THE APPLICABILITY OF AGE RATIO AND BROOD SIZE COUNTS IN POPULATION DYNAMIC STUDIES OF THE BRENT GOOSE *Branta b. bernicla*

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ABSTRACT In wintering Brent Geese, annual assessments of the proportion of juveniles and the mean brood size have been made since the 1950s, allowing population dynamic analyses. Field procedures have never been quantitatively explored and were studied in four areas along the Dutch Wadden Sea in 1975/76. Juveniles were shown to be overrepresented in the front and adults in the centre of grazing flocks. A separation between families and other birds is accomplished already at landing. As a consequence of the flock structure, the composition of temporary subflocks can differ largely. The proportion of juveniles went down from 50% in autumn to 25% in midwinter, and increased to 40% in spring. With normally 15-20% of the Brent wintering in the entire Wadden Sea, age counts from the southern areas will overestimate the population average. In late winter and spring systematic differences in age ratio were found between different feeding habitats. Brood size ranged from 1 to 7 juveniles. The average declined from 4 in autumn to 3.2 in spring. The mean brood size in a flock was positively related with its proportion of juveniles. Changes in family behaviour with season are discussed. Field counts can best be run in conjuction with the annual midwinter census, but require a tightly organised scheme. Sampling techniques are discussed. Results will probably apply to other goose species, but consequences of shooting warrant more study.

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INTRODUCTION

Population studies on geese are mainly based on ringing data. Most data sets, however, are not consistent enough to provide statistically precise annual survival figures, in spite of a sometimes respectable number of ringed birds, as illustrated by a study of Atlantic Brant *Branta bernicla hrota* (Kirby *et al.* 1986). High standards are only reached in very intensive ringing programs such as operated for some North American ducks (Anderson & Burnham 1976, Boyd & Hyslop 1985). But theoretical objections remain, because conditions such as a constant annual survival per year-class and a constant reporting rate are often not fulfilled (Martinson & McCann 1966, Anderson *et al.* 1981, Conroy 1985, Parkin & White-Robinson 1985). This can result in serious errors (Lakhani & Newton 1983). Potential biases also emerge from demographic heterogeneity (Pollock & Raveling 1982).

Mark-recapture studies are only feasible in atypical cases like the small, nearly closed population of the introduced Canada Goose *B. canadensis* in England (Parkin & White-Robinson 1985). Individual marking, allowing live sightings, is a successful extension of ringing programs (St. Joseph 1979, Prevett & McInnes 1980, Owen 1982, Ebbinge & van Biezen 1987). As in traditional ringing, long-term programs have, however, practical, financial or even political limitations. A general drawback of ringing is, finally, that catches do not necessarily reflect the composition of a goose population (e.g. Raveling 1966, Higgins *et al.* 1969, Sulzbach & Cooke 1978).

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In several species, first-year birds are readily distinguished in the field by their plumage, allowing field assessments of their proportion in a flock. Given a time-series of these so-called age ratios and population counts, estimations of the annual recruitment and survival can be made. In combination with data on the age of first breeding and the average number of juveniles per family - parents and their offspring normally stay together until spring (Sherwood 1967, Prevett & McInnes 1980) - a population model can be set up, as shown by Boyd (1959) and Lynch & Singleton (1964).

Such field observations provide a potential alternative to ringing or at least a "parallel research" as recommended by Lakhani & Newton (1983). In Europe several long-term studies are running, which have resulted in population models of e.g. Icelandic Pink-footed *Anser brachyrhynchus* and Greylag Goose *A. anser* (Ogilvie & Boyd 1976) and the Spitzbergen Barnacle Goose *Branta leucopsis* (Owen & Norderhaug 1977). Annual age ratio counts in the Dark-bellied Brent Goose *B. b. bernicla* were started in the 1950s by Burton (e.g. 1958, 1961), mainly in Essex (UK), and continued and extended since then (Ogilvie & St. Joseph 1976, St. Joseph 1982). Data were used for analyses of survival and recruitment in relation to changes in population numbers (Lambeck 1973, Ogilvie & St. Joseph 1976, Ebbinge 1985).

Although potential snags are well-known (Boyd 1959, Owen 1980), the methodology of age ratio assessments has not been quantitatively explored so far. This study therefore examines the feasibility of obtaining reliable data on Brent flocks, the homogeneity of the population as reflected by the composition of flocks within the same area or from different places, and the constancy of the proportion of first-year birds during the wintering season.

Behaviour and integrity of marked goose families have been studied by e.g. Sherwood (1967), Raveling (1968) and Prevett & McInnes (1980), but little is known about seasonal variation of the family size on a population level (cf. Black & Owen 1989a), or differences between areas. Some data were collected in conjuction with the age ratio assessments.

STUDY AREAS AND METHODS

The study was carried out in four areas around the Dutch Wadden Sea, a coastal sea with extensive intertidal flats, during the 1975/76 season. Two islands, Texel and Schiermonnikoog, and two mainland areas, the Balgzand and a part of the coast of the Province of Groningen, were selected for their geographic position (east and west), their different type of feeding areas and for their accessibility. A map of their location, a description of each, and details of local Brent dynamics during the study is found in Lambeck (1990).

Field work started on Schiermonnikoog in the second half of October, and was conducted at approximately biweekly intervals. After some occasional counts in autumn, a similar schedule was operated for Texel and the Groningen coast from January onwards. Frequency in all three areas was increased to mostly once a week from March onwards. Field work in the fourth area, the Balgzand, started on April 1 and followed a biweekly schedule. Data collection on Schiermonnikoog ended prematurely in early May, when the Brent switched from the polder to the poorly accessible mudflats and salt marshes (see Lambeck 1990). Only one of the three separate feeding areas in the surveyed section of the Groningen coast was permanently occupied by Brent (Lambeck 1990). Local data on seasonality in age composition will, therefore, be confined to that sub-population.

First-year (=juvenile) Brent have white edges of the wing coverts, a 'chevron' lacking in older birds (for convenience called adults, irrespectively of their sexual maturity). For further details see Cramp & Simmons (1977). With a telescope and under good light conditions ageing is feasible from 400 m. Nearly all counts were done from a dike, giving a good overview. Flock size was determined by counting individual birds with a hand-counter, assuring independence of repeated counts. Estimates were only made occasionally (e.g. when birds disappeared prematurely because of a disturbance). For the study of flock structure, the telescope was moved slowly against the walking direction of a cohesive flock, so from 'head' to 'tail', inspecting over the whole cross-section as many birds as possible and recording, on tape or with the help of an assistant, their ages one by one. Sample size was, therefore, variable, being determined by flock size and the ad hoc field situation. Additionally, samples were taken from different parts of a flock (front, centre, etc.) with the aid of two hand-counters, providing a lump sum of the two age classes. To obtain an age ratio of a flock, Burton (1961) amalgamated a series of standard (block) samples of 50 birds. Such a procedure is not practicable under all field conditions, however, and the independence of samples is difficult to assure. Age ratios in this study were mostly based on a large 'head-to-tail' sample, including minimally 25% of the birds present. Coverage was usually much higher, reaching to over 90% in smaller flocks (< 1000 birds). A second, occasionally used method was an integral count of all juveniles in the flock. Age counts were only made when the flock behaved quietly, i.e. without running or 'milling' on the water. Consecutive age ratios for the different haunts were based on all birds present. In cases of more than one flock, a weighted average was calculated.

In contrast to the block-sampling technique, one large cross-sample does not provide a direct measure of its precision. Repetition of the estimation may give an indication. In 26 cases with more than one (mean 2.6) sample, the largest difference between the percentages of juveniles obtained ranged from 0.3-9.7 percentiles, with an average of 3.6%. For a theoretical analysis of sample sizes required to detect a 'true' difference between percentages of juveniles in two random samples at a desired probability level, see e.g. Sokal & Rohlf (1981). In comparisons of the proportion of juveniles in samples a *G*-test of independence was used. Seasonal trends were analyzed with the related RxC test of independence (Sokal & Rohlf 1981).

Only distinct groups, composed of two or sometimes one adult plus one or more juveniles, recognizable by a spatial separation from other birds or a common activity like walking, swimming or agression directed towards others, have been regarded as a family. Productivity parameter is the number of juveniles: the so-called brood size.

RESULTS

Flock structure

Because data are influenced by variations in sample size and age composition of the flocks studied, all samples of at least 200 birds ($n = 37$, range 207-1683) were made comparable by plotting the proportion of juveniles in a percentual segment against the proportion in the whole sample. The rationale is that any segment should provide an unbiased estimate of the sample average and, hence, the flock composition, when individuals or social units are randomly distributed over a flock. The two parameters are not independent, but with segments of 10 or 20% of the whole sample the interrelation is rather limited. It is, therefore, justifiable to analyse possible differences by a simple sign-test. The procedure is illustrated for the first 20% of a sample, taken as a measure of the leading edge of a flock (Fig. 1).

Juveniles were overrepresented in this segment ($p < 0.001$). Linear regression functions for six

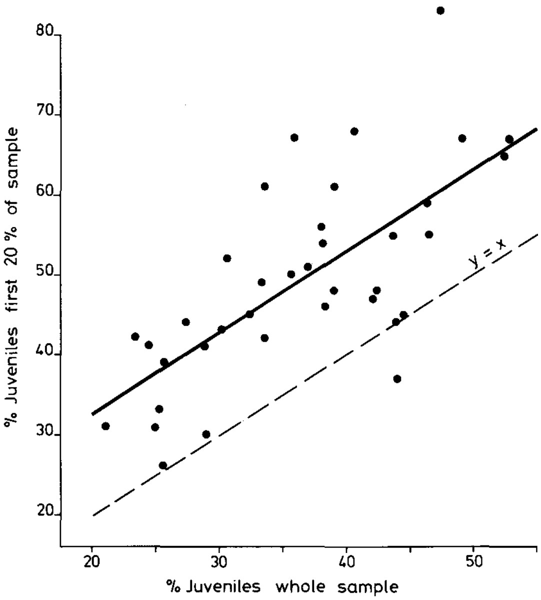

Fig. 1. The relation between the percentage of juveniles in the first 20% of the birds sampled, representing the head of a flock, and the percentage of juveniles in all birds sampled.

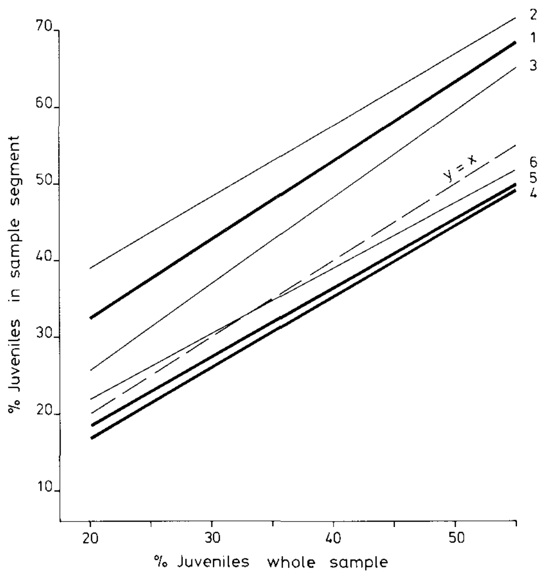

Fig. 2. Calculated linear regression functions, representing the relation between the percentage of juveniles in a number of sample segments (Y) and the percentage of juveniles in all birds sampled (X).
1= segment 0- 20%; $Y = 11.94 + 1.026 \cdot X$
2= segment 0- 10%; $Y = 20.49 + 0.932 \cdot X$
3= segment 10- 20%; $Y = 3.24 + 1.125 \cdot X$
4= segment 40- 60%; $Y = -1.41 + 0.918 \cdot X$
5= segment 80-100%; $Y = 0.52 + 0.897 \cdot X$
6= segment 90-100%; $Y = 4.89 + 0.850 \cdot X$

sample segments (Fig. 2) show a quick drop in the percentage of juveniles behind the leading edge: the difference between the 0-10 and 10-20% segments is highly significant (Wilcoxon two sample test, $p < 0.001$). The percentage of juveniles of the latter was still higher than the sample average ($p < 0.001$). In contrast, the centre of the flock, supposed to be represented by the 40-60% segment, had a lower level ($p < 0.01$). On average, the percentage of juveniles in the leading edge was twice as high as in the centre. The composition of the tail of a flock, for which the 80-100% segment was taken as an index, did not significantly differ from both the sample average and the 40-60% segment. The rise in the percentage of juveniles towards the rear end, as found in some cases, is reflected by a somewhat higher level for the 90-100% segment (Fig. 2). If within each sample the 80-90 and 90-100% segments are compared, values for the latter were mostly higher ($p < 0.05$).

The structure of a flock is not influenced by its age ratio: the slopes of all regression functions were not significantly different from 1.0 (the $y = x$ line in Figs. 1 and 2).

Seasonal and inter-area differences in age ratio

Data on the age ratio of the Brent populations studied over the 1975/76 season (Fig. 3) show a distinct seasonal pattern (RxC test of independence, $p < 0.001$). The percentage of juveniles gradually declined from around 50 in early autumn to a 25 in midwinter. During a severe frost period in late January-early February, Schiermonnikoog and the Groningen coast were abandoned. The first flocks to return had a low proportion of juveniles, but it subsequently increased in all areas to about 40% in early April. Around that time the bulk of the population, having wintered in southern areas, returned to the Wadden Sea. A similar age ratio was found in the Balgzand, then sampled for the first time.

Autumn figures do not indicate striking inter-area differences, but the incomplete data do not justify any conclusion. Differences certainly occurred in late winter, and patterns in the four areas widely diverged in April-May. The Texel and Schiermonnikoog populations maintained a high percentage of juveniles, that of the Groningen coast was similar to the winter population, and the Balgzand population declined to an intermediate level (Fig. 3). On corresponding dates, the differences were significant between the two latter areas on the one hand and Texel (G-test, $p < 0.001$) and Schiermonnikoog (respectively $p < 0.001$ and $p < 0.05$) on the other. The higher proportion of juveniles in the Balgzand as compared to the Groningen coast was significant ($p < 0.01$) in May. Figures for the Schiermonnikoog population seemed to stay somewhat behind those of Texel, but differences were too small to be significant.

Summarizing, age ratios from the Dutch Wadden Sea will heavily depend on the time of the year and, at least in the second half of the season, on the sampling area.

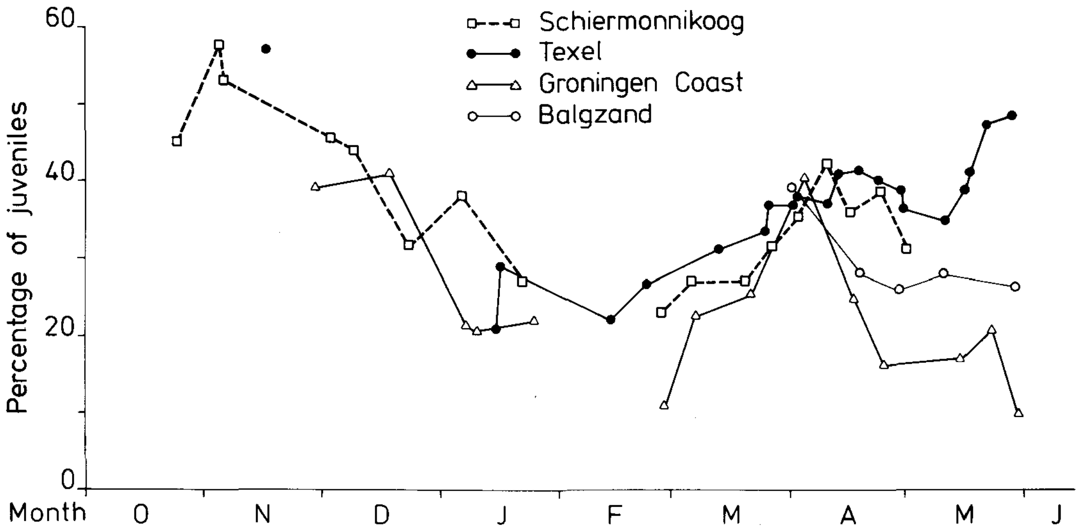

Fig. 3. Seasonal patterns in the mean percentage of juveniles in the four study areas during the 1975/76 season. Schiermonnikoog and the Groningen coast were temporarily abandoned during a cold spell around 1 Feb. Texel was sampled only once in autumn; the Balgzand study was confined to April-May.

Brood size

In only 2.5% of the families, one of the two parents was missing. The number of juveniles ranged from 1 to 7 with a mode of 4 (Fig. 4a). The assessed families are unequally spread over the areas and over the season, impeding a thorough analysis. Taken over the whole of the season no significant differences in mean brood size between the areas could be detected. Using all single size-date pairs (n = 327), the mean size declined from near 4 in early autumn to about 3.2 in spring. The best fitting polynomial curve suggests this decline is realised already around February (Fig. 5). Separate linear regression functions (size versus time) were calculated for two categories: the families assessed before and after February 1, respectively (the cold spell being a natural break). The slope over time in the former data set was significantly (p < 0.001) negative, the slightly positive one in the latter did not significantly deviate from zero.

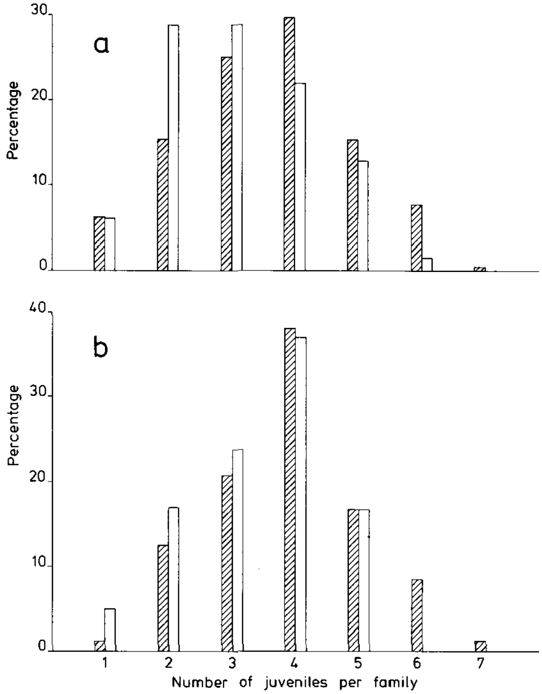

Fig. 4. Seasonal change in the frequency distribution of brood sizes. (a) a comparison between all families assessed before (hatched, n = 195) and after 1 Feb.(blank, n = 132); (b) a comparison between the two most coherent (see text) data sets in autumn (hatched, Schiermonnikoog 24 Oct. - 11 Dec., n = 71) and spring (blank, Texel 13 Mar. - 2 Apr., n = 41).

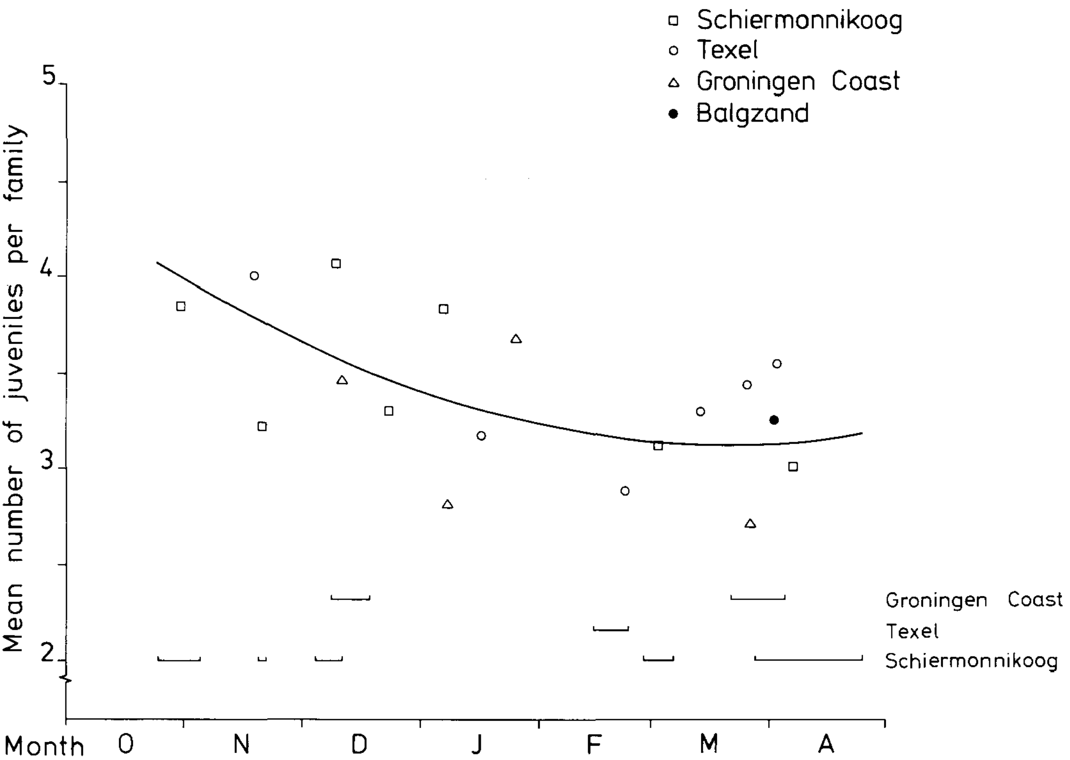

Fig. 5. Mean brood sizes in the study areas during the 1975/76 season. Horizontal bars represent the period length when data were combined for a sufficient sample size.

Size-frequencies for the two periods illustrate the distinct shift (*G*-test, $p < 0.01$) towards smaller families (Fig. 4a). This change is much less pronounced and, moreover, not significant when the two largest coherent data sets (originating from one area in a period without a substantial change in age ratio) from autumn (Schiermonnikoog) and spring (Texel) are compared (Fig. 4b).

The relation between age ratio and brood size

The mean brood size in a flock appeared to be positively correlated with its percentage of juveniles ($n = 17, r = 0.79, p < 0.001$). However, such a correlation may be the result of their concomitant decrease until February (Figs. 3 and 5) and, besides, too few samples in spring. Short-term changes within one area may be more illustrative. Although sample sizes were too small to justify firm conclusions, the parallel fluctuations of brood size and percentage of juveniles on Schiermonnikoog in December-January and their simultaneous increase on Texel in early spring are quite suggestive in this respect (Figs. 3 and 5).

Results, therefore, provide evidence that a higher percentage of juveniles not only depends on a higher share of families in a flock, but also on a relative increase in the abundance of larger families.

DISCUSSION

Flock structure and behaviour

The shape of a Brent flock is continuously changing. More than one frontline is not uncommon, which results in splitting up and reuniting of groups of birds. But the non-random flock structure, as found in this study, holds also for such complex situations.

An unequal distribution of Brent families has been noted already by Burton (1958), who presumed that it arose only gradually after a mixed landing. White-fronted Goose *Anser albifrons* parents move longer in the same direction than other adults, which according to Owen (1972) explains the higher abundance along the edges of a flock. This is probably not the prime factor, however, as shown by the structure of a Brent flock immediately after landing at sea (Fig. 6). Qualitative observations on small groups arriving later indicate that families mostly land on the edge or between other families, while single or paired adults drop between other adults. (Sub)adults often graze in packed subgroups, with both families and solitary juveniles nearly exclusively confined to the edges. Later in the season blocks of juveniles, with hardly any adults, were seen. These observations suggest that the incomplete mixing is not due to the persistence of family flocks (Boyd 1966) alone, but is merely the result of an associative tendency within the different social categories. This may arise from the close relation between social status and position in the dominance rank (cf. Boyd 1953, Raveling 1970, Black & Owen 1989b).

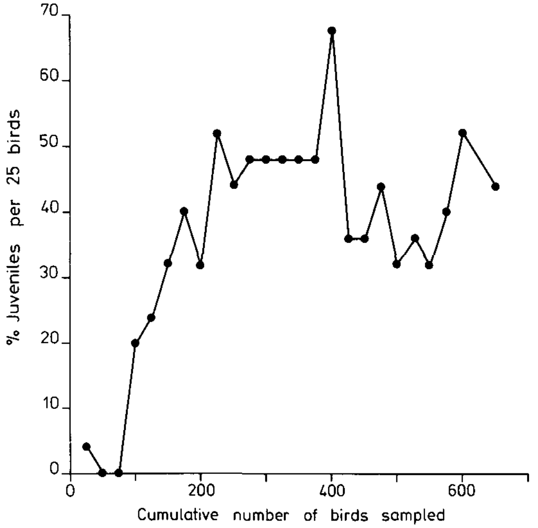

Fig. 6. The percentage of juveniles per successive 25 birds in an age ratio sample of a flock on Schiermonnikoog, taken immediately after landing at sea.

Differences in flock composition within and between areas

A local population may temporarily break up into subflocks. Small ones (< 100 birds) may have extremely varying age ratios. A comparison of pairs of larger subflocks ($n = 13$) revealed differences ranging from 1-24 percentiles of juveniles. Even subflocks of over 500 birds each could differ up to 20 percentiles. Such differences between temporary subflocks are presumably a consequence of the described flock structure.

Observations of colour-ringed individuals (cf. St. Joseph 1979) also demonstrated the existence of permanent subflocks. This may occur when a flock makes a stopover in the area of a 'resident' flock. A large difference in composition between the two may emerge from the differential migration found (see Lambeck 1990). But permanent subflocks with a systematically different age ratio may also coexist for a longer period, as was found on Texel during spring. The two groups of 4000 Brent each used separate feeding areas in the polder and on the mudflats. On all seven sampling dates, the southern subflock consistently comprised more juveniles (on average 12 ± SE 2.3 percentiles; Wilcoxon two sample test, $p < 0.05$). Of 15 colour-ringed individuals six were (almost) exclusively observed in the northern and five in the southern subflock. Exchanges were mostly induced by disturbances.

Permanent subflocks were also found in wintering Canada Geese (Koerner *et al.* 1974). Raveling (1969b) suggested that such entities represent different breeding populations. There is no evidence for permanent associations amongst colour-ringed Brent, however (Ebbinge, pers. comm.). A partitioning of birds related to differences in carrying capacity and quality between feeding areas on the one hand, and the dominance hierarchy in the population on the other seems a more plausible explanation. This mechanism is supposed to accomplish the systematic differences in population composition found between habitats: fewer juveniles in areas with only mudflats and salt marshes (Groningen coast and Balgzand) than in areas with additional inland grasslands (Texel and Schiermonnikoog) (Lambeck 1990).

Results stress the importance of sampling all subflocks present. Knowledge of the distribution of numbers over habitat types is equally essential. Given a higher proportion of juveniles amongst inland feeding geese (see also Round 1982), age counts tend to be positively biased because, in general, such birds are easier to observe than those in tidal habitats.

Seasonal trends in age ratio

Differences in energy requirement and foraging efficiency between adults and juveniles, and a limited food supply probably play a part in the relatively low proportion of juveniles found in the study areas during winter (Lambeck 1990). As a consequence, a 1975/76 population average of 46% that is based mainly on counts in England and some in France (Ogilvie & St. Joseph 1976) will be an exaggeration by 4-5% juveniles, assuming our winter figure to be representative of all Wadden Sea birds (18% of the population in mid-January (Ganzenwerkgroep Nederland 1977)), and the 'English' figure for the rest. This indeed better agrees with a proportion of 40% found in all areas around April 1, when most Brent returned to the Wadden Sea. Because the distribution of birds in 1975/76 was typical of other winters (Ogilvie & St. Joseph 1976, St. Joseph 1982), 'English' age counts presumably overestimate the population average in all good breeding years.

Numbers in autumn were relatively small and the turnover was high (Lambeck 1990). The decline in the age ratio indicates that Brent families depart on average earlier from the main autumn areas in the German/Danish Wadden Sea for the southern wintering areas. Reversely, the low proportion of juveniles amongst the first returning groups shows them to stay there longer (see Lambeck 1990). Although more buffered, some seasonal fluctuation in the age ratio may be expected for the southern areas too. This was confirmed in the Dutch Delta area (own obs.). Hence, the distribution of age counts over the season should be taken into account in all wintering areas.

Moult may contribute to seasonal variation. In captivity, some juvenile Brent are known to have renewed their wing-coverts in late winter (Burton 1961, Ebbinge pers. comm.). In agreement with Burton, no evidence for such an early moult was found in this field study. From early April on the chevron feature faded away in some juveniles. Although additional characteristics such as the lighter coloured ruffled plumage were still available, in May some mistakes will have been made. The impact on the results is presumably small, as illustrated by the very high percentage of juveniles found in some spring flocks. Observation distance, however, should be considerably smaller than in autumn/winter, particularly under less favourable atmospheric conditions.

Brood size assessments

The family archetype as found in this protected Brent population contrasts with the high proportion of disrupted families in hunted geese (Sherwood 1967, Prevett & McInnes 1980). In some species, extra adults might be associated with a family, probably young of the previous year (Sherwood 1967, Raveling 1969a, Prevett & McInnes 1980). The absence in this study will not exclude the possibility as such because 1974 was a non-breeding year for Brent. It was, however, extremely rare in other seasons too (own obs.).

Family sizes are often based on group counts at the moment of landing, when social units split from unrelated birds (Raveling 1968, Prevett & McInnes 1980). This technique is vital in species that lack a conspicuous juvenile plumage. Inland feeding Brent mostly operate as a herd, even at landing, which impairs such counts. Brent feed quite dispersed on intertidal flats and families can most easily be distinguished here. In inland flocks the criterion of temporary segregation restricts the observations to the edges of the flock. Because most of the families are to be found here, a bias due to an unequal distribution of large and small families is unlikely. Large families may, however, attract more attention resulting in an overestimation of the mean brood size. This is presumably not important in the analysis of seasonal or inter-area differences but may affect inter-annual comparisons. This warrants a more detailed study.

As pointed out earlier, the correlation between percentage of juveniles and mean brood size is probably not attributable to differences in breeding success of geographical subpopulations. Considering (1) the positive relation between dominance and the size of a family (Boyd 1953, Hanson 1953, Raveling 1970, Black & Owen 1989b), and (2) the higher demands of juveniles (e.g. Charman 1979), competition for the better feeding areas is supposed to bring larger families together. This correlation complicates the interpretation of the seasonal decline in brood size. An earlier departure of family flocks from the northern Wadden Sea may initially inflate the population average in an area en route. Also habitat may interfere. The high autumn figures were mainly derived from the inland feeding population of Schiermonnikoog. In the same period Ebbinge (pers. comm.) assessed a brood size of 2.9 (*n* = 53) for the intertidal feeders of two adjacent islands (with 30% juveniles). Although the extent may be overrated (cf. Fig. 4), some seasonal decline is likely, however. Qualitative observations suggested an increase in the number of unattached juveniles. This agrees with recent data on Barnacle Geese wintering in Scotland (Black & Owen 1989a). Even in a protected species the chance to lose contact will increase with time. Some extra mortality in juveniles on their first migration is also possible (cf. Owen & Black 1989).

It is unknown when Brent families start to disintegrate. On the basis of a decline in mean brood size, Black & Owen (1989a) claim that 20% of the juvenile Barnacles is unattached in late April and 60% in early June, prior to the departure to the Spitsbergen colonies. However, the majority of marked Lesser Snow Goose *Anser c. caerulescens* families arrived intact in the breeding area (Prevett & McInnes 1980). Brent families were common up to late May, but ties between family members were much looser in spring than in autumn, hampering size assessments. Nevertheless, on some occasions separate flocks of hundreds of birds, comprising 70% and more juveniles, were observed. The few flocks staying behind in England in late spring 1976 had a similar composition (Cadbury & St. Joseph 1978). Moreover, adult Brent became more aggressive towards juvenile birds in spring (see also Black & Owen 1989a). A disintegration of part of the families before the final departure is therefore not unlikely.

The applicability of field counts in population studies

Age counts have shown to be subject to four sources of error. The first, variability related to flock structure, can be sufficiently counteracted by taking large head-to-tail samples such as applied in this study. This is underlined by the consistency within the seasonal pattern in age ratio found. A count of the total number of juveniles requires more time and the final age ratio is subject to errors in both the juvenile and the flock count. This method is to be preferred only when few juveniles are present. The other three sources (season, habitat and geographic position) may easily cause systematic biases. A reliable, weighted population average therefore requires a carefully planned international scheme of field counts.

The limited data showed brood size to be subject to seasonal variation. Other systematic biases, such as a difference between habitat types, are not unlikely, considering the correlation between brood size and percentage of juveniles in a flock. These aspects and the representativeness of size assessments in general (e.g. a possible bias towards larger families) should be studied in more detail.

A proper scheme of brood size and age counts can best be run in conjuction with the annual population census in mid-January, when migratory movements are at a minimum (Ogilvie & St. Joseph 1976). Although the distribution of birds is relatively stable also in April/May and, moreover, largely confined to the Wadden Sea, results have shown spring to be unsuitable.

For Spitsbergen Barnacle Geese, Owen (1982) made a so far unique comparison between survival rates based on either field counts or sightings of colour-ringed birds. Long-term averages were similar, but the variability of annual figures in the former was two times larger. Key factor is the accuracy of the population census. The error of a single count may amount to tens of percents (Owen 1980, Ebbinge 1985). The statistical precision of the sum of all local counts is much better, however (cf. Rappoldt & Kersten 1985). Duplicate population appraisals for Brent differed indeed less than 10% (St. Joseph 1982). Presuming the error in age ratio to be insignificant within the procedure outlined above, the theoretical range for a survival estimate will be twice as large as the one in the census. The advantage of Brent is their high frequency of breeding failures (Ogilvie & St. Joseph 1976), allowing the regular reset of parameters in a population model. Besides, the accuracy of the estimates based on life sightings, as obtained by Owen (1982), may be unattainable in other species: his Barnacle population is small and, moreover, almost confined to one wintering area.

Because death of a marked individual can only be ascertained after some years of being not observed, survival estimates for a specific season will be intrinsically postponed. Compared to field counts, this is a drawback when an active population management is required. Field counts are certainly preferable to conventional ringing programs.

Considering the similarities in family behaviour, conclusions on sampling problems related to flock structure are probably valid in all goose species. Age ratios derived from catches already indicated a non-random distribution for Pinkfoot (Boyd 1956) and Canada Goose (Raveling 1966). By studying marked Barnacle Geese, Black & Owen (1989b) recently arrived at a flock structure similar to that in Brent. Whether season and habitat affect the age ratio in other species too warrants more study. In hunted populations, serious problems may arise in brood size counts. Prevett & McInnes (1980) showed a continuous breakup and reuniting of families under intensive shooting. The proportion of unattached juveniles in midwinter may increase to over 20% (van Impe 1978, Prevett & McInnes 1980). Bartelt (1987) found, additionally, a reduced cohesiveness within families that suffered losses. This may explain the aberrant results of brood counts in White-fronted Geese found by van Impe (1978). Because juveniles are more vulnerable to shooting than adults (cf. Boyd 1956, Higgins *et al.* 1969, Owen 1982), age ratios may also be affected. Since a midwinter census falls within the shooting season, quantitative consequences should be studied.

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REFERENCES

Anderson, D.R. & K.P. Burnham 1976. Population ecology of the mallard. 6. The effect of exploitation on survival. U.S. Fish Wildl. Serv. Res. Publ. 128, Washington.

Anderson, D.R., A.P. Wywialowski & K.P. Burnham 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. Ecology 62:1121-1124.

Bartelt, G.A. 1987. Effects of disturbance and hunting on the behavior of Canada goose family groups in eastcentral Wisconsin. J. Wildl. Manage. 51:517-522.

Black, J.M. & M. Owen 1989a. Parent-offspring relationships in wintering barnacle geese. Anim. Behav. 37:187-198.

Black, J.M. & M. Owen 1989b. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. Anim. Behav. 37:199-209.

Boyd, H. 1953. On encounters between wild White-fronted Geese in winter flocks. Behaviour 5:85-129.

Boyd, H. 1956. Statistics of the British population of the Pink-footed Goose. J. Anim. Ecol. 25:253-273.

Boyd, H. 1959. The composition of goose populations. Ibis 101:441-445.

Boyd, H. 1966. The assessment of the effects of weather upon the breeding success of geese nesting in the arctic. The Statistician 26:171-181.

Boyd, H. & C. Hyslop 1985. Are hunting losses of young Black Ducks (*Anas rubripes*) too high? In: B.J.T. Morgan & P.M. North (eds.), Statistics in Ornithology: 181-195. Springer, Berlin.

Burton, P.J.K. 1958. Brent Geese in Essex. Wildf. Trust Ann. Rep. 9:73-79.

Burton, P.J.K. 1961. Brent Goose age-group counts 1959-60. Wildf. Trust Ann. Rep. 12:113-115.

Cadbury, C.J. & A.K.M. St. Joseph 1978. Brent Geese on the Wash in late spring. Brit. Birds 71:268-269.

Charman, K. 1979. Feeding ecology and energetics of the dark-bellied Brent Goose (*Branta bernicla bernicla*) in Essex and Kent. In: R.L. Jefferies & A.J. Davy (eds.), Ecological processes in coastal environments: 451-465. Blackwell, Oxford.

Conroy, M.J. 1985. Maximum likelihood methods for investigating reporting rates of rings on hunter-shot birds. In: B.J.T. Morgan & P.M. North (eds.), Statistics in Ornithology: 215-241, Springer, Berlin.

Cramp, S. & K.E.L. Simmons (eds.) 1977. The birds of the Western Palearctic, Vol. I. Oxford University Press, Oxford.

Ebbinge, B.S. 1985. Factors determining the population size of arctic-breeding geese, wintering in Western Europe. Ardea 73:121-128.

Ebbinge, B.S. & J.B. van Biezen 1987. Estimation of annual survival rates using resightings of individually marked Barnacle geese (*Branta leucopsis*) wintering in The Netherlands and Northern Germany. Acta Ornithologica 23:101-114.

Ganzenwerkgroep Nederland 1977. Voorlopige resultaten van de ganzentellingen in Nederland in het winterhalfjaar 1975/76 - 2e bericht. Watervogels 2:102-115.

Hanson, H.C 1953. Inter-family dominance in Canada Geese. Auk 70:11-16.

Higgins, K.F., R.L. Linder & P.F. Springer 1969. A comparison of methods used to obtain age ratios of Snow and Canada Geese. J. Wildl. Manage. 33:949-956.

Impe, J. van, 1978. La rupture de la cohesion familiale chez l'oie rieuse, *Anser alifrons albifrons*, dans les quartiers d'hivernage. Le Gerfaut/de Giervalk 68: 651-679.

Kirby, R.E., M.J. Conroy, T.W. Barry & R.H. Kerbes 1986. Survival estimates for North American Atlantic Brant, 1956-75. J. Wildl. Manage. 50:29-32.

Koerner, J.W., T.A. Bookhout & K.E. Bednik 1974. Movements of Canada Geese color-marked near southwestern Lake Erie. J. Wildl. Manage. 38:275-289.

Lakhani, K.M. & I. Newton 1983. Estimating age-specific bird survival rates from recoveries - can it be done? J. Anim. Ecol. 52:83-91.

Lambeck, R.H.D. 1973. Oecologie en beheer van wilde ganzen in Nederland. Doctoral Thesis, Zool. Lab. Rijksuniversiteit Groningen/Centraal Bureau voor de Statistiek, Voorburg.

Lambeck, R.H.D. 1990. Differences in migratory pattern and habitat choice between social classes of the Brent Goose *Branta b. bernicla*. Ardea 78:...-...

Lynch, J.J. & J.R. Singleton 1964. Winter appraisals of annual productivity in geese and other waterbirds. Wildf. Trust Ann. Rep. *15*:114-126.

Martinson, R.K. & J.A. McCann 1966. Proportion recovered goose and brant bands that are reported. J. Wildl. Manage. 30:856-858.

Ogilvie, M.A. & H. Boyd 1976. The numbers of Pink-footed and Greylag Geese wintering in Britain: observations 1969-1975 and predictions 1976-1980. Wildfowl 27:63-75.

Ogilvie, M.A. & A.K.M. St. Joseph 1976. Dark-bellied Brent Geese in Britain and Europe, 1955-76. Brit. Birds 69:422-439.

Owen, M. 1972. Some factors affecting food intake and selection in White-fronted geese. J. Anim. Ecol. 41:79-92.

Owen, M. 1980. Wild geese of the world. Batsford, London.

Owen, M. 1982. Population dynamics of Svalbard Barnacle Geese 1970-1980. Aquila 89:229-247.

Owen, M. & J.M. Black 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. J. Anim. Ecol. 58:603-607.

Owen, M. & M. Norderhaug 1977. Population dynamics of Barnacle Geese *Branta leucopsis* breeding in Svalbard, 1948-1976. Ornis Scand. 8:161-174.

Parkin, D.T. & R. White-Robinson 1985. The effect of age on survival in the Canada Goose, *Branta canadensis*, in Nottinghamshire. In: B.J.T. Morgan & P.M. North (eds.), Statistics in Ornithology: 323-340. Springer, Berlin.

Pollock, K.H. & D.G. Raveling 1982. Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. J. Wildl. Manage. 46:88-98.

Prevett, J.P. & C.D. McInnes 1980. Family and other social groups in Snow Geese. Wildl. Monogr. 71:6-46.

Rappoldt, C., M. Kersten & C. Smit 1985. Errors in large-scale shorebird counts. Ardea 73:13-24.

Raveling, D.G. 1966. Factors affecting age ratios of samples of Canada geese caught with cannon-nets. J. Wildl. Manage. 30:682-691.

Raveling, D.G. 1968. Can counts of groups sizes of Canada Geese reveal population structure? In: R.C. Hine & C. Schoenfeld (eds.), Canada Goose Management: 87-91. Dembar Educ. Res. Services, Madison (USA).

Raveling, D.G. 1969a. Social classes of Canada Geese in winter. J. Wildl. Manage. 33:304-318.

Raveling, D.G. 1969b. Roost sites and flight patterns in Canada Geese in winter. J. Wildl. Manage. 33:319-330.

Raveling, D.G. 1970. Dominance relationships and agonistic behaviour of Canade Geese in winter. Behaviour 37:291-319.

Round, P. 1982. Inland feeding by Brent geese *Branta bernicla* in Sussex, England. Biol. Conserv. 23:15-32.

Sherwood, G.A. 1967. Behavior of family groups of Canada Geese. Trans. N. Am. Wildl. Nat. Res. Conf. 32:340-355.

Sokal, R.R. & F.J. Rohlf 1981. Biometry, 2nd. ed.. Freeman, New York.

St. Joseph, A.K.M. 1979. The seasonal distribution and movements of *Branta bernicla* in Western Europe. In: M. Smart (ed.), Proc. First Techn. Meet. on Western Palearctic Migr. Bird Management: 45-59. IWRB, Slimbridge.

St. Joseph, A.K.M. 1982. Review of the status of *Branta bernicla bernicla*. In: D.A. Scott & M. Smart (eds.), Proc. 2nd Techn. Meet. on Western Palearctic Migr. Bird Management: 16-31. IWRB, Slimbridge.

Sulzbach, D.S. & F. Cooke 1978. Elements of nonrandomness in mass-captured samples of snow geese. J. Wildl. Manage. 42:437-441.

SAMENVATTING

Juveniele Rotganzen zijn in het veld te onderscheiden van overjarige dieren. Sedert de jaren vijftig worden, vooral in Engeland, ieder seizoen gegevens verzameld over zowel het jongenaandeel als de gemiddelde familiegrootte (ouders en jongen leven het eerste jaar in familieverband). In kombinatie met jaarlijkse populatietellingen vormen beide de grondslag voor populatiedynamische berekeningen. Zo'n werkwijze is een alternatief voor of een aanvulling op de traditionele ringstudies, waaraan nogal wat bezwaren kleven. Methodiek en representativiteit van veldbepalingen zijn nader onderzocht op vier pleisterplaatsen in de Nederlandse Waddenzee in het seizoen 1975/76.

Juvenielen bleken het gehele jaar oververtegenwoordigd te zijn in de kop van een troep en adulten in het centrum. Een zekere scheiding tussen families en andere vogels kwam reeds bij de landing tot stand. Willekeurige steekproeven kunnen daardoor aanzienlijk verschillen in jongenpercentage. Dat geldt ook voor de samenstelling van tijdelijke subgroepen. Het jongenpercentage was seizoensafhankelijk; het liep van ca. 50% in de vroege herfst terug tot 25% in de midwinter en steeg weer tot 40% in de lente. Aangezien doorgaans 15-20% van de Rotganzen in het totale Waddengebied overwintert, overschatten Engelse cijfers het populatiegemiddelde (in 1975/76 met 4-5%). Er zijn aanwijzingen dat ook in de zuidelijker overwinteringsgebieden het jongenpercentage enige seizoensvariatie vertoont, hetgeen daar het tijdstip van bepaling eveneens van belang maakt. De differentiële migratie kan verder leiden tot een flink verschil in samenstelling tussen een groep op doorreis en de "plaatselijke" vogels. In nawinter/voorjaar bestonden er systematische verschillen in jongenpercentage tussen de studiegebieden (zie verder in volgend Ardea artikel). Bepalingen uit één gebied zijn dus vaak niet representatief. In grotere pleisterplaatsen kunnen bovendien subpopulaties opereren, met onderling weinig uitwisseling en een permanent verschil in leeftijdsamenstelling.

Het aantal jongen per familie varieerde in 1975/76 van 1 tot 7, met in de herfst een modus van 4. De gemiddelde grootte daalde van 4 tot 3.2 jongen. De beperkte gegevens laten een positieve relatie tussen jongenpercentage en familiegrootte zien. Gebiedsverschillen kunnen niet worden uitgesloten. De variaties zijn echter kleiner dan bij het jongenpercentage.

Het voorjaar is ongeschikt voor grootscheepse bepalingen, daar een begin van rui de waarnemingsafstand verkleint, terwijl Rotganzen zich dan juist concentreren op minder toegankelijke, uitgestrekte kwelders en slikken. Bovendien worden door gedragsveranderingen ook familiebepalingen bemoeilijkt. Een koppeling met de jaarlijkse midwintertellingen lijkt het meest praktisch. De voorwaarden worden nader besproken, evenals de beperkingen van het op deze wijze verkregen populatiemodel. De resultaten gelden waarschijnlijk ook voor andere soorten. Meer onderzoek is nodig naar de gevolgen van jacht, met name op de familiegrootte.