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POTENTIAL POLYGAMOUS BREEDING BEHAVIOR IN NORTHERN BOBWHITE

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Abstract: Breeding behavior of radio-tagged northern bobwhite (*Colinus virginianus*) was observed at Fort Bragg Military Reservation (n = 19), North Carolina, in 1985–88, and Tall Timbers Research Station (n = 27), Florida, during 1984–86. We observed apparent polygamous breeding behavior in 95% (18 of 19) of the radio-tagged northern bobwhite at Fort Bragg, and 93% (25 of 27) of the birds at Tall Timbers. We documented 5 cases of double-clutching by radio-tagged females. Twenty-seven percent of Fort Bragg clutches (n = 30), and 20% of Tall Timbers clutches (n = 56) were incubated by radio-tagged males. Northern bobwhite exhibited characteristics of both rapid multiclutch and ambisexual polygamous mating systems. Northern bobwhite are capable of uniparental care, have long breeding seasons, live in an environment with fluctuating resources, suffer high predation pressure during the nesting season, and raise precocial young; all traits that are similar to other bird species which have evolved polygamous mating systems.

Key words: breeding behavior, *Colinus virginianus*, Florida, North Carolina, northern bobwhite, polygamy.

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Despite more than 50 years of research, the breeding biology of the northern bobwhite is poorly understood. Most researchers have assumed bobwhite form monogamous pairs, and will renest after the loss or abandonment of a previous nest (Stoddard 1931, Lehmann 1946, 1984, Rosene 1969, Johnsgard 1973, Roseberry and Klimstra 1984). Stettner et al. (1966) examined monogamous behavior by switching mates of several pairs of penned northern bobwhite. The high level of aggression observed when new birds were introduced in a captive environment was thought to be indicative of strong monogamous bonds. Brill (1934) reported polygyny in captive northern bobwhite with a ratio of 1 male:2 females or 2 males:7 females. Baldini et al. (1952) noted that these sex ratios were likely only under laboratory conditions, and stated that northern bobwhite were monogamous in the wild.

Stanford (1953) examined the breeding behavior of captive northern bobwhite, and found that 3 pairs attempted a second nest after the first one was successful. When the first brood reached 13-15 days old, the female started a second nest, leaving the male to assume parental care for the first brood. Kiel (1976) also observed renesting attempts by captive northern bobwhite after pairs had successfully hatched initial clutches.

Stoddard (1931) documented that males may take over incubation duties, and either sex may be found at a nest. One sex assumed the primary role of incubating eggs for each nest. Studies in Georgia (Stoddard 1931) and Illinois (Roseberry and Klimstra 1984) indicated that males incubated about 26% of clutches. Male incubation of eggs and subsequent brood-rearing emancipates the female and increases the possibility of her mating again (Emlen and Oring 1977) with either the same or a different male. When uniparental care can meet brood-rearing requirements, desertion by 1 parent may lead to higher reproductive success than staying with the brood (Maynard Smith 1977). However, previous research provides little direct evidence of either monogamy or polygamy for the northern bobwhite.

Recent advances in transmitter design (Shields et. al. 1982) have allowed researchers to locate

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individually-marked northern bobwhite throughout the breeding season (Sermons and Speake 1987, Curtis 1990). During 1985, Sermons and Speake (1987) observed that 6 of 16 (38%) females had broods which disappeared when the chicks were 7-35 days of age. These 6 females soon paired with males, and 4 renested. During 1986, 2 of these 6 females again successfully produced second broods. It was not known if juvenile mortality, brood abandonment (Lehmann 1984), surrogate parenting (Stoddard 1931), or some combination of these factors was responsible for brood disappearance. Sermons and Speake (1987) did not say whether radio-tagged females paired with the same males for their second nest attempt. If broods or clutches were left in the care of the male that fertilized the eggs, and females mated with different males for a second nest attempt (i.e., polyandry), then the potential exists for a polygamous mating system in northern bobwhite.

The purpose of this paper is to describe the breeding behavior of radio-tagged northern bobwhite in North Carolina and Florida.

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STUDY AREAS

We observed the breeding behavior of northern bobwhite at TTRS in 1984-86, and at FB during 1985-88. Tall Timbers encompasses nearly 1,300 ha in northern Leon County, Florida. This site lies within the Tallahassee Red Hills subregion of the Coastal Plain, and is characterized by rolling clay hills with gentle to moderate slope (Hendry and Sproul 1966). Approximately 85% of TTRS is woodland, primarily open stands of loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) interspersed with live oak (*Quercus virginiana*). Smith (1980) provided a detailed habitat description of the area. Habitat at TTRS supports some of the highest northern bobwhite numbers in the southeastern United States Coastal Plain, and densities greater than 1 bird/0.4 ha have been observed. However, northern bobwhite populations have declined at TTRS since peak numbers were observed in the early 1970's. Based on Petersen estimates from recaptures of banded bobwhite, O'Brien et al. (1985) estimated there were 976 birds occupying TTRS in 1979, compared to 515 bobwhite in 1982.

Fort Bragg lies within the Sandhills region of Cumberland and Hoke counties, North Carolina. Sandhills vegetation has been described by Wells (1932) and Wells and Shunk (1931). The longleaf pine-scrub oak-wiregrass (*Pinus palustris-Quercus laevis, Q. marilandica, Q. incana, Q. margaretta-Aristida stricta*) community is found on undisturbed upland sites. Fort Bragg contains approximately 55,000 ha, of which about 70% are woodland. Long burning rotations (5 years) and infertile soils result in a sparse herbaceous layer with few native legumes. Estimates from covey-mapping, trapping, and following radio-tagged northern bobwhite, indicated fall densities of approximately 1 bird/8.1 ha. Data from controlled check stations at FB indicated bobwhite populations peaked during 1972 (approximately 9,000 birds harvested postwide), and then declined dramatically through 1986 (approximately 650 bobwhite harvested postwide; Curtis et al. 1989).

METHODS

Northern bobwhite were captured primarily in funnel traps similar to those described by Stoddard (1931:443). Peak trapping occurred in January and February at both study areas. Additional bobwhite were captured during May through October at FB, and throughout the year at TTRS. Funnel trap sites were usually prebaited with cracked corn at least 10 days before each capture attempt. At TTRS, traps were placed at a density of 1 per 2-2.5 ha, and covered with vegetation to conceal them from predators. At FB, trap densities were about 1 per 4-4.5 ha, and traps were concealed at problem locations. Additional bobwhite were caught by night-netting at roost sites (Labisky 1968), and males were captured during breeding season in mist nets to which they were attracted by a tape-recorded call (Cink 1975).

Northern bobwhite caught for the first time were sexed and marked with an aluminum leg band. Once a bird was captured and radio-tagged, additional efforts were made to radio-tag at least 1 other covey member. The transmitter used at both study sites was a logic-operated, crystal-controlled oscillator designed by Shields et al. (1982). The 6-8 g collar was worn as a medallion below the crop and concealed under breast feathers. During a field test of this transmitter, no differential mortality was detected between radio-tagged

and banded northern bobwhite (Mueller et al. 1988).

Radio-tagged northern bobwhite were located once daily throughout the breeding season (April through October) to determine breeding status. Nesting behavior was usually detected after incubation commenced, when a radio-tagged bird was found at the same location for 3 consecutive days. Associations with other radio-tagged northern bobwhite, unmarked adults, or broods were recorded in the daily tracking records. Ornithological studies have typically relied on association patterns to evaluate mating systems or individual reproductive success (Gowaty and Mock 1985:11). We realize that apparent mating patterns based on associations, and actual (genetically-effective) mating patterns, may not be the same, and additional electrophoretic exclusion research will be necessary to elucidate the differences. Electrophoretic exclusion techniques have documented multiple maternity and paternity between care-giving adults and putative offspring in apparently monogamous eastern bluebirds (*Sialia sialis*) (Gowaty and Karlin 1984).

Monogamy has been termed a "mating-system-by-default" (Gowaty and Mock 1985:4), and has served as a catch-all, where species are assigned only when they fail to satisfy more easily specified criteria of polygyny or polyandry. Consequently, monogamous mating systems include a diverse array of reproductive strategies that may have little in common.

We defined apparently monogamous breeding behavior based on social organization (1 male-1 female social units; Gowaty and Mock 1985:12). If a radio-tagged bobwhite was associated (flushed or observed) with >1 individual of the opposite sex during a breeding season, we considered this potentially polygamous behavior, even if no nest was found. Radio-tagged bobwhite were associated with both tagged and untagged individuals on many occasions, and it was impossible to determine the actual outcome of these encounters. Our definition based on social observations may result in an overestimate of the actual proportion of genetically-effective matings. However, it was the best estimate of potential polygamy, given that <20% of the bobwhite at both study sites were radio-tagged (based on trapping records and visual observations), and no electrophoretic exclusion work was conducted during this study. Biweekly flush counts of radio-tagged birds or coveys were used to document associations prior to the onset of incubation and during brood-rearing activities. It was impossible to flush radio-tagged bobwhite more frequently without affecting survivorship, and some associations with untagged birds were likely missed. Nesting bobwhite of either sex were monitored daily during the 23-day incubation period (Rosene 1969) to determine status of the tagged bird. Broods were checked at TTRS by night-lighting to determine chick mortality and parental associations.

RESULTS

It was possible to determine the breeding status of 19 radio-tagged bobwhite at FB. Eighteen (95%) exhibited potentially polygamous breeding behavior, and 1 (5%) tagged male bobwhite apparently stayed with the same tagged female until his death during June (Table 1). This female was subsequently associated with 2 other males, and produced a clutch with another radio-tagged bird during July. The breeding behavior of 41 bobwhite at FB could not be determined because they were observed for only a portion of the breeding season (e.g., males captured and tagged during midsummer), or they were associated with untagged birds on several occasions, and it was impossible to determine if the same untagged bobwhite was involved during each observation. At TTRS, 25 radio-tagged northern bobwhite (93%) exhibited potentially polygamous behavior, and 2 birds (7%) remained with the same mate. The breeding status of 74 radio-tagged bobwhite at TTRS could not be classified.

During 1988 at FB, we documented 3 cases of double-clutching by radio-tagged females. One female successfully raised 2 broods with a tagged male, who cared for her first brood while she incubated a second clutch of eggs. While it is impossible to confirm the paternity of the second brood from observations alone, the same radio-tagged male was repeatedly seen with the female during the month before her second nest was found. The other 2 radio-tagged females raised their first broods until 3-4 weeks of age, then either lost or abandoned the chicks, and were found incubating second nests (it is not known whether they mated with the same male for both nests). Both second nests were lost to predation. We also observed a radio-tagged male incubating 2 different nests during a 5-day period. The following day, this male joined a radio-tagged female and her brood, and he stayed with this group until he was killed by a predator 1 month later.

Table 1. Breeding behavior of radio-tagged northern bobwhite at Fort Bragg Military Reservation (FB), NC, 1985-88; and at Tall Timbers Research Station (TTRS), FL, 1984–86.

		1984	1985	1986	1987	1988	Total
Breeding behavior of radio-tagged bobwhite, n (%)							
Monogamous	FB				1		1 (5)
	TTRS	2					2 (7)
Polygamous	FB		4		7	7	18 (95)
	TTRS	5	15	5			25 (93)
Not classifiable	FB		8	12	11	10	41
	TTRS	7	31	36			74
Number of bobwhite (%) radio-tagged							
Males	FB		5	7	12	8	32 (53)
	TTRS	7	24	18			49 (49)
Females	FB		7	5	7	9	28 (47)
	TTRS	7	22	23			52 (52)
Number of nests (%) incubated							
Males	FB		2	1	2	3	8 (27)
	TTRS	1	8	2			11 (20)
Females	FB		4	4	3	11	22 (73)
	TTRS	3	17	25			45 (80)
Number of bobwhite (%) not associated with a nest or brood							
Males	FB			1	8	2	11 (34)
	TTRS		10	12			22 (45)
Females	FB				4	1	5 (18)
	TTRS		6	1			7 (13)
Number of broods (%) reared							
Pairs	FB		5	5	2	10	22 (71)
	TTRS	2	5	9			16 (50)
Lone females	FB		2	2		3	7 (23)
	TTRS		4	5			9 (28)
Lone males	FB				2		2 (6)
	TTRS	1	3	3			7 (22)

During 1986 at TTRS, we observed 2 cases of double-clutching by radio-tagged females. Both females again raised their first broods to 3 weeks of age, and then either lost or left the chicks to incubate second nests. Both second nests were lost to predation, and the paternity of broods was unknown.

During 1985-88 at FB, 60 radio-tagged northern bobwhite (53% male, 47% female) were observed during the breeding season (Table 1). Radio-tagged bobwhite incubated 30 clutches, and only 1 tagged bird was responsible for incubation duties at each nest. Twenty-seven percent of clutches found were incubated by radio-tagged males; radio-tagged females incubated the remaining 73%. Of the 30 clutches observed, 17 (57%) were the first documented nest of the breeding season for tagged females, and 7 (23%) were first nests for males. Four females (13%) and 1 male (3%) were located at 2 different nests during the same breeding season, and 1 female (3%) attempted 3 nests in 1 year.

During 1984-86 at TTRS, 101 radio-tagged northern bobwhite (49 males, 52 females) were monitored during the breeding season (Table 1). Radio-tagged bobwhite incubated 56 clutches, and again, only 1 tagged bird was responsible for incubation duties at each nest. Twenty percent of nests were incubated by radio-tagged males, and 80% by tagged females. These proportions were similar between sites ($X^2 = 0.50$, df = 1, $0.25 < P < 0.50$). Of 56 clutches observed, 37 (66%) were the first documented nest of the breeding season for tagged females, and 10 (18%) were first nests for males. Seven females (13%) and 1 male (2%) were located at 2 different nests during the same breeding season, and 1 female (2%) attempted 3 nests in 1 year. These proportions were similar between sites for both females ($X^2 = 0.30$, df = 2, $P > 0.50$) and males ($X^2 = 0.09$, df = 1, $P > 0.50$).

The proportion of broods reared by male and female pairs, lone females, and lone males was similar ($X^2 = 3.90$, df = 2, $0.10 < P < 0.25$) between FB and TTRS (Table 1); however, there was a trend for lone males to raise a greater percentage of broods at TTRS. Thirty to 50% of the broods were uniparent (of either sex), and 50-70% were cared for by pairs (usually mixed sexes, but male only pairs were observed).

We describe the following case histories of radio-tagged bobwhite to illustrate potentially polygamous breeding behavior.

Case History 1.—During summer 1984 at TTRS, 5 radio-tagged and 2 untagged bobwhite interacted throughout the breeding season (Fig. 1). Female 748 was associated with 2 males prior to incubation, and both possibly fertilized a portion of the eggs in her nest. Male 749 was observed during the early egg-laying stage of female 748's nest, and eventually assisted with raising her brood. Male 742 was found incubating female 744's nest with 11 eggs. Male 742 hatched 11 eggs, and was then joined by another untagged male which assisted with raising the brood.

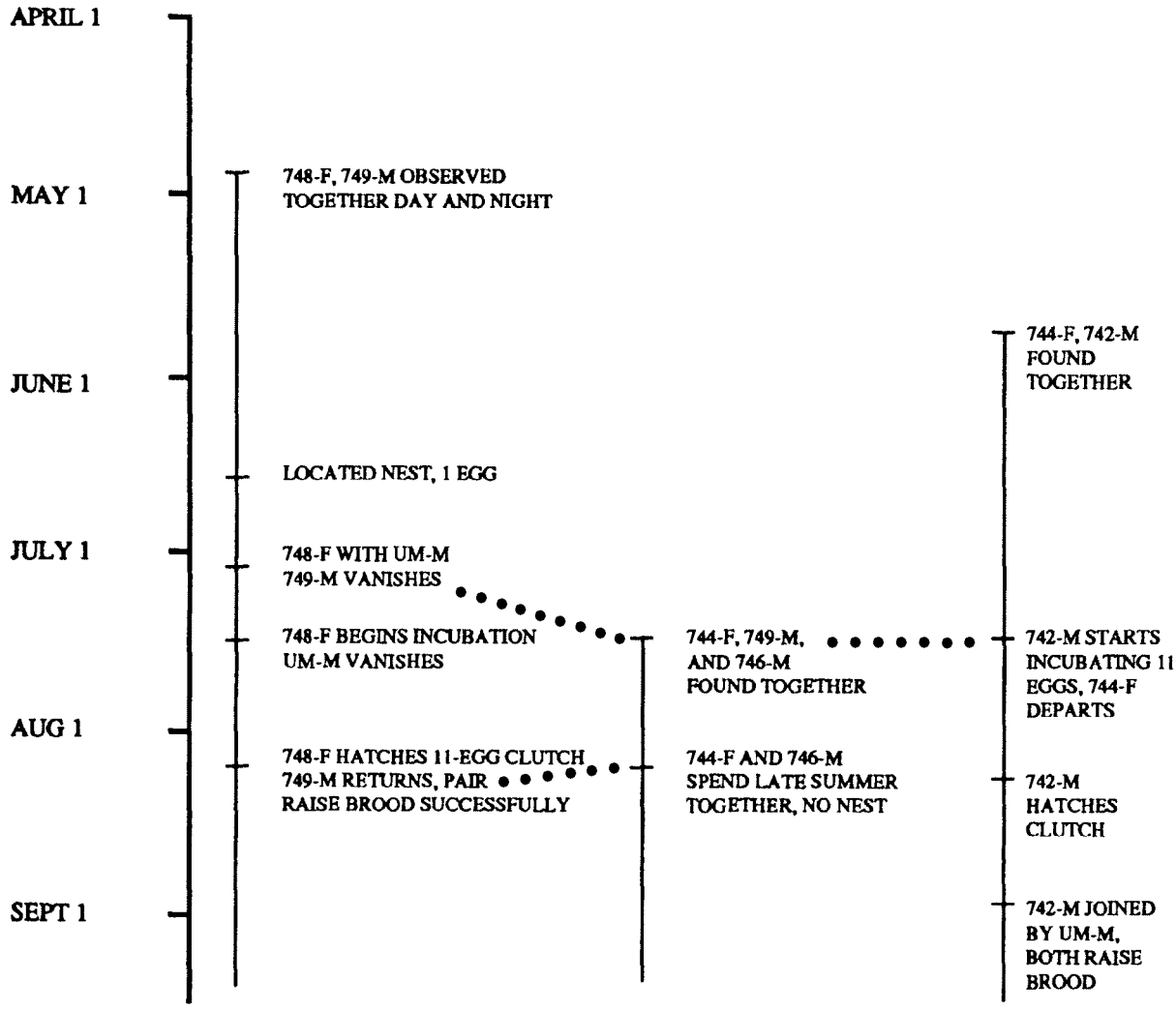

Fig. 1. Case history of the breeding biology of 5 radio-tagged and 2 untagged northern bobwhite from Tall Timbers Research Station, FL, summer 1984 (M = male, F = female, UM = unmarked bobwhite).

Case History 2.—Double-clutching is described for a radio-tagged female at FB during summer 1988 (Fig. 2). Female 938 and male 941 successfully raised 2 broods, with male 941 caring for the first brood while female 938 incubated and hatched the second clutch. Male 941 was also observed with at least 2 other females while female 938 was incubating her first clutch, and during her first month of brood-rearing as a single parent.

DISCUSSION

Lack (1968) indicated that about 90% of all bird species are monogamous and, although the actual proportion may be less, monogamy is the predominant mating system for most bird species. More recently, it has become clear that several individual breeding strategies may be exhibited by birds classified as apparently monogamous breeders (Gowaty and Mock 1985). It is unclear how many "covert" matings outside the 1 male-1

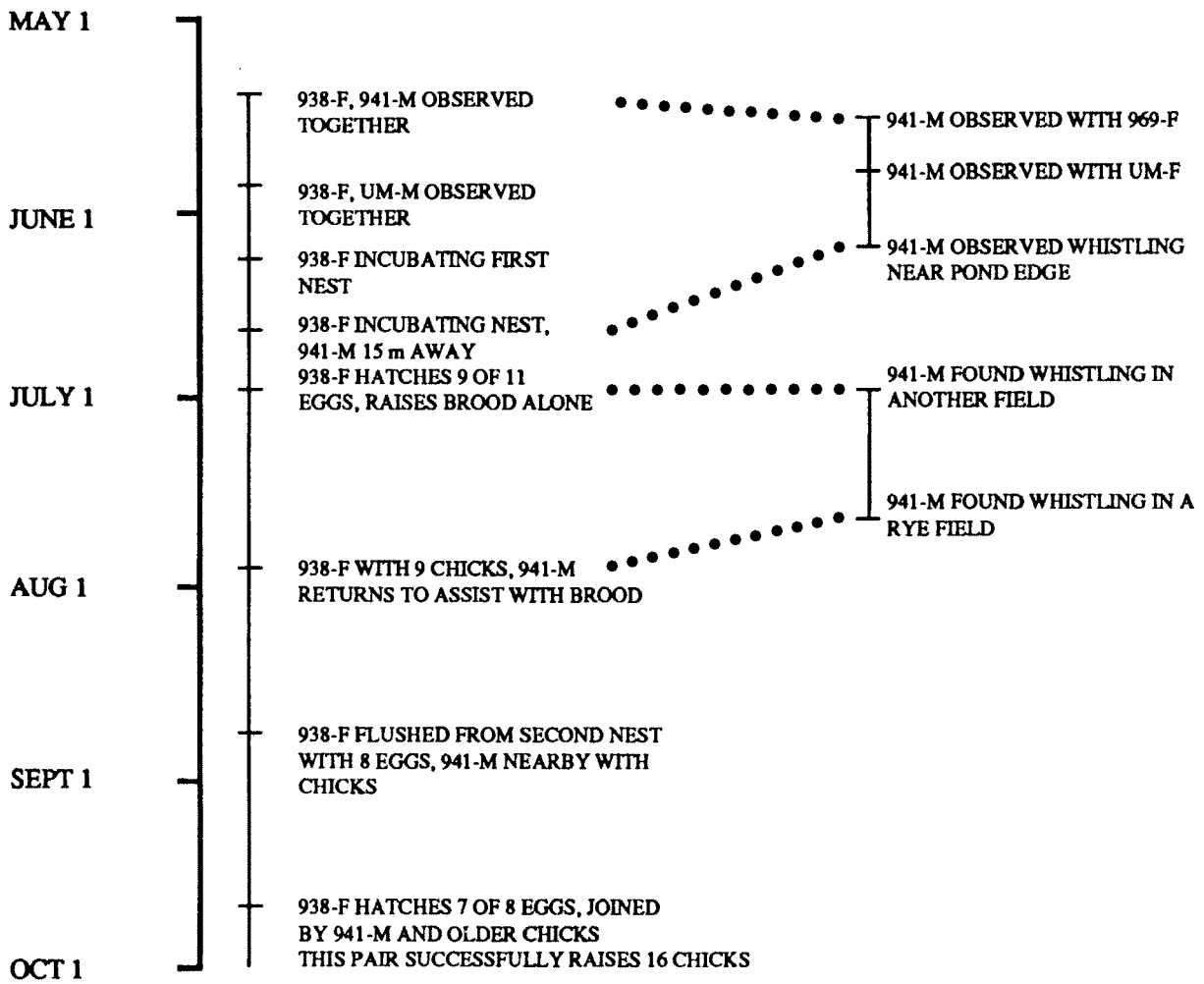

Fig. 2. Case history of the breeding behavior of 3 radio-tagged and 2 untagged northern bobwhite from Fort Bragg, NC, summer 1988 (M = male, F = female, UM = unmarked bobwhite).

female social unit must occur for a monogamous system to be classified as polygynous or polyandrous (Gowaty and Mock 1985), although the 5% benchmark has been used by others (Carey and Nolan 1979). Variations in mating tactics for apparently monogamous birds often confound concepts and definitions of mating systems.

Polygamous mating systems are especially common in precocial birds that do not feed their young (Lack 1968, Orians 1969), presumably because demands on parents are more often insensitive to brood size in such species (Walters 1982). Rapid multiple-clutch mating systems have been defined by Hilden (1975), and first described by Graul (1973). In these systems, the female lays a clutch that is attended by a male. The female then forms a second clutch that she incubates, or gives to a second male (in which case she may incubate a third clutch). This avian social system is not common, and may occur regularly only in a few species of shorebirds and galliformes (Emlen and Oring 1977). When environmental conditions (e.g., unpredictable food supply, variable weather conditions) are favorable, reproductive output can be enhanced with only a slight increase in breeding time.

Rapid multiple-clutch polygamy has been documented for the red-legged partridge (*Alectoris rufa*; Jenkins 1957), sanderling (*Calidris alba*; Parmelee and Payne 1973), mountain plover (*Charadrius montanus*; Graul 1973), and Temminck's stint (*Calidris temminckii*; Hilden 1975). The California quail (*Callipepla californica*), which occasionally practices this mating system (Francis 1965, Leopold 1977:92-93), experiences severe biotic and abiotic environmental fluctuations. All of these ground-nesting species have precocial young that suffer moderate to high predation losses (Emlen and Oring 1977), similar to northern bobwhite.

Northern bobwhite are apparently similar to California quail because females which exhibit double-brooding leave their young when the chicks are about 2 weeks old (Leopold 1977:93). For California quail, double-brooding seems to occur once or twice per decade in years highly favorable for reproduction. Male California quail rarely incubate clutches, and unmated males act as foster parents in years when chicks are abundant.

Persson and Ohrstrom (1989) recently described a new avian mating system, ambisexual polygamy, in which sequential polygyny and polyandry may occur simultaneously. Penduline tits (*Remiz pendulinus*) exhibited uniparental clutch and brood care; of 140 clutches observed, 48% were attended by females, 18% by males, and 34% were deserted by both parents before incubation. Polyandry was exhibited by 31% of females, and 69% attended their first brood. Thirty percent of males assumed parental responsibilities. It appeared likely that the female made the primary choice to leave a clutch or stay to incubate the eggs (Persson and Ohrstrom 1989). If the female decided to incubate, the male could become polygynous. If the female departed, the male could assume parental care or abandon the clutch. Two females attended both their first and second clutches, and mate-shifting occurred between clutches.

The number of female penduline tits available to breed diminished as the breeding season progressed, and the operational sex ratio (Emlen and Oring 1977) became increasingly male-biased. As males found their chances for successfully breeding reduced, the best way to increase their reproductive output was to assume parental care. Females also may have exploited the skewed sex ratio by becoming polyandrous, as they had a greater probability of finding another mate. By spending less time with each male, a female could mate more often and increase the probability that a male would care for some of her eggs. Persson and Ohrstrom (1989) indicated that all males attempted to practice polygyny, but some were unable to do so because of female choice and behavior. Uniparental care and a long breeding season are necessary for this mating system to develop.

We noted in both case histories, that northern bobwhite females were associated with >1 male during egg laying. Consequently, it is impossible to determine the paternity of a brood without electrophoretic exclusion analyses. In both cases, the male that was present during early laying stages eventually returned to help the female care for the chicks. Schom and Abbott (1974) reported that the fertility of eggs laid by naturally-inseminated, captive bobwhite females dropped from approximately 95 to 68% 4 days following the removal of males. Roseberry and Klimstra (1984) reported that only 3% of 3,249 eggs from 234 wild nests were infertile. Therefore, female bobwhite must be mating frequently to maintain high fertility rates. In cases where a female has associated with 2 males during egg-laying, the paternity of the brood could possibly be shared.

Stoddard (1931) noted the strong adoption tendencies of northern bobwhite. More than 90% of males, females, or pairs not engaged in nesting

readily adopted chicks put with them. Sermons and Speake (1987) suggested that brood abandonment or surrogate parenting may lead to double-clutching. We observed 4 cases of apparent brood abandonment during this study (6% of all broods monitored). Polygamous mating behavior may be more likely to increase reproductive output than brood abandonment and subsequent renesting. In fact, pairs helped raise 50% ($n = 32$) of the broods at TTRS and 71% ($n = 31$) of the broods at FB.

Northern bobwhite should potentially be considered polygamous breeders, as mating behavior may shift between variations of polygyny, polyandry, or promiscuity. Northern bobwhite appear to exhibit characteristics of both the rapid multiclutch and ambisexual polygamous mating systems, although neither system completely describes the breeding associations we observed. Northern bobwhite live in a fluctuating environment, suffer high predation pressure during the nesting season, and raise precocial young, similar to other galliformes and shorebirds that have evolved multiclutch systems. About 95% of the radio-tagged bobwhite for which we were able to document breeding status exhibited apparently polygamous behavior at FB and TTRS, and our case histories describe several mating and brood-rearing associations.

MANAGEMENT IMPLICATIONS

The importance of successful nesting and brood-rearing cannot be overemphasized during development and implementation of northern bobwhite habitat management programs. When environmental conditions are favorable, bobwhite reproductive output may be enhanced with only a slight increase in breeding time due to the flexibility in breeding behavior. Because 70-80% of the fall harvest usually consists of juvenile northern bobwhite (Rosene 1969), the number of birds in the fall population may be influenced by the proportion of bobwhite exhibiting polygamous mating strategies.

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