Three-bird flights in migratory geese - a review

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Three-bird flights (3BF) have been reported amongst seven species of geese: 12 populations of *Branta* and seven of *Anser*. The phenomenon has been recorded from mid-winter to the start of incubation, being most frequent and intense during the period of first egg laying. As previously reported, pursuit flights (often involving more than three geese) in wintering and staging areas seem not to be of crucial importance. Pursuits at breeding places offer opportunities for males to achieve forced extra-pair copulations (FEPC) with paired sexually-mature females. This may represent both a primary strategy for solitary mature males and a secondary strategy for paired males with incubating females, which can secure extra-pair copulations (EPC) without cost to their primary reproductive investment. The authors suggest also that 3BF enable females to assess the relative strength and condition of the males to whom they are attached and of the males seeking to usurp them. This may allow females to make choices about accepting EPC from attacking males to contribute to the paternal composition of their reproductive effort. It also seems likely that 3BF offer females not yet paired an opportunity to choose between potential partners prior to the establishment of long-term monogamous bonds.

Key Words: three-bird flights, extra-pair copulation, pair bonds, geese, behaviour, pursuit flights

Despite great progress in the study of the behavioural ecology of geese in recent years, many activities, including pair formation and maintenance, defence of mate, progeny or nesting area and even copulation, remain difficult to observe and challenging to record or analyse in any systematic way. These crucial events are both infrequent and of very short duration. They may also take many forms and have outcomes that are often unseen by the observer. This is especially true of those activities that have consequences for paternity and the reproductive success of an individual. These include aerial pursuits amongst geese. Rarely described in the literature and often dismissed when they are, their precise function remains obscure and their frequency throughout the year unreported. Since most chases have a sexual basis, and most aerial pursuits involve two or three individuals, it seems highly likely that aerial chases have some function that relates to reproduction. Although monogamy is the primary system amongst waterbirds (Black 1996), extra-pair copulations (EPC) have been documented in several taxa, primarily in temperate duck species (McKinney *et al.* 1983). Whilst such behaviour has been observed amongst geese, it remains relatively rarely described in the field (eg Welsh & Sedinger 1990), even during intense observations (eg Mineau & Cooke 1979).

Much of what is generally known about reproductive behaviour in northern geese relates to observations of captive or semi-wild flocks. Most notable amongst these were the construction of an ethogram of Greylag Geese *Anser anser* by Lorenz (1988) and his co-workers and observations of Canada Geese *Branta canadensis* by Hanson (1953), Collias & Jahn (1959) and Wood (1965).

In this brief review, the authors attempt to summarise information in the literature and their own observations of pursuit flights in free-living northern breeding geese to address two major questions:

1. Do pursuit flights at breeding places have a direct sexual function?

2. Are pursuit flights in wintering and staging areas more important in pair formation than previous studies suggest?

Finally, they attempt to draw general conclusions from the scant observations available in the hope that this will stimulate others to offer their own observations or to initiate new studies.

Timing of pair formation in geese

There is a general belief, largely derived from observed increases in the proportion of paired birds in spring flocks, that most new pairing of geese occurs increasingly during the late winter or early spring (Weller in Delacour 1954; Ogilvie 1978; Owen 1980). This is certainly the case amongst the best-studied population, that of the Svalbard Barnacle Goose *Branta leucopsis*, in

which pair formation, Triumph Ceremonies (Lorenz 1965) and agonistic behaviour peak in March prior to departure to breeding areas (Owen *et al.* 1988; Black & Owen 1988). Similarly, the proportion of Wrangel Island Snow Geese *Anser caerulescens* in pair bonds increased throughout the winter, so although pairing did not take place exclusively in winter most apparently occurred in late winter and early spring (Ganter *et al.*, in litt.). In some years, pairing apparently occurred after departure from the wintering grounds, but first pairing may involve long trial periods and probable changes in partners. However, amongst Greenland White-fronted Geese *Anser albifrons flavirostris* pairing is thought to occur away from the wintering grounds, although two pairs are known to have paired in Scotland during winter (Warren *et al.* 1992). Only studies of a range of known unpaired geese amongst different populations will resolve the apparent differences between populations.

After the death or divorce of a partner, new pair bonds were formed in Swedish Greylag Geese on the breeding area during three periods: just after return in spring, just after moult or just before departure in autumn (Nilsson & Persson 2001). Two of the most detailed accounts of the process of pair formation derive from observations on the re-mating of a nesting female Canada Goose and a nesting Lesser Snow Goose *Anser c. caerulescens* immediately after their mates had been killed (Jones & Obbard 1970; Abraham *et al.* 1981). Radio-marking of Greater Snow Geese *Anser c. atlanticus* showed that during autumn migration male parents often arrived at Cap Tourmente at different times from the female and young, and then re-united (A. Reed, pers. comm.), so caution is necessary to differentiate re-pairing from re-uniting when observing unmarked birds.

With the advent of individual marking schemes, it becomes increasingly possible to register the point at which a young goose, a conspicuous member of a family group consisting of parents and siblings, is either driven away by its parents or breaks away to form a pair bond with a new mate. Despite the impracticability of monitoring associations between individuals along migratory corridors, it is remarkable that scientists remain so ignorant of the precise timing of pair formation in most goose populations. In any case, as Lorenz's studies of Greylag Geese showed, the strength of pair bonds waxes and wanes, so it is difficult to determine a particular point when a long-term monogamous bond becomes established. On the limited evidence currently available, it would seem that pair formation takes place mostly in late winter and in spring. Pair re-formation (ie after death or divorce of a mate) may, however, occur in spring, the reproductive period and in autumn (perhaps at moulting or staging areas where mixing of birds of widely differing provenance occurs).

The role of pursuits in pair formation

Heinroth (1911) first described pair formation amongst a small captive group of Greylag Geese. Lorenz (1988) and his students lived for more than 30 years among an artificially created flock of 50-200 free-flying Greylag Geese and constructed an ethogram that offers the most complete account yet given of the behavioural repertoire of any goose. These authors described a variety of highly ritualised heterosexual displays, mostly centred on the Triumph Ceremony but including a number of chases, which in the latter stages of courtship frequently involve the two birds of a pair displacing third individuals on the ground. They saw pursuit flights but did not describe them in detail and seem not to have regarded them as essential elements in pair formation. In their small, almost sedentary flock, all the individuals were well known to each other. The social behaviour of large populations of long-distance migrants, most of which live in large temporary flocks in winter, might differ in some respects, perhaps including the occurrence and importance of pursuit flights.

Boyd (1953), studying agonistic behaviour in wintering flocks of White-fronted Geese *Anser albifrons*, saw many activities on the ground that seemed to be attempts to form pairs or to break up existing ones. He also saw a few aerial pursuits but did not publish details of them, as they did not seem to be important in the functioning of winter flocks. Prevett (1972), studying the social behaviour of Lesser Snow Geese, saw many activities in late winter directed towards pair formation. These included occasional pursuit flights, but chases on the ground were much more frequent and Prevett concluded that the flights were not all necessarily part of pair formation, although Barry (1967) was convinced that 3BF were associated with pair formation in Canada Geese. Owen (1980) undertook long-term studies of the behaviour of Barnacle Geese in the wild and in a full-winged collection of tame birds. He agreed with Prevett, noting that pursuit flights "tend to occur in exceptional cases of intense competition such as in the Barnacle Goose flock at Slimbridge, England, which had a surplus of mature males". As a result of considerable study on the wintering grounds, Black & Owen (1988) were able to state that aerial chases (usually the culmination of vigorous Mate Search behaviour) were rare in wintering Barnacle Goose flocks and therefore did not consider them further.

What is the nature of pursuit flights in geese?

Most pursuit flights involve three individuals, either one bird conspicuously chasing two, or two chasing a single bird. When the sexes of the individuals have been determined, often by relative body size, most reliably by reading numbered collars or leg bands on marked birds, the trios have usually consisted of one female and two males (eg Mowbray *et al.* 2000). The pursuing

individual is a male, apparently intent on disrupting the bond between an existing 'pair' and attaching himself to the female. Some observations apparently relate to a male (who has a female on a nest already) who is defending his territory against a prospecting/intruding pair. This has been reported amongst Canada Geese *B. c. moffitti* at breeding colonies (especially during early incubation) in the western United States (J.M. Black, in litt.), amongst Barnacle Geese at the Diabas nesting colony on Svalbard, and in the Slimbridge collection during May/June (J.M. Black, in litt.). Similar territorial 3BF have also been recorded during incubation amongst Red-breasted Geese *Branta ruficollis* on the breeding grounds in Taimyr. Typically, a neighbour chases a pair (in flight) and when the female lands the two males continue to fly around and chase each other (J. Prop, in litt.). The pursuit of a single bird by a pair extends the process, perhaps a strongly bonded pair combining to drive off an interloper. However, since ground chases are characteristic of the early stages of pair formation, aerial chases could originate from this source in pairing birds as well. Quite often other pairs join the pair, simultaneously or in succession, in chasing the single bird. Pursuit flights amongst Lesser Snow Geese on spring migration through the North American continent have involved up to six individuals (R.T. Alisauskas, in litt.). One potentially complicating factor in the discussion of pursuit behaviour is the often contagious nature of such behaviour within small groups of geese, also evident amongst other activities, including bathing (and its extension 'dashing-and-diving'), pre-copulatory displays and copulation itself.

An uncommon form of pursuit flight involves a male chasing closely after a female, without a third bird becoming involved. In the few cases when individual identification has been possible, the birds had previously behaved like a 'normal' pair and resumed that status after the flight had ended. Chases on the ground of a female by her mate are more frequent, though still not common. They are probably associated with early stages of pair formation or pair bond reinforcement and have been seen at staging areas and in winter.

Nest site selection sometimes looks like a pursuit flight, for instance a site-searching female often takes flight suddenly, without the usual pre-flight head-shaking or head-rolling (this has especially been observed in Canada Geese in Walker Bay, Kent Peninsula, Nunavut). She often settles again quickly close by. At other times, she may fly for several minutes before pitching a kilometre or more away to resume her search. Her mate follows, often very closely. Occasionally, the male appears to be leading the search on the ground, though not in the air.

When are pursuit flights most frequent?

Pursuit flights by geese have been seen most often in spring at, or very close to, breeding places, both before

snow melt has become sufficient to allow a search for nest sites to begin and during site-selection and early egg laying (see **Table 1** for species summary). Perhaps most significantly, the frequency of pursuit flights amongst Lesser Snow Geese (followed in 1983 and 1984 from Texas and Louisiana north to Manitoba), when corrected for flock size, increased as the spring migration progressed (R.T. Alisauskas, in litt.). Similarly, although 3BF have been seen in Ross's Geese in Saskatchewan during spring (from c.25 April to c.15 May when they are present there), they become very common during the early nesting period at Karrak Lake (R.T. Alisauskas, in litt.). These combined observations tend to suggest that the frequency of pursuit flights increases from late winter, becomes more common on spring migration and peaks during early nesting.

Pursuit flights seem to be highly infrequent after incubation is well advanced and have not been seen in late summer or early autumn, prior to southward migration. However, in early October in 1965 and 1966, pursuit flights were seen among Pink-footed Geese *Anser brachyrhynchus* using a roost at Loch Leven, east Scotland, shortly after their arrival from Iceland. These flights looked less intense than they do in spring and seemed to be related to conflicts between family groups, not to competition between males for a mate (H. Boyd, unpublished data). There are records of pursuits in winter for many species (**Table 1**), and in spring staging areas (eg in Iceland and north Norway). The latter may be under-represented because less time has been invested in the study of geese at this time of the year than on the winter quarters.

Pursuit flights away from breeding places

Ely & Scribner (1994) reported that, whilst such chases were common during the pre-nesting period in the Yukon-Kuskokwim Delta amongst Cackling Canada *Branta c. minima* and White-fronted Geese, they were extremely rarely (if ever) observed at staging or wintering grounds (C.R. Ely, in litt.). These temporal differences are especially notable given the much greater chance of observing such behaviour when birds are aggregated in large flocks and subject to more intensive human observation. Hence, the impression remains that 3BF in winter are unusual, and that those that do occur are associated with directed aggression or pair formation, rather than being of a direct sexual nature. Nevertheless, such flights have been witnessed, though rarely, amongst White-fronted Geese *Anser albifrons* at Slimbridge, England, in the 1950s (HB) for example:

S1- 3 January 1953, Dumbles:

"3 adults circle round flying very low, rather fast, over the flock on the saltmarsh, with leader A turning inside B and C who keep station. At length they

Table 1. Summary tabulation of observations of three-bird flights in migratory geese, broken down by area/season and population. + = rare, ++ = infrequent-frequent, +++ = observations made daily. Source of observations identified as follows: [1]ADF (this manuscript), [2]ADF and HB (this manuscript), [3]HB (unpublished), [4]Paul Shimmings (in litt.) and HB (unpublished), [5]Black & Owen (1988), [6]R.M. McLandress quoted in Mowbray *et al.* (2002), [7]Ely & Scribner (1994), [8]HB (Walker Bay, NWT unpublished), [9]Prevett (1972), [10]Einarsen (1968), [11]M. O'Briain (in litt.), [12]C.R. Ely (in litt.), [13]J.M. Black (in litt.), [14]R.T. Alisauskas (in litt), [15]R.H. Drent (pers. comm.), [16]J. Madsen (pers. comm.), [17]B. Ebbinge, (Strangford Lough, Northern Ireland, in litt.), [18]B. Ebbinge, (Taimyr Peninsula, Russia, in litt.), [19]J. Prop (Taimyr Peninsula, Russia, in litt.), [20]J. Prop (in litt.).

Goose population	Staging Areas April/May	Breeding Areas May/June	Winter Quarters October/March
Red-breasted Goose *Branta ruficollis*		++[19]	
Svalbard Barnacle *Branta leucopsis*	+[4,20]	+++[1,13]	+[4,5,20]
Russian Barnacle *Branta leucopsis*		+++[15]	
Light-bellied Brent Canada & Svalbard *Branta bernicla hrota*	+[3,11]	++[11,16]	+[17]
Dark-bellied Brent *Branta bernicla bernicla*		"never"[18]	+[3]
Black Brant *Branta bernicla nigricans*		+++[12]	+[10]
Canada (introduced) *Branta canadensis/maxima*	+[3]	++[3]	
Canada *Branta canadensis maxima*		+++[12]	
Canada *Branta canadensis interior*	+[3]		
Canada *Branta canadensis hutchinsii*		+++[6,8]	
Canada *Branta canadensis moffitti*		++[13]	
Canada *Branta canadensis minima*		+++[7]	
Pink-footed *Anser brachyrhynchus*	+[3]	++[3]	+[3]
Eurasian White-fronted *Anser anser albifrons*		"never"[18]	+[3]
Greenland White-fronted *Anser anser flavirostris*	+[3]		
North American White-fronted *Anser anser frontalis*		+++[2,7,12]	
Greater Snow *Anser canadensis atlanticus*	+[3]	++[3]	
Lesser Snow *Anser canadensis caerulescens*	+[14]	++[3,9]	+[7,9]
Ross's *Anser canadensis rossi*	+[14]	+++[14]	+[7]

pitch. A and B go at once into low head-wave and head-low-threat, at each other then at geese sitting nearby. C does not join them but general-shakes, forward head-waves and head-low-threat at its neighbours. A and B walk off together [followed by lengthy notes on attentiveness of B to A]."

If most pairs are formed in winter, and if 3BF play an important part in pair formation, why are there relatively so few records of winter pursuit flights? One reason may be that most mature adults are in well-bonded pairs, remaining together as long as both are alive. Most of the geese forming new pairs must be pre-breeders, in their second or third winters. Geese 16-32 months old are likely to form no more than 10-15% of a flock, so may receive little attention from an observer focussing on other topics. The study of pair formation has been a principal concern only in the study of Barnacle Geese by Black (1996) and his co-workers, and they found aerial pursuits to be rare. Three-bird flights therefore appear much less frequent in winter than in spring.

In most Northern Hemisphere birds, the refractory period that begins in mid-summer ends in December and testis volume increases steadily from January to April or May. The ovaries increase later, rapid oocyte development being restricted to the 2-3 weeks before egg laying in geese (Dawson 2002). Akesson & Raveling (1981, 1982, 1984) have provided the fullest account of the spring recrudescence of the sex organs of wild geese, with accompanying endocrine, body mass and behavioural changes. They studied a captive flock of *Branta c. moffitti*, a long-distant migrant, held in captivity in California. The birds were full winged but with the primaries of one wing clipped, preventing 3BF. The conditions may have led to maturation earlier in the spring than in the wild (cf. Owen 1980 on *Branta leucopsis*), but the sequence of events was not likely to have been altered. Akesson & Raveling (1981) reported that "Androgen levels of reproductively active males rose 4 weeks before ... egg-laying and remained high ... through the incubation period". They suggested that androgen secretion in male geese was more dependent on environmental cues than stimulation from the mate. Patterns of change in estrogens, corticosterone and body weights were clearly identifiable in reproductively active female geese (but lacking in unpaired females) and appeared later, suggesting that "the development of reproductive capacity in the female goose was tied to stimulation provided by the gander" (Akesson & Raveling 1981). This account is consistent with the generally tepid responses by females to male approaches in winter, or in early staging areas, reported above. Generally, females assume an outwardly passive role throughout courtship (Prevett & MacInnes 1980), yet pair-bond behaviours are generally positively correlated with oestrogen levels in breeding females (Akesson & Raveling 1984).

Overt sexual behaviour thus appears earlier in males than females, so that indifferent responses by females to male enthusiasm should be expected, in winter even more than at staging areas. As one very experienced observer responded when asked about 3BF flights by Barnacle Geese: "Very unusual to see in winter, but increasingly frequent in spring in Helgeland. I guess it's even more intense in Svalbard when the hormones are going absolute bananas" (P. Shimmings, in litt.). None of the pursuit flights Boyd saw in winter led to an apparent change in mate, nor were they followed by any attempts at copulation, however incomplete. The apparent outcomes of pursuit flights that the authors have seen in spring staging areas included a few cases in which short-term changes in pairs looked to have occurred, though they did not see whether the new pairs persisted, or the displaced male returned successfully. Again, in stark contrast to aerial pursuits on the breeding areas, the authors saw no 3BF at staging areas that led to attempts at copulation.

Pursuit flights at breeding places

In this section, two sets of specific observations are used to support three different (but not mutually exclusive) hypotheses relating to their function. These are that 3BF offer (i) opportunities for males to achieve forced extra-pair copulation (FEPC) with paired, sexually mature females, (ii) opportunities for paired females to assess the relative strength and condition of males to whom they are attached and of the males seeking to usurp them, and (iii) opportunities for young birds to choose between partners prior to the establishment of a long-term pair bond. The first set of observations relates to newly arrived White-fronted Geese at Walker Bay, Nunavut, made in spring 1992 by both authors. Here, geese concentrated along snow melt inundation wetlands associated with a small river, which were the first areas to melt and flood. The geese continued to roost there, or on the river, while spreading out across slightly higher and more rolling country to feed and in search of nesting sites. Pursuit flights were relatively common, but their frequency was difficult to assess, since birds indulged in aerial pursuit over long distances, and so were frequently lost from sight. Furthermore, 3BF were frequently prolonged, geese landing before resuming chases, often several times (up to at least six episodes were observed) over prolonged periods (one was followed for 21 minutes, but undoubtedly they extended for longer). No regular sampling of the behaviour could be undertaken, and observations were fragmentary with hardly any 3BF watched from start to finish. Most observations were recorded on 8-10 June 1992, and were noted throughout the period of most intensive diurnal activity from 0630 to 2140h. The second set of observations involved Barnacle Geese indulging in pre-nesting feeding post arrival in the main part of Sassendalen, Svalbard, 22

May - 5 June 2003, prior to their movement into peripheral breeding areas in adjacent tributary canyons (ie 3BF occurring away from nest sites). All of the following quotes from field notes have been shortened, and clarified where necessary.

(i) Male FEPC

No 3BF involving White-fronted Geese in Walker Bay ended in clear attempts at rape, whereas six attempts at forced copulation were witnessed during episodes on the ground in the course of five different 3BF involving Barnacle Geese in Sassendalen. All these instances involved what appeared to be established pairs with a lone satellite male, and all the females were apparently ready to breed, showing abdominal profile scores (AP, Owen 1981) of 3 or more. In all cases, the pursuits were rapid and the behaviour of the following male was frequently highly aggressive, pressing violently against the other male in each case. These involved clashes of wings in the air (on five occasions), ramming in the air (twice) and on the ground to displace males during rape attempts (on four occasions). These pursuits looked like attempts by a third male to secure copulation on the ground after a period of aerial pursuit of the female to displace her from her guarding gander, for instance:

B1 - 22 May, between 1700 and 1800 h:

"... A classic 3-bird chase .... the smaller female always in the lead, followed by an extremely persistent male....followed in the air by another male, 3-10 bird lengths behind. In the initial chase, the pursuing male eventually pressed the female to the ground, there grabbing her hind neck with his bill .... and attempting to mount. The following male slammed into the struggling pair, displacing the male. In the tumble, the pursuing [paired] male forced the attacker away with head-low threat posture and much calling. The paired male returned to the female, adopting the classic Triumph Ceremony, with neck stretch and wing-flap posturing, then positioned himself close to the female ... the satellite male wore a light green colour ring on its right leg ... helping to distinguish the two males. The ringed male sat c.15m from the pair and after 2 minutes he flew at the other male whilst it seemed not to be paying attention to him. The female ran 1-1.5m and again became separated from her male. The ringed male pressed her into flight again, at which point the paired male took to the air in close pursuit. Once in the air, the ringed male was trying to keep on the female's tail ... often conspicuously trying to get above her and force her to the ground. The paired male's role seemed simply to keep up with the fast-moving birds in front of him. The second pursuit flight ended with the female being pressed to the ground, the ringed male attempting to mount her. Again the

following [paired] male violently knocked the attacking male from the back of his mate and the displaced male initially turned head-on on his attacker, but swiftly retreated. Having put the ringed male to flight, the paired male returned with Triumph Ceremony to his mate. She eventually sat down, positioned immediately by his side whilst he stood alert, the attacker standing some 15m away at a position to which he had run. After some five minutes of the attacker preening, the pair began headshake pre-flight signals and flew off. The ringed bird watched, then followed passively, flying some 30-40 bird lengths behind - presumably content to continue to press his opportunity for insemination elsewhere".

The ringed Barnacle Goose of B1 on 22 May 2003 was unattached and, from its size and AP 1, a male. Its intent was clearly to rape the paired female (AP 3), potentially about to breed. If an unmated mature male is present on the breeding grounds early in the season, with his chance of finding an unpaired mature female just before egg-laying probably low, his best individual reproductive strategy may be to rape a mated female. It may well be better to risk minor injury in an FEPC of a sexually mature female than lose any chance of immediate parental success by pairing in readiness for a breeding attempt in the next summer. However, it was also possible that the ringed male was mated to another female (perhaps already nesting elsewhere, though the date was early), in which case this attack represented a secondary sexual strategy, namely to secure the chance of extra-pair parental investment in a clutch of an established pair. A similar adult male bearing a pale green leg ring was seen indulging in another 3BF some 300m from the site of the previous encounter two days later. It seemed likely that this was the same triangle, suggesting some persistence on the part of this individual, although the ring markings could not be read.

All the 'active' males observed in 3BF lacked a mate and so should have been free to feed more at less at will, in contrast to paired males, which have to spend much time ensuring that their mates are able to feed uninterruptedly and in repelling rival males.

(ii) Female mate assessment

It was conspicuous that, despite the violent behaviour of the males to each other during these aerial chases in Canada and Svalbard, the females were never the objects of aggressive behaviour, nor was their behaviour in the air especially stressed by the presence of the two pursuing males. Indeed on more than one occasion, especially in the 3BF involving apparently non-breeding females, they showed every suggestion to the human observer of 'leading' the direction and speed of the flight. For example:

B2-31 May, Brattlid Delta Marsh, 1131 h:

"Three-bird flight witnessed only well into the pursuit, by which time the

female seemed very much in control, leading the two rather passively following males around the sky in a manner that suggested she was testing their abilities. The two males were both AP 1, the female AP 1.5, again suggesting this was a trial of young birds in some way."

A 3BF could provide the pursued female with the opportunity of assessing the condition of the attacker and that of her mate, in circumstances favouring the former. The way in which pursued female geese appear to 'loiter' in flight is less striking than in dabbling ducks (Dzubin 1957), but it may give the female time and opportunity to make such a comparison.

(iii) Pair formation

There is considerable evidence that, although new pairing occurs mainly in late winter and early spring prior to departure from wintering grounds, pairing is also known to occur away from the winter quarters and may involve long trial liaisons and potential changes in partners. Following the energetic challenges of migration to the breeding grounds, young birds yet to have fully established long-term pair bonds may indulge in activities that confirm the quality of birds with which they have established trial liaisons. This is most likely to be evident in subadults, newly arrived at nesting areas, that are unlikely to breed successfully. There are few reports in the literature of such behaviour, but the authors' observations suggest that such behaviour may explain some of the 3BF seen amongst White-fronted Geese at Kent Peninsula, since two of the chases involved pursuits of second-calendar year females (one based on the dark bill tip, the other on neck collar identification). In both cases, the chases were neither persistent nor did either of the pursuing males remain with the female, for example:

W1 - 8 June, 2116-2137 h:

"....prolonged chase of....yearling female by two males....chases very frenetic - wing clashes frequent....yearling female eventually settles and commences preening, a local pair see off the two males which (fly and)....are lost from sight."

In Sassendalen, three separate 3BF involved pursuits of females with AP scores of 1.5-2 during 22 May - 3 June. Usually at this time, an AP score of 3 or more suggests the female is in condition to breed, her abdomen distended by accumulated fat and enlarged reproductive organs. In most of the observed cases, the female was relatively thin (AP 1.5-2), and these birds were probably not potential breeders or, given the late attainment of condition in each case, would breed late. In each case, the trailing male behaved in a way that suggested youth. The parties rarely physically clashed in the air and, in one case, the trailing male later fed in loose association with another (different) pair, and then with a group of three birds all with low AP scores, suggesting no long-term association with the pursued female. It was regrettable that in all cases the preludes to the flights

were not witnessed and nor were the relationships established prior to the birds' taking to the air, but the impression gained was that these pursuits were less intense than most of those witnessed involving females with higher AP scores. It appeared that these 3BF involved some trial temporary liaisons associated with early stages of pair formation or a possible usurpation.

Discussion

The broad conclusion of this review is that 3BF in northern nesting geese remain rarely observed, observations being at present confined to 19 populations of seven species (**Table 1**). What is interesting is the absence of observations from particular species at particular sites at appropriate times in the annual cycle, even at high goose densities (eg amongst Pink-footed Geese in Sassendalen, Svalbard, and Greylag Geese in lowland Iceland in spring). Although 3BF were mostly witnessed between late winter and the onset of incubation, the authors do not know the temporal frequency distribution of such behaviour, though observations from Walker Bay, Nunavut, and Sassendalen, Svalbard, strongly suggest a major peak immediately prior to the initial period of egg laying. At Walker Bay, the intensity of the behaviour amongst White-fronted Geese peaked on 8-10 June 1992, coincident with the first egg dates that year which continued until 18 June (see Fox *et al.* 1995). In Sassendalen, most observations amongst Barnacle Geese came from the period 22 May - 3 June 2003, the period during which the first nests were initiated in adjacent breeding canyons. Other reports (eg Dark-bellied Brent Geese on Russian breeding areas, Light-bellied Brent Geese on Tusinøya, Svalbard, and Barnacle Geese in the Russian Pechora Delta, information courtesy of R.H. Drent and J. Madsen) also suggest a peak in 3BF after arrival at the nesting grounds, immediately prior to first egg dates. This coincidence of timing gives some support to the hypothesis that such activity could be associated with reproductive investment. The attempted mounting of apparently paired female Barnacle and White-fronted Geese following chases at this time suggests that the 3BF were associated with attempted FEPC by permanently or temporarily unattached males.

Since the first study of 'rape' in the Lesser Snow Goose by Mineau & Cooke (1979), FEPC have also been reported among Black Brant *Branta bernicla nigricans* (Welsh & Sedinger 1990) and Greater Snow Geese (A. Reed and H. Boyd, unpublished data). These sexual assaults on nesting females seem to increase in frequency and ferocity after the females have begun to incubate. Perhaps as a consequence of the increase in intruding males seeking FEPC, there is a conspicuous peak in alertness behaviour (ie mate guarding) of male Snow Geese during pre-laying and laying phases (Mowbray *et al.* 2000). EPC are rarely unforced: the

'attacking' male runs at the sitting female and is sometimes harassed by her mate (if he is not engaged in similar activities elsewhere). The female usually remains on the nest, while trying to avoid damage to her eggs, and herself, as the male mounts. Such FEPC are typically from neighbouring paired males and frequently involve females nesting asynchronously, often outside the female's fertile period (Dunn *et al.* 1999; Mowbray *et al.* 2000). Though geese usually copulate in the water, some of these attempts on dry land have appeared successful. The degree to which FEPC is successful and to which intra-specific nest parasitism occurs has only been able to be investigated since the development of genetic techniques (eg DNA-fingerprinting). It has been studied in Lesser Snow Geese (where 2-5% of goslings were fathered by extra-pair males, Quinn *et al.* 1987; Lank *et al.* 1989; Dunn *et al.* 1999) and in Barnacle Geese (where one offspring amongst nine families analysed was related to the nesting father but not the mother, Choudhury *et al.* 1993). Many of these studies were carried out more to demonstrate the efficacy of a new molecular technique than to address a specific biological question by appropriate sampling. The low apparent rate of extra-pair fertilisations may therefore not be typical, especially given the high rate of incidence of forced FEPC in general (46-56% of all attempted copulation in Lesser Snow Geese) and of successful FEPC attempts (>33%, Dunn *et al.* 1999). Rape on the nest is a potentially risky strategy for a lone male, who risks injury from the attendant paired gander in an attempt, which is perhaps too late to successfully fertilise eggs. It is not clear how much less risk, however, is associated with attempts to inseminate a female by FEPC attempts during the pre-nesting, intensive feeding phase, when the probability of successful insemination prior to egg laying may greatly enhance the males' probability of securing paternity of offspring through FEPC. Incubating female White-fronted Geese at Walker Bay were extremely cryptic, concealing nests and always assuming 'head low' postures to avoid detection by passing geese, so rape attempts may be averted, although rape attempts may also be difficult to observe as a result. In Brattliddalen, Svalbard, in the vicinity of the 3BF observations presented here, the Barnacle Geese nest on ledges on steep cliffs where invariably the attendant gander is positioned within 1m of the incubating female. Successful FEPC in such a precarious and defended position would be hard to achieve. In both species, attempts at FEPC by males on paired females would probably be more successful immediately prior to first egg dates, when such behaviour was observed to be more prevalent, than at the nest.

The impression gained from all of the interactions was always that one male was attempting to maintain contact with a female that another male was attempting in some way to usurp.

The behaviour involves some test of male strength, since for them, though perhaps less so for the female, the pursuit is more strenuous, tortuous and vigorous than normal flight. The physical contact, clashes of wing in flight and aerial ramming undertaken by some of the male protagonists all imply some test of relative strength. These attributes would certainly fit within the predictions from the hypothesis that serially monogamously paired males would seek to ensure their paternity through protection of their exclusive copulatory rights to their female, when she is most fertile. Certainly, some male-male encounters can be violent, ending in battles between male Canada Geese of the *B. c. maxima* race (C.R. Ely, in litt.). It seems likely that a lone male can, by initiating a 3BF, gain valuable seconds in a rape attempt from the distancing of a sexually mature and receptive female from her attendant gander (who suffers reduced condition because of his investment in mate-guarding).

But what of the female? In one of the observations from Walker Bay, the female involved landed on water after a pursuit and commenced ritual bathing, an incitement pre-copulation behaviour normally initiated by the male. In a series of observations involving that female, she actively initiated at least one of the 3BF. Since the observer is most often drawn to the behaviour as a result of noticing an aerial pursuit once it is conspicuously under way in the air, it may be that the female initiates flights more often than is apparent from the descriptions presented here or published elsewhere. Finally, despite the vigorous nature of the aerial chase, the human observer is often left with the impression that the female is not especially stressed by the pursuit (especially those involving young individuals) and that the aggression is most often directed from the trailing male at the pursuing male. Indeed it is often the case that the female determines the pace and the route of the flight path followed during a 3BF, frequently 'hanging in the air' to permit pursuing males to catch up. These features suggest the possibility that the female may actually use these flights to test the relative quality of the males involved in the chase. In several cases in Kent Peninsula and Sassendalen it was known or suspected that the female involved was not immediately likely to breed, so that these 3BF could well have been trial liaisons between sub-adult birds, still in the process of pair formation. Hence, under some circumstances, aerial chases may offer the female the opportunity to pose a trial of strength to assist her in an assessment of male quality prior to full pair formation which, under normal circumstances, is highly likely to last a lifetime (Black 1996). If 3BF are attempts by unattached males to attain FEPC, paired adult females may also exploit this facility. That is to say, paired females may actually exploit EPC as a secondary reproductive strategy to attain mixed paternity and use 3BF as a

means of assessing the quality of a male from whom she permits a rape attempt after such a test against her attendant male.

The authors conclude that earlier observers were correct in judging that pursuit flights in wintering and staging were not of crucial importance, merely representing cases in which terrestrial conflicts and chases become unusually intense. In contrast, they contend that pursuits at breeding areas may be highly significant by providing opportunities for females and males to achieve EPC outwith the confines of the normal pair structure. Perhaps most importantly, 3BF offer the opportunity for females to assess the relative strength and condition of the males to whom they are attached and of the males seeking to supersede them. This might enable a female to make choices about accepting EPC from attacking males to contribute to the paternal composition of her reproductive attempt. In addition, 3BF may represent both a primary strategy for mature males lacking a mate close to the point of nesting and a secondary strategy for paired males with incubating females that may be able to secure FEPC after 3BF, without cost to their primary reproductive investment.

However, both Barry (1967) and Mowbray *et al.* (2000) report that the phenomenon is most frequent in Canada Geese and Snow Geese during pair formation, and other observations suggest that, although rare, such pursuits may play such a role in late winter through to nesting. Observation W1, for example, showed that membership of 3BF could be ephemeral rather than relate to established pair and assailant. The Walker Bay and Sassendalen observations suggest young birds indulge in such activity, which may neither involve overt aggression nor culminate in copulation. Hence, it seems likely that 3BF also represent part of the pair-formation behaviour repertoire, used by young females to chose between potential partners, prior to the establishment of long-term monogamous bonds. In addition, observations suggest that 3BF involved territorial defence in three *Branta* populations (J.M. Black and J. Prop, in litt.). The authors conclude that we remain remarkably ignorant of 3BF, considering that they could have consequences for the reproductive tactics of northern geese. Yet considerable challenges to the study of 3BF remain, if researchers are to be able to measure their frequency and significance, since 3BF are apparently relatively infrequent, of short duration and difficult to study from initiation to completion.

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