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Author(s): Gordon H. Orians

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ON THE EVOLUTION OF MATING SYSTEMS  
IN BIRDS AND MAMMALS

GORDON H. ORIAN

Department of Zoology, University of Washington, Seattle, Washington 98105

Mating systems and the selective factors that molded them have had an important place in the history of the theory of natural selection. Darwin (1871) himself gave considerable thought to the nature of sexual selection and its consequences for sexual dimorphism and mating patterns. He proposed two major forces in the evolution of sexual differences. First, that the fighting and display among males for the possession of females, which is especially prominent among mammals, accounted for the evolution of secondary sexual characteristics, such as horns and antlers, which are useful in battle. This aspect of sexual selection has been generally accepted. Second, Darwin suggested that the extreme development of plumage characters among males of some birds, such as pheasants and birds of paradise—features which did not seem of use in intermale combat—could be explained as being due to the cumulative effects of sexual preference exerted by the females at the time of mating. This aspect of his theory of sexual selection was challenged by a number of workers, but Fisher (1958) clearly showed that the notion of female choice is reasonable, notwithstanding the fact that direct evidence was then scarce for species other than man.

More recently, mating systems and sexual dimorphism have been assigned an important role in the theory of Wynne-Edwards (1962) as a device for regulating the reproductive output of populations. According to Wynne-Edwards, polygyny is one of a series of restrictive population adaptations arising through group selection which controls populations by reducing collective fecundity. He argues (1962, p. 515) that this restriction of breeding activity is possible because the territorial males of polygynous and promiscuous species can be fully informed about their own reproductive activity and, if the species engages in displays at communal mating grounds, of the total of matings performed by the group as well. These males could be conditioned to respond by becoming sexually inactive when an appropriate number of matings had taken place. The value of polygyny and group displays would lie in the fact that the assessment of total reproductive output by the population would be much easier than with a monogamous mating system in which the individuals are spaced out through the environment. He further suggested (1962, p. 525) that a balanced sex ratio would be maintained in nonmonogamous species because it would facilitate

more intensive intermale competition and thereby provide a more sensitive index of population density and total reproductive output.

This theory would best be tested by direct demonstration of the processes that are postulated to occur. For example, if females of polygynous species are unable to mate because males withhold coition after a certain number of copulations have been achieved, if low-ranking males do not attempt to solicit copulations after the quota has been reached, or if females are not receptive to their advances if they are made, then confidence in the theory would be strengthened.

Such evidence is extremely difficult to gather in the field, but there are now available data from a number of intensively studied polygynous species of birds, indicating that all females which appear in the breeding areas are able to obtain males and raise young. Jared Verner (personal communication) has not found any evidence for unmated females in the long-billed marsh wren (*Telmatodytes palustris*), and my own intensive work on red-winged blackbirds (*Agelaius phoeniceus*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) has failed to reveal a nonbreeding population of females in either of these species. In both species, there is a large and readily observable floating population of males. In the great-tailed grackle (*Quiscalus mexicanus*), a highly promiscuous species, adult males remain in full breeding condition and continue to attempt copulations after all females are nesting and are no longer receptive (Selander 1965). Therefore, in these species if there is some mechanism for limiting reproductive output, it must be due either to the failure of more females to present themselves at the breeding grounds or to a lowered effort per reproducing individual. At present, there is no evidence from any species that males withhold coition from receptive females.

It is the purpose of this paper to present an alternative theory of mating systems among birds and mammals which is based upon the assumption that the evolution of mate-selection behavior by individuals of both sexes has been influenced primarily by the consequences of these choices for individual fitness. The model is based upon mate-selection processes that can be observed directly in the field, and it is capable of generating a set of predictions which can be tested against the general mating patterns of broad groups of species for which there are no detailed observations of the factors influencing mating behavior.

#### A NATURAL SELECTION MODEL OF MATING SYSTEMS

This model is built upon the work of a number of people, especially Maynard Smith (1958), Verner (1964), Verner and Willson (1966), Lack (1968), and Willson and Pianka (1963), to which I have added some original ideas. Existing knowledge of the mating patterns of birds and mammals has been summarized by Lack (1968) and Eisenberg (1966), respectively. All theories of sexual selection involve an element of choice, and mine is no exception. In order for discrimination to be selected for, it is

necessary that (a) the acceptance of one mate generally precludes the acceptance of another, and (b) the failure to accept one mate will be followed by an opportunity to mate with other individuals with such a high probability that the loss in reproductive output resulting from rejection of a potential mate is, on the average, less than the average gains that can be realized by obtaining a mate of superior fitness (Fisher 1958, p. 144).

The first condition is met by both sexes of many species and by females in virtually all species. Basically, a female produces gametes with a large amount of stored energy, while a male produces gametes with a complete set of genetic instructions but no significant amount of stored energy. Consequently, the number of gametes that can be produced by males is potentially, and in most cases actually, very large. On the other hand, the number of eggs produced by females is ultimately limited by the amount of energy that can be mobilized for their production or subsequent care. It follows that males can be expected to increase the number of offspring they produce by mating with more than one female, but females should not have more offspring by successive matings with more than one male unless one male were to provide insufficient gametes to fertilize all the eggs, an unlikely condition (Maynard Smith 1958, p. 146).

For the same reason, errors in mate selection are more serious for females than for males. An interspecific mating that produced inviable or sterile offspring might claim the entire season's gamete production for a female, while the male could have erred to the extent of no more than a few minutes and a few readily replaced gametes.

The inescapable conclusion is that mate selection will be practiced whenever sensory capabilities and locomotor abilities permit it and that females will, in the vast majority of cases, exercise a stronger preference. It is a well-known fact that males of many species court rather indiscriminately and can, especially when deprived of sexual activity for some time, be induced to mate with remarkably incomplete stimulus objects. Such behavior could not have evolved if errors were strongly selected against among males. For this reason, the following model assumes that females make a choice among available males. Since polygyny must always be advantageous to males, its presence or absence must depend primarily upon the advantages or disadvantages to the females.

I also assume that the environment inhabited by a species is variable and that mean reproductive success uncomplicated by density effects is correlated with this variation in quality of the habitat. For the purposes of graphic presentation, environments are treated as though they can be ordered linearly with respect to their intrinsic quality, as measured by reproductive success, but this is not essential to the argument. A model based upon these assumptions is presented in figure 1.

There are two bases upon which female choice could be made. The first, already mentioned, is the genetic quality of the male, that is, the nature of the genes that will be given to the offspring from a mating with that male. Given the existence of such differences, female choice must inevitably be

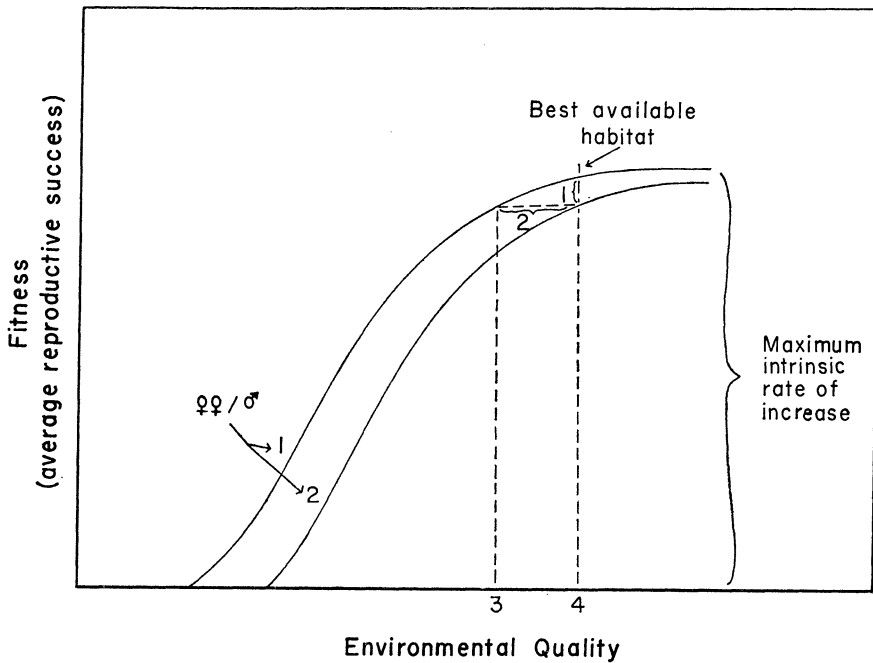


FIG. 1.—Graphic model of conditions necessary for the evolution of polygynous mating patterns. Average reproductive success is assumed to be correlated with environmental differences and females are assumed to choose their mates from available males. The distance 1 is the difference in fitness between females mated monogamously and females mated bigamously in the same environment; the distance 2 is the *polygyny threshold*, which is the minimum difference in quality of habitat held by males in the same general region sufficient to make bigamous matings by females favored by natural selection.

under strong selection, since those females mating with more fit males will thereby produce offspring that are more fit, on the average, than females mating with less fit males. Therefore, females should evolve to be especially responsive to those morphological and/or behavioral traits of males which reflect their fitness (Fisher 1958, p. 151).

In many species, however, the role of the male in reproduction is more extensive, involving provision of food for the offspring, possession of a territory within which resources can be gathered, protection against predation or inclement weather, and so forth. In these cases, I expect selection by the females to be influenced also by the quality of the territory and the probability that the male is capable of and disposed toward taking an active role in the care and defense of the offspring. The model accommodates both cases.

The model assumes that mean reproductive success is correlated with the quality of the environment in which the individuals are living. The exact shape of the function is immaterial as long as the slope is everywhere positive. Given this condition, the best strategy for a female is to mate with

a male on the best quality habitat and to rear her offspring, with or without his help, in that environment. However, as more individuals settle in these optimal environments, the average reproductive success will be expected to drop for three major reasons. First, the more individuals that are exploiting a given environment, the greater the likelihood that reduction of resources will adversely influence reproductive success. Second, the higher density of individuals may attract more predators, thereby increasing the probability of nest destruction. Third, if the male does play a role in the care of the offspring and females settle at a greater density than the males, then the aid of the male will have to be shared among the females, each getting less than if the male were able to devote his full attention to the offspring of one of them. For this reason, a curve representing the average reproductive success of females mated to males having more than one mate is drawn below the curve for females involved in monogamous matings.

Whatever the relative positions of these two curves, a situation may eventually be reached at which the quality of habitat on the territories of unmated males is such that the expected reproductive success of a newly arriving female is higher if she attempts to mate with a male already with one female but on a superior-quality habitat, rather than mating with an unmated male on poorer habitat. The difference in quality of habitats occupied by mated and unmated males required to make a bigamous mating advantageous for a female may be designated the *polygyny threshold* (Verner and Willson 1966), and polygyny is expected to evolve only when this situation regularly presents itself to the females of a species.

It follows that the likelihood that polygyny will evolve is influenced by all factors which determine how broad a range of environmental conditions will be occupied by the individuals of a species. For example, if the territories of the males of a species are nearly equal in quality and there are still unpaired males available, it is unlikely that the mean reproductive success of females attempting bigamous matings would be higher. Similarly, all factors that influence the amount of difference in mean reproductive success of females in monogamous and bigamous matings in equivalent environments will affect the likelihood that polygyny will evolve. More specifically, the greater the difference, that is, the farther apart the two curves are, the farther to the left will lie the polygyny threshold, and there must be greater differences in habitat quality for polygyny to pay for the females. Conversely, with less difference, that is, closer curves, a smaller difference in habitat will push part of the population to the left of the polygyny threshold.

a) *Factors promoting occupancy of habitats differing widely in quality:* The existence of individuals to the left of the polygyny threshold will be facilitated by (1) low mortality rates during the nonbreeding season, so that not all individuals can be accommodated in the better areas, and (2) the existence of large differences in the quality of habitats actually occupied by the species.

b) *Factors influencing the differences in average reproductive success of*

*monogamously and bigamously mated females*: A major factor affecting the differences in reproductive success of females will be the role of the male in the care of the offspring. If his role is limited to the provision of genetic information, that is, if the male provides no food, territory, or protection, the success of the females will not be affected by the number of other females that have mated with the male unless his fertility declines with successive matings. Thus, in the limiting case of no male parental care, the two curves become congruent, and the mating choice by the females is based strictly upon the genotype of the male. A high degree of promiscuity is to be expected in such species.

Even if the male also cares for the offspring, in which case the number of other females he already has is a major factor in female choice, there are conditions which tend to minimize the reduction in reproductive success attendant upon polygynous matings. For example, if the successive females of a male are staggered in their breeding so that the periods of dependence of their offspring overlap little or not at all, more support from the male could be available (Verner 1964). This should give selective advantage to two different forms of female behavior. The first is the attempt to exclude additional females from the territory of the male until such time as the overlap in dependency periods of the young would be minimized, and second, the avoidance by newly arriving females of territories in which a prior female was just beginning to breed.

Another factor influencing the difference in reproductive success of monogamously and bigamously mated females is the nature of the food resources present in the area. If the food for the young is not being replenished during the breeding period, the individuals breeding earliest should experience the best foraging conditions, while later-breeding individuals are exploiting an already depressed supply. However, if the recruitment to the food supply is considerable during the breeding period, conditions for later breeders may be no worse (or may even be better) than conditions for earlier breeders. Therefore, other things being equal, species exploiting food supplies that are continually renewed are more likely to cross the polygyny threshold.

The above arguments all assume that the number of offspring being raised by a female (or pair) has evolved under the influence of natural selection to correspond to that which, on the average, is the largest number for which sufficient energy can be mobilized. The theoretical basis for this assumption and the supporting empirical data have been extensively summarized by Lack (1954 p. 21-44). However, in some species the number of offspring produced is strongly influenced by other factors. In such cases, the existence of male parental care may be of little consequence, and mate choice should be made primarily or strictly on the basis of phenotype and territory quality. Cases in which this situation may be operative will be discussed later.

The model implies the existence of several processes which can be directly observed in nature. For example, it should be true that females mate with

already mated males when unmated males are readily available and perceived by the females. Evidence that this is true has been gathered for the long-billed marsh wren (Verner 1964), the red-winged blackbird, and the yellow-headed blackbird (Orians, unpublished observations). The great variations in number of females mated with different males in other polygynous species are suggestive of the widespread occurrence of this phenomenon. Verner has also shown that the number of females attracted to a male long-billed marsh wren is correlated with the features of his territory relative to the available food.

The model also predicts that there should not be a negative correlation between average reproductive success per female and number of females mated with a given male, since females are assumed to enter polygynous matings only when it is advantageous for them to do so. This prediction has been verified for the red-winged blackbird (Haigh 1968).

The model does not require a skewed sex ratio in the breeding population for the initiation and evolution of polygynous mating patterns. This is important because there are theoretical reasons for expecting a sex ratio near equality when the young become independent in most species (Fisher 1958; Kolman 1960) and because sex ratios at the time of fledging are near equality in all polygynous species so far investigated (Haigh 1968; Selander 1960, 1961; Williams 1940).

Using the postulates upon which the polygyny model was erected, a series of seven predictions about mating patterns can be made. These predictions are subject to direct verification or falsification. Current knowledge of mating patterns among mammals, though by no means complete, is extensive enough that I can reasonably assess the goodness of the predictions. Moreover, the predictions from the model serve to draw attention to those cases which would be most rewarding of further study. Though predictions of wide application can be made, I restrict my present consideration to birds and mammals, the groups with which I am most familiar.

1. *Polyandry should be rare among all animal groups.* This prediction follows directly from the basic attributes of maleness and femaleness. A female could presumably increase her reproductive output if several males could be induced to care for her offspring, but such a situation would in most cases be sufficiently disadvantageous to the males to cause the evolution of male behavior patterns that would prevent the system from evolving. However, once a basic sexual role reversal had evolved in a species, males might profit by associating themselves with females on better territories, thus leading to polyandry.

The actual incidence of polyandry among birds and mammals is difficult to assess. Among mammals, Eisenberg (1966) reviewed several polygynous or promiscuous mating patterns but found no good case of a simultaneous association of a female with more than one male. Among birds the situation is confused by the fact that there has been a tendency to assume polyandry in all those species with a reversal of sexual roles. Most such species are tropical and subtropical in distribution and are not well known ecologically,



making comparisons even more difficult. For example, it was formerly believed that the phalaropes (Phalaropodidae) were polyandrous, but recent data indicate that, though incubation and care of the young are exclusively the role of the males, the species are nonetheless monogamous (Höhn 1967). However, there is good evidence of polyandry for at least some species in five groups of birds, all with precocial young: the button quails (Turnicidae), painted snipe (Rostratulidae), jacanas (Jacanidae), tinamous (Tinamidae) and rails (Rallidae). Details in all these cases are summarized by Lack (1968).

Among rheas (Rheidae), emus (Dromiceidae), cassowaries (Casuariidae), kiwis (Apterygidae), tinamous and button quails, the males normally incubate the eggs and care for the young, but most species are apparently monogamous. In the best-studied species, the brushland tinamou (*Nothoprocta cinerascens*), the males defend territories while the females travel in small groups. Several females lay eggs in a single nest, but each female may mate with several males in rapid succession (Lancaster 1964). The classification of this type of pattern is somewhat ambiguous since the male may have several females at once, but each female may nevertheless mate with several different males during the laying of a single "clutch" of eggs. A clearer case of polyandry with a reversal of parental role is provided by the pheasant-tailed jacana (*Hydrophasianus chirurgus*) (Hoffmann 1949).

The evolution of sexual role reversal in birds may have had its origins in a monogamous system with equal sharing of parental care by the two sexes. In many such species, the males incubate first while the females recover the energy lost during egg production. Under such circumstances, especially among species with precocial young, if the females were able to obtain enough energy to produce more eggs, it would be advantageous to mate with another male were one available. It would also be advantageous for the incubating males to induce other females to mate with them and deposit their eggs in the nests, so that the tinamou type of system could readily evolve. A further advantage of such a system is that the length of time the nest is available to be destroyed by predators is reduced, since a full clutch of eggs is placed in the nest in a shorter period of time than if a single female were doing all the laying.

2. *Monogamy should be relatively rare among mammals but should be the predominant mating pattern among birds.* The physiology of mammalian reproduction dictates a minor role of the male in the care of the offspring, whereas among birds the only activity for which males are not equally adept as females is egg laying. This prediction is readily verified. In his extensive review of mammalian social organization, Eisenberg (1966) pointed out that there are very few cases of known monogamy among mammals, the apparent exceptions being the marmosets (Callithricidae), gibbons (Hylobatinae), beavers (Castoridae), the hooded seal (*Cystophora cristata*), the only pinniped known to form a stable family unit, and a number of terrestrial carnivores, such as foxes, badgers, and viverrids. The situation is more difficult to determine among large ungulates, but tem-

porary pair bonds that are apparently monogamous may form in hyraxes (*Dendrohyrax*), rhinoceroses, and some deer (*Capreolus capreolus*, *Odocoileus*).

The mammals among which monogamy is probably the most prevalent are the terrestrial carnivores, and they provide the most prominent exception to the generalization that the role of the male is limited or nonexistent in the care of offspring. For a carnivore, capturing food is a difficult task, and males can and do make kills and deliver the prey to either the female, who converts it to milk, or to the young once they are old enough to be able to ingest meat. It is difficult to imagine a comparable role for a male herbivore.

In contrast, monogamy is the prevalent mating pattern in the majority of bird species in virtually all families and orders. Assuming that all hummingbirds are promiscuous, Lack (1968) surmises that about 91% of all bird species are monogamous. Given the properties of the model, this is to be expected; but polygyny and promiscuity do exist among birds, and the model, if it is to be generally useful, must provide predictions capable of explaining those cases. Because polygyny should seldom evolve among birds, this group provides a particularly useful test case for the validity of the model. Fortunately, the mating patterns of birds are well enough known to allow tests of the predictions in most cases.

3. *Polygyny should evolve more readily among precocial birds than among altricial species.* This prediction follows from the ability of many precocial young to find their own food and be relatively independent of the provisioning activities of the adults. This decreases the potential role of the male. There are species with precocial young, such as gulls, in which the young, though able to run around actively at birth, are not able to forage for themselves. These species are not included in this prediction.

This prediction is only partially fulfilled in nature. Polygynous and promiscuous species are numerous among upland game birds (Phasianidae, Tetraonidae), and there are a few species among the shorebirds (ruff, *Philomachus pugnax*; buff-breasted sandpiper, *Tryngites subruficollis*; pectoral sandpiper, *Erolia melanotos*; and great snipe, *Capella media*), but most members of the Charadriidae (plovers) and Scolopacidae (sandpipers) are monogamous (Lack 1968, p. 116). Polygyny is also rare in the Anatidae (swans, geese, and ducks). In many of the monogamous species, both sexes take an active role in the care of the young, leading them to suitable foraging areas and keeping on the alert for predators. In geese the male defends the nest and young from predators, but in most species of ducks the female alone cares for the young, and yet monogamous pair bonding seems to be the rule. It is significant that the known exceptions among ducks are all tropical species (Lack 1968, p. 123), suggesting that perhaps the prevalence of monogamy among high latitude species may be the result of the advantage of pair formation on the wintering ground and rapid initiation of breeding which give a stronger advantage to monogamy for the males than would otherwise be the case.

4. *Polygyny is likely to evolve in species with altricial young that nest*

*in marshes.* The marsh environment possesses several features that make it more likely that the polygyny threshold will be crossed than in any other environment. First, the range in productivity of marshes greatly exceeds that found in upland habitats (Verner and Willson 1966). Differences of over tenfold are not unusual in aquatic environments, whereas the difference between the most productive and least productive woods is much less. Moreover, great differences in productivity in a terrestrial environment are likely to result in a sufficiently altered vegetational profile to cause a change in species rather than the occupation of a broad gradient by one species (L. L. Wolf, personal communication). In marshes, however, productivity differences are not necessarily associated with vegetation structure, and striking changes in vegetational features regularly occur within the span of a few years (Weller and Spatcher 1965), so that opportunities for evolving species that occupy only a small segment of the marsh vegetation pattern are more limited than in terrestrial environments.

The food supply for insectivorous birds in marshes is often rapidly renewed. Many of the breeding passerine birds of marshes exploit primarily the emerging individuals of insects with aquatic larval and terrestrial adult stages. These insects are vulnerable for only a few hours during their lives, and those not taken on the day they emerge are mostly unavailable on subsequent days. Therefore, the supply of food on a given day is not significantly affected by the number of insects removed from the system on previous days but rather upon those factors that regulate the size of the emergence on that particular day. In contrast, the supply of insects on the foliage of trees and shrubs may be seriously depleted by the foraging activities of birds, which lowers the expected reproductive success of later arriving individuals.

In a review of the mating systems of North American passerines, Verner and Willson (1966) demonstrated that, though marsh-nesting species constitute only a small fraction of the total species (about 5%), eight of the 15 polygynous species breed in marshes. Polygyny is also prevalent among the marsh-nesting weaverbirds (Ploceidae) in Africa (Crook 1963, 1964). Also, the only known nonpasserine species with altricial young that is regularly polygynous is the bittern (*Botaurus stellaris*), a marsh-nesting species (Gaukler and Kraus 1965).

5. *Polygyny should be more prevalent among species inhabiting early successional habitats.* Like marshes, early successional terrestrial vegetation changes rapidly, thus discouraging the evolution of species adapted specifically to minor variants of it. In addition, there are reasons for suspecting that variations in food supply in early successional sites might be considerable. Early successional plants are characterized by rapid growth and the apportionment of large amounts of energy to reproduction. They probably also devote less energy, on the average, to antiherbivore devices than plants of later successional stages. Accordingly, they should be vulnerable to insect attack when found, and may owe their success in part to the fact that many patches escape detection. If this is true, patches of early

successional vegetation should consist of some not yet found by insects, therefore containing relatively little food, and others supporting large populations of grazing insects. Five of the 15 regularly polygynous species of North American passerines breed in prairie or savannah habitats (Verner and Willson 1966; Zimmerman 1966), and some of them, notably the dickcissel (*Spiza americana*) and the bobolink (*Dolichonyx oryzivorus*) are restricted to the very early successional stages of grassland vegetation (Zimmerman 1966). Differential food supply and its possible correlation with the number of females per male in different patches of early successional vegetation has never been measured, but it should not be difficult to do so.

6. *Polygyny should be more prevalent among species in which feeding areas are widespread, but nesting sites are restricted.* If nest sites are restricted and a single male holds several of them, it should be advantageous for females to mate with such males even if they are already mated, particularly if the alternative is accepting an inferior site or no site at all. Two of the polygynous passerines of North America, the house wren (*Troglodytes aedon*) and the winter wren (*T. troglodytes*), nest in cavities but are unable to excavate their own, and the same is true of the polygynous pied flycatcher (*Muscicapa hypoleuca*) of Europe (Curio 1959; von Haartman 1954). This may also be the explanation of the prevalence of polygyny among savannah species of weaverbirds in Africa and Asia (Crook 1962, 1963, 1964), since these are species that feed in grassland but require trees for their nests.

7. *Polygyny and promiscuity should be more prevalent among species in which clutch size is strongly influenced by factors other than the number of offspring that can be supported by the parents.* Clutches smaller than the number of young the parents can feed successfully might occur in species in which the adults feed primarily on low-energy food sources such as pulpy fruits and nectar which, though sufficient for maintenance energy, are not good for egg production. This supposition is supported by the fact that hummingbirds, unlike most avian species, lay no more than two eggs in all geographical areas and do not show the latitudinal gradient in clutch size characteristic of most birds. In addition, high predation rates may select against high feeding rates in tropical environments, reducing clutches below what the parents could feed (Skutch 1949). Finally, in stable environments competitive ability may demand considerable time expenditure (Cody 1966), so that foraging time is reduced and males may spend all or most of their time at these activities. If any of these factors are operating, the contribution of the male to reproductive success by means of food delivery to the nestlings would be decreased, and conditions favorable for polygyny would be created.

This prediction cannot be tested directly at present, but it is noteworthy, as pointed out by Snow (1963), that polygyny or promiscuity associated with lek displays in the tropics occur only among fruit- and nectar-eating birds such as hummingbirds, manakins (Snow 1962a, 1962b), cotingas

(Snow 1961; Gilliard 1962), birds of paradise (Iredale 1950) and bowerbirds (Marshall 1954; Gilliard 1959*a*, 1959*b*), and not among insectivorous species, including insectivorous species in the same families, all of which are apparently monogamous. Only one of the lek species has been studied in detail (Snow 1962*a*, 1962*b*), and it was shown that fruits supporting the adults could not have been in short supply during the breeding season, but the effects of this kind of food source on egg production and nature of the food delivered to the young are completely unknown. There is evidence from the bowerbirds that frugivorous species feed their young on insects (Marshall 1954). Conversely, obligatory fruit eaters, such as parrots, have extremely long nestling periods, suggesting that rapid nestling growth and a fruit diet are mutually incompatible.

#### CONSEQUENCES OF THE EVOLUTION OF POLYGYNY

If polygynous mating systems evolve from monogamous ones as a result of the existence of choice situations in which it is advantageous for females to select mates already having at least one mate, the very existence of this choice system creates other selective forces that further influence the mating pattern and the morphology of the sexes.

First, in polygynous birds, there should be very keen competition among males for the better-quality territories, because possession of a high-quality territory is likely to result in the attraction of more than one female. The increased intermale competition for good areas should lead to stronger selection for secondary sexual characteristics useful in these contests. The existence of these characteristics, as indicated earlier, is well known among mammals, and Selander (1958) has demonstrated a strong correlation between the amount of sexual dimorphism in size and the degree of polygyny and promiscuity in mating pattern among American blackbirds (Icteridae). Great dimorphism in size is also characteristic of the polygynous marsh-nesting weaverbirds in Africa, the males even showing remarkable convergence toward the plumage patterns shown by males of polygynous species of icterids.

Nevertheless, unless the species are continually evolving to become more highly dimorphic, there must be counterselection against the more dimorphic individuals that stabilizes the degree of dimorphism at its present value. There are two obvious candidates for this counterselection. The first is predation, since the males are rendered exceedingly conspicuous by both their appearance and their behavior patterns. The second derives from the adverse ecological effects of larger size. In polygynous species, females are presumably not normally under selection for size other than that dictated by their basic ecological relationships with their environment (Amadon 1959). The greater the degree to which males depart from the presumably optimal size of the females, the more poorly adapted they should be for general existence, unless by their increased size they are able to exploit food resources not available to the smaller females. To date the only dem-

onstratation of a higher mortality rate during the nonbreeding season for males of a highly dimorphic species is that of Selander (1965) for the great-tailed grackle in south-central Texas. Sexing birds returning to communal roosts by examination of greatly enlarged photographs, Selander was able to show that males died at about twice the rate of the females during the winter. He also observed that the large tails of the males interfered with flying in strong winds, and that extremely strong winds completely prevented males from flying, while females were still able to navigate, though with difficulty.

Contrary to the theory of Wynne-Edwards, the model developed here predicts delayed maturation on the part of the males but not of females. Unless females are capable of preventing other females from settling in the area, all females should be able to obtain mates and reproduce. In fact, it should be extremely difficult for females to exclude other females from the territory of their mate. During the nest-building and egg-laying periods, defense of the area is easy; but once incubation has begun, eviction of a persistent intruder can only be accomplished at the expense of chilling and possible loss of the clutch of eggs. It is highly unlikely that the adverse effects of the second female could be so great as to select for such behavior. Moreover, by the time the first female is already incubating, the potential period of overlap in time when young are being fed is already minimized.

On the other hand, the strong competition among males for suitable territories and the failure of males with poor territories to obtain mates at all should produce a floating population of nonbreeding males. Such floating populations are known to be characteristic of a number of polygynous species of birds. Assuming that older and more experienced birds will be at an advantage in competition for territories, the chances of success for younger birds should be very low. If attempts to obtain territories result in higher mortality rates of the young birds and probability of success is sufficiently low, individuals making vigorous attempts might be selected against and delayed maturation would result. Selander (1965) gives a more detailed development of this argument. In the red-winged blackbird, first-year males do not acquire the full adult plumage, their testes develop later in the spring and do not reach the size characteristic of older males (Wright and Wright 1944), and they usually do not breed, though they may do so if the supply of adult males is reduced in some manner (Orians, unpublished field data).

#### SUMMARY

Predictions from a theory assuming mate selection on the part of females, which maximizes reproductive success of individuals, are found to accord closely, though not completely, with known mating patterns. These predictions are that (1) polyandry should be rare, (2) polygyny should be more common among mammals than among birds, (3) polygyny should be more prevalent among precocial than among altricial birds, (4) conditions

for polygyny should be met in marshes more regularly than among terrestrial environments, (5) polygyny should be more prevalent among species of early successional habitats, (6) polygyny should be more prevalent among species in which feeding areas are widespread but nesting sites are restricted, and (7) polygyny should evolve more readily among species in which clutch size is strongly influenced by factors other than the ability of the adults to provide food for the young. Most cases of polygyny in birds, a group in which monogamy is the most common mating pattern, can be explained on the basis of the model, and those cases not apparently fitting into the predictions are clearly indicated. Thus, there is no need at present to invoke more complicated and restrictive mechanisms to explain the mating patterns known to exist.

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