and many were territorial, which would further limit local population densities. Western Amazonia, therefore, may have few areas where shorebirds are concentrated and in need of special protection (Myers 1983).

Perhaps the major reason why migrant shorebirds do not occur in large numbers is the unpredictability of the onset of the rainy season. The peak numbers of most shorebirds occurred in October, which also coincides with the beginning of the wet season (Terborgh 1983). Early rainy season floods cover mudflats and leave behind a layer of silt which may impede foraging. Only the Spotted Sandpiper, which uses steep river banks and logjams, remains after the first wet season floods. We know nothing, however, of prey concentrations, which may also influence shorebird abundance.

Nevertheless, the large extent of habitat available on the many tributaries of the Amazon may provide important shorebird habitats. Areas south of the equator such as the Manu River may be used primarily as stopovers during the southward migration. Areas north of the equator, where the seasons are reversed, may be used primarily during the northward migration. Indeed, some shorebirds could winter entirely within the Amazon basin by staying south of the equator from August to November, and then migrating north of the equator from December to April, where they occur in Venezuela (Thomas 1987). There are, however, no comparable data on the occurrence of shorebirds from a site in northwestern Amazonia.

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EXTRA-PAIR COPULATIONS IN BLACK BRANT[1]

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Monogamy is the primary mating system among waterfowl, but extra-pair copulations (EPCs) have been documented in at least 39 species (McKinney et al. 1983). Extra-pair copulations occur in most Holarctic species of dabbling ducks (*Anas* spp.), but have been recorded in only three species of geese: Lesser Snow Geese, *Chen caerulescens caerulescens* (Mineau and Cooke 1979a), Ross' Geese, *C. rossii* (J. Ryder in McKinney et al. 1984), and Greater White-fronted Geese, *Anser albifons frontalis* (C. R. Ely, pers. comm.).

In colonial Lesser Snow Geese, the close proximity of nesting conspecifics may enable males to pursue EPCs as a secondary reproductive strategy (Mineau and Cooke 1979a, 1979b). Copulatory behavior of other geese has not been studied in sufficient detail to permit comparison with Lesser Snow Geese. Here we report on timing and rates of pair copulations (PCs) and EPCs, and describe behaviors associated with EPCs in colonially nesting Black Brant (*Branta bernicla nigricans*).

METHODS

This study was conducted on the Tutakoke River Black Brant colony (61°15′N, 165°40′W), on the coast of the Yukon Delta National Wildlife Refuge, Alaska, during 1984–1986. Habitat consisted of coastal tundra dom-

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TABLE 1. Nesting chronology of Black Brant at Tutakoke River, 1985–1986.

Year	Date of first egg	Date of last egg	Dates EPC observed	Dates PC observed
1985	27 May	10 June	7 June ($n = 1$)	28 May–2 June ($n = 5$)
1986	27 May	10 June	30 May–5 June ($n = 6$)	26 May–4 June[a] ($n = 13$)

[a] One copulation that occurred on the date that the pair's eggs pipped (28 June) is excluded because it could not possibly have resulted in fertilization.

inated by sedges (*Carex* spp.), grasses (*Poa eminens, Elymus arenarius,* and *Calamagrostis* sp.), and dwarf willow (*Salix* sp.). Black Brant were observed at distances of 50–250 m using a spotting scope from elevated (2.5–4.5 m) blinds.

Based on opportunistic observations of one pair during the 1984 pilot study, focal sampling methods (Altmann 1974) were developed for 1985 and 1986. Data collection began when nest prospecting pairs entered nesting areas. The earliest pairs to begin nest construction at observable sites near observation towers were selected as focal pairs for the duration of their nesting attempt. Later-nesting pairs were added to replace initial pairs that failed due to predation, and to minimize bias associated with observing only early pairs (Mineau and Cooke 1979a). Most focal birds were not individually distinguishable at the range from which they were observed, but pairs present at focal nests on subsequent days were assumed to be the pairs originally selected.

Focal samples were collected during the following time periods: 05:00–08:59, 09:00–12:59, 13:00–16:59, 17:00–20:59, and 21:00–00:59. Light was insufficient for data collection between 01:00–05:00. A microcomputer was used to record behavior of both members of focal pairs continuously during focal samples, which lasted 20 min or until the focal pair went out of sight, whichever came first.

Throughout the nesting season, data were recorded opportunistically on all observed copulations, including those that did not occur during focal samples. Only focal sample data were used in estimates of rates (number of copulations/hours of focal sample data) of PCs and EPCs, but data from nonfocal birds were useful in delineating the timing of copulations relative to nesting chronology of the population.

Copulations not involving members of focal pairs were considered EPCs if they were not preceded by pre- or postcopulatory displays (Burns et al. 1980), were resisted by females, and occurred between birds that did not remain together after copulating. All displays were as described by Johnsgard (1965).

Nests of focal pairs were visited at 3- to 7-day intervals to establish nesting chronology. Some later-nesting focal pairs had begun incubation by the time of the first visit to their nests; nesting chronologies of these pairs were estimated by egg flotation (Westerskov 1950). Dates of initiation of laying and incubation were determined by backdating, assuming one egg was laid per day and incubation commenced with laying of the final egg in the clutch. Using similar methods, nesting chronology of the entire colony was established from nests located on a series of randomly located 50-m radius circular plots (Sedinger, unpubl.).

RESULTS

BEHAVIORS ASSOCIATED WITH EPCS

Focal pairs were involved in three EPC attempts, one per year. The first involved the focal male from 1984 and an unescorted female that swam onto his territory. This was not a forced EPC; both birds performed precopulatory bill-dipping displays, the female did not attempt to escape, and the female remained on the male's territory for several minutes after the copulation. The copulating birds were interrupted by an aggressive Glaucous Gull (*Larus hyperboreus*), and did not perform postcopulatory displays.

In 1985, a focal male engaged in a forced EPC with the female of an intruding pair of brant. The nesting stage of the female was unknown. Although the female resisted by diving, the focal male appeared to achieve cloacal contact and performed tail-wags and postcopulatory displays, which are considered indicative of successful copulations (McKinney et al. 1983). The female's mate did not intervene in the interaction.

In 1986, an unknown male attempted a forced EPC with a focal female on her nest. The male mounted but did not achieve cloacal contact before being dislodged and chased away by the focal male.

The remaining five EPCs occurred in 1986 and involved nonfocal birds of unknown nesting stage. All females resisted by running or diving. Two interactions ended in fights between males, but in both cases it was unclear whether the males that intervened were mates of the involved females.

TIMING AND RATES OF EPCs

Mates of the two focal males that participated in EPCs had already begun incubation and thus were no longer fertilizable. The focal female with whom an unidentified male attempted an EPC was still laying and thus fertilizable. The reproductive status of the nonfocal birds which participated in EPCs during 1986 was unknown. However, these EPCs occurred during the period when females on the colony were laying eggs (Table 1).

In 1985 and 1986, respectively, 25.6 hr (88 focal samples of 56 pairs) and 34.3 hr (106 focal samples of 55 pairs) of focal-sample data were collected during the portions of the nesting seasons in which copulations (PC and EPC) potentially resulting in fertilization were observed (Table 1). These data were distributed between time periods as follows: 05:00–08:59, 19% and 6%; 09:00-12:59, 20% and 29%; 13:00-16:59, 30% and 20%; 17:00–20:59, 12% and 13%; 21:00–00:59, 19% and 32%.

Since one EPC was observed per year during focal samples, the rates of EPC during the above portions of the nesting seasons were 0.9/pair/day in 1985 and 0.7/pair/day in 1986 (assuming equal rates of EPC among pairs, among days, and for all hours within a 24-hr day). Rates of PC over the same intervals were 1.9 and 2.8 copulations/pair/day in 1985 ($n = 2$) and 1986 ($n = 4$), respectively. In all, seven of the 28 (25%) copulations we observed in 1985 and 1986 were EPCs, 19 (68%) were PCs, and two (7%) were of unknown status.

DISCUSSION

Our rate estimates are based on small samples, but suggest that an average female would participate in more than one EPC during her fertile period. The significance of this behavior to the fitness of the individuals involved is presently unknown for Black Brant; however, the occurrence of EPCs during the period when females are fertilizable could result in multiply-fathered clutches as found in other species (Burns et al. 1980, Evarts and Williams 1987, Quinn et al. 1987).

Extra-pair copulations have been reported less frequently for geese than for ducks, particularly dabbling ducks in the tribe Anatini. This difference undoubtedly results partly from the limited number of behavioral studies of geese during the period when copulations are most likely, and may also reflect variation in social organization of these two groups (McKinney et al. 1984). Most ducks do not defend exclusive territories and pair-bonds seldom persist much beyond the completion of egg laying; furthermore, nesting is asynchronous and females may renest if their clutches are destroyed (McKinney 1985). Taken together, these factors provide increased opportunities for male ducks to seek EPCs, particularly after their own mates have completed egg laying.

Geese, in contrast, maintain long-term pair-bonds and males defend exclusive territories during nesting (Owen 1980). Nest and mate defense limit the opportunities for males to seek EPCs, even after their own mates are incubating (Heinroth 1911). In the Arctic, nesting synchrony and lack of renesting further limit opportunities for EPCs (Owen 1980).

Occurrence of EPCs in colonially nesting Black Brant is consistent with the hypothesis that males of colonial species of geese have more opportunities for EPCs than dispersed nesters, despite the constraints of nest and mate defense. Studies of other colonial geese are needed to test this assertion. More data are also needed from dispersed nesting species, since Ely's (pers. comm.) observation of an EPC in dispersed nesting Greater White-fronted Geese suggests that EPCs are not limited to colonial species.

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