Ibis (2005), **147**, 57–66

First pairing in Snow Geese *Anser caerulescens*: at what age and at what time of year does it occur?

BARBARA GANTER,[1]* W. SEAN BOYD,[2] VASILY V. BARANYUK[3] & FRED COOKE[4]
[1]*Schückingstrasse 14, 25813 Husum, Germany*
[2]*Pacific Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, RR1, 5241 Robertson Road, Delta, British Columbia V4K 3N2, Canada*
[3]*State Nature Reserve 'Ostrov Wrangelya', Russia*
[4]*Larkins Cottage, 6 Lynn Road, Castle Rising, Norfolk PE31 6AB, UK*

In migratory birds, the place and time of pair formation are important parameters for population structure and dynamics. Geese are not only migratory but also exhibit long-term monogamy, and therefore the first pairing event in a bird's lifetime is of particular importance. Through behavioural observations of young, known-age, marked birds conducted on the wintering grounds during three winter seasons we investigated two aspects of the timing of first pair formation in the Wrangel Island population of Snow Geese *Anser caerulescens*: (1) the age at which birds first form pair bonds, and (2) the seasonal pattern of first pair formation. Wrangel Island Snow Geese paired considerably later in life than Snow Geese from a low-Arctic population: almost none of the birds formed pairs in their second winter, and many were still in sibling groups for at least part of that season. The proportion of birds in pairs continued to increase until at least 5 years of age. Most pairing took place during the observation periods, and in general the proportion of birds in pair bonds increased gradually throughout the winter season. The amount of pairing during spring migration or summer varied annually and among cohorts, indicating that even very young birds may be able to form pair bonds quickly if conditions on the breeding grounds are unusually favourable. Pairing later and remaining in family groups longer may be a response to breeding conditions in this high-Arctic colony. Here, productivity is typically low due to harsh weather and predation, whereas Snow Geese breeding in the low Arctic are less restricted and form pairs and start to breed when younger. The fact that most, but not all, pairing takes place on the wintering grounds helps explain why a previous study found a certain amount of gene flow between the two Wrangel Island subpopulations with separate wintering grounds.

In long-lived birds with long-term monogamy, such as geese and swans, the first pairing event in a bird's lifetime is of particular importance. Pair bonds formed early in life persist over many years. Divorce is rare and if re-pairing occurs, it is usually after the death of a partner (Black 1996). Therefore, the timing of first pairing, both within a bird's lifetime and within the annual cycle of bird populations, has an important influence on population structure and dynamics of long-term monogamous birds.

Genetic mixing of populations is directly linked to the stage of the annual cycle when pairing (for long-term monogamous birds this will be predominantly first pairing) occurs (Rockwell & Barrowclough 1987). Population units can generally be defined according to time and place of initial pair formation. This is especially important for migratory populations, which intermingle with neighbouring populations to different degrees at different times of the year. The age at which birds pair for the first time sets a lower limit to the age of first breeding, which in turn is an important life-history trait (Stearns 1992) with direct influence on population growth rate.

A prerequisite for the study of both aspects of first pairing (age of birds at first pairing and timing of first pairing within the annual cycle) is the presence of marked birds of known age in the population. Ideally,

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*Corresponding author.
Email: barbara.ganter@t-online.de

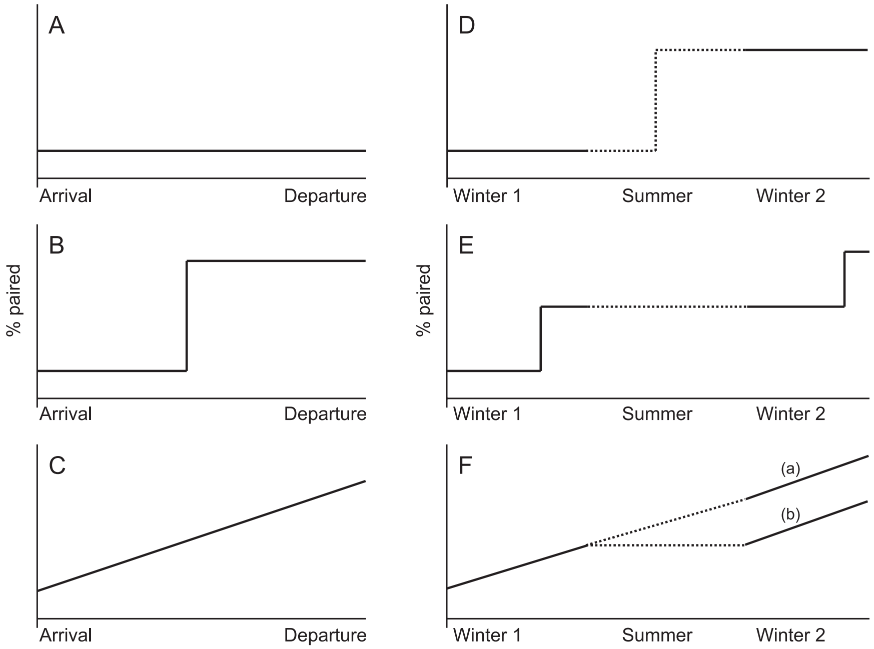

Figure 1. Examples of hypothetical scenarios of the timing of pair formation. A–C: timing within the non-breeding season; A: no pairing, B: sudden pairing, C: gradual pairing. D–F: timing throughout the year (observation seasons in winter); D: all pairing suddenly in summer, E: all pairing suddenly in winter, F: gradual pairing in winter (a) with or (b) without pairing in summer.

these birds should be followed throughout the year. However, the study of pairing events requires considerable effort in behavioural observation, and most intensive studies of migratory populations are confined to either breeding grounds or migration/wintering sites. Even if birds are observed for only part of the year, an observation period of several months during the non-breeding season allows evaluation of several hypothetical scenarios of the annual chronology of pairing (Fig. 1). Within and between observation periods pairing could take place gradually, suddenly or not at all. The proportion of birds of each age class paired at the end of each observation season will give a lower limit to the proportion paired during the following breeding season.

Previous studies on the chronology of first pairing in several Arctic-breeding goose species indicate that pairing occurs mostly in winter and spring when birds are a long way from their breeding grounds (Cooke *et al.* 1975, Prevett & MacInnes 1980, Black & Owen 1988, Owen *et al.* 1988, Warren *et al.* 1992). Little, if any, pairing occurred in summer, although one studies showed that associations formed between yearlings on or near the breeding areas were important in determining the choice of future mates (Owen *et al.* 1988, Choudhury & Black 1994). No birds were paired before their second winter. The average age of first pairing varied among species: in Greenland White-fronted Geese *Anser albifrons flavirostris*, most birds formed pairs in their third or fourth winter, but some even later (Warren *et al.* 1992); in Svalbard Barnacle Geese *Branta leucopsis*, about half of the birds were paired by the age of 2 years and all were paired by the age of 4 years (Black & Owen 1995); in Snow Geese *Anser caerulescens* from the La Pérouse Bay colony on Hudson Bay, Canada, almost all 2-year-old birds were already paired and up to 50% of them were breeding (Cooke *et al.* 1995, Cooch *et al.* 1999). In summary, the above studies suggest that both age and annual timing of pair formation differ among goose species, but there may also be differences in age and timing among populations within a species. These differences may translate into differences in population dynamics.

In this paper, we present the results of a study on first pairing in a population of Snow Geese breeding in the Russian High Arctic. We use intensive observations of known-age birds during the winter season to address the questions of (i) when during the annual cycle and (ii) at what age pair formation occurs.

METHODS

Study population

We studied a population of Snow Geese breeding on Wrangel Island in the Russian High Arctic (71°N 180°E/W). Breeding birds from this remnant Snow Goose colony separate into two subpopulations in winter, a northern one on the Fraser and Skagit River Deltas near the border of British Columbia (Canada) and Washington State (USA), and a southern one in central California (Kerbes *et al.* 1999). On spring migration, the subpopulations do not mingle until at least the Yukon–Kuskokwim Delta (Alaska), and in some years they may even arrive separately on Wrangel Island (V.V. Baranyuk pers. observ.). The northern wintering subpopulation of Wrangel Island Snow Geese currently numbers about 60 000 birds, slightly more than half of the total population (Kerbes *et al.* 1999, W.S. Boyd unpubl. data). Population dynamics of the Wrangel Island colony are characterized by comparatively low overall productivity and frequent breeding failures due to adverse weather conditions and high predation pressure (Bousfield & Syroechkovskiy 1985).

Marking and resighting

Birds were caught on Wrangel Island during the annual wing moult. All birds within a ringing drive were marked with metal leg rings and individually engraved red plastic neck collars, and sexed by cloacal examination. Although a general neck-collaring programme of adult breeding birds on Wrangel Island has been ongoing since 1988 (Kerbes *et al.* 1999), capturing effort for the present study specifically targeted yearlings in moulting non-breeder flocks; in that way, neck-collared birds of known age were introduced into the population. (Although many goslings are caught annually with their parents and leg-ringed, they are too small to be fitted with neck collars.) Yearling Snow Geese can be identified by plumage characteristics (Mowbray *et al.* 2000). We marked 198 yearlings in 1998 (1997 cohort, i.e. hatched in 1997), 171 in 1999 (1998 cohort) and 183 in 2000 (1999 cohort; Table 1). Only yearlings with intensively red-stained faces were marked in this study; these birds were suspected to winter on the Fraser and Skagit River Deltas (see Baranyuk *et al.* 1999).

During a previous project, some known-aged birds from the 1986 and 1987 cohorts (225 and 321 birds, respectively) had been captured and marked either on the Fraser–Skagit Delta or on Wrangel Island (W.S. Boyd & V.V. Baranyuk unpubl. data); observations of these birds on the breeding colony in subsequent summers are used as supplementary information (see below).

In the following, cohorts of marked birds are referred to by their hatch year. To avoid ambiguity in referring to age classes, we use the number of winters in a bird's lifetime when referring to age in the winter season (second-, third-, fourth-winter bird, a second-winter bird being approximately 1.5 years of age etc.) and the bird's true age (2-, 3-, 4-year-old) in the summer season.

Table 1. Number of different birds seen (number of observations in parentheses) per cohort and observation season, and total number of birds ringed per cohort.

	Cohort			
Observation season	1997	1998	1999	Old*
1998–1999	110 (298)			
1999–2000	98 (445)	88 (559)		
2000–2001	59 (160)	57 (183)	124 (600)	169 (437)
2001–2002	8 (10)	10 (12)	22 (31)	
Total ringed	198	171	183	

*Ringed as adults prior to 1998.

Neck-collared birds were resighted on the wintering grounds of the northern subpopulation on the Fraser and Skagit River Deltas from October 1998 to April 1999 (26 observation days), from January to April 2000 (44 observation days) and from October 2000 to April 2001 (52 observation days), with a few additional records from October and November 2001. As behavioural observations of marked birds in large flocks are time-consuming, observation effort in this study was directed specifically at the known-age birds ringed in 1998–2000, which were recognizable by the letter series of the engraved alphanumeric codes on the neck collars, although a large number of unknown-age marked birds were also present in the population. Observers recorded neck-collar code and status (unpaired, paired or member of a group) of each marked bird. In the winter of 2000/01, observation effort was extended and the pair status of a number of marked birds of unknown age, ringed as adults prior to 1998 and thus at least 5 years old, was also recorded for comparison. Observations were carried out by a different observer each winter.

Paired status of neck-collared birds was identified by the focal (ringed) bird walking closely together with an unringed bird or displaying courtship behaviour, or by triumph displays; only clearly paired birds were recorded as such. Most unpaired birds were alone. However, we also classified birds as 'unpaired' if they were observed associating with birds from the same cohort and the same ringing drive (same neck-collar series). These associations were interpreted as sibling groups that were ringed together as yearlings on Wrangel Island. Siblings tend to remain together on the breeding grounds in their yearling summer (Prevett & MacInnes 1980), so many would have been captured in the same ringing drives. Because all birds in a ringing drive were ringed, sibling groups consisting of both marked and unmarked birds would be highly unlikely. To test the assumption that associated birds of the same cohort were siblings and not members of a pair, we checked the 'sibling groups' for persistence throughout the season and, where possible, persistence to subsequent years. Moreover, we checked how many of the 'two-sibling groups' consisted of birds of the same or of opposite sexes.

Data were grouped by month of observation, and pairing status was determined for each existing combination of bird and month (not every bird was seen in every month). In cases where birds were classified as alone, paired or in sibling groups within the same month, sibling group and pair status was given precedence over 'alone' status. Exceptions to this were made in only a few cases where, within the same month, birds were recorded first as paired and subsequently several times as alone; in these cases, birds were regarded as alone in this month, the paired observation probably having been an error. Ambiguous records (e.g. a bird recorded once as paired and later once as unpaired in the same month) were deleted.

In the summer of 2001, a number of known-age birds of the 1997–1999 cohorts were resighted on the breeding colony on Wrangel Island. Observations of the status of these birds (paired or unpaired, breeding or non-breeding) were used to supplement the information from the 2000/01 winter season.

In addition, some observations of young, known-age birds were made on Wrangel Island in the summers of 1989 and 1990 (V.V. Baranyuk unpubl. data). These data are presented for comparison, although we have no information on the pairing status of these birds in winter.

RESULTS

Numbers of observations and of different birds observed in each winter season are shown in Table 1. In addition, there were a large number of resightings of neck-collared birds where pairing status could not be determined, but only those with information on pairing status were retained. However, for more than 90% of all known-aged birds seen in a given year, pairing status was recorded at least once. Owing to the chronology of ringing and resighting, we observed known-age birds from one cohort in the 1998/99 winter, two cohorts in 1999/2000, and three cohorts in 2000/01 and autumn 2001. We thus have three years of observations on the 1997 cohort, two on the 1998 cohort and one on the 1999 cohort, with additional information on all three cohorts from autumn 2001. Sample sizes per month and cohort ranged from 7 to 87 birds, with an average of 36 (Fig. 2).

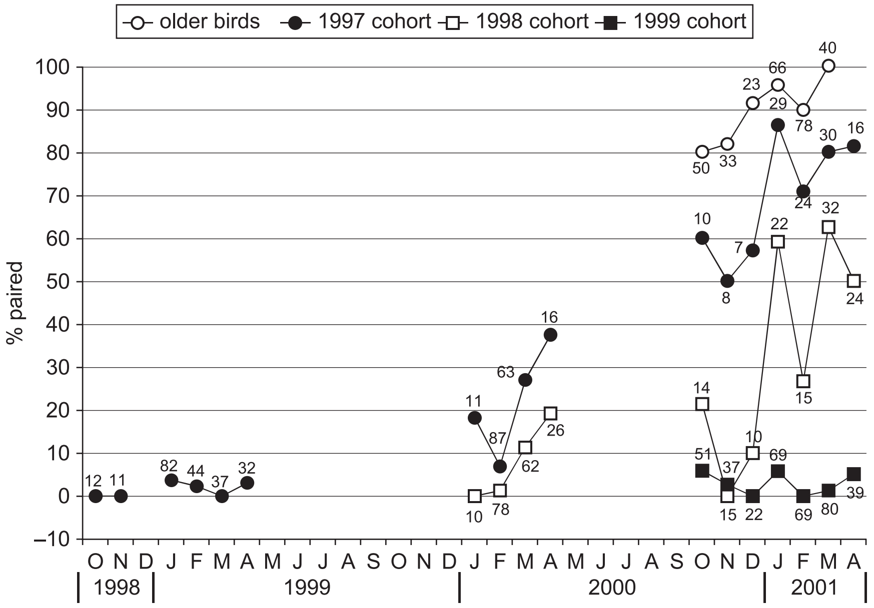

Figure 2. Proportion of birds in pair bonds. Included are three known-age cohorts observed during three winter seasons; in the 2000/01 season, older birds were also observed for comparison. No observations were made between departure of birds from the wintering grounds and their return in the following autumn. Numbers against data points are sample sizes (number of different birds per month).

Table 2. Status of birds from sibling groups when they were last seen before departure. Included are all birds that had been observed in sibling groups at least once during the season.

	Last sighting in						
	Oct	Nov	Dec	Jan	Feb	Mar	Apr
1998–1999 season ($n = 60$)							
in sibling group when last seen	3	2	–	4	15	–	7
alone when last seen	–	1	–	1	–	12	15
paired when last seen	–	–	–	–	–	–	–
2000–2001 season ($n = 55$)							
in sibling group when last seen	1	2	1	2	–	–	–
alone when last seen	–	1	–	1	6	24	16
paired when last seen	–	–	–	–	–	–	1

Sibling groups during the second winter

Associations between birds from the same cohort that were ringed together were observed almost exclusively in the birds' second winter (approximately 2–5 months after ringing). Such groups were observed in the winters of 1998/99 and 2000/01, but not in 1999/2000 when observations were carried out from January to April only. In 1998/99, a total of 60 birds from the 1997 cohort was seen in a group of birds from the same ringing drive at least once; in 2000/01, 55 birds from the 1999 cohort were seen in such a group at least once. Groups consisted of 2–5 ringed birds and were seen mostly during the first part of the season (October to January). Most birds that had been recorded as part of a ringed group in autumn or early winter were alone when last seen before departure (Table 2).

We assumed that birds that were ringed together as yearlings and seen together in the following winter were sibling groups, and indeed the distribution of groups, with most comprising 1–4 similarly aged birds, is consistent with this assumption. However, an alternative explanation is that some of the 'siblings', at least those in groups of two birds, could have been yearling pairs. If this had been the case then such groupings should comprise one male and one female, whereas if they were all siblings the sex ratio distribution should be in a ratio of 1 : 2 : 1. We tested this and found that among all 34 groups of two 'siblings', six consisted of two males, 18 of one male and one female, and 10 of two females; this distribution is close to a random (binomial) distribution of sexes, assuming a 1 : 1 sex ratio (goodness-of-fit test for binomial distribution: $\chi^2 = 1.06$, $df = 2$, $P = 0.58$). These findings strongly support the assumption that groups of two birds from the same cohort that were ringed together as yearlings are indeed either siblings or associated in some other way (see Discussion), but not partners of a pair formed early in life. Therefore, we feel confident in regarding all birds seen in ringed groups as 'unpaired'.

There is some evidence that sibling groups associate occasionally in subsequent winters. Although none of the sibling groups observed in the 1998/99 winter (1997 cohort of birds) were seen together again in the following winter season, two birds from this cohort that had been members of a three-bird group in 1998/99 were repeatedly seen together in autumn 2001 (i.e. three winters later), although they had not been observed together in the two intervening years. Similarly, three groups of two siblings from the 1999 cohort had separated by the end of the 2000/01 season (all birds were recorded as 'alone' in the spring), but were seen together again in October/November 2001. Although anecdotal, this information clearly indicates that even though sibling groups usually separate toward the end of the birds' second winter (see Table 2), some of these groups may re-unite in the following autumn or even years later.

Rate of pair formation: seasonal and age class patterns

Data for three cohorts of Wrangel Island Snow Geese show that very few of these birds (< 5%, < 20% and < 10% for the 1997, 1998 and 1999 cohorts, respectively) had formed pair bonds by the end of their second winter (Fig. 2). For third- and fourth-winter birds, the proportion of paired birds increased markedly throughout the winter, reaching levels of 37.5% (1997 cohort) and 50% (1998 cohort) at the end of the third winter and of 81.3% at the end of the fourth winter (1997 cohort; Fig. 2). In the unknown-age older birds (5 years old and older) observed in the 2000/01 winter, the proportions paired were even higher than in fourth-winter

Table 3. Pairing of 2-year-old birds during summer. Compared are proportions of birds seen in pairs before departure from and after return to the wintering grounds (March/April vs. October/November sightings).

Cohort	% paired in spring (*n*)		% paired in autumn (*n*)
1998	12.3 (65)	(summer 2000)	13.0 (23)
1999	3.2 (93)	(summer 2001)	36.4 (22)

birds, increasing from 80% in October to 100% in March. The seasonal increase in recorded proportions of paired birds was not monotonic but underwent some fluctuations (Fig. 2), which may be explained by the fact that not all birds were observed in every month, sample sizes differed among months and each monthly figure probably represents a different set of birds.

Overall, the increase in proportion of paired birds took place mostly in late winter/early spring (i.e. between January and April). When cohorts returned after the 2000 summer season, the proportion of birds in pairs had not increased in the 1998 cohort (2-year-old birds) and had increased slightly in the 1997 cohort (3-year-old birds), indicating that little pairing occurred during spring migration or during the summer (Fig. 2). However, observations of 2-year-old birds returning to the wintering grounds in autumn 2001 suggest that the rate of pair formation during summer was higher in that year, with about one-third of the returning 2-year-olds recorded as paired (Table 3; see below for information on 2001 summer conditions on Wrangel Island).

Breeding ground data

In the summer of 2001, 39 known-age birds from the 1997–99 cohorts were resighted on the breeding colony on Wrangel Island; of these birds, 30 had been observed and their pairing status determined in the previous winter. On Wrangel Island, birds were classified by their behaviour on the colony and presence or absence of a nest/territory; birds were either paired and breeding or alone and non-breeding. It should be noted that the sample of birds seen on Wrangel is not representative for the population because observations were only made on the breeding colony and marked birds in non-breeding flocks were not recorded. A number of birds from all cohorts were seen paired and breeding on Wrangel, but had still been recorded as alone when last seen on the wintering grounds (Table 4). The 2001 breeding season on Wrangel was characterized by unusually favourable conditions with the highest spring temperatures in 30 years, resulting in early snow melt and good weather throughout the arrival and laying periods (Baranyuk *et al*. 2001).

In comparison, in 1989 and 1990, the two previous years during which known-age birds had been observed in the colony, spring conditions were good, but not exceptional (V.V. Baranyuk pers. obs.). Of the birds seen in the colony in these years, some 2-year-olds, most 3-year-olds and all 4-year-olds were breeding (again, the sample of birds seen in the colony is not representative for the whole population). However, the proportion of observed 2- and 3-year-olds that were still single was higher than in 2001 (Table 5).

DISCUSSION

Timing of pairing: seasonal pattern

In our study, the proportion of young birds in pairs increased throughout the winter season from October to April, although there were some fluctuations in recorded proportions because different subsets of birds were seen every month. First pairing did not occur suddenly, but gradually throughout the season, mostly in late winter and early spring; this pattern is similar to that reported in Barnacle Geese

Table 4. Pair status of birds during the 2001 breeding season on Wrangel Island and when last seen in winter 2000–2001.

Cohort	Summer 2001	Winter 2000–2001	*n*	Last seen in winter
1997 (4-year-old)	paired, breeding	paired	5	Jan. (2), Feb. (2), Mar. (1)
	paired, breeding	alone	3	Feb. (1), Mar. (2)
1998 (3-year-old)	paired, breeding	paired	4	Jan. (2), Mar. (2)
	paired, breeding	alone	2	Feb. (1), Mar. (1)
1999 (2-year-old)	paired, breeding	alone	13	Dec. (1), Jan. (1), Feb. (2), Mar. (8), Apr. (1)
	alone	alone	3	Mar. (1), Apr. (2)

Table 5. Proportion of paired birds among known-age birds observed on the breeding colony. Note that birds seen on colony are not a representative sample of the population.

Breeding season	Spring conditions	2-year-olds			3-year-olds			4-year-olds		
		n	% single	% paired	*n*	% single	% paired	*n*	% single	% paired
1989	good	29	55.2	44.8	14	21.4	78.6	n/a	n/a	n/a
1990	good	n/a	n/a	n/a	32	28.1	71.9	4	0	100
2001	exceptionally good	16	18.8	81.2	6	0	100	8	0	100

n/a: no marked known-age birds in this cohort.

(Owen *et al.* 1988), Greenland White-fronted Geese (Warren *et al.* 1992) and mid-continent Snow Geese (Prevett & MacInnes 1980).

Because the partners of our marked known-aged birds were all unringed, we cannot exclude the possibility that birds were seen with more than one partner on subsequent occasions. Geese may enter a series of trial partnerships before finally choosing their long-term mate (Choudhury & Black 1993). If some of the pairings we observed were only temporary trial partnerships this would bias our estimate of timing of pairing towards earlier pairing, meaning that definitive pair formation may have taken place slightly later on average (affecting both seasonal and age-related patterns).

Our data indicate that some first pairing may also take place on migration (possibly at spring staging areas further north) or even on the breeding grounds. In some cohorts and some years more birds returned paired in autumn than had left paired in spring (Fig. 2, Table 3), and some birds that were recorded as 'alone' when last seen on the wintering grounds in spring 2001 were seen paired and breeding on Wrangel Island in the following summer (Table 4). Again, this is similar to results from previous studies in which some first pair formation occurred during summer (or, at least, outside the winter observation season). However, because not every bird was observed on the wintering grounds right until the end of the season, we cannot exclude the possibility that even in these cases, pair bonds were still formed on the wintering grounds just before departure. One might also suspect that some birds recorded as 'alone' on the wintering grounds were, in fact, paired although they were not seen in close association with a partner. However, the example of older birds observed in 2000/01, 100% of which were recorded as paired at the end of the season (Fig. 2), emphasizes the reliability of our method of recording pairing status.

Overall, it appears that the majority of first pair bonds are formed on the wintering grounds during the observation season (October–April). This corresponds roughly with scenarios C and F(b) in Figure 1, although annual variation in the amount of pairing during summer suggests that scenario F(a) may also apply in some years. Data from different breeding seasons on Wrangel Island suggest that this variation may be related to the conditions encountered by the birds during the arrival and laying periods (Table 5).

If pairing took place exclusively in winter, one might expect that the northern-wintering subpopulation of Wrangel Island birds would be genetically isolated from the southern-wintering one. However, Syroechkovsky *et al.* (1994) found that there was a certain amount of gene flow between the two subpopulations, and they pointed out that genetic mixing may occur through events on the breeding grounds such as extra-pair copulations or intraspecific nest parasitism. Our data suggest that, at least in some years, some pairing occurs during spring migration or even on the breeding grounds where both subpopulations intermingle, thus allowing additional gene flow through formation of pairs with one partner from each subpopulation.

Timing of pairing: patterns across age classes

Compared with the previously studied Snow Geese of the La Pérouse Bay population (Cooke *et al.* 1995), Wrangel Island birds appear to form pair bonds on average considerably later in life. Very few are paired at the end of their second winter, and the proportion of paired birds continues to increase gradually throughout the third and fourth winters. Even at the end of the fourth winter the proportion of birds in pair bonds has not yet reached that found in older birds. By contrast, most 2-year-old Snow Geese arrive on the breeding grounds in La Pérouse

Bay already paired. Note that these observations are not directly comparable with the present study because all information on La Pérouse Bay birds was collected on the breeding grounds, not on the wintering grounds. Some unpaired La Pérouse Bay females may not have returned to the breeding grounds, leading to an overestimation of the proportion of young birds in pairs when seen in the summer. However, because up to 50% of all 2-year-olds are already breeding each year (Cooch *et al.* 1999), an even larger proportion must have been paired at the age of 2 years. By the age of 4 years, the breeding propensity of La Pérouse Bay birds no longer differs from that of older birds (Cooch *et al.* 1999), whereas some Wrangel Island birds have not even found a partner at this age. The slow and gradual process of pair formation over the first few years that we found in Wrangel Island birds is more similar to the pattern found in Greenland White-fronted Geese (Warren *et al.* 1992) than to that in the La Pérouse Bay Snow Goose population, or in Barnacle Geese (Black & Owen 1995).

In geese, being part of a pair confers a dominance advantage over single birds within a feeding flock, although this advantage is small compared with that of being part of a family including parents and juveniles (Gregoire & Ankney 1990). Moreover, being paired well before arrival on the breeding grounds is a prerequisite for a successful breeding attempt (Owen *et al.* 1988), and some birds do breed when 2 years old. Why, then, should so many more young Snow Geese defer pairing in the Wrangel Island population compared with La Pérouse Bay? There are several possible explanations for the difference in age of first pairing between the two populations.

The first explanation is concerned with a possible methodological artefact. Wrangel Island birds are marked with conspicuous neck collars, whereas La Pérouse Bay birds wear tarsal rings only, and the presence of a neck collar might inhibit pairing. However, all of the 'old' neck-collared birds in our sample were paired by the end of the season. These birds were originally ringed several years earlier, and even if most of them were paired at the time of ringing many must have lost mates in the meantime; the fact that currently all of them were paired shows that they apparently did not have any difficulty in acquiring a new partner. Therefore, we are confident that the mere presence of a neck collar does not present a problem for birds searching for a partner.

A second, ecological explanation arises from the differences in breeding environment of the two populations. Whereas La Pérouse Bay is a low-Arctic colony where successful breeding is possible every year (for a rare exception see Ganter & Boyd 2000), Wrangel Island has a much harsher high-Arctic climate with frequent near-complete breeding failures (Bousfield & Syroechkovskiy 1985), and in most years young birds may not have much of a chance to breed. Breeding at a young age does carry a cost in terms of successful breeding in the following season at La Pérouse Bay (Viallefont *et al.* 1995), and this cost may be even higher in a harsher environment. However, when spring conditions near and on the Wrangel Island breeding colony are unusually favourable young birds may be able to form pairs relatively quickly during the last part of migration or perhaps even after arrival on the breeding grounds. A study by Reed *et al.* (2003) on Snow Geese on Bylot Island (Eastern Canadian High Arctic), although not concerned with age of first pairing, showed that recruitment (i.e. age of first breeding) was influenced by environmental conditions on the breeding grounds (lemming densities, but not spring snow conditions). In our study, even under very favourable conditions the proportion of paired 2-year-old birds in the Wrangel Island population still remains much lower than in La Pérouse Bay birds (about one-third vs. most birds paired), and we can assume that the same is true for 3-year-old or even older birds.

If breeding at a young age is not an option, it may be advantageous for young birds to remain in family units for a longer period of time. Our data indicate that many birds remain in 'sibling groups' well into their second winter, and sometimes unpaired 'siblings' reunite months or years later even if they had separated at the end of the second winter. Because birds were not marked in the nest at hatching, we cannot say with certainty that groups of birds of the same cohort associating in winter are indeed true siblings. However, we can exclude the possibility that these associations are permanent pairs formed at an early age, and if they are not true siblings they are early life associates of some other kind staying together for an extended period of time. A similar phenomenon was described in Greenland White-fronted Geese, many of which remain in extended family units throughout the first years of life (Warren *et al.* 1993). If birds are still in 'sibling groups' for part of their second winter there may be little chance for them to find a partner before departing for the breeding grounds; in our sample, only one of 115 birds seen in a sibling group during the winter was observed as paired before departure (Table 2).

Pairing at a later age and remaining in family groups longer may be part of a different life history pattern in this high-Arctic population, resulting in an expected lower population growth rate. Greenland White-fronted Geese, which behave in a similar way, also have low average annual productivity (Fox *et al.* 1999). By contrast, data at La Pérouse Bay were collected during a period when productivity was very high and the colony was expanding at a rate of about 8% per year (Cooke *et al.* 1995). Although Cooch *et al.* (1999) did not find a systematic change in age of recruitment over time in this population, their study included only cohorts until 1981, and age of first pairing and breeding may have changed since then.

Another possible source of variation in timing of pair formation among cohorts is annual variation in the pool of potential mates. In the Wrangel Island population, where annual breeding output and therefore the size of cohorts is highly variable, the age structure of the pool of unpaired birds must differ from year to year: more so than in the La Pérouse Bay population where annual breeding success is less variable. Because we have no information on the relative proportions of available unpaired birds of different ages, we can only speculate on the influence of this factor on the average age of first pairing.

Overall, the apparent difference in age of first pairing and breeding among goose populations suggests that these aspects of life history are highly flexible and can differ or change according to environmental conditions (Newton 1998), which may be climatic or related to intra- or interspecific interactions. In addition to differences among populations, annual variation in breeding conditions within a population may influence not only the average age of first successful breeding but also the average age at which pairs are formed.

Our sincere thanks go to Chris Tucker, Darren Lissimore, Byron Andres and Mary Taitt who observed birds on the Fraser and Skagit Deltas in winter. We also thank two anonymous reviewers for their helpful comments on the manuscript. Financial assistance was provided by Canadian Wildlife Service, Pacific Wildlife Research Centre, Delta and by the British Columbia Waterfowl Society.

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Received 17 October 2003; revision accepted 10 June 2004;

(doi: 10.1111/j.1474-919x.2004.00341).