

Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*

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Large-sized Barnacle Geese *Branta leucopsis* of both sexes had a higher probability of breeding successfully in any particular year and produced more goslings than did smaller birds. Large females paired at an earlier age, suggesting that they were preferred as mates and were likely to have entered the breeding population earlier. The relative sizes of the pair bond members also affected fitness. Most birds were able to maximize their breeding performance by mating with relatively similar sized partners; the greater the size disparity of mates, the lower the breeding performance. This supports the idea that compatibility of mates may be important in determining fitness of the pair. The success of different pair types was also affected by environmental conditions, with certain size combinations doing better in some years and poorly in other years.

Body size variation in birds often significantly affects fecundity and survival (Fretwell 1969, Boag & Grant 1981, Fleischer & Johnston 1982, Price & Grant 1984, Monaghan & Metcalfe 1986, Schluter & Smith 1986, Alatalo *et al.* 1990). Since body size has been shown to be heritable in most bird species (Smith & Zach 1979, Boag & Grant 1981, Van Noordwijk *et al.* 1988), it is likely that natural selection will operate on this trait.

Body size variation in geese has not only been shown to be heritable (Davies *et al.* 1988, Larsson & Forslund 1992b) but is thought to be of paramount importance in determining reproductive success (Ryder 1970, Ankney & MacInnes 1978, Drent & Daan 1980, Alisauskas & Ankney 1990). Since food on the arctic breeding grounds is scarce during the pre-laying and laying periods, northern geese are largely dependent on stored endogenous nutrient reserves for egg production (Ryder 1970, Raveling 1979). Females with small body reserves at the onset of breeding may either fail to breed or have a reduced clutch size. Ryder (1970) suggested that the absolute levels of reserves which can be stored by a bird may be limited by its structural size. This has led to the prediction that body size should be directly related to reproductive output in geese; small birds will be able to acquire less reserves than large birds and have less surplus for egg production. Despite this clear prediction, studies attempting to relate body size variation to fecundity in geese have obtained conflicting results both within (Davies *et al.* 1988, Alisauskas & Ankney 1990, Cooch *et al.* 1992) and between species (Ankney & MacInnes 1978, Larsson & Forslund 1992a, C.M. Lessells, 1982, unpubl. PhD thesis, University of Oxford).

Most studies attribute successful breeding to phenotypic characteristics of the individual (see Clutton-Brock 1988,

Newton 1989). However, the majority of birds are socially monogamous, sharing their reproductive experience with a member of the opposite sex (Lack 1968); therefore taking account of only one member of the pair when explaining reproductive performance is presenting only half of the picture. Coulson (1972) pointed out that the compatibility or complementarity of partners may affect the fitness of both individuals. In seabirds, for example, one bird must incubate, or brood the chick, while the other is at sea collecting food. If the partners do not alternate their behaviours in a synchronous manner, the eggs or chicks are at an increased risk from chilling, starving or predation during periods that both partners are off at sea. Although there is much evidence for assortative mating in birds for various traits (Davies *et al.* 1988, Marzluff & Balda 1988a, Black & Owen 1995), this does not mean that choice is for compatibility. Most claims that compatibility is selected for can also be explained by birds choosing high-quality mates. In order to test the compatibility hypothesis, it is necessary to demonstrate that an individual will do better when paired to a similar type of mate than to a dissimilar but higher quality individual. This has rarely been achieved (Marzluff & Balda 1988a, Ens *et al.* 1996). Here we will show that, on average, large male and large female Barnacle Geese *Branta leucopsis* tend to have the highest reproductive success but that small individuals of either sex do better when mated to a small individual of the opposite sex.

Previous workers have tested whether body size is related to egg size, clutch size, laying date, hatching success and fledging success in geese (Ankney & MacInnes 1978, Davies *et al.* 1988, Alisauskas & Ankney 1990, Cooch *et al.* 1992, Larsson & Forslund 1992b, C.M. Lessells, 1982, unpubl. PhD thesis, University of Oxford). We explore the effect of body size variation on other fitness components, namely the

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age of first pairing and the time taken to re-pair with a new mate (as measures of sexual selection, see Choudhury & Black 1993, 1994), and the probability of returning with at least one young to the wintering grounds and also the total number of goslings produced in a particular year (as measures of natural selection). A combination of cross-sectional and longitudinal approaches is used to examine the possibility of opposing directional selection at different stages of the life cycle or under different environmental conditions.

METHODS

Study population

Data were collected between 1973 and 1989 from a migratory population of Barnacle Geese that breeds in arctic Spitsbergen and winters on the Solway Firth in northern Britain. Birds were caught at regular intervals and fitted with individually coded plastic rings. Although the population increased from 5000 to 12,000 birds during the study period, the percentage of marked birds was maintained at around 20–30% of the individuals. The coded leg rings were readable with a telescope from a distance of up to 250 m, and birds were regularly resighted at all stages of the migration route, particularly on the wintering grounds where pair formation generally occurs. At each sighting, standard data were collected on the pair and family status of the individual, identity of the mate and the number of goslings (Black & Owen 1989). Ninety-five percent of birds alive and ringed were resighted annually, with most birds being seen between five and eight times each season (Owen & Black 1989b).

Body size measurements

Body size measures (skull, tarsus and weight) were collected on the breeding grounds during the 4 weeks (July–August) before the young had fledged and the adults were in moult. Male Barnacle Geese are larger (mean skull = 87.3 ± 2.7 mm, tarsus = 71.5 ± 4.1 mm, weight = 1843 ± 198 g, $n = 1615$) than females (mean skull = 83.1 ± 2.6 mm, tarsus = 67.3 ± 3.5 mm, weight = 1623 ± 171 g, $n = 1593$). Repeatability of body measures collected on the same individuals in different years was high ($r = 0.71$ – 0.76 , $n = 69$ – 105 , $P < 0.01$). Since body-weight varies with season, year, breeding area and breeding status (Owen & Black 1989b, Choudhury *et al.* 1992), we generally restricted the analyses to structural measures of size (skull and tarsus), which are constant once birds are over 1 year old, unless otherwise mentioned. Only body size measures of fully grown birds (>1 year old) were used, and, for individuals measured in more than 1 year, a mean value was taken. We used principal component analysis to combine skull and tarsus measures to give a single derived variable, the first principal component (PC1). PC1 has been found to be the best index of overall body size (Rising & Somers 1989), and

in our population, PC1 accounted for over 80% of the total variance of both measures. Each sex was assigned to one of three size categories. Medium-sized birds were those within half a standard deviation of the mean PC1 score, small birds below and large birds above this.

Measures of fitness

In Barnacle Geese, only a minority of the breeding population (3–40%) succeeds in raising young to fledging each year (Owen & Black 1989a, Prop & de Vries 1993). Some pairs do not try to breed at all, whilst of those that attempt to nest, some will suffer partial or total brood loss, e.g. because of predation by gulls and foxes (Prop *et al.* 1984, Prop & de Vries 1993). Mortality of goslings is highest on the breeding grounds and during migration (Owen & Black 1989b). Once a gosling reaches the wintering grounds in its first year, it has an 83% chance of becoming a breeder (Owen & Black 1989b). The number of goslings a pair has on arrival on the wintering areas is therefore a good measure of recruitment of young into the breeding population. We used two measures of reproductive success. The first was the probability of breeding successfully, i.e. of returning to the wintering grounds with any offspring at all. Here birds were assigned to two categories: those that returned with goslings and those that returned without goslings. Birds that returned to the wintering grounds without any goslings included individuals that had not attempted to breed as well as those that had lost their brood prior to arrival in the wintering areas. The second measure was the number of goslings produced, and this varied between zero and six goslings.

We also looked at the age of first pairing in relation to body size. In Barnacle Geese, first-time pairing generally occurs between 2 and 3 years of age and mates usually stay together for life (Owen *et al.* 1988). Birds that pair earlier may be preferred as mates and recruited into the breeding population earlier, hence increasing the number of potential breeding years. The date of pair formation was taken as the first of many subsequent sightings when two birds were first recorded as paired. Since approximately 35% of geese have more than one mate during their lifetime, mainly because of the loss or death of their first partner (Black *et al.* 1996), the time taken to re-pair with a new mate may also indicate bird quality. We therefore also investigated the relationship between body size and the time taken to obtain a new mate.

Data analysis

In long-lived birds like geese, measuring reproduction in 1 year may not accurately reflect lifetime production and fitness. We therefore used both cross-sectional data, where reproductive success in a particular year was compared between size categories, and longitudinal data, where reproductive success of an individual was calculated over a period of 5 years, during which the average bird had a chance of breeding successfully at least once (Owen & Black 1989a).

Since many birds produced no offspring in any particular year, the measures of reproductive success follow a Poisson distribution, thus precluding the use of normal multiple regressions. We therefore analysed the data using logistic regressions (for the binomial, breeding success measure) and log-linear models (for the Poisson, recruitment rate measure) (GLIM; NAG 1986).

In the cross-sectional analyses, we added age, year and breeding area as independent explanatory variables with the last two entered as categorical variables. Reproductive success varies with age in geese (Larsson & Forslund 1992a, Rockwell *et al.* 1993, Black & Owen 1995). Larsson and Forslund (1992a) showed that in Barnacle Geese, clutch size, hatching and fledging success increase up to an age of 4–5 years, and Black and Owen (1995) found that gosling recruitment increases up to 6 years of age. Reproductive success also varies significantly between years and areas on the arctic breeding grounds (Owen 1984, Owen & Black 1989a,b). By including these variables in the model, we were able to pool data across years, breeding areas and age classes. After fitting complete models, terms were successively removed and changes in deviance recorded. Significant terms were retained in the model whilst nonsignificant terms were removed. The significance of removing an explanatory variable from a log-linear model can be calculated from the resultant change in variance which follows a χ^2 distribution. Fitted values were derived from the final model, which contained only significant interaction terms and variables.

In the longitudinal analyses, we selected birds that survived and formed part of the breeding population throughout the 5-year period 1982–1986. We used this 5-year period because it was the time span for which we had consecutive breeding data for the largest number of birds. We controlled for confounding effects of age by using only birds older than 5 years at the start of the period. It was not necessary to control for year because the data were from the same 5 years for all birds. This analysis compares the success of birds that survived throughout these 5 years, which in effect controls for the potentially confounding feature of bird quality in analyses of reproductive data (see e.g. Thomas & Coulson 1988). Breeding success was measured as the probability of successful breeding during the 5-year period, whilst the total number of goslings produced was summed over the 5 years.

In order to determine whether the interaction of male and female size affected the reproductive success of a pair, we combined the male and female size categories to give nine unique combinations of pair types (e.g. small male + small female, small male + medium female, small male + large female, etc.). Logistic and loglinear regression (GLIM; NAG 1986) was used to determine whether breeding success and number of goslings produced varied with male–female size type (entered as a factor) after controlling for year of breeding.

Table 1. Pearson correlation coefficients of body size measures with age of first pairing (in years) in male and female Barnacle Geese (see text for explanation about PC1)

Size measures	Females			Males		
	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
Skull	−0.219	183	<0.01	−0.099	140	n.s.
Tarsus	−0.274	183	<0.01	−0.158	140	n.s.
PC1	−0.284	183	<0.01	−0.146	140	n.s.
Weight	−0.287	165	<0.01	−0.119	134	n.s.

RESULTS

Timing of pairing

Although more than 90% of birds obtained their first mate between the ages of 1 and 5 years, the age of first pairing varied between 1 and 8 years in males (mean = 2.5, s.e. ± 0.05 , $n = 530$) and 1 and 15 years in females (mean = 2.6, s.e. ± 0.05 , $n = 611$). In order to identify whether males or females of a particular size paired earlier, we determined the age of first pairing in relation to body size in the single largest cohort (1976) born in the Nordenskiöld area of Spitsbergen. To control for annual fluctuations in body-weight and condition, we used measures collected in 1977, when all birds were 1 year old. Yearling weights were correlated with adult weights (males: $r = 0.578$, $n = 48$, $P < 0.001$; females: $r = 0.676$, $n = 89$, $P < 0.001$).

There was a significant negative correlation of all body size measures with age of first pairing for females but not for males (Table 1), indicating that large females paired at a younger age. We also looked at the relationship between body size and the time taken to re-pair after mate loss. There was a weak but significant positive correlation between the time taken to re-pair (number of days) and tarsus-length ($r = 0.160$, $n = 499$, $P < 0.01$) and PC1 ($r = 0.104$, $n = 499$, $P < 0.05$) in males. However, this correlation was mainly a result of five birds which took longer than 2000 days to re-pair. On excluding these outliers, the correlations were in the opposite direction and no longer significant (tarsus: $r = -0.094$, n.s.; PC1: $r = -0.049$, n.s.). There was no effect of body size on time taken to re-pair in females.

Cross-sectional analyses

Breeding success

Once the effects of year, age and breeding area were removed, variation in body size significantly affected the probability of breeding in any particular year for both males and females (Table 2). The means and fitted values plotted in Figure 1 show that breeding success increased with body size in both sexes. Small birds had a low probability of returning to the wintering grounds with goslings, whilst large birds had a high probability and medium ones were inter-

Table 2. The importance of body size for breeding success (returning with or without goslings) in male and female Barnacle Geese for each year (cross-sectional analysis). Significance of a variable is determined by the change in deviance (Delta deviance) of the null model

Sex	Variable	Delta deviance	Delta d.f.	P
Male	Null model	1448	1780	
	Final model	1211	1751	
	Year	38.4	13	<0.001
	Area	10.7	3	<0.05
	Age	41.6	11	<0.001
	Size	10.3	2	<0.01
Female	Null model	1618	2006	
	Final model	1326	1980	
	Year	30.0	13	<0.01
	Area	1.6	3	n.s.
	Age	54.5	11	<0.001
	Size	12.8	2	<0.005

mediate. Since none of the interaction terms was significant, this suggests that body size affected breeding success in a similar manner in most years, breeding areas and age classes.

Number of goslings produced

The cross-sectional analysis of number of goslings produced with body size also showed a significant relationship between the size of both male and female parents and the number of goslings they brought back to the wintering grounds (Table 3). Plotting the mean values for each size category showed that the number of goslings produced in any particular year increased with increasing body size in both sexes (Fig. 1). However, since the interactions between body size, year and age were significant for males, this suggests that, in some years or age classes, the numbers of goslings produced are highest for large males, whilst in other years or age classes small males do equally well or better (see below).

Longitudinal analyses

Breeding success

The longitudinal analysis of the probability of successful breeding of 58 males and 52 females over a 5-year period

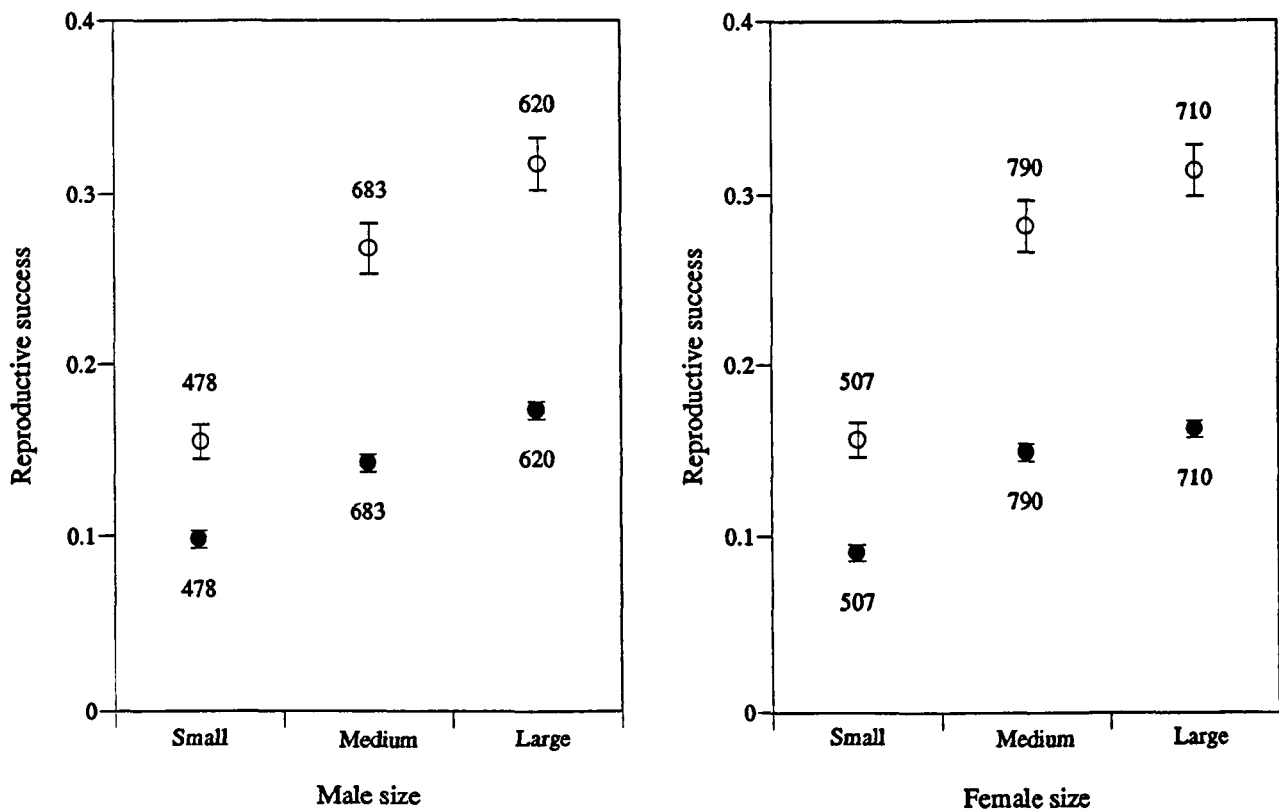


Figure 1. Mean breeding success (successful breeding attempts) and number of goslings produced by different size male and female Barnacle Geese. Dots refer to breeding success and circles refer to number of goslings. Sample sizes appear above s.e. bars.

Table 3. The importance of body size for recruitment rate (number of goslings) in male and female Barnacle Geese each year (cross-sectional analysis). Significance of a variable is determined by the change in deviance (Delta deviance) of the null model. Only significant interaction terms are presented in table

Sex	Variable	Delta deviance	d.f.	P
Male	Null model	1924	1843	
	Final model	1330	1693	
	Year	48.5	13	<0.001
	Age	83.8	11	<0.001
	Size	21.6	2	<0.001
	Area	11.4	5	<0.05
	Year*size	43.3	26	<0.05
	Age*size	46.8	22	<0.005
	Year*age*size	111.6	71	<0.005
	Female	Null model	2191	2020
Final model		1704	1994	
Year		49.1	13	<0.001
Age		94.9	11	<0.001
Size		23.3	2	<0.001
Area		8.5	5	n.s.

showed no significant difference between small, medium and large birds (Table 4).

Number of goslings produced

When we fitted a log-linear model to the total number of goslings that were produced over the 5-year period, we found that small birds of both sexes had a lower number of goslings than did medium or large birds (Fig. 2), but this was significant only for males (Table 4). There was no significant difference between medium and large birds in the number of goslings produced in either sex (males: $F = 0.23$, d.f. = 1; females: $F = 0.70$, d.f. = 1).

Pair-size combinations

The number of goslings produced varied significantly between different pair-size combinations (Table 5), but breeding success (returning with or without goslings) was not significantly different. Figure 2 shows the fitted means of goslings produced for each pair-size type. It is striking that most birds maximized their reproductive output when paired to a relatively similar sized partner. For example, small females and small males performed best with small mates and progressively worse with medium and large ones. Similarly, large males and large females improved their breeding performance increasingly from small to medium to large mates. For medium-sized individuals, the effect of partner size on reproductive success was not as marked; although birds paired to small individuals produced the least number of

Table 4. The importance of body size for breeding success and gosling recruitment in male and female Barnacle Geese over a 5-year period (longitudinal data). Significance of a variable is determined by the change in deviance (Delta deviance) of the null model

	Variable	Delta deviance	d.f.	P
Breeding success				
Males	Null model	96.5	57	
	Final model	90.7	55	
	Size	5.86	2	n.s.
Females	Null model	77.6	51	
	Final model	74.9	49	
	Size	2.67	2	n.s.
Gosling recruitment				
Males	Null model	182.9	57	
	Final model	163.6	55	
	Size	19.38	2	<0.001
Females	Null model	140.5	51	
	Final model	136.6	49	
	Size	3.87	2	n.s.

goslings, there was little difference between success with medium or large partners.

Cooke and Davies (1983) identified that large-large pairs of Lesser Snow Geese *Chen caerulescens caerulescens* had the highest clutch size and hatching success and interpreted this as an explanation for the observed assortative mating in Lesser Snow Geese. We plotted their data in a manner similar to ours, and it appears that not only do large birds paired to large mates do best, but most birds have the highest fitness with similar-sized mates (Fig. 3), as in the Barnacle Geese.

In Barnacle Geese, reproductive success is known to vary seasonally with differences in climatic factors, particularly the timing of snow melt (Prop *et al.* 1984, Owen & Black 1989a). We also found that certain pair-size combinations performed best in some years and poorly in others (Table 5; significant interaction between year and pair size). This is illustrated in Figure 4 in three example years. In 1985, the highest number of goslings was produced by large male + large female pairs, followed by the medium-sized pairs. In 1988, medium-sized pairs did best, whilst in 1990, gosling recruitment was highest in small male + small female partnerships.

DISCUSSION

Body size and reproductive success

Studies attempting to relate body size variation to fecundity in geese have obtained conflicting results. C.M. Lessells (1982, unpubl. PhD thesis, University of Oxford) found that females paired to large male Canada Geese *Branta canadensis*

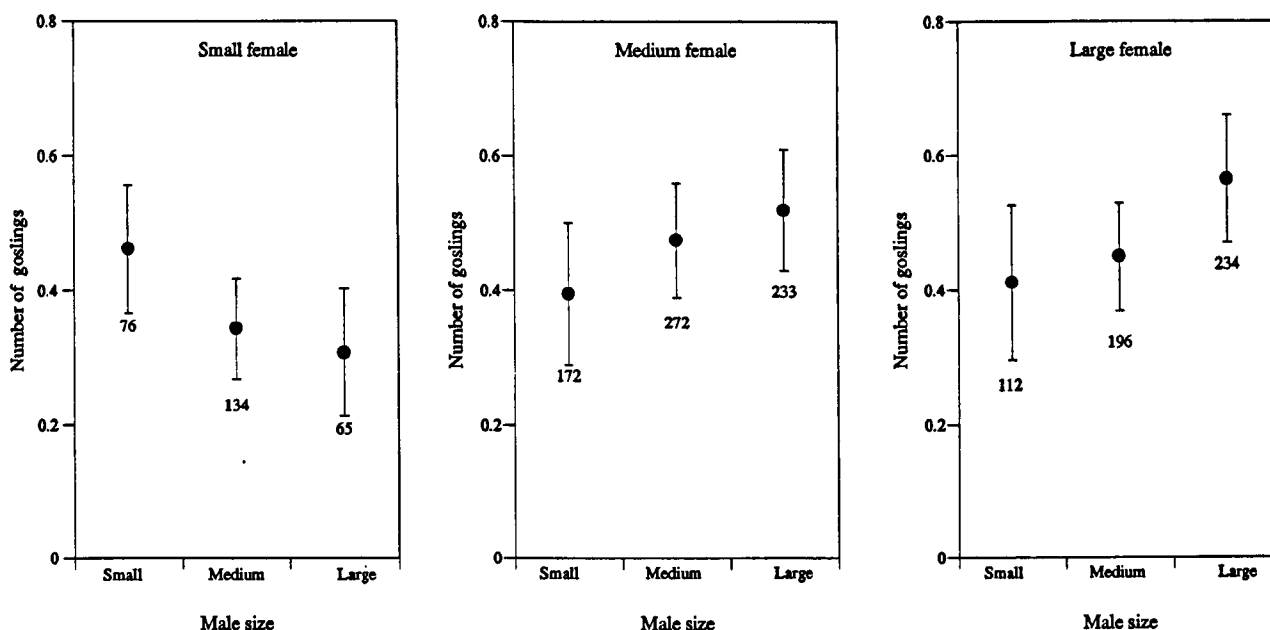


Figure 2. Mean number of goslings produced by different male-female size combinations in Barnacle Geese. Sample sizes appear below s.e. bars.

had larger clutch sizes, and Larsson and Forslund (1992b) and Larsson (1992) showed that larger female Barnacle Geese laid larger eggs and had larger clutches. In the Lesser Snow Goose, however, although Ankney and MacInnes (1978) found a positive relationship between female culmen length and clutch size, Davies *et al.* (1988) and Cooch *et al.* (1992) used a multivariate index of structural size and found no evidence that it affected clutch size or laying date.

Cooch *et al.* (1992) argued that the positive associations between structural size and breeding performance detected by other studies were a result of lack of control for covariation of age with structural size. However, we also controlled for such confounding variables, but our results clearly show that body size in Barnacle Geese is correlated with fitness. Examining both males and females separately, we found that larger sized birds had a higher probability of breeding successfully in any particular year and producing a greater number of offspring than smaller birds in that year. When reproductive success was measured over a 5-year period, larger birds had a greater number of successful breeding seasons and produced more goslings than smaller birds, although this was only significant for males.

There were three major differences between our approach and Cooch *et al.*'s. First, Cooch *et al.* could look at fitness only in relation to female size, whilst we were able to include male size, as well as the interaction of male and female phenotypes. Second, we used components of fitness derived at a later stage, i.e. after fledging of the goslings. Since total or partial brood loss is high in geese and occurs mainly before fledging (Prop *et al.* 1984, Larsson & Forslund 1992b), measures of clutch size and egg mass are likely to show less variation than post-fledging measures. Indeed, Larsson and Forslund (1992b) observed density-dependent

effects in the Gotland population of Barnacle Geese and found no effect on clutch size or hatching success but a reduced fledging success. We therefore suggest that natural selection on breeding performance is more likely to be expressed in post-fledging success. Third, we measured fitness both on a yearly basis and over a longer 5-year period. In long-lived species, annual and lifetime production can be highly variable (Owen & Black 1989a), and longitudinal analyses using a long-term measure, ideally lifetime fitness, should be used in addition to the standard cross-sectional analyses.

Body size and mate choice

We found that larger females paired at an earlier age, which may suggest that they were selected out of the mate pool and preferred as mates. This would be a reasonable explanation because large females will produce more offspring (see above) and males should therefore attempt to pair with the largest available females first. Alternatively, large females may have paired earlier if they were able to achieve a fitness advantage from pairing early. Pairing early could be advantageous because geese apparently need to establish a workable relationship with their mates before they succeed in a reproductive attempt (Cooke *et al.* 1981, Raveling 1981, Black & Owen 1988, Owen *et al.* 1988). Geese that pair early will have more time to gain experience with their mate and may thereby increase the number of potential breeding years.

Although large females paired earlier in first-time partnerships, this was not the case in subsequent pairings. The reason for this is not clear. It may be that body size is more important in mate choice for initial pair bonds, since they

Table 5. Importance of size for reproductive success in Barnacle Geese. Significance of a variable is determined by the change in deviance (Delta deviance) of the null model. Only significant interaction terms are presented

	Variable	Delta deviance	d.f.	P
Breeding success	Null model	1643	1493	
	Final model	1532	1484	
	Year	110.7	9	<0.001
	Size	9.7	8	n.s.
Gosling recruitment	Null model	2133	1493	
	Final model	1760	1405	
	Year	182	9	<0.001
	Size	21.5	8	<0.01
	Year*pair size	173.9	71	<0.001

all tend to be of similar age and experience (Black & Owen 1995). Subsequent pairings, in contrast, include birds of all ages and backgrounds that may have lost or divorced a mate (Black *et al.* 1996). For these birds, criteria other than body size may be of greater importance when selecting a mate, e.g. age, breeding experience and familiarity (Black & Owen 1995).

The functional significance of large body size

In arctic-nesting geese, the functional significance of body size on fitness may be that structural size limits the amount

of nutrient reserves a bird can acquire (Ryder 1970, Ankney & MacInnes 1978, Alisauskas & Ankney 1990, R.T. Alisauskas, 1988, unpubl. PhD thesis, University of Western Ontario). However, Cooch *et al.* (1992) argued that body size variation should affect fecundity only if the relative increase in nutrient reserves is sufficient to allow the formation of at least one additional egg. Although this may be true, body condition of parent birds may affect not only fecundity but also subsequent parental care. Females in poorer condition have to feed more frequently during incubation, thus exposing their nests to greater risk of predation (Ankney & MacInnes 1978, Aldrich & Raveling 1983, Prop *et al.* 1984). Similarly, after the young have hatched, males in better condition may need less time to replenish their own body reserves and can devote more time to vigilance and protecting their young (Ankney 1977).

Apart from a possible link between body size and the nutrient reserves a bird can store, large body size may be related to favourable conditions experienced during growth and hence indicate a healthier constitution (Cooch *et al.* 1991, Larsson & Forslund 1992b). In the Lesser Snow Goose, a decline in suitable feeding habitat on the breeding grounds resulted in a decline in mean gosling weight and subsequently in the weights of the adults from those cohorts (Cooch & Cooke 1991). Small goslings will either fledge at a lower weight or fledge later, either of which could adversely affect survival during migration and future reproduction (see Owen & Black 1989b, 1991). At present, we do not know whether there is a relationship between body size and survival in Barnacle Geese.

Larger size may also increase fitness via behavioural mechanisms. Larger birds often have a higher social rank

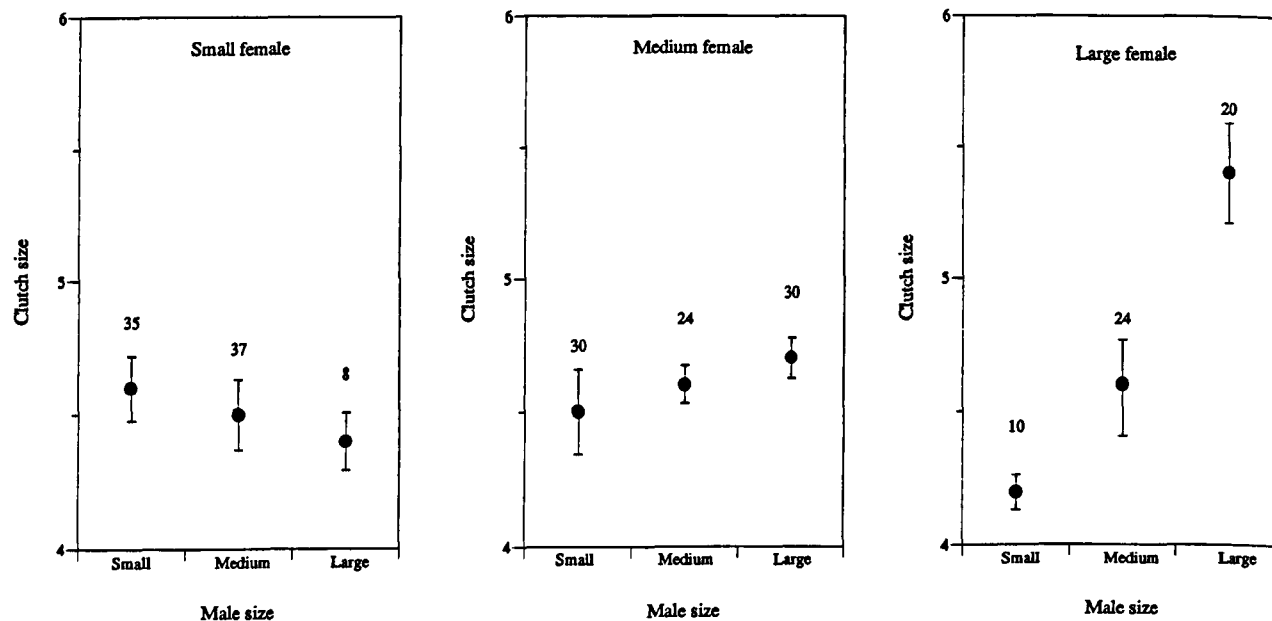


Figure 3. Mean clutch size of different male–female size combinations in the Lesser Snow Goose (adapted from Cooke & Davies 1983). Sample sizes appear above s.e. bars.

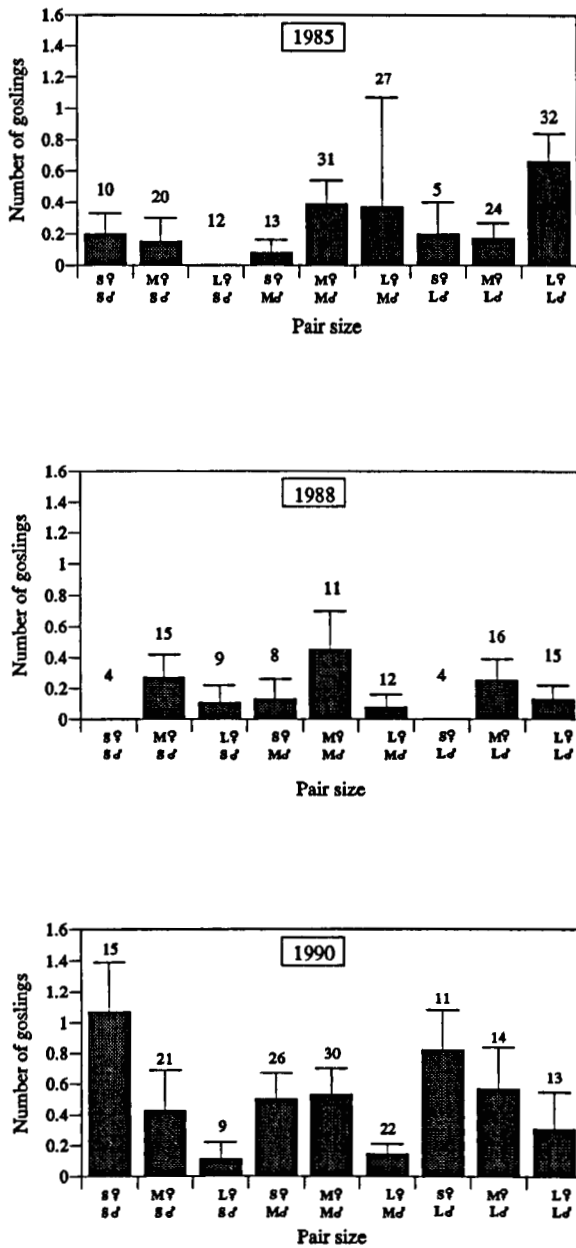


Figure 4. Mean number of goslings produced by different male-female size combinations in Barnacle geese in different years (S♂ = small male, M♂ = medium male, L♂ = large male, S♀ = small female, M♀ = medium female, L♀ = large female). Sample sizes appear above s.e. bars.

(Fretwell 1969, Scott 1980), and this may ensure better access to food resources, nest sites and high-quality mates and hence a higher breeding success (Owen & Wells 1979, Raveling 1981, Lamprecht 1986a,b). However, in geese there is as yet little evidence that body size greatly influences dominance rank within flocks (Raveling 1970, Lamprecht 1986a,b, Black & Owen 1987).

Pair size and fitness

Traditionally, studies of life-history strategies have looked at fitness in relation to the phenotype of one sex (Clutton-Brock 1988, Newton 1989). However, the reproductive success of an individual will always be influenced in part by the investment or actions of the other partner, and recent studies are becoming more and more aware of this interactive process (Black 1996). In Barnacle Geese, both males and females appear to be able to maximize their breeding performance with similar-sized partners. The larger the size mismatch is between mates, the lower the breeding performance will be. This effect was particularly striking for small and large birds but less so for intermediate sizes, possibly because medium-sized birds have relatively small size disparity with any partner. These results suggest that reproductive success of a pair may be determined not only by their qualities as individuals but also by their degree of compatibility or complementarity.

The reason for the lower fitness in partners disparate in body size is not clear but may be related to discrepancy in social status, lack of coordination or intrapair aggression. In Pinyon Jays *Gymnorhinus cyanocephalus*, aggressive encounters are rarer between partners similar in size, and this was suggested to enhance survivorship and pair duration (Marzluff & Balda 1988b). In geese, the male is larger than the female and also is more aggressive and dominant. Increasing size disparity of mates could increase risk of injury to females during social display and copulation (Radesäter 1974, Black & Owen 1988). Small females may be over stressed by social interactions with very large mates, thus inhibiting the flow of reproductive hormones (Greenberg & Wingfield 1987). The smaller the size disparity is between male and female partners, the less the male may be able to harass the female, and this may reduce intrapair aggression and strengthen the partnership in terms of increased pair coordination.

Since the interaction of male and female body sizes has a pronounced effect on reproductive success, we would expect birds to preferentially pair with similar-sized mates in order to maximize breeding performance. Previous work has failed to find evidence of positive assortative mating for body size in Barnacle Geese (Choudhury *et al.* 1992), but geese use multiple criteria in mate choice (Choudhury & Black 1994) and all birds may not be able to achieve their preferred mating option in terms of body size.

Limitations on body size

Body size variation is known to have a genetic basis in geese (Davies *et al.* 1988, Larsson & Forslund 1992b). If larger body size confers fitness advantages to Barnacle Geese, what prevents the evolution of increasingly larger birds? One possibility is that body size may be limited by physical constraints, ensuring that at some level there is no further increase in size. For example, increasing structural size may pose problems for flight manoeuvrability or long-distance

migrations (Pennycuik 1989). In Lesser Snow Geese, large males compared with females are more sensitive to food limitations, showing a greater decrease in growth rate and survival when conditions are poor (Cooke *et al.* 1995).

Increasing body size may also carry costs of delayed maturation, which affects age at fledging and first breeding. Owen (1980) showed that 84% of variability in fledging periods in geese is a result of body-weight alone. Barnacle goslings have only about 10 weeks from the date of hatch until they undertake the 3000-km migration from the arctic breeding grounds to the wintering areas (Owen & Black 1989b). During this time, they have to complete body and wing growth as well as acquire sufficient reserves to undertake the journey (Prop & de Vries 1993). Since larger birds have slower growth rates (Ricklefs 1973), longer fledging periods (Carrier & Auriemma 1992) and require larger absolute amounts of food, there may be an upper limit to the structural size of geese that can cope with these life-history and environmental constraints.

Phenotypic variation may also be maintained if selection acts in opposite directions under different environmental conditions (Searcy 1979, Boag & Grant 1981, Endler 1986). Arctic-nesting geese are particularly susceptible to variable weather conditions (Ebbinge 1989, Owen & Black 1989a,b, Prop & de Vries 1993). It seems likely, therefore, that the importance of the size and condition of a bird on its reproductive output is likely to vary with the harshness of the breeding season. Small individuals, for example, may be more susceptible to starvation during extreme weather conditions and food shortages (Ankney & MacInnes 1978). In Barnacle Geese, there is evidence that large birds and pairs do better in some years and small individuals do better in others (Fig. 4).

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