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DELAYED BREEDING IN YEARLING MALE GROUSE: AN EVALUATION OF TWO HYPOTHESES¹

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Key words: Blue Grouse; *Dendragapus obscurus*; delayed breeding; territory quality; female choice; polygyny; survival.

In most monogamous species of birds males and females commence breeding at approximately the same ages, whereas in species with polygynous mating patterns males often initiate breeding at older ages than females (Selander 1965, Orians 1969, Wiley 1974). Although yearling males in these latter species may be physiologically able to breed (e.g., Orians 1961, Eng 1963, Hannon et al. 1979), they usually are presumed to be nonbreeders if they do not defend breeding territories. In contrast, yearling females of the same species often lay eggs and are capable of raising young.

In papers on the evolution of mating patterns in grouse, Wiley (1974) and Wittenberger (1978) proposed explanations for a postponement of breeding by males relative to females in polygynous species. Both authors believed that females may breed preferentially with older males, and hence that female choice of mates could be a factor selecting for delayed breeding by males. Further, Wiley suggested that the cost of breeding for young males of polygynous species may be greater than that for older males, this possibly owing to their relative inexperience in defending territories, advertising to females, and performing courtship displays, which could increase their susceptibility to mortality. This would be particularly true if young males were relegated to taking low quality territories (Wiley 1981). According to Wiley then, both female choice and a greater cost of breeding for younger males relative to older males likely contributed to the evolution of delayed breeding.

Wittenberger (1978), however, argued that within

species the cost of breeding for young males should be similar to that of older males. He therefore concluded that a difference in cost of breeding for young and old males was unimportant as a factor favoring delayed breeding. The two hypotheses proposed by Wiley and Wittenberger are not mutually exclusive in that both consider female choice to be a factor in the evolution of delayed breeding. However, they differ in that Wittenberger considered female choice by itself sufficient to explain delayed breeding by males, whereas Wiley believed a cost factor also was important in the evolution of this behavior pattern.

We studied the demography and behavior of Blue Grouse (*Dendragapus obscurus*) in two areas of coastal British Columbia from 1977 to 1983. This species has a mating system in which there are no pair bonds between males and females, and thus males breed promiscuously. Our objective is to use information from this intensive study of a single species to evaluate Wiley's and Wittenberger's hypotheses for the evolution of delayed breeding in male grouse. In doing so we recognize that it is problematic to test hypotheses on the origin of a behavior pattern. Nevertheless, we can examine how delayed breeding might currently be maintained by selection pressure. We ask the question: is female choice by itself an adequate explanation for the postponement of breeding by yearling male Blue Grouse?

RESULTS

GENERAL BEHAVIOR OF MALE BLUE GROUSE

Adult male Blue Grouse occupy territories that serve primarily as areas for advertising and displaying to females (Bendell and Elliott 1967, McNicholl 1978). Territories generally range between 1 and 4 ha in size and usually include elevated portions of land such as hills, knolls, or ridges (Bendell and Elliott 1967, McNicholl 1978, Lewis 1985). Males generally hoot (sing) from these elevated regions, which probably fa-

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cilitates the broadcasting of their hooting. Occupancy of a territory is considered a prerequisite for breeding in this species (Bendell and Elliott 1967, McNicholl 1978).

Yearling male Blue Grouse rarely are territorial (Bendell and Elliott 1967, Lewis and Zwickel 1981, Jamieson 1985), but in spring most localize their movements around the territories of a few males (Jamieson and Zwickel 1983). If yearlings interacted with females on adults' territories, or approached territorial males, they were quickly displaced (Jamieson 1985). Yearling males never gave the customary precopulatory "whoop" call (Stirling and Bendell 1970) when they interacted with females away from adults' territories (Jamieson 1985).

The lack of territorial behavior by yearling males, and their apparent inability to perform complete courtship displays, strongly suggests that they are unlikely to obtain copulations. However, these results do not favor one hypothesis over the other, as both Wiley and Wittenberger believed that females may preferentially breed with older males. Recent studies also have found that some young adult males are nonterritorial (Lewis and Zwickel 1980, 1982; Jamieson and Zwickel 1983; Lewis 1984a). Therefore delayed breeding apparently is not limited to the yearling age class.

QUALITY OF TERRITORIAL SITES AND SURVIVAL OF MALES

Over a 10-year period on one of our study areas, Comox Burn on Vancouver Island, some areas were used for territories almost every year whereas other areas were occupied sporadically. Areas used at least 9 of the 10 years were termed persistent sites and those used less frequently transient sites (Lewis and Zwickel 1981). Males on persistent sites survived significantly longer than did males on transient sites (Lewis and Zwickel 1981); overall, they survived 8% better annually and had mean life expectancies that were one year longer (Lewis and Zwickel 1982). The average number of males that occupied each persistent site over the 10 years also was greater than that on transient sites. Thus, continuous occupancy on these areas was not merely a consequence of better survival of the males occupying them.

Differences in survival of males occupying persistent and transient sites should be related to differences in the habitat characteristics of these areas and/or to individual differences in the "quality" of the males occupying them. Persistent sites did not contain more cover than transient sites, but the elevated regions on them were higher relative to surrounding areas than they were on transient sites (Lewis 1981). Being high relative to surrounding areas may enhance the detection of aerial predators which are a major source of mortality for grouse. Thus, persistent and transient sites differ structurally in a way that could affect the survival of their residents. Therefore, in terms of survival we believe that persistent sites are higher in quality than transient sites.

In general, yearling males arrive on breeding ranges later in spring (Bendell and Elliott 1967) and at lighter weights (Redfield 1973) than do adult males. Under these conditions the probability of a yearling male ac-

quiring a persistent, or high quality, territorial site seems very low. Almost all persistent sites on Comox Burn were occupied each year (399/410, 97%), all by adults (Lewis and Zwickel 1981). Therefore, if yearling males were to take territories, they would have had to do so on areas where survival is relatively low.

REMOVAL STUDIES

One method of experimentally testing Wiley's and Wittenberger's hypotheses is to remove adult males from an area and observe the response of yearling males. If young males delay breeding primarily as a consequence of female choice, with costs being unimportant, then yearlings should take territories in the absence of adults. In the year following the almost total removal of adults from two large areas (360 and 625 ha) on Vancouver Island, yearling males were observed hooting and hence presumably holding territories (Bendell et al. 1972, Zwickel 1972). Wittenberger (1978) cited these results as direct experimental support for his hypothesis.

In the above studies, however, most yearling males did not take territories after adults were removed. Zwickel removed 62 of an estimated 74 adult males that were present on his 625-ha area in 1970. In 1971 only 16 adult males were identified and a total of 21 were estimated to be present. Of the 59 yearlings identified in 1971, only 21 (36%) were observed hooting. Thus, even with only a few adults present and previously used territorial sites available, most yearling males still did not take territories. Bendell et al. (1972) also state that most yearlings did not take territories after the removal of adults but they do not give exact numbers. In neither of these studies was the quality of territorial sites known.

In a more recent study, Lewis and Zwickel (1980) removed original occupants from 11 persistent and 11 transient sites on Comox Burn in early spring 1978. Throughout the remainder of the breeding season in 1978 and again in 1979 all replacement males at these sites also were removed as soon as they were heard hooting. High quality territorial sites therefore always were available for settlement. Only two yearlings in 1978 and six in 1979 took territories, seven of these being on persistent sites. During these two years 14 other yearling males were identified that did not take territories. The percentage of yearlings that took territories (8/22, 36%) likely is lower than that indicated because silent males are harder to find and identify than hooting males.

In 1982, Lewis (1984b) removed residents from 14 of 17 occupied territories on a 95-ha area on Hardwicke Island, British Columbia. As in the previous experiment, replacement males were removed as soon as they were heard hooting. Four yearlings took territories in 1982 and a minimum of four others were nonterritorial. In 1983, only six territorial adults were present, yet only one of four yearlings that were identified were territorial. Thus, in all four removal experiments most yearlings did not take territories when adults were removed, this being so even when high quality areas were available. In the latter two studies all known nonterritorial adults took territories when residents were removed from high quality sites.

DISCUSSION

If delayed breeding by yearling males is almost solely an evolutionary consequence of female choice, then most yearlings should take territories when adult males are not present. This clearly does not occur in Blue Grouse as substantial proportions of yearlings did not take territories even when most adults were removed, and when high quality areas for territories were known to be available. Wittenberger's female choice hypothesis therefore is not supported by these results. However, if Wiley's hypothesis, which advocates that delayed breeding occurs at least partly because the cost of breeding is higher for younger than older males, is to be accepted as an alternative, the fact that some yearling males do take territories in the absence of adults must be reconciled.

Whether or not an individual delays breeding presumably depends on the balance between the costs and benefits of defending a territory and undertaking advertisement and courtship activities. The likelihood of a yearling breeding increases when adults are absent, which increases potential benefits accruing from holding a territory and soliciting females. It might then be advantageous for yearlings to take territories if such an increase in potential benefits is sufficient to counterbalance a high cost associated with doing so, if such a high cost does exist. Further, the almost total removal of adults creates an artificial situation in which encounter rates between yearling males and receptive females likely are high. This may provide a stimulus for these males to take territories. Therefore, we do not consider the taking of territories by some yearling males, when adults are removed, inconsistent with Wiley's hypothesis.

Is the cost of breeding for yearling male Blue Grouse greater than it is for adults? Given that yearlings likely would be relegated to using poor quality areas where survival is relatively low if they were to take territories, the cost of attempting to breed almost certainly would be higher, on average, for them than it is for adult males. Further, the greater probability of mortality would persist into future years since males, even if on transient sites, rarely change the location of their territory from one year to the next (Lewis and Zwickel 1981), a situation Wittenberger (1978) assumed would not occur.

Even when most adult males were removed, and high quality sites were available, most yearlings did not take territories. That implies that any difference in the cost of breeding for yearling and adult males is greater than that resulting from a difference in quality among territorial sites. Perhaps a higher cost of breeding for yearling males also is related to their relative inexperience in performing territorial and courtship activities and their lack of familiarity with the area on which their territory would be located. Adult territorial males are active throughout the day during the breeding season whereas yearling males spend most of the daytime inactive and close to cover (Jamieson 1985). However, yearlings do become more active in the early morning and late evening (Jamieson 1985) and this may enable them to gain experience in interactions with conspecifics. Additionally, all radio-tagged yearling males ($n = 6$) that subsequently took territories as two-year-olds

did so on areas within their yearling home range (Jamieson and Zwickel 1983). Thus, males may use time as yearlings to gain familiarity with the area where they subsequently are likely to take a territory. Such familiarity may enhance future survival (e.g., Metzgar 1967).

In conclusion, since most yearling males still did not take territories when adults were removed, we consider Wittenberger's female choice hypothesis an insufficient explanation for delayed breeding by yearling male Blue Grouse. Present evidence suggests that costs associated with breeding, in terms of quality of territorial site that is likely to be obtained, would be higher for yearling than adult males; the relative inexperience of yearling males may incur an additional cost. Therefore, we believe that an explanation for delayed breeding by yearling male Blue Grouse, and probably other Tetraonids, should include a consideration of the effect of both female choice and a difference in cost of breeding for young and old males. Because Wiley did this we consider his hypothesis more inclusive than that proposed by Wittenberger.

However, before it will be possible to understand the basis for delayed breeding more fully, more information is needed and other factors should be considered. Irrespective of what the presumed benefits of postponing breeding might be, we should not expect all young males to show the same degree of delayed breeding since the propensity to do so will be affected by many factors, such as age, physiological state, quality of territorial sites available, number of competitors, experience, familiarity with an area, and inherent individual variability. Evidence suggests that there is much individual variation among males in these respects (McNicholl 1979, Jamieson and Zwickel 1983). We suggest that future research on this problem should include intensive studies of individuals, including studies of their morphology, physiology, behavior, movements, etc., as that might help to understand why the tendency for young males to delay breeding varies both in the presence and absence of adults.

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PYRAMIDING BEHAVIOR IN THE INCA DOVE: ADAPTIVE ASPECTS OF DAY-NIGHT DIFFERENCES¹

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Key words: Behavior; huddling; Texas; thermo-regulation; dove.

Huddling, primarily at night but occasionally during the day, is well documented as an energy-saving behavior during cold weather in a number of passerines

and nonpasserines, particularly in small and medium-size species (Dorst 1974, Welty 1978). Protected places such as tree holes, rock crevices, and ledges are common huddling sites. A significant increase in efficiency has been demonstrated. Brenner (1965) found an energy saving of 92% in food-stressed starlings huddled in groups of four and Le Maho (1977) noted reductions in fat loss up to 50% in huddled Emperor Penguins. Huddling in rows is common in some dove species (Bent 1932) and a rather exaggerated version, pyra-

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