

EXTRA-PAIR COPULATION IN THE GREATER WHITE-FRONTED GOOSE¹

CRAIG R. ELY²

Alaska Cooperative Wildlife Research Unit, University of Alaska,
209 Irving Building, Fairbanks, AK 99775

Key words: Greater White-fronted Goose; Anser albifrons; extra-pair copulation; copulation; mixed reproductive strategies.

Controlled experiments and quantitative field studies with both captive and wild waterfowl (Family Anatidae) have demonstrated that extra-pair copulations (EPCs, both forced and unforced) may be a viable alternative reproductive strategy for males (Mineau and Cooke 1979; Burns et al. 1980; Cheng et al. 1982, 1983; Afton 1985; Everts and Williams 1987). In a review of EPCs in waterfowl, McKinney et al. (1983) stressed the need for additional information on the extent of such behavior in seemingly monogamous species of birds. Such information would increase our understanding of the extent of mixed reproductive strategies as formally hypothesized by Trivers (1972). Extra-pair copulations have been reported for only three of 22 (14%) species of geese and swans (Tribe Anserini), but are known to occur in 37 of 122 (30%) of the remaining species of waterfowl (McKinney et al. 1983, 1984; Welsh 1988). Socioecological differences between Anserini and most other anatids may provide insight into the evolution of extra-pair copulatory behavior, as male Anserini (unlike most other Anatidae) provide extensive parental care and maintain long-term pair-bonds (Owen 1980, p. 76). Cuckolded male Anserini thus stand to lose more in the form of reproductive investment than other male anatids, which may invest less in a given clutch and generally have short-term pair-bonds.

I describe here an observation of extra-pair copulation in wild Greater White-fronted Geese (*Anser albifrons frontalis*). The observation is significant not only because it augments our meager documentation of the behavior within the Anserini, but it is the first observation of such behavior in a noncolonial goose (Mineau and Cooke 1979, McKinney et al. 1983). The occurrence of EPC behavior in a dispersed-nesting goose is important, as proximity to potential mates has been hypothesized as a factor possibly selecting for EPC behavior in geese (McKinney et al. 1983) and other species of monogamous birds (Gladstone 1979, but see Westneat 1987).

Observations of the breeding behavior and ecology of Greater White-fronted Geese were made from the

time geese arrived on the nesting grounds on the Yukon-Kuskokwim Delta, Alaska, in early May through early incubation (late May/early June) in 1985-1986. Geese were observed from blinds near feeding areas (prior to nesting), and later at nearby nesting areas. Geese were identified by the unique patterns of their belly markings (Boyd 1953).

I spent approximately 162 hr during 1985 and 1986 observing an average of 2.2 pairs of Greater White-fronted Geese from the time they arrived on the nesting grounds, through the first week of incubation. During 356 pair hours of observation I observed nine pair copulations and one EPC.

On 29 May 1986, I observed a paired Greater White-fronted Goose (from pair B) copulate with a female from another pair (pair A). Preceding the EPC, pair A had been looking for a nest site for nearly 5 hr, during which time they were followed intermittently by pair B. The male of pair A followed his mate as closely as possible, but was noticeably limping, and often lagged behind. On two occasions pair B threatened or bit a member of pair A. At 18:26 the female of pair A settled at a nest site and engaged in nest building, while her mate stood nearby. Pair B followed the pair to the site; at 18:31 pair B engaged in a triumph ceremony (Fischer 1965), and then male B mounted female A on the nest. Female A did not resist, but remained motionless during the 15-20 sec that male B was treading her back and biting the nape of her neck. After male B dismounted he again engaged in a triumph ceremony with female B who remained seated next to the nest. Male A did not attempt to dislodge male B, but remained 7-8 m from the nest during the incident. There were no pre- or postcopulatory displays typical of pair copulations (Johnsgard 1965).

The next day (30 May) I flushed a pair of birds from the nest, which contained two eggs; the incubating bird was not female A, but could not be positively identified as female B. Both eggs in the nest pipped on 23 June, indicating that the first egg was probably laid on 29 May (based on a 26-day incubation period and a deposition rate of one egg per day [Ely and Raveling 1984]).

The presence of more than one female at a single nest site and the weakened physical condition of the mate of the female in the EPC complicate interpretations of the EPC. However, opportunistic copulations by males of this species are probably not aberrant, as indicated by an observation on the study area in 1985, when a paired male was observed copulating with an unpaired female at the beginning of the incubation period (D. Budeau, pers. comm.). The latter incident occurred on water, and both members participated in precopulatory display. These two observations estab-

¹ Received 27 January 1989. Final acceptance 24 May 1989.

² Present address: Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, AK 99503.

lish that promiscuity is a part of the repertoire of yet another seemingly monogamous bird (cf. Lamprecht and Buhrow 1987).

The EPC behavior of Greater White-fronted Geese was similar to that reported for Lesser Snow Geese (*Chen caerulescens*) by Mineau and Cooke (1979). There was no precopulatory display, the female did not resist the copulation attempt, and she was mounted while on the nest (pair copulations in geese occur almost exclusively on water [Owen 1980, p. 81]). The EPC also lasted longer (15–20 sec) than pair copulations (4–8 sec, $n = 5$), as also reported for Lesser Snow Geese (Mineau and Cooke 1979). Mineau and Cooke (1979), following terminology used for other anatids (McKinney et al. 1983), referred to EPCs in Lesser Snow Geese as forced copulations, as females on occasion actively resisted copulation attempts of foreign males. The present observation is referred to simply as an EPC, as the female involved did not actively resist copulation.

Timing of copulation in relation to female fertility is critical in determining if forced copulations (FCs) are of reproductive significance (Cheng et al. 1982). Mineau and Cooke (1979) reported that over 80% of the FCs in Lesser Snow Geese occurred after egg laying was completed, and the females were thus infertile. In this observation the EPC occurred during nest initiation, and hence the female was probably capable of being fertilized.

Extra-pair copulations probably occur in other species of dispersed-nesting geese, but are not observed due to the low frequency of occurrence and a lack of observational effort. Also, observations of reproductive behavior of dispersed-nesting waterfowl are most often made during the incubation period when females can be dependably observed, but EPC attempts may be less likely to occur.

I thank Alan Afton, Kim Cheng, Scott Hatch, Frank McKinney, and David Westneat for helpful comments on an earlier draft of this manuscript. Fieldwork was made possible by a cooperative agreement between the U.S. Fish and Wildlife Service and the University of Alaska, Fairbanks (E. Murphy, principal investigator).

LITERATURE CITED

- AFTON, A. D. 1985. Forced copulation as a reproductive strategy of male Lesser Scaup: a field test of some predictions. *Behaviour* 92:142–167.
- BOYD, H. 1953. On encounters between wild white-fronted geese in winter flocks. *Behaviour* 5:85–129.
- BURNS, J. T., K. M. CHENG, AND F. MCKINNEY. 1980. Forced copulation in captive Mallards. I. Fertilization of eggs. *Auk* 97:875–879.
- CHENG, K. M., J. T. BURNS, AND F. MCKINNEY. 1982. Forced copulation in captive Mallards. II. Temporal factors. *Anim. Behav.* 30:695–699.
- CHENG, K. M., J. T. BURNS, AND F. MCKINNEY. 1983. Forced copulation in captive Mallards. III. Sperm competition. *Auk* 100:302–310.
- ELY, C. R., AND D. G. RAVELING. 1984. Breeding biology of Pacific White-fronted Geese. *J. Wildl. Manage.* 48:823–837.
- EVARTS, S., AND C. J. WILLIAMS. 1987. Multiple paternity in a wild population of Mallards. *Auk* 104:597–602.
- FISCHER, H. 1965. Das Triumphgeschrei der gaugans (*Anser anser*). *Z. Tierpsychol.* 22:247–304.
- GLADSTONE, D. E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.* 114:545–557.
- JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, NY.
- LAMPRECHT, J., AND H. BUHROW. 1987. Harem polygyny in Bar-headed Geese. *Ardea* 75:285–292.
- MCKINNEY, F., S. R. DERRICKSON, AND P. MINEAU. 1983. Forced copulation in waterfowl. *Behaviour* 86:250–294.
- 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.
- MINEAU, P., AND F. COOKE. 1979. Rape in the Lesser Snow Goose (*Anser caerulescens*). *Behaviour* 70:280–291.
- OWEN, M. 1980. Wild geese of the world. B. T. Batsford, London.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. *In* B. G. Campbell [ed.], Sexual selection and the descent of man. Aldine, Chicago.
- WELSH, D. 1988. The relationship of nesting density to behavior and reproductive success of Black Brant. M.S. thesis, Univ. of Idaho, Moscow.
- WESTNEAT, D. F. 1987. Extra-pair copulations in a predominantly monogamous bird: observations of behavior. *Anim. Behav.* 35:865–876.