

Do barnacle geese pair assortatively? Lessons from a long-term study

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In the field, mate choice is usually studied by looking for non-random mating patterns in established pairs (Cooke & Davies 1983; Marzluff & Balda 1988; Reid 1988; Johnston & Johnson 1989). It has been recognized, however, that these patterns alone do not necessarily imply that active mate choice is taking place. Two main factors have been identified that can confound mate choice and produce non-random mating patterns: intra-sexual competition (Wishart 1983; Johnson 1988) and differential availability of mates during pair formation (Cooke & Davies 1983; Reid 1988). We propose another factor that needs to be investigated before interpreting non-random mating patterns. Traits that show lifetime variation (e.g. body weight, dominance rank, plumage, vocalization and behaviour) may change after pair formation and produce the observed non-random mating pattern. This is especially likely for traits that have a strong environmental component (e.g. body weight and rank) and for species in which mates remain together throughout the year. Thus when two geese pair up, they acquire the same rank (Lamprecht 1986; Black & Owen 1989). Similarly, traits that involve a learning process (e.g. vocalizations) may change over time (Mundinger 1970; Payne 1982).

Here we use field data on a wild population of barnacle geese, *Branta leucopsis*, collected over 17 years to determine whether there is non-random mating for body size or body reserves and discuss whether this could be due to mate choice. We look for correlations in the body measurements of mates both before and after pair formation.

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, which were readable with a telescope from a distance of up to 250 m. During

the study period the population increased from 5000 to 12 000 birds, but the percentage of marked birds was maintained at around 20–30% of the total number.

Body size measures (skull, tarsus and weight) were collected on the breeding grounds during the 4 weeks (July–August) when the young had fledged and the adults were in moult. Repeatability of body measures collected on the same individuals in different years was high ($r=0.7$, $N=69-105$, $P<0.01$). 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 it accounted for over 80% of the total variance of both measures.

Body weight includes a component of structural size and of body condition. For the purpose of this study we regressed weight on PC1, using the residuals as an index of general body condition. We assume that body weight corrected for size in this way gives a better indication of a bird's general condition than weight alone (Owen & Cook 1977).

The pair status of birds was determined from resighting data of ringed individuals, mostly collected on the wintering grounds, where pair formation generally takes place (Owen et al. 1988). The resighting rate was high, with 95% of ringed birds being resighted five to eight times each year. The date of pair formation was taken as the first of multiple sightings when a pair was recorded as paired.

Assortative mating for body size was investigated by correlating body measures of the male and female of all known pairs. The biometric measures were collected in 4 years and in eight different breeding areas in Spitsbergen. For pairs that were measured in more than 1 year, mean values were used. Thus each distinct pair was used only once in the analysis, though individual birds might appear more than once, if they had more than one partner

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Table 1. Correlation coefficients between mates of standardized body size variables (corrected for breeding area and year of measurement) collected before and after pairing

Size variable	Before pairing			After pairing		
	<i>r</i>	<i>P</i>	<i>N</i>	<i>r</i>	<i>P</i>	<i>N</i>
Skull	0.050	NS	125	0.051	NS	336
Tarsus	-0.016	NS	125	0.038	NS	336
PC1*	0.032	NS	125	0.080	NS	336
Weight	0.115	NS	125			
Non-breeders				0.414	<0.01	148
Failed breeders				0.311	<0.01	135
Successful breeders				0.271	<0.05	47
Condition	0.149	NS	125			
Non-breeders				0.445	<0.01	149
Failed breeders				0.309	<0.01	135
Successful breeders				0.274	<0.05	47

*First principal component; see text for explanation.

during their lifetime. Since there was a strong year-of-measurement and breeding-area effect (unpublished data), all measures were standardized by subtracting the mean and dividing by the standard deviation. We were then able to lump all pairs for the analysis. In all cases we used only adult measurements (2 years or more) and measures collected from both sexes of a pair in the same year. Barnacle geese reach full size by the time they are 1 year old, but they do not attain full adult weight until the age of 2 years (Owen & Ogilvie 1979).

The measures from birds prior to pairing were those collected nearest to the time of pair formation. For measures collected after pairing, we carried out separate analyses for body weights and conditions of (1) non-breeders, (2) birds that had attempted but failed to breed, and (3) birds that had bred successfully in the year the measurements were collected. Body weight and reserves vary significantly during the moult period between these categories of birds (Owen & Ogilvie 1979).

Members of a pair showed no correlation in body size or body condition before pairing. However, after pairing, we found a significant positive correlation in weight and condition of mates, and no correlation in body size measures (Table 1). This suggests that there was no assortative mating for body size, but that members of a pair build up similar amounts of body reserves after they pair up.

Our results contrast with those of Davies et al. (1988) on lesser snow geese, *Chen caerulescens*

caerulescens. They found a significant positive correlation between mates for all body measures including size. However, they pooled data from a number of sub-colonies and over a number of years. If we repeat our analysis on barnacle geese by pooling data from all years and breeding sites without standardizing the variables, we also find significant positive correlations for all body measures of mates (unpublished data). In geese, body size varies significantly between cohorts (Davies et al. 1988; Cooch et al., in press; unpublished data), and there may be geographical clustering of cohorts on the breeding grounds (Cooke et al. 1983). The findings of Davies et al. were therefore probably confounded by cohort effects.

The results of this study illustrate that patterns of non-random pairing derived from post-pairing measures are potentially suspect, because phenotypic traits may change after pairing. In our investigations of assortative mating in geese, we discovered that, before pairing, the weight and condition measures of mates were not correlated, but after pairing they were. This suggests that mates apparently attain similar body conditions and weights as a consequence of pairing.

Goose mates tend to remain together throughout the year. They migrate together, are exposed to similar environmental stresses, and use the same habitats which differ in resource availability and/or quality (Black et al. 1991), with the most competitive pairs gaining access to the best food sources

(Teunissen et al. 1985; Black & Owen 1989). In addition, both sexes show a high degree of parental care and lose a substantial amount of their body reserves in breeding attempts (Ankney 1977; Ankney & MacInnes 1978). These differences in habitat usage and life history give rise to the gradient of body weights that exists across the population of pairs, with some pairs growing fat together while others do not.

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