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Ecology, Sexual Selection, and the Evolution of Mating Systems

Stephen T. Emlen and Lewis W. Oring

Mating systems (1) were first discussed in evolutionary terms by Darwin (2). Since then, major developments in genetic theory have allowed a better understanding of sex ratios, sexual dimorphism, and differential patterns of parental care (3-7). Important milestones toward an ecological understanding of mating systems have also been reached (8-16). Nevertheless, attempts at synthesizing natural history data into a unified theory of mating system evolution have lagged behind the development of population genetics theory.

One factor hindering development of a sociobiological framework of mating system theory has been a recurring tendency for field workers to search for and to discuss "adaptiveness" in the context of the survival or well-being of the population or species. To understand mating systems, we must abandon species- or group-selection viewpoints and return to the evolutionary tenet of natural selection operating at the level of the individual genome (17).

Fitness, in genetic theory, measures the reproductive success of an individual (or a genotype) measured relative to the reproductive success of other individuals (or genotypes) in the same or in other populations. Thus, we should expect a strong competitive element in many aspects of reproductive behavior. Darwin was fully aware of this intraspecific competition when he introduced the theory of sexual selection (2). Stated simply, when one sex becomes a limiting factor for the other, the result is an increase in intrasexual competition among members of the available sex for access to mates

of the limiting sex. The greater the "shortage" of one sex, the more intense the sexual selection. Sexual selection is relatively slight in monogamous groups while it is intense in highly polygamous societies. A better understanding of the causes of sexual selection is thus pivotal to the development of any mating system theory.

What accounts for the differing intensities of sexual selection found in different species and, frequently, between populations of the same species? We hypothesize that one important cause is the *ability of a portion of the population to control the access of others to potential mates*. This control can be direct, as in the physical herding of potential mates, and the physical exclusion of other members of the same sex from these mates, or indirect, by controlling resources that are critical either for mate attraction or for successful reproduction. The greater the degree of control or monopolization, the greater the resulting variance in mating success. As the difference in reproduction success of "haves" and "have nots" increases, so too does intrasexual competition to be in the former category. It becomes crucial to understand the manner in which access to mates can be controlled.

One of the emerging findings of sociobiology is that many aspects of an animal's social organization can be predicted on the basis of an understanding of a limited set of environmental variables. We propose that certain environmental factors determine the degree to which mates can be defended or monopolized. In effect, *ecological constraints impose*

limits on the degree to which sexual selection can operate. The greater the potential for multiple mate monopolization, the greater should be the potential intensity of sexual selection and the tendency for polygamy.

In this article, we discuss various ecological factors that influence the degree and form of polygamous mating systems. Our intention is to develop a theory adequate for predicting environmental influences on the evolution and expression of avian mating systems. We believe these predictions are also broadly applicable to many mammalian groups, as well as to certain insects and lower vertebrates. They are less applicable to strongly "r"-selected species (18), or for species that normally live in permanent groups with restricted membership where the potential for reciprocal interactions is high (19).

Economic Monopolizability and the Environmental Potential for Polygamy

There are two preconditions for the evolution of polygamy (see Fig. 1). First, multiple mates, or resources sufficient to attract multiple mates, must be energetically defendable by individuals. Many environmental factors affect the potential for such control. But primary among these are the spatial and temporal patterns of resource dispersion. The potential for controlling access to multiple mates should be viewed in a cost-benefit context. Stated simply, the prerequisite for a monogamous mating system is the economic defendability of a mate. The prerequisite for a polygamous mating system is the economic monopolizability of several mates. The *environmental potential for polygamy* depends on the degree to which multiple mates, or resources critical to gaining multiple mates, are economically defendable.

A second prerequisite is the ability of the animals to utilize this potential. Critical resources might be distributed such

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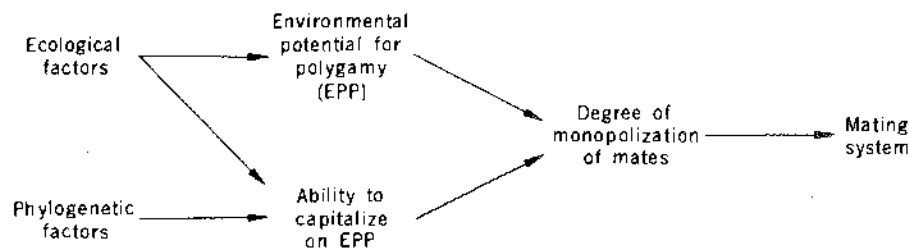


Fig. 1. A general schema of the determinants of a mating system.

that they are economically defensible for an individual that expends most of its time budget on such defense, but not for one that devotes considerable time to alternative activities. The degree to which an animal can take advantage of the "polygamy potential" of the environment depends in large part on the degree of parental care required for successful rearing of young.

Recent attempts at synthesizing the literature on mating systems have focused on this latter point. Polygamy is more prevalent in species where one sex is freed from parental care duties. Members of this sex can expend increased time and energy on intrasexual competition for resources and mates. Several predictions logically follow and have been stressed by others: polygamy should be more common among animals where (i) one sex is predisposed to assume most of the parental care (for example, mammals); (ii) parental care requirements are minimal (for example, birds with precocial as compared with altricial young); and (iii) a superabundant food resource enables a single parent to provide full parental care (7, 11-13). Emancipation by itself, however, need not lead to the evolution of polygamy. It merely assures that one sex can fully exploit the potential for mate monopolization inherent in the environment (see discussion on resource defense polygyny, below).

The spatial distribution of resources. Brown introduced the concept of economic defendability to the study of animal spacing patterns (20). We extend his approach to encompass mating systems.

When important resources are distributed uniformly in space, there is little opportunity for resource monopolization. If the resources are sufficiently abundant and stable through time, territoriality typically occurs. Members of the breeding population would tend toward even dispersion and the potential for multiple matings would be low. Sexual selection would be minimal, and the fitness of individuals might be maximized by sharing equally in parental care duties (see monogamy).

As critical resources become unevenly distributed in nature, the potential for obtaining additional mates increases. This is because some individuals may be able to control a larger quantity or better quality of resource than other individuals. To the degree that this influences mate choice, polygamous matings may be expected (Fig. 2, horizontal axis).

When important resources are highly clumped, the possibility arises for a small percentage of the population to monopolize a large proportion of the available resources. Sexual selection and variance in reproductive success should be high, and we speak of the environment as having a high polygamy potential (EPP).

The temporal distribution of mates. In our model, the benefits derived from resource defense lie in an increased probability of mate attraction and acquisition. The magnitude of this benefit is strongly influenced by the temporal pattern of availability of sexually receptive partners.

If females in a population become sexually receptive in unison, there is little potential for individual males to monopolize multiple females. This will be especially true if each female is sexually active for only a brief period. By the time

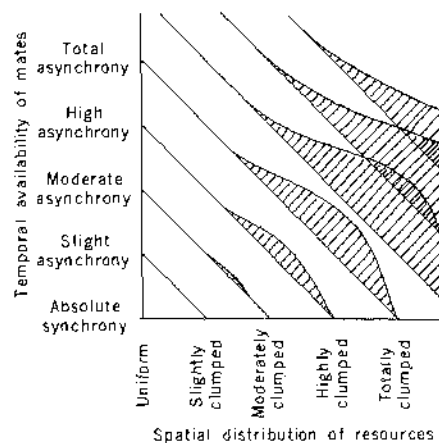


Fig. 2. Graphic representation of the environmental potential for polygamy (indicated by the perpendicular height of the shaded area) and its relation to the spatial distribution of resources and temporal availability of receptive mates.

the sexes have located one another, and normal courtship and mating have taken place, most of the remaining available females have already been inseminated and few new partners are available. As long as the time involved in servicing a single sexual partner constitutes a significant portion of the total time that potential mates are available, trends toward polygamy will be minimal.

With increasing degrees of asynchrony among members of one sex, the potential for individuals of the other sex to accumulate multiple mates increases. Among species in which both sexes contribute to parental care, a moderate degree of asynchrony is essential for the expression of polygamy. In species where one sex is largely freed from parental duties, individuals of this sex should remain sexually active for the duration of the period during which members of the other sex become sexually receptive. The intensity of sexual selection then will be determined by the degree to which critical resources are differentially controlled by members of the limited sex, by the availability of members of the limiting sex (21), and by the process of mate selection.

As the degree of asynchrony becomes extreme, the rate of appearance of new potential mates reaches a point at which the cost of continued resource defense necessary for attracting an additional mate exceeds the additional benefits gained. Continued mate accumulation would no longer be energetically practical and tendencies toward polygamy will decrease (see Fig. 2, vertical axis).

The concept of operational sex ratios. To understand the intensity of sexual selection it is not the overall population ratio of males to females that is of importance but rather what we term the operational sex ratio (OSR)—defined as the average ratio of fertilizable females to sexually active males at any given time (22). This ratio is strongly affected by the degree of spatial and temporal clumping of the limiting sex. For example, continuous long periods of sexual activity by males, coupled with brief and asynchronous periods of receptivity by females, will produce a strong skew in the OSR.

The OSR provides an empirical measure of the degree of monopolizability of mates. The greater the degree of imbalance in the OSR, the greater the expected variance in reproductive success among members of the limited sex and the greater the degree of polygamy. Where the OSR is skewed toward males, polygyny is expected; when the skew is toward females, polyandry should occur (23).

Types of Mating Systems

Attempts to categorize mating systems have been hampered by a lack of generally accepted terminology. Classically, mating systems have been defined according to the number of mates that one sex can accumulate. Sometimes this is modified to separate simultaneous from sequential multiple mate acquisition. Selander (14) has proposed a new classification based, in part, on the duration of the pair bond or mate association. The difficulty with these classification schemes is that they leave functionally or causatively unrelated situations (or both) in the same category. They ignore the importance of environmental pressures on parental care and sexual selection, and the influence of these factors on mating system evolution. In this article we have characterized mating systems on the basis of the ecological and behavioral potential to monopolize mates, and by the means through which such monopolization takes place. Where male and female strategies conflict, we use terms appropriate for the sex that controls the resource base or monopolizes multiple mates (or both) (see Table 1).

Monogamy

Neither sex has the opportunity to monopolize additional members of the opposite sex, directly or through resource control. Multiple breedings per season may occur in sequence.

Monogamy is expected to occur when (i) there is no environmental "polygamy potential," or (ii) there is no opportunity to take advantage of what "polygamy potential" the environment affords. Monogamy is the dominant avian mating system, occurring in more than 90 percent of the species studied (24), but it is believed rare among mammals (25).

The prevalence of monogamy among birds is due primarily to the inability of most species to take advantage of any environmental "polygamy potential." Considerable parental care by both parents often is required for successful rearing of young. Thus, losses to an individual parent accrued by withholding care from one set of offspring while courting and mating with additional mates may be greater than the gains resulting from such behavior.

In mammals, the preponderance of female parental care allows males of most species to exploit whatever "polygamy potential" exists. Nevertheless, monogamy may be more common than is usually supposed, especially in populations

Table 1. An ecological classification of mating systems.

<i>Monogamy</i> : Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care.
<i>Polygyny</i> : Individual males frequently control or gain access to multiple females.
<i>Resource defense polygyny</i> : Males control access to females <i>indirectly</i> , by monopolizing critical resources.
<i>Female (or harem) defense polygyny</i> : Males control access to females <i>directly</i> , usually by virtue of female gregariousness.
<i>Male dominance polygyny</i> : Males or critical resources are <i>not economically monopolizable</i> . Males aggregate during the breeding season and <i>females select mates</i> from these aggregations.
<i>Explosive breeding assemblages</i> : Both sexes converge for a short-lived, highly synchronized mating period. The operational sex ratio is close to unity and sexual selection is minimal.
<i>Leks</i> : Females are less synchronized and males remain sexually active for the duration of the females' breeding period. Males compete directly for dominant status or position within stable assemblages. Variance in reproductive success and skew in operational sex ratio reach extremes.
<i>Rapid multiple clutch polygamy</i> : Both sexes have substantial but relatively <i>equal</i> opportunity for increasing fitness through multiple breedings in rapid succession. Males and females each incubate separate clutches of eggs.
<i>Polyandry</i> : Individual females frequently control or gain access to multiple males.
<i>Resource defense polyandry</i> : Females control access to males <i>indirectly</i> , by monopolizing critical resources.
<i>Female access polyandry</i> : Females do not defend resources essential to males but, through interactions among themselves, may limit access to males. Among phalaropes, both sexes converge repeatedly at ephemeral feeding areas where courtship and mating occur. The mating system most closely resembles an explosive breeding assemblage in which the OSR may become skewed with an excess of females.

where individuals are widely dispersed over relatively uniform environments (26). As was mentioned previously, male emancipation by itself should only lead to polygyny under permissive environmental conditions.

If the potential of, or the gain from, mate monopolization is nonexistent, an individual should benefit by remaining with its initial mate and acting in such a manner as to maximize the survival chances of its offspring. Recent studies of long-lived birds show a clear advantage to long-term mate fidelity (27). Birds breeding with former mates show low levels of aggression and a high degree of within-pair synchronization, allowing them to breed more rapidly and efficiently and leading to a demonstrable increase in reproductive success. The longer the period of mate fidelity, the more the future physical condition of a mate becomes of importance to its partner. It then becomes adaptive to equalize the energetic burden of reproduction and to share in parental care.

Forms of Polygyny

Polygyny occurs if environmental or behavioral conditions bring about the clumping of females, and males have the capacity to monopolize them. Types of polygyny are classified according to the means that males use to control females.

1) *Resource defense polygyny*. Males defend resources essential to females. To

the degree that males can monopolize these resources, they can monopolize females.

When important resources are unevenly distributed or spatially clumped, certain males can defend areas containing a larger quantity or better quality of resource than others. If these resources are critical for female reproduction, then competition among males should revolve around subdividing and defending these resources. Female choice of mate should be influenced both by the quality of the defending male and the resources under his control (territory quality). The extent of polygyny will tend to increase with increasing variance in territory quality among the males of the population.

Among bird species where both sexes provide at least some parental care for offspring, females stand to lose if their mates take on additional females. Polygynous matings will be advantageous to the female only if the benefits gained by genetic access to a high-quality male or to the resources controlled by him more than offset her compensatory costs for the decreased contribution of the male in parental care. As stressed by Verner, Willson, and Orians, polygyny is expected when the distribution of resources is sufficiently irregular that a female mating with an already paired male on a superior-quality territory will have equal or better reproductive success than if she mated with an unpaired male occupying a poorer quality territory (8, 12, 13).

Studies on mating systems of North American passerines support these views. Resource defense polygyny is most prevalent in habitats with uneven resource distribution that results in a mosaic of male territories of different qualities (12, 28). Demographic studies further show that females forming polygynous pair bonds realize a reproductive success as great or greater than monogamous females (29-31). The specific resource attributes that comprise "territory quality" are expected to vary between species. Similarly, the extent of difference between territories that is sufficient to favor polygyny [the "polygyny threshold" of Orians (13)] will vary with such factors as the distribution of male parental care among his various mates, the total amount of parental care required by the young (for example, precocial versus altricial young), and the degree of dependency on the territory itself (for example, whether just for nesting or also for feeding).

Under certain environmental situations, the cost to the male of resource control or mate accumulation might be relatively low, while the potential benefit is extremely high. The cumulative advantage of multiple matings to the male could far outweigh the decreased reproductive success of individual females. In such conflict situations, females could be forced into assuming a larger fraction of the total parental care, even if it necessitated such long-term adaptations as reduced brood size or decreased growth rates of young. We suggest that some cases of male emancipation might best be viewed as an evolutionary result of a high environmental potential for polygamy rather than as an independently derived precursor to the evolution of polygamy.

Many passerine species believed to be monogamous show disparate parental investment by the male and female. (The female alone incubates the eggs while both sexes bring food for the nestlings.) Many of these species are sexually dimorphic, the male assuming a conspicuous breeding plumage while the female remains cryptically colored. The decreased male involvement in parental care preadapts such species to respond to slight changes in the environmental potential for polygamy by enabling them to become opportunistically or facultatively polygynous (31). We expect that many additional cases of such facultative polygyny will be discovered when individually marked populations are studied in areas where the feeding or nesting resources are limited or highly localized in space.

When male parental investment is minimal or nonexistent, a limited and clumped resource distribution can lead to extreme development of polygyny. In the orange-rumped honeyguide (*Indicator xanthonotus*), beeswax forms an essential part of the diet. Males do not provide defense of the nest site or food for the young, but they do maintain year-around territories at the locations of bee nests. These bee nests are found only on exposed cliffs; they are in short supply and a small proportion of the male population is able to control access to this resource. When females become sexually active, they enter the male territories and feed on the wax of the bee comb. Courtship is centered at the locations of bees' nests and copulation success is high for territory owners. One male was observed to copulate 46 times with at least 18 different females while nonterritorial males had minimal, if any, copulatory success. This species exemplifies an extreme degree of polygyny, based primarily on the ability of a small number of males to monopolize access to a critical resource (32).

Analogous, but less extreme, examples of resource defense polygyny have been reported for fiery-throated (*Pantherpe insignis*) and Anna hummingbirds (*Calypte anna*) (33, 34). Many aspects of hummingbird biology are closely linked to their habit of nectar feeding. When suitable flowers are sufficiently clumped and nectar production is high, territorial defense becomes economically feasible (34-36). Females incubate and rear the young alone, but they require a reliable nectar source to do so. In several species males allow females nesting within their territory to feed therein, but aggressively exclude all other hummingbirds (34, 35). The extent of polygyny presumably is determined by the distribution pattern of nectar-producing flowers which leads to differences in territory quality among males.

The yellow-bellied marmot (*Marmota flaviventris*) provides a mammalian example of resource defense polygyny. Overwintering sites constitute a monopolizable resource. Studies by Armitage and Downhower (37) suggest that areas of rock outcroppings provide the most suitable underground retreats for predator escape and for hibernation. Such sites are limited in number and are vigorously defended by males. High-quality locations are occupied by a colony including one or (rarely) a few dominant males, a variable number of mature females, plus young and juveniles. These units have been called "harems," but we feel they are better understood in the

context of resource defense polygyny. Male marmots achieve high reproductive success not by forcibly accumulating a harem of females but rather by economically monopolizing a resource that leads to female clumping.

2) *Female (or harem) defense polygyny.* Females are gregarious for reasons unrelated to reproduction. Their self-clumping tendencies facilitate direct monopolization by males.

If females themselves are defendable, we might expect males to forcibly accumulate females and to herd or maintain them under their jurisdiction by aggressively excluding all other males from the area. Such harem formation or "female defense polygyny" does occur, but usually in conjunction with male resource defense.

In many ungulates, females and young aggregate into small herds for part or all of the year. During times of parturition and sexual receptivity, these groups move into areas of preferred habitat (generally affording increased cover or abundant food, or both). Among the African impala (*Aepyceros melampus*) and waterbuck (*Kobus defassa*), for example, males at this time of year divide the habitat into defended territories. "The frequency with which a male has females in his territory is related to the amount of preferred habitat for that season that his territory contains. This may mean that a restricted number of territories may attract all the females for the duration of a limited mating season, and holders of those territories alone will contribute to breeding. In such circumstances it may be found that the marginal territories are held by young or old, rather than prime males" (38).

The reasons for female clumping may be totally unrelated to reproduction. Ungulates gain through increased predator detection and avoidance; other groups might gain through information exchange about locations of unpredictable food resources, increased foraging efficiency by observational learning, or cultural transmission of learned habits. But one result of the clumping is to increase the male potential for differential access and control of multiple mates.

Among many pinnipeds, females are sexually active shortly after giving birth (39). Females "haul out" onto land or ice to give birth, and the combination of female gregariousness, a shortage of suitable parturition locations, and a tendency to return annually to traditional areas gives rise to dense aggregations of sexually active females. By monopolizing access to these sites, dominant males are able to realize phenomenal

numbers of copulations. Competition among males is extremely intense and the resulting sexual selection presumably has led to the marked sexual dimorphism and intensity of aggressive behavior found in these species (10, 40).

The result of female clumping in pinnipeds may result in mates being directly defended as a resource (for example, in elephant seals) or may greatly increase the benefits derived from resource (site) defense (in many otariids such as the fur seals). In either case it leads to intensified sexual selection and increased imbalances in the reproductive success of different males in the population.

Female defense polygyny is rare among birds, being known for certain only in the greater rhea, a few tinamous, and several pheasants. The rhea provides one of the best known examples, but since males incubate and females sometimes mate with several males in succession, this system is described in the section on female selection and the evolution of polyandry.

In a number of pheasants and possibly in peafowl and chachalacas, female self-clumping occurs in combination with male resource defense. Female ring-necked pheasants (*Phasianus colchicus*) form groups that are attracted to certain male territories during the breeding season. Males directly defend female groups, and limited evidence suggests that larger harems and harems comprised of experienced females associate preferentially with males on prime territories (41). Membership in female groups is variable, and new individuals join throughout the summer. The result is a staggering of female breeding readiness (that is, asynchrony) enabling a single male to inseminate all sexually receptive members of the female group.

3) *Male dominance polygyny.* Males do not directly defend females or resources essential to females, but rather sort out among themselves their relative positions of dominance. Females choose males primarily on the basis of male status.

Communal displaying is frequent among species in which the male is totally emancipated from parental care and the environment provides little potential for resource or mate control. This is expected (i) when critical resources are superabundant but widely dispersed, or (ii) when they are sufficiently unpredictable in space and time as to be economically undefendable. It is also expected (iii) when resources or mates are clumped in a defensible pattern but the cost of successful defense is too high. High population density (increasing the number of

competitors) and increased intensity of competition (resulting from extreme limitation of resources or from strong skew in the OSR) can lead to situations where successful defense is energetically unfeasible. Cases where territorial defense is abandoned as the cost of defense increases have been documented in a variety of taxa (34, 36, 42). When access to females cannot be controlled through resource defense, male competition may take the form of direct male-male encounters, resulting in differential dominance relationships between the male members of the population.

Under what conditions should individual males aggregate and display communally? Such aggregations provide a forum for male-male competition and should increase the variance in reproductive performance among males. The copulation success of a high-ranking male would be increased by joining such a group; that of a low-ranking individual might decrease. Why then should subordinate males enter communally displaying groups?

If female movements or concentration areas are predictable, encounter rates would be high for males that position themselves in these areas, leading to localized concentrations of males. As males start to aggregate, their advertising and courtship signals become pooled, creating an enhanced stimulus situation that attracts females preferentially to larger aggregations (22, 43, 44). If isolated males have minimal chances of successfully attracting males, low-ranking males will be expected to adopt alternative, cryptic, or satellite strategies for obtaining females within the communal display areas rather than avoiding male aggregations altogether (45).

Females also benefit by male clumping since they can better compare a large number of potential mates in a minimum period of time. By relying on the male-male interactions to have done a preliminary sorting for them, females can preferentially select from a predetermined group of "tested" and "proven" males.

Other advantages have been suggested for male display aggregations. These include increased alertness and defense against potential predators as well as pooling of information about locations of patchy or ephemeral food resources (24, 46, 47). We believe that these are secondary advantages, accruing after the development of group displaying and being of greatest importance in species that remain sexually active and aggregated for long periods of time.

The form of male dominance polygyny will depend on the degree of synchrony

of sexual activity among females of the population. Where females are highly synchronized and converge at the male aggregation within a short period of time, a highly promiscuous, "explosive" breeding situation will occur. This is typical of many singing insects and chorusing amphibians (16, 48). As was discussed previously, the synchrony of the females restricts the potential for individual males to monopolize matings. Breeding activity is frenzied, but the operational sex ratio should not be highly skewed and sexual selection should not be intense (49).

If the females of a population are relatively asynchronous in their periods of sexual receptivity (50), the operational sex ratio becomes increasingly skewed and sexual selection intensifies. Males generally remain active for the duration of the population's breeding season. The intensity of male-male competition, together with the longer duration of the mating period, result in the establishment of stable dominance or position effects among the advertising males. The result is an organized aggregation usually referred to as a *lek*.

A lek is defined as a communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating (51). Males jockey for a status or position that conveys maximal attractiveness to females. Frequently, central positions are occupied by older, more dominant, males that achieve a disproportionate share of female copulations (22, 44, 46, 47, 52, 53). Females visit the lek when sexually receptive and "sample" numerous males before selecting a mate. After copulation, the female leaves the display area and proceeds, on her own, to rear the young.

Lek mating systems have been described for several species of insects, mouth breeding fish, bullfrogs, a scattering of mammals and approximately 30 species of birds (54-56). We hypothesize that all cases will be typified by a fairly long breeding season, a heavily skewed operational sex ratio, and by the inability of individual males to economically control or monopolize the resources essential for female acquisition.

Male Incubation, Female Emancipation

Among most animals, female parental investment greatly exceeds that of males (3, 5-7). Consequently, most cases of polygamy involve male emancipation and the development of polygyny. However, a significant portion of avian spe-

cies share rather equally in parental care duties, including incubation of the eggs. And, in a very small percentage of species, males have assumed the full burden of incubation and brood rearing, emancipating the female and increasing the possibility of her mating repeatedly.

Males should assume the bulk of parental care only when their individual fitness is increased through such an action. This might occur in two general situations: (i) when the future physical condition of the female is of direct importance to the male (discussed under Monogamy), and (ii) when the lack of dependability of breeding conditions places a premium on female ability to produce additional or replacement clutches for the male. Lack of dependability can result either (i) from great fluctuations in environmental suitability for breeding or (ii) from very low success rates of reproductive attempts (caused, for example, by high predation rates).

From a female's viewpoint, the principal advantage of male incubation is a lessening of her metabolic burden, freeing her to devote increased time and energy to replenish nutrient and mineral reserves drained through egg production (57, 58).

From the male's point of view, female emancipation can be viewed as an insurance strategy—when the failure rate is sufficiently high, the cost involved in incubation may be less, on average, than the gain accrued by having a mate physiologically able to rapidly produce new clutches of eggs.

Complete male parental care is most likely to develop in groups with slight to moderate parental care needs (precocial young) and a phylogenetic history of shared incubation. It should also be more prevalent among determinate than indeterminate egg layers (59).

Rapid multiple clutch polygamy. Both sexes have substantial but relatively equal opportunity for increasing fitness through multiple breedings in rapid succession. Simultaneous brooding of two clutches usually occurs.

In some shorebirds and galliforms, the female may lay a first clutch that is incubated solely by the male, and a second clutch that she herself incubates. When conditions are good, the result is a doubling of reproductive potential with only a minimal increase in breeding time; when conditions are poor, the result is an increased ability to produce replacement clutches.

Species exemplifying such rapid multiple clutch polygamy include red-legged partridge (*Alectoris rufa*), sand-

erling (*Calidris alba*), mountain plover (*Charadrius montanus*), and Temminck's stint (*Calidris temminckii*) (58, 60, 61). All are ground-nesting birds whose precocial young suffer moderate to extremely high predation losses. The mountain plover inhabits marginal short-grass prairies and is further subjected to severe fluctuations in environmental suitability due to great variations in rainfall. The short arctic breeding season of the sanderling is characterized by great fluctuations in suitability for breeding. The California quail (*Lophortyx californicum*), which, at least occasionally, practices this mating system (62) also is subject both to severe fluctuations in environmental suitability and to extreme predation (63).

Rapid multiple clutch polygamy is probably more common than is currently known, especially among shorebirds. It may also prove to be common among small phasianids, where males of a number of species are known to sometimes incubate or brood young (or both) without female help (64).

Advantages of male incubation to males are maximized (i) when females preferentially return to their original mates to lay a subsequent clutch of eggs, and (ii) when males remain sexually active for as long as possible during or before the initiation of incubation.

Preferential treatment by females for their original mates has been investigated in red-legged partridge, mountain plover, and Temminck's stint [see also (77)]. In the former two species, females lay second clutches in the territories of their original mate and copulate with him providing he is sexually active. In Temminck's stint, on the other hand, mate fidelity between first and second clutch is reported from one locality (U.S.S.R.) but not from another (Finland) (58, 65).

Males exhibiting rapid multiple clutch polygamy continue to actively court additional females for a period following the completion of the first clutch. Such behavior is rarely reported among species that share incubation. In the mountain plover, this is accomplished by maintaining sexual activity during part of incubation, while in the Temminck's stint, sanderling, and red-legged partridge, males frequently delay incubation, leaving the first clutch untended for as long as 6 to 12 days while continuing to court additional females.

As a result of this behavior, rapid multiple clutch polygamy can lead to a doubling of reproductive potential without producing a strong skew in the operational sex ratio.

Female Sexual Selection and the Evolution of Polyandry

Male incubation preadapts a species for possible evolution toward polyandry. Emancipation allows the female opportunity to increase her fitness through continued production of multiple clutches. Female fitness can be increased only to the degree that males are sexually receptive and available to assume incubation of these additional clutches.

Since an individual male is not able to maintain sexual activity indefinitely during incubation, males sitting on eggs normally must be considered sexually "unavailable." To the degree that females can produce more clutches than can be serviced by males (caused either by high production rates of females or low failure rates of existent clutches), the operational sex ratio will become skewed with a shortage of males. These conditions lead to increased intrasexual competition among females for access to available males. The degree to which polyandry will develop then depends on the intensity of female sexual selection and the environmental potential for monopolization of mates (in this case female monopolization of males).

True polyandry is extremely rare among birds, being found in less than 1 percent of the species studied to date (24, 66). Most documented cases are restricted to the avian orders Gruiformes and Charadriiformes. Comprehensive studies involving individually marked, wild birds have been conducted on only three species, the spotted sandpiper (*Actitis macularia*), the American jacana (*Jacana spinosa*), and the northern phalarope (*Phalaropus lobatus*). The mating systems of the first two are considered resource defense polyandry, while the latter represents an explosive type of female access polyandry. There are no documented examples of female dominance polyandry with stable organization analogous to that typical of leks.

1) **Resource defense polyandry.** Females compete for and defend resources essential to males. To the degree that these resources are clumped and monopolizable, females can monopolize multiple males.

In the spotted sandpiper, males often perform all incubation and brood care. Incubation begins during egg laying, and by the time of clutch completion males are sexually disinterested. Predation losses are extremely high (67, 68), and the ability of females to rapidly lay replacement clutches is impressive (69).

Spotted sandpipers breed throughout

the mid- and lower latitudes of North America. Under favorable conditions, the long breeding season, coupled with a high egg-producing ability, results in the female reproductive output exceeding the availability of males to assume incubation responsibilities. Because of male incubation, the operational sex ratio is skewed in favor of females, competition exists for available mates, and female sexual selection is moderately strong.

The extent of polyandry seems to be determined, in part, by the "availability" of males and by the quality and the spatial dispersion pattern of essential resources. In one population in Minnesota, male density was low and breeding females on average mated with 1.17 males. In contrast, in dense populations in Minnesota and New York, where birds were concentrated on patches of high-quality habitat, successful females averaged 2.4 mates (67, 70). High nest predation and asynchronous patterns of arrival of males both influenced the incidence of polyandry through their effect on increasing the "availability" of males to accept additional clutches of eggs (71).

The American jacana exhibits the most extreme polyandry known. In parts of Costa Rica their breeding habitat is severely limited, and only a small fraction of either the male or female population is believed to breed in any one year. The few suitable ponds or lagoons are subdivided into small territories by males. Females control "super-territories," often encompassing the nesting areas of several males. Females frequently have multiple mates incubating clutches simultaneously. Predation of nests is high, and females readily provide replacement clutches for their males, who perform most parental care duties (66, 72).

As the degree of female sexual selection increases, so too does behavioral and size dimorphism. In spotted sandpipers the female is 25 percent larger than the male, both sexes defend territories although the female is dominant, and the female frequently shares incubation with her last mate of the year. In the jacana, breeding females weigh 50 to 75 percent more than males, are totally dominant over males in aggressive interactions, and provide minimal parental care for eggs or young. In essence, female jacanas are specialists in egg production.

2) *Male defense or "harem" polyandry?* Several species of tinamous as well as the greater rhea exhibit unique mating systems that have been termed harem polyandry. On the basis of under-

lying resource control, we interpret these cases not as polyandry but rather as specialized cases of polygyny coupled with male incubation.

Tinamous are primitive, ground-nesting birds that inhabit the neotropics. Most defend all-purpose territories from which they advertise vocally. Females of some species are loosely gregarious and travel between male territories. Males may have pair bonds simultaneously with several females who lay a communal clutch of eggs. Males then perform all incubation and care for the precocial young without female help. Competition for females appears to exist and indirect evidence suggests a considerable differential in reproductive success of neighboring males (73-76).

Male tinamous recoup the cost of incubation in three ways. (i) Females freed from parental duties are better able to provide replacement clutches when predation does occur (73, 77). (ii) If several females lay communally, the male obtains a compound clutch rapidly, thereby minimizing the times during which eggs are unattended and, hence, exposed to extreme predation pressure. (iii) A male can inseminate many females and increase his reproductive success if he is able to attract groups of synchronized females. Variance in clutch size is large among tinamous, and individual male *Tinamus* and *Rhynchotus* have been seen incubating as many as 12 eggs (76, 78).

Once incubation has begun, a male ceases calling and becomes sexually unavailable. Females maximize their fitness by continuing to produce additional eggs, but they now must seek out additional males that are sexually active and able to accept a new clutch. Because of the long, tropical breeding season, females are frequently able to breed with a number of males in sequence. The wandering of females between neighboring males can be viewed as a strategy that is maximally advantageous to both sexes.

Female gregariousness is highly pronounced in the greater rhea (79). At the onset of the breeding season, older males compete for possession of a self-clumping group of females. Males defend no resources other than females and nest sites. Subordinate males are physically driven from the vicinity of females. In this way, a dominant male gains access to or monopolizes a group of females that then communally lay a clutch of eggs. The male assumes full incubation. The emancipated females continue to produce eggs and move on, laying a communal clutch for a second, third, or even

fourth male. Many aspects of this breeding situation, including the reasons underlying male incubation, are presumed to be basically similar to those in the tinamous.

There is little evidence for sexual selection among females in the tinamous and rhea. Females are subordinate to males and sexual dimorphism is slight. All of this suggests a specialized form of resource defense polygyny (tinamous) or mate-defense polygyny (rheas) rather than an ecologically based polyandry.

3) *Female access polyandry.* Females do not directly defend resources essential to males but, through interactions among themselves, may limit access to males. Females sometimes defend males. This defense is longer than the reciprocal defense noted in male dominance polygyny since a female must remain with a male until a clutch is completed and incubation begins.

Phalaropes are highly specialized shorebirds that breed at mid- and high latitudes. They feed on a relatively small variety of insects and aquatic invertebrates in or adjacent to wetlands. They utilize a narrow range of nest sites located near these feeding areas. Because of the extremely unpredictable and ephemeral nature of their food resource, courting areas shift from year to year and even from week to week. Males perform all parental care, but there is no opportunity for a stable resource defense.

In all three phalarope species, males and females congregate at bodies of water where they feed, display, and copulate. In our opinion, the mating system is most analogous to an explosive breeding assemblage with the difference that the females can be the limited, and males the limiting, sex. We predict that the operational sex ratio will become increasingly skewed and polyandry will occur when (i) males arrive asynchronously on the breeding grounds, (ii) the breeding season is sufficiently long to allow re-nesting attempts, and (iii) nesting failure is frequent, increasing the importance of such replacement nestings. Female competition then occurs, and polyandry has been reported (80). Pair bonds are brief, and females attempt to maximize fitness through repeated matings (81). At high population levels, female-female interactions become severe and some members of these ephemeral aggregations are prevented from breeding (82). To the degree that certain females can influence the access of others to males during the period of copulation and nest initiation, the mating system can be called female access polyandry (83).

Plasticity of Mating Systems

Throughout this article, we have stressed that ecological variables influence or constrain the intensity of sexual selection. This, in turn, profoundly influences the form of the resulting mating system. Certain individual strategies for resource or mate control are adaptive to one set of ecological conditions, but not necessarily to another. As stated by Emlen "... ecological parameters impose limits on the range of types of social organization that will be adaptive. With differences in the dispersion of a critical resource, the availability of mates, or other factors, optimal social strategies shift, resulting in a fine tuning of social organization to ecological constraints" (84).

If the productivity or the spatial or temporal distribution of a critical resource changes from year to year or from area to area, we should expect corresponding changes in the environmental potential for polygamy. Similarly, if the energetic cost of resource or mate monopolization changes as a result of changes in population density, length of breeding season, and the like, we should expect corresponding changes in the ability to take advantage of the environmental potential for polygamy.

Considerable lability in mating systems is thus expected between different populations of a given species in different environmental or density situations. The form of the plasticity, as well as the conditions under which it should occur, should in themselves be predictable on the basis of the ecological framework presented here.

Shifts from monogamy to facultative polygyny (resource defense polygyny) and shifts in degree of polygyny have been documented in a wide variety of avian species—invariably in accordance with ecological predictions (8, 30, 31, 85). Similar variability in the amount of polyandry and its dependence on male availability and degree of resource monopolization has already been mentioned among spotted sandpipers. Predictable shifts along the continuum of monogamy (with shared incubation)—rapid multiple clutch polygamy—resource defense polyandry have also been suggested in both sanderlings and spotted sandpipers (61, 67).

Several organisms, including dragonflies, bullfrogs, turkeys, puku, topi, and Uganda kob, are known to exhibit lekking behavior at high population densities, but shift to a resource defense polygyny or mate defense polygyny at low densities (53, 54, 86, 87). We hypoth-

esize that these shifts are due to the changing energetic costs of mate or resource defense associated with density-related changes in the intensity of intrasexual competition (87).

Until recently, many field biologists have worked under a preconception that species specificity was a characteristic not only of courtship behavior but of mating systems as well. We are now coming to realize that variability in social organization, including mating systems, is widespread. The ecological model presented in this article should provide a basis for generating testable predictions concerning the expected form of such mating system variability.

Summary

We have attempted to provide an ecological framework for understanding and predicting the forms of animal mating systems. The underlying assumption is that intrasexual interactions associated with mating are basically competitive. An individual member of the limited sex is expected to maximize its inclusive fitness by attempting to control access to mates of the limiting sex. The degree to which this is possible depends on the costs and benefits associated with such control. Certain environmental factors, particularly the spatial dispersion pattern of key resources and the temporal availability of receptive mates, are important determinants of these costs and benefits. The greater the potential for individuals to monopolize resources or mates, the greater the intensity of sexual selection and the greater the environmental potential for polygamy.

The precise form of the mating system will depend on which sex is limiting and on the manner and the degree to which the limited sex controls the resource base or monopolizes mates (or both).

An ecological categorization of mating systems is presented (Table 1) that allows a better understanding of the selective forces shaping one mating system over another. Within this ecological framework, specific examples are discussed ranging from the occurrence of leks to the evolution of polyandry.

References and Notes

1. The term "mating system" of a population refers to the general behavioral strategy employed in obtaining mates. It encompasses such features as: (i) the number of mates acquired, (ii) the manner of mate acquisition, (iii) the presence and characteristics of any pair bonds, and (iv) the patterns of parental care provided by each sex.
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17. We intend this to encompass the concept of inclusive fitness, as developed by W. D. Hamilton [*J. Theor. Biol.* 7, 1 (1964); *ibid.*, p. 17] and M. J. West-Eberhard [*Q. Rev. Biol.* 50, 1 (1975)], among others.
18. "r"-selected species generally tend to maximize quantity rather than quality of propagules. Parental care is relatively unimportant, if present at all. Hence the form of the mating system is less influenced by minor differences in resource control or mate assistance in the rearing of young.
19. The effects of competition or selfish behavior may not be fully expressed among long-lived animals that spend much of their lives in small, closed groups. This may be due to (i) the effects of kin selection, whereby selfish behavior might reduce the actor's inclusive fitness as a result of its negative effects on close relatives within the group, (ii) reciprocal interactions including reciprocal altruism, sensu R. L. Trivers [*Q. Rev. Biol.* 46, 35 (1971)], or (iii) the general advantages of group living being sufficiently great that selfish behavior is not carried to the point where it results in subordinate individuals leaving the group, sensu R. D. Alexander [*Ann. Rev. Ecol. Syst.* 4, 325 (1974)].
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21. In species where one sex provides the bulk of parental investment, this sex becomes temporarily "unavailable" for further reproductive attempts (for example, during incubation of eggs or lactation for young). This can cause a skew in the operational sex ratio that will lead to intensified competition for access to the few remaining partners of the limiting sex.
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49. To the extent that certain males limit the access of other males to females, some polygynous matings would occur. This situation could be called "male access polygyny" and would be analogous to the mating situation described for phalaropes under the section on female access polyandry.
50. Degree of asynchrony in a female population should be characterized relative to the time necessary for a male to attract, court, and service an individual female of the species in question—not in absolute units such as hours, days, or weeks. Asynchrony generally results from differences in the times at which individual females first become sexually active; but it may be augmented by high failure rates of early nests, causing females to return to the "sexually active" pool at later dates.
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