

A long-term study of recruitment in the Tundra Bean Goose overwintering in Zeeland (The Netherlands)

J. Van Impe

Dr. Van de Perrelei, 51B, B - 2140 Borgerhout, Belgium; jacques.vanimpe@telenet.be

INTRODUCTION

Juvenile recruitment in adult populations has a great influence on the evolution of life-history strategies (Ferrer *et al.*, 2004; Krüger, 2005; Robertson, 2008). Changes in demographics among long-lived species may be identified before changes in numbers (Baillie *et al.*, 1999). Therefore it is important to monitor demographic factors as they may give the first warning signs of problems that may lead to population declines (Clark *et al.*, 2004).

Wild geese wintering in Western Europe breed in a large area of the tundras of northern Europe and Western and Central Siberia (Dement'ev and Gladkov, 1967; Kishchinskiy, 1979; Lebedeva, 1979; Litzbarski, 1979). In order to reach the wintering grounds from their breeding sites in autumn, these geese undertake, either alone or as a family, a long migratory journey of up to 5000 km (Cramp and Simmons, 1978; Ebbinge, 2014, amongst others). During this long journey, young birds learn from their parents not only the migration route and resting places (Raveling, 1969, 1970; Robertson and Cooke, 1999), but also dangers they need to avoid (Fox *et al.*, 2002). Valuable information is gained from studying flocks of wild geese that winter in Western and Central Europe, because the immature geese stay with their parents for a large part of the winter. This makes it possible to determine two crucial factors in studies of population dynamics, the proportion of geese in first-winter plumage (= juvenile plumage, juveniles), and family size (in winter). Methods of determining these values were developed in the USA for the Black Brant *Branta bernicla nigricans* during the 1930s (Phillips, 1932; Moffitt, 1934). In Western Europe, the techniques were first applied to the White-fronted Goose *Anser a. albifrons* in The Netherlands by Le Bret (1948, 1956) around 1947 and by Philippona (1972) around 1957. Boyd (1952–53, 1953, 1965) first studied population dynamics in White-fronted geese in Great Britain in 1947–48. At the same time, a long-term study of the population dynamics of the Dark-bellied Brent Goose *Branta b. bernicla* was also launched in Great Britain (Burton, 1958, 1962).

Research on the Tundra Bean Goose *Anser fabalis rossicus* (hereinafter referred to as TuBG) and the Taiga Bean Goose *A. f. fabalis* started much later (Van Impe, 1973). This lag was due to uncertainty about the systematic position of both taxa and to the difficulty in differentiating between the age groups of Bean Geese in the field.

The breeding sites of *A. f. rossicus* include the tundras of European Russia and Western Siberia. These Bean Geese belong to the Western Tundra group of Bean Geese *A. f. rossicus* (Coombes, 1947, 1951; Huyskens, 1977; Van Impe, 1980a). Until the 1970s small flocks of *A. f. fabalis* were observed only occasionally in Zeeland, and only in severe, cold weather. After 1980 few records of this nominative form exist (Huyskens, 1977; J. Everaers *in litt.*, 2013; personal observations).

The world population of this subspecies has been estimated at 300,000 individuals (Madsen, 1991; Scott and Rose, 1996; Fox and Madsen, 1999). More recently, Koffijberg *et al.* (2010), Fox *et al.* (2010), and Wetlands International (2016) estimated the world population at, respectively, 522,000; 550,500; and 550,000 individuals. According to other reliable estimates, 184,000 TuBG currently winter in the Netherlands and this number is increasing (Ebbinge *et al.*, 1986; Koffijberg *et al.*, 2010; Koffijberg and Hornman, 2011) between the winters of 2000/01

and 2009/10. The latter report on an annual increase by 6% on average between these winters. Since 1989 the population overwintering in the area of the Baltic and North Sea increased by 4.4 % (Fox *et al.* 2010).

However, counts on the breeding grounds show a decline in the population of *A. f. rossicus* (Flint and Krivenko 1990; Krivenko 1993; Ryabitsev, 2008). On the Yamal Peninsula, a slight reduction of the breeding population has been observed (Ryabitsev, 1995). Whereas in the northeastern Malozemel'skaya Tundra, an important breeding ground for *rossicus* in European Russia, the number of nesting individuals has dropped to only one-sixth to one-fifth of the numbers observed in this region in the 1980s (Mineev and Mineev, 1997). According to the authors of these studies, the main causes behind this reduction can be attributed to disturbances due to hunting and fishing activities: fishing in the delta of the Pechora River and in Korovinskaya Bay and hunting during migration and on the wintering grounds. Because of these conflicting observations about the numbers of *A. f. rossicus* on the nesting and wintering grounds, we can only speculate about the demographic trends in a population of this subspecies. The purpose of the current study of the Tundra Bean Goose in the province of Zeeland (The Netherlands) is twofold. Firstly, to describe and analyse the two crucial factors of population dynamics (the proportion of juveniles and family size in its winter flocks). Secondly, to discuss factors that may affect the results when assessing reproductive performance in the wintering grounds.

MATERIAL AND METHODS

The studies were carried out on the wintering grounds in the province of Zeeland (The Netherlands). For decades, large numbers of wintering flocks have visited the agricultural land surrounding the residential centres of the villages of Ossenisse (51°23' N, 3°59' E), Rilland (51°25' N, 4°11' E), Zonnemaire (51°43' N, 3°57' E), and the town of Goes (51°30' N, 3°53' E). The landscape is characterised by polders just a few metres below sea level.

Every winter the percentage of first-year birds was assessed 10 to 15 times. All counts were carried out from a car with a 40× spotting telescope with a zoom lens, on undisturbed flocks in normal weather conditions, without frost or snow, and with winds not exceeding 4–5 on the Beaufort scale. Examined flock size varied greatly, between 20 and 400 individuals. Flocks with < 20 birds were not examined, because in general, juveniles in these flocks were overrepresented.

Field determination of age classes in the Tundra Bean Goose

The observed TuBG were split into two age groups: birds in first-winter plumage (= juvenile plumage), and birds older than one year (= adult plumage). Two-year-old birds cannot be reliably distinguished from older birds in the field.

Determination of percentage of first-year birds is more difficult among TuBG than among White-fronted geese and can only be performed in favourable conditions: in good lighting and at not too great a distance (< 150–250 m). It is impossible to differentiate age classes of birds in flight. Studying birds on the ground is complicated because the TuBG are shier than White-fronts. They take to the wing more quickly when researchers approach than do White-fronts; in mixed flocks of *A. anser*, *A. albifrons*, and *A. f. rossicus*, the last almost always take to the wing first when disturbed.

The number of sitting birds in the flocks of wintering TuBG increases considerably in frosty weather, and/or when there is a strong wind (4–5 on the Beaufort scale). Under those conditions young geese adopt a resting posture more frequently than adults do. Research involving age

categories should therefore not be carried out in frost or very windy weather. We observe also the same behaviour after the flock has been disturbed and has landed at the end of the flight. After even a short flight, an abnormally large number of birds can rest on the ground and no longer forage, sometimes for a considerable period of time. As a result of this behaviour, half or two-thirds of the members of a flock of TuBGs are not sufficiently visible to the observer and cannot be classified by age, because the sides of their bodies and their bellies remain undeterminable. Adults, on the other hand, are generally more active than the young birds and most of them forage even in very windy weather.

Illustrations from several manuals indicate clear differences between the plumage of first-year and adult TuBG (Alphéraky, 1905; Hartert, 1915; Delacour, 1954; Cramp and Simmons, 1978), but the drawings of immature birds in these books present a very static picture of the juvenile plumage. Birds with juvenile plumage always moult their typical immature plumage gradually during their first winter before taking on full adult plumage, although this moulting of juvenile body plumage occurs more quickly than it does in immature White-fronted geese. In February, and even more so in March, it is impossible to reliably distinguish an increasing number of the birds in juvenile plumage from birds in adult plumage (Van Impe, 1973). That is why we stopped counting immatures on 15 January each year (1970/71–2013/14, $n = 44$ winters).

Differences between adult and the changing spectrum of juvenile plumage in TuBG.

1. The white “sidebar”, clearly visible in birds in adult plumage, is absent in the first stages of juvenile plumage, but becomes visible in first-year birds during November and December. Unfortunately, some birds in adult plumage lack this field characteristic. Naumann (1902) mentioned the sidebar as the most important point of differentiation between birds in adult and juvenile plumage without indicating any exceptions to this rule though.

2. In adults, the white tips on the greater and median wing coverts form distinct white scalloping. In immatures, such scalloping is absent or less pronounced during the first stages of body moulting (Bauer and Glutz von Blotzheim, 1968) or is browner (Witherby *et al.*, 1941; Dement’ev and Gladkov, 1967). In some first-year birds, however, the adult pattern of these bars becomes visible as early as December because of a rapidly proceeding moult.

3. First-year geese do not show alternating bright and dark transverse streaks on the lower belly. These may also become visible in juvenile plumage as early as December, again because of an early moulting process.

Field marks of secondary importance in first-year birds are the presence of more or less extended dark patches on the sides of the breast and the belly in many but not all individuals (481/1300 (37.0 %)) and a bright colour of the breast or belly or both (602/1082 individuals (55.5 %)). But these dark patches and the bright belly colour may also occur in adults.

4. Other field marks mentioned in the literature (leg colour, presence of white feathers at the base of the bill) do not reliably allow a distinction to be made between the two age classes.

Because all these characteristics develop during winter at individual rates, it is only possible to make a reliable distinction between the two age classes if all the characteristics are taken into account as a whole (Van Impe, 1973).

Calculating the percentage of immature TuBG

During the winters from 1970/1971 through to 2013–2014 ($n = 44$) the proportion of immature TuBG has been investigated within their winterflocks. In order to ensure that there is no overrepresentation of first-year birds in the calculation, it is necessary to make an equivalent sampling in the central as well as the peripheral parts of the flocks.

The percentage of first-year birds in overwintering flocks of TuBG cannot be determined by using the same method as for the White-fronted Goose. In the latter, it is relatively easy to

classify individual geese by age. Because individuals of this species move continually, observers do not have to wait long before the field marks on their belly and flanks become visible. However, it is not possible to use the same method with TuBGs, because it is not easy to differentiate between the plumage of adults and juveniles, but above all because foraging TuBGs move much more slowly than White-fronts do, often remaining in fixed orientation for minutes at a time. As their upper parts, belly sides and flanks are thus insufficiently visible, it is impossible to classify the birds with regard to age. These challenges are overcome with the following methodology.

First, all geese in the flock of 20 to 400 birds are counted or their number estimated and we gain an overall impression of the arrangement of the flock, i.e. we observe whether the whole flock is enough visible for an investigation and whether or not enough families are separate from the central part of the flock. Thereafter we determine the age category of all geese that are clearly visible during a quick screen, ignoring birds that are not clearly visible. We now have a partial and incomplete count, the result of which may be very different from the final result we shall obtain. This first, incomplete screen is repeated six to nine times, depending on the circumstances and the size of the flock in question. The sum of all adults and juveniles obtained in each of these succeeding sub-counts are then added up. The total number of TuBGs sampled in the succeeding counts should be at least four times higher than the number of geese counted/estimated at the beginning of the survey for the result to be representative. The sum of all observed partial adult-to-juvenile ratios is then reduced to the number of birds counted/estimated at the beginning of the survey.

In order to establish whether the adult-to-juvenile ratio for the overwintering TuBG remained about the same during the entire winter season, 35 winters were split into two periods: mid-November to mid-December and mid-December to mid-January, because especially during the second half of December large movements of geese occur between the different parts of the wintering ground. We were able to work with the data from only 35 winters of a total of 44: nine winters did not present an approximately equal number of examined birds for both periods or the number of examined birds was too low. The percentages of first-year birds obtained in the two periods were then compared.

Observing the family size

A family is defined as one or two birds in adult plumage (the parents) closely accompanied by individuals in juvenile plumage. However, six juveniles or more accompanied by one or more parents were considered “gang broods” (see below). These rare big families were not included in the calculation of the mean number of immatures per family on the wintering grounds.

Families in the middle of flocks of wintering geese can be identified because several birds, closely clustered together, move in the same direction within the flock. Parents of families that have lost all their young before arriving in their wintering grounds can no longer be classified as families.

During the winters from 1974/1975 through to 2013/2014 ($n = 40$), the number of offspring for 4,440 TuBG families in the province of Zeeland were counted.

Detection of ‘good’ and ‘poor’ breeding seasons

For the sake of convenience, breeding seasons were defined as ‘good’ if during the following winter the reproductive parameters exceeded the value of the long-term mean plus one standard deviation ($\xi > +1 SD$). Breeding seasons were identified as ‘poor’ if these parameters fell below the long-term mean minus 1 *SD* ($\xi < -1 SD$). To get more security in the judgment concerning a ‘good’ or a ‘poor’ breeding season, differences from the obtained values ($\pm 1\%$ for the age count

and $\pm 0,1$ juveniles per family for the family size) were ignored in order to come to a decision. Failed breeding was also ignored.

Detecting different behavioral patterns between adult and juvenile birds

To investigate whether some elements of the behavioral pattern of juvenile birds differed from these of adults, we spent more than 5,000 observation hours in the field. During 220 hours of this time, both age groups were divided into behavioral classes (foraging, conflict, resting, etc.) following the sampling method described by Altmann (1974).

RESULTS

Table 1. Numbers of Tundra Bean Geese present in four important observation areas during the two ten-year periods 1970 - 1979 and 2004 - 2013 in the province of Zeeland, The Netherlands. They correspond with the start and the end of the observation period respectively.

| Area | Numbers 1970-1979 | Numbers 2004-2013 |
|------------|-------------------|-------------------|
| Ossensisse | 1000 - 1500 | 600 - 800 |
| Rilland | 4500 - 5500 | 500 - 700 |
| Goes | 4500 - 6000 | 1500 - 2500 |
| Zonnemaire | 4000 - 5000 | 2500 - 3000 |

On the numbers, the phenology, and the association with other geese of A. f. rossicus in the province of Zeeland

In the area covered in our survey, the actual numbers of *A. f. rossicus* have obviously declined compared to the period between 1970 and 1979 (**Table 1**).

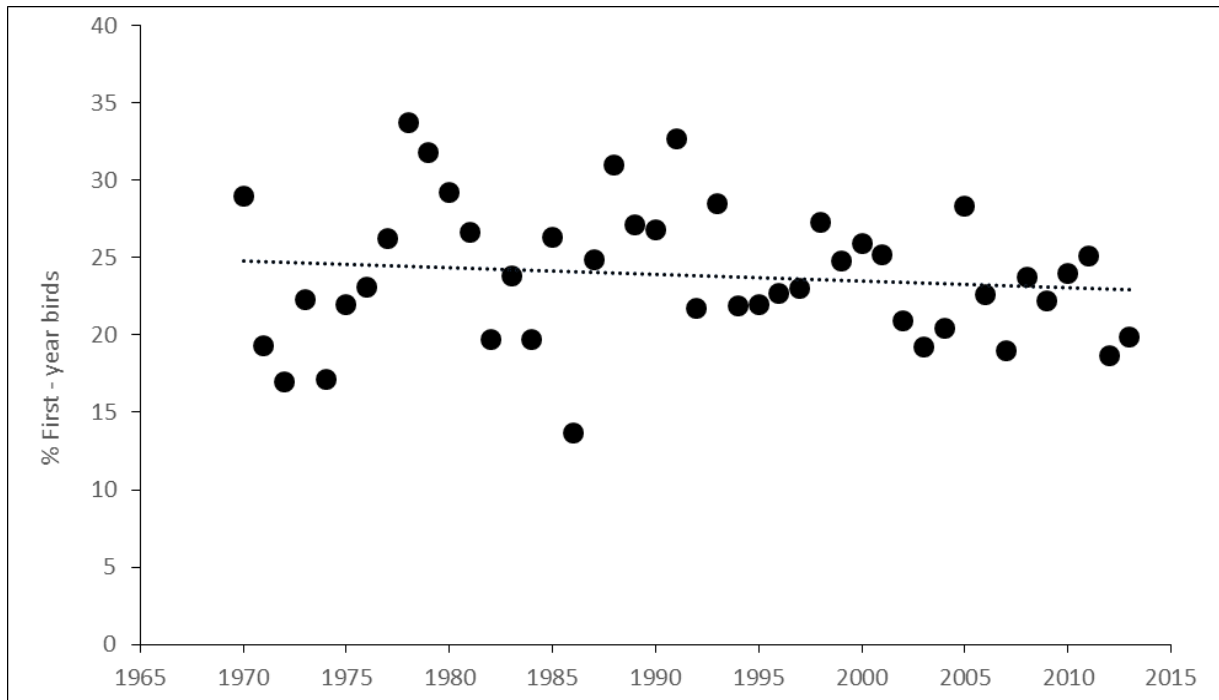
Between 1960 and 1970 the first TuBG arrived on the Zeeland wintering grounds in mid-November, with the first big flocks arriving around 5 December. Currently the arrival is a month or more earlier than these dates. Between the winters of 1994/1995 and 2013/2014, the average date of first arrival of individual geese or very small flocks was 21.10 (13.10 – 20.10) ($n = 17$) and the date for the first arrival of flocks was 27.10 (17.10 – 6.11) ($n = 14$). On their arrival the TuBG fed on the waste left in harvested fields of beets and potatoes. There were therefore very few sightings on pasture land. Once the fields had been ploughed up, there were fewer remains of the beets and potatoes available as a source of food. This is why at the end of December, and even more so in January, the geese sought pastureland and meadows. During this period many wintering birds were observed in fields of winter wheat.

Table 2. Yearly proportions of first-year birds (juveniles) ($n = 44$) and of mean family- sizes ($n = 40$) among Tundra Bean Geese wintering in the province of Zeeland, The Netherlands.

| | Percent juveniles | | Mean family - size | |
|---------|-------------------|------|--------------------|------|
| | n | % | n | mean |
| 1970-71 | 1184 | 29 | | |
| 71-72 | 1024 | 19.3 | | |
| 72-73 | 1412 | 17 | 17 | - |
| 73-74 | 2140 | 22.3 | 22 | - |
| 74-75 | 3047 | 17.1 | 37 | 2.17 |
| 75-76 | 2234 | 22 | 39 | 2.15 |
| 76-77 | 2155 | 23.1 | 69 | 1.77 |
| 77-78 | 1877 | 26.2 | 83 | 1.89 |
| 78-79 | 2601 | 33.7 | 172 | 2.22 |
| 79-80 | 2234 | 31.8 | 100 | 2.28 |
| 80-81 | 3234 | 29.2 | 115 | 2.4 |
| 81-82 | 5572 | 26.6 | 181 | 2.25 |
| 82-83 | 3700 | 19.7 | 84 | 1.91 |
| 83-84 | 4301 | 23.8 | 78 | 2.2 |
| 84-85 | 3895 | 19.7 | 67 | 1.89 |
| 85-86 | 3469 | 26.3 | 106 | 2.11 |
| 86-87 | 4105 | 13.7 | 83 | 1.6 |
| 87-88 | 4834 | 24.9 | 104 | 2 |
| 88-89 | 2917 | 31 | 102 | 2.29 |
| 89-90 | 2683 | 27.1 | 86 | 1.94 |
| 90-91 | 2788 | 26.8 | 56 | 2.14 |
| 91-92 | 3850 | 32.7 | 134 | 2.63 |
| 92-93 | 2864 | 21.7 | 56 | 1.92 |
| 93-94 | 3150 | 28.5 | 129 | 2.16 |
| 94-95 | 4553 | 21.9 | 102 | 2.21 |
| 95-96 | 3618 | 22 | 87 | 1.79 |
| 96-97 | 3429 | 22.7 | 116 | 2.1 |
| 97-98 | 4306 | 23 | 110 | 1.88 |
| 98-99 | 4481 | 27.3 | 115 | 2.14 |
| 99-00 | 4197 | 24.8 | 115 | 2.06 |
| 00-01 | 7174 | 25.9 | 149 | 1.97 |
| 2001-02 | 9598 | 25.2 | 139 | 2.16 |
| 2002-03 | 6539 | 20.9 | 138 | 1.85 |
| 2003-04 | 6598 | 19.2 | 127 | 1.9 |
| 2004-05 | 6398 | 20.4 | 168 | 1.88 |
| 2005-06 | 7739 | 28.3 | 193 | 2.36 |
| 2006-07 | 6826 | 22.6 | 130 | 2.13 |
| 2007-08 | 8267 | 19 | 87 | 1.72 |
| 2008-09 | 8424 | 23.7 | 145 | 2.18 |
| 2009-10 | 6578 | 22.2 | 139 | 2.12 |
| 2010-11 | 7255 | 24 | 95 | 1.84 |

| Table 2 : continued | | | | |
|---------------------|-------------------|------|--------------------|------|
| | Percent juveniles | | Mean family - size | |
| | n | % | n | mean |
| 2011-12 | 7424 | 25.1 | 112 | 2.13 |
| 2012-13 | 3772 | 18.7 | 115 | 1.96 |
| 2013-14 | 6515 | 19.9 | 119 | 2.08 |
| | mean | 23.9 | | 2.06 |
| | SD | 4.40 | | 0.20 |

Fig. 1. Regression line of proportions of first-year birds (juveniles) among Tundra Bean Geese on years. Period 1970-1971 – 2013-2014 (n = 44). Province of Zeeland, The Netherlands.



Fifty years ago, the wintering flocks of TuBG often appeared in monospecific flocks. It is rare today to see unmixed flocks of overwintering geese. In recent decades, an increasing number of White-fronted geese have been observed foraging in fields rather than in meadows or pastureland, so that almost all flocks are now a mix of TuBG and White-fronts. The Greylag Goose (*A. anser*) and the Barnacle Goose (*Branta leucopsis*) have increased tenfold in the last 20 years and these species now, too, mix with the flocks of overwintering TuBG.

Table 3. Differences between the percentages of juvenile Tundra Bean Goose during two winter periods of the same winter: from mid - November until mid - December and from mid - December until mid - January. Province of Zeeland, The Netherlands.

| Differences between the proportions of juveniles during two winterperiods of the same winter | Number of winters | % of winters |
|--|-------------------|--------------|
| < 1.5 % | 14 | 40 |
| 1.5 – 3.0 % | 9 | 26 |
| 3.0 – 4.5 % | 8 | 23 |
| > 4.5 | 4 | 11 |

Percentage of first-year birds

The percentage of immatures recorded within flocks of wintering TuBGs during a 44-year period (1970/1971–2013/2014) ranged from 13.7 % (1986/1987) to 33.7 % (1978/1979), with an overall mean of 23.9 ± 4.4 % (**Table 2; Fig. 1**). During this long period, no specific overall increase or decrease was observed. The regression coefficient r_s in a model I regression amounted to -0.042 , and the linear regression equation: $y = 24,8 - 0,042x$; degrees of freedom = $n - 2$; $t_{42} = 0.579$; $P > 0,5$. However, it is worth noting that over a period of five successive years, from the end of the 1970s to the beginning of the 1980s, relatively large numbers of first-year birds were observed (**Table 2; Fig. 1**).

It is also worth noting that the winters prior to the winter of 1992/1993 produced more varied results than the more recent winters. For the earlier period, the coefficient of variation (CV) was 10.6 % and for the more recent period it was just 5.5 %. The reason for this striking difference is not known. Apparently, there has been a more constant winter recruitment in recent decades than in earlier ones.

In order to establish whether age ratio remained constant during winter, we compared the percentages of first-year birds calculated for two periods each winter: mid-November to mid-December and mid-December to mid-January. We observed notable shifts in the composition of wintering TuBGs during some winters (**Table 3**). In 14 of 35 winters (40 %), the difference in the percentages of first-year birds within the wintering flocks from one time period to the next was < 1.5 %. However, nine winters (26 %) showed a difference of 1.5 to 3.0 %, eight winters (23 %) a difference of 3.0 to 4.5 % and four winters (11 %) a difference of > 4.5 %. Of these four, the discrepancies amounted to 6.2 % (winter 2013/2014), 6.7 % (1986/1987), 7.5 %, 1980/1981) and as much as 9.1 % (1989/1990). These differences may well be an indication of the fact that there were important relocations of the populations of TuBG within the wintering grounds. This observation also points to the need to determine the ratio of adults to juveniles in different periods within the same winter season.

Mean family size (Table 2; Fig. 2)

The mean number of first-year birds per family on the Zeeland wintering grounds for this 40-year period (1974/1975-2013/2014) was 2.06 ± 0.20 . In 36 (90%) of these cases the mean family size fell between 1.70 to 2.30. With a coefficient of regression of $r_s = -0,0023$; $y = 2,11 - 0,0023X$; degrees of freedom = $n - 2$; $t_{38} = 0,493$; $P > 0,5$) (**Table 2; Fig. 3**), it is impossible to see a clear trend during this period.

The results of the percentage of wintering immatures and the number of first-year birds per family are well correlated over a long period ($Y = 1.59 + 1.28 X$; $r = 0.688$; $n = 38$; $t_{38} = 7.600$; $P = < 0.001$) (Fig. 4).

Fig. 2. Number of juveniles per family ($n = 4,440$) among Tundra Bean Geese. Period 1974-1975 – 2013-2014 ($n = 40$). Province of Zeeland, The Netherlands. Numbers above columns indicate sample sizes of families.

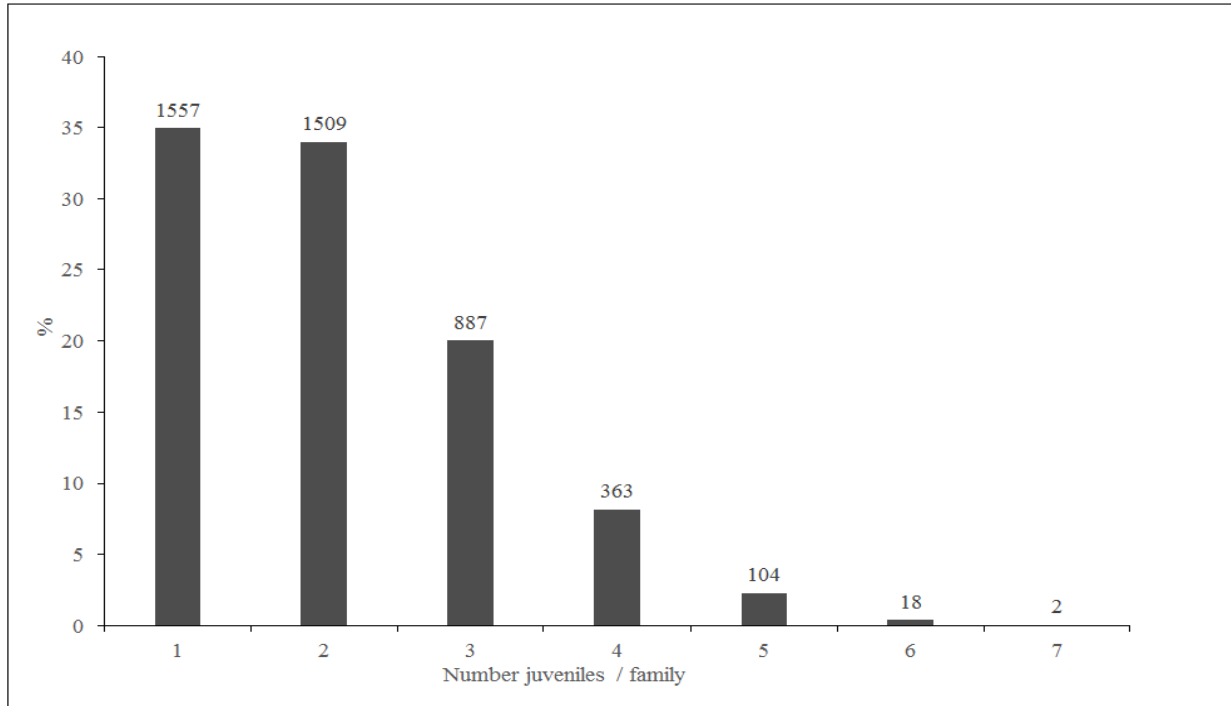
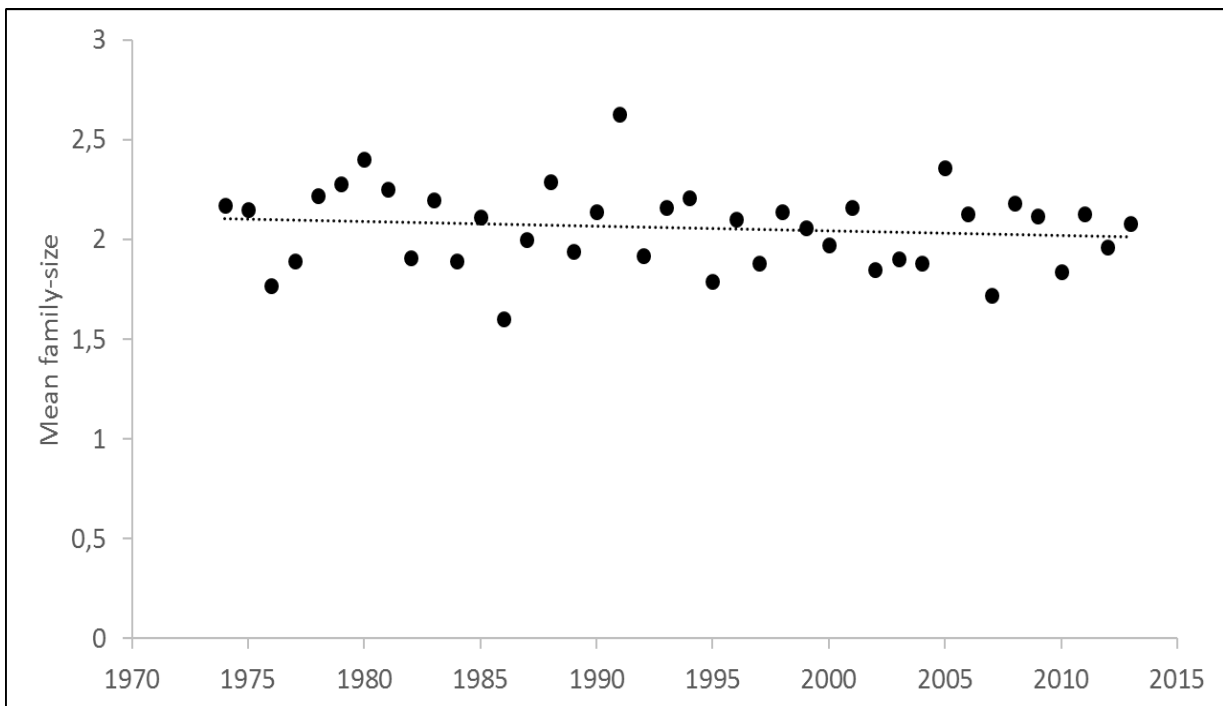


Fig. 3. Regression line of mean family-sizes among Tundra Bean Geese on years. Period 1974-1975 – 2013-2014 ($n = 40$). Province of Zeeland, The Netherlands.



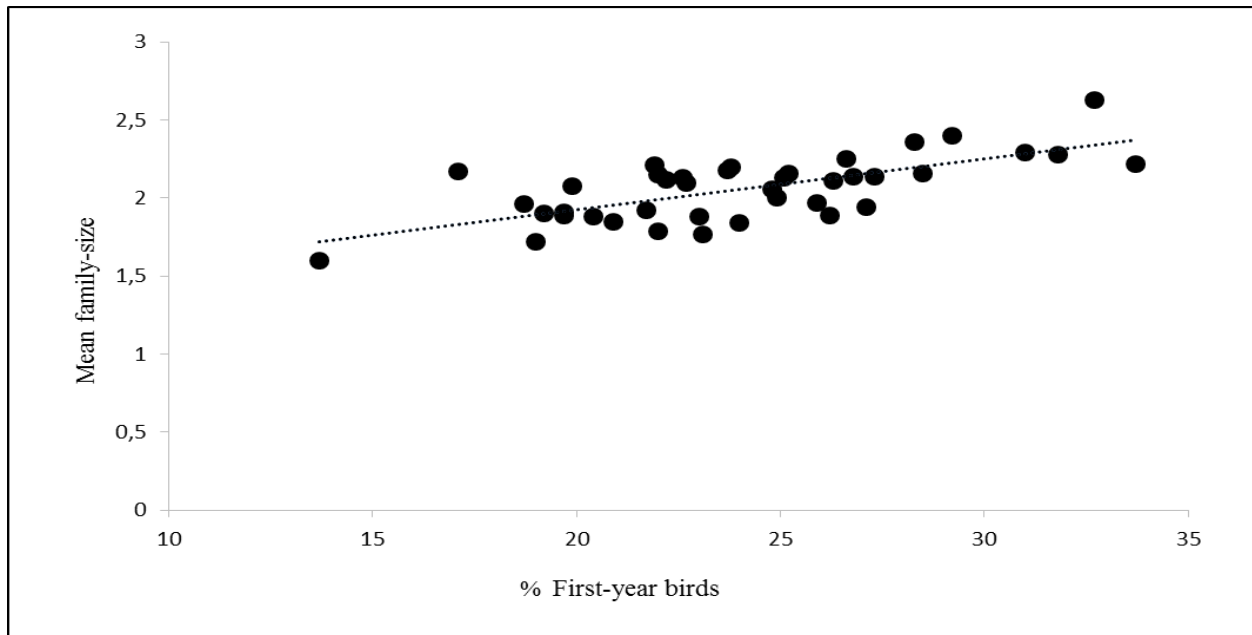


Fig. 4. Regression line and correlation between mean family-sizes and the proportions of first-year birds among Tundra Bean Geese. Period 1974-1975 – 2013-2014 ($n = 40$). Province of Zeeland, The Netherlands.

Table 4. Years with reproductive parameters above ('good' reproductive year) and below ('poor' reproductive year) the limits of the long-term mean $\pm 1SD$ among Tundra Bean Geese. Province of Zeeland, The Netherlands

| | % First-year birds or juveniles | | Family - size | |
|----------------|---------------------------------|-----------------------------|---------------------------|---------------------------|
| N winters | 44 | | 40 | |
| Mean ξ | 23.9 \pm 4.4% juv. | | 2.06 \pm 0.20 juv./fam. | |
| $\xi \pm 1 SD$ | 19.5 – 28.3 % juv. | | 1.86 – 2.26 juv./fam. | |
| | > 28.3 % | < 19.5 % | > 2.26 | < 1.86 |
| | 1978 (33.7%) + 5.4% | 1972 (17.0 %) – 2.5% | 1980 (2.40) + 0.14 | 1986 (1.60) - 0.26 |
| | 1979 (31.8 %) + 3.5% | 1974 (17.1 %) – 2.4% | 1991 (2.63) + 0.37 | 2007 (1.72) – 0.14 |
| | 1988 (31.0 %) + 2.7% | 1986 (13.7 %) – 5.8% | | |
| | 1991 (32.7 %) + 4.4% | | | |

Occurrence of 'good' and 'poor' breeding years in the Arctic

The limits for the normal percentage of first-year birds in overwintering TuBG were 19.5 – 28.3 % (23.9 \pm 4.4%). As for family size, 2.06 \pm 0.20 (1.86 – 2.26) first-year birds per family was the calculated mean for the entire four decades (**Table 4**). We do not take into account small differences from the four mentioned extreme values i.e. $\pm 1.0\%$ for the proportion of juveniles and ± 0.1 juveniles for the mean brood size (see methods). Based on percentage of first-year birds, four reproductive seasons were termed 'good' (first-year birds comprised more than 28.3%

of the observed birds) and three seasons were termed ‘poor’ (<19.5 %). However, based on the mean number of juveniles per family, two seasons were deemed “good” (> 2.26 juveniles per family) and two “poor” (< 1.86 juveniles per family). In terms of the percentage of juveniles, 37 of 44 breeding seasons remained within normal limits and in terms of the family size, 36 of 40 breeding seasons remained within limits of the mean. Only 1991 gave a positive discrepancy for both parameters and in 1986 there was a negative discrepancy for both (**Table 4**).

DISCUSSION

General remarks concerning the age ratios and comparison with results for the whole of The Netherlands

Age Ratios

In TuBG the percentage of first-year birds and the mean number of offspring in winter were not characterized by a three-year or other multi-year cycle. Such cycles have been described by Summers (1986) and Summers and Underhill (1987) for overwintering Dark-bellied Brent geese and White-fronted geese (Van Impe, 1996). The year 1986 produced poor reproductive results for all species of Arctic-nesting geese (Van Impe, 1988; Zöckler and Lysenko, 2000; Syroechkovskiy *et al.* 1991). This was also the case for many species of waders nesting on the Taimyr Peninsula (Underhill, 1987). It is worth to note that during the summer of 1986 Syroechkovskiy *et al.* (1991) found poor reproductive results for geese and swans on the island of Vaygach during a cold summer coinciding with very heavy egg-predation by Arctic foxes (*Alopex lagopus*). It is possible that also the North Atlantic Oscillation (NAO) played a role in this phenomenon (Boyd 2007 and Hugh Boyd *in litt.* 2003)

Data from the whole of The Netherlands were available for the period 2000/2001 – 2013/2014 ($n = 14$) in the yearly reports “Watervogels in Nederland” [Waterbirds in The Netherlands] (Hustings *et al.* 2008, 2009; Hornman *et al.*, 2009, 2011, 2012, 2013a, 2013b, 2015a, 2015b).

In all 14 years, immature TuBG were more numerous in Zeeland than elsewhere in the country. Differences between the two sampling pools ranged from 3.1 to 11.9 %, with a mean of 7.2 ± 3.2 % (Mann-Whitney U test, $n_1 = n_2 = 14$; $U = 4$; $P < 0.01$). It seems that the percentage of young birds varies depending on the geographic location of the wintering grounds. A study of the age ratio in the Dark-bellied Brent Goose in The Netherlands by Lambeck (1990) also refers to this phenomenon. Otsu *et al.* (1981) discovered that there were more first-year birds present in wintering flocks of White-fronts in the southern than in northern Netherlands. During the winter of 2009/2010, there were considerable differences in the percentages of first-year birds among TuBGs wintering in different countries : 5.2% (Sweden); 10.0% (Germany); and 15.1% (The Netherlands). These were noted by Koffijberg (2010), who also recorded higher values in the province of Zeeland than in other parts of The Netherlands.

In the present study the same pattern could clearly be observed in all winters. Families seem to prefer to winter in a warmer climate. The long-term mean minimum December temperature in Zeeland is on average 2°C higher than in the more northerly provinces of Groningen and Frisia, and for January and February these differences are as high as 3°C.

(<http://www.klimaatinfo.nl/nederland>). We compared the percentage of overwintering first-year TuBG with the nesting-season conditions on the tundras of northeastern Europe and northwestern Siberia collected in a long-term study by Soloviev and Tomkovich (1999-2011); (Tomkovich and Soloviev (2013); <http://www.arcticbirds.net>). We come to the conclusion that in years with a low number of rodents on the tundras of Europe ($n = 10$) and Siberia ($n = 12$), there were 1.0 – 1.5 % fewer first-year TuBG in Zeeland (period 1988-2013) than the long-term mean,

whereas in years with high numbers of rodents in northwestern Siberia, there was no significant difference.

Family size

The above-mentioned Dutch sources also gave results concerning family size for the whole of The Netherlands during the winters of 2008/2009 through to 2013/2014 ($n = 6$). In five of the six year-to-year comparisons, the mean number of first-year birds per family in Zeeland was greater than that for the rest of The Netherlands by 0.10 to 0.42 per winter (0.24 ± 0.10 on average for the positive results). The difference between the two sets was also significant (Mann-Whitney U test, $n_1 = n_2 = 6$; $E = 5$; $C = 31$, $P = 0.021$). The results for the overall percentage of immatures and for the number of first-year birds per family are comparable: more first-year TuBG winter in the warmer southwest corner of The Netherlands than elsewhere in the country.

Different behaviour of adult and juvenile birds

The daytime activity of wild geese consists of multi-phased cycles, as described by Szymanski (1916, 1920). During the day, overwintering flocks of TuBG alternate phases of high (foraging, moving around, conflicts) with those of low (resting, sleeping) activity. If one observes flocks of wild geese over a whole day, these alternations are clearly visible. These rhythmic activities have been studied in greater depth by Aschoff (1959, 1964) and Pohl (1968), among others, and by Philippona (1972) for the White-fronted Goose and by Van Impe (1980b) for *A. f. fabalis* and *A. f. rossicus*. Owing to such changes in activity that affect young and adult behaviour differently, only flocks that have been studied in a phase of high activity can reveal a realistic ratio of adults to juveniles. A phase with low activity will result in an age-ratio count skewed toward adults, because they are standing up and are more active than young birds at this time.

Examples of notes from a long series of observations:

(a) Ossensisse, 20.12.2013, 322–355 TuBG on potato fields: 1st count 11:30 a.m.: 355 TuBG, slightly mixed with *A. anser* and *A. albifrons*, high flock activity = 29.6 % juveniles; 2nd count 12:30 p.m.: 322 TuBG, id., low flock activity = 19.4 % juveniles;

(b) Perkpolder, 06.11.2007, 415–550 TuBG on beet fields: 1st count 10:00 a.m., 415 TuBG, mixed with 40 *A. albifrons*, high flock activity = 19.2 % juveniles; 2nd count 12:15 p.m.: 550 TuBG, mixed with a few *A. anser* and *A. albifrons*, low flock activity = 13.5 % juveniles.

Movement of families between adjacent flocks

A great number of observations have demonstrated that TuBG families generally can be found in higher percentages in energy-rich foraging places (remains of potatoes and beets after harvesting), than in less energy-rich feeding areas (e.g., meadowlands). This is also true for wintering White-fronted geese and Bewick's swans (*Cygnus bewickii*) (a.o. Rees *et al.* 1997; personal observations).

At the beginning of the winter season, remains of harvested beets and potatoes are favoured by geese over the grasses of meadowlands. Each winter, when small groups of TuBG are observed flying away from a big flock (A) to a nearby flock (B), these small flocks are determined to be predominantly families, and their destination field richer in nutrients than the departure field. Due to these relocations, the ratio of adults to juveniles in flock A tilts in favour of adults and in flock B in favour of first-year birds.

These important changes in the ratio of adults to juveniles can occur relatively quickly (within an hour).

Examples of notes from a long series of observations:

(a) Zonnemaire, 17.12.2012, TuBG on beet fields. Flock A. Almost all unmixed TuBG. 1st count 10:15 a.m., 640 TuBG = 28.6 % juveniles; 2nd count 2:00 p.m., 310 TuBG = 14.2 % juveniles;

(b) Zonnemaire, 18.12.2009, TuBG on potato fields. Flock B. TuBG mixed with 70 *A. anser* and 40 *A. albifrons*. 1st count 11:30 a.m., 540 TuBG = 20.4 % juveniles; 2nd count 12:15 p.m., 1080 TuBG, mixed with 90 *A. anser* and 70 *A. albifrons* = 27.2 % juveniles.

It is possible, therefore, for neighbouring flocks of overwintering TuBG (only a few hundred metres apart), to consist of very different percentages of immature birds.

Considerable deviations from the norm with regard to age ratio have also been observed among White-fronts during the space of a single day. The same phenomenon has been observed among waders (Clark *et al.*, 2004; Harrington, 2004). Researchers should not limit themselves to studying one single flock. Sampling one flock several times during the day, and several flocks on the same day should give a more accurate picture of the age ratio.

“Gang broods” among TuBG on the Zeeland wintering grounds

Families that include goslings other than those hatched by the parent pair were first called “gang broods” by Williams and Marshall (1938) and by Hochbaum (1944). Pre-hatch brood amalgamation is the result of intraspecific nest parasitism such as egg dumping. Post-hatch amalgamations result from crèching, kidnapping, and adoption of young (Eadie *et al.*, 1988). It is clear that egg-dumping on the breeding grounds complicates the assessment of the family-size in the winter haunts. On the Russian nesting grounds of the TuBG, egg dumping is not a rare event (Syroechkovskiy and Litvin 2005), especially on Vaigach Island, where, during six breeding seasons, 17 % to 36 % of all nests ($n = 512$) were parasitized (Syroechkovskiy and Baranyuk 2003; Syroechkovskiy, 2004).

The number of “families” that included 6 and 7 first-year birds represented only 0.44% of the 4,440 sampled families studied in Zeeland (**Fig. 2**). Gang broods occur also in other species of wild geese (*a.o.* Lynch *in* Miller and Dzubin, 1965; Miller and Dzubin, 1965; Raveling, 1969; Prevett and MacInnes, 1980; Zicus, 1981; Johnson and Raveling, 1988; Choudhury *et al.*, 1993; Ely, 1993; Williams, 1994). This can lead to counts of brood sizes, which do not reflect the real brood size on the breeding grounds. It is widely understood that this phenomenon is exacerbated by banding procedures and hunting activities. However, amalgamation or break-up of families during the winter is often only temporary and families can reunite within one day after hunting or banding (a. o. Miller and Dzubin, 1965).

The value of the studies concerning adult-to-juvenile ratio and family size

The ratio of adults to juveniles and family size have been studied in all species of wild geese in many countries in Western and Central Europe. The very first publications showed that this research was of great value in studies of population dynamics in wild geese. However, great care needs to be taken in applying appropriate methods of counting. In TuBGs age- and family-counts can be dependent on the exact period within the winter season, the geographical location of the winter grounds, the activity of the flocks, and the nutritional value of their food. Isolated results need to be compared with information from other studies. The study of the percentage of first-year birds without knowledge of other factors can lead to erroneous decisions about the management of wild geese (Caughley, 1974). The mechanisms by which populations increase or decrease can rarely be attributed to a single parameter. It is well established that a change in survival affecting all age classes equally has no effect on the age distribution. Both fecundity and survival are very important. The number of juveniles per family in winter provides a partial

picture of fecundity, but already involves survival; survival itself can only be studied by capture/recapture (including sighting) operations. In long-lived species the age of breeding individuals and especially the age of first breeding is also an important demographic factor, because it is correlated with reproductive performance (review *in* Newton, 1989; Saether, 1990; Ferrer and Bisson, 2003; Penteriani *et al.*, 2003; Pandolfi *et al.*, 2004).

CONCLUSIONS

The proportion of juveniles (the adult-to-juvenile ratio) and family size within the winter flocks of Tundra Bean Goose in the province of Zeeland (The Netherlands) were investigated during 44 and 40 winters respectively. The long term means for the first amounted to $23.9 \pm 4.40\%$ and for the latter to 2.06 ± 0.20 .

For the percentage of juveniles, the regression coefficient amounted to -0.042 during the course of the study and for the family size to -0.0023 . It is impossible to see a trend for either parameter.

Based on percentage of first-year birds in a family, four reproductive seasons were termed “good” and three “poor”. Based on the mean number of immatures per family, two seasons were deemed “good” and two “poor”. Only 1991 gave a positive discrepancy for both parameters and in 1986 there was a negative discrepancy for both.

In 14 year to year comparisons, flocks of Tundra Bean Geese wintering in Zeeland showed significantly more juveniles than elsewhere in The Netherlands. The same was true for five out of six year to year comparisons of the family size. These differences seem to be connected with higher average winter temperatures in Zeeland.

These results, when assessing the adult-to-juvenile ratio, do not only seem depend on the mean winter temperatures in the winter quarters, but also on what fields the counts were made, high-energy foods (sugar beet waste) attract relatively a higher number of families than do low-energy foods.

Adults and juveniles have a different behavioural pattern, which may give rise to divergent results in the adult-to-juvenile ratio. A reliable method to investigate winter flocks is of great importance.

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REFERENCES

- Alphéraki S. 1905. The Geese of Europe and Asia. – London, Rowland Ward: 1–198 .
- Altmann, J. 1974. Observational study of behavior, sampling methods. – Behaviour, 49: 227–267.
- Aschoff J. 1959. Zeitliche Strukturen biologischer Vorgänge. – Nova Acta Leopoldina, 21: 147–177.
- Aschoff J. 1964. Die Tagesperiodik licht-und dunkelaktiver Tiere. – Rev. Suisse Zool., 71: 528–558.
- Baillie S. R., Wernham C. V. and Clark J. A. 1999. Development of the British and Irish Ringing Scheme and its role in conservation biology. – Ringing & Migration, 19 (suppl.): 5–19.
- Bauer K. M. and Glutz von Blotzheim U. N. 1968. Handbuch der Vögel Mitteleuropas. Band 2. Anseriformes (1 Teil). – Frankfurt am Main, Akademische Verlagsgesellschaft: 1–534.
- Boyd H. 1952–53. White-fronted Goose statistics, 1952–53. – Wildfowl Trust 6th Annual Report, 73–79.
- Boyd H. 1953. On encounters between wild White-fronted Geese in winter flocks. – Behaviour, 5: 85–129.
- Boyd H. 1965. Breeding success of White-fronted Geese from the Nenets National Area. – Wildfowl, 16: 35–40.
- Boyd H. 2007. Seasonal variations in the North Atlantic Oscillation and the breeding success of arctic-nesting geese. – Wildfowl, 57: 40–53.
- Burton P. J. K. 1958. Brent Geese in Essex. – Wildfowl Trust 9th Annual Report, 73–79.
- Burton P. J. K. 1962. Brent Goose population studies, 1960–61. – Wildfowl, 13: 93–98.
- Caughley G. 1974. Interpretation of age ratios. – J. Wildl. Manage., 38: 557–562.
- Choudhury S., Jones C. S., Black J. M. and Prop J. 1993. Adoption of young and intraspecific nest parasitism in Barnacle Geese. – Condor, 95: 860–868.
- Clark J. A., Robinson R. A., Clark N. A. and Atkinson P. W. 2004. Using the proportion of juvenile waders in catches to measure recruitment. – Wader Study Group Bull., 104: 51–55.
- Coombes R. A. H. 1947. On the races of the Bean Goose in The Netherlands. – Limosa, 20: 229–230.
- Coombes R. A. H. 1951. Two races of Bean Goose *Anser arvensis* in Western Europe. – Proceedings of the 10th International Ornithological Congress (Uppsala, Sweden, June 1950): 185–188.
- Cramp S. and Simmons K. E. L. 1978. Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 1. Ostrich to Ducks. – Oxford, Oxford University Press: 1–732.
- Delacour J. 1954 The Waterfowl of the World. Vol. 1. – London, Country Life Ltd.: 1–284.
- Dement'ev G. P. and Gladkov N. A. (eds.). 1967. Birds of the Soviet Union. Vol. 4. – Jerusalem, Israel Program for Scientific Translations: 1–683.
- Dementiev, G. P. and Gladkov, N. A. (eds.). 1967. Birds of the Soviet Union. Vol. 2. Trans. by Israel Program for Scientific Translations, U.S. Dept. Interior & Natl. Sci. Foundation, Washington, D.C.
- Eadie J. McA., Kehoe F. P. and Nudds T. D. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. – Can. J. Zool., 66: 1709–1721.
- Ebbing B. 2014. De Rotgans. – Amsterdam/Antwerpen, Atlas Contact: 1–368.
- Ebbing B., van den Bergh L., van Haperen A., Lok M., Philippona J., Rooth J., and Timmerman A. 1986. Numbers and distribution of wild geese in The Netherlands 1979–1984. – Wildfowl, 37: 28–34.
- Ely C. R. 1993. Family stability in Greater White-fronted Goose. – Auk, 110: 425–435.

- Ferrer M. and Bisson I. 2003. Age and territory-quality effects on fecundity in the Spanish Imperial Eagle (*Aquila adalberti*). – *Auk*, 120: 180–186.
- Ferrer M., Ojalora F. and Garcla-Ruiz J. M. 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. – *Ecol. Appl.*, 14: 616–624.
- Flint V. Ye. and Krivenko. V. G. 1990. The present status and trends of waterfowl in the USSR. – *Managing Waterfowl Populations (Proceedings of IWRB Symposium, Astrakhan, 2–5 October 1989)*. IWRB Special Publication No 12. IWRB, Slimbridge, UK: 23–26.
- Fox A. D. and Madsen J. 1999. Introduction. – *Goose Populations of the Western Palearctic. A Review of Status and Distribution*. Pp. 8-18 *in*: Madsen J., Cracknell G. and Fox A. D., eds.). Wetlands International Publ. N 48. Wetlands International, Wageningen, The Netherlands; National Environmental Research Institute, Rønde, Denmark.
- Fox A. D., Hilmarsson J. O., Einarsson O., Walch A. J., Boyd H. and Kristiansen J. N. 2002. Staging site fidelity of Greenland White-fronted Geese *Anser albifrons flavirostris* in Iceland. – *Bird Study*, 49: 42–49.
- Fox A. D., Ebbinge B. S., Mitchell C, Heinicke T., Aarvak T., Colhoun K., Clausen P., Dereliev S., Faragó S., Koffijberg K., Kruckenberg H., Loonen M. J. J. E., Madsen J., Mooij J., Musil P., Nilsson L., Pihl S. and van der Jeugd H. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. – *Ornis Svecica*, 20: 115–127.
- Harrington B. 2004. Use care in determining age-ratios in shorebirds: they may differ relative to flock position, flock location and behaviour. – *Wader Study Group Bull.*, 104: 92–93.
- Hartert E. 1915. Die Vögel der paläarktischen Fauna. Band II. – Berlin, R. Friedländer und Sohn: 1–1004.
- Hochbaum A. H. 1944. The Canvasback in a Prairie Marsh. – Publ. American Wildlife Institute, Washington D.C.: 1–201.
- Hornman M., Hustings F., Koffijberg K., van Winden E., SOVON Ganzen- en Zwanenwerkgroep and Soldaat L. (2009, 2011, 2012, 2013a, 2013b, 2015a, 2015b) (in series). Watervogels in Nederland 2008/2009, 2009/2010, 2010/2011, 2011/2012 2012/2013, 2013/2014). Waterdienst-rapporten en SOVON-monitoringsrapporten. SOVON Vogelonderzoek Nederland, Nijmegen.
- Hustings F., Koffijberg K., van Winden E., van Roomen M., SOVON Ganzen- en Zwanenwerkgroep and Soldaat L. 2008. Watervogels in Nederland in 2006/2007. Waterdienst-rapport 2008.061; SOVON-monitoringsrapport 2008/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen: 1–176.
- Hustings F., Koffijberg K., van Winden E., van Roomen.M., SOVON Ganzen- en Zwanenwerkgroep and Soldaat L. 2009. Watervogels in Nederland in 2007/2008. Waterdienst-rapport 2009.020; Sovon-monitoringrapport 2009/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen: 1–128.
- Huyskens G. 1977. De verspreiding van *Anser fabalis fabalis* en *Anser fabalis rossicus* in Europa buiten het broedseizoen. – *Watervogels*, 2: 69–75.
- Johnson J. C. and Raveling D. G. 1988. Weak family associations in Cackling Geese during winter: effects of body size and food resources on goose social organization. Pp 71-89 *in*: Weller M. J. (Ed.) – *Waterfowl in winter* Minneapolis, Univ. Minnesota Press.
- Kishchinskiy A.A. 1979. Migrations of Bean Geese (Conclusions). - Pp. 160–163 *in*: Il'icev V.D. and Kishchinskiy A.A. *Migrations of Birds of Eastern Europe and Northern Asia: Ciconiiformes - Anseriformes*. Moscow, "Nauka". (Russ.)
- Koffijberg K. 2010. Breeding success amongst Greater White-fronted Geese in 2009/10 – a progress report. – *Goose Bulletin*, 11: 32–34.

- Koffijberg K., Beekman J., Cottaar Fr., Ebbinghe B., van der Jeugd H., Nienhuis J., Tanger D., Voslamber B., van Winden E. 2010. Wintering and migratory geese in The Netherlands. – *De Levende Natuur*, 111: 3–9.
- Koffijberg K. and Hornman M. 2011. Recent numbers and trends in wintering and migratory geese and swans in The Netherlands. – *Goose Bulletin*, 13: 20–23.
- Krivenko V. G. 1993. The current status of waterfowl resources and their habitats in the middle region of the former USSR. – *Wetlands and Waterfowl Conservation in South and West Asia: proceedings of an International Symposium, Karachi, Pakistan, 14–20 December 1991*. IWRB Spec. Publ. No 25 and AWB Publ. 85. Slimbridge, GB; IWRB; Kuala Lumpur, MY: Asian Wetland Bureau: 72–77.
- Krüger O. 2005. Age at first breeding and fitness in Goshawk *Accipiter gentilis*. – *J. Anim. Ecol.*, 74: 266–273.
- Lambeck R. H. D. 1990. The applicability of age ratio and brood size counts in population dynamic studies of the Brent Goose *Branta b. bernicla*. – *Ardea*, 78: 414–425.
- Lebedeva M.I. 1979. Migrations of Bean Geese according to banding results obtained in the U.S.S.R. - Pp 150-160 *in: Il'icev V.D. and Kishchinskiy A.A. Migrations of Birds of Eastern Europe and Northern Asia: Ciconiiformes - Anseriformes*. Moscow, "Nauka", (Russ.).
- Lebret T. 1948. Waarnemingen over leeftijdsklassen bij Kolganzen (*Anser a. albifrons* (Scop.)). – *Ardea*, 36: 198–200.
- Lebret T. 1956. Are group-size counts of wild geese an index of productivity? – *Ardea*, 44 (2): 284–288.
- Litzbarski H. 1979. Migrations of Bean Geese according to data obtained in the German Democratic Republic. - Pp. 145-150 *in: Il'icev V.D. and Kishchinskiy A.A. - Migrations of Birds of Eastern Europe and Northern Asia: Ciconiiformes - Anseriformes*: Moscow, "Nauka". (Russ.).
- Madsen J. 1991. Status and trends of goose populations in the Western Palearctic in the 1980s. – *Ardea*, 79 (2): 113–122.
- Miller H. and Dzubin A. 1965. Regrouping of family members of the White-fronted Geese (*Anser albifrons*) after individual release. – *Bird-Banding*, 36: 184–191.
- Mineev Yu. N and Mineev O. Yu. 1997. Geese numbers and their changes in the Pechora Delta and northeastern Malozemelskaya Tundra. – *Casarca*, 3: 347–354 [Russ., Eng. summary].
- Moffitt J. L. 1934. Fourth Annual Black Brant census in California. – *California Fish and Game*, 20: 355–364.
- Naumann J. F. 1902. Johann Andreas Naumann's Naturgeschichte der Vögel Mitteleuropas. Vol. IX. – Gera, Verlag Fr. Eugen Köhler: i–iv; 1–408.
- Newton I. 1989. Lifetime Reproduction in Birds. – London & San Diego, Academic Press: i–x; 1–479.
- Otsu M., van den Bergh L. and Van Impe J. 1981. Age-ratio's bij Kolganzen (*Anser albifrons*) in Noord- en Zuid-Nederland (unpublished report).
- Pandolfi M., Gaibani G., Tanferna A. 2004. Depicts the number of breeding pairs reliably the status of Peregrine Falcon *Falco peregrinus* populations? – *Ardea*, 92 (2): 247–251.
- Penteriani V., Balbontin J. and Ferrer M. 2003. Simultaneous effects of age and territory quality on fecundity in Bonelli's Eagle *Hieraetus fasciatus*. – *Ibis*, 145 (online): E77–E82.
- Philippona J. 1972. Die Blessigans. – *Die Neue Brehm-Bücherei* 457. Wittenberg – Lutherstadt, A. Ziemsen Verlag: 1–135.
- Phillips J. C. 1932. Fluctuations in numbers of the Eastern Brent Geese. – *Auk*, 49: 445–453.
- Pohl H. 1968. Einfluss der Temperatur auf die freilaufende circadiane Aktivitätsperiodik bei Warmblütern. – *Zeitschr. Vergleichende Physiol.*, 58: 364–380.

- Prevett J. P. and MacInnes C. D. 1980. Family and other social groups in Snow Geese. – Wildlife Monographs, N°71: 3–46.
- Raveling D. G. 1969. Roost sites and flight patterns of Canada geese in winter. – J. Wildl. Manage., 33: 319–330.
- Raveling D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. – Behaviour, 37: 291–319.
- Rees E. C., Kirby J. S. and Gilburn A. 1997. Site selection by swans wintering in Britain, the importance of habitat and geographic location. – Ibis, 139: 337–352.
- Robertson G. J. 2008. Using Winter Juvenile/Adult Ratios as Indices of Recruitment in Population Models. – Waterbirds, 31 (Special Publication 2): 152–158.
- Robertson G. J. and Cooke F. 1999. Winter philopatry in migratory waterfowl. – Auk, 116: 20–34.
- Ryabitsev V. K. 1995. Short review of geese at Yamal Peninsula. – Bulletin of Geese Study Group of Eastern Europe and Northern Asia, 1: 164–166 [Russ., Eng. summary].
- Ryabitsev V.K. 2008. Birds of the Ural, the Pre-Ural area and Western Siberia: reference book of determination. 1-634. Yekaterinburg, Ed. of the Ural University. (Russ.).
- Sæther B.-E. 1990. Age-specific variation in reproductive performance of birds. – Current Ornithology, 7: 251–282.
- Scott D. A. and Rose P. M. 1996. Atlas of Anatidae populations in Africa and Western Eurasia. Publication 41. Wetlands International. Wageningen, The Netherlands: 1–336.
- Soloviev M. Y. and Tomkovich P. S. (compilers). 1999–2011 (in series). Arctic Birds: an International Breeding Conditions Survey, NN°1–12. Available at: <http://www.arcticbirds.net> (Accessed 3 December 2016).
- Summers R. W. 1986. Breeding production of Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to lemming cycles. – Bird Study, 33: 105–108.
- Summers R. W. and Underhill J. G. 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. – Bird Study, 34: 161–171.
- Syroechkovskiy E. V. 2004. Egg dumping and family structure in the *Anser* genus. – Casarca, 10: 81–106 [Russ., Eng. summary].
- Syroechkovskiy E. V. and Baranyuk V. V. 2003. Quantitative criteria for detection of dumped eggs in clutches of Anseriformes. – Casarca, 9: 23–42 [Russ., Eng. summary].
- Syroechkovskiy E. V. and Litvin K. E. 2005. Goose eggs: what can they tell us about? – Casarca English Supplement, 1: 69–89.
- Syroechkovskiy E.V., Litvin K.E. and Ebbinge B.S. 1991. Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988; interplay of weather and Arctic Fox predation. – Ardea, 79/3: 373-382.
- Szymanski J. S. 1916. Die Haupt-Tiertypen in Bezug auf die Verteilung der Ruhe und Aktivitätsperioden im 24-stündigen Zyklus. – Biol. Zentralblatt, 36: 537–541.
- Szymanski J. S. 1920. Aktivität und Ruhe bei Tieren und Menschen. – Zeitschr. für Allg. Physiol., 18: 105–162.
- Tomkovich P. S. and Soloviev M. Y. 2013. Breeding Bird Conditions in the Circumpolar Arctic during 2011. –ABBCS report: 1–13. Available at: <http://www.arcticbirds.net> (Accessed 4 December 2016).
- Underhill L. G. 1987. A poor breeding season for ground-nesting birds in the Taimyr Peninsula in 1986. – Safring News, 16: 13–15.
- Van Impe J. 1973. Bepaling in het veld van leeftijdsklassen bij de Rietgans *Anser fabalis*. – Limosa, 46: 192–198.
- Van Impe J. 1980a. Etude de deux populations de l’Oie des moissons *Anser fabalis*. – Alauda, 48: 1–20.

- Van Impe J. 1980b. Ecologie et ethologie des Oies des Moissons *Anser fabalis fabalis* et *Anser fabalis rossicus*. Le Gerfaut, 70: 499–558.
- Van Impe J. 1988. Poor breeding success in northern Wild Geese in 1986. Description and analysis of probable causes. – Le Gerfaut, 78: 43–68.
- Van Impe J. 1996. Long-term reproductive performance in White-fronted Geese *Anser a. albifrons* and Tundra Bean Geese *A. fabalis rossicus* wintering in Zeeland (The Netherlands). – Bird Study, 43: 280–289.
- Wetlands International. 2016. Waterbird Populations Estimates. Retrieved from wpe.wetlands.org on 7 November 2016.
- Williams C. S. and Marshall W. H. 1938. Survival of Canada Goose goslings, Bear River Refuge, Utah 1937. – J. Wildl. Manage., 2: 17–19.
- Williams T. D. 1994. Adoption in a precocial species, the Lesser Snow Goose: intergenerational conflict, altruism or a mutually beneficial strategy? – Anim. Behav. 47: 101–107.
- Witherby H. F. Jourdain F. C. R., Ticehurst N. F. and Tucker B. W. 1939. The Handbook of British Birds. Vol. III. Hawks to Ducks. – London, H. F. and G. Witherby Ltd.: i-x; 1–387.
- Zicus M. C. 1981. Canada Goose brood behaviour and survival estimates at Crex Meadows, Wisconsin. – Wilson Bull., 93 (2): 207–217.
- Zöckler C. and Lysenko, I. 2000. First circumpolar assessment of climate change impact on Arctic breeding water birds. – Biodiversity Series, N°11. WCMC World Conservation Press: 1-20.