

- SKUTCH, A. F. 1961. Helpers among birds. *Condor* 63:198-226.
- STOUFFER, P. C., E. D. KENNEDY, AND H. W. POWER. 1987. Recognition and removal of intraspecific parasite eggs by Starlings. *Anim. Behav.* 35:1583-1584.
- VEHRENCAMP, S. L. 1977. Relative fecundity and parental effort in communally nesting anis (*Crotophaga sulcirostris*). *Science* 197:403-405.
- VEHRENCAMP, S. L. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga sulcirostris*). *Behav. Ecol. Sociobiol.* 4:1-33.
- WOLFORD, J. H., R. K. RINGER, AND T. H. COLEMAN. 1964. Ovulation and egg formation in the Beltsville Small White Turkey. *Poultry Sci.* 43:187-189.
- WOODARD, A. E., AND F. B. MATHER. 1964. The timing of ovulation, movement of the ovum through the oviduct, pigmentation and shell deposition in Japanese Quail. *Poultry Sci.* 43:1427-1431.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative breeding bird. Princeton Univ. Press, NJ.
- YOM-TOV, Y., G. M. DUNNET, AND A. ANDERSON. 1974. Intraspecific nest parasitism in the Starling *Sturnus vulgaris*. *Ibis* 116:87-90.
- ZAHAVI, A. 1974. Communal nesting by the Arabian Babbler. *Ibis* 116:84-87.

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## EARLY PAIR AND EXTRA-PAIR COPULATIONS IN WILLOW PTARMIGAN<sup>1</sup>

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In Willow Ptarmigan (*Lagopus lagopus*), males and females are paired from the onset of territoriality until after independence of the brood, a situation unique among grouse. Despite pairs being together on the territory for up to 33 days prior to laying, copulations have rarely been observed in the wild. Copulations between pairs have been seen immediately before and during egg laying and during incubation in Red Grouse (*L. l. scoticus*, Watson and Jenkins 1964), Rock Ptarmigan (*L. mutus*, MacDonald 1970), and White-tailed Ptarmigan (*L. leucurus*, Schmidt 1969). The three species of ptarmigan are the only monogamous grouse in North America and no instances of extra-pair copulation have been reported for them (McKinney et al. 1984). Here we document nine copulations between pairs of Willow Ptarmigan that occurred much earlier in the season than reported previously for ptarmigan and five instances of attempted extra-pair copulations between paired females and unpaired males.

### STUDY AREA AND METHODS

Copulation behavior was observed opportunistically at the Chilkat Pass (CP) in northwestern British Columbia, and at La Perouse Bay (LPB) near Churchill,

Manitoba, Canada. We considered a copulation to be completed if both members of the pair placed their tails to make cloacal contact. The majority of copulations were observed in 1986 and 1987 at CP while we monitored monogamous and experimentally-produced polygynous hens for over 100 hr, 2.5 weeks prior to and up to egg laying. Except when indicated otherwise, observations occurred at Chilkat Pass. In both areas birds were color-banded and the pairing and territorial status of each bird were known. Date of first egg was determined by backdating from hatch date (subtracting 21 days for incubation period and 1 day for each egg laid) or was known directly for hens whose nests were found during egg laying. Terminology for calls and postures follow that of Watson and Jenkins (1964).

### OBSERVATIONS

Completed copulations were observed between mated birds in May between 7 and 16 days before hens laid their first eggs (Table 1). Copulations were similar to those described for Red Grouse by Watson and Jenkins (1964). In addition, an apparently unsuccessful copulation between a mated pair was observed on 22 May 1986 when a hen approached her mate who was engaged in a border dispute. The other male ran toward her and she flew away, followed by her mate. Without preliminary display he jumped on her back, grabbed her nape feathers and treaded on her back. The female struggled throughout, and when her mate flew away to continue the border dispute, she remained crouched

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TABLE 1. Dates and number of days before hens laid their first eggs that completed copulations between mated pairs were observed.

Hen #	Date of copulation	Days before first egg
1	24 May 1986 (LPB)	?
2	27 May 1986	15
3	28 May 1986	8
4	23 May 1987	11
5	24 May 1987	16
6	27 May 1987	7
7	28 May 1987	10
8	28 May 1987	11

under a bush. This took place 18 days before she laid her first egg.

We observed five instances where unmated males attempted to copulate with paired hens, described in (A) to (E) below. (A) On 14 June 1983, in the only successful extra-pair copulation observed, a laying hen at LPB copulated with a nonterritorial male while her mate was involved in a border dispute. (B) In an unsuccessful copulation attempt on 5 June 1986, a paired hen head-wagged and crouched when approached by a displaying nonterritorial male. The male had placed his foot on her back when her mate, who had been 15 m away in dense vegetation, flew in and landed beside them. The intruder flew away immediately. This hen laid her first egg 6 days later. (C) On 19 May 1984 a paired hen was chased by an unmated male when she walked onto his territory. The unmated male attempted to mount the hen while she clucked and struggled and her mate attacked him. After about a 40-sec struggle, the mated male knocked the unmated male off the hen and chased him away. This occurred 11 days prior to initiation of laying. (D) and (E) Finally, two more instances of attempted copulation were witnessed on 23 and 25 May 1986 when nonterritorial males approached females that had been left alone by their polygynous mates. In both cases the intruding males displayed to the hens, and the hens responded by clucking and flying away. Their mates immediately chased the intruding males. One hen laid her first egg 14 days later. The second disappeared later and date of laying was not determined.

## DISCUSSION

All copulations observed between paired birds for which the date of first egg was known, occurred much earlier in the season than has been reported previously for ptarmigan. In Willow Ptarmigan, sperm can reliably fertilize eggs up to about 6 days after copulation (Parker 1981). The seven completed copulations observed between paired birds for which we have first egg dates, occurred between 7 and 16 days prior to laying, and most were unlikely to have fertilized eggs. Pairs probably copulate several times during the prelaying period. Copulations between mates early in the prelaying period may function to reinforce the pair bond and/or, as Lumpkin (1983) has suggested, females may solicit copulations so that males will guard them. This could increase the hen's feeding efficiency, deter predation, or reduce harassment by unmated males. Mate guarding by male Willow Ptarmigan begins soon after pairing

and lasts until late incubation (Martin 1984). Males may guard females for periods longer than necessary to defend their paternity if they are unable to tell when the hen is fertile.

Attempted extra-pair copulations were observed when a female's mate was absent for a short period, when her mate was having a border dispute, or when he was separated visually from the hen. We observed females attempting to escape from "cuckolders" only when a copulation was highly unlikely to result in fertilized eggs. In two cases females did not resist extra-pair copulations and these copulations could have resulted in fertile eggs (one during laying and the other 6 days prior to laying). Nonterritorial males have developed testes (Hannon and Roland 1984) and they can sire young once they have become territorial (Martin and Cooke 1987).

Although we have only a few observations of attempted extra-pair copulations, the fact that hens accepted intruder males shortly before and during their egg-laying period suggests that unmated males may father some young. The receptive behavior of hens as they approach laying, the long laying period occasioned by large clutches (8 to 14 eggs laid at a rate of one per day) and the frequent production of replacement clutches after failure of early nests (Martin 1984), means that mated males may face substantial risks of kleptogamy from late May (1 week before laying) until late July, a period of 9 to 10 weeks.

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## LITERATURE CITED

- HANNON, S. J. AND J. ROLAND. 1984. Morphology and territory acquisition in Willow Ptarmigan. *Can. J. Zool.* 62:1502-1506.
- LUMPKIN, S. 1983. Female manipulation of male avoidance of cuckoldry behavior in the Ring Dove, p. 91-112. *In* S. K. Wasser [ed.], *Social behavior of female vertebrates*. Academic Press, New York.
- MACDONALD, S. D. 1970. The breeding behavior of the Rock Ptarmigan. *Living Bird* 9:195-238.
- MARTIN, K. 1984. Reproductive defence priorities of male Willow Ptarmigan (*Lagopus lagopus*): enhancing mate survival or extending paternity options? *Behav. Ecol. Sociobiol.* 16:57-63.
- MARTIN, K., AND F. COOKE. 1987. Bi-parental care in Willow Ptarmigan—a luxury? *Anim. Behav.* 35:369-379.
- MCKINNEY, F., K. M. CHENG, AND D. J. BRUGGERS. 1984. Sperm competition in apparently monogamous birds, p. 523-545. *In* R. L. Smith [ed.], *Sperm competition and the evolution of animal mating systems*. Academic Press, New York.
- PARKER, H. 1981. Duration of fertility in Willow Ptarmigan hens after separation from the cock. *Ornis Scand.* 12:186-187.
- SCHMIDT, R. K. 1969. Behavior of White-tailed Ptarmigan in Colorado. M.Sc.thesis, Colorado State Univ., Fort Collins, CO.
- WATSON, A., AND D. JENKINS. 1964. Notes on behaviour of the Red Grouse. *Br. Birds* 57:137-170.