

Barnacle geese preferentially pair with familiar associates from early life

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Abstract. Wild barnacle geese, *Branta leucopsis*, pair assortatively with individuals from their own breeding areas, even though pair formation mainly occurs away from the breeding grounds. Two alternative mechanisms for assortative mating by breeding area have been suggested: (1) geese recognize and choose mates from early life associates, or (2) geese choose mates with phenotypic traits common to their own breeding area. These hypotheses were tested in two experiments with 78 young geese. Birds given a choice between familiar and unfamiliar potential partners paired significantly more often with familiar individuals; those that had a choice between unfamiliar individuals from their own and from a different population paired randomly. It is suggested that pairing with a 'known' individual from the same breeding area may enhance mate complementarity in adaptation to the same local habitat.

Halliday (1983) suggested that the reproductive success of a mating pair is affected not only by their qualities as individuals, but also by their degree of genetic and behavioural complementarity. Partner compatibility may be particularly pertinent where ecological conditions vary over the species' natural range, so that positive assortative pairings between individuals adapted to the same local habitat may be favoured (Shields 1982; Greenwood 1987).

The barnacle goose, *Branta leucopsis*, is a long-term monogamous species and first-time pairing generally occurs at 2–3 years of age. On the breeding grounds in Spitsbergen, the geese breed in fairly discrete colonies of about 100 pairs (Prestrud et al. 1989), and there is evidence that young geese preferentially mate with individuals they summered with in the arctic (Owen et al. 1988). They usually, however, form pairs in the winter, where the whole population of 12 000 individuals is concentrated in a much smaller site in Scotland and birds from all breeding areas intermingle. Three mechanisms could underlie the observed assortative mating pattern. (1) Birds from the same breeding units may cluster within wintering flocks, increasing the probability of pairing with an individual from the same area; (2) geese may recognize previous associates, i.e. familiar individuals from the breeding grounds,

within the wintering flocks; or (3) there may be phenotypic differences between birds from different breeding areas, and geese may choose mates with phenotypic traits common to their own area. At present there is little evidence for the first hypothesis, i.e. clustering of geese from the same breeding colonies within wintering flocks (Owen et al. 1988; Choudhury 1992). This suggests that young geese may be actively searching for individuals from their own breeding area during pair formation. Re-locating members of the same breeding colony within wintering flocks of thousands of birds, however, requires some form of recognition. Our aim in this study was to test whether recognition and mating preferences for colony associates is based on familiarity due to prior association, or on a phenotype matching mechanism. Since animals may use multiple criteria in mate choice (Burley 1981), and other selection criteria could operate besides familiarity or genetic relatedness, we also looked at the role of other traits on mate choice.

METHODS

We reared 78 young barnacle geese from incubator-hatched eggs in the summer of 1989, in two experiments and in unisexual groups of 6–12 birds each (Fig. 1). No more than two goslings from the same clutch were used in each exper-

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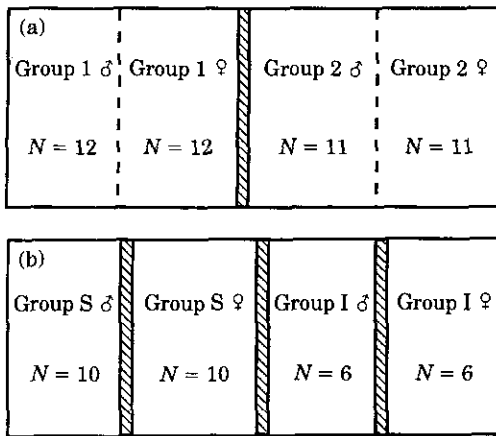


Figure 1. Experimental set-up for mate-choice experiment with captive barnacle geese. (a) Experiment 1: testing the effect of familiarity, i.e. early life associations, on future mate choice. (b) Experiment 2: testing whether geese can distinguish between birds from different populations purely by phenotype.

iment, and these were always of the same sex, so that genetic relatedness could not interfere with mate choice.

Experiment 1

In experiment 1 we tested the effect of familiarity, i.e. early-life associations, on future mate choice. All birds were reared from eggs of the Slimbridge semi-captive geese. Twelve males and 12 females were raised in two enclosures separated by a wire-mesh fence so that they could see, and could become familiar with, each other. A separate set of 11 males and 11 females were raised in a similar manner (Fig. 1). Birds from the two sets were separated by a solid fence, which did not allow visual contact, although vocal contact could not be excluded. The geese called very little, however, until the start of the pair formation period in their second spring, and it seems unlikely that recognition of individuals would have occurred purely by vocal means.

In the wild, goslings stay with their parents for up to 11 months (Black & Owen 1989a) and have only limited contact with other birds. Similarly, our goslings were not allowed to mix during the first 11 months and had only limited (i.e. visual) contact with the group with which they were to become familiar. On the arctic breeding grounds, young birds spend their second summer in non-

breeding flocks (Owen et al. 1978), possibly associating quite closely with future mates. To simulate this, we moved the 12 males and 12 females into one enclosure and the 11 males and 11 females into another enclosure during their second summer to facilitate closer association. To ensure that no pairbonds were formed prematurely, birds were kept together for only 2 weeks at a time, separated again for 4 weeks, and so on throughout the summer.

In the wild, young birds generally pair during their second winter (Owen et al. 1988). We therefore moved all birds into one large enclosure in October, at the beginning of their second winter, and allowed them to pair freely until the following summer. If assortative mating occurs because of a preference for familiar associates from early life, we would expect more pairs to form between birds that were familiar with each other.

Experiment 2

In experiment 2 we tested whether geese can distinguish between birds from different populations, i.e. distant and close genetic relatives, purely by phenotype. We obtained eggs from two different genetic stocks: the Slimbridge semi-captive flock (England) and the Islay semi-captive flock (Scotland). Although the origins of the birds cannot be traced, the Slimbridge flock originated mainly from the wild Svalbard population, while the Islay flock consists mainly of birds from the wild Greenland population (M. Owen & M. A. Ogilvie, personal communication). However, both semi-captive flocks have been genetically isolated for decades.

The birds were reared in four unisexual groups of 10 Slimbridge males, 10 Slimbridge females, six Islay males, and six Islay females (Fig. 1). For the first 16 months of life none of the groups had visual contact with each other. As in experiment 1, all birds were moved into one large enclosure at the beginning of their second winter, and allowed to pair freely until the following summer. If assortative mating occurs via phenotype matching, we would expect birds from the Slimbridge stock to pair with other Slimbridge birds, and Islay birds to choose Islay mates.

Ideally, we should have tested each bird separately for its mating preferences, but geese will not behave naturally unless they are in a flock. We therefore compromised and attempted to gain

as much information as possible on mating preferences of geese under the given constraints. This means that, strictly speaking, the samples were not independent of each other. Besides the possibility that the action or choice of one bird could influence those of another, there is a lack of external validity. Although this means that one has to be more cautious when drawing general conclusions, we do not believe that it invalidates the results.

Rearing Conditions

In both experiments, the enclosures of the initial unisexual rearing groups were 7×21 m, and the large enclosures for the pairing process were 21×63 m in size. All birds had access to ad libitum food, water and nesting materials. Birds were fitted with individually marked, yellow plastic leg bands which could be easily read from the hide erected outside the enclosures. We observed the birds regularly every fortnight for 8–12 h, from the age of 6 months. In the spring, when courtship behaviour suddenly increased, observations were stepped up to 1–2 h virtually every morning, which was the peak time for courting behaviour.

Birds were allowed to establish nests and lay eggs during the breeding season; however, all eggs were replaced by wooden ones as soon as the clutch was complete, so that birds continued to sit on and guard their nests. Reproductive success was measured in terms of the number of eggs laid.

Pair-formation Behaviour

Pair-formation behaviour was collected by continuous observation. This included all courtship behaviour, i.e. mate searching, vocalizations, herding, mock attacks, triumph ceremonies, precopulatory head-dipping and copulations (see Black & Owen 1988), as well as leading/following (Lamprecht 1992), food sharing (Black & Owen 1989a) and friendly approaches (Lamprecht 1991). Proximity between pair members was measured as the percentage of time seen as nearest neighbours and as the mean distance between them in goose lengths (ca 45 cm). The three nearest neighbours were recorded at least once during each observation session for each individual. We defined the start of a partnership as the point from which the female started to join in the triumph

ceremonies, or where the female was observed to show a combination of at least three other positive responses towards the male, for example, following, food sharing, friendly approach, continuous nearest neighbour.

Phenotypic Qualities

Most traits were measured prior to pair formation, since phenotypic traits may change after pairing (Burley 1983; Choudhury et al. 1992).

Dominance

Dominance ranks within each experiment were established from aggressive interactions, displacements and greetings (Radesäter 1974). Appleby's (1983) test for linearity was used to confirm that goose ranks were linear, and Clutton-Brock et al.'s (1979) index was used to rank birds in a linear hierarchy.

Body measures

Body size (skull, tarsus, wing, weight) was measured for all birds once they had attained full adult size at the age of 1 year. Principal Component Analysis (Rising & Somers 1989) was used to combine skull and tarsus measures to give a single index of overall body size (PC1). We also assessed body condition according to a visual score of the abdominal fat reserves of the goose, the abdominal profile index (Owen 1981).

Plumage patterns

Since the main plumage variability appears to be in the face patterns, we photographed all faces once the birds had attained adult plumage, and calculated the percentage of black and white surface areas.

Vigilance

In geese, vigilance for predators is one of the main forms of parental care (Lazarus & Inglis 1978; Sedinger & Raveling 1990). To obtain a vigilance measure as an indicator of mate quality, we carried out an experiment with an artificial predator on birds in experiment 2. A stuffed fox on a stick was 'walked' past the enclosure, resulting in all birds taking on the vigilant 'head-up'

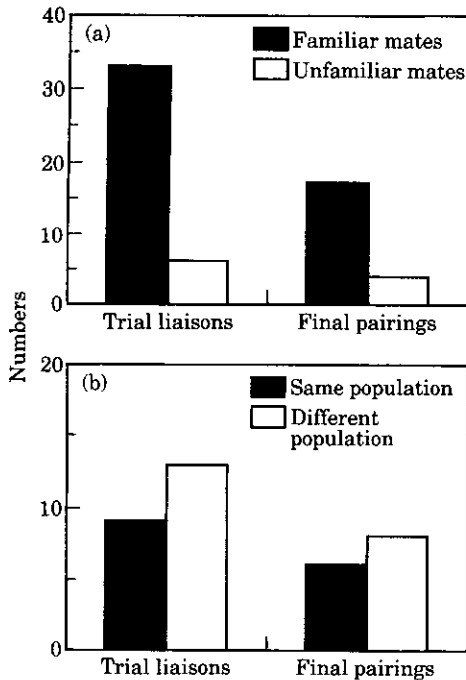


Figure 2. (a) Frequency of pairings between familiar and unfamiliar birds. (b) Frequency of pairings between unfamiliar birds from the same and from different populations.

posture. We scanned the flock every minute for 15 min following the treatment, recording individuals as vigilant (with head-up) and non-vigilant (with head-down). Two independent measures of vigilance were obtained. (1) Head-down latency: birds were ranked according to when they put their head down the first time after the incident, and (2) Head-up score: birds were ranked according to the number of head-ups during the 15-min sampling period.

Nest defence

Nest defence, i.e. aggression towards the observer, was scored on an index of 1–4 (Black & Owen 1987) for both male and female when the eggs were replaced by wooden ones.

RESULTS

Recognition: Familiarity versus Phenotype Matching

Most birds went through a number of trial

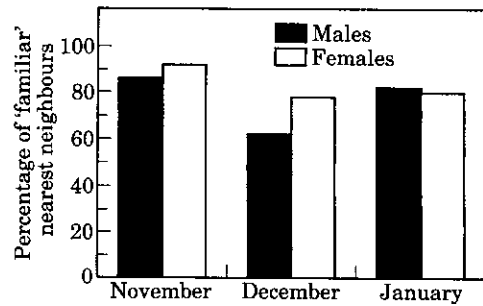


Figure 3. Social preferences of geese prior to pairing.

liaisons or partnerships lasting a few days before settling with a consistent mate. In experiment 1, birds sampled more familiar than unfamiliar individuals ($\chi^2=18.69$, $df=1$, $N=39$, $P<0.001$), and eventually paired with familiar individuals more than would be expected by chance ($\chi^2=8.05$, $df=1$, $N=21$, $P<0.005$; Fig. 2a). Even during November to January, when virtually none of the birds had started mate sampling, familiar males and females were nearest neighbours more than expected by chance (males: $\chi^2=49.3$, $df=2$, $P<0.01$; females: $\chi^2=68.9$, $df=2$, $P<0.01$; Fig. 3).

In experiment 2, pairing was random with respect to population and/or genotype, i.e. birds did not prefer mates from the same genetic stock either in the mates they sampled ($\chi^2=0.7$, $df=1$, $N=22$, NS) or in their final partners ($\chi^2=0.29$, $df=1$, $N=14$, NS) (Fig. 2b).

We have assumed that birds were free to pair with any other bird throughout the pairing period. This assumption may be false, since the pool of available partners may decrease in a finite population of birds as individuals pair up. We tested this by comparing the observed pairings with all random pairings under hypothetical conditions in a simulated randomization model (see Marzluff & Balda 1988; Reid 1988; Johnston & Johnson 1989). The pairing process was simulated by repeatedly drawing males and females randomly from the pool of all available birds (200 times). In model (1) we replaced birds as soon as they were drawn so that they were continuously available as potential mates. In model (2), birds were removed and not replaced. There were significantly more pairings between familiar individuals in our experimental design than in both simulation models: for model (1) $P<0.005$ and for model (2) $P<0.02$.

Table I. Relationship between male and female traits and timing of pairing

	Experiment 1		Experiment 2	
	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>
Males				
Body size (PC1)	-0.378*	23	-0.421	16
Body weight	-0.047	23	-0.322	16
Body condition	0.010	23	-0.305	16
Face pattern (% black)	-0.204	23	0.040	16
Dominance rank group	0.454*	23	0.100	16
Vigilance: Head-up			-0.017	15
Head-down			0.242	15
Vocalization rate	0.057	23	-0.251	16
Females				
Body size (PC1)	-0.029	23	0.003	16
Body weight	0.028	23	-0.129	16
Body condition	-0.048	23	-0.083	16
Face pattern (% black)	0.192	23	-0.416	16
Dominance rank group	0.329	23	-0.012	16
Vigilance: Head-up			0.122	12
Head-down			0.038	12
Vocalization rate	-0.183	23	0.260	16

r=Spearman rank correlation coefficient.

**P*<0.05.

Selective Advantages

Familiar birds tended to pair earlier ($\bar{X} \pm \text{SE} = 166 \pm 50$ days) than unfamiliar ones (188 ± 22 days; $t = -1.59$, $df = 21$, $P = 0.064$), but there was no difference in mean clutch size ($t = 0.29$, $df = 25$, NS). Nor was there any difference in proximity, the amount of courtship behaviour, or the degree of nest defence of familiar versus unfamiliar partners.

Other Mate-choice Criteria

We investigated in three ways whether the geese also used body size, body condition, plumage pattern, dominance rank, vigilance and vocalization rate as criteria when selecting mates. (1) Timing of pairing: high quality mates may be in greater demand and hence pair earlier (Reid & Weatherhead 1990). Larger and more dominant males in experiment 1 paired earlier to their final mate (Table I). For females there was no evidence that individuals with particular traits paired earlier. (2) Assortative mating patterns: we found no evidence of correlations between male and female traits within pairs. (3) Comparison of accepted and rejected mates sampled: neither sex appeared

to be consistent in preferring mates with a particular trait.

DISCUSSION

Familiarity versus Phenotype Matching

Wild barnacle geese pair assortatively with individuals from their own breeding areas, even though pair formation mainly occurs away from the breeding grounds (Owen et al. 1988). We found that young barnacle geese show a strong social attachment to familiar individuals prior to pair formation, and subsequently also prefer as mates familiar associates from early life to unfamiliar individuals. They did not appear to discriminate between close and distant colony mates purely by phenotype.

Young geese spend their summers in flocks of non-breeding and unpaired birds (Owen et al. 1978). Associations during this time may well be responsible for shaping future mate preferences. In wild lesser snow geese, *Anser caerulescens caerulescens*, birds from the same cohort tend to cluster and nest together on the breeding grounds, and this association may be maintained over a

number of successive seasons (Cooke et al. 1983). Cooke et al. (1983) suggested that this group cohesiveness originates from the social interactions of young birds both on the wintering and breeding grounds and is maintained by individual recognition and group association into adulthood.

Selective Advantages of Pairing with Familiar Individuals

Early pairing

By choosing a partner from a group of familiar individuals, a bird may be able to reduce the costs involved in searching for and assessing a mate (Janetos 1980; Real 1990), and hence pair earlier. We found that geese that had a choice of mates from a familiar set of individuals tended to pair earlier than birds that had to pair with unfamiliar mates. Early pairing may have numerous advantages, for example increasing social status and access to the best food sources (Teunissen et al. 1985; Black et al. 1992); giving the birds more time to establish a workable relationship with a mate, which is necessary for successful breeding (Cooke et al. 1981; Black & Owen 1988; Owen et al. 1988); and ensuring a better choice of mates, and avoiding the risk of remaining unpaired altogether (Rohwer & Anderson 1988).

Mate complementarity and local adaptation

On the arctic breeding grounds, where nesting and feeding conditions for barnacle geese are variable (Prop & de Vries 1993) successful breeding may require both partners to be adapted to the same habitat and to know the local area well in order to optimize their use of resources. Assortative pairing between individuals from the same breeding area may ensure mate complementarity in local adaptation. We did not detect any difference in pair quality or breeding success of familiar and unfamiliar partners, but our geese experienced near to optimal conditions for breeding, so that the inter-pair variations in breeding success were negligible.

Inbreeding and genetic adaptation

Assortative pairing between individuals from the same breeding area may lead to a certain degree of 'inbreeding', and could ensure genetic

complementarity of mates and hence transmission of the successful genotype to the offspring (Shields 1982; Bateson 1983). Adaptation to a local area is likely to be of fitness value to barnacle geese; however, there is no evidence of a genetic basis to such adaptations and our results suggest that geese do not appear to differentiate mates specifically on the basis of kinship or genetic cues, and hence are unlikely to be selecting for genetic adaptations.

Other Mate-choice Criteria

There has been increasing evidence that animals may use multiple criteria in mate choice (Burley 1981; Johnson 1988a, b; Johnston & Johnson 1989). In barnacle geese, female weight, vigilance and face patterns, as well as male vigilance, have previously been shown to play a role in the selection of mates (Choudhury & Black 1993). Our results show that male body size and dominance status may also be of importance in mate choice. Body weight and size are related to breeding success in geese (Ebbinge 1989; Lessells 1982; Larsson & Forslund 1992), possibly because structurally large birds may be able to acquire larger nutrient and fat reserves, and hence invest relatively more in their offspring (Ankney & MacInnes 1978; but see Cooch et al. 1992). Dominance may predict access to nesting and feeding sites, which in turn affects life-time reproductive success (Owen & Wells 1979; Black & Owen 1989b).

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