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EVOLUTION OF SOCIAL ORGANIZATION AND LIFE-HISTORY PATTERNS AMONG GROUSE

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ABSTRACT

Correlations of social structure, life-history patterns, and ecology among the seventeen species of grouse exemplify some general patterns in the evolution of mating systems among higher vertebrates. The species of grouse differ in the aggregation of displaying males, the permanence of heterosexual affiliations, the contributions of males to parental care, and the breeding sex ratio. Promiscuous species (no durable heterosexual affiliation) are probably all polygynous (the breeding sex ratio less than unity), but fall into two groups depending on whether the displaying males congregate at leks or disperse relatively evenly. In all of these promiscuous, polygynous species and in three monogamous species, the female cares for the young; dual parental care appears only in one monogamous species.

During their first year, the males of polygynous species do not mate or mate much less frequently, although females normally breed at one year of age, a situation termed sexual bimaturism. At least among birds and mammals, polygyny is normally associated with sexual bimaturism. Sexual bimaturism and polygyny among grouse correlate well both with large overall size, as indicated by female weight, and with greater sexual dimorphism in weight. These correlations also recur in other vertebrate families. Among the promiscuous grouse, the dispersion patterns of displaying males probably relate to the differences in predation pressures in open and forested habitats. In contrast with some other avian families, differences in social structure among grouse have little relationship to major differences in diet.

Single parental care is not a sufficient condition for the evolution of polygyny among grouse. The association of sexual bimaturism with polygyny requires, in addition, an explanation of the adaptive advantages of deferred reproduction among males. Postponed reproduction by males will reduce the spread of their genes in a population unless compensated by a sufficient gain in early survival or increased fecundity later. Calculations of rates of reproductive increase for hypothetical lineages of males indicate that these compensating conditions can plausibly explain the evolution of delayed reproduction among male grouse.

Theoretical considerations further suggest that larger size could favor the evolution of deferred reproduction, especially in males, and thus could contribute to the evolution of sexual bimaturism and polygyny in the larger species of grouse. Ecological circumstances, including the details of food dispersion, could thus influence the evolution of mating systems indirectly, through effects on the evolution of body sizes. As polygyny among higher vertebrates is normally associated with sexual bimaturism and is incompatible with full dual parental care, polygyny should evolve under ecological conditions in which the adaptive advantages of sexual bimaturism outweigh those of dual parental care.

INTRODUCTION

ONLY RECENTLY has it become clear how intricately a species' social organization is adapted to ecological circumstances. Studies by Crook (1962) and Orians (1961) provided

pioneering evidence for the adaptedness interspecific differences in social organization, and subsequent studies have explored this theme further (Crook, 1964, 1965, 1970; Eisenberg, 1966; Lack, 1968; Orians, 1969, 1972; Crook and Goss-Custard, 1972; Selander, 1972;

Eisenberg, Muckenhirn, and Rudran, 1972). Especially fruitful have been investigations of related species that differ markedly in social structure.

Among birds, the grouse (Tetraonidae) provide unusual opportunities for such comparisons. The range and gradations of social structure among these seventeen species are probably not surpassed in any other avian family. Particularly striking is the spectrum of mating systems among grouse, ranging from monogamy to extreme polygyny. Yet the hypotheses developed to explain the adaptedness to social systems in passerine birds, while applicable in part to grouse, do not provide complete explanations for the evolution of their societies. For example, the relationship of mating systems to strategies of parental care is less clear than in certain passerine families.

The grouse also illustrate a general problem in the evolution of polygynous mating systems. A widespread correlate of polygyny, at least among birds and mammals, is the later onset of reproduction among males than among females. Grouse exemplify this correlation well. The evolution of polygyny in grouse also seems inseparable from the evolution of large body size. The ecological consequences of both of these features must contribute to the evolution of their social systems. In this review a systematic comparison of grouse social systems and an examination of the correlations between social structure and other attributes will allow a closer analysis of the coevolution of mating systems, body sizes, and sexual differences in life history.

COMMENTS ON METHODOLOGY

By deducing the ecological consequences of differences in social behavior and its correlates, one can begin to specify the selection pressures that bear on the evolution of these differences. When constellations of correlated traits coincide with phyletic groups, however, the possibility exists that these similarities depend primarily on the common ancestry of the species, rather than on current adaptation. If natural selection in similar environments has resulted in the evolution of similarly coordinated adaptations, these correlations should recur in separate phyletic groups.

Within the Tetraonidae phyletic groups are difficult to distinguish. Systematic studies have

repeatedly confirmed their close relationships (Sibley, 1957; Short, 1967). Yet aside from the five traditionally polytypic genera (*Lagopus*, *Tympanuchus*, *Tetrastes*, *Tetrao*, *Lyrurus*), the species are not easily grouped. It seems possible that some nine or ten phyletic lines radiated from early tetraonid ancestors, so that attempts to identify only a few phyletic groups would prove illusory. Any similarities in social behavior among the recognized congeneric species provide only equivocal evidence for adaptation. Also the similarities between *Canachites* and *Falci pennis* and probably those between *Tympanuchus* and *Pedioecetes* are likely to depend heavily on common ancestry (Short, 1967).

RADIATION OF GROUSE SOCIAL SYSTEMS

The social systems of grouse comprise three general categories, differentiated on the bases of the dispersion of displaying males during the breeding season and the duration of heterosexual associations (Hjorth, 1970): (1) promiscuity, with males aggregated at leks; (2) promiscuity, with dispersed males; (3) monogamy, with dispersed males (Table 1). As Hjorth (1970) has reviewed much of the literature of grouse behavior, the present discussion will compare more systematically certain critical features of tetraonid social systems, particularly territorial behavior, interactions between the sexes, and age-related differences in behavior.

The term *polygamy* is used in this paper to denote an unequal sex ratio among breeding individuals (termed the *breeding sex ratio*). If more individual females than males contribute gametes to zygotes during any one season, the mating system is further specified as polygyny. Thus the words polygamy and polygyny will here imply nothing about the duration of the heterosexual association. The term *promiscuous* describes a mating system in which no preferential bonds unite individuals of opposite sex. Sexual bonds are easily recognized when individuals coordinate their behavior or remain in close spatial proximity for an appreciable length of time. But less noticeable sexual affiliations might also occur. An individual might develop a preference for mating with a particular partner even though their associations are brief, and such preferences might not prove reciprocal. On the other hand, an apparent preference could arise when two individuals share attach-

TABLE 1

Species That Form Leks (Category I)

Categories of social structure among grouse

CATEGORY I:	PROMISCUOUS SPECIES THAT FORM LEKS Sage Grouse, <i>Centrocercus urophasianus</i> (NA) ^b Black Grouse, <i>Lyrurus tetrix</i> (EA) ^a Caucasian Black Grouse, <i>Lyrurus mlokosiewiczzi</i> (A) Greater Prairie Chicken, <i>Tympanuchus cupido</i> (NA) ^a Lesser Prairie Chicken, <i>Tympanuchus pallidicinctus</i> (NA) Sharp-tailed Grouse, <i>Pedioecetes phasianellus</i> (NA) Capercaillie, <i>Tetrao urogallus</i> (EA) ^a Small-billed Capercaillie, <i>Tetrao parvirostris</i> (A)
CATEGORY II:	PROMISCUOUS SPECIES WITH DISPERSED MALES Blue Grouse, <i>Dendragapus obscurus</i> (NA) Spruce Grouse, <i>Canachites canadensis</i> (NA) ^a Sharp-winged Grouse, <i>Falcipecten falcipecten</i> (A) Ruffed Grouse, <i>Bonasa umbellus</i> (NA)
CATEGORY III:	SPECIES THAT FORM PAIR-BONDS Hazel Grouse, <i>Tetrastes bonasia</i> (EA) ^a Amur Grouse, <i>Tetrastes sewerzowi</i> (A) White-tailed Ptarmigan, <i>Lagopus leucurus</i> (NA) Rock Ptarmigan, <i>Lagopus mutus</i> (NA, EA) Willow Ptarmigan, <i>Lagopus lagopus</i> (Red Grouse, <i>L. l. scoticus</i>) (NA, EA)

^aSpecies whose behavior remains largely unknown. Available evidence suggests that in their social behavior they resemble their nearest relatives (Dementiev and Gladkov, 1967; Hjorth, 1970).

^bApproximate distribution within the Holarctic region: NA, North America; EA, Europe and Asia; A, Asia.

The five adequately known lek-forming species share many basic similarities in their social organization (Hjorth, 1970; Wiley, 1973a). Displaying males aggregate for several hours each morning and evening, and sometimes all night, at communal display grounds, also called arenas or leks. These aggregations recur from year to year at the same traditional locations. Females come there to mate, although at least in some of the species a small fraction of the copulations are performed by solitary males (Hamerstrom and Hamerstrom, 1960; Hjorth, 1970; Kruijt, de Vos, and Bossema, 1972). The period of two or three weeks during which females visit a lek is considerably shorter than the period of several months during which the males attend regularly. Males make no contribution to parental care.

Within each lek, individual males occupy territories demarcated by boundary zones in which neighbors encounter each other. The size of the males' territories and the degree to which males intrude into neighbors' territories vary with the species and with the presence or absence of females on the lek. Male Sage Grouse and Black Grouse usually remain within or near their boundaries even when females are present elsewhere on the lek (Wiley, 1973a; Höhn, 1953; Kruijt and Hogan, 1967; Kruijt, de Vos, and Bossema, 1972). Male Greater Prairie Chickens and Capercaillie, on the other hand, often leave their territories to approach females elsewhere on the lek, although when females are absent they remain within nearly exclusive territories (Hamerstrom and Hamerstrom, 1960; Robel, 1964; Lumsden, 1961; Hjorth, 1970).

Most copulations are performed near the center of the lek by a minority of the attending males (Schwartz, 1945; Lumsden, 1965; Kruijt and Hogan, 1967; Koivisto, 1965; Wiley, 1973a). Only a few studies have estimated the distribution of matings among the males attending a lek. In his studies of Black Grouse, Koivisto (1965) reported that one male on a lek attended by ten males performed nearly three-quarters of the copulations observed (17 of 24). One-third of the males performed 75 per cent of the matings observed by Kruijt and Hogan (1967) during two years on one lek. On three Sage Grouse leks, about 10 per cent of the males performed 75 per cent of the

ments to a common area. In such situations, a full understanding of heterosexual relationships would require intensive studies and experimentation.

populations (Wiley, 1973a). A three-year study at one Sage Grouse lek also revealed that only a few males performed a preponderant majority of the copulations (Hartzler, 1972). The Sage Grouse is possibly the most polygynous of all birds.

Females apparently visit one or a few leks on several mornings before copulating, at least in Sage Grouse (Lumsden, 1968), Greater Prairie Chickens (Hamerstrom and Hamerstrom, 1955; Robel, Briggs, Cebula, Silvy, Viers, and Watt, 1970) and Black Grouse (Kruijt, de Vos, and Bossema, 1972). The number of times a female mates each season is unclear. In Sage Grouse the available evidence indicates that females need to copulate only once in order to lay a fertile clutch and that females normally mate only once or perhaps a few times each season (reviewed in Wiley, 1973a). Whether or not females develop preferences for particular males, particular leks, or particular sites within leks remains uncertain (see below, Female Choice). The behavior of first-year and older females might differ significantly in these respects.

Females evidently normally breed in their first spring (Dalke, Pyrah, Stanton, Crawford, and Schlatterer, 1963). There are some suggestions that in Sage Grouse year-old females ovulate on the average a week or two later than older females (Dalke et al., 1963).

Studies of permanently marked males have shown that they tend to return to the same lek in successive years and to occupy territories at or near the same sites within a lek (Greater Prairie Chickens: Hamerstrom and Hamerstrom, 1960; Robel, 1967; Black Grouse: Koivisto, 1965; Hjorth, 1970; Kruijt, de Vos, and Bossema, 1972; Sharp-tailed Grouse: Evans, 1969; Sage Grouse: Hartzler, 1972). Territorial positions do change, usually when a male occupies part or all of an adjacent vacancy, both within a season and from year to year. These shifts often bring the territorial male closer to the center of the lek (Evans, 1969; Wiley, 1973a; Kruijt, de Vos, and Bossema, 1972). However, this centripetal tendency in territorial shifts is not invariable (Kruijt, de Vos, and Bossema, 1972; Hartzler, 1972). Although vacancies occurring during the breeding season, at least in Sage Grouse and Black Grouse, are usually occupied by males with contiguous territories, on occasion a newcomer will appro-

priate a vacancy near the center of a lek or even expel the original resident (Hjorth, 1970; Kruijt, de Vos, and Bossema, 1972; Hartzler, 1972).

In all lek-forming grouse, year-old males attend leks less constantly than do older males. They establish territories on leks later in the season and then occupy peripheral positions (Lack, 1939; Lumsden, 1965; Koivisto, 1965; Kruijt and Hogan, 1967; Robel, 1967; Patterson, 1952; Wiley, 1973a). Some young males never become territorial (Black Grouse: Robel, 1969). Owing in part to their later establishment and peripheral positions, year-old males almost never copulate. Hjorth (1970), however, did observe a number of copulations by first-year male Sharp-tailed Grouse when one of the older, central males failed to return after he was trapped.

In first-year male Sage Grouse, and probably in other lek-forming species as well, growth of the testes is delayed in comparison with that of older males, and the average testis weight never reaches the average for older males at the peak of the mating season. Year-old males do, however, produce spermatozoa (Eng, 1963). In several lek-forming species year-old males have noticeably less well-developed plumage than do older males. The tail feathers, an important component of their display postures, are often shorter and less distinctively developed (Sage Grouse: Patterson, 1952; Eng, 1963; Wiley, 1973a,b; Black Grouse and Capercaillie: Fuschlberger, 1956). Males of the latter two species are also browner and less iridescent in their first year. Male Caucasian Black Grouse retain a relatively female-like plumage through their first year (Dementiev and Gladkov, 1967), an extreme example of a trend apparent in the other lek-forming species. Acoustic signals that are characteristic of behavior on leks also differ somewhat in first-year and older males (Wiley, 1973b; Fuschlberger, 1956). In general, then, year-old males among the lek-forming species lag behind older males in their physiological maturation, manifest somewhat less well-developed plumage and displays, and seldom, if ever, copulate.

A Variant Among Lek-Forming Grouse

The Capercaillie, as Hjorth (1970) indicates,

is the most divergent of the lek-forming species. Hjorth even suggests that their aggregations are not appropriately termed leks. However, the differences lie primarily in the large territories of the males and the small number of males on most leks. The displaying males definitely congregate, except perhaps in regions of very low population density. This clustering remains apparent in spite of the males' large territories.

Where the territories of two neighbors adjoin, the boundary zone is wide, perhaps 20 to 50 meters across in most cases (Lumsden, 1961). In relation to the diameters of their territories (about 100 meters), however, the widths of these boundary zones seem hardly greater than in Sage Grouse (Wiley, 1973a). Boundary encounters between neighbors are less frequent than in other lek-forming species but are often severe and protracted (Hjorth, 1970). When females visit the lek, the males often desert their territories to approach the females, behavior that recalls that of the Greater Prairie Chicken. One limited study has indicated that, of the adult males in one aggregation, a minority performed most of the copulations (Lumsden, 1961).

The Capercaillie's social organization on the ground, then, aside from being more spread out, resembles that of other lek-forming grouse. In their forested habitat, male Capercaillie display from arboreal sites as well. Each male Capercaillie usually performs from a specific tree in the evening and again early in the morning, before he begins to display nearby on the ground (Fuschlberger, 1956; Hjorth, 1970). These trees used for "Hochbalz" and for roosting are often more dispersed than the positions occupied during terrestrial display ("Bodenbalz") (Hjorth, 1970), so aggregation of males is less pronounced in the former. In their arboreal behavior male Capercaillie approach those species in which displaying males have widely dispersed stations (Category II, below); however, even in arboreal display, the males form aggregations.

As in the other lek-forming species, year-old male Capercaillies begin to display later in the spring than do older males and they occupy peripheral positions on the leks. Indeed, Kirikov (cited in Dementiev and Gladkov, 1967) concluded that even two-year-old males were later than older males in their seasonal onset of display.

*Promiscuous Species with Displaying Males
Widely Dispersed (Category II)*

In three species of grouse (Blue, Ruffed, and Spruce), the males display at widely separated sites, yet the sexes apparently do not form durable pair-bonds. Most reports of these species suggest that the males and females do not remain together for an appreciable time at any stage of the breeding cycle. The movements of female Blue Grouse and Ruffed Grouse, for instance, are not confined to the vicinity of any one male (Bendell, 1955a; Bendell and Elliott, 1967; Brander, 1967). Boag (1966) found that female Blue Grouse occupy overlapping home ranges, which are much larger than the territories of individual males. However, Blackford (1963) reported an association between one pair of Blue Grouse, although the female often left the male's territory. This case might represent an apparent bond that resulted from the two individuals' attachments to an overlapping area. Female Spruce Grouse choose somewhat more open habitat for nesting than do the males for display posts (Ellison, 1971). As a result, the females often nest at a distance from the males' stations, a situation that indicates only transitory relationships between the sexes. Heterosexual associations in these species thus seem nearly as transitory as in the lek-forming species.

Displaying male Blue Grouse, Ruffed Grouse (Bump, Darrow, Edminster, and Crissey, 1947; Gullion, King, and Marshall, 1962; Gullion, 1967), and Spruce Grouse (MacDonald, 1968; Ellison, 1971) disperse themselves more or less evenly throughout the suitable habitat. In all three species males with established display sites produce long-range acoustic signals. Gullion (1967) noted, without quantification, a slight clustering of Ruffed Grouse display sites, but it is not clear from his account whether this clustering is explained by the males' habitat preferences. By challenging or attacking intruders, male Blue Grouse defend nearly exclusive territories, averaging 4 hectares or more around their display sites (Blackford, 1963; Boag, 1966; Bendell and Elliott, 1967). In contrast, resident male Ruffed Grouse and Spruce Grouse occupy areas without definite, defended boundaries. Male Spruce Grouse nevertheless react quickly when they detect the presence of nearby conspecific males (MacDonald, 1968). Male Ruffed Grouse will use tempo-

rary display sites to approach neighbors who are displaying nearby, but overt aggression is virtually never reported (Gullion, 1967). The dispersion of displaying males distinguishes these species from the lek-forming grouse. Although three males whose territories or ranges adjoin at a common point might occasionally approach each other, in none of these species do displaying males regularly aggregate in the clear way that even male Capercaillie regularly do.

Once a male Blue Grouse has established a territory, he normally returns to that territory in successive seasons as long as he survives (Bendell and Elliott, 1966, 1967). Male Ruffed Grouse, on the other hand, often change their display posts if they survive several years, but the factors that influence the choice of a new site remain unknown (Gullion, 1967).

Many male Blue Grouse in their first year do not establish display territories (Bendell and Elliott, 1967). These unestablished yearlings remain silent and move around widely. In this species first-year males have smaller testes, shorter tails, and weigh less than older birds (Bendell, 1955b; Bendell and Elliott, 1967; Swarth, 1926). Bendell and Elliott (1967) have suggested that resident male Blue Grouse attract unestablished year-old males to their territories. These yearlings sometimes occupy these sites if the usual occupant is removed. Resident Ruffed Grouse and Spruce Grouse also seem to attract first-year males (Gullion, 1967; Ellison, 1971). Often a year-old male Ruffed Grouse regularly frequents the vicinity of another male's display site, yet rarely displays. Marshall (1965) and Gullion (1967) have noted that on several occasions when the resident male had disappeared, such a yearling occupied the vacated display site. In this way some display sites are used by a succession of males, so that the locations of these sites become traditional.

The experimental removal of resident males in both of these species allows some first-year males to establish themselves in the vacated sites, but many vacancies remain unoccupied at least until the following year. When Bendell and Elliott (1967) removed from their territories 31 male Blue Grouse, less than a third of which were yearlings, two-thirds of the new occupants were first-year males. Eighteen of the vacated territories (58%) remained unoccupied. If resident male Ruffed Grouse are removed, only

a minority of the display sites are reoccupied in the same season, but the newcomers again are usually first-year males (Dorney and Kabat, 1960). The mechanisms underlying the reoccupation of vacancies remain unclear. In no study so far have the newcomers' previous locations been known in detail. Nor has any study compared vacancies created early in the season, prior to most of the mating, and vacancies created later, after the mating.

Nothing is known about the distribution of matings among the males of Category II species, owing to the difficulties of observing widely dispersed birds in forested habitats. It remains unknown whether sites occupied by a succession of males offer advantages in attracting females, and whether females develop preferences for mating with particular males or at particular sites.

Both in Blue Grouse and in Ruffed Grouse, most females breed in their first year (Bendell and Elliott, 1967; Zwickel and Bendell, 1967; Bump et al., 1947). On the other hand, in all three species many first-year males evidently do not mate, to judge from their less well-developed territorial behavior, less persistence in displaying, and, at least among Blue Grouse, smaller testes and somewhat less well-developed plumage. If most first-year females do mate, while year-old males usually do not, and provided that the mortality of females is not much greater than males (see below), then polygyny is the probable result.

Species That Form Persistent Pair-Bonds (Category III)

The only grouse that normally form durable pair-bonds are the three species of ptarmigan (*Lagopus*) and the Hazel Grouse (*Tetrastes bonasia*). Of these, the Red Grouse (*L. lagopus scoticus*), an insular race of a widespread arctic and subarctic species, is by far the best known. Male Red Grouse establish territories in autumn, but these territories, several hectares in area, are not intensively defended until the following February. Hens associate with territorial males during the autumn and winter, but they often move from one male to another until pair-bonds are firmly established in early spring (Watson and Jenkins, 1964). Males intrude into their neighbors' territories in pursuit of a female or when the resident male is occupied at a

distance. When challenged, however, the intruder normally retreats within his own boundary. Confrontations of neighboring males define relatively narrow boundary zones between their territories (Jenkins, Watson, and Miller, 1963).

The behavior of male and female Red Grouse gradually changes as the pair-bond is formed. The male becomes less aggressive, and concurrently the female's tendency to avoid him decreases. Eventually, during the period before incubation, the male closely follows the female's movements. The female, in turn, sometimes lures her mate away from other nearby females. During incubation the hen often joins her mate during her periods off the nest. After the eggs hatch both parents attend the brood (Nethersole-Thompson and Nethersole-Thompson, 1939; Jenkins, Watson, and Miller, 1963; Watson and Jenkins, 1964; also other subspecies of *L. lagopus*: Swarth, 1926; Dixon, 1927; Rajala, 1962; Weeden, 1965b; Dementiev and Gladkov, 1967). Both sexes attack predators near the brood or the nest, or lure them away, often by feigning injury. In addition, males lure potential predators away from their mates (Nethersole-Thompson and Nethersole-Thompson, 1939; Watson and Jenkins, 1964). Red Grouse broods often, although not invariably, remain within the male's territory for several months after hatching (Jenkins, Watson, and Miller, 1963), though in other populations broods might prove less sedentary. Paired Red Grouse thus maintain their association for nearly six months each year.

A small fraction of the territorial male Red Grouse mate with two females, while a few territorial males remain unmated. Bigamous males usually devote more attention to one of their mates (Watson and Jenkins, 1964). Those males that fail to attract a mate often have smaller than average territories.

Many male Red Grouse establish territories and breed successfully in their first year, although older males become territorial one to two months earlier in autumn (Jenkins, Watson, and Miller, 1963; Watson, 1967). Whether this lead gives older males an advantage over first-year males in establishing territories is unclear. On one hand, Jenkins, Watson, and Miller, (1963, 1967) deduce that territorial birds survive much better than non-territorial birds and that August to August survival of males during

their first year is about equal to that of older males. Consequently, first-year and older males would seem to have about the same chances of establishing territories.

The results of removal experiments suggest, on the other hand, that older males might have some advantages in the establishment of a territory. When Watson and Jenkins (1968) removed territorial Red Grouse during early autumn (August and September), before first-year males normally establish territories in undisturbed populations, most of the vacancies were filled within a few days by yearling males only a few months old. Thus, in the early stages of territory establishment, the presence of older males seems to prevent territorial behavior in yearlings. Vacancies created from November through June sometimes remained unoccupied for weeks or months. The eventual newcomers during these months included about equal numbers of first-year males without previous territories and older males that moved their territories into the vacancies, in one case from a distance of one kilometer. A few older males that had previously lacked territories also took positions in the vacancies.

By mid-winter, then, all but a few older males have either established territories or have become permanently non-territorial; perhaps they have died or emigrated. It appears that some first-year males, however, are still excluded by previously established birds. The fraction of spring territories occupied by year-old males and the interactions between first-year and older males during territory establishment have yet to be reported.

Rock and White-tailed Ptarmigan also normally form monogamous pairs, which maintain large territories. Like Red Grouse, two females will occasionally settle in one male's territory, in which case the male tends to favor one of them (MacDonald, 1970). In these species, though, the association of the mated pair usually ends during incubation or shortly after hatching (Swarth, 1926; Choate, 1963; Watson, 1965, 1972; Weeden, 1965a,b; Dementiev and Gladkov, 1967; MacDonald, 1970). Male Rock Ptarmigan in some arctic regions leave the nesting region altogether, in order to molt (Semenov-Tyan-Shanskii, 1960). The pair-bond can terminate even sooner, at the start of incubation. Female White-tailed Ptarmigan, for instance, sometimes nest outside their mate's

territory, in one case at a distance of 400 meters, so that in this case the female terminated the pair's association (Choate, 1963).

Some male Rock Ptarmigan do accompany broods and help to distract predators (Parmelee, Stephens, and Schmidt, 1967; Watson, 1972). Usually, however, only females feign injury or otherwise defend the brood from potential predators (MacDonald, 1970). Males regularly perform these activities only while the female is incubating (Watson, 1972). In an alpine population in Scotland, females with broods often remained within their mate's former territory (Watson, 1965), but in arctic populations broods tend to move widely (Weeden, 1965a; MacDonald, 1970).

First-year male White-tailed Ptarmigan usually arrive on the breeding grounds later than older males and are less successful in establishing territories. The one available study suggests that when they do establish territories, these tend to be smaller, and their chances for successful mating are low (Choate, 1963). Although Watson (1965) did not differentiate first-year males, males that displayed less persistently and had smaller territories were less successful in attracting mates. By comparison with Choate's (1963) studies of banded White-tailed Ptarmigan, it seems possible that many of Watson's less successful males were yearlings.

Territoriality and heterosexual associations in Hazel Grouse closely resemble those of Rock and White-tailed Ptarmigan. Males establish territories in autumn, but pair-bonds are not firmly made until early spring. Males rarely have more than one mate. Before incubation begins, the pair clearly coordinate their behavior, by calling back and forth to each other, for instance, but the association does not usually persist through incubation. Males usually do not accompany broods; apparently only the female feigns injury to protect the brood (Pynnönen, 1954; Fuschlberger, 1956; Dementiev and Gladkov, 1967). Occasional reports of males with broods might result from chance occurrence or from some individual variation in male behavior.

Winter Behavior

During the winter most grouse form flocks, which sometimes include large numbers of individuals. Tendencies toward unisexual

flocking appear in a number of species (Weeden, 1964; Seiskari, 1962), and studies of other species might uncover similar tendencies. Although our information on winter behavior is still limited, one is struck by a similarity among species that contrasts with the diversity in their mating behavior.

Gradations within the Proposed Classification

Although I have presented the social systems of grouse during the breeding season in three categories, variations within the categories suggest that they actually intergrade. The enduring pair-bond of the Red Grouse, and presumably other subspecies of Willow Ptarmigan, clearly is one extreme in grouse social organization. In other ptarmigan and the Hazel Grouse, the association of the sexes, although lasting a number of weeks, usually soon ends once incubation begins. Among the four species in Category II interactions of the sexes prove still more evanescent. Pair-bonds probably vary somewhat among individuals and perhaps among populations of the same species.

Categories II and III probably also intergrade in the roles taken by first-year males and in breeding sex ratios. While many first-year male Red Grouse breed successfully, first-year male White-tailed Ptarmigan, according to the one report available, were less successful in attracting mates. In their heterosexual relations the difference then between the White-tailed Ptarmigan (Category III) and the Ruffed Grouse (Category II) thus appears to lie in the longer association of male and female ptarmigan prior to copulation.

Categories I and II are probably similar in their heterosexual relations. However, our knowledge of the interactions between identified individuals of both sexes is insufficient to allow firm conclusions. Perhaps when males are widely dispersed there are greater opportunities for longer and more intricate relationships between individuals of opposite sex.

Direct evidence is lacking for the distribution of matings among individual males of the Category II species. For this reason, it remains unclear how the species in Categories I and II compare in their degree of polygyny. Breeding sex ratios might well vary among populations or years in the same species.

Promiscuity, Polygyny, Male Dispersion, and Male Parental Care

The aggregation or dispersion of displaying males clearly has no necessary connection with promiscuity (Hjorth, 1970; Selander, 1972). Although the species in Categories I and II are all promiscuous, the two categories differ in the dispersion of displaying males. All grouse that form pair-bonds also manifest dispersed territoriality.

Polygyny probably always accompanies promiscuity among the grouse. The evidence for this point will remain incomplete until we have direct estimates of breeding sex ratios for Category II species. Our present knowledge of the behavior of year-old males and of mortality rates in these species, however, suggests that they are indeed polygynous (see above). If this conclusion is correct, all promiscuous grouse are polygynous to varying degrees, while all grouse that form pair-bonds are normally monogamous.

A third feature of social organization, the reduction of male parental care, is associated with both monogamous and polygynous mating systems (Table 2). All polygynous, promiscuous species lack male parental care. Among species that form monogamous pair-bonds, however, the males vary in their contributions to parental care. In all grouse the female alone incubates the eggs. The precocial young are not fed by their parents, although the mother helps by leading her chicks to appropriate feeding areas and by directing their attention to food items. A parent, in addition, contributes substantially to the security of the brood. For grouse some

of the greatest risks in parental care probably accompany the parent's attempts to deflect predators from the nest or young.

Only in the Willow Ptarmigan does the male normally aid in guarding the brood from predators. His attentiveness near the nest during incubation might, in addition, reduce a predator's chances of surprising and killing the female on her nest. In the other two species of ptarmigan and the Hazel Grouse, although all form stable pair associations before nesting begins, the bond usually terminates during incubation. Among grouse, then, reduced male parental care is not restricted to species with promiscuous or polygynous sexual relations.

In conclusion, the radiation of tetraonid social organization has involved at least three dimensions: the dispersion of displaying males; the breeding sex ratio; and the male's contribution to parental care.

CORRELATES OF SOCIAL STRUCTURE AMONG GROUSE

The following sections will review evidence that reproduction by year-old males, overall size as indicated by female weight, sexual dimorphism in weight, and habitat structure all correlate in some degree with social structure. On the other hand, available evidence suggests little association between variations in social organization in grouse and their diets, mortality rates, or clutch sizes.

Reproduction by Year-old Males

The preceding review of tetraonid social systems has already documented one striking correlate of social organization: in polygynous species first-year males generally do not breed, although year-old females do (Table 3). This correlation recurs in other groups of birds, notably the Ploceidae (Crook, 1964) and Icteridae (Selander, 1965, 1972). Furthermore, sexual differences in the age at onset of reproduction also characterize polygynous mammals (see, for instance, Carrick, Csordas, Ingham, and Keith, 1962; Geist, 1968a,b; McCullough, 1969).

The association of polygyny with deferred reproduction in male grouse seems to be consistent. In the most polygynous, lek-forming species, such as the Sage Grouse, first-year males essentially never breed. In the species that form

TABLE 2

Parental care by male grouse in different social systems

TYPE OF SOCIAL SYSTEM	INCIDENCE OF PARENTAL CARE BY MALES		
	NEVER	OCCASION-ALLY	USUALLY
Category I	<i>Centrocercus</i> <i>Tympanuchus</i> <i>Pedioecetes</i> <i>Lyrurus</i> <i>Tetrao</i>		
Category II	<i>Dendragapus</i> <i>Bonasa</i>		
Category III		<i>L. mutus</i> <i>Tetrastes</i>	<i>L. lagopus</i>

TABLE 3

Breeding by first-year male grouse in different social systems

TYPE OF SOCIAL SYSTEM	INCIDENCE OF BREEDING BY FIRST-YEAR MALES		
	NEVER, OR RARELY	OCCASIONALLY	USUALLY
Category I	<i>Centrocercus</i> <i>Tympanuchus</i> <i>Pedioecetes</i> <i>Lyrurus</i> <i>Tetrao</i>		
Category II	<i>Dendragapus</i> ^a <i>Bonasa</i> ^a		
Category III	<i>L. leucurus</i>	<i>L. lagopus</i> <i>L. mutus</i>	

^aSome year-old males establish territories or display sites but their breeding status remains unknown.

smaller leks, such as the Sharp-tailed Grouse, year-old males are occasionally reported to copulate, but normally they do not.

Among the Category II species, some first-year males establish territories, but most do not. However, it remains uncertain whether even territorial yearlings mate successfully. Among the species that form pair-bonds, the most persistent heterosexual affiliation occurs in that species, the Willow Ptarmigan, in which first-year males normally breed. In the other two species of ptarmigan, both of which have briefer pair associations, first-year males seem less likely to breed successfully, and the incidence of polygynous relationships seems somewhat higher.

Females in all species of grouse normally do breed in their first year. Thus in males of polygynous species the age at first reproduction is later than in females and is later than in males of related monogamous species.

It remains uncertain whether mating success among males of polygynous species increases with age even beyond their first year, though indirect evidence suggests that this may be so in Sage Grouse (Wiley, 1973a). Unlike year-old males, some two-year-olds definitely do copulate (Hartzler, 1972), but it still is not known how their mean frequency of mating compares with that of older males. There are also suggestions of age-correlated mating success beyond the first year among male Black Grouse, Capercaillie, and Greater Prairie Chickens (Koivisto, 1965; Kirikov, cited in Dementiev and Gladkov,

1967; Robel, 1967; Kruijt, de Vos, and Bossema, 1972).

At least in Blue Grouse and Sage Grouse year-old males have smaller testes on the average than older males. Also their testicular growth is delayed in comparison with older males, although first-year males of both species produce spermatozoa (see above; Bendell, 1955a; Eng, 1963; Bendell and Elliott, 1967). Although other species of grouse have not yet been investigated in this regard, two polygynous icterids, the Red-winged Blackbird *Agelaius phoeniceus* and the Great-tailed Grackle *Quiscalus mexicanus*, also show age-related differences in testicular growth (Wright and Wright, 1944; Selander and Hauser, 1965; Selander, 1972). Deferred reproduction by first-year males of polygynous birds is thus associated with retarded maturation of the gonads. The term *sexual bimaturism* is appropriate to describe a substantial difference between the sexes in the age at which adult reproductive physiology is attained.

Weight of Female and Sexual Dimorphism in Weight

Polygamous, sexually dimorphic species often tend to be larger than related monogamous species (Amadon, 1959; Selander, 1972). This relationship applies with a few exceptions to the grouse. A striking correlation also pertains between the degree of sexual dimorphism in weight and the overall size of a species, as indicated by the average female weight.

The ratio of male to female weights increases almost linearly with increases in female weight (Fig. 1). Information on the weights of grouse, it should be noted, includes many uncertainties. Weights vary somewhat from season to season, from year to year, and from place to place even within relatively limited regions (Koskimies, 1958), and the weights of only a few species have received careful study. I have used published means from samples of at least five weights for each sex. All these weights were obtained during summer and autumn, or at unspecified times of year. If wing length is used as a measure of size, instead of weight (see Amadon, 1943), the correlation of sexual dimorphism in size with female size remains virtually the same.

Within the Tetraonidae sexual dimorphism

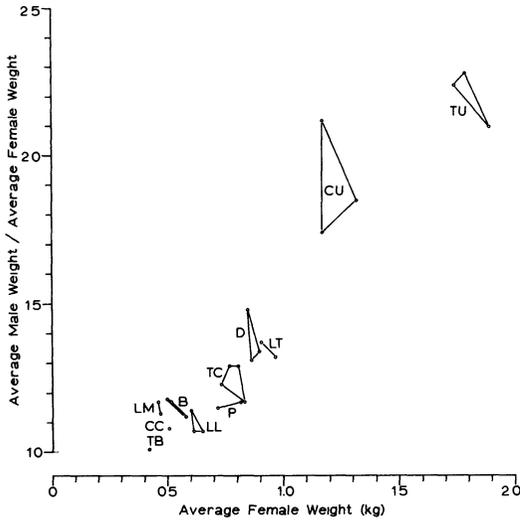


FIG. 1. RELATIONSHIP BETWEEN OVERALL SIZE, AS INDICATED BY FEMALE WEIGHT, AND SEXUAL DIMORPHISM IN WEIGHT AMONG THE SPECIES OF GROUSE.

Each point presents the average female weight and the ratio of average female weight to average male weight for one published sample. Solid lines connect two or more published samples for one species. Letters identify the pertinent species: TU, *Tetrao urogallus*; CU, *Centrocerus urophasianus*; D, *Dendragapus obscurus*; LT, *Lyrurus tetrrix*; TC, *Tympanuchus cupido*; P, *Pedioecetes phasianellus*; B, *Bonasa umbellus*; CC, *Canachites canadensis*; LL, *Lagopus lagopus*; LM, *L. mutus*; TB, *Tetrastes bonasia*.

in weight provides a good discriminant for differences in mating systems. The Hazel Grouse and the ptarmigans, species that form pair-bonds, have the lowest sexual dimorphism. Among the lek-forming species, the Sage Grouse, which forms the largest leks, has the second highest discrepancy in weight between the sexes. The species that form smaller leks in open country have less dimorphism. This relationship suggests that among promiscuous species the more polygynous ones are also more dimorphic in size. Full evaluation of this suggestion is impossible until the degree of polygyny among Category II species and Capercaillie is better known.

Average female weight can also serve to discriminate differences in mating systems. The promiscuous species are larger as well as more dimorphic, except for the Ruffed and Spruce Grouse. The females of these two promiscuous

species are about the size of female ptarmigan, which form monogamous pair-bonds. If the Ruffed Grouse is instead compared with its approximate ecological counterpart in the Old World, the Hazel Grouse, the promiscuous species is then both larger overall and more dimorphic in weight than the pair-bonding species. Promiscuity among grouse is thus related not only to increased sexual dimorphism but also to increased size of the species. This triple relationship holds both for the forest species and for the open-country ones.

Habitat Preferences

Differences in social organization among grouse show one clear association with differences in habitat type: promiscuous species in open habitats form leks, while the males of most promiscuous species in forested habitats remain dispersed. The promiscuous species are almost evenly divided between open and forested habitats in the temperate zone. Those species that form leks (Category I), however, all occur in open habitats, with the exception of the Capercaillie, a denizen of mature coniferous forests. The Black Grouse favors an interspersed forest and open areas, often moor or steppe. Their leks, though, are generally in the open. In contrast, those species in which males take dispersed positions (Category II) occur primarily in forests. Thus among promiscuous grouse, the habitat has a more definite influence on the dispersion of displaying males than on the breeding sex ratio.

In habitats with restricted visibility, the risks of predation on a congregation of grouse could militate against the evolution of leks. The fact that only Capercaillie form leks in forests is perhaps the exception that proves the point. Of all grouse the Capercaillie, owing to its large size, should have the fewest potential predators. Although they are the only forest grouse to form leks, male Capercaillie keep farther apart than the males of any other lek-forming grouse.

The few monogamous species occupy a great diversity of vegetation formations. Particularly catholic in habitat preferences are the various subspecies of the Willow Ptarmigan. The race endemic in the British Isles, *L. l. scoticus*, occupies open moors, a habitat as exposed as the steppes and prairies of western North America. Another subspecies of the Willow

Ptarmigan, *L. l. major*, ranges along the interface between steppe and deciduous forest in central Asia (Dementiev and Gladkov, 1967), a situation favored by several races of the Sharp-tailed Grouse in North America. Most populations of the Willow Ptarmigan, however, occur in the shrubby tundra near or beyond the tree line. The Hazel Grouse occupies a variety of relatively mature forest types, deciduous, mixed, and coniferous, across the breadth of Eurasia.

Food Habits

All grouse are primarily herbivorous, although all probably eat considerable numbers of insects during the summer months. The chicks of all species seem to take many insects in their diets. Thus, in contrast to the remarkable divergence in their social organization, their food habits are basically similar. There are no gross differences in diet correlated with differences in social structure, as there are among the Ploceidae, for instance (Crook, 1962).

Species and populations of grouse do differ in the diversity of their diets and the uniformity of the dispersion of their food plants. Kruijt, de Vos, and Bossema (1972) have related the differences in the social structure of Red Grouse and Black Grouse to differences in the variety and dispersion of their foods. The Red Grouse subsists primarily on the leaves and shoots of one plant, *Calluna vulgaris*, which is dominant over large areas. Female Black Grouse preceding and during egg-laying have a more diverse diet and range over a larger area. Kruijt, de Vos, and Bossema (1972) point out that only when food is more or less uniformly distributed can a male efficiently defend a territory large enough to supply his mate's nutritional requirements (see Brown, 1964).

Among grouse, however, uniformly distributed food resources are not always associated with large male territories or monogamy. The Sage Grouse (Category I), in particular, consumes little except the leaves of one species of plant, *Artemisia tridentata*, which is the dominant plant in the Sage Grouse's habitat. Nor do more diverse diets and less uniformly dispersed food always imply promiscuity and absence of large male territories. Populations of the Willow Ptarmigan other than the Red Grouse consume twigs, buds, leaves, and catkins from a variety of shrubby plants. In a population in Alaska, pairs with territories in poor habitat

trespassed on territories in optimal habitat in order to feed there (Moss, 1972). Here the failure of a female to restrict her movements to her mate's territory evidently does not preclude pair-bonding. Hazel Grouse and Ruffed Grouse occupy similar habitats and presumably experience similarly dispersed food supplies, but they differ appreciably in their social behavior.

Among the grouse with dispersed males and promiscuous sexual relations (Category II), female movements prior to egg-laying are normally not restricted to any one male's territory (see above). To decide whether this tendency is a cause or a consequence of promiscuity would require careful analysis. For instance, although female Ruffed Grouse wander widely with respect to the males' stations, such large, widely overlapping ranges might arise either because the females have no attachments to individual males or because no smaller area would include adequate food resources. When food supplies are uniformly distributed, females could presumably find as much food on larger, more overlapping ranges as they could on smaller, more exclusive ranges. The evolution of large male territories in grouse and the restriction of females' movements to these territories evidently requires both a uniformly distributed food supply and monogamy. A uniform dispersion of food resources seems necessary, but not sufficient, for the evolution of large male territories in grouse.

The effects of food dispersion on the movements of individuals thus seem not to explain the evolution of grouse social structure. The effects of food dispersion on social structure, however, do not necessarily act directly through effects on the movements of individuals. A later section will discuss the relations among social structure, sexual bimaturism, and body size in grouse and will raise the possibility that a species' food supply might affect its social structure more indirectly, through an effect on the evolution of its body size. Elucidation of the relationship between feeding strategies and social structure in grouse will probably require a more exact knowledge of feeding strategies and food dispersion than is now available.

Mortality Rates and Clutch Sizes

Mortality rates and clutch sizes vary considerably from population to population and from

year to year within any one species. Differences among the species are generally not apparent from the evidence now available, and no correlations with social systems are evident. Measurements of adult mortality rates have ranged from 25 per cent to 80 per cent per year (see Wiley, 1973a; also Robel, Henderson, and Jackson, 1972). Several comparisons of mortality rates in the second and later years of life have suggested that mortality rates remain constant after the first year. Three reports on two species, the Red Grouse and the Blue Grouse, indicated that there are no differences between the sexes in mortality (Jenkins, Watson, and Miller, 1967; Bendell and Elliott, 1967; Boag, 1966). Male Ruffed Grouse, however, evidently survive slightly better than do females (Gullion and Marshall, 1968). Some limited evidence suggests that the same holds for male White-tailed Ptarmigan (Choate, 1963).

The only comparison of mortality rates for two species in the same region is Helminen's (1963) report on Capercaillie and Black Grouse in Finland. The larger species had much lower mortality, about 40 per cent in comparison with roughly 80 per cent.

Clutch sizes likewise vary considerably within a single species, when samples from different areas or years are compared. The nutrition of the females in the period preceding and during laying can affect the average clutch size (Jenkins, Watson, and Miller, 1967). For most species the average clutch sizes reported in the literature fall between 5 and 9 eggs per clutch, and usually between 6 and 8. Three species consistently average 11 to 12 eggs per clutch: Greater Prairie Chicken, Sharp-tailed Grouse, and Ruffed Grouse. Large average clutch sizes thus have no clear relationship with habitat or social system.

THEORIES OF THE EVOLUTION OF POLYGyny

Theories of the adaptedness of polygynous mating systems among birds fall into two groups. Although they share a number of features, they may be labeled for convenience the "surplus-food" and the "patchy-environment" theories. The surplus-food theory, the earlier of the two, proposes that the absence or reduction of male parental care, a prerequisite for the evolution of polygyny, should prove adaptive only in species that have a superabundance of food available to the breeding females.

Once males are liberated from parental duties, competition among them will restrict mating opportunities to a minority (see Armstrong, 1955; Crook, 1962, 1964; D. Snow, 1963; Lack, 1968).

According to this theory, polygyny should evolve frequently in species whose food supply during the breeding season is so abundant that one parent can feed the young nearly as successfully as two. The rate at which a parent can supply food, for a given investment of time and energy in foraging, will depend both on the rate at which the food supply is generated in the environment and on the number of other individuals simultaneously exploiting that same supply. Consequently, for food to remain easily available during the breeding season, the density of hungry nestlings must not rise in proportion to the supply of food to feed them.

These arguments can help explain why polygyny evolves among species with dense but highly seasonal food sources, like the seed-eating ploceine weaver birds of tropical savannas (Crook, 1962, 1964), an environment in which seeds become available in great quantities for that brief period each year during which the finches breed. With this sudden surge in the food supply, food evidently becomes easily available in spite of the increased demand for food during the breeding season. Polygyny also emerges frequently among tropical fruit- and nectar-eating birds that build open nests (D. Snow, 1962, 1963; B. K. Snow, 1970, 1972). The high mortality sustained by such nests in the tropics would favor cryptic nests, small clutch sizes, and infrequent visits to feed the young. In these circumstances, the density of nestlings and the parental time and energy required to feed them might remain relatively low in relation to the food supply.

Long-distance foraging to feed the nestlings could also favor full parental cooperation (Orlans, 1969). Thus species that nest colonially in protected sites, such as isolated trees or marshes, at some distance from their source of food, tend to have less polygynous breeding sex ratios and more male parental care than do related species that forage nearer their nests (Orlans, 1961; Crook, 1962).

Although two parents could presumably always provide more food than could one, two might not provide food as efficiently as one, if the second parent by his own food consumption sufficiently reduced the supply of food

nearby. In some species polygyny might decisively increase the availability of food near nests by reducing the number of males foraging there. Under these conditions, it could prove more efficient for one parent to feed the young on food found nearer the nest than for both parents to rear the young on food collected at greater distances.

The surplus-food theory thus focuses on the evolution of single parental care as the critical process in the evolution of polygyny. Reduced male parental care leads to competition among males, which in turn is assumed to generate an unequal distribution of matings and consequently polygyny.

The patchy-environment theory, like the surplus-food theory, proposes that polygyny will evolve only when a reduction in parental care by the male has minor consequences for the female's nesting success. The patchy-environment theory, however, formulates more precisely the conditions under which polygyny will evolve, especially for species in which females nest within the territories of individual males (Verner, 1964; Verner and Willson, 1966; Orians, 1969, 1972). Polygyny should evolve only when those females mated bigamously with males in prime habitat breed more successfully, in spite of reduced help from their mates, than do females mated monogamously in poor habitat. In optimal areas, any disadvantages of single parental care are offset by the greater availability of food near the nest. For polygyny to evolve according to this model, the availability of food must differ considerably from one male's territory to another. Such patchy environments apparently often confront insectivorous birds nesting in fresh-water marshes. The availability of food is again a critical consideration. The density of nesting females in optimal areas must remain low enough to insure a high ratio of supply to demand for food there.

It should be noted that, among birds with nidicolous young, polygyny is often partially compatible with male parental care (Verner and Willson, 1969). When the females mated to one polygynous male have staggered nesting cycles, the male can contribute some time to feeding the young of both his mates (Haartman, 1951; Williams, 1952; Lanyon, 1957; Verner, 1964; Willson, 1966). In these circumstances one female, usually the first, receives preferential treatment from the male (Haartman, 1951; Williams, 1952).

The patchy-environment theory assumes that competition among males will limit the number of males that can establish territories in prime areas. Both theories of the evolution of polygyny thus directly address the evolution of single parental responsibility and assume that competition among males will restrict successful mating to a few as male parental care wanes.

Certainly, among grouse, the advantages of dual parental care seem minimal, owing to their predominantly herbivorous diets and precocial young (Orians, 1969). It is not clear, then, why dual parental care should have greater advantages for one of the species, the Willow Ptarmigan, than for the others. Furthermore, single parental care is not inevitably associated with polygyny, for three species in two genera practice monogamy although the males rarely contribute to brood care: Hazel Grouse, Rock and White-tailed Ptarmigan. Although the grouse are evidently all closely related species, many of them have evolved polygyny, whereas others with reduced male parental care have not. Monogamy with single parental care is also frequent among the Anatidae and Scolopacidae (Lack, 1968).

The specific features of the patchy-environment theory do not easily apply to grouse. In only three species does a female regularly restrict her choice of a nest-site to her mate's territory: Willow Ptarmigan, including Red Grouse; Rock Ptarmigan; and Hazel Grouse. These species are all normally monogamous. The patchy-environment theory might well explain the occasional instances of bigamy in these species. For most grouse, though, the availability of food or nest-sites within the male's territory probably has had little influence on the evolution of polygyny. Although the adaptedness of single parental care is perhaps necessary for the evolution of polygyny among grouse, it evidently is not sufficient.

SEXUAL BIMATURISM AND THE EVOLUTION OF POLYGyny

The coincidence of polygyny with deferred reproduction among males suggests a second contributing adaptation. Selection for sexual differences in the age at onset of breeding, provided that females survive about as well as males, would tend to produce unbalanced breeding sex ratios, and hence polygyny. When the consequent polygyny is incompatible with

fully shared parental care, the evolution of mating systems would then depend on a balance between the adaptive advantages of dual parental care and the adaptive advantages of sexual bimaturism.

The two theories reviewed above both accept without much comment the notion that competition among males will inevitably generate polygyny, once the need for male parental care wanes. This assumption is accepted because the evolutionary benefits of multiple mating have seemed self-evident. Yet, owing to the deferment of breeding among males of polygynous species, the advantages of polygyny to males are not so simple.

By delaying reproduction, males considerably jeopardize their rates of reproductive increase (Birch, 1948; Cole, 1954; Lewontin, 1965) and hence the spread of their genes in the population. Early breeding must therefore have counteracting disadvantages in order to allow the evolution of delayed reproduction (Lack, 1954; Williams, 1966a,b; Gadgil and Bossert, 1970). Any complete theory of the evolution of polygyny must thus consider the conditions necessary for the evolution of deferred reproduction among males.

The suggestion that sexual bimaturism might provide one key to the evolution of polygyny in grouse raises a number of questions, which the following sections will consider. It is important at the outset to separate clearly the proximate and ultimate controls of deferred breeding by polygynous males (see Lack, 1954, 1965; Mayr, 1961; Orians, 1962). Accordingly, I will consider the development of male reproductive behavior in polygynous species before considering its evolution.

Development of Reproductive Behavior in Males

Delayed reproduction among males in polygynous species is associated with prolonged physiological immaturity. I have reviewed above the evidence for this correlation among grouse, and similar patterns of delayed maturation are probably found in most polygynous birds. Plumages of first-year males in polygynous species often resemble female plumages or are intermediate between adult male and female plumages (Crook, 1962, 1964; Selander, 1965). Among certain polygynous mammals young males usually reach full size only at about the age when successful breeding begins (Carrick

et al., 1962; Geist, 1968, 1971).

Because spermatogenesis in males of polygynous birds can begin well before successful breeding or full maturity, year-old males probably have the capacity to copulate successfully. The testes of younger males, however, do not match in size those of older males. At least in the lek-forming grouse, the later and lesser growth of the yearlings' testes probably insures that the older males arrive earlier on the leks in the spring and have stronger motivation to defend their positions on the lek. The infrequency with which younger males mate is thus most likely an immediate result both of the inadequate development of their secondary sexual characters and of their inadequate motivation to defend positions and perform displays attractive to females.

This retarded maturation might result from behavioral subordination of younger males to older males, or it might occur independently of any interactions with older males. In flocks of domestic fowl, full development of the testes is inhibited in subordinate cocks, a process that Guhl, Collias, and Allee (1945) term "psychological castration." This effect also occurs in house mice (Lloyd, 1971). As older animals are likely to dominate younger ones, the importance of social interactions in the delayed reproductive maturation of males seems likely.

In field experiments, the removal of older territorial males often results in disproportionate recolonization by younger males. Such results have been obtained with Blue Grouse and Ruffed Grouse, as reviewed above, and with other birds (Orians, 1961; Krebs, 1971). Apparently the presence of older males inhibits the expression of territorial behavior by younger males. The behavioral mechanisms that produce this inhibition remain largely unexplored. Young male Red-winged Blackbirds only colonize vacancies late in the breeding season (Orians, 1961). This observation suggests either that adult males become progressively less motivated to establish new territories (see Peek, 1971) or that first-year males become aggressive later in the season than do adults, or that both changes occur.

Other evidence suggests that social interactions with older males probably do not completely determine the physiological immaturity of young males. Field experiments by Kirikov (cited in Dementiev and Gladkov, 1967) indicated that young male Capercaillie retained the

usual seasonal retardation in their activities even after all the older males had been removed from their leks. Those first-year male Blue Grouse that obtain territories have testes similar in size to those of other year-old males and smaller than those of older males (Bendell and Elliott, 1967). In spite of this difference in gonadal development, territorial first-year males occupy areas of about the same size as those occupied by older males. However, they tend to abandon their territories earlier in the spring. It is not known whether those first-year males that establish territories mate as successfully as older territorial males.

The developmental processes that regulate the onset of successful breeding in males of polygynous species probably involve both (1) behavioral interactions between older and younger males, and (2) maturational processes independent of social interaction. To my knowledge, no experiments on the control of reproductive maturation in males have evaluated these two possibilities or have compared related monogamous and polygynous species.

Evolution of Deferred Reproduction among Males

The physiological and behavioral mechanisms that control the development of reproductive capacity in males do not explain the selection pressures behind the evolution of these ontogenetic processes. An explanation for the evolution of any trait requires some demonstration that the trait increases an individual's fitness, the rate at which an individual transmits his genes to his descendants. The rate at which descendants propagate is specified by the rate of reproductive increase, the Malthusian parameter (Lotka, 1956; Fisher, 1958). Unless some form of balancing selection has produced a stable polymorphism, genes associated with higher rates of propagation would eventually replace those associated with lower rates of propagation. Any lineage of a male and his sons that had a higher rate of reproductive increase would thus spread its genes in the population relative to other genes. Females would also acquire advantages in disseminating their genes by mating with males with relatively higher rates of reproductive increase.

The rate of reproductive increase depends not only on fecundity but also on the age of reproduction. For any schedule of age-specific

survival, delayed reproduction must reduce an individual's expected production of offspring. For delayed reproduction to evolve, this disadvantage must have compensations. Recent mathematical analyses (Williams, 1966a; Gadgil and Bossert, 1970; Wiley, 1974) have suggested that two conditions, when sufficiently pronounced, could favor the evolution of delayed reproduction: a high risk of mortality during reproduction; and fecundity increasing with age. Lack (1954, 1968) had proposed these explanations for the evolution of delayed breeding by both sexes in a number of monogamous species.

These arguments might also apply to deferred reproduction among males in polygynous species, as Selander (1965, 1972) has recognized. If a young male, by reproducing, so jeopardizes his chances of survival to the following breeding season and yet gains a sufficiently small expectation of progeny that would survive to reproduce, then by breeding at an early age a male might actually reduce the dissemination of his genes in the population.

As a result of any postponement of reproduction among males to a later age than among females, the breeding sex ratio in a population will increase. This ratio will also depend on the age-specific survival rates of the sexes, as sex ratios at hatching are about equal in birds regardless of their mating systems (Willson and Pianka, 1963; Selander, 1960, 1965), and on the rate of increase of the population. Could these increased chances for mating at later ages compensate for the effects of postponed reproduction on a male's rate of reproductive increase?

To explore this possibility I have calculated the increase in fecundity that would maintain a rate of reproductive increase (r) equal to zero in spite of a delay in the onset of reproduction from Age 1 to Age a (Appendix; Fig. 2). This value exactly equals the increase in expected fecundity of males that would result from delayed reproduction by all males in a population from Age 1 to Age a (Appendix). Thus, an increase in the expected fecundity of males, owing to sexual bimaturism in a stable population, would just compensate for the effects of delayed reproduction on the rate of reproductive increase for males.

These calculations assumed a stable population ($r = 0$). In reality, grouse populations

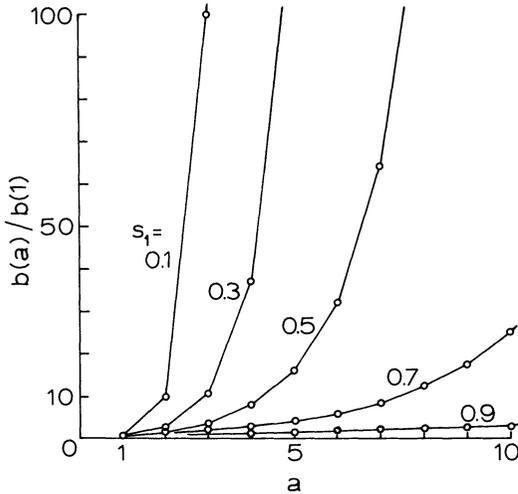


FIG. 2. THE INCREASE IN EXPECTED FECUNDITY, $b(a)/b(1)$, NEEDED TO MAINTAIN $r = 0$ WHEN THE AGE AT ONSET OF REPRODUCTION IS DELAYED FROM AGE 1 TO AGE a

The different curves represent different values of pre-breeding survival, s_1 . See Appendix for derivation of the functions.

fluctuate in size considerably over periods of several years, owing to changes in mortality or fecundity, or both, from year to year. Lotka's standard equation for r , on the other hand, assumes that age-specific mortality and fecundity remain constant with time. In the long run, however, r usually averages close to 0, and age-specific mortality and fecundity, when averaged over relatively long periods, probably do remain nearly constant. In a steadily increasing population, the proportion of younger individuals would be greater than in a steady population, and consequently the expected fecundity of males in a population with sexual bimaturism would also be greater. In this circumstance, therefore, males would have an expected rate of reproductive increase greater than 0, like the population as a whole.

A comparison of two populations, one with sexual bimaturism and one without, is not strictly pertinent to the initial stages of the evolution of bimaturism. Initially, in a population without sexual bimaturism, delayed reproduction by an individual male and his male descendants would not produce much change in their expected fecundities later in life. For postponed breeding to evolve when the expect-

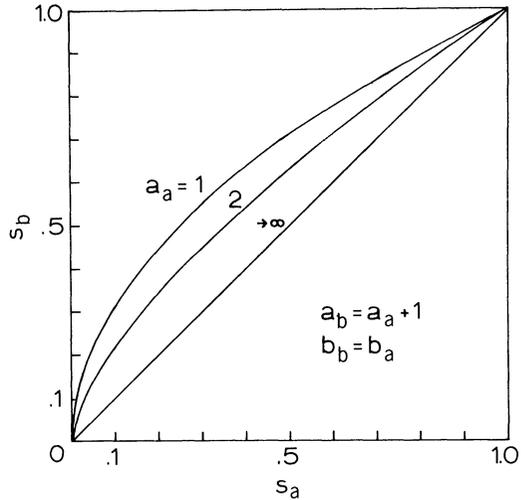


FIG. 3. PRE-BREEDING SURVIVAL WITH DELAYED REPRODUCTION, s_b , AS A FUNCTION OF PRE-BREEDING SURVIVAL WITH EARLIER REPRODUCTION, s_a

For both strategies $r = 0$, although the ages at onset of reproduction differ by one year (a_a and $a_a + 1$) and the annual fecundity of a breeding male does not change. The different curves represent different ages, a_a , at onset of reproduction in the early-breeding strategy. See Appendix for derivation of the functions.

ed fecundity of a breeding male does not change, compensatory increases must occur in early survival. I have calculated, again when $r = 0$, the increase in survival prior to reproduction that will just compensate for a delay in the onset of reproduction from Age 1 to Age a , when fecundity does not change (Appendix; Fig. 3). Thus, when delayed breeding is accompanied by this compensatory increase in early survival, a male's genes will just reproduce themselves and thus will not change in frequency in a stable population. Any greater increase in early survival as a result of delayed breeding, or any concurrent increase in later fecundity, would allow the relevant genes to reproduce faster than the population as a whole. With sufficiently reduced survival as a consequence of early reproduction with or without increasing fecundity at later ages, males that postpone the onset of breeding might increase the dissemination of their genes.

This conclusion takes into account the fact that survival and reproduction are not usually independent attributes of an organism. The

limited time and energy available to an individual are partitioned among its various metabolic activities or are temporarily stored in the form of chemical bonds. Expenditure of time and energy for reproduction is often incompatible with expenditures for other activities, all of which in different ways subserve the maintenance and growth of the organism. The allocation of time and energy at each stage of an individual's life to reproduction and maintenance will in part determine his age-specific fecundity and survival and the spread or persistence of his genes in the population. The genes of individuals with more nearly optimal age-specific allocations of time and energy should prevail. At different ages there will pertain different optimal compromises between investing time and energy in reproduction and investing time and energy in individual maintenance. At older ages, as life-expectancy decreases, natural selection should favor a greater investment of time and energy in reproduction.

Although this approach provides a suitable framework for analyzing the evolution of life-history patterns (cf. Tinkle, Wilbur, and Tilley, 1970; Tinkle and Ballinger, 1972), it has not previously entered into discussions of the evolution of mating systems. It seems probable that the evolution of sexual differences in life-history strategies would contribute to the evolution of polygynous mating systems. Sexual bimaturism, however, might not completely explain the distribution of matings among males in polygynous species. Males of the same age could also differ systematically in mating success, a situation to be considered later (see below, Intrasexual Competition).

Possible Effects of Reproduction on Survival in Male Grouse

To demonstrate that deferred reproduction enhances a young male's chances of survival would require a comparison of mortality rates among young males that engage in different amounts of reproductive activity. That information would prove difficult to obtain. Comparisons of mortality in young, non-breeding males and older, breeding males might present difficulties in interpretation, because reproduction might have greater effects on the

survival of the young, less experienced birds.

In view of the difficulties in obtaining the necessary information regarding survival rates, a more practical approach might indirectly measure the effects of breeding on individual maintenance. Knowledge of the time- and energy-budgets of breeding and non-breeding males would indicate whether young, non-breeding males devote more time than do adults to feeding, resting, and other activities contributing to individual maintenance. Positive results would suggest that breeding activities do limit the time available for individual maintenance. Comparisons made in both monogamous and polygynous species of non-breeding and breeding males would best elucidate the energetic basis for life-history patterns in different mating systems. These comparisons are not yet available for any species. Reports of lek-forming grouse, however, definitely imply that young males devote less time and energy to reproductive activities (see Wiley, 1973a).

Reproductive behavior and morphology might also reduce survival by increasing the conspicuousness or vulnerability of males to predators. Among most of the promiscuous species of grouse, however, males acquire nearly full plumage in their first year. Could year-old males then have any advantage in avoiding predators? Even full-plumaged males are more or less camouflaged in their environments until they assume display postures. Only when neck ruffs are elevated, esophageal sacs inflated, and tails fanned do males become truly conspicuous. Long-distance sounds also only accompany displays. It appears plausible, then, that first-year males might reduce their encounters with predators by refraining from display.

Fights among males appear to have little effect on survival in promiscuous grouse. Although serious injuries are periodically reported in the literature, in three seasons of work with Sage Grouse I never saw a male sustain an obvious injury in a fight. Hartzler (1972), in his extensive work on this species, also never observed a major injury. Fighting might still have indirect effects on survival, as it represents an appreciable expenditure of energy.

Although the evidence is so far only circumstantial, it does seem plausible that young male grouse might actually enhance their survival appreciably by postponing reproduction.

COMPETITION AMONG MALES AND THE EVOLUTION OF
FEMALE CHOICE

Intrasexual Competition

One idea often advanced since Darwin's time to explain the evolution of postponed breeding in males of polygynous species is that year-old males have less chance to mate successfully in competition with older, more experienced males. This explanation defers the question, since one must then explain why intrasexual competitive abilities develop later rather than earlier in life. If other features of their life histories remained constant, males would do best to develop their full abilities for attracting mates early in life. For instance, if a certain intensity of display or coloration were necessary to obtain mates, males that reached this level early in life rather than later, without other changes in life-history parameters, would have the evolutionary advantage. Only when full reproductive activity at early ages sufficiently reduced early survival would deferred development of reproductive abilities increase the rate of reproductive increase for a male's genes.

The evolutionary consequences of competition between males of different ages will thus depend on the consequences of competition for the males' life-history strategies. Competition with other males is one component of male reproductive activities. For the evolution of delayed reproduction, the important thing is thus not competition between males of different ages but competition between males with different overall life-history strategies.

It bears repeating that developmental processes do not explain evolution; instead, these processes themselves evolve to produce adapted individuals. A demonstration that full reproductive capacity required two years of experience would not mean that his developmental process explained the evolution of delayed reproduction. For an evolutionary explanation we need to know how a later development of intrasexual competitive abilities increases an individual male's fitness.

Intrasexual competition between males of different ages needs to be distinguished from intrasexual competition among males of the same age. If inequities in the distribution of matings pertain among like-aged males, the

genes of the more fecund males will spread, provided again that the greater fecundity of these males does not entail overcompensating disadvantages in survival and later reproduction. Other conditions that might allow differences in fecundity to persist among like-aged males include forms of balancing selection, such as heterosis, disruptive, or frequency-dependent selection. Such variation would also persist if the differences in fecundity arose at random with respect to genetic differences among the males.

Individual differences in mating success among like-aged males of polygynous species, although not fully documented for any species, are likely to prove appreciable (for Sage Grouse, see Hartzler, 1972). Among males of a polygynous species one might expect a pattern of progressively increasing average fecundity throughout life, with considerable variance among individuals at each age. Far too little information is available to compare the within-age and the between-age variance in breeding success among the males of any polygynous species. At least in the lek-forming grouse, both contributions to the total variance in the distribution of matings among males are probably substantial.

Female Choice

The behavioral and physiological mechanisms that regulate a female's choice of a mate must once again not be confused with the selection pressures that explain why these behavioral mechanisms increase a female's fitness.

The behavioral mechanisms that regulate a female's choice might include differential responses to variations in the behavior or morphology of individual males. In flocks of domestic fowl, for instance, males that mate frequently also frequently perform those displays that lead to copulation (Lill, 1966). Ethologists have also repeatedly demonstrated in experimental situations that females in breeding condition prefer conspecific males with fully developed secondary sexual characters, or models that mimic these features (for instance, Noble and Curtis, 1939; Hunsaker, 1962; Liley, 1966). Such responses are clearly important in preventing dysgenic hybridization and in coordinating reproductive behavior in mated indi-

viduals. It remains less clear, though, that they can completely explain the operation of polygynous mating systems in the field.

In my study of Sage Grouse, I concluded that the major behavioral differences between successful and unsuccessful adult males were the result, rather than the cause, of their more persistent association with females (Wiley, 1973a). Subsequently, Hartzler (1972) has found some behavioral differences correlated with mating success that do seem to hold in comparisons of adult males at similar distances from females. Female Black Grouse apparently respond differently to differences in the tactics of displaying males (Kruijt, de Vos, and Bossema, 1972; Kruijt and Hogan, 1967). These observers concluded that experience is necessary before a male achieves full success in attracting females ready to copulate. Females here base their choice on features of male behavior that develop with age.

Although female choice might rely partly on individual differences among males, female behavior could also include responses to other females and to the environment. Female Sage Grouse arriving on a lek appear attracted to each other (Wiley, 1973a). One possibility is that females in this species remember the positions of mating centers and tend to return there in subsequent years, and that older females attract younger ones to these sites. Evidence for this possibility is still indirect; one difficulty is that the positions of mating centers on some leks shift considerably from one year to the next, although this seems not to occur on most leks. Female Long-billed Marsh Wrens appear to choose their nesting sites on the basis of the food supply or habitat within a male's territory rather than the male's behavior (Verner, 1963; Verner and Engelson, 1970). This principle might apply to the females of other territorial, polygynous species as well (Kluyver, 1955; Zimmerman, 1966; Wolf and Stiles, 1970).

Female behavior thus might depend on at least three sorts of stimuli: individual differences among males, behavior of other females, and characteristics of particular sites or features of the habitat. Certainly females might respond to more than one class of cues in choosing a mate.

Regardless of what behavioral mechanisms

underlie a female's choice of a partner, these mechanisms should evolve to maximize her chances of mating with fit males and her breeding success. Unless delayed reproduction of the male increased the spread of his genes, a female's genes would propagate faster if she selected a younger male and thus left sons that would also tend to breed at an early age. In general, then, females should not evolve mechanisms for choosing older mates, unless early breeding by a male decreases his fitness.

An assertion that females choose older males because these have demonstrated their ability to survive (for instance, Robel, 1967; Koivisto, 1965) assumes incorrectly that male fitness consists only in survival. Likewise, an assertion that a male's fitness consists in the number of females with which he mates is also only partially correct, because reproductive rate depends not only on fecundity but also on the age of breeding and on the consequences that breeding at a given age have for survival. An explanation for the evolution of the females' behavior requires a full understanding of the adaptive significance of males' life histories.

EVOLUTION OF SEXUAL BIMATURISM: TENTATIVE CONSIDERATIONS

Granted that the adaptedness of sexual bimaturism might contribute to the evolution of polygyny, what ecological differences might explain the evolution of sexual bimaturism in some species of grouse but not others? Here again the correlations between social structure and other attributes can provide some clues. The only identified correlates of sexual bimaturism and polygyny among the grouse are greater sexual dimorphism in size and larger overall size. The adaptive advantages of these characteristics, in the absence of overriding disadvantages for single parental care, could plausibly predispose a species to evolve sexual bimaturism and thus polygyny.

Larger size might prove adaptive for grouse because of changes in their energy balance and susceptibility to predation. A larger size should normally reduce the number of potential predators and thus might increase life expectancies. This possibility receives tentative support from Helminen's (1963) study of mor-

tality among Black Grouse and Capercaillie in Finland (see above). Larger size, especially in homeotherms, also entails proportionately lower rates of heat loss and consequently both lower metabolic rates per gram of body weight and greater resistance to temperature fluctuations (Rensch, 1960; Kendeigh, 1972). For these reasons, larger animals in a given biotope are probably more likely to have population densities consistently near the limit of resources. In these circumstances, a greater emphasis on survival, especially early in life, might well favor the spread of an individual's genes (MacArthur and Wilson, 1967; Pianka, 1972; MacArthur, 1972). Larger size might in this way contribute to the evolution of deferred reproduction. For grouse, the diversity of their mating systems and their life-history patterns might thus depend in part on the diversity of their body sizes.

Species differences in body size among grouse are not easily explained with our present knowledge. The reason why some species have not evolved large size might have to do with the availability of their particular food supply. It is particularly at times of food shortage that the additional food required by larger animals would put them at the greatest disadvantage. The energetic advantages of larger size presuppose that the amount of food an animal can assimilate increases in proportion to the absolute increase in its energy requirements. If this proportionality does not obtain, animals might be expected to evolve a body size that assured a minimum but sufficient margin between the amount of food an individual could collect per day and the amount normally required for existence metabolism. The rate of food acquisition as a function of body size would depend in turn on such factors as the dispersion and abundance of food items, the mobility of the animal, and the animal's capacity to locate and harvest the food.

Sexual dimorphism in size and sexual bimaturation would evolve if large size and delayed reproduction did not have the advantages for females that they do for males. Egg production requires an additional margin between the amount of energy a female can collect as food and the amount of energy she needs for existence metabolism. If the amount of food a larger female grouse could collect each day does not

increase in proportion to the increase in her existence energy requirements, egg production could prove incompatible with larger size. Instead, to allow a large clutch, a female would do better to evolve a body size that maximized the margin between normal existence energy requirements and the rate of food acquisition. That production of a clutch of eggs is in fact a nutritional strain on a female is suggested by evidence that female grouse lay fewer eggs when food quality is low (Jenkins, Watson, and Miller, 1967). In addition, unlike a male, a female grouse cannot increase her fecundity by postponing breeding. Her annual fecundity will always equal the number of eggs she produces during her short breeding season. The potential advantages of postponing reproduction at early ages in favor of greater survival are thus reduced for females. In polyandrous birds the selection pressures on female body size are probably very different (Jenni and Collier, 1973).

Sexual dimorphism in size could also evolve to reduce intersexual competition for limited food supplies (Selander, 1966, 1972; Schoener, 1967, 1969). However, because the diets of all species of grouse are similar in kind, the advantages of reducing intraspecific competition for food thus seem equal for all. Nevertheless, this advantage might contribute to the evolution of sexual dimorphism in size among grouse, even if it does not completely explain it. Male and female Capercaillie tend to feed in different parts of spruce trees, for instance (Seiskari, 1962).

A standard explanation for the evolution of sexual differences in body size is that large size is an advantage for males in intrasexual competition (Selander, 1972). A corollary is that females are a more nearly optimal size for the species' particular food habits and habitat. The additional growth of males is thus viewed as one component of the male's reproductive effort. In polygynous grouse, however, first-year males attain virtually full adult weight, although in other respects their reproductive physiology remains immature. It would thus seem that larger size is an advantage in itself to these younger males, independent of any advantage in reproduction. Among certain polygynous mammals, on the other hand, males attain full size only around the beginning of full repro-

ductive activity (Carrick et al., 1962; Geist, 1968a,b). Among these mammals, then, changes in body size during a male's life parallel changes in other components of reproductive effort.

Body size clearly evolves in response to a variety of selection pressures with complex interactions. Energy balance, exposure to predators, niche differentiation, and agonistic success probably constitute only a partial list of these selection pressures. Our present knowledge is insufficient to specify the particular ecological conditions that make larger size and greater sexual dimorphism in size advantageous for some grouse and not others. The adaptive pattern for polygyny among grouse nevertheless seems clear: for large grouse the combination of larger males with postponed breeding and smaller females that lay large clutches beginning in their first year evidently represents the optimal combination of male and female life histories. The ecological circumstances that affect the evolution of social systems among grouse thus probably act in part indirectly, through their influence on the evolution of sexual differences in body size and life-history strategies.

CONCLUSIONS: A TWO-FACTOR THEORY FOR THE EVOLUTION OF POLYGyny

Polygyny among grouse has evolved as one component in a coadapted complex, which also includes adaptations in body size, life-history patterns, and parental care. Because polygyny entails both sexual bimaturism and single parental care, polygyny should evolve only when the advantages of deferred reproduction among males outweigh any disadvantages of single parental care. When delayed reproduction occurs among males, single parental care and intrasexual competition among males are not alone sufficient conditions for the evolution of polygyny. The ecological conditions that influence the evolution of polygynous mating systems thus act through their dual effects in reducing the advantages of dual parental care and increasing the advantages of sexual bimaturism.

Among grouse, the evolution of sexual bimaturism appears related to the evolution of sexual dimorphism in size and larger overall size of the species. The evolutionary advantages of

deferred reproduction probably increase in saturated environments. At least among grouse, this condition should pertain especially to those with larger size. Deferred reproduction will evolve more readily among male grouse than among females, when a female's size is limited by the energy required for egg production, and her annual fecundity is limited to one clutch.

In other groups of birds as well, sexual bimaturism and polygyny probably correlate with large overall size and sexual dimorphism in size. Although thorough studies are needed for verification, correlations between overall size and mating system probably obtain within the Phasianidae, Cotingidae, Paradisaeidae, and Icteridae. In several tropical avian families, however, notably the Pipridae and Trochilidae, polygyny appears unrelated to size. At least in the Pipridae, polygyny is associated with sexual bimaturism (D. W. Snow, 1962, 1963), as usual among birds and mammals. In these families the evolution of sexual bimaturism and polygyny presumably depends on different patterns of adaptation than those pertaining to grouse.

The general principles underlying the evolution of polygynous mating systems in grouse should, nevertheless, apply widely. Whenever sexual bimaturism is a concomitant of polygyny, the evolution of mating systems is inextricably associated with the evolution of sexual differences in life-history strategies. As a general rule, sexual bimaturism should evolve when the optimal age-dependent expenditure of reproductive effort differs for the two sexes. To the extent that polygyny is incompatible with dual parental care, the evolution of polygyny would then depend on the relative advantages of delayed reproduction in males and dual parental care.

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APPENDIX

(1) The increase in fecundity that is necessary to compensate for a delay in the onset of reproduction from Age 1 to Age a , when $r = 0$:

Using the standard equation for discrete breeding seasons (Andrewartha and Birch, 1954),

$$1 = \sum_{x=0}^{\infty} e^{-rx} l(x)m(x),$$

and setting $r = 0$, $m(x) = 0$ when $x < a$, $m(x) = b$ when $x \geq a$, and $l(x) = s_1 s_1^{(a-1)} s_2^{(x-a)}$ where s_j is survival from Age 0 to Age 1, s_1 is annual survival from Age 1 to Age a , and s_2 is annual survival after Age a , we obtain

$$1 = b s_1 s_1^{(a-1)} \sum_{x=1}^{\infty} s_2^{(x-1)} = \frac{b s_1 s_1^{(a-1)}}{1 - s_2}.$$

Consequently,

$$b = \frac{1 - s_2}{s_1 s_1^{(a-1)}},$$

and

$$\frac{b(a)}{b(a=1)} = s_1^{(1-a)}.$$

(2) The increase in expected fecundity of males that results from delayed reproduction of all males in a population from Age 1 to Age a , when $r = 0$:

The expected fecundity of a male was taken as the ratio of breeding females to breeding males, the reciprocal of the breeding sex ratio, which depends on the mortality rates and ages at first breeding for both sexes. I have assumed here that all males of breeding age fertilize equal numbers of eggs each year or, at least, that differences in fecundity among breeding males arise randomly.

If we assume a constant birth rate and a primary sex ratio equal to one, then the reciprocal of the breeding sex ratio,

$$1/BSR = \frac{\sum_{x=1}^{\infty} S_j S_1^{(A-1)} S_2^{(x-1)}}{\sum_{x=1}^{\infty} s_j s_1^{(a-1)} s_2^{(x-1)}},$$

where upper and lower case designate parameters for females and males, respectively. If $S_j = s_j$ and $A = 1$, then

$$1/BSR = \frac{\sum_{x=1}^{\infty} S_2^{(x-1)}}{s_1^{(a-1)} \sum_{x=1}^{\infty} s_2^{(x-1)}} = \frac{(1 - s_2) s_1^{(1-a)}}{(1 - S_2)}$$

Consequently,

$$\frac{BSR(a)}{BSR(a = 1)} = s_1^{(1-a)}$$

(3) The increase in early survival that will compensate for a delay of k years in the onset of breeding,

when $r = 0$ and fecundity of breeding males does not change:

Here I compare two strategies, (a) one in which the age at first breeding is a , $s_1 = s_a$, and $s_j = cs_a$, $c < 1$; and (b) another in which the age at first breeding is $a + k$, k an integer greater than 0, $s_1 = s_b$, and $s_j = cs_b$. The fecundity (b_a and b_b) and survival of breeding males (s_2) is equal in both strategies.

Using an equation derived in section (1) above,

$$\frac{b_b}{b_a} = \frac{s_a^a}{s_b^{(a+k)}} \quad \text{or} \quad s_b = s_a^{(a/(a+k))}$$

Because a and k are both positive, $s_b > s_a$.