with internal fertilization, competition between sperm of different males can be an important component of male-male competition (see the excellent review by Parker 1970b): In rare cases, competition between males may continue after eggs are fertilized. For ex-

ample an adult male langur (*Presbytis entellus*) who ousts the adult of a group may systematically kill the infants of that group (presu fathered by the ousted male) thereby bringing most of the adult fe quickly into estrus again (Sugiyama 1967). While clearly disadvanta for the killed infants and their mothers, such behavior, benefiting th male, may be an extreme product of sexual selection. Female mice taneously abort during the first four days of pregnancy when expos the smell of a strange male (Bruce 1960, reviewed in Sadleir 1967), a tion subject to several interpretations including one based on male competition.

Sperm competition may have important effects on competition be males prior to release of sperm. In those insects in which later-ar sperm take precedence in fertilizing eggs, selection favors mating w female just prior to release of eggs, thereby increasing competition at lation sites and intensifying selection for a postovulatory guarding by the male (see Parker 1970bcd, Jacobs 1955). I here concentrate on male competition prior to the release of sperm in species showing little male parental investment.

The form of male-male competition should be strongly influenced b distribution in space and time of the ultimate resource affecting ma productive success, namely, conspecific breeding females. The distrib can be described in terms of three parameters: the extent to which fe are clumped or dispersed in space, the extent to which they are clu or dispersed in time, and the extent to which their exact position in and time is predictable. I here treat females as if they are a passi source for which males compete, but female choice may strongly infl the form of male-male competition, as, for example, when it favors clumping together on display grounds (for example, S. Emlen 1968) females then search out (see below under "Female Choice").

DISTRIBUTION IN SPACE

Cervids differ in the extent to which females are clumped in space o domly dispersed (deVos, Broky & Geist 1967) as do antelopes (Eise 1965), and these differences correlate in a predictable way with diffe in male attributes. Generally male-male aggression will be the more the greater the number of females two males are fighting over at any moment. Searching behavior should be more important in highly dis species especially if the dispersal is combined with unpredictability.

DISTRIBUTION IN TIME

Clumped in time refers to highly seasonal breeders in which many fe become sexually available for a short period at the same moment (f ample, explosive breeding frogs; Bragg 1965, Rivero & Estevez 1 while highly dispersed breeders (in time) are species (such as chimpanzees; Van Lawick-Goodall 1968) in which females breed more or less randomly throughout the year. One effect of extreme clumping is that it becomes more difficult for any one male to be extremely successful: while he is copulating with one female, hundreds of other females are simultaneously being inseminated. Dispersal in time, at least when combined with clumping in space, as in many primates, permits each male to compete for each newly available female and the same small number of males tend repeatedly to inseminate the receptive females (DeVore 1965).

PREDICTABILITY

One reason males in some dragonflies (Jacobs 1955) may compete with each other for female oviposition sites is that those are highly predictable places at which to find receptive females. Indeed, males display several behaviors, such as testing the water with the tips of their abdomen, that apparently aid them in predicting especially good oviposition sites, and such sites can permit very high male reproductive success (Jacobs 1955). In the cicada killer wasp (*Sphecius spheciosus*) males establish mating territories around colony emergency holes, presumably because this is the most predictable place at which to find receptive females (Lin 1963).

The three parameters outlined interact strongly, of course, as when very strong clumping in time may strongly reduce the predicted effects of strong clumping in space. A much more detailed classification of species with non-obvious predictions would be welcome. In the absence of such models I present a partial list of factors that should affect male reproductive success and that may correlate with high male mortality.

SIZE

There are very few data showing the relationship between male size and reproductive success but abundant data showing the relationship between male dominance and reproductive success: for example, in elephant seals (LeBoeuf & Peterson 1969), black grouse (Koivisto 1965, Scott 1942), baboons (DeVore 1965) and rainbow lizards (Harris 1964). Since dominance is largely established through aggression and larger size is usually helpful in aggressive encounters, it is likely that these data partly reveal the relationship between size and reproductive success. (It is also likely that they reflect the relationship between experience and reproductive success.)

Circumstantial evidence for the importance of size in aggressive encounters can be found in the distribution of sexual size dimorphism and aggressive tendencies among tetrapods. In birds and mammals males are generally larger than females and much more aggressive. Where females

are known to be more aggressive (that is, birds showing reversal in roles) they are also larger. In frogs and salamanders females are usu larger than males, and aggressive behavior has only very rarely been corded. In snakes, females are usually larger than males (Kopstein 19 and aggression is almost unreported. Aggression has frequently been served between sexually active crocodiles and males tend to be la (Allen Greer, personal communication). In lizards males are often la than females, and aggression is common in some families (Carpe 1967). Male aggressiveness is also common, however, in some specie which females are larger, for example, *Sceloporus*, (Blair 1960). Ther a trivial reason for the lack of evidence of aggressiveness in most ampl ians and reptiles: the species are difficult to observe and few behavi data of any sort have been recorded. It is possible, however, that this relation between human ignorance and species in which females are la is not accidental. Humans tend to be more knowledgeable about th species that are also active diurnally and strongly dependent on vision, example, birds and large mammals. It may be that male aggressivenes more strongly selected in visually oriented animals because vision prov long-range information on the behavior of competitors. The male can, example, easily observe another male beginning to copulate and can o quickly attempt to intervene (for example, baboons, DeVore 1965 and grouse, Scott 1942).

Mammals and birds also tend towards low, fixed clutch sizes and may favor relatively smaller females, since large female size may be r tively unimportant in reproductive success. In many fish, lizards and s manders female reproductive success as measured by clutch size is kn to correlate strongly within species with size (Tinkle, Wilbur & Tilley 1 Tilley 1968).

Measuring reproductive success by frequency of copulation, I h analyzed male and female reproductive success as a function of siz *Anolis garmani* (Figures 7.9 and 7.10). Both sexes show a significant p tive correlation between size and reproductive success, but the tren males is significantly stronger than the trend in females ($p < .01$). C sistent with this tendency, males grow faster at all sizes than females (ure 7.11) and reach an adult weight two and one-half times that of a females. The sex ratio of all animals is unbalanced in favor of fem which would seem to indicate differential mortality, but the factors might produce the difference are not known. Males are highly aggres and territorial, and large males defend correspondingly large territ with many resident females. No data are available on size and success in gressive encounters, but in the closely related (and behaviorally similar) *A. lineatopus*, 85 per cent of 182 disputes observed in the were won by the larger animal (Rand 1967). Females lay only one eg a time, but it is likely that larger adult females lay eggs slightly more o

Figure 7.9. Male and female Anolis garmani *copulating face down four feet up the trunk of a cocoanut tree.* Photo by Joseph K. Long.

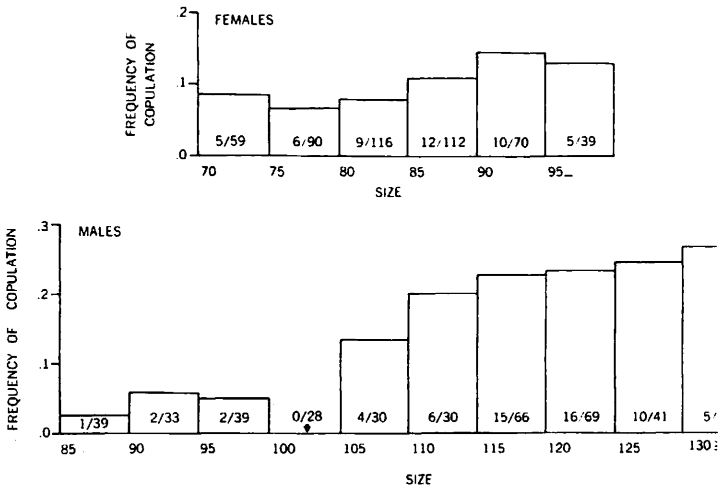

Figure 7.10. Reproductive success in male and female A. garmani *as a fi tion of size. Reproductive success is measured by the numbe copulations observed per number of individuals (male or fem in each nonoverlapping 5 mm size category. Data combined f five separate visits to study area between summer 1969 and s mer 1971.*

than smaller ones, and this may partly be due to advantages in feec through size-dependent aggressiveness, since larger females wander sigı cantly more widely than smaller adult ones. An alternate interpreta (based on ecological competition between the sexes) has been propc for sexual dimorphism in size among animals (Selander 1966), and interpretation may apply to *Anolis* (Schoener 1967).

METABOLIC RATE

Certainly more is involved in differential male mortality than size, evei species in which males grow to a larger size than females. Although (show convincingly that nutritional factors strongly affect human male vival *in utero*, a sexual difference in size among humans is not dete until the twenty-fourth week after conception whereas differences in n tality appear as soon as the twelfth week. Sellers et al. (1950) have sh that male rats excrete four times the protein females do; the differenc removed by castration. Since males suffer more from protein-defic diets than females (they gain less weight and survive less well) the linked proteinuria, apparently unrelated to size, may be a factor in cau lower male survival in wild rats (Schein 1950). (The connection betw

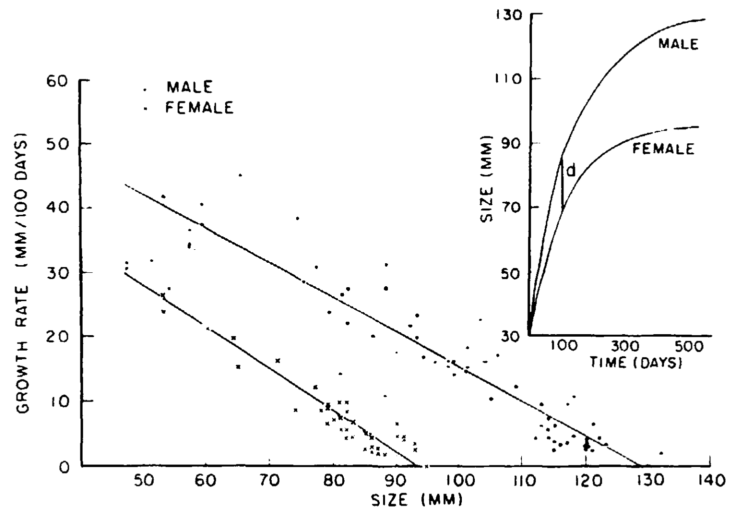

Figure 7.11. Male and female growth rates in A. garmani *as a function of initial size based on summer 1970 recaptures of animals marked 3 to 4 months before. A line has been fitted to each set of data;* d *indicates how much larger a male is when a similar aged female reaches sexual maturity.*

proteinuria and male reproductive success is obscure.) Again, although human male survival is more adversely affected by poor nutritional conditions than female survival, Hamilton (1948) presents evidence that the higher metabolic rate of the male is an important factor increasing his vulnerability to many diseases which strike males more heavily than females. Likewise, Taber & Dasmann (1954) argue that greater male mortality in the deer, *Odocoileus hemionus,* results from a higher metabolic rate. High metabolic rate could relate to both aggressiveness and searching behavior.

EXPERIENCE

If reproductive success increases more rapidly in one sex than the other as a function of age alone (for example, through age-dependent experience), then one would expect a postponement of sexual maturity in that sex and a greater chance of surviving through a unit of time than in the opposite sex. Thus, the adult sex ratio might be biased in favor of the earlier maturing sex but the sex ratio for all ages taken together should be biased in favor of the later maturing sex. Of course, if reproductive success for one sex increases strongly as a function of experience and experience only partly

correlates with age, then the sex may be willing to suffer increased mor if this mortality is sufficiently offset by increases in experience. Sel: (1965) has suggested that the tendency of immature male blackbir exhibit some mature characteristics may be adaptive in that it incr the male's experience, although it also presumably increases his ri: mortality.

MOBILITY

Data from mammals (reviewed by Eisenberg 1965 and Brown 1966) from some salamanders (Madison & Shoop 1970) and numerous li (Tinkle 1967 and Blair 1960) suggest that males often occupy larger ranges and wander more widely than females *even when males are sn* (Blair 1965). Parker (1970a) has quantified the importance of mo and searching behavior in dung flies. If females are a dispersed resc then male mobility may be crucial in exposing the male to a large nu of available females. Again, males may be willing to incur greater mor if this is sufficiently offset by increases in reproductive success. This f should only affect the male during the breeding season (Kikkawa 1 unless factors relevant to mobility (such as speed, agility or knowled the environment) need to be developed prior to the reproductive se Lindburg (1969) has shown that macaque males, but not females, cl troops more frequently during the reproductive season than otherwis that this mobility increases male reproductive success as measured b quency of copulation, suggesting that at least in this species, gi mobility can be confined to the reproductive season (see also Miller 1 On the other hand, Taber & Dasmann (1954) present evidence th early as six months of age male deer wander more widely from their r ers than females—a difference whose function, of course, is not kr Similar very early differences in mobility have been demonstrated lizard (Blair 1960) and for several primates, including man (Je Bobbitt & Gordon 1968).

Female Choice

Although Darwin (1871) thought female choice an important e tionary force, most writers since him have relegated it to a trivial (Huxley 1938, Lack 1968; but see Fisher 1958, and Orians 1969). notable exceptions the study of female choice has limited itself to sh that females are selected to decide whether a potential partner is c right species, of the right sex and sexually mature. While the ad: value of such choices is obvious, the adaptive value of subtler discri tions among broadly appropriate males is much more difficult to visi or document. One needs both theoretical arguments for the adaptive of such female choice and detailed data on how females choose. Neither of these criteria is met by those who casually ascribe to female (or male) choice the evolution of such traits as the relative hairlessness of both human sexes (Hershkovitz 1966) or the large size of human female breasts (Morris 1967). I review here theoretical considerations of how females might be expected to choose among the available males, along with some data on how females do choose.

SELECTION FOR OTHERWISE NEUTRAL OR DISFUNCTIONAL MALE ATTRIBUTES

The effects of female choice will depend on the way females choose. If some females exercise a preference for one type of male (genotype) while others mate at random, then other things being equal, selection will rapidly favor the preferred male type and the females with the preference (O'Donald 1962). If each female has a specific image of the male with whom she prefers to mate and if there is a decreasing probability of a female mating with a male as a function of his increasing deviation from her preferred image, then it is trivial to show that selection will favor distributions of female preferences and male attributes that coincide. Female choice can generate continuous male change only if females choose by a relative rather than an absolute criterion. That is, if there is a tendency for females to sample the male distribution and to prefer one extreme (for example, the more brightly colored males), then selection will move the male distribution toward the favored extreme. After a one generation lag, the distribution of female preferences will also move toward a greater percentage of females with extreme desires, because the granddaughters of females preferring the favored extreme will be more numerous than the granddaughters of females favoring other male attributes. Until countervailing selection intervenes, this female preference will, as first pointed out by Fisher (1958), move both male attributes and female preferences with increasing rapidity in the same direction. The female preference is capable of overcoming some countervailing selection on the male's ability to survive to reproduce, if the increased reproductive success of the favored males when mature offsets their chances of surviving to reproduce.

There are at least two conditions under which one might expect females to have been selected to prefer the extreme male of a sample. When two species, recently speciated, come together, selection rapidly favors females who can discriminate the two species of males. This selection may favor females who prefer the appropriate extreme of an available sample, since such a mechanism would minimize mating mistakes. The natural selection of females with such a mechanism of choice would then initiate sexual selection in the same direction, which in the absence of countervailing selection would move the two male phenotypes further apart than necessary to avoid mating error.

Natural selection will always favor female ability to discriminate sexual competence, and the safest way to do this is to take the extre a sample, which would lead to runaway selection for male display case is discussed in more detail below.

SELECTION FOR OTHERWISE FUNCTIONAL MALE ATTRIBUTES

As in other aspects of sexual selection, the degree of male investment offspring is important and should affect the criteria of female c Where the male invests little or nothing beyond his sex cells, the f has only to decide which male offers the ideal genetic material for h spring, assuming that male is willing and capable of offering it. This tion can be broken down to that of which genes will promote the su of her offspring and which will lead to reproductive success, assumi offspring survive to adulthood. Implicit in these questions may be th tion between her genes and those of her mate: do they complemen other?

Where the male invests parental care, female choice may still invol above questions of the male's genetic contribution but should also in perhaps primarily involve, questions of the male's willingness and to be a good parent. Will he invest in the offspring? If willing, dc have the ability to contribute much? Again, natural selection may fav male attentiveness to complementarity: do the male's parental at complement her own? Can the two parents work together smo Where males invest considerable parental care, most of the same con ations that apply to female choice also apply to male choice. The alt criteria for female choice are summarized in Table 7.1.

SEXUAL COMPETENCE

Even in males selected for rapid, repeated copulations the ability to is not unlimited. After three or four successive ejaculations, for exa the concentration of spermatozoa is very low in some male chi (Parker, McKenzie & Kempster 1940), yet males may copulate as of 30 times in an hour (Guhl 1951). Likewise, sperm is completely de in male *Drosophila melanogaster* after the fifth consecutive mating c same day (Demerec & Kaufmann 1941, Kaufmann & Demerec 1942) ration of copulation is cut in half by the third copulation of a male du on the same day and duration of copulation probably correlates sperm transferred (Parker 1970a). In some species females may be a judge whether additional sperm are needed (for example, house Riemann, Moen & Thorson 1967) or whether a copulation is at least b iorally successful (for example, sea lions; Peterson & Bartholomew 1 but in many species females may guarantee reproductive success by

Table 7.1. Theoretical criteria for female choice of males

- I. All species, but especially those showing little or no male parental investment
  - A. Ability to fertilize eggs
    - (1) correct species
    - (2) correct sex
    - (3) mature
    - (4) sexually competent
  - B. Quality of genes
    - (1) ability of genes to survive
    - (2) reproductive ability of genes
    - (3) complementarity of genes
- II. Only those species showing male parental investment
  - C. Quality of parental care
    - (1) willingness of male to invest
    - (2) ability of male to invest
    - (3) complementarity of parental attributes

ing with those males who are most vigorous in courtship, since this vigor may correlate with an adequate supply of sperm and a willingness to transfer it.

When the male is completely depleted, there is no advantage in his copulating but selection against the male doing so should be much weaker than selection against the female who accepts him. At intermediate sperm levels, the male may gain something from copulation, but the female should again be selected to avoid him. Since there is little advantage to the male in concealing low reproductive powers, a correlation between vigor of courtship and sperm level would not be surprising. Females would then be selected to be aroused by vigorous courtship. If secondary structures used in display, such as bright feathers, heighten the appearance of vigorousness, then selection may rapidly accentuate such structures. Ironically, the male who has been sexually most successful may not be ideal to mate with if this success has temporarily depleted his sperm supply. Males should not only be selected to recover rapidly from copulations but to give convincing evidence that they have recovered. It is not absurd to suppose that in some highly promiscuous species the most attractive males may be those who, having already been observed to mate with several females, are still capable of vigorous display toward a female in the process of choosing.

GOOD GENES

Maynard Smith (1956) has presented evidence that, given a choice, female *Drosophila subobscura* discriminate against inbred males of that species and that this behavior is adaptive: females who do not so discriminate leave about ¼ as many viable offspring as those who do. Females may

choose on the basis of courtship behavior: inbred males are apparently able to perform a step of the typical courtship as rapidly as outbred m. The work is particularly interesting in revealing that details of court behavior may reveal a genetic trait, such as being inbred, but it su from an artificiality. If inbred males produce mostly inviable offspı then, even in the absence of female discrimination, one would expect few, if any, inbred males to be available in the adult population. Only cause such males were artificially selected were there large numbers to pose to females in choice experiments. Had that selection continued generation further, females who chose inbred males would have been successful females.

Maynard Smith's study highlights the problem of analyzing the poteı for survival of one's partner's genes: one knows of the adult males meets that they have survived to adulthood; by what criterion does one cide who has survived better? If the female can judge age, then all o things being equal, she should choose older males, as they have den strated their capacity for long survival. All other things may not be ec however, if old age correlates with lowered reproductive success, as it (in some ungulates (Fraser 1968) through reduced ability to impregr If the female can judge the physical condition of males she encoun then she can discriminate against undernourished or sickly individı since they will be unlikely to survive long, but discrimination against : individuals may occur for other reasons, such as the presumed low ability of such males to impregnate successfully due to the weak condition.

In some very restricted ways it may be possible to second-guess future action of natural selection. For example, stabilizing selection been demonstrated to be a common form of natural selection (see M 1963) and under this form of selection females may be selected to exe their own discrimination against extreme types, thereby augmenting effects of any stabilizing selection that has occurred prior to reproduct Mason (1969) has demonstrated that females of the California Oak M discriminate against males extreme in some traits, but no one has sh independent stabilizing selection for the same traits. Discrimina against extreme types may run counter to selection for diversity; the sible role of female choice in increasing or decreasing diversity is discu below as a form of complementarity.

Reproductive success, independent of ability to survive is easier for female to gauge because she can directly observe differences in reproı tive success before she chooses. A striking feature of data on lek beha of birds is the tendency for females to choose males who, through comı tion with other males, have already increased their likelihood of maı Female choice then greatly augments the effects of male–male competit On the lek grounds there is an obvious reason why this may be adap

By mating with the most dominant male a female can usually mate more quickly, and hence more safely, than if she chooses a less dominant individual whose attempts at mating often result in interference from more dominant males. Scott (1942) has shown that many matings with less dominant individuals occur precisely when the more dominant individuals are unable, either because of sexual exhaustion or a long waiting line, to quickly service the female. Likewise, Robel (1970) has shown that a dominant female prevents less dominant individuals from mating until she has mated, presumably to shorten her stay and to copulate while the dominant male still can. A second reason why choosing to mate with more dominant males may be adaptive is that the female allies her genes with those of a male who, by his ability to dominate other males, has demonstrated his reproductive capacity. It is a common observation in cervids that females placidly await the outcome of male strife to go with the victor. DeVore (1965) has quantified the importance of dominance in male baboon sexual success, emphasizing the high frequency of interference by other males in copulation and the tendency for female choice, when it is apparent, to be exercised in favor of dominant males. That previous success may increase the skill with which males court females is suggested by work on the black grouse (Kruijt, Bossema and deVos, *in press*), and females may prefer males skillful at courting in part because their skill correlates with previous success.

In many species the ability of the male to find receptive females quickly may be more important than any ability to dominate other males. If this is so, then female choice may be considerably simplified: the first male to reach her establishes thereby a *prima facie* case for his reproductive abilities. In dung flies, in which females must mate quickly while the dung is fresh, male courtship behavior is virtually nonexistent (Parker 1970a). The male who first leaps on top of a newly arrived female copulates with her. This lack of female choice may also result from the *prima facie* case the first male establishes for his sound reproductive abilities. Such a mechanism of choice may of course conflict with other criteria requiring a sampling of the male population, but in some species this sampling could be carried out prior to becoming sexually receptive.

There are good data supporting the importance of complementarity of genes to female choice. Assortative mating in the wild has been demonstrated for several bird species (Cooch & Beardmore 1959, O'Donald 1959) and disassortative mating for a bird species and a moth species (Lowther 1961, Sheppard 1952). Petit & Ehrman (1969) have demonstrated the tendency in several *Drosophila* species for females to prefer mating with the rare type in choice experiments, a tendency which in the wild leads to a form of complementarity, since the female is presumably usually of the common type. These studies can all be explained plausibly in terms of selection for greater or lesser genetic diversity, the female choosing a male

whose genes complement her own, producing an "optimal" diversity in offspring.

GOOD PARENT

Where male parental care is involved, females certainly sometimes cho males on the basis of their ability to contribute parental care. Ori (1969), for example, has recently reviewed arguments and data suggesi that polygyny evolves in birds when becoming the second mate of an ready mated male provides a female with greater male parental contri tion than becoming the first mate of an unmated male would. This will so, for example, if the already mated male defends a territory considera superior to the unmated male's. Variability in territory quality certainly curs in most territorial species, even in those in which territories are used for feeding. Tinbergen (1967), for example, has documented tendency for central territories in the black-headed gull to be less vul able to predation. If females compete among themselves for males v good territories, or if males exercise choice as well, then female choice parental abilities will again tend to augment intra-male competition for relevant resources (such as territories). The most obvious form of this lection is the inability of a nonterritory holding male to attract a female.

Female choice may play a role in selecting for increased male pare investment. In the roadrunner, for example, food caught by a male se to act on him as an aphrodisiac: he runs to a female and courts her v the food, suggesting that the female would not usually mate without s a gift (Calder 1967). Male parental care invested after copulation is p sumably not a result of female choice after copulation, since she no lor has anything to bargain with. In most birds, however, males defend te tories which initially attract the females (Lack 1940). Since males with suitable territories are unable to attract a mate, female choice may pla role in maintaining male territorial behavior. Once a male has investe a territory in order to attract a mate his options after copulating with may be severely limited. Driving the female out of his territory would most certainly result in the loss of his investment up until then. He cc establish another territory, and in some species some males do this (Haartman 1951), but in many species this may be difficult, leaving with the option of aiding, more or less, the female he has already ma Female choice, then, exercised *before* copulation, may indirectly force male to increase his parental investment *after* copulation.

There is no reason to suppose that males do not compete with each o to pair with those females whose breeding potential appears to be h Darwin (1871) argued that females within a species breeding early nongenetic reasons (such as being in excellent physical condition) wc produce more offspring than later breeders. Sexual selection, he argı would favor males competing with each other to pair with such females. Fisher (1958) has nicely summarized this argument, but Lack (1968, p. 157) dismisses it as being "not very cogent," since "the date of breeding in birds has been evolved primarily in relation to two different factors, namely the food supply for the young and the capacity of the female to form eggs." These facts are, of course, fully consistent with Darwin's argument, since Darwin is merely supposing a developmental plasticity that allows females to breed earlier if they are capable of forming the eggs, and data presented elsewhere in Lack (1968) support the argument that females breeding earlier for nongenetic reasons (such as age or duration of pair bond) are more successful than those breeding later (see also, for example, Fisher 1969, and Coulson 1966). Goforth & Baskett (1971) have recently shown that dominant males in a penned Mourning Dove population preferentially pair with dominant females; such pairs breed earlier and produce more surviving young than less dominant pairs. It would be interesting to have detailed data from other species on the extent to which males do compete for females with higher breeding potential. Males are certainly often initially aggressive to females intruding in their territories, and this aggressiveness may act as a sieve, admitting only those females whose high motivation correlates with early egg laying and high reproductive potential. There is good evidence that American women tend to marry up the socioeconomic scale, and physical attractiveness during adolescence facilitiates such movement (Elder 1969). Until recently such a bias in female choice presumably correlated with increased reproductive success, but the value, if any, of female beauty for male reproductive success is obscure.

The importance of choice by both female and male for a mate who will not desert nor participate in sex outside the pair bond has been emphasized in an earlier section ("Desertion and cuckoldry"). The importance of complementarity is documented in a study by Coulson (1966).

CRITERIA OTHER THAN MALE CHARACTERS

In many species male–male competition combined with the importance of some resource in theory unrelated to males, such as oviposition sites may mitigate against female choice for male characters. In the dragonfly *Parthemis tenera* males compete with each other to control territories containing good oviposition sites, probably because such sites are a predictable place at which to find receptive females and because sperm competition in insects usually favors the last male to copulate prior to oviposition (Parker 1970b). It is clear that the females choose the oviposition site and not the male (Jacobs 1955), and male courtship is geared to advertise good oviposition sites. A male maintaining a territory containing a good oviposi-

tion site is *not* thereby contributing parental investment unless that m
tenance benefits the resulting young.

Female choice for oviposition sites may be an especially important de
minant of male competition in those species, such as frogs and salan
ders, showing external fertilization. Such female choice almost certainly
disposed these species to the evolution of male parental investm
Female choice for good oviposition sites would tend to favor any male
vestment in improving the site, and if attached to the site to attract o
females the male would have the option of caring more or less for tl
eggs already laid. A similar argument was advanced above for birds.
ternal fertilization and development mitigate against evolution of r
parental care in mammals, since female choice can then usually only o
ate to favor male courtship feeding, which in herbivores would be ne
valueless. Female choice may also favor males who mate away from
position sites if so doing reduced the probability of predation.

Where females are clumped in space the effects of male competition
render female choice almost impossible. In a monkey troop a female p
erence for a less dominant male may never lead to sexual congress if
pair are quickly broken up and attacked by more dominant males.
parent female acquiescence in the results of male–male competition
reflect this factor as much as the plausible female preference for the
victor outlined above.

Summary

The relative parental investment of the sexes in their young is the
variable controlling the operation of sexual selection. Where one se
vests considerably more than the other, members of the latter will com
among themselves to mate with members of the former. Where investi
is equal, sexual selection should operate similarly on the two sexes.
pattern of relative parental investment in species today seems strongl
fluenced by the early evolutionary differention into mobile sex cells fer
ing immobile ones, and sexual selection acts to mold the pattern of rel
parental investment. The time sequence of parental investment anal
by sex is an important parameter affecting species in which both sexe
vest considerable parental care: the individual initially investing
(usually the female) is vulnerable to desertion. On the other han
species with internal fertilization and strong male parental investr
the male is always vulnerable to cuckoldry. Each vulnerability ha
to the evolution of adaptations to decrease the vulnerability an
counter-adaptations.

Females usually suffer higher mortality rates than males in monoga
birds, but in nonmonogamous birds and all other groups, males us

suffer higher rates. The chromosomal hypothesis is unable to account for the data. Instead, an adaptive interpretation can be advanced based on the relative parental investment of the sexes. In species with little or no male parental investment, selection usually favors male adaptations that lead to high reproductive success in one or more breeding seasons at the cost of increased mortality. Male competition in such species can only be analyzed in detail when the distribution of females in space and time is properly described. Data from field studies suggest that in some species, size, mobility, experience and metabolic rate are important to male reproductive success.

Female choice can augment or oppose mortality selection. Female choice can only lead to runaway change in male morphology when females choose by a relative rather than absolute standard, and it is probably sometimes adaptive for females to so choose. The relative parental investment of the sexes affects the criteria of female choice (and of male choice). Throughout, I emphasize that sexual selection favors different male and female reproductive strategies and that even when ostensibly cooperating in a joint task male and female interests are rarely identical.

References

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24: 546–559.

Bastock, M. 1967. *Courtship: An ethological study*. Chicago: Aldine.

Bateman, A. J. 1948. Intrasexual selection in Drosophila. *Heredity* 2: 349–368.

Beebe, W. 1925. The variegated Tinamou *Crypturus variegatus variegatus* (Gmelin). *Zoologica* 6: 195–227.

Beer, J. R., L. D. Frenzel, & C. F. MacLeod. 1958. Sex ratios of some Minnesota rodents. *American Midland Naturalist* 59: 518–524.

Beverton, J. M., & S. J. Holt. 1959. A review of the lifespan and mortality rates of fish in nature and their relation to growth and other physiological characteristics. In *The lifespan of animals*, ed. G. Wolstenhome & M. O'Connor, pp. 142–177. London: J. & A. Churchill.

Blair, W. F. 1960. *The Rusty Lizard*. Austin: University of Texas.

Bouliere, Z. F., & Verschuren, J. 1960. *Introduction a l'ecologie des ongules du Parc National Albert*. Bruxelles: Institut des Parcs Nationaux du Congo Belge.

Bragg, A. N. 1965. *Gnomes of the night*. Philadelphia: University of Pennsylvania Press.

Brown, L. E. 1966. Home range and movement of small mammals. *Symposium of the Zoological Society of London* 18: 111–142.

Bruce, H. 1960. A block to pregnancy in the mouse caused by the proximity of strange males. *Journal of Reproduction and Fertility* 1: 96–103.

Burns, J. M. 1968. Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. *Proceedings of the National Academy of Sciences* 61: 852–859.

Calder, W. A. 1967. Breeding behavior of the Roadrunner, *Geococcyx californianus*. *Auk* 84: 597–598.

Carpenter, C. 1967. Aggression and social structure in Iguanid lizards. In *Lizard ecology*, ed. W. Milstead. Columbia, Mo.: University of Missouri

Chapman, A. B., L. E. Casida, & A. Cote. 1938. Sex ratios of fetal calves. *Proceedings of the American Society of Animal Production* 1938, pp. 303–

Cooch, F. G., & M. A. Beardmore. 1959. Assortative mating and reciprocal difference in the Blue-Snow Goose complex. *Nature* 183: 1833–1834.

Corbet, P., C. Longfield, & W. Moore. 1960. *Dragonflies*. London: Collins.

Coulson, J. C. 1960. A study of the mortality of the starling based on ring recoveries. *Journal of Animal Ecology* 29: 251–271.

———. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*. *Journal of Animal Ecology* 35: 2 279.

Cowan, I. M. 1950. Some vital statistics of big game on overstocked mountain range. *Transactions of North American Wildlife Conference* 15: 581–588.

Darley, J. 1971. Sex ratio and mortality in the brown-headed cowbird. *Auk* 560–566.

Darwin, C. 1871. *The descent of man, and selection in relation to sex*. London: John Murray.

Demerec, M., & Kaufmann, B. P. 1941. Time required for *Drosophila* male to exhaust the supply of mature sperm. *American Naturalist* 75: 366–379.

DeVore, I. 1965. Male dominance and mating behavior in baboons. In *Sex behavior*, ed. Frank Beach. New York: John Wiley and Sons.

deVos, A., P. Broky, & V. Geist. 1967. A review of social behavior of the N American Cervids during the reproductive period. *American Midland Naturalist* 77: 390–417.

Dunn, E. R. 1941. Notes on *Dendrobates auratus*. *Copeia* 1941, pp. 88–93

Eaton, T. H. 1941. Notes on the life history of *Dendrobates auratus*. *Co* 1941, pp. 93–95.

Eisenberg, J. F. 1965. The social organizations of mammals. *Handbuch Zoologie* 10 (7): 1–92.

Elder, G. 1969. Appearance and education in marriage mobility. *American Sociological Review* 34: 519–533.

Emlen, J. M. 1968. A note on natural selection and the sex-ratio. *American Naturalist* 102: 94–95.

Emlen, J. T. 1940. Sex and age ratios in the survival of the California Q *Journal of Wildlife Management* 4: 91–99.

Emlen, S. T. 1968. Territoriality in the bullfrog, *Rana catesbeiana*. *Co* 1968, pp. 240–243.

Engelmann, F. 1970. *The physiology of insect reproduction*. Oxford: Pergamon Press.

Fiedler, K. 1954. Vergleichende Verhaltensstudien an Seenadeln, Schlangennadeln und Seepferdchen (Syngnathidae). *Zeitsch. Tierpsych.* 11: 358–41 358–416.

Fisher, H. 1969. Eggs and egg-laying in the Laysan Albatross. *Diomedea mutabilis*. *Condor* 71: 102–112.

Fisher, R. A. 1958. *The genetical theory of natural selection*. New York: D Publications.

Fraser, A. F. 1968. *Reproductive behavior in Ungulates*. London and New Academic Press.

Gadgil, M., & W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* 104: 1–24.

Goethals, G. W. 1971. Factors affecting permissive and nonpermissive rules regarding premarital sex. In *Studies in the sociology of sex: a book of readings*, ed. J. M. Henslin. New York: Appleton-Century-Croft.

Goforth, W., & T. Baskett. 1971. Social organization of penned Mourning Doves. *Auk* 88: 528–542.

Guhl, A. M. 1951. Measurable differences in mating behavior of cocks. *Poultry Science* 30: 687.

Haartman, L. von. 1951. Successive polygamy. *Behavior* 3: 256–274.

————. 1969. Nest-site and evolution of polygamy in European Passerine birds. *Ornis Fennica* 46: 1–12.

Hamilton, J. B. 1948. The role of testicular secretions as indicated by the effects of castration in man and by studies of pathological conditions and the short lifespan associated with maleness. *Recent Progress in Hormone Research* 3: 257–322.

Hamilton, J. B., & M. Johansson. 1965. Influence of sex chromosomes and castration upon lifespan: studies of meal moths, a species in which sex chromosomes are homogenous in males and heterogenous in females. *Anatomical Record* 24: 565–578.

Hamilton, J. B., & G. E. Mestler. 1969. Mortality and survival: comparison of eunuchs with intact men and women in a mentally retarded population. *Journal of Gerontology* 24: 395–411.

Hamilton, J. B., R. S. Hamilton, & G. E. Mestler. 1969. Duration of life and causes of death in domestic cats: influence of sex, gonadectomy and inbreeding. *Journal of Gerontology* 24: 427–437.

Hamilton, W. D. 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology* 7: 1–52.

————. 1967. Extraordinary sex ratios. *Science* 156: 477–488.

Harris, V. A. 1964. *The life of the Rainbow Lizard.* Hutchinson Tropical Monographs. London.

Hays, F. A. 1947. Mortality studies in Rhode Island Reds II. *Massachusetts Agricultural Experiment Station Bulletin* 442: 1–8.

Hershkovitz, P. 1966. Letter to *Science* 153: 362.

Hirth, H. F. 1963. The ecology of two lizards on a tropical beach. *Ecological Monographs* 33: 83–112.

Höhn, E. O. 1967. Observations on the breeding biology of Wilson's Phalarope (*Steganopus tricolor*) in Central Alberta. *Auk* 84: 220–244.

Huxley, J. S. 1938. The present standing of the theory of sexual selection. In *Evolution*, ed. G. DeBeer. New York: Oxford Univ. Press.

Jacobs, M. 1955. Studies in territorialism and sexual selection in dragonflies. *Ecology* 36: 566–586.

Jensen, G. D., Bobbitt, R. A. & Gordon. B. N. 1968. Sex differences in the development of independence of infant monkeys. *Behavior* 30: 1–14.

Johns, J. E. 1969. Field studies of Wilson's Phalarope. *Auk* 86: 660–670.

Kaufmann, B. P., & Demerec, M. 1942. Utilization of sperm by the female *Drosophila melanogaster*. *American Naturalist* 76: 445–469.

Kessel, E. L. 1955. The mating activities of baloon flies. *Systematic Zoology* 4: 97–104.

Kikkawa, J. 1964. Movement, activity and distribution of small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *Journal of Animal Ecology* 33: 259–299.

Kluijver, H. N. 1933. Bijrage tot de biologie en de ecologie van den spreeuw (*Sturnus vulgaris* L.) gedurende zijn voortplantingstijd. *Versl. Plantenziektenkundigen dienst, Wageningen* 69: 1–145.

Koivisto, I. 1965. Behaviour of the black grouse during the spring display. *Finnish Game Research* 26: 1–60.

Kolman, W. 1960. The mechanism of natural selection for the sex ratio. *American Naturalist* 94: 373–377.

Kopstein, F. 1941. Über Sexualdimorphismus bei Malaiischen Schlangen. *minckia*, 6: 109–185.

Kruijt, J. P, I. Bossema, & G. J. deVos. *In Press.* Factors underlying choi mate in Black Grouse. *15th Congr. Intern. Ornith.*, The Hague, 1970.

Kruijt, J. P., & J. A. Hogan. 1967. Social behavior on the lek in Black Gı *Lyrurus tetrix tetrix* (L.) *Ardea* 55: 203–239.

Lack, D. 1940. Pair-formation in birds. *Condor* 42: 269–286.

————. 1954. *The natural regulation of animal numbers.* New York: O University Press.

————. 1968. *Ecological adaptations for breeding in birds.* London: Met

LeBoeuf, B. J., & R. S. Peterson. 1969. Social status and mating activity i phant seals. *Science* 163: 91–93.

Lee, R., 1969, King Bushman violence. Paper presented at meeting of Am Anthropological Association, November, 1969.

Leigh, E. G. 1970. Sex ratio and differential mortality between the sexes. *ican Naturalist* 104: 205–210.

Lin, N. 1963. Territorial behavior in the Cicada killer wasp *Sphecius sphe* (Drury) (Hymenoptera: Sphecidae.) I. *Behaviour* 20: 115–133.

Lindburg, D. G. 1969. Rhesus monkeys: mating season mobility of adult *Science* 166: 1176–1178.

Lowther, J. K. 1961. Polymorphism in the white-throated sparrow, *Zonoı albicollis* (Gmelin). *Canadian Journal of Zoology* 39: 281–292.

Ludwig, W., & C. Boost. 1951. Über Beziehungen zwischen Elternalter, grösse und Geschlechtsverhältnis bei Hunden. *Zeitschrift fur indukt. Al mungs und Vererbungslehre* 83: 383–391.

Madison, D. M., & Shoop, C. R. 1970. Homing behavior, orientation, and range of salamanders tagged with tantalum–182. *Science* 168: 1484-

Mason, L. G. 1969. Mating selection in the California Oak Moth (Lepid Droptidae). *Evolution* 23: 55–58.

Maynard Smith, J. 1956. Fertility, mating behaviour and sexual select *Drosophila subobscura*. *Journal of Genetics* 54: 261–279.

Mayr, E. 1939. The sex ratio in wild birds. *American Naturalist* 73: 15

————. 1963. *Animal species and evolution.* Cambridge: Harvard Uni Press.

Miller, R. S. 1958. A study of a wood mouse population in Wytham Berkshire. *Journal of Mammalogy* 39: 477–493.

Morris, D. 1952. Homosexuality in the Ten-spined Stickleback (*Py pungitius*). *Behaviour* 4: 233–261.

————. 1967. *The naked ape.* New York: McGraw Hill.

Myers, J., & C. Krebs. 1971. Sex ratios in open and closed vole popul demographic implications. *American Naturalist* 105: 325–344.

Nevo, R. W. 1956. A behavior study of the red-winged blackbird. 1. Mati nesting activities. *Wilson Bulletin* 68: 5–37.

O'Donald, P. 1959. Possibility of assortative mating in the Arctic Skua. 183: 1210.

————. 1962. The theory of sexual selection. *Heredity* 17: 541–552.

Orians, G. H. 1969. On the evolution of mating systems in birds and ma *American Naturalist* 103: 589–604.

Parker, G. A. 1970a. The reproductive behavior and the nature of sexua tion in *Scatophaga stercoraria* L. (Diptera: Scatophagidae) 2. The f tion rate and the spatial and temporal relationships of each sex around of mating and oviposition. *Journal of Animal Ecology* 39: 205–228.

———. 1970b. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45: 525–568.
———. 1970c. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae) VI. The adaptive significance of emigration from the oviposition site during the phase of genital contact. *Journal of Animal Ecology* 40: 215–233.
———. 1970d. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). VI. The adaptive sig- evolution of the passive phase. *Evolution* 24: 774–788.
Parker, J. E., F. F. McKenzie, & H. L. Kempster. 1940. Observations on the sexual behavior of New Hampshire males. *Poultry Science* 19: 191–197.
Peterson, R. S., & G. A. Bartholomew. 1967. *The natural history and behavior of the California Sea Lion.* Special Publications #1, American Society of Mammalogists.
Petit, C., & L. Ehrman. 1969. Sexual selection in *Drosophila*. In *Evolutionary biology*, vol. 5, ed. T. Dobzhansky, M. K. Hecht, W. C. Steere. New York: Appleton-Century-Crofts.
Potts, G. R. 1969. The influence of eruptive movements, age, population size and other factors on the survival of the Shag (*Phalacrocorax aristotelis* L.). *Journal of Animal Ecology* 38: 53–102.
Rand, A. S. 1967. Ecology and social organization in the Iguanid lizard *Anolis lineatopus*. *Proc. U.S. Nat. Mus.* 122: 1–79.
Riemann, J. G., D. J. Moen, & B. J. Thorson. 1967. Female monogamy and its control in house flies. *Insect Physiology* 13: 407–418.
Rivero, J. A., & A. E. Estevez. 1969. Observations on the agonistic and breeding behavior of *Leptodactylus pentadactylus* and other amphibian species in Venezuela. *Breviora No.* 321: 1–14.
Robel, R. J. 1966. Booming territory size and mating success of the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*). *Animal Behaviour* 14: 328–331.
Robel, R. J. 1970. Possible role of behavior in regulating greater prairie chicken populations. *Journal of Wildlife Management* 34: 306–312.
Robinette, W. L., J. S. Gashwiler, J. B. Low, & D. A. Jones. 1957. Differential mortality by sex and age among mule deer. *Journal of Wildlife Management* 21: 1–16.
Rockstein, M. 1959. The biology of ageing insects. In *The lifespan of animals*, ed. G. Wolstenhome & M. O'Connor, pp. 247–264. London: J. A. Churchill.
Rowley, I. 1965. The life history of the Superb Blue Wren *Malarus cyaneus*. *Emu* 64: 251–297.
Royama, T. 1966. A re-interpretation of courtship feeding. *Bird Study* 13: 116–129.
Sadleir, R. 1967. *The ecology of reproduction in wild and domestic mammals.* London: Methuen.
Savage, R. M. 1961. *The ecology and life history of the common frog.* London: Sir Isaac Pitman and Sons.
Schein, M. W. 1950. The relation of sex ratio to physiological age in the wild brown rat. *American Naturalist* 84: 489–496.
Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155: 474–477.
———. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2: 369–404.
Scott, J. W. 1942. Mating behavior of the Sage Grouse. *Auk* 59: 477–498.

Selander, R. K. 1965. On mating systems and sexual selection. *American* *ralist* 99: 129–141.
———. 1966. Sexual dimorphism and differential niche utilization in *Condor* 68: 113–151.
Sellers, A., H. Goodman, J. Marmorston, & M. Smith. 1950. Sex differen proteinuria in the rat. *American Journal of Physiology* 163: 662–667.
Sheppard, P. M. 1952. A note on non-random mating in the moth *P* *dominula.* (L.) *Heredity* 6: 239–241.
Stephens, M. N. 1952. Seasonal observations on the Wild Rabbit (*Oryct* *cuniculus cuniculus* L.) in West Wales. *Proceedings of the Zoological S* *of London* 122: 417–434.
Stokes, A., & H. Williams. 1971. Courtship feeding in gallinaceous birds 88: 543–559.
Sugiyama, U. 1967. Social organization of Hanuman langurs. In *Social co* *nication among primates*, ed. S. Altmann. Chicago: University of C Press.
Taber, R. D., & R. F. Dasmann. 1954. A sex difference in mortality in Columbian Black-tailed Deer. *Journal of Wildlife Management* 18: 30
Tilley, S. 1968. Size-fecundity relationships and their evolutionary implic in five Desmognathine salamanders. *Evolution* 22: 806–816.
Tinbergen, N. 1935. Field observations of East Greenland birds. 1. The be of the Red-necked Phalarope (*Phalaropus lobatus* L.) in Spring. *Ard* 1–42.
———. 1967. Adaptive features of the Black-headed Gull *Larus ridib* L. *Proceedings of the International Ornithological Congress* 14: 43–59.
Tinkle, D. W. 1967. The life and demography of the Side-blotched Lizar *stansburiana*. *Miscellaneous Publications of the Museum of Zoology, U* *sity of Michigan* 132: 1–182.
Tinkle, D., H. Wilbur, & S. Tilley. 1970. Evolutionary strategies in lizard duction. *Evolution* 24: 55–74.
Tyndale-Biscoe, C. H. and R. F. C. Smith. 1969. Studies on the marsupial *Schoinobates volans* (Kerr). 2. Population structure and regulatory n nisms. *Journal of Animal Ecology* 38: 637–650.
Van Lawick-Goodall, J. 1968. The behavior of free-living chimpanzees Gombe Stream Reserve. *Animal Behaviour Monographs* 1: 161–311.
Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. *Ev* 18: 252–261.
———. 1965. Selection for sex ratio. *American Naturalist* 99: 419–421.
Verner, J., & M. Willson. 1969. Mating systems, sexual dimorphism, and t of male North American passerine birds in the nesting cycle. *Ornitho* *Monographs* 9: 1–76.
Williams, G. C. 1966. *Adaptation and natural selection.* Princeton: Pri University Press.
Willson, M., & E. Pianka. 1963. Sexual selection, sex ratio, and mating s *American Naturalist* 97: 405–406.
Wood, D. H. 1970. An ecological study of *Antechinus stuartii* (Marsupia a Southeast Queensland rain forest. *Australian Journal of Zoology* 18 207.