



British Ecological Society

Reproductive Performance and Assortative Pairing in Relation to Age in Barnacle Geese

Author(s): Jeffrey M. Black and Myrfin Owen

Source: *Journal of Animal Ecology*, Vol. 64, No. 2 (Mar., 1995), pp. 234-244

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/5758>

Accessed: 04/11/2009 07:39

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=briteco>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*.

<http://www.jstor.org>

Reproductive performance and assortative pairing in relation to age in barnacle geese

JEFFREY M. BLACK and MYRFYN OWEN

The Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK

Summary

1. The pattern of reproductive success (RS) in barnacle geese varied significantly as a function of age. RS continued to increase through the sixth year and peaked in the eleventh. It declined between the eleventh and fifteenth year.
2. The decline in RS in old age was not, as suggested by other workers, due to loss of mate and re-pairing with a young bird; individuals that retained their mates also had diminishing RS in the later years.
3. Low RS in the early years was attributable to the female. We suggest that this is because of inexperience in food and feeding area selection, which affects the build-up of body reserves in preparation for nesting and hence breeding potential. Low RS in the later years was, on the other hand, attributable to the male. We suggest that this is caused by a decline in fighting ability which determines both the acquisition of optimal feeding sites for the female and the ability to acquire and defend a nesting site.
4. At whatever age they re-paired, geese tended to choose replacement mates that were similar in age to themselves. This was despite the fact that, at all times, birds from the young, unpaired cohort (1–2 years) were considerably more numerous than older unpaired geese.
5. We argue that pairing with a familiar individual is advantageous both from the point of view of partner compatibility and of familiarity with the feeding and nesting habitat.

Key-words: age, assortative mating, barnacle goose, *Branta leucopsis*, reproductive success.

Journal of Animal Ecology (1995) **64**, 234–244

Introduction

When describing the pattern of reproductive output over an animal's lifetime, authors often attribute the improvement in performance to the combined effect of experience and age, and any decline in performance in later life to the wear and tear of competing for resources and of breeding (Clutton-Brock 1988; Newton 1989). Under a stable environmental situation successful breeding has been attributed to numerous phenotypic and behavioural characteristics of one sex or the other, e.g. age, experience, dominance, etc. However, in birds, the majority of species are socially monogamous, sharing their reproductive experience with a member of the opposite sex (Lack 1968) so that taking account of only one member of the pair when explaining reproductive performance is presenting only half of the picture. For example, if large females produce most offspring, high reproductive rates may be attributed to large female size; however, if large

females pair with males with the best territories perhaps the females' success is attributable to the males' qualities, which enable the acquisition of good territories.

In this paper we examine the interplay between partner characteristics in terms of the female + male types that combine to make a productive team (e.g. Coulson 1966; Mills 1973; Coulson & Thomas 1983; Perrins & McCleery 1985; Marzluff & Balda 1988; McCleery & Perrins 1988; Newton 1988; Ollason & Dunnet 1988; Scott 1988). Considering both sexes concurrently is particularly relevant for geese since pair members maintain constant association (Black & Owen 1988) and pair bonds generally persist for life (Owen, Black & Liber 1988; Raveling 1988).

Recent analyses of long-term reproductive success (RS) in lesser snow geese *Anser caerulescens caerulescens* and barnacle geese *Branta leucopsis* have indicated that gosling recruitment increases in the early years, peaks between 7 and 9 years, and then appar-

ently declines in the later years of life (Ratcliffe, Rockwell & Cooke 1988; Owen & Black 1989a). However, since few older birds remained in the data sets, both studies were less certain about the trend in later years than in the early improvement. In the early years, clutch size increases up until age 4–5 years in barnacle geese (Forsslund & Larsson 1992) and to 5–6 years in snow geese (Rockwell *et al.* 1993).

Apart from enhanced physical ability, the increase in the early years, which is common across many species, has been linked with increased effort and improved access to resources (Hamann & Cooke 1987; Partridge 1989). The reasons for the decline in reproductive performance in later years, especially in birds (Clutton-Brock 1984; Newton 1989), are less well understood. There are three possible areas of explanation for apparent old-age decline: biological features, environmental features, and other qualities in the animals' life history. The lesser snow goose workers favoured two of the three considered alternatives, a biological and an environmental feature: the effects of senescence on females and the degradation of the older birds' habitat (Rockwell *et al.* 1993). They were unable to test the third possibility, a life-history feature, concerning the replacement of mates when first partners disappear or die.

Owen *et al.* (1988) described how the chances of successful breeding were reduced after loss of the first mate and re-pairing with a second. The proportion of birds that bred successfully (average for all ages) in the first (8%) and second year (16%) after re-pairing with a new mate was lower than in longer-established pairs (21%). With advancing age, individuals that lose mates are presented with a choice of potential partners from a pool of younger, less experienced geese and fewer older birds whose loss of mate coincides. Without data on mate choice, workers have understandably assumed that old birds which have lost mates preponderantly re-pair with birds from the young, unpaired cohort. Re-pairing with a younger goose may mean that the new pair will experience lower rates of fitness until the younger mate gains in experience and ability (Forsslund & Larsson 1991).

Since the average length of the first pair-bonds in barnacle geese is about 5 years (Owen *et al.* 1988), the old-age decline in RS may result from a progressive number of mate changes in the population (Rockwell *et al.* 1993). We explored this possibility by comparing the ages of partners in first and subsequent pairings. We also investigated whether the choice of mates is influenced by the size and availability of the cohort of unpaired young birds in the population. Our first exercise, however, was to re-evaluate the effect of age on gosling recruitment for both sexes throughout their life span.

Methods

Between 1973 and 1990, 5890 of the barnacle geese that breed in Svalbard, Spitsbergen, were marked indi-

vidually with an engraved plastic leg band on one leg and a metal ring on the other; they were either rounded up during the moult or caught with rocket nets. When in the hand, the birds were sexed by cloacal examination and aged, by plumage characteristics, as goslings, yearlings or adults. Birds ringed as breeding adults were assigned a minimum age, assumed to be from 1 July prior to banding.

The geese spend the autumn and winter on the Solway Firth, UK (7 months), the spring in Helgeland, Norway (1 month) and the summer in Svalbard (4 months). The journey is about 3000 km from one end of their range to the other.

The population has risen from 5100 individuals in 1973 to 12 100 in 1990, and in most years between 10 and 25% of these have been individually identifiable (ringed). The leg bands are readable with a telescope at up to 250 m. Because in winter the birds use the managed fields that are bordered by numerous blinds and observation towers at The Wildfowl & Wetlands Trust's Caerlaverock reserve, we have been able to resight at least 95% of the marked birds in most years (Owen & Black 1989a). The geese were also observed in Helgeland ($n = 13$ years) and Svalbard ($n = 11$ years). Most bands were seen between 3 and 25 times (mean = 8 times) each year. In addition to the code on the ring, we recorded the identity of the mate and goslings and whether banded or unbanded (see Black & Owen 1989a,b for details). The date of pair formation with a particular partner was taken as the first of multiple sightings of the pair. The end of their partnership was attributed to the last date they were recorded together (Owen *et al.* 1988).

Geese enter into a number of trial partnerships prior to choosing a long-term mate (Choudhury & Black 1993). To reduce the possibility of accepting trial partners as true mates, we excluded pairings lasting less than 2 months and included only pairs that went to or returned from the breeding grounds as a pair. Our method of determining first and last dates of a partnership was influenced by the timing of first sightings in each winter season. We assumed that pairs seen for the first time between October and December had come back from the breeding grounds together: in other words, that they had had the opportunity to reproduce that year. The first opportunity for reproduction in pairs that were first seen between January and May, on the other hand, was assumed to be the following summer. This method is necessarily conservative and provides a minimum value for pair durations and reproductive success.

Goslings and parents maintain close and continuous proximity each day throughout the first months of the goslings' life (Black & Owen 1989a). On each sighting we counted the number of goslings that were with each pair. Three measures of fecundity were used. (i) Gosling recruitment – the number of goslings (ranging from 0 to 6) that survived the autumn migration (minimum 3 months of age). This measure

includes partial brood loss after fledging and on migration (Owen & Black 1989b). This is a combined measure, including an element of non- or failed breeding and an element of family size. (ii) Brood success – the proportion of birds that had reared at least one gosling to the age of 3 months, i.e. to arrival on the wintering grounds. This measure allows comparisons between those that succeed versus those that fail or do not attempt to breed. (iii) Brood size – the number of goslings in the brood (i.e. ranging from 1 to 6). This is a relative measure of success that excludes failed and non-breeders. Failed breeding attempts and partial brood loss in this species have been attributed to severe climatic conditions, parental quality and poor feeding opportunity prior to the first migration (Prop, van Eerden & Drent 1984; Owen & Black 1989b, 1991b). Once goslings reach the wintering grounds they have an 83% chance of surviving to 2 years, when they enter the population of potential breeders (Owen 1984).

Since only one in 10 birds died each year (Owen 1984; Owen & Black 1989a), data from an individual could be included each year throughout its life, resulting in a significant interaction between age and year. In order to limit this problem we chose one record at random from each bird's lifetime (SAS Institute 1990). Whilst this technique is appropriate for use in statistical tests, we used pooled data for the plotting exercises as these provided an accurate measure of the pattern of change in RS over time. To augment samples for older birds (i.e. ≥ 9 years) we included a sample of minimum-aged birds (consistent with the methods of Rockwell *et al.* 1993). A composite of

individuals was included in age-class 15+ for use in the ANOVA, and a cut-off of 16 years was used for plotting. To detect the precise pattern of change in reproductive performance in the middle and older ages we used two subsets of the data (i.e. 6–11 years, 11–15+ years). All reproductive records were included in this analysis because multiple records from the same individuals at different ages were less frequent within the shorter span of years. Year was included as a covariate in all analyses to control for possible contamination of age effects by annual variation (Owen & Black 1989b; Rockwell *et al.* 1993). Non-significant interaction terms between age and year were removed from the final models. We calculated least square means, adjusting for the effects of year and unequal sample sizes, to compare specific age-classes. Curves were fitted to plotted points and linear or quadratic contrasts were computed. All exercises were performed with the SAS Procedure GLM (SAS Institute 1990), unless otherwise stated.

Results

PATTERN OF REPRODUCTIVE SUCCESS IN MALES AND FEMALES

Age significantly affected gosling recruitment and brood success but not brood size, after controlling for year (Table 1). Figure 1a,b shows that the overall reproductive rates increased with age to a peak in the tenth or eleventh year, after which they declined to moderate levels (Table 2). The significant linear effect between 2 and 11 years was reflected by an overall

Table 1. Analysis of variance test of reproductive success for 1062 female and 1029 male barnacle geese as a function of their ages, 2–15 years*

Reproductive measure	Females				Males		
	df	SS‡	F	P	SS‡	F	P
Gosling recruitment							
Year 1977–90	13	21.54	2.69	0.001	22.23	3.11	<<0.001
Age 2–15+ years†	13	21.08	2.63	0.001	21.60	3.02	<<0.001
Linear 2–11 years	1	7.28	11.33	<0.001	15.97	23.69	<<0.001
Brood success							
Year 1977–90	13	4.24	2.72	<0.001	2.78	1.58	0.084
Age 2–15+ years†	13	3.70	2.37	0.004	6.30	3.59	<<0.001
Linear 2–11 years	1	0.83	6.87	0.009	3.70	27.27	<<0.001
Brood size							
Year§	10	15.67	1.48	0.145	10.25	0.99	0.453
Age 2–15+ years†	13	12.33	0.89	0.560	10.47	0.78	0.653
Linear 2–11 years	1	2.35	2.10	0.148	2.42	2.52	0.113

*Analyses include one reproductive record per bird; using the RANDOM feature in the GLM procedure (SAS Institute 1990). The non-significant interaction term, year \times age, was removed in each analysis.

†Age class 15+ is a composite of individuals 15 years and older. Only one record per bird was included in the analysis.

‡Partial (Type III) SS from GLM procedure (SAS Institute 1990).

§Years with fewer than 25 recorded broods before random selections were excluded, leaving 1978, 1980–90.

Note: Gosling recruitment and brood success sample sizes for ages 2–15+ years: females 176, 124, 105, 67, 39, 29, 33, 157, 132, 64, 46, 30, 28, 32; males 160, 110, 104, 48, 36, 31, 24, 192, 120, 74, 52, 31, 20, 27. Brood size sample sizes for ages 2–15+ years: females 19, 19, 58, 17, 52, 23, 104, 69, 60, 47, 28, 8, 13, 13; males 19, 12, 49, 15, 29, 24, 104, 87, 61, 49, 36, 10, 11, 17.

Table 2. Analysis of variance tests of reproductive success for barnacle geese in middle and older age classes*

Reproductive measure	Females				Males		
	df	SS‡	F	P	SS‡	F	P
Gosling recruitment							
Year 1980–90	10	41.07	4.88	<<0.001	102.11	11.84	<<0.001
Age 6–11†	5	1.90	1.12	0.813§	2.84	0.66	0.655
Linear 6–11	1	0.46	0.54	0.462	1.09	1.26	0.261
Year 1983–90	7	12.54	2.88	0.006	14.80	3.17	0.003
Age 11–15+†	4	5.43	2.19	0.069	4.62	1.73	0.141
Linear 11–15+	1	3.52	5.67	0.017	2.41	3.61	0.058
Brood success							
Year 1980–90	10	10.14	6.39	<<0.001	22.58	13.65	<0.001
Age 6–11†	5	0.28	0.35	0.880	1.14	1.38	0.227
Linear 6–11	1	0.46	2.91	0.088¶	0.56	3.39	0.066
Year 1983–90	7	4.06	3.92	<0.001	4.39	4.05	<<0.001
Age 11–15+†	4	0.41	0.69	0.601	1.05	1.70	0.148
Linear 11–15+	1	0.18	1.19	0.277	0.41	2.63	0.105
Brood size							
Year 1980–90	10	29.68	2.58	<0.005	14.21	1.36	0.194
Age 6–11	5	8.40	1.46	0.202	1.58	0.30	0.912
Linear 6–11	1	3.05	2.64	0.104	0.85	0.82	0.366
Year 1983–90	7	7.92	1.22	0.292	7.10	1.08	0.375
Age 11–15+†	4	8.11	2.19	0.072	1.65	0.44	0.780
Linear 11–15+	1	5.91	6.38	0.012	0.27	0.29	0.591

* Analyses include all reproductive records. The non-significant interaction term, year × age, was removed in each analysis.

† Age class 15+ is a composite of individuals 15 years and older. Only one record per bird was included in the analysis.

‡ Partial (Type III) SS from GLM procedure (SAS Institute 1990).

§ Age × year interaction was significant, SS = 9.26, df = 32, $F = 1.82$, $P = 0.003$.

¶ Age × year interaction was significant, SS = 14.66, df = 32, $F = 1.62$, $P = 0.015$.

Note: sample sizes for gosling recruitment and brood success: ages 6–11 years (1980–90), respectively, for females 288, 258, 917, 811, 500, 354; males 240, 235, 908, 821, 493, 375; ages 11–15 years (1983–90), respectively, for females 354, 261, 188, 144, 107; males 375, 267, 201, 137, 133. Brood size sample sizes: ages 6–11 years (1980–90) for females 64, 45, 214, 166, 93, 84; males 54, 46, 214, 167, 105, 93; ages 11–15 years (1983–90) for females 84, 54, 18, 22, 20; males 93, 63, 19, 20, 29.

Table 3. Analysis of variance test of reproductive success for 1526 barnacle goose pairs as a function of the sum of the partners' ages while controlling for year. Data include one record per pair between 1977 and 1990. The combined age index ranged between 2 (young+young partners) to 6 (old+old partners)

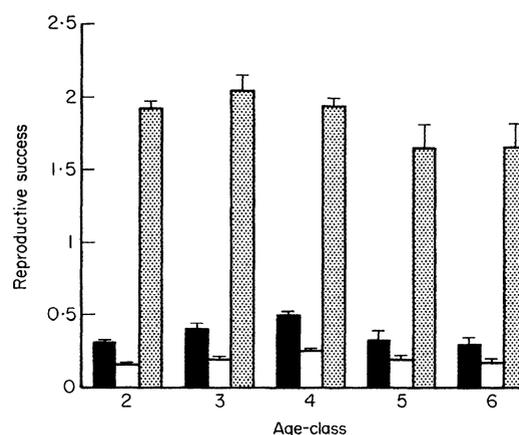
Reproductive measure	df	SS*	F	P
Gosling recruitment				
Year 1977–90	13	67.68	7.77	<<0.001
Combined age†	4	10.56	3.94	<0.004
Brood success				
Year 1977–90	13	12.08	6.68	<<0.001
Combined age†	4	2.67	4.81	<0.001
Brood size‡				
Year 1977–90	13	41.65	3.14	<<0.001
Combined age†	4	3.68	0.90	0.463

*Partial (Type III) SS from GLM procedure (SAS Institute 1990).

†The non-significant interaction term, year × combined age, was removed.

‡Based on data from 740 pairs.

Note: Sample sizes for gosling recruitment and brood success: combined ages of partners (1977–90) 1002, 143, 327, 26, 28; brood size 376, 75, 257, 19, 13.

**Fig. 2.** The distribution of gosling recruitment (■), brood success (□) and brood size (▨) with respect to the combined age of partners (quadratic curve test, gosling recruitment – quadratic contrast, SS = 10.10, $F = 13.47$, $df = 1$, $P < 0.001$; brood success – quadratic contrast, SS = 2.03, $df = 1$, $F = 13.85$, $P < 0.001$; brood size – quadratic contrast, SS = 2.03, $df = 1$, $F = 13.85$, $P < 0.001$). Values are presented in least square means and standard errors are indicated. Sample sizes of pooled gosling recruitment and brood success records for the index of combined ages, ranging between 2 and 6, were 3331, 552, 2045, 210, 270; brood size records were 571, 106, 497, 42, 43.

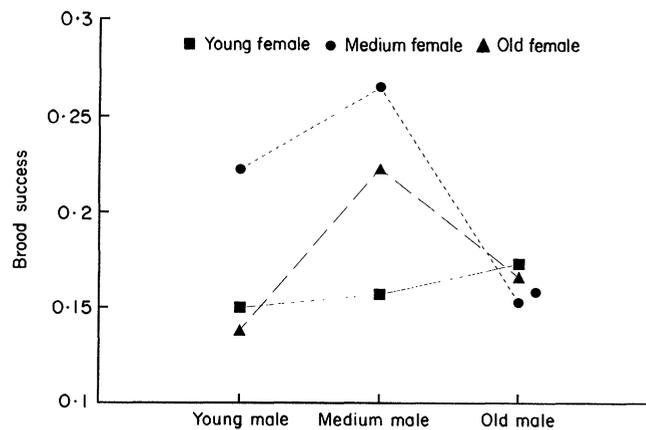


Fig. 3. The pattern of brood success in relation to the mates' ages. Sample sizes and (SE) of pooled male-female age class comparisons: young-young 3331 (0.01), young-middle 290 (0.02), young-old 84 (0.04), middle-young 262 (0.02), middle-middle 1878 (0.01), middle-old 112 (0.04), old-young 83 (0.04), old-middle 98 (0.04), old-old 270 (0.02).

formance (Fig. 3). These plots indicated that the highest brood success was achieved by middle-aged females that were paired with males also in their middle years. Middle-aged females also performed well when paired with young males. Regardless of their mates' ages, young females and old males achieved a consistent, low mean brood success value of around 0.15–0.18. Young and middle-aged males achieved peak performance when paired with middle-aged females, whereas the RS even of middle-aged females was very low when they were paired with old males. The reproductive performance of old females was substantially higher when paired with middle-aged males.

POTENTIAL CAUSES OF APPARENT SENESCENCE

This section tests three potential explanations for the apparent downward trend in RS in later years: (i) the old-age decline in RS in the population may be caused by an increasing number of older birds re-pairing with younger birds that are known to be poor breeders; (ii) declining RS may simply reflect the frequency of re-pairing in the population, since RS is temporarily lower in new pairs; and (iii) the decline may be linked to a real decline in some fitness parameter which controls RS. If (i) is the correct case, we would predict that there would be a disparity in the age of partners that re-pair after the loss of first mates. If (ii) is correct individuals that do not re-pair should have sustained success beyond middle-age. If both these hypotheses are rejected, we would conclude that RS decline is due to a decline in fitness, explanation (iii).

Age correlations between partners

The geese in this data set paired for the first time between the first and fourth year of age. The majority of geese tended to choose mates that were born in the same year. This might be expected, since males and females tend to pair at the same age. However, the

probability was extremely high; only five cases in the sample of the 113 known-aged, first-time pairings consisted of different-aged partners, all involving 2 and 3 year olds (Fig. 4a). The probability of the choice of a mate from the same cohort is difficult to estimate, since the number of unpaired birds of different ages in the population at any one time is not known. However, since more than half the sample did not pair until they were more than 2 years old, when they would also have the choice of the next cohort as well as their own, the degree of choice is remarkable.

After loss of the first partner, re-pairing occurred between 2 and 19 years of age. Although ages did not match as closely as in first-time pairings, partner ages were significantly correlated (Fig. 4b,c). The comparison was more revealing using the larger minimum-age data set ($F = 23.7$, $df = 235$, $R^2 = 0.09$, $P < 0.001$); partners were the same age in 46% of 236 re-pairings. The oldest case of re-pairing between two birds of the same age occurred in their twelfth year (two cases). The oldest, similar-aged re-pairing was between a 13- and 14-year-old male and female, respectively. When ages did not match ($n = 128$) the older sex was only slightly and not significantly skewed towards females (57% older female, 43% older male). The greatest disparity in ages of replacement mates was 15 years, in two cases with the male and in two with the female as the older sex.

Of 39 re-pairings in which the age and pair histories were known, in 21 cases the replacement mate was a younger bird that had not been paired previously (Fig. 4b). Based on the population demographics for each year (Owen & Black 1989a,b, unpublished data) we checked the relative 'abundance' of young unpaired birds (1–3 year olds) in the population to see if the pairing opportunity affected the choice of either type of mate, a bird that had had no previous mates (inexperienced) vs. a bird whose loss of mate coincided (experienced). In the years when re-pairing occurred there were between 976 and 2331 unpaired individuals available, which means that one in 3.2–9.5 birds in the

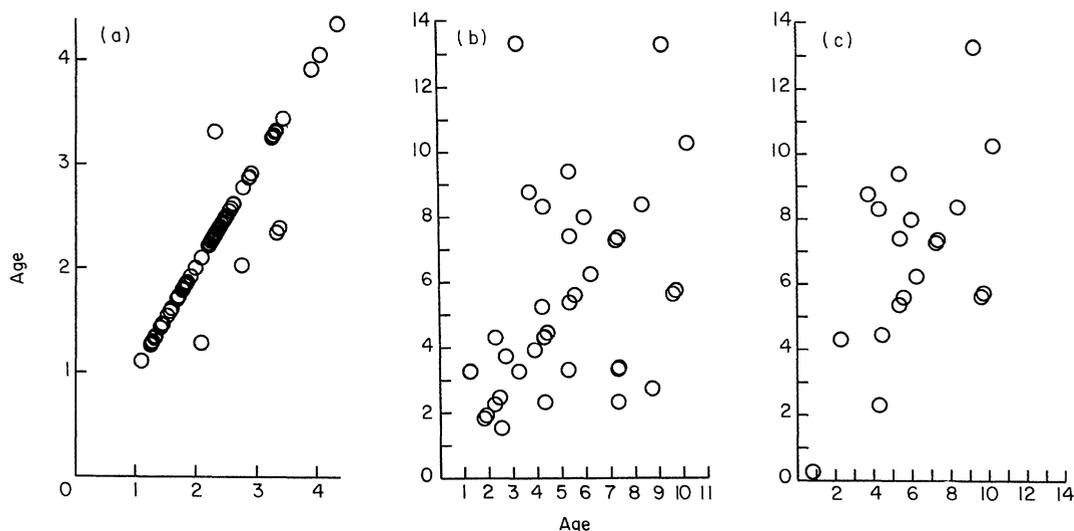


Fig. 4. The age of partners at the time of pairing (in years). (a) First-time pairings: both partners had no previous mates ($F = 1045.7$, $df = 111$, $R^2 = 0.90$, $P < 0.001$). (b) Second plus pairings: at least one partner had one or more previous mates ($F = 8.93$, $df = 37$, $R^2 = 0.19$, $P = 0.005$). (c) Second plus pairings: both partners had one or more previous mates ($F = 3.82$, $df = 16$, $R^2 = 0.19$, $P = 0.068$).

population was a young, unpaired bird (see footnotes to Table 4).

The probability of choosing an inexperienced vs. an experienced partner was not influenced by either measure of the unpaired birds' abundance (Kruskal-Wallis test using total available, $\chi^2 = 1.63$, $df = 1$, $P = 0.202$; abundance ratio, $\chi^2 = 2.43$, $df = 1$, $P = 0.119$).

On searching the backgrounds of the 18 pairs that chose experienced mates, we discovered that 14 pairs had previously associated with each other (Table 4; binomial test, $P = 0.015$). In these cases the partners had been seen or captured on the same coastline in Spitsbergen prior to pairing (Nordenskiöldkysten). This finding is consistent with our previous studies which reported that the majority of first-time pairings were of partners that were from the same natal areas (Owen *et al.* 1988) and that this was largely due to active choice of familiar individuals (Choudhury & Black, 1994). In the current study the geese could have become acquainted in the first or subsequent summers on Spitsbergen; both birds in eight of the 14 pairs were caught in the same natal area in their first or second summer.

Reproductive success excluding re-pairing

To test whether re-pairing frequency was responsible for the declines in reproductive performance, we checked the RS pattern for pairs that remained together over 1–14 years, thus excluding the effect of re-pairing. Figure 5 shows that the pattern of brood success by these stable pairs mirrors that of the previous sample (Fig. 1) which included birds which had re-paired (Spearman rank correlation, comparing RS over 2–14 years of life with 2–14 years of pair life:

$r^s = 0.719$, $n = 14$, $P < 0.01$). The pattern shows that RS increased from 1 to 6 years and peaked in the eighth year, after which it declined to the lowest value in the twelfth year. Therefore, the pattern of RS change shown in Fig. 1 is apparently not due to the occurrence of re-pairing in middle to older age classes.

Discussion

We have shown that reproductive performance of male and female barnacle geese continues to improve in the first 6 years and declines again after age 11. Reproductive performance for most individuals, therefore, could improve throughout their lives, since the average life span in these geese is about 9 years (Owen & Black 1989a). For comparison, fledging success in short-tailed shearwaters *Puffinus tenuirostris*, which also live for an average of 9 years, peaks at age 10 (Wooller *et al.* 1989). Bewick's swans *Cygnus bewickii* live for 10 years on average and their breeding success peaks at age 11 (Scott 1988). Fulmars *Fulmarus glacialis* live more than 30 years and their peak RS is at 12–14 years (Ollason & Dunnet 1988).

Our study confirmed the existence of a decline in reproductive performance in older-aged individuals after the eleventh year. In lesser snow geese (Ratcliffe *et al.* 1988; Rockwell *et al.* 1993) and Hawaiian geese *Branta sandvicensis* (Kear & Berger 1980) the decline occurs after 6–7 and 5 years, respectively. The usual explanation for old-age decline in RS is that individuals tire from the wear and tear of breeding and competing (Clutton-Brock 1984; Newton 1989). We explored an alternative explanation: that the decline in the mean values may be caused by an increasing number of older birds re-pairing with younger birds that are poor breeders, or that declining reproductive

Table 4. Case histories of re-pairing for 18 known-aged male and female geese, and the number of young unpaired birds in the population after the loss of the previous mate

Pair	Mate number M/F	Age at re-pairing (years) M/F	Date of re-pairing	Time taken to re-pair (months) M/F	Cause of previous split†	Place of re-pairing	Number and ratio of young, unpaired geese‡	Same rearing area?
AGLCPR	3/2	8/4	Oct 1980	3/1	MD/MD	Spitsbergen	1942 1 in 3·6	No
LIYLIV	2/2	5/5	Jun 1981	4/6	MD/MD	Scotland	1830 1 in 3·8	Yes
*DYDTP	2/2	6/6	Feb 1982	16/3	UPD/SPL	Scotland	1721 1 in 4·3	Yes
CLVDIP	3/2	7/7	Nov 1983	0§/7	MD/UNK	Scotland	995 1 in 7·8	Yes
*DYDUK	3/2	7/7	Oct 1983	8/23	MD/MD	Spitsbergen	1127 1 in 6·9	Yes
\$PHXJU	2/2	4/4	Dec 1984	1/0	UNK/UPD	Scotland	1056 1 in 7·4	Yes
CZPCRP	2/2	8/8	Nov 1984	5/6	UPD/UPD	Scotland	900 1 in 8·6	Yes
YRPYFK	2/2	6/6	Sep 1984	7/6	UPD/UNK	Spitsbergen	1204 1 in 6·5	No
*YM*SF	3/2	9/4	Apr 1984	7/5	MD/MD	Scotland	800 1 in 9·7	Yes
DUZYLC	2/2	8/6	Jun 1984	4/2	UPD/UNK	Spitsbergen	1204 1 in 6·5	No
>CC\$JC	2/2	9/5	Nov 1985	5/1	UPD/UNK	Scotland	2355 1 in 4·0	Yes
YRUXCF	2/2	7/5	Nov 1985	7/9	MD/MD	Spitsbergen	2690 1 in 3·5	No
\$FAHFC	2/3	6/10	Mar 1986	11/1	MD/MD	Scotland	1909 1 in 4·9	Yes
XBICRP	2/3	6/10	Feb 1986	8/2	UPD/MD	Scotland	1717 1 in 5·4	Yes
DNG *SF	4/3	13/9	Oct 1989	7/6	MD/MD	Spitsbergen	1804 1 in 6·0	Yes
*PSEND	3/2	4/2	Oct 1990	8/6	MD/SPL	Spitsbergen	1276 1 in 8·3	Yes
NJF*YN	2/3	2/4	Oct 1990	8/6	SPL/MD	Spitsbergen	1276 1 in 8·3	Yes
XCCXAH	2/2	10/10	Oct 1990	5/8	UNK/UNK	Spitsbergen	1276 1 in 8·3	Yes

†Codes for status of previous mate: SPL, split with previous mate; MD, mate disappeared/died; UPD, seen as unpaired prior to re-pairing, hence could have split with previous mate or the mate could have died, mate was unbanded; UNK, unknown status as mate was unbanded.

‡Calculated from data in Owen *et al.* (1988) (e.g. the timing of pairing for young birds is 8% by age 15 months, 19·2% by 21 months, 30·1% by 27 months and 42·7% in later months) and unpublished demographic data.

§Mates overlapped in summer months, i.e. one male and two females. This male, CLV, had three different polygynous trios in his 11-year lifetime—a rare occurrence.

rates simply reflect the frequency of re-pairing in the population. This second possibility could occur in this population, since it has been established that RS is low for the first 2 years after re-pairing (Owen *et al.* 1988; also see Coulson & Thomas 1983; Scott 1988; Wooller *et al.* 1989).

We conclude that the old-age decline of RS in geese is not caused by re-pairing with young mates or with re-pairing frequency for three reasons. First, geese tended to choose replacement mates that were the same age as themselves, despite the larger availability of younger unpaired birds. Secondly, the analysis of the combined-age index of partners showed the same

pattern of increasing RS in early years, peaking in the middle years, followed by a decline in the later years (Fig. 2). Thirdly, we found this same quadratic pattern, including the decline in old age, for geese that kept the same mate throughout life (Fig. 5).

We therefore suggest that the decline in reproductive success in old age, is indeed due to the loss of some fitness measure that affects the likelihood of breeding, e.g. hatching success or brood success, or more likely a combination of these. From Fig. 3, it is clear that the lower RS in early life can largely be attributed to the female (middle-aged females breed well even with young males), whereas the decline in

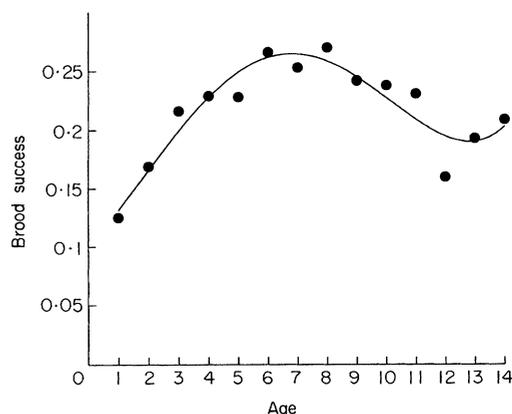


Fig. 5. The distribution of brood success for 1526 pairs with respect to number of years with the same mate (quadratic contrast, $SS = 2.06$, $df = 1$, $F = 14.04$, $P < 0.001$). Sample sizes and (SE) of pooled brood success records for pairs that were together for between 1 and 14 years: 1555 (0.01), 1346 (0.01), 952 (0.01), 775 (0.01), 590 (0.02), 327 (0.02), 265 (0.02), 198 (0.03), 158 (0.03), 100 (0.04), 60 (0.05), 43 (0.06), 26 (0.08), 13 (0.11).

later life is due to a decline in male fitness (even middle-aged females perform poorly with old mates).

Underlying evolutionary explanations for old-age decline were reviewed by Partridge (1989) and Lessells (1992). These include two hypotheses entitled mutation accumulation and negative genetic correlations (also referred to as antagonistic pleiotropy). The phenotypic manifestation of ageing in males may be physiological. For example, old ganders may fail to reproduce well due to inadequate sperm. However, evidence from captive geese suggests that this is not the case (Kear & Berger 1980). A more plausible reason for low RS in old males may be that their ability to compete for some limited resource deteriorates with age. Male geese spend the better part of their non-feeding time scanning their surroundings and protecting their female and offspring by warding off neighbours that get closer than about 2 m (Black & Owen 1988, 1989a,b). Female feeding performance during the spring fattening period has been linked with ganders' aggressiveness (Teunissen, Spaans & Drent 1985; Lamprecht 1989). During fights, males can sustain blows from the enlarged bone on the carpometacarpus (i.e. the wrist). On the breeding grounds, while protecting nests or goslings, ganders may also suffer wounds in encounters with large gulls and foxes. We have noticed that injured geese are usually unable to maintain pair bonds and that their social status declines to the lowest level (e.g. lower than young unpaired geese). Such wear and tear linked to a lifetime of physical activity has also been attributed to male black grouse *Tetrao tetrix*, red deer *Cervus elaphus* and northern elephant seals *Mirounga angustirostris* (de Vos 1983; Clutton-Brock, Guinness & Albon 1982; le Boeuf & Reiter 1988).

Replacement mates were not always of similar age. About 33% of the 113 re-pairings in Fig. 4B were

between partners whose ages differed by more than 2 years. In addition to detecting the consequences of choosing an older or younger mate, the comparison of success in relation to the partners' age may hold some clues about the variation in RS. Figure 3 indicates that lowest reproductive rates, regardless of the mates' age, occur in young females and old males. The proximate mechanisms behind these could be physiological and/or behavioural. We know that clutch size in this species is smallest for females younger than 5–6 years (c. 3 eggs), after which it peaks (c. 4.2 eggs) and probably remains constant for the rest of life (Forslund & Larsson 1992), therefore initial low values of recruitment in this study may be related to the initial clutch size. Young birds may lay smaller clutches due to physical immaturity and/or reduced feeding opportunity (Perrins & Birkhead 1983). Smaller clutches in 2-year-old geese can be attributed solely to immaturity. In captivity, where food is not limiting, clutch size is still small in Hawaiian geese and barnacle geese (Kear & Berger 1980; Owen 1980).

Lower RS in young females, compared to older more experienced birds, could be due to lower intake rates or inability to select high-quality vegetation during the fattening and incubation periods. During the spring fattening period we found that the geese adjusted foraging routines and pathways, thus improving foraging performance on subsequent visits within and between seasons (J. Prop and J.M. Black, unpublished data). During nest pauses females feed on their own and males stand guard at the nest. Prop *et al.* (1984) show that hatching success is positively correlated with female feeding performance during the incubation period (see also Aldrich & Raveling 1983). For geese, high intake rates on vegetation that is rich in nutrients and readily digestible lead to larger fat reserves (Prop & Deerenberg 1991), which enable larger clutches (Ankney & MacInnes 1978) and greater RS (Teunissen *et al.* 1985).

The worst combination of partners in terms of RS is between old females and young males (Fig. 3). If all young males were poor breeders we would attribute the shortfall to an inability to protect the female and to inadequately developed foraging routines (see above). Or perhaps young males have low fertility rates in the early years, as was found in the Hawaiian goose (Kear & Berger 1980). If all old females were poor breeders we might argue that there may be a reduction in egg and/or clutch size after age 11, as was found for the Hawaiian goose (Kear & Berger 1980). However, neither sex appears wholly responsible for the shortfall since combinations with middle-aged partners can be very productive. The interplay between the potential limiting factors is apparently compounded in this combination of ages and sexes. Deteriorating ability in older males may also explain the declining reproductive performance in pairs that are together for 10 or more years (Fig. 5).

Alternative explanations for the increase in RS with

increasing age include the possibility that birds with low RS only contribute data in early years because of reduced longevity, or perhaps older birds try harder than younger birds (Curio 1983). Black & Owen (1989a) showed that parents of increasing ages cared for goslings for longer periods. Similarly, Lamprecht (1986) and Black & Owen (1989b) found a correlation between age and dominance, and aggressiveness in ganders. However, these studies could not rule out the possibility that older geese simply learn the skills for enhanced parental care and fighting ability. Further studies, particularly dealing with variation in survival rates, are needed.

Can geese improve on age-assortative pairing and long-term monogamy by switching to a mate of a different age? We attempted to answer this question by calculating a range of hypothetical lifetime reproductive success (LRS) values. The calculation uses the percentage breeding success for each sex, times five (the number of years in each age segment: young, middle-aged and old; Fig. 4), times two (the mean brood size). We assumed that a bird would lose 1 year's worth of breeding opportunity for each re-pairing event; most geese replace a mate at least once in a lifetime, thus missing the opportunity to breed in 1 or more years; the average length of the pair bond is 4.5 years (Owen *et al.* 1988). Depending on the age combinations and the number of mate changes (one or two in a lifetime) the range of LRS values was 3.92–5.96 goslings for females and 3.88–5.90 goslings for males. Birds that initially chose the same-aged mate and kept that mate for 15 years produced 5.90 goslings, top of the range for both sexes. We conclude that in terms of LRS the system of age-assortative pairing and long-term monogamy can achieve near-optimal performance.

We have recorded changes in several demographic parameters as numbers have increased in this population. These include an expansion in the range of nesting and foraging sites, increased age of first breeding, a huge increase in the non-breeder contingent and an increase in gosling and adult mortality during autumn migration (Prop *et al.* 1984; Owen & Black 1989a, 1991a,b; Prestrud, Black & Owen 1989; Black, Deerenberg & Owen 1991). The results in this paper, which deal with individuals, seem inextricably linked with these records. The social feedback system between age, dominance, foraging ability and reproductive success that has been suggested for geese (Raveling 1981; Lamprecht 1986; Black & Owen 1989b), probably explains the age-related RS in the first 6–11 years of life in geese. Therefore, when food is limited, as it appears to be in the arctic for this population (Prop *et al.* 1984; Owen & Black 1989, 1991a), only the older more dominant competitors will reproduce. Detecting the link between the old-age decline in reproductive performance and population demographics may be more difficult due to reduced sample sizes in older age classes. We suspect the interplay to

be between older age, a high degree of site fidelity, declining food resources and lower reproductive rates in colonies with different histories and age structures (Larsson & Forslund 1994).

We have shown that geese replace deceased or divorced mates with individuals from the same breeding areas in Spitsbergen. During the 3 months in summer there is ample opportunity for geese to become familiar with a select number of individuals. During incubation neighbouring pairs co-defend their nests against marauding gulls and intruding conspecifics. After hatching and during the moult groups of families travel as a unit across the tundra between lakes to localized feeding areas (Prop *et al.* 1984; personal observation). First-time pairings also tend to consist of familiar birds from the same breeding areas, probably from the same non-breeder, moulting flocks (Owen *et al.* 1988; Choudhury & Black 1994). It will be challenging to discover whether neighbouring pairs monitor each other's progress and failure and choose replacement mates according to some criteria assessed from previous pair bonds. We suspect that choosing a mate with complementary knowledge of the intricacies of the arctic system may influence a pair's reproductive performance.

Acknowledgements

We thank the staff and volunteers at Caerlaverock for their efforts, and Sharmila Choudhury for comments and support. We are particularly grateful for the statistical training from Evan Cooch and the many years of dedication to the project from Paul Shimmy Shimmings.

References

- Aldrich, T.W. & Raveling, D.G. (1983) Effects of experience and body weight on incubation behavior of Canada geese. *Auk*, **100**, 670–679.
- Ankney, C.D. & MacInnes, D.C. (1978) Nutrient reserves and reproductive performance of female lesser snow geese. *Auk*, **95**, 459–471.
- Black, J.M., Deerenberg, C. & Owen, M. (1991) Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea*, **79**, 349–358.
- Black, J.M. & Owen, M. (1988) Variations in pair bond and agonistic behaviors in barnacle geese on the wintering grounds. *Wildfowl in Winter* (ed. M. Weller), pp. 39–57. University of Minnesota Press, Minneapolis.
- Black, J.M. & Owen, M. (1989a) Parent–offspring relationships in wintering barnacle geese. *Animal Behaviour*, **37**, 187–198.
- Black, J.M. & Owen, M. (1989b) Agonistic behaviour in goose flocks: assessment, investment and reproductive success. *Animal Behaviour*, **37**, 199–209.
- Le Boeuf, B.J. & Reiter, J. (1988) Lifetime reproductive success in northern elephant seals. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 344–362. University of Chicago Press, Chicago.
- Choudhury, S. & Black, J.M. (1993) Mate selection behav-

- our and sampling strategies in geese. *Animal Behaviour*, **46**, 747–757.
- Choudhury, S. & Black, J.M. (1994) Barnacle geese choose familiar mates from early-life. *Animal Behaviour*, **48**, 81–88.
- Clutton-Brock, T.H. (1984) Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Clutton-Brock, T.H. (1988) *Reproductive Success*. Chicago University Press, Chicago.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behaviour and Ecology of Two Sexes*. Edinburgh University Press, Edinburgh.
- Coulson, J.C. (1966) The influence of the pair-bond and age on breeding biology of the Kittiwake gull *Rissa tridactyla*. *Journal of Animal Ecology*, **35**, 269–279.
- Coulson, J.C. & Thomas, C.S. (1983) Mate choice in the kittiwake gull. *Mate Choice* (ed. P. Bateson), pp. 361–76. Cambridge University Press, Cambridge.
- Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, **125**, 400–404.
- Forslund, P. & Larsson, K. (1991) The effect of mate change and new partner's age on reproductive success in the barnacle goose, *Branta leucopsis*. *Behavioral Ecology*, **2**, 116–122.
- Forslund, P. & Larsson, K. (1992) Age-related reproductive success in the barnacle goose. *Journal of Animal Ecology*, **61**, 195–204.
- Hamann, J. & Cooke, F. (1987) Age effects on clutch size and laying dates of individual female lesser snow geese *Anser caerulescens*. *Ibis*, **129**, 527–532.
- Kear, J. & Berger, A. (1980) *The Hawaiian Goose*. T&D Poyser, Calton.
- Lack, D. (1968) *Ecological Adaptations of Breeding in Birds*. Methuen, London.
- Lamprecht, J. (1986) Social dominance and reproductive success in a goose flock (*Anser indicus*). *Behaviour*, **97**, 50–65.
- Lamprecht, J. (1989) Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? *The Sociobiology of Sexual and Reproductive Strategies* (eds A.E. Rasa, C. Vogel & E. Voland), pp. 48–66. Chapman & Hall, London.
- Larsson, K. & Forslund, P. (1994) Population dynamics of the barnacle goose in the Baltic area: density-dependent effects on reproduction. *Journal of Animal Ecology*, **63**, 954–962.
- Lessells, C.M. (1992) The evolution of life histories. *Behavioural Ecology*, 3rd edn (eds J.R. Krebs & N.B. Davies), pp. 32–68. Blackwell Scientific Publications, Oxford.
- McCleery, R.H. & Perrins, C.M. (1988) Lifetime reproductive success of the great tits *Parus major*. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 136–153. University of Chicago Press, Chicago.
- Marzluff, J.M. & Balda, R.P. (1988) Pairing patterns and fitness in a free-ranging population of pinyon jays: what do they reveal about mate choice? *Condor*, **90**, 201–213.
- Mills, J.A. (1973) The influence of age and pair-bond on the breeding biology of the red-billed gull (*Larus novae-hollandiae scopulinus*). *Journal of Animal Ecology*, **42**, 147–162.
- Newton, I. (1988) Age and reproduction in the sparrowhawk. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 201–219. University of Chicago Press, Chicago.
- Newton, I. (1989) *Lifetime Reproduction in Birds*. Academic Press, London.
- Ollason, J.C. & Dunnett, G.M. (1988) Variation in breeding success in fulmars. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 263–278. University of Chicago Press, Chicago.
- Owen, M. (1980) *Wild Geese of the World*. Batsford, London.
- Owen, M. (1984) Dynamics and age structure of an increasing goose population – the Svalbard barnacle goose *Branta leucopsis*. *Norsk Polarinstitutt Skrifter*, **181**, 37–47.
- Owen, M. & Black, J.M. (1989a) Barnacle goose. *Lifetime Reproduction in Birds* (ed. I. Newton), pp. 349–362. Academic Press, London.
- Owen, M. & Black, J.M. (1989b) Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal Animal Ecology*, **58**, 603–618.
- Owen, M. & Black, J.M. (1991a) Geese and their future fortune. *Ibis* (suppl), **1**, 28–35.
- Owen, M. & Black, J.M. (1991b) The importance of migration mortality in non-passerine birds. *Bird Population Studies—Relevance to Conservation and Management* (eds C.M. Perrins, J.D. Lebreton & G.J.M. Hirons), pp. 360–372. Oxford University Press, Oxford.
- Owen M., Black, J.M. & Liber, H. (1988) Pair bond duration and the timing of its formation in barnacle geese. *Wildfowl in Winter* (ed. M. Weller), pp. 23–38. University of Minnesota Press, Minneapolis.
- Partridge, L. (1989) Lifetime reproductive success and life-history evolution. *Lifetime Reproduction in Birds* (ed. I. Newton), pp. 421–440. Academic Press, London.
- Perrins, C.M. & Birkhead, T.R. (1983) *Avian Ecology*. Blackie, Glasgow.
- Perrins, C.M. & McCleery, R.H. (1985) The effects of age and pair bond on the breeding success of great tits *Parus major*. *Ibis*, **127**, 306–315.
- Prestrud, P., Black, J.M. & Owen, M. (1989) The relationships between an increasing barnacle goose *Branta leucopsis* population and the number and size of colonies in Svalbard. *Wildfowl*, **40**, 32–38.
- Prop, J. & Deerenberg, C. (1991) Feeding constraints in spring staging brent geese and the impact of diet on the accumulation of body reserves. *Oecologia*, **87**, 19–28.
- Prop, J., van Eerden, M.R. & Drent, R. (1984) Reproductive success of the barnacle goose in relation to food exploitation on the breeding grounds, western Spitsbergen. *Norsk Polarinstitutt Skrifter*, **181**, 87–117.
- Ratcliffe, L., Rockwell, R.F. & Cooke, F. (1988) Recruitment and maternal age in lesser snow geese *Chen caerulescens caerulescens*. *Journal of Animal Ecology*, **57**, 553–563.
- Raveling, D.G. (1981) Survival, experience and age in relation to breeding success of Canada geese. *Journal of Wildlife Management*, **45**, 817–829.
- Raveling, D.G. (1988) Mate retention in giant Canada geese. *Journal of Canadian Zoology*, **66**, 2766–2768.
- Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. (1993) Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. *Journal of Animal Ecology*, **62**, 323–333.
- SAS Institute (1990) *Version 6 Edition*. SAS Institute, Cary, North Carolina.
- Scott, D.K. (1988) Breeding success in Bewick's swans. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 220–236. University of Chicago Press, Chicago.
- Teunissen, W., Spaans, B. & Drent, R.H. (1985) Breeding success in the brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea*, **73**, 109–119.
- de Vos, G.J. (1983) Social behaviour of black grouse: an observational and experimental study. *Ardea*, **71**, 1–103.
- Wooler, R.D., Bradley, J.S., Skira, I.J. & Serventy, D.L. (1989) Short-tailed shearwater. *Lifetime Reproduction in Birds* (ed. I. Newton), pp. 405–417. Academic Press, London.