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THE EVOLUTION OF MATING SYSTEMS IN GROUSE

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The evolution of polygyny in birds has been clarified by recent theory based on female choice of mates (Verner 1964, Orians 1969), but the evolution of promiscuity has remained difficult to explain (Selander 1972). Wiley (1974) recently suggested that promiscuity evolved in grouse as a consequence of delayed maturation of males. This hypothesis reverses the usually accepted causal relationship between delayed breeding and polygamy. It also emphasizes the optimization of male rather than female reproductive tactics. Therefore, the intent of this paper is to examine Wiley's (1974) hypothesis and present an alternative based on the assumption that female choice determines the evolution of grouse mating systems.

Polygamy must normally be advantageous to both sexes before it can evolve. The only known exceptions occur when females cannot determine the true mated status of potential mates (Wittenberger 1976). According to sexual selection theory, polygamy should nearly always be advantageous to males because males can usually increase their fitness by copulating with as many females as possible (Bateman 1948). In contrast, females usually gain little advantage by copulating with more than one male per season because their reproductive output is limited by energetic constraints rather than ability to get eggs fertilized. In addition, females risk losing a much larger investment of time and energy than males when they accept a mate (Orians 1969). As a result, males generally compete among themselves for mates, while females generally select their mates from an array of competing males. According to this principle of female choice, factors affecting female success should normally determine the type of mating system that evolves (Orians 1969).

The Orians-Verner model follows directly from the female choice principle. It predicts that polygyny should evolve only when some females can be more successful as second mates of already mated males than as first mates of any remaining unmated males (Verner 1964, Orians 1969). This can occur whenever habitat differences between male territories or genetic differences between males are large enough to offset any costs incurred by females as a result of their choice to become second mates. Because females of promiscuous birds do not rely upon resources located on male territories while nesting or rearing young, the Orians-Verner model can suggest that promiscuity evolved only as a result of variation in male genetic quality. This hypothesis is plausible only if ecological differences between species make male genetic quality a larger component of female fitness in some species than in others.

The literature on mating systems is still confused by conflicting definitions of terms. In the following discussion, "polygyny" refers to the regular occurrence of males which are pair bonded to more than one female at a time (after Lack 1968). "Promiscuity" is characterized by the absence of prolonged pair bonds and the insemination of multiple females by at least some males in the population. This definition does not imply that mating occurs at random or that females necessarily copulate with more than one male per season. "Polygamy" is used here as a general term encompassing all nonmonogamous types of mating systems.

CRITIQUE OF THE SEXUAL BIMATURISM HYPOTHESIS

Wiley (1974) proposed that promiscuity evolved in grouse because natural selection favored sexual bimaturism (i.e., a sexual difference in the age when breeding is first attempted). According to Wiley, sexual bimaturism could skew the ratio of breeding males to breeding females toward an excess of females. This, in turn, would force at least some females to accept already mated males as mates. As a result, males would spend a greater proportion of their time seeking mates, and the species would become promiscuous. In the following discussion, Wiley's hypothesis will be referred to as the sexual bimaturism hypothesis.

An alternative hypothesis is that sexual bimaturism evolves as a response to competition among males for females after the species has become polygamous (Lack 1954, 1968; Selander 1965, 1972; Orians 1969). According to the sexual selection hypothesis, breeding is delayed in males because young males cannot compete effectively for mates with older, more experienced males. If the sexual selection hypothesis is correct, the sexual bimaturism hypothesis cannot explain promiscuity in grouse.

Delayed breeding is advantageous for males when their lifetime fitness is increased by postponing reproduction until an older age. This can occur when delayed breeding increases expected longevity sufficiently to compensate for the reproductive output lost by not breeding immediately. Sexual bimaturism evolves when this effect favors delayed breeding in males but not in females.

It is possible to calculate the threshold conditions determining whether a young male should attempt breeding at age $x = a - 1$ or defer breeding for one additional year (Wittenberger, in press). This derivation is based on the Euler-Lotka life table equation and assumes age-independent survival and reproductive rates following maturity. An approximation of the threshold for delayed breeding is given by

$$\frac{b_{a-1}}{b_a} < \frac{\Delta s}{1 - s_a}, \qquad (1)$$

where a = age at maturity, b_{a-1} = male reproductive rate at age $x = a - 1$, b_a = male reproductive rate at ages $x \geqslant a$, Δs = reduction in survival rate (i.e., risk) resulting from attempts to breed at age $x = a - 1$, and s_a = annual male survival rate at ages $x \geqslant a$. In words, equation 1 states that males one year short of maturity should delay breeding another year only if the ratio of their expected reproductive success to that of adult males is less than the risk of attempting to breed divided by adult male mortality rate. The accuracy of this approximation depends on how closely the intrinsic rate of increase for the population approaches zero. Threshold values are shown in Fig. 1 for several values of adult male survival rate.

This derivation differs from Wiley's (1974) original model in that it includes the factors of risk and adult male survival. Wiley's derivation assumed that earlier breeding by subadults reduces their survival rate by a constant amount that affects every year of life rather than just the year they begin breeding. This assumption is inappropriate because earlier breeding should not affect survival rate in subsequent years.

According to Wiley (1974), males typically do not breed as yearlings in promiscuous grouse but typically do breed as yearlings in monogamous grouse. This is not always true, as will be pointed out later. In contrast, females of all grouse species normally begin breeding as yearlings. The basic question here is why delayed breeding by males is more likely to evolve in promiscuous grouse than in monogamous grouse. Factors potentially influencing the age males first attempt breeding can be deduced from equation 1. These are summarized in Table 1. Not all of these factors can be evaluated on the basis of present evidence.

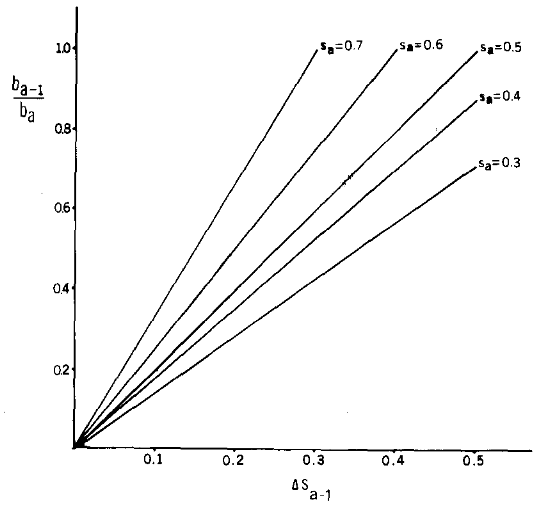

FIGURE 1. The conditions determining age at onset of breeding. Delayed breeding is advantageous to males when the value of b_{a-1}/b_a lies below the line specified by s_a for a given value of Δs_{a-1}. Symbols are defined in Table 1.

The risk of breeding for subadult males is difficult to measure directly because it entails comparison of survival rates for breeding and nonbreeding subadults within the same population. However, the relative magnitude of risk may be indicated by predation rates affecting adults. If predation on breeding adult males is high, the risk for subadult males is also likely to be high. Similarly, if predation on breeding adults is low, the risk for subadults is probably also low.

Although mortality from all causes is low in monogamous grouse during most of the breeding season (Choate 1963, Watson 1965, Bergerud 1970, Watson and Moss 1971), predation mortality is often high in early spring when pair formation commences (Watson 1965, Dement'ev and Gladkov 1967, Bergerud 1970). In promiscuous grouse, predation on breeding adult males is heavy in Ruffed Grouse (Bump et al. 1947, Eng and Gullion 1962, Gullion and Marshall 1968, Rusch and Keith 1971a) and Blue Grouse (Zwickel, pers. comm.), but it is rare in Sage Grouse (Wiley 1973), Sharp-tailed Grouse (Ammann 1957), and Greater Prairie Chickens (Berger et al. 1963, Hamerstrom et al. 1965) (see Appendix for scientific names). Therefore, assuming that the magnitude of risk for subadults is correlated with predation rates on breeding

TABLE 1. Some factors potentially influencing the evolution of delayed breeding in male grouse. (b_{a-1}/b_a = ratio of subadult to adult male reproductive rate; Δs = risk of attempting to breed as a subadult; s_a = adult male survival rate.)

b_{a-1}/b_a

1. Male experience in competing for better breeding habitats.
2. Male experience in competing for more fit females.
3. Male experience in enhancing survival of offspring.
4. Male experience in competing for more females once polygamy has evolved.

Δs

1. Frequency or intensity of courtship displays.
2. Male experience in evading predators during displays.
3. Male experience in maximizing foraging efficiency.
4. Habitat structure.

s_a

1. Body size.
2. Resource availability.
3. Habitat structure.
4. Population density.
5. Densities of predator and buffer prey populations.
6. Weather.

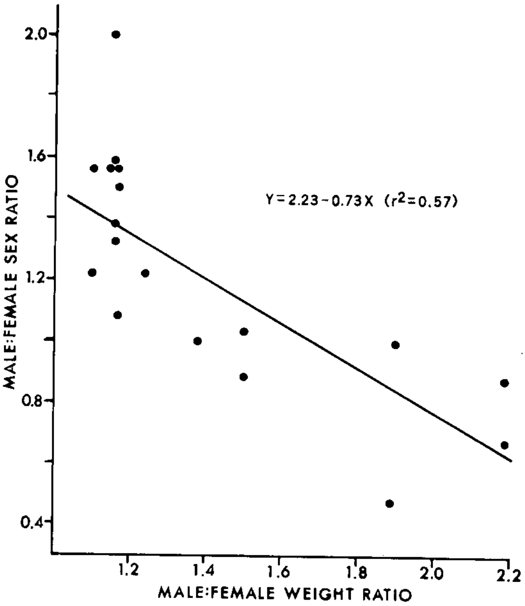

FIGURE 2. The relationship between increased sexual size dimorphism and autumn male:female sex ratios. The regression line is significant at $P < 0.01$. Weight ratio data are from Johnsgaard (1973) and Wiley (1974). Sex ratio data are from Baker (1953), Bergerud (1970), Bezdek (1944), Boag (1966), Campbell (1972), Choate (1963), Dorney (1963), Girard (1937), Jenkins et al. (1967), Patterson (1949), Pulliainen and Loisa (1972), Rajala (1974), Robel et al. (1972), Rusch and Keith (1971a), Viht (1974), Watson (1965), and Zwickel (1972).

adults, differences in risk cannot explain why sexual bimaturism is more likely to evolve in promiscuous grouse.

Wiley (1974) proposed that sexual bimaturism evolved because male survival rates were higher than female survival rates in grouse populations ancestral to present-day promiscuous species. He attributed this difference to sexual size dimorphism in ancestral forms. Large-sized males would, according to Wiley, survive longer than smaller-sized females because their energy balance would be more favorable and their vulnerability to predation would be less. Larger body size could reduce heat loss, lower metabolic requirements, and increase resistance to temperature fluctuations (Rensch 1960, Kendeigh 1972). Large size could also reduce the number of predators capable of attacking adult males. According to Wiley, females remained small in these species because larger size would have conflicted energetically with egg production. Thus, Wiley (1974) suggested that sexual size dimorphism led to sexual bimaturism, which in turn forced females to become polygamous. According to this hypothesis, monogamy should evolve only when ecological constraints prevent males from becoming larger than females.

One problem with Wiley's hypothesis is that some promiscuous species of grouse are no more dimorphic in size than monogamous species. Thus, males are about 8% larger than females in Spruce Grouse, 15% larger in Lesser Prairie Chickens, 16% larger in Ruffed Grouse, and 17% larger in Sharp-tailed Grouse, as compared to 10–15% larger in monogamous species of ptarmigan (data from Johnsgaard 1973, Wiley 1974).

Wiley's (1974) hypothesis rests on the assumption that larger size increases male longevity in sexually dimorphic species. This assumption can be tested directly, since the survival rate of males relative to females determines the adult (i.e., nonjuvenile) sex ratio. A positive correlation between sexual size dimorphism and sex ratio would therefore support Wiley's hypothesis. A negative correlation would support the alternate hypothesis that increased size dimorphism is a reproductive cost paid by males of polygamous species in order to compete more effectively for females. A plot of data from the literature shows a significant negative correlation (Fig. 2) supporting the sexual selection hypothesis that size dimorphism is a consequence rather than a cause of polygamy in grouse.

It is possible that this negative correlation is an artifact of biased data. Some data used in the analysis were based on the composition of hunter kills, which are frequently biased in favor of excess males. Kill data were used only if there was evidence that hunter kills were not biased toward either sex or if the data were the best available and the expected bias ran counter to the sexual selection hypothesis. Thus, Campbell (1972) stated on the basis of eariler studies that vulnerability to hunting was not a function of either age or sex in Lesser Prairie Chickens. Kill data for Capercaillie (Pulliainen and Loisa 1972) and Sage Grouse (Girard 1937, Patterson 1949) were the best available, and the expected bias toward excess males would weaken the evidence for a negative correlation. Kill data for Ruffed Grouse should not be biased because males are only slightly larger than females. This assumption is supported by evidence that sex ratios based on hunter kills (Bezdek 1944, Dorney 1963, Rusch and Keith 1971a) are similar to the sex ratio obtained by eliminating an entire population (Bump et al. 1947).

A second source of bias stems from the effects of long-term selective hunting on extant population sex ratios. If hunters kill more than the "surplus" males for many years in succession, there is likely to be an abnormally low proportion of males in the population. This bias may have had a particularly pronounced effect on the most dimorphic species. Rajala (1974) pointed out that this bias probably influenced sex ratios in Capercaillie, but he argued that the observed preponderance of females cannot be entirely explained by selective hunting pressure. He noted that females also predominate in unhunted populations and that juvenile sex ratios before the hunting season are the same as adult sex ratios during and after the hunting season. In relatively nondimorphic species, hunting should have little effect on sex ratios unless the sexes are unequally distributed in habitats receiving different intensities of hunting pressure. Palmer (1956), for example, found no difference in fall-to-spring mortality between hunted and unhunted populations of Ruffed Grouse. Nevertheless, additional studies of unhunted populations would be desirable to evaluate this potential source of bias.

The sexual bimaturism hypothesis implies that males delay breeding because the risks are too high, not because they are unable to obtain mates. Therefore, subadult males of promiscuous grouse should not attempt breeding even when they can gain access to receptive females. This can be tested by removing all adult males from an area and observing the behavior of colonizing subadults. Removal experiments have been performed for Blue Grouse (Bendell and Elliott 1967, Bendell et al. 1972, Zwickel 1972), Ruffed Grouse (Boag and Sumanik 1969, Rusch and Keith 1971a, Fischer and Keith 1974), and Sharp-tailed Grouse (Rippin and Boag 1974). In every study, yearling males occupied the removal area, established territories, advertised for mates, and presumably copulated with one or more females. These results are corroborated by observations of subadult males attempting to breed under natural conditions. Yearling Ruffed Grouse sometimes display on vacated territories following natural mortality of adult males (Marshall 1965). Yearling Sharp-tailed Grouse were observed occupying the center of one lek and successfully copulating despite the presence of adult males on the lek (Hjorth 1970). Yearling Greater Prairie Chickens performed 18% of all observed copulations by known-aged males during a 20-year study (Hamerstrom 1972). Thus, the evidence shows that yearling males of promiscuous grouse defer breeding only when they cannot compete effectively for mates. There is no evidence that yearling males who have access to receptive females ever defer breeding because of an associated high risk, and present evidence contradicts the sexual bimaturism hypothesis proposed by Wiley (1974).

A FEMALE CHOICE MODEL

As explained in the introduction, females usually select mates while males usually compete for mates. According to sexual selection theory, females should generally select mates on the basis of phenotypic traits which reflect male genetic quality (Fisher 1958). When females nest on male territories, they should also select mates on the basis of territory quality (Orians 1969). By the same reasoning, females should, in general, select the best breeding situations available, where "breeding situation" refers to the breeding context a female accepts by mating with a particular male (after Emlen 1957).

Two behavioral components define avian mating systems: the duration of pair association and the extent that individuals of either sex obtain more than one mate at a time. Both components can be influenced by female mating preferences. Females can preferentially select males with a propensity toward prolonged pair bonding by withholding copulations until an extensive courtship period has been completed. They can minimize the duration of pair bonding by copulating as quickly as possible after testing the phenotypic suitability of the male. Likewise, fe-

TABLE 2. Behavioral comparison of monogamous and promiscuous grouse. General information is based on Hjorth (1970), Johnsgaard (1973), and Wiley (1974).[a] English names are in the Appendix.

Mating system and species	Duration of pair-bond[b]	Female use of male territory[c]	Male vigilance[d]	Winter dispersion[e]	References[f]
Monogamous species					
Lagopus lagopus	Y	C,F,C	F,N,Y	UF	16,20,67
L. l. scoticus	Y	C,F,N,Y	F,N,Y	P	36,66
L. leucurus	EI-I	C,F,(N)	F,(N)	MF,S	6,17,37,60
L. mutus	EI-I	C,F,N,(Y)	F,N	UF,P,S	20,50,65,67
Tetrastes bonasia	MI-I	C,F,N	F,(N)	P,S	16,20,65,67
T. sewerzowi	MI?	C,F,N	F,N?	?	20
Promiscuous species, males dispersed					
Bonasa umbellus	C	C	None	B,S,UF	6,13,23,30
Falcipennis falcipennis	C	C	None	MF?	20,34
Canachites canadensis	C	C	None	MF,S	25,26,49
Dendragapus obscurus	C	C[g]	None	B,S?	4,5,46
Tetrao urogallus[h]	C	C	None	UF,S	20,34,42,48,63
T. parvirostris[h]	C	C	None	?	16,20
Promiscuous species, males on leks					
Pedioecetes phasianellus	C	C	None	MF	1,33,34
Tympanuchus cupido	C	C	None	MF,UF	2,6,32,34,47
T. pallidicinctus	C	C	None	MF	6,15,35
Lyrurus tetrix	C	C	None	MF	42,43,45,63
L. mlokosiewiczi	C	C	None	MF,S	20
Centrocercus urophasianus	C	C	None	UF	18,56,69

[a] Parentheses indicate that the trait varies among populations.

[b] EI = male leaves early in incubation; MI = male leaves in middle of incubation; I = male leaves after young hatch; Y = male remains with female and young; C = female leaves after courtship and copulation.

[c] C = copulation; F = foraging; N = nesting; Y = rearing of young.

[d] F = male guards pre-incubating female; N = male guards incubating female and nest; Y = male guards female and young.

[e] UF = unisexual flocks; MF = mixed sex flocks; S = solitary; P = pairs; B = broods.

[f] 1. Ammann 1957. 2. Baker 1953. 3. Beer 1943. 4. Bendell 1955. 5. Bendell and Elliott 1967. 6. Bent 1932. 7. Bergerud 1970. 8. Berner and Gysel 1969. 9. Blackford 1958. 10. Blackford 1963. 11. Boag 1966. 12. Børset and Krafft 1973. 13. Brander 1967. 14. Brown 1946. 15. Campbell 1972. 16. Cheng 1964. 17. Choate 1963. 18. Dalke et al. 1963. 19. Darrow 1939. 20. Dement'ev and Gladkov 1967. 21. Doerr et al. 1974. 22. Eastman and Jenkins 1970. 23. Edminister 1947. 24. Ellison 1966. 25. Ellison 1971. 26. Ellison 1973. 27. Fowle 1960. 28. Girard 1937. 29. Gullion and Marshall 1968. 30. Hale and Dorney 1963. 31. Hamerstrom 1939, 1963. 32. Hamerstrom and Hamerstrom 1955. 33. Hamerstrom and Hamerstrom 1951. 34. Hjorth 1970. 35. Hoffman 1963. 36. Jenkins et al. 1963, 1967. 37. Johnsgaard 1973. 38. Jones 1963. 39. Jones 1964. 40. Jones 1966. 41. Klebenow 1969. 42. Koskimies 1957. 43. Kruijt and Hogan 1967. 44. Kruijt et al. 1972. 45. Lack 1939. 46. Lance 1970. 47. Lehmann 1941. 48. Lumsden 1961. 49. MacDonald 1968. 50. MacDonald 1970. 51. Marshall 1946. 52. Marshall and Jensen 1937. 53. Martin et al. 1951. 54. May 1970. 55. Moss 1969. 56. Patterson 1952. 57. Pendergast and Boag 1970. 58. Peters 1958. 59. Pynnönen 1954. 60. Quick 1947. 61. Robinson 1969. 62. Rusch and Keith 1971b. 63. Seiskari 1962. 64. Stewart 1944. 65. Watson 1965. 66. Watson and Jenkins 1964. 67. Weeden 1963, 1964. 68. Weeden 1969. 69. Wiley 1973.

[g] In some populations females form prolonged pair bonds and nest on male territories (Blackford 1963).

[h] Sometimes considered a lek species (e.g. Wiley 1974), but display arenas are larger than typical leks (see Lumsden 1961).

males can determine how many mates males obtain by accepting or rejecting already mated males as their mates.

Behavioral comparisons of promiscuous and monogamous grouse should indicate the time of year when ecological differences are most likely to influence the evolution of mating systems. Table 2 shows that females of monogamous species remain paired with males from the beginning of courtship until at least the onset of incubation, while females of promiscuous species associate with males only briefly during courtship and copulation (by definition). Only in Red Grouse and some populations of Willow Ptarmigan do males help in any way with the rearing of offspring. Therefore, male parental care and ecological conditions during the rearing period apparently do not determine which mating system evolves. Likewise, wintering behavior appears unrelated to the evolution of grouse mating systems. The decisive ecological differences between monogamous and promiscuous species are apparently those affecting females during and immediately preceding egg laying.

There are two major differences in female behavior during the prelaying and laying periods. First, females of all monogamous species forage on male territories, while females of promiscuous species do not to any significant extent (Table 2). Females of monogamous species usually also nest on male territories, although female White-tailed Ptarmigan do not (Choate 1963). Females of promiscuous species nest on male territories only coincidentally, and they do not associate with males during the nesting period except to copulate. Secondly, females of monogamous species apparently rely on male vigilance to detect predators during egg laying and sometimes during part or all of incubation, while females of promiscuous species do not. For instance, female Rock Ptarmigan forage continuously in spring and are vigilant only when alerted by the male, who remains close to her until the onset of incubation (MacDonald 1970). Male Hazel Grouse and Amur Grouse remain in the treetops while females forage in the understory (Cheng 1964, Dement'ev and Gladkov 1967). Male White-tailed Ptarmigan and Willow Ptarmigan accompany females continuously until the onset of incubation and presumably also serve as sentinels (Choate 1963, Dement'ev and Gladkov 1967). Two ecological factors potentially influencing the evolution of these differences in female behavior are availability of food resources and vulnerability to predation during the prelaying and laying periods.

Food availability during the prelaying and laying periods can affect female reproductive success in several ways. In Red Grouse, there is evidence that early chick mortality is largely determined before the eggs hatch, possibly reflecting the condition of laying females (Jenkins et al. 1963, 1965). In Capercaillie and Black Grouse, viability of eggs and chicks is correlated with early spring weather conditions (Siivonen 1957), which are presumably correlated with early spring foraging conditions (Lack 1966). However, conflicting evidence seems to minimize the importance of this effect in at least some species (Marcstrom 1960, Helminen 1963, Zwickel and Bendell 1967).

Food availability probably limits clutch size in all species of grouse. Lack (1964, 1968) suggested that clutch size in grouse and other precocial birds should be determined by average availability of food during laying, along with the mean size of each egg. Johnsgaard (1973) has questioned this hypothesis and proposed instead that clutch size is limited by the cumulative effects of vulnerability to nest predation through time. According to Johnsgaard, the longer a female spends laying eggs, the higher her risk of losing the entire clutch to a predator. Food availability remains an important determinant of clutch size in Johnsgaard's hypothesis because it should limit the rate at which females can lay eggs. Food availability during the laying period must surely be important, since female energy requirements increase by an estimated 20–30% during that time (King 1973).

Theoretically, females should be able to alleviate competition for food by nesting on male territories (Brown 1964). They should also be able to devote more time to foraging and less time to surveillance by relying on males to detect predators. Therefore, food scarcity should favor nesting on male territories and reliance on male vigilance. This is possible only if females form prolonged pair bonds with males. Hence, competition for food resources should favor monogamy or polygyny, provided that these resources are defensible.

When food is abundant, females need not forage on male territories to obtain adequate food. Females gain little advantage by reducing competition for food when their success is limited by digestive rate rather than food intake rate or nutritive quality. They can avoid any increased conspicuousness caused by the presence of a male by minimizing their association with males. If food is abundant, females can rely on their own vigilance for detecting predators, or they can form flocks to obtain more effective vigilance than a male can provide. Unless suitable nesting substrate is scarce, food abundance should therefore lead to promiscuity.

A comparison of the diets and habitats of monogamous and promiscuous grouse suggests two trends (Table 3). First, monogamous species of ptarmigan occupy open arctic or alpine habitats, and the monogamous Hazel Grouse and Amur Grouse occupy open temperate forests. In contrast, promiscuous grouse occupy temperate forests, boreal forests, or grasslands, all of which provide relatively dense cover. Second, all but one of the species predominantly exploiting a single type of food during spring are promiscuous. Species with more diversified spring diets can be either monogamous or promiscuous.

It would be interesting to know whether monogamy is associated with more open habitats because food availability is generally lower, because predation vulnerability is generally higher, or because of other factors. I can find no data to test these hypotheses. It may be significant that a similar trend exists in pheasants. Monogamous pheasants prevail at high altitudes, polygynous pheasants occur within a broad range of intermediate altitudes, and promiscuous and harem polygynous pheasants are restricted to low altitudes (Beebe 1926, Delacour 1951, Smythies 1953, Ali 1962, Cheng 1964).

The sole exception to the correlation between monotypic diet and promiscuity is the Red Grouse, which exploits heather. Availability of food for this species is limited by nutritive quality of the heather and the length of the growing season prior to the end of egg laying (Moss 1969, Watson and Moss 1972, Moss et al. 1975). In contrast, availability of conifer needles taken by several species of

TABLE 3. Comparison of habitats and diets of monogamous and promiscuous grouse. English names are in the Appendix.

Mating system and species	Preferred habitat[a]	Staple spring diet of females[a]	References[b]
Monogamous species			
Lagopus lagopus	arctic and alpine tundra	buds, berry seeds, foliage; berries	20,58,68
L. l. scoticus	heather	heather	22,55
L. leucurus	rocky alpine tundra	heath, moss, new shoots, leaves, flowers	17,37
L. mutus	arctic and alpine tundra	leaves, flowers, berries, buds	20,50,55,68
Tetrastes bonasia	spruce-aspen-birch forest	catkins, buds, leaves; insects	16,20,34
T. sewerzowi	alpine aspen-birch-alder	herbaceous flowers and leaves	20,34
Promiscuous species, males dispersed			
Bonasa umbellus	mixed deciduous forest	buds, twigs, leaves; herbaceous foliage	14,19,23,29,51,53,62
Falcipennis falcipennis	spruce-fir; spruce-larch	conifer needles; shoots, buds?	20
Canachites canadensis	spruce; pine	conifer needles; leaves, berries	24,25,49,57,61
Dendragapus obscurus	open conifer-deciduous	wide variety of plant materials	3,5,9,10,27,51,53,64
Tetrao urogallus[c]	spruce-fir forest	conifer needles; new shoots, buds	12,16,20,34
T. parvirostris[c]	spruce-fir forest	herbaceous foliage; berries	20
Promiscuous species, males on leks			
Pedioecetes phasianellus	bogs, short grass, brush;	aspen forbs, grass, leaves; insects	1,31,34,40,53
Tympanuchus cupido	prairie, meadows	seeds, fruits, buds, leaves	1,31,38,47,53
T. pallidicinctus	short-grass prairie	insects, seeds, leaves	38,39,53
Lyrurus tetrix	bogs, open birch-aspen	herbaceous foliage; heather	12,16,20,34
L. mlokosiewiczi	alpine meadows, low scrub	herbaceous foliage; shoots, buds	20,34
Centrocercus urophasianus	sagebrush	sagebrush; weeds, insects	28,41,56

[a] Predominant habitat or diet precedes semicolon.
[b] See Table 2 for references.
[c] Sometimes considered a lek species (see footnote h of Table 2).

promiscuous grouse is not limited by nutritive quality (Zwickel and Bendell 1967, 1972, Ellison 1976). This correlation is significant because monoculture food resources such as conifer needles and sagebrush seem to be superabundant, thus supporting the prediction that promiscuity evolves when food is plentiful in spring. Further data are needed to confirm this conclusion and to test whether food availability is higher for promiscuous than for monogamous grouse with diversified diets.

Some evidence indicates that females of monogamous grouse nest on male territories because food is scarce. Competition for food has been demonstrated in Red Grouse, where many individuals of both sexes are excluded from suitable habitats (Watson and Moss 1971, 1972). Habitat quality in this species is greatly influenced by the quality and quantity of heather (Moss et al. 1975). Competition for suitable nesting habitat is indicated in all species of ptarmigan by the regular, though infrequent, occurrence of polygyny (Choate 1963, Watson and Jenkins 1964, MacDonald 1970, Weeden and Theberge 1972). Polygyny should not occur unless some females cannot find unmated males in suitable habitats (Orians 1969). However, the importance of food availability in determining habitat quality for these species has not been established. The value of nesting on male territories appears somewhat different for female Hazel Grouse. In this species male territories are centered around spruce groves which provide dense cover amid the open birch, aspen, and willow where females forage (Dement'ev and Gladov 1967). This suggests that female Hazel Grouse nest on male territories because it enables them to forage near dense cover.

There is also evidence that females of promiscuous grouse compete for habitats. Removal experiments show that adult female

Blue Grouse exclude yearling females from suitable nesting habitat (Bendell and Elliott 1967, Bendell et al. 1972, Zwickel 1972). Nesting female Spruce Grouse and Blue Grouse are overdispersed (Bendell and Elliott 1967, Lance 1970, Ellison 1971, 1973), and evidence for Blue Grouse suggests that this may result from conflicts between females (Stirling 1968, Zwickel, pers. comm.). Whether these spatial interactions are a response to competition for food or to other factors has not been determined.

It is not presently clear whether females of monogamous grouse are more vulnerable to predation than females of promiscuous grouse during early spring. Predation rates on female ptarmigan are relatively high (Watson 1965, Dement'ev and Gladkov 1967, Bergerud 1970), but predation on female Ruffed Grouse is also high (Edminister 1947). Very high vulnerability to predation may even preclude reliance on male vigilance. For example, Gardnarsson (cited by Johnsgaard 1973) reported that Willow Ptarmigan in Iceland are promiscuous under conditions of heavy predation by Gyrfalcons (*Falco rusticolus*). Males suffer much higher mortality from predation than females, suggesting that association with males may be sufficiently hazardous to preclude prolonged pair bonding. Therefore, differences in predator pressure alone seem insufficient for explaining why some grouse are monogamous while others are promiscuous.

To summarize, evidence is somewhat confusing, and the relative importance of various ecological factors may differ among species. One possible interpretation is that female grouse in relatively open habitats compete strongly for food and are often required to forage in areas containing little cover during the prelaying and laying periods. Under these conditions, females can alleviate competition for food by foraging on male territories, and they can enhance foraging efficiency and improve their chances for survival by relying on vigilant males to detect predators. Concealment alone would be ineffective against predators because of the openness of their habitat and females could ill afford the time necessary to maintain vigilance for themselves. In more closed habitats females are not required to forage in the open, and they might best avoid predation by maximizing concealment. One way to enhance concealment is to stay away from males and prevent close proximity to other females. This should be advantageous only if the rate of food consumption is not limiting and if there is no scarcity of suitable nest sites. In open habitats where cover is poor but food is abundant, females might best avoid predation by forming flocks to enhance their ability to detect predators. For example, female Sage Grouse breed in relatively open sagebrush and remain in flocks throughout the breeding season (Patterson 1952). This interpretation of how grouse mating systems evolved has by no means been proven, but it is consistent with both the existing evidence and sexual selection theory. It also provides concrete hypotheses that are amenable to future testing.

Two additional aspects of grouse mating systems are of general interest. Both can be explained in terms of the female choice principle. Mating typically occurs at traditional display sites in all promiscuous grouse, and these display sites are generally organized into leks in promiscuous species that occupy open habitats (reviewed by Hjorth 1970). Blue Grouse usually display at dispersed sites in their forest habitats, but they sometimes breed in open habitats following forest fires, where they have a tendency to perform communal displays (Hoffmann 1956, Blackford 1958, 1963). This adds support to the causal relationship between habitat structure and lekking behavior. Capercaillies are sometimes considered lek species (Wiley 1974), but their display arenas are much larger than those of typical lek species (Lumsden 1961). Lek behavior probably evolved in open country grouse after they invaded open habitats (Hjorth 1970, Johnsgaard 1973).

Lack (1968) suggested that traditional display sites are used by males because they have proven safe from predation. However, the location and appearance of traditional sites can be quickly learned by predators, so vulnerability may actually be higher at such sites. For example, Gullion and Marshall (1968) found that male Ruffed Grouse using perennial drumming logs have a lower life expectancy than males using transient logs. An alternate explanation is that females can more safely approach and mate at familiar sites than at unfamiliar [redacted] In this event, males would attract and copulate with more females at traditional sites even though their expected longevity is reduced. The use of traditional sites should evolve whenever the propensity for females to mate at familiar sites offsets any reduction in male life expectancy.

Two factors probably select for lek behavior in grouse. Lack (1939) and later Hjorth (1970) suggested that the combined displays of several males might increase the attractiveness or conspicuousness of a display arena, thereby increasing the average number of females obtained by each male on the arena. The same hypothesis was advanced by Snow (1963) to explain manakin leks. Hamerstrom and Hamerstrom (1960) found that the number of female Greater Prairie Chickens attracted to a lek per territorial male increased as predicted with lek size, until 11–15 males were present on the lek. Males on still larger leks averaged fewer females than on leks of this size. Koivisto (1965), however, failed to find any relationship between lek size and the number of visiting female Black Grouse. Similarly, Lill (1976) found no correlation between lek size and number of visiting females in Golden-headed Manakins (*Pipra erythrocephala*). A major problem with this hypothesis is that it fails to explain why lek behavior has evolved only in open country grouse. A second hypothesis resolves this problem. Lek behavior should reduce vulnerability of males displaying in open habitats because several individuals can detect predators better than can a single individual (Koivisto 1965, Lack 1968, Powell 1974). Leks may also be more attractive to females than solitary males because females should be safer there for the same reason. The hypothesis that leks enhance protection against predators is supported by the fact that leks are usually on elevated terrain in the most open parts of the habitat available (reviewed by Hjorth 1970).

SUMMARY

Promiscuity in grouse has been explained by the theory that delayed breeding by males causes an unbalanced breeding sex ratio, which forces females to accept polygamy. Subadult males are said to delay breeding because the risks are too high, not because they cannot effectively compete for mates. Evidence contradicts several predictions of this hypothesis.

This paper offers another hypothesis, derived from sexual selection theory and published information. Sexual selection theory predicts that selection affecting females should determine mating system characteristics. Comparative evidence shows that the principal differences between monogamous and promiscuous grouse occur in spring. These are: (a) females of monogamous species use male territories to acquire food and build a nest, while females of promiscuous species do not, and (b) females of monogamous species rely on male vigilance to detect predators during the prelaying and laying periods, unlike females of promiscuous species. There is no evidence for consistent behavioral differences during other stages of the breeding cycle.

The observed behavioral differences can be explained by the hypothesis that females of monogamous grouse are limited by the availability of food in spring, while females of promiscuous grouse are limited by digestive rate. In monogamous species females should be able to increase their rate of food intake by foraging on male territories to reduce competition and by relying on male vigilance for predators to increase the amount of time available for finding food. Females of promiscuous species would not be able to increase digestive rate by these behaviors, and they would be able to avoid increased conspicuousness by minimizing their association with males. Hence, scarce food resources should favor monogamy, while abundant food resources should favor promiscuity. The available evidence is consistent with this hypothesis but is insufficient to prove it.

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APPENDIX. Names of grouse species discussed in the text and tables. Willow Ptarmigan, *Lagopus lagopus*; Red Grouse, *L. l. scoticus*; White-tailed Ptarmigan, *L. leucurus*; Rock Ptarmigan, *L. mutus*; Hazel Grouse, *Tetrastes bonasia*; Amur Grouse, *T. sewerzowi*; Ruffed Grouse, *Bonasa umbellus*; Sharp-winged Grouse, *Falcipennis falcipennis*; Spruce Grouse, *Canachites canadensis*; Blue Grouse, *Dendragapus obscurus*; Capercaillie, *Tetrao urogallus*; Small-billed Capercaillie, *T. parvirostris*; Sharp-tailed Grouse, *Pedioecetes phasianellus*; Greater Prairie Chicken, *Tympanuchus cupido*; Lesser Prairie Chicken, *T. pallidicinctus*; Black Grouse, *Lyrurus tetrix*; Caucasian Black Grouse, *L. mlokosiewiczi*; Sage Grouse, *Centrocercus urophasianus.*

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