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Mutual benefits of associations between breeding and non-breeding White-fronted Geese *Anser albifrons*

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The relationships between yearlings and adult pairs of White-fronted Geese *Anser albifrons* were studied during pre-nesting, laying and early incubation in the central Canadian Arctic. Prior to nesting, females of lone pairs spent 75–81% of their time feeding, while males spent only 42–47% of time feeding and 46–50% alert. In pairs with one or more associated yearlings, both females and males fed significantly more and spent less time vigilant. Yearlings spent significantly less time (59%) feeding when alone compared with 71–76% when with pairs. Associations between yearlings and paired adults were most frequent before adult females began prospecting for nest sites. No prospecting pairs were associated with yearlings. After the egg-laying period, groups of geese, predominantly yearlings, made distraction flights over humans and terrestrial predators approaching nests, in contrast to the more cryptic behaviour of nesting pairs. The presence of groups of geese associated with some nest sites suggests that continuing parent–offspring relationships may involve assistance with nest defence.

Much of the theory relating to the potential costs and benefits of prolonged parent–offspring relationships in birds has been developed from observations of cooperatively breeding nidicolous species, in which offspring actively assist with the care or feeding of subsequent offspring of their parents (Brown 1987). In contrast, relatively little attention has been paid to such behaviour in nidifugous species, such as waterfowl.

Parent–offspring relationships persisting for more than 1 year are well documented for swans (Braithwaite 1981, Scott 1984, 1988) but have been reported rarely amongst geese (Black & Owen 1989). Recent studies have shown that extended parent–offspring and sibling–sibling relationships lasting several years occur in the White-fronted Goose *Anser albifrons* (Warren *et al.* 1993). Most observations of family behaviour have been made during the winter, when subadults are more dominant in the social hierarchy when associating with parents than when alone (Scott 1980, Black & Owen 1989). In White-fronted Geese, large families show dominance over smaller families, pairs without goslings and individuals (Boyd 1953). Such behaviour increases access to restricted food resources and safe roost sites (Raveling 1966, 1970), presumably enhancing fitness and thus survival.

In this paper we document the association of yearling geese with adult pairs during pre-nesting, laying and early incubation by White-fronted Geese in the Central Canadian Arctic during consecutive years. In particular, we test the hypothesis that adults are more vigilant (and thus bear additional costs) when associated with yearling geese than without (Lazarus & Inglis 1986).

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METHODS

Study areas

Observations of pre-nesting goose behaviour were made from 25 May to 17 June 1992 in an area of some 16 km² around the Walker Bay Field Station of the Department of Renewable Resources on the Kent Peninsula, Northwest Territories, Canada (68°20′N, 108°05′W), an important breeding area for White-fronted Geese. Details of non-breeding geese associating with incubating birds were recorded to assess potential involvement in nest defence during nest searches of six transects (400 m × 10 km) in the northern part of the Queen Maud Migratory Bird Sanctuary (centred around 67°38′N, 102°39′W and about 270 km southeast of Walker Bay), 20–30 June 1991 and 19–29 June 1992.

Age determination and breeding status

Geese were sexed in the field on the basis of upper body shape (males are larger overall and demonstrably thicker set in the neck and head), larger body size and behaviour

(males tend to be more vigilant and present a more upright stance, even at rest).

Yearling geese can be identified in the field by the presence of a black nail on the bill. The absence of black belly barring is also restricted to birds of 1 year old or less (Cramp & Simmons 1977), although some yearling birds begin to develop restricted barring by their second summer. We scored all geese encountered in the field according to the 11-point scale of Stroud (1981b). This gave a range from 0 (barring covering 0–10% of the belly) to 5 (100% of belly black) by 10% (0.5) increments. Throughout this analysis, we have assumed that White-fronts with belly-bar indices (BBI) of zero or 0.5 had hatched in the preceding calendar year.

As a result of intensive feeding after arrival on breeding areas and prior to nesting, male White-fronts accumulate fat in the undertail region of the body, whilst females exhibit gonadal development in addition to fat deposition. We used the abdominal profile index (API) of Owen (1981) to provide a field assessment of body condition and breeding activity.

Compilation of vigilance schedules

From 27 May to 9 June 1992, using four observation towers at Walker Bay, we compiled activity budgets for groups of actively foraging White-fronted Geese that included paired individuals and associated yearlings. These observations were made opportunistically whenever yearlings were seen associating with adult pairs. Each pair had either one or two yearlings associated with them; 1991 had been a relatively poor breeding year, so that few young returned in 1992. The activities of all members of such groups were recorded every 15 s for a period of 10 min. Inter-bird distances of the group and the distance to the nearest other White-fronts were estimated in goose-lengths. Behavioural categories comprised feeding, alert (head-up and extreme head-up postures), locomotion, comfort, agonistic interaction and resting. We sampled activity budgets of neighbouring pairs without associated yearlings immediately following the observation bouts on groups to provide a pairwise comparison between pairs with and without associated yearlings. Data are presented for four-bird groups (i.e. adult pairs with two associated juveniles; 14 bouts in all totalling 140 min, 560 observations) and three-bird groups (pairs with one juvenile; 56 bouts, 560 min, 2240 observations).

Assessment of behaviour of nesting and non-breeding geese

Once laying had commenced at Walker Bay, breeding pairs fed in the wetlands, whilst non-breeders were scattered less conspicuously throughout the study area. As we searched for nests, we recorded the behaviour of all geese encountered (using the categories defined above) and, in particular, group size, distance at flushing, whether geese flew over the observer or departed the area and, where possible, the BBI and API. Pairs were considered to be breeding if the female API exceeded 2.5 or when they were associated with a nest.

In Queen Maud Gulf, three 10-km transects 400 m wide were searched in 1991 and three more in 1992 by ten observers strung out at 20-m intervals searching for nests. Full details of all nests and associated geese were recorded, as well as group size, distance at flushing, reaction to flushing, BBI and API score.

Table 1. *Percentage of time spent by paired male and female White-fronted Geese in feeding or alert activity prior to nesting at Walker Bay, Northwest Territories, Canada, during spring 1992. Values represent mean values ± s.e. for observation bouts on lone pairs (n = 40) and pairs accompanied by one (n = 28) or two yearlings (n = 7)*

	Lone pairs (%)	Pairs with one yearling (%)	Pairs with two yearlings (%)
Male foraging	42.0 ± 2.7	63.8 ± 2.3	68.7 ± 4.3
Female foraging	80.7 ± 2.8	93.9 ± 1.2	97.1 ± 0.9
Male alert	47.5 ± 3.0	33.7 ± 2.2	29.0 ± 3.0
Female alert	8.4 ± 1.8	6.1 ± 1.2	2.9 ± 0.9

RESULTS

Vigilance and feeding schedules of parents and yearlings during pre-nesting

Paired males spent less time alert when in association with one (Wilcoxon $T^+ = 366$, $n = 28$, $P < 0.0001$) or two yearlings ($T^+ = 27$, $n = 7$, $P < 0.05$) than did males of pairs without yearlings (Table 1). Correspondingly, males spent more time feeding when accompanied by one ($T^+ = 51$, $n = 28$, $P < 0.001$) or two yearlings ($T^+ = 25.5$, $n = 7$, $P < 0.05$) than did those that were unaccompanied (Table 1). Paired adult females spent less time alert when one ($T^+ = 165$, $n = 28$, $P < 0.05$) or two yearlings ($T^+ = 28$, $n = 7$, $P < 0.01$) were present and more time feeding ($T^+ = 386$, $n = 28$, $P < 0.0001$ and $T^+ = 28$, $n = 7$, $P < 0.01$, respectively) compared with unaccompanied paired females (Table 1).

Those yearlings associated with paired geese fed significantly more ($U = 3$, $P < 0.001$) and spent less time alert ($U = 5$, $P < 0.001$; Table 2) than did lone yearlings. The pattern was similar for yearlings associating with another yearling and a pair of adult geese ($U = 3$, $P < 0.001$ and $U = 4$, $P < 0.001$; Table 2).

Weakening yearling–adult associations during the pre-laying period

Increase in distance between adults and offspring

The distance between yearlings and the adult female in associations increased with time, although data for more than

Table 2. *Percentage of time spent by yearling White-fronted Geese in feeding or alert activity prior to nesting at Walker Bay, Northwest Territories, Canada, during spring 1992. Values represent mean values ± s.e. for observation bouts on lone yearlings* (n = 10), *those associating with pairs* (n = 28) *and those accompanying pairs with another yearling* (n = 7)

	Lone yearling (%)	Yearling with adult pair (%)	Yearling with adult pair and other yearling (%)
Yearling foraging	59 ± 2.1	76 ± 1.9	72 ± 3.2
Yearling alert	41 ± 2.1	24 ± 1.9	28 ± 3.2

40 continuous observations were available for only four dates (29 and 30 May and 2 and 7 June 1992). Median distances differed significantly between 29 and 30 May (median 2.41 goose-lengths, n = 98 and 4.03 goose-lengths, n = 125; median test χ^2_1 = 13.75, $P < 0.001$) and 2 and 7 June (median 5.60 goose-lengths, n = 128 and 9.99 goose-lengths, n = 42; χ^2_1 = 43.44, $P < 0.001$) but not between 30 May and 2 June (χ^2_1 = 0.33, n.s.).

Decline in frequency of observations of associated yearlings

Yearling associations with adult pairs were encountered less frequently as time went on (r_s = 0.74, n = 6, $P < 0.05$). Lone yearlings and those associating with other yearlings were encountered more frequently as nesting was initiated (r_s = 0.67, n = 6, $P < 0.05$). It would appear, therefore, that goslings from previous years tended to be displaced from the vicinity of potentially breeding pairs as the pre-breeding phase progressed.

Differences in behaviour between breeding and non-breeding geese during laying and early incubation

Nest-site selection, nest construction and egg-laying were observed rarely because of the secretive nature of White-fronts. However, five prospecting females which were observed were always seen accompanied only by their mates. During nest searches in Queen Maud Gulf, breeding pairs during laying and incubation flushed from the nest at less than 50 m (Fig. 1) always flushed away from observers, and in 12 out of 15 observed cases, they flew silently a short distance (<400 m) and landed. Pairs or groups of birds not known to be associated with nests flushed most frequently at distances greater than 500 m from observers (Fig. 1), and in 39 instances out of 48 observations, they flew either directly or in a long arc towards and over the observers, uttering the loud alarm call. Birds giving the loud alarm call at both study areas comprised more than 40% yearlings (Fig. 2), a greater proportion than would have been expected to be present in the local population given the poor breeding success in 1991.

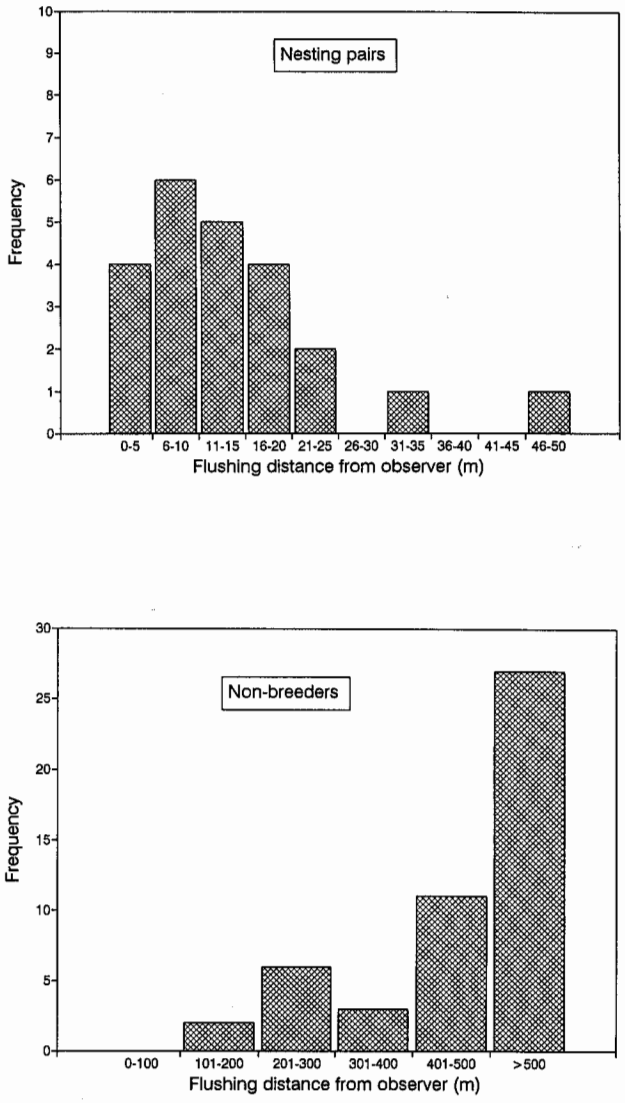

Figure 1. Frequency distributions of (upper) flushing distances of breeding White-fronted Geese displaced from nests and (lower) flushing distances of non-breeding White-fronted Geese disturbed from open areas during nest searches in the Queen Maud Gulf Migratory Bird Sanctuary. Northwest Territories, Canada, spring 1992.

Attendance of non-breeding geese at nest sites

In late June 1991 and again in 1992, we searched three transects in Queen Maud Gulf and found 7 and 18 White-fronted Goose nests, respectively. At most nests, two geese were flushed from the immediate vicinity of the nest site,

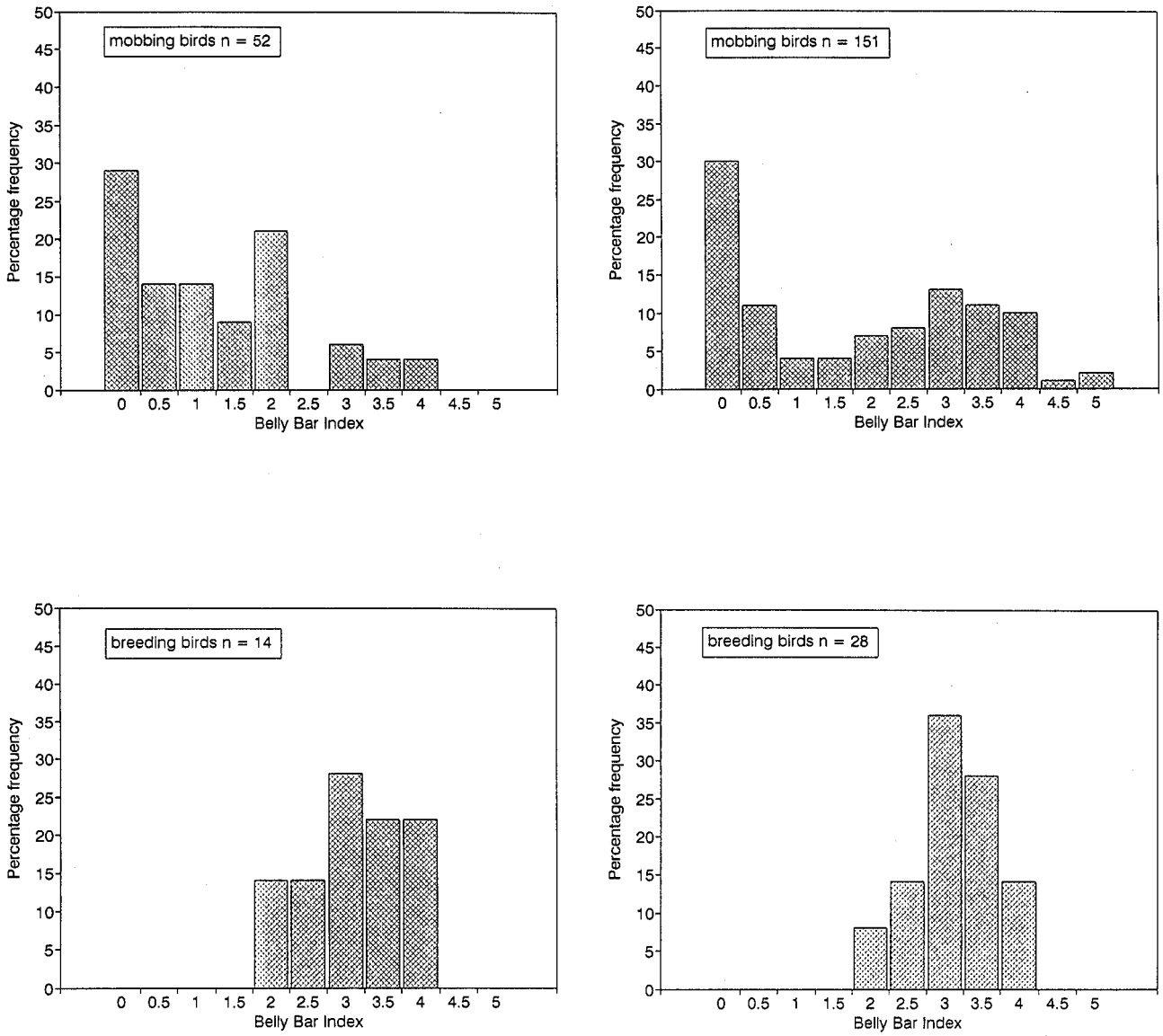

Figure 2. Frequency distributions of belly-bar indices (BBI) of White-fronted Geese recorded in Walker Bay Field Station (left) and Queen Maud Gulf Migratory Bird Sanctuary, Northwest Territories, Canada (right), contrasting nesting birds (lower) with loud alarm calling ("yea chorus") overflying birds (upper, see text for details). Distributions of "overflying" *v* breeding bird BBIs are significantly different for Walker Bay (Kolmogorov-Smirnoff Test $K_D = 15$, $P < 0.001$) and Queen Maud Gulf ($K_D = 45$, $P < 0.001$).

and although other White-fronts were occasionally present in the general area, none was seen on the ground close to the nesting pair at the time of discovery. In 1992, 4 of the 18 nests found had more than two birds present. At one nest, observers flushed six geese in a tight group at a range of 15 m, all of them within a mean of 2.4 m of the nest (maximum 5 m measured from droppings); the incubating female remained on the nest until approached to within 7 m. The group included two yearlings (with BBIs of 0) as well as birds with BBIs of 1.5, 2, 3.5 and 4. At a second nest, observers flushed three birds (including a yearling, BBI of 0) from within 7 m of the nest before the attendant pair was flushed. This nest contained eight eggs, which makes it probable that it had been "parasitized" by at least one other female. Six birds were present at the discovery of a third nest, standing within 15 m of it: three of these geese had BBIs of 0 and therefore were likely to be yearlings. At a fourth nest, two geese (BBIs of 2.0 and 3.0 and hence unlikely to be yearlings) stood within 12 m of the nest; both flew off well before the nesting pair.

DISCUSSION

Extended parent–offspring association appears characteristic of grey geese. Owen (1980) concluded that most offspring of *Anser* species remain with their parents throughout the first year of life, whilst break-up is more variable amongst *Branta* species (but most often in the first winter, e.g. Black & Owen 1989). Up to 15% of yearling Canada Geese *Branta canadensis* (Raveling 1969) and 10% of yearling Lesser Snow Geese *Anser caerulescens* (Prevett & MacInnes 1980) remained with their parents throughout their first year.

Our results suggest that some parent–offspring associations in White-fronted Geese may persist on the breeding grounds. If offspring learn migratory routes to and from the wintering areas from their parents (Owen 1980), association on spring migration potentially enhances recruitment into future breeding age classes with low costs of intraspecific competition for resources during migration and pre-nesting. Our observations suggest that, during the early arrival period on nesting areas, males about to breed tolerate yearlings in close proximity. By doing so, the male shares the vigilance, yielding benefits to all members of foraging groups by increasing feeding time (Fox & Madsen 1981). This may be especially important in late springs (as in 1992) when snow cover severely restricts feeding areas.

Yearlings were threatened by the male when the feeding opportunities of the female were compromised by the close presence of an attached yearling. Only one adult female was seen to threaten a yearling, although females did join males in threats to nearby Canada Geese and other White-fronts. Yearlings following feeding adult pairs relieved adults and themselves of some share of vigilance while avoiding direct competition with the female for food at a time when the accumulation of reserves by the female has a direct bearing on her fitness and reproductive potential (Budeau *et al.* 1990).

As egg-laying began, males became more aggressive towards yearlings. Distances between yearlings and adults increased, as did the number of unattached yearlings observed. White-fronts are extremely cryptic in their behaviour during nest-site selection and nest construction. The presence of associated geese with prospecting pairs might unduly advertise the nest site to predators. Yearlings appeared to remain in the vicinity of nests and, with other non-breeding geese, provided an aerial protective canopy by flying up to 900 m to distract terrestrial predators (such as human observers).

Most geese first breed at 3 or 4 years of age (Owen 1980), as does the Greenland White-fronted Goose *A. a. flavirostris* (Warren *et al.* 1992). Adult-plumaged birds include prebreeders; Warren *et al.* (1993) have shown that unpaired geese remain associated with parents and/or siblings. On arrival at Walker Bay, only 3.1–4.8% of pairs were accompanied by yearlings; in Queen Maud Gulf, 16% of nests were attended by geese in addition to the breeding pair.

Many nest sites become well known to predators, especially to Arctic Foxes *Alopex lagopus*, which locate potential food by smell and frequently mark nests by scat marking for subsequent predation (Birks & Penford 1989). Associated geese assisting in nest defence may reduce the risk of nest loss. The presence of single associating White-fronts at nests has been reported before (Ely, unpubl. MSc thesis, University of California-Davis, Stroud 1981a), including one case of a group of three associating yearlings close to a nest at the time of hatch (Stroud 1982). We also saw groups of yearling and other non-breeding White-fronts actively assisting nesting pairs in defence of nests against Arctic Foxes. In 1991, a known 3-year-old male was killed by an Arctic Fox in defence of the nest of a different pair in the presence of three other geese.

The benefits of highly dispersed nesting for White-fronted Geese have been discussed (e.g. Stroud 1982, Fox *et al.* 1983, Barry, unpubl. PhD thesis, University of Alberta). The low densities and variety of nest sites used may make it difficult for a potential predator to develop a search image. Hence, when predators are abundant, it seems likely that the benefits of associated birds assisting with predator location and nest defence outweigh the cost of increased conspicuousness and territorial defence in White-fronts.

With few uniquely marked geese, this study could not determine the lineal relationships of geese associating with breeding pairs. Adult males performed head-low rush threat displays at other pairs of geese and lone yearlings at distances up to 30 m from the female whilst tolerating yearlings immediately adjacent to their feeding females. It seems extremely likely that birds associating with breeding pairs were close relatives and that the shared defence of reproductive potential of related individuals and the ability to learn social skills and about the reproductive process without suffering reproductive cost confer benefits to all the individuals involved.

These observations show that (1) yearling association enhances foraging time of males and females in pairs during the pre-laying period and (2) social groups of yearlings and non-breeding adult-plumaged geese play an active role in distracting predators in the vicinity of nests. Thus, the hypothesis of Lazarus & Inglis (1986) that adult geese are more vigilant when associating with yearling geese cannot be extended to the White-front. We conclude that prolonged association of family groups is a feature of the summer ecology of White-fronted Geese. Indeed, there appears to be a developmental switch from offspring as dependents (eliciting additional vigilance in parents during their first summer, e.g. Madsen [1981], Lessells [1987]) to offspring as cooperators (sharing vigilance with the parents during the prelude to nesting). Such behaviour benefits breeding pairs by increasing feeding time during pre-nesting and contributing to nest defence during incubation. Non-breeding geese also benefit from such behaviour through the acquisition of reproductive and other social skills.

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