Mate-selection behaviour and sampling strategies in geese

SHARMILA CHOUDHURY*† & JEFFREY M. BLACK*

The Wildfowl & Wetlands Trust, Slimbridge, Gloucester GL2 7BT, U.K.

†*EGI, Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.*

Abstract. Captive barnacle geese, *Branta leucopsis*, were allowed to choose mates in large social groups, over 2 years, simulating natural pairing conditions. During the mate-choice process, geese sampled from one to six potential mates in temporary 'trial liaisons', which lasted from a few days to several weeks. The number of trial liaisons did not differ significantly between the sexes, but was greater in heavier and more vigilant females. More vigilant males were sometimes able to acquire more than one long-term partner. Birds that started mate searching earlier in the season sampled more mates and invested more time on individual liaisons. A combination of two mate-sampling strategies was apparently used: (1) the 'one-step-decision strategy', where a bird decides at each encounter whether to accept or reject a mate, before moving onto the next candidate, and (2) the 'partner-hold strategy', where a bird holds onto the previously sampled mate whilst sampling a new one, comparing the relative qualities of both, before making a decision whether to leave the old for the new trial mate. The partner-hold strategy will yield the highest fitness of all mates sampled, yet puts no constraints on a bird of having to remember the qualities of all mates encountered and of re-locating the best mate.

Most studies of mate choice have been restricted to showing its existence, identifying the traits chosen, and providing evidence for the selective advantage of the chosen trait. Few studies have attempted to demonstrate the mate-choice process of sampling, selecting and rejecting potential partners (Brown 1981; Dale et al. 1990; Petrie et al. 1991).

Mate choice has typically been viewed as a mere acceptance or rejection of prospective partners that happen to present themselves to the choosing individual (Wittenberger 1983). Yet selecting a mate is a complex process involving searching, sampling, information gathering and decision making. Each step in the mate-choice process is generally subject to some constraints and animals may use different strategies to find the most suitable mate under given conditions. Little attention has been given to the alternative strategies that animals may use in mate choice, except for some theoretical investigations (Janetos 1980; Wittenberger 1983; Real 1990). It is only recently that field or experimental studies have attempted to address the question of how animals choose mates (Moore & Moore 1988; Zuk et al. 1990; Bakker & Milinski 1991; Petrie et al. 1991; Dale et al. 1992).

With no constraints on time, movement or memory, an animal's best strategy of mate choice would obviously be to inspect all available partners and then to select the best one. However, animals are usually subject to one or more constraints and unable to sample all available individuals. Several models have been proposed as to how animals may go about choosing mates under given constraints: (1) random mating (Janetos 1980); (2) fixed-threshold strategy (Janetos 1980; Wittenberger 1983); (3) one-step-decision strategy (Janetos 1980); (4) sequential-comparison strategy (Wittenberger 1983); and (5) best-of-*N*-mates strategy (Janetos 1980; Wittenberger 1983). Random mating suggests that there is no mate choice and that animals settle with the first mate encountered. The fixed-threshold strategy predicts that animals will sample mates until they encounter an individual that meets some minimum requirements or threshold value. This strategy requires animals to have an absolute standard of assessing potential mates. In the one-step-decision process, an animal has to decide at each encounter whether to accept or reject the potential mate. It cannot go back to a previously rejected individual once a decision has been made. In the one-step-decision process, the accepted mate needs only to have a fitness greater than the mean

*Address for correspondence.

fitness of all available mates, and a rejected mate may have been of higher quality than an accepted one (Janetos 1980). The sequential comparison tactic also predicts that mates are sampled in sequence, but the choosing animal always compares the two most recent candidates according to some rule. In the best-of-N-mates strategy an animal examines N potential partners, ranks them on a relative basis, and choses the best one; N may be the maximum number an animal can sample within the given time and space or within its memory capacity.

Here we use a monogamous species, the barnacle goose, *Branta leucopsis*, to investigate the mate-selection strategies of both sexes. Geese generally pair for life, mates stay together throughout the annual cycle and both help to rear the young (Owen et al. 1988; Black & Owen 1989). Mate choice and pair formation have been little studied in waterfowl species, mainly because the large, often very social, species do not lend themselves easily to captive experimental situations (but see Cooke et al. 1972; Cooke & McNally 1975; Bluhm 1985). However, in a species in which both partners depend on each other to rear young successfully, and mates stay together for life, we might expect selection to favour the careful choice of the initial mate.

METHODS

Seventy-eight young barnacle geese, 39 males and 39 females, were reared from incubator-hatched eggs in May 1989 in eight unisexual 'sibling' groups of 6–15 birds each. Each sibling group contained no more than two real genetic siblings. In the wild, young geese generally form pairs in their second winter (Owen et al. 1988). In October 1990, the start of the second winter for our captive geese, all birds were moved into two large enclosures, each containing four sibling groups. Within each enclosure sex ratios were balanced and birds were allowed to pair up freely until the end of the following summer (July 1991).

After the birds had been moved into the large enclosures for pair formation, we carried out observations once a fortnight for 8–12 h. In February, courtship behaviour suddenly increased, and observations were stepped up to 1–2 h virtually every morning, which was the peak time for courting behaviour. Birds were provided with nesting

materials during the breeding period in June–July, and allowed to establish nests and lay eggs.

Pair formation in barnacle geese consists of a series of stages. The male initiates the courtship by herding a female with loud calls and neck stretches. The female may either reject the male's advances or encourage him (Hausberger & Black 1990). If the female responds positively, the courtship proceeds to the next stage of mock attacks and triumph ceremonies, initially by the male alone, but gradually by the female too (Black & Owen 1988). As the pair bond increases in strength, both birds maintain greater proximity and respond to each other in courtship displays.

Pair Formation Behaviour

Behavioural data related to pair formation were mostly collected by continuous all-occurrence sampling (Martin & Bateson 1986). This included all courtship behaviour, i.e. mate searching, vocalizations, herding, mock attacks, triumph ceremonies, head-dipping and copulations (Black & Owen 1988), as well as leading/following, food sharing and friendly approaches. To obtain measures of proximity between birds, the three nearest neighbours of each individual were recorded at least once during each observation session. In addition, a category termed a 'consort' was used, and this was defined as two birds carrying out the same behaviour in the same direction at not more than one goose length apart and at least three goose lengths from another bird. Although pair formation is a continuous process, we decided to define the start of a partnership as the point from which the female started to join in the triumph ceremonies, or where she was observed to show a combination of at least three other positive responses to the male, for example, following, food sharing, friendly approach, continuous nearest neighbour, consort.

Phenotypic Qualities

To investigate mate-selection strategies in a species, it is essential to have some information on the qualities of individuals which might play an important role in affecting the outcome of an encounter. We therefore measured a range of phenotypic traits that might be of importance to the mating process, for example, as mate-choice criteria or in competition with conspecifics.

Dominance

Prior to pair formation dominance ranks were established from aggressive interactions, displacements and greetings. Appleby's (1983) test for linearity was used to confirm that goose ranks are linear, and Clutton-Brock et al.'s (1979) index was used to rank birds in a linear hierarchy.

Body Measures

We measured the skull, tarsus, wing and weight of all birds once they had attained full adult size at the age of 1 year (Owen & Ogilvie 1979). Principal Component Analysis (Rising & Somers 1989) was used to combine skull and tarsus measures to give a single index of overall body size (PC1). Although weight contains a component of body condition or reserves of a bird, we also obtained an index of abdominal profiles (Owen 1981). The indices of abdominal profile increase with body reserves, but there is no evidence of linearity, so that a mean cannot be used. The weighted median devised by Owen & Black (1989), which adjusts the median according to the number of values above and below it, was used: weighted median = (median (no. at median) (no. above − no. below))/(no. at median).

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. With a video-camera the face patterns were transformed to a computer and the image digitized (program by J.-P. Richard). The digitized data were used to calculate the percentage of black and white surface areas (Arc Info Program).

Vigilance

In geese, vigilance for predators is one of the main provisions of care provided by the parents, particularly the male (Lazarus & Inglis 1978; Black & Owen 1989; Sedinger & Raveling 1990). Male vigilance is also of considerable importance to the female in the pre-breeding season, whilst she is acquiring reserves for egg laying and incubation (Inglis 1977; Lamprecht 1989). To obtain vigilance ranks as a measure of mate quality, we carried out an experiment with an artificial predator on all birds in one of the two enclosures. Birds were split by sex into two groups and each group was subjected to the same treatment. A stuffed fox on a stick was 'walked' past the enclosure, resulting in all birds taking on the vigilant 'head-up' 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 score': 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 total number of head-ups during the 15-min sampling period. We repeated the experiment in order to get more samples, but found that the birds had habituated to the fox after one trial, and thus only used data from the first trial. The vigilance measures obtained in this way obviously only measure one kind of vigilance, i.e. a bird's reaction to the sight of a predator and subsequent attentiveness. In the wild, vigilance also includes continuous scanning for predators throughout the day and this may be a more important measure. However, in our captive set-up, birds had no experience with predators or other dangers and thus did not engage in regular vigilance bouts as geese in the wild do. They did react strongly to sudden disturbances or unknown stimuli, which enabled us to obtain a reaction to the stuffed fox.

RESULTS

Mate Sampling

Number of trial liaisons

About half the birds (51%) settled with the first mate they sampled, whilst the other half (49%) went through one or more trial partners or liaisons before settling with a consistent mate (Table I). Trial liaisons appeared to be indistinguishable from permanent pairs except for their temporary nature. We found no significant difference in the frequency of courtship behaviour and the proximities between partners of trial and final pairings on the first day of the association (Table II).

In geese, the male always initiates courtship bouts and it is thus not possible to determine choosiness on the basis of which individual initiated an encounter. However, the formation of a trial partnership has to be a mutual decision on the

Table I. Sequences of mates sampled by barnacle geese during mate choice (for birds sampling more than one partner)

Males	Mate sequence	Females	Mate sequence
BVE	LSS LZS–LSV*	LZS	LPA BVE BEF LPC*
BEF	LZS–LXI–LZS LZS–LSV–LZS LSZ–LSS*	LSS	BVE PAB BEF*
DEA	EEE–DEK DEK–LLU LLU–LYT–LLU*	LZX	LYU–KAP–LYU*
DEG	LJA–LXC–LJA*	EEE	DEA NAB*
LPA	LZS–LSP*	DEK	DEA–LSJ–DEA NAD*
NAB	LYT EEE*	LXI	BEF PAB*
PAB	LSS–LXC–LSS LSS–EEV* EEV–LXI*	LXC	PAB DEG
PAF	LPY* LPY–PAH*	LSV	LPT–BVE BVE–BEF–BVE*
LTF	BJT–LLU–BJT*	LLU	LTF DEA*
KAP	LIS–LZX–LIS*	LYT	DEA NAB
LYU	KHR* KHR–LZX*	LXN	KKC ECE*
KKC	LXN EXE LIN* LIN–DEI* DEI–NAU* NAU–LUT*	NAT	LTZ–NAZ NAZ–EIE*
LTZ	NAT–DEF* DEF–BEA*	LIN	LVD KKC*
LVD	LIN LYF*	NAU	LNV KKC*
NAZ	NAT–BEA DJE LVH*	LUT	BUJ–KKC*
		BEA	NAZ–LTZ*

a–b, Partner-hold strategy, animal moves from a to b. a–b–a, Partner-hold strategy, animal stays with a.
*Final mate (some males are polygynous).

Table II. Comparison of courtship behaviour and proximities between partners of trial and final pairings on day 1 (2 h) of the association

Behaviour	Mean number of occurrences ($\pm$ SE)		P^*
	Trial pairs ($N = 22$)	Final pairs ($N = 29$)	
Herding	4·3 ($\pm 0·8$)	5·2 ($\pm 0·7$)	NS
Triumph ceremony	0·4 ($\pm 0·2$)	0·6 ($\pm 0·2$)	NS
Head-dipping	0·4 ($\pm 0·2$)	0·3 ($\pm 0·1$)	NS
Follow	3·1 ($\pm 1·2$)	1·8 ($\pm 0·4$)	NS
Consorts	1·1 ($\pm 0·3$)	1·0 ($\pm 0·3$)	NS

*Mann–Whitney U-test at 5% significance.

part of both sexes (Hausberger & Black 1990) and indicates that both were sampling. Both male and female are therefore recorded as having sampled one potential mate for each trial liaison formed. Between one and six mates were sampled per bird, excluding individuals that sampled no mates, and there was no significant difference between the sexes (males: $\bar{X} \pm$ SE $= 1·91 \pm 0·23$, $N = 32$; females: $\bar{X} \pm$ SE $= 1·58 \pm 0·13$, $N = 38$; Mann–Whitney U-test: $z = -0·67$, $P = 0·5$). In most cases it was possible to determine which sex terminated a trial liaison, because one partner would start to direct threats at the other, respond negatively to or ignore any courtship advances, and/or start courting a new trial mate. There was no difference

in the number of liaisons terminated by males and females (males = 10, females = 10, Table III).

Duration of trial liaisons

The duration of individual trial liaisons varied greatly from 1 day to over 9 months, but the majority lasted only a few days (Fig. 1). There was a clear relationship between the duration of individual trial liaisons and the time of year (Fig. 2). Trial liaisons early in the season tended to be longer, and became shorter, the closer it got to the time of breeding (Spearman rank correlation, $r_S = 0·523$, $N = 24$, $P < 0·01$). We used liaisons only from February onwards, because the two liaisons formed earlier (in June and November the previous

Table III. Outcomes of individual liaisons and the identity and sex of the bird that terminated the liaison

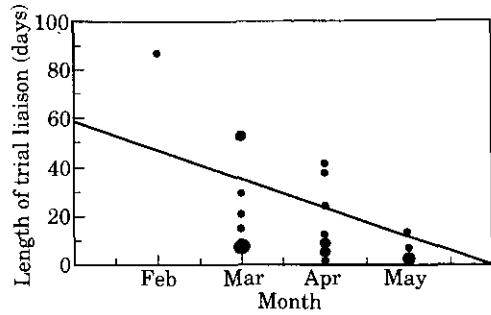| Trial pair	Terminated the liaison	Sex
BVE/LSS	BVE	M
BVE/LZS	Both	M/F
BEF/LXI	BEF	M
BEF/LSV	?	?
BEF/LZS	BEF	M
DEA/DEK	DEK	F
DEA/EEE	DEA	M
DEA/LYT	?	?
DEG/LXC	DEG	M
LPA/LZS	Both	M/F
NAB/LYT	LYT	F
LSJ/DEK	Both	M/F
PAB/LXC	PAB	M
PAB/LSS	?	?
LPT/LSV	LSV	F
LTF/LLU	LLU	F
KAP/LZX	LZX	F
KKC/LXN	LXN	F
KKC/EXE	KKC	M
LTZ/NAT	NAT	F
LVD/LIN	LVD	M
NAZ/NAT	NAT	F
NAZ/BEA	NAZ	M
NAZ/DJE	NAZ	M
LNV/NAU	NAU	F
BUJ/LUT	LUT	F

Figure 2. Effect of nearness to breeding season on length of trial liaisons. Circles of different sizes represent multiple points.
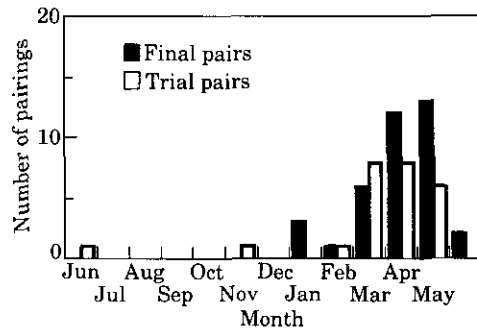

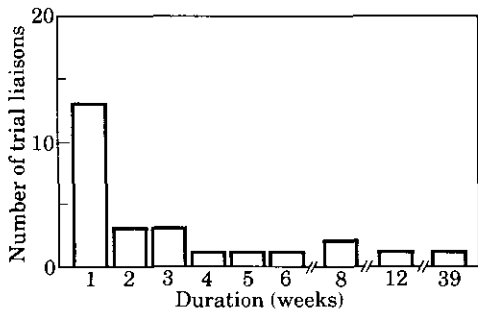**Figure 3.** Timing of pair formation in barnacle geese.

Figure 1. Duration of individual trial liaisons during mate selection in barnacle geese.
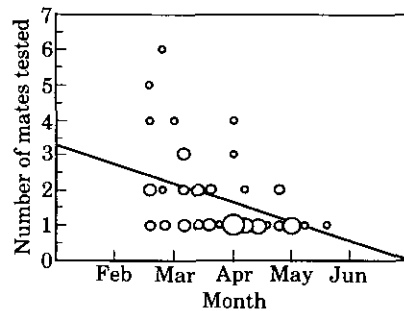

Figure 4. Relationship between date of starting mate searching and the number of trial partners sampled (Spearman rank correlation: $r = 0.44$, $N = 62$, $P < 0.01$). Circles of different sizes represent multiple points.

year) appeared to be outliers, i.e. they occurred before courtship behaviour increased in spring (see Methods). If these two points are included, the correlation is even higher ($r_s = 0.848$).

Timing of pair formation

The peak time for pair formation was March–May, with most of the trial liaisons as well as final pair bonds being established at this time (Fig. 3). Birds that started searching for a mate earlier in the season sampled more partners than those that started late (Fig. 4).
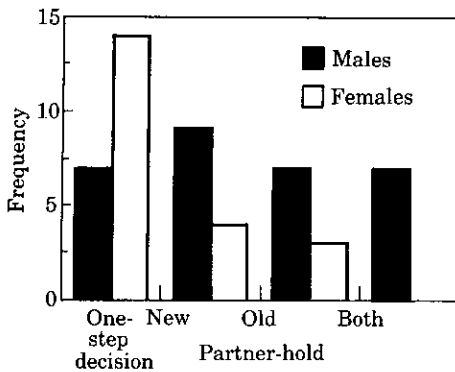
Figure 5. Sampling strategies used by geese during mate selection. During the partner-hold strategy, birds either moved on to the new trial mate, stayed with the old one, or formed a polygynous association with both trial mates.

Sampling Strategies

We looked at the sampling procedures used by geese that sampled more than one potential mate during the mate-choice process (Table I; Fig. 5). In about 40% of the cases ($N=21$), geese moved step-wise from one trial partner to the next. In these cases it is difficult to identify which strategy is being used, particularly as a number of these birds ($N=15$) sampled only two mates. Since none of the birds returned to a previous mate, it seems likely that the best-of-N-mates process can be ruled out. However, it is difficult to distinguish between the one-step-decision and the threshold-criterion strategy, since animals may move step-wise in both strategies. With the threshold rule, we would expect animals to continue sampling until a particular threshold quality of mate is encountered, and thus the accepted mate should always be of higher quality than a rejected one. Therefore, we compared the qualities of selected mates with those of rejected mates in mate-sampling sequences, to see whether the mate chosen at the end was of higher quality with respect to a particular phenotypic character. Neither sex appeared to be consistent in preferring mates with a particular trait (Choudhury 1992), which seems to suggest that birds were not aiming to obtain a particular threshold quality mate. However, it is also possible that individual birds had different choice criteria and were selecting for different qualities. The evidence seems to suggest, though, that birds are most likely to be using the one-step-decision process.

In the remaining 60% of cases ($N=30$), birds did not immediately forsake the first trial mate for the next, but used a 'partner-hold' strategy, where they continued to associate closely with the previous trial partner for a length of time, before deciding which partner to keep. Often this resulted in temporary trios, where three birds moved through the flock in a close unit. A male using the partner-hold strategy would usually start by alternating between the two females he was courting. He would direct most of his attention at the new female and return regularly to the old one, as if to reassure her of his intentions. Females, however, did not take the initiative in courtship, and the partner-hold process simply involved the female responding positively to the attentions of two males at once. The female would either alternate between the two males in approaching and maintaining proximity to them, or she would be courted and herded alternately by two males, both vying and competing for her attention. During the partner-hold strategy, birds ultimately either opted for the new partner (43%), stayed with the old mate (33%), or, in the case of males, sometimes paired with both the old and new female (24%). Although both males and females used both strategies, males used the partner-hold strategy significantly more often, whilst in females the one-step-decision process was most common ($\chi^2 = 5.85$, $df = 1$, $P < 0.05$).

Selectivity

To investigate whether the number of mates a bird sampled reflected its quality and choosiness, we looked at various bird characters in relation to the number of trial partners it had (Table IV). Heavy females in better body condition, more vigilant females, and those with darker face patterns tended to have more trial partners. There was no evidence that the amount of black in the face signalled either dominance rank (males: $r = -0.39$, $N = 23$; females: $r = -0.231$, $N = 23$) or more vigilance (males: $r = -0.095$, $N = 16$; females: $r = -0.219$, $N = 11$; Pearson correlation coefficient, NS). For males, none of the qualities investigated was related to the number of trial mates.

Although males sometimes had two female partners for a while during the partner-hold sampling process, in most cases the trio-relationship lasted only a few days. However, five males were able to form lasting partnerships with two or more

Table IV. Relationship between female and male characteristics and number of potential mates sampled

	Females			Males		
Character	r^*	N	P	r^*	N	P
Weight	0·377	39	<0·02	−0·033	38	NS
Abdominal profile	0·419	23	<0·05	0·079	23	NS
Size (PC1)	0·204	39	NS	0·060	38	NS
Vigilance 1 (head-up score)	0·697	12	<0·02	−0·251	12	NS
Vigilance 2 (head-down score)	0·570	12	<0·05	−0·046	12	NS
Dominance	0·076	23	NS	0·018	23	NS
Vocalization rate	0·016	39	NS	−0·139	39	NS
Face pattern (% black)	0·366	37	<0·05	−0·109	39	NS

*Pearson correlation coefficient.

females right up to or through the breeding season. To determine what types of males are able to attract more than one female, we compared various phenotypic traits of trio males with those of paired and unpaired males. Trio males were more vigilant (prior to pairing) than males with a single mate and unpaired males ($F=5·69$, $N=15$, $P<0·05$). There was no difference in body size, dominance rank or vocalization rate of trio males and others.

DISCUSSION

Mate-sampling Strategies

Conventional experimental methodology in mate choice tends to require animals to choose mates in a way quite different from the natural situation. Simultaneous choice situations, where animals are able to compare directly the qualities of potential mates, are likely to be uncommon in nature; animals will usually have to visit mates sequentially, comparing the present mate with information stored in memory about past mates sampled (Janetos 1980; Real 1990; Bakker & Milinski 1991). Most experimental studies on mate choice also restrict the time available to assess potential mates. This may limit the amount of information an animal can acquire on which to base its choice, and it ignores the possibility that some traits may vary over the normal mate-sampling period of the species (Sullivan 1990). Experimental investigations of mate choice should take into

consideration the species' natural sampling period and allow animals to choose in a natural manner and to base their decisions on similar amounts of information as they would normally have access to.

In this study, barnacle geese in captivity were allowed to choose mates freely in large social groups and over 2 years, closely simulating natural pairing conditions. We found that geese sampled between one and six potential mates in temporary trial liaisons or partnerships which lasted from a few days to a few weeks. Janetos (1980) showed that the expected fitness of the chosen mate increases with the number of mates sampled (N), but it does not do so linearly. For $N>5$, the potential gain from inspecting more mates is of diminishing value and may be outweighed by the costs of mate searching. This prediction is supported by our observations, although in our captive situation, we might well expect the number of mates sampled to be slightly lower than in the wild, because there is a limited number of birds to choose from and because birds are likely to gain some prior knowledge of mate quality from daily contacts in a confined situation. These figures are also likely to underestimate actual mate sampling, because they include only those mates sampled that were picked up by our classification of a trial liaison (see Methods). The mate-choice process, however, may be far more subtle, and some mate sampling and decisions may occur before trial liaisons are formed. Mate sampling could, for example, take place at two levels. Animals might eliminate totally

unsuitable or unattractive mates in a first selection round, without forming a trial partnership. The next selection step may involve going through trial liaisons with the potentially suitable candidates. Indeed, pair formation in geese consists of a series of courtship phases, and we observed a number of cases where a male initiated courtship towards a female, but then moved onto a different female, before obtaining a positive response. These cases were not included in the study and it is difficult to tell from such brief encounters, whether the male terminated the pairing process, or whether the female's lack of response or rejection caused the male to leave. These problems will occur in studies of any species where animals may assess the quality of mates without any recordable sampling behaviour. Thus we were able only to analyse mate-sampling behaviour that occurred above a certain threshold, namely beyond the level of forming a trial liaison.

In 40% of cases birds moved step-wise from trial partner to trial partner in the way predicted by the one-step-decision process, and since they never returned to a previously sampled mate nor appeared to be using a threshold criterion, it seems unlikely that they were using the best-of-N-mates or the threshold criterion strategies. In the remaining 60% of cases, the geese appeared to use a modified version of the 'sequential comparison rule' described by Wittenberger (1983). Instead of leaving one trial partner for the next, they held onto the old partner for a time, whilst sampling the new one. This 'partner-hold strategy' allows the choosing individual to compare the relative qualities of two mates before making a decision on whether to leave the old partner for the new one. A bird sequentially samples a number of prospective mates, always attempting to stay with the better of two consecutive mates. The partner-hold strategy should thus also give the best mate of all those sampled, yet have the advantage of freeing birds from the constraints of remembering the qualities of all mates encountered and of re-locating the best mate.

Barnacle geese therefore appear to use a combination of the one-step-decision and partner-hold strategies, with females predominantly using the former and males the latter strategy. This may partly be related to the fact that males could often retain the interest of two females for quite a while, even to the extent of forming a polygynous breeding association. However, both sexes may be exercising choice simultaneously, and the response of the sampled mate may affect the outcome of the encounter. The differences in sampling strategies of the sexes may thus simply be an artefact of differences in choosiness. If, for instance, females are the choosier sex, then two females choosing to sample the same male at the same time would result in an apparent 'partner-hold' process by the male. Similarly, if males are more choosy, then females may only proceed into a new liaison once the previous male has rejected them. This would result in the observed prevalence of the one-step-decision strategy in females. It is thus necessary to view results on mate sampling strategies in monogamous species with caution.

The few other studies that have empirical data on mate sampling have also found evidence for different strategies. Brown (1981) showed that female mottled sculpins, *Cottus bairdi*, pick the first male that is larger than the last one visited (sequential comparison; Wittenberger 1983), whilst Moore & Moore (1988) and Zuk et al. (1990) have evidence for the fixed-threshold strategy (Janetos 1980) in the cockroach, *Periplaneta americana*, and red jungle fowl, *Gallus gallus spadiceus*, respectively. Petrie et al. (1991) found that peahens, *Pavo cristatus*, appear to use the best-of-N-males rule (Janetos 1980) and visit up to five displaying males at a lek before selecting to copulate with one of them. Peacocks display in leks of a few birds, so the female has no difficulty in re-locating the best male. Barnacle geese, however, choose their mates in wintering flocks that number in their thousands (Black & Owen 1988; Owen et al. 1988). It seems unlikely that a bird searching for a mate will be able to find and return to the best candidate after sampling a number of potential mates very easily. This would severely limit the best-of-N-mates strategy for this species. The one-step-decision and the partner-hold strategies seem more suited to a flock-living species, since they do not require re-locating previously sampled individuals. The mate-choice strategy used by a species is thus likely to be determined by its life style and habitat.

Costs of Mate Sampling

Animals usually operate under a number of constraints when searching for a mate. One of the most obvious is a limit in time (Janetos 1980; Real 1990). This may reflect on the mate-sampling process in two ways, i.e. it may limit the number of

potential mates an animal can sample, or it may reduce the time the animal can spend on sampling individual candidates. We found that birds that started mate searching earlier in the season were able to invest more time in mate selection and test more potential partners. Also, the nearer it got to the breeding season, the less time birds were able to afford on each trial liaison and therefore the shorter the associations. Alternatively, these results could suggest that birds sampling mates at the beginning of the season are not yet efficient and therefore require more time. Towards the end of the mate-sampling period, birds may be more practised and thus able to sample mates more quickly.

In geese, pairing early may be advantageous for two reasons. First, when birds pair, they rise in rank above unpaired birds and may gain access to better feeding sites (Teunissen et al. 1985; Black et al. 1992). Sharing the burden of vigilance may also increase time available for feeding, particularly for females, who need to build up body reserves prior to breeding (Lazarus & Inglis 1978; Sedinger & Raveling 1990). The second advantage of pairing early arises from the observation that pairs apparently need to establish a workable relationship, before they succeed in a reproductive attempt (Black & Owen 1988; Owen et al. 1988). Successfully hatching and rearing goslings is usually achieved only after several seasons (Cooke et al. 1981; Owen 1984). The importance of the pair as a unit may also explain why geese, during the mate-choice process, form temporary pairs or trial liaisons in which they 'try out' the candidate as a partner. Most common mate-choice criteria, such as size, condition, plumage, dominance rank or vocalizations, can presumably be assessed fairly quickly by a bird, without requiring a closer association. However, assessing mate complementarity or compatibility may require more intensive and prolonged association, where both partners get a chance to test how well they function as a unit.

Birds are constrained not only by time when searching for a mate, but probably also by energetic costs (Parker 1982; Real 1990). In the wild, barnacle geese on the wintering grounds spend almost all daylight hours grazing. Although the longer days and favourable feeding conditions in spring allow the birds some leeway in their tight energy budget (McLandress & Raveling 1981; Black & Owen 1988), time spent on searching for and sampling a mate may reduce time available for feeding. This may explain our findings that females

in better body condition are able to invest the additional time in sampling more trial partners.

Selectivity

Studies investigating the traits selected in mate choice have first to rule out intra-sexual competition as a confounding mechanism for any observed mating patterns (Halliday 1983; Johnson & Marzluff 1990). When choice and competition interact, it is difficult to know whether dominants are being chosen or whether they simply monopolize access to mates. In barnacle geese, dominance rank is not related to the number of mates sampled, the time to acquire a consistent partner, or the number of final partners acquired (Choudhury 1992). This suggests that competition for mates is unlikely to be a major determinant of pairing success in geese. Hausberger & Black (1990) showed that the pairing process in barnacle geese requires mutual cooperation of both partners in social display, and that the male's persistence in courtship is influenced by the female's response.

Selectivity of the sexes is expected to be related to the relative amount of parental care (Trivers 1972). Although, male and female do not invest equally in offspring even in species with bi-parental care, the discrepancy is relatively small. In geese, lifetime monogamy, a virtually balanced sex ratio, and high parental investment of both male and female, suggest that both sexes should be selective in mate choice. We found no difference in the number of mates sampled and rejected by both sexes during mate sampling, suggesting that there may be little difference in choosiness.

Within sexes, choosiness is expected to be based on relative attractiveness of the choosing individual (Burley 1977). High quality birds will be in greater demand as mates and can thus afford to be more choosy themselves. We found heavy and more vigilant females as well as those with darker face patterns to have more trial liaisons, i.e. possibly being more choosy. Since greater body weight means greater fat reserves for breeding, and therefore a better chance of rearing goslings successfully (Ankney & MacInnes 1978; Ebbinge 1989), heavier females may be higher quality mates. Similarly, increased vigilance of the female may reduce the vigilance burden of the male when protecting nest and young, thus making the female more attractive as a mate. It is unclear what selective advantage darker face patterns in female barnacle geese could have.

In this study, some males continued to associate for a prolonged period with two or more females. We found that males with more than one female were more vigilant, even prior to pairing, than other males. Secondary females may benefit from the male's increased vigilance directly in terms of increased time for feeding, or indirectly by providing her offspring with the male's predisposition for high vigilance. Members of polygynous associations may also benefit from the higher dominance status of larger social units (Lamprecht 1987).

Problems of Interpreting Mate Choice in Monogamous Species

In monogamous species, especially those with bi-parental care, both sexes are expected to be selective when choosing a mate (Trivers 1972). Mate choice is thus likely to be an interactive process, with both sexes exercising choice, and with the action of one sex influencing the actions of the other and consequently the outcome of the encounter (Real 1990). They may use different choice criteria or different mate-choice strategies (Burley 1981). Within sexes, individuals may also differ in their choosiness, depending on their own quality or relative parental investment (Burley 1977). All these potential variables in the mate-choice process make it exceedingly difficult to interpret data even from experimentally controlled situations. Since it is difficult to assess the relative influence of each sex, the mate-choice process is generally simplified to being the outcome of an 'active' mate accepting or rejecting the 'passive' mate (Parker 1983). We have already stressed that our results on the mate-sampling strategies used by barnacle geese have to be viewed with caution, since the apparent pattern used by one sex could be strongly influenced by the responses of the other sex. Similarly, apparent selectivity or qualities chosen by one sex may be greatly influenced by the outcomes of previous encounters. Although experimental studies using more controlled situations, for example, where only one sex is permitted to exercise choice at a time, may indicate how animals may choose if they had unrestricted choice, this is an unnatural situation for most species. Pair formation eventually requires mutual acceptance by both mates.

ACKNOWLEDGMENTS

REFERENCES

Ankney, C. D. & MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk*, **95**, 459–471.

Appleby, M. C. 1983. The probability of linearity in hierarchies. *Anim. Behav.*, **31**, 600–608.

Bakker, T. C. M. & Milinski, M. 1991. Sequential female choice and the previous male effect in sticklebacks. *Behav. Ecol. Sociobiol.*, **29**, 205–210.

Black, J. M., Carbone, C., Wells, R. L. & Owen, M. 1992. Foraging dynamics in goose flocks: the cost of living on the edge. *Anim. Behav.*, **44**, 41–50.

Black, J. M. & Owen, M. 1988. Variations in pair bond and agonistic behaviours in barnacle geese on the wintering grounds. In: *Waterfowl in Winter* (Ed. by M. W. Weller), pp. 39–57. Minneapolis: University of Minnesota Press.

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

Bluhm, C. 1985. Mate preferences and mating patterns of canvasbacks (*Aythya valisineria*). In: *Ornithological Monographs No. 37: Avian Monogamy* (Ed. by P. A. Gowaty & D. Mock), pp. 45–56. Washington D.C.: American Ornithologists' Union.

Brown, L. P. 1981. Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Anim. Behav.*, **29**, 375–382.

Burley, N. 1977. Parental investment, mate choice, and mate quality. *Proc. natn. Acad. Sci. U.S.A.*, **74**, 3476–3479.

Burley, N. 1981. Mate selection by multiple criteria in a monogamous species. *Am. Nat.*, **117**, 515–528.

Choudhury, S. 1992. Mate choice in barnacle geese (*Branta leucopsis*). Ph.D. thesis, University of Oxford.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elephus I.*). *Anim. Behav.*, **27**, 211–225.

Cooke, F., Bousfield, M. A. & Sadura, A. 1981. Mate change and reproductive success in the lesser snow goose. *Condor*, **83**, 322–327.

Cooke, F., Mirsky, P. J. & Seiger, M. B. 1972. Colour preferences in the lesser snow goose and their possible role in mate selection. *Can. J. Zool.*, **50**, 529–536.

Cooke, F. & McNally, C. M. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour*, **53**, 151–170.

Dale, S., Amundsen, T., Lifjeld, J. T. & Slagsvold, T. 1990. Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behav. Ecol. Sociobiol.*, **27**, 87–91.

Dale, S., Rinden, H. & Slagsvold, T. 1992. Competition for a mate restricts mate search of female pied flycatchers. *Behav. Ecol. Sociobiol.*, **30**, 165–176.

Ebbinge, B. S. 1989. A multifactorial explanation for variation in breeding performance of brent geese *Branta bernicla*. *Ibis* **131**, 196–204.

Halliday, T. R. 1983. The study of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 3–32. Cambridge: Cambridge University Press.

Hausberger, M. & Black, J. M. 1990. Do females turn males on and off in barnacle goose social display? *Ethology*, **84**, 232–238.

Inglis, I. R. 1977. The breeding behaviour of the pink-footed goose: behavioural correlates of nesting success. *Anim. Behav.*, **25**, 747–764.

Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.*, **7**, 107–112.

Johnson, K. & Marzluff, J. M. 1990. Some problems and approaches in avian mate choice. *Auk*, **107**, 296–304.

Lamprecht, J. 1987. Female reproductive strategies in bar-headed geese (*Anser indicus*): why are geese monogamous? *Behav. Ecol. Sociobiol.*, **21**, 297–305.

Lamprecht, J. 1989. Distance regulation of hand-reared goslings (*Anser indicus*) to an unresponsive parent: a study of the short-term dynamics of attachment. *Behaviour*, **108**, 209–240.

Lazarus, J. & Inglis, I. R. 1978. The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour*, **65**, 62–82.

McLandress, M. R. & Raveling, D. G. 1981. Hyperphagia and social behaviour of Canada geese prior to spring migration. *Wilson Bull.*, **93**, 310–324.

Martin, P. & Bateson, P. 1986. *Measuring Behaviour: an Introductory Guide.* Cambridge: Cambridge University Press.

Moore, A. J. & Moore, P. J. 1988. Female strategy during mate choice: threshold assessment. *Evolution*, **42**, 387–391.

Owen, M. 1981. Abdominal profile: a condition index for wild geese in the field. *J. Wildl. Mgmt*, **39**, 227–230.

Owen, M. 1984. Dynamics and age structure of an increasing goose population: the Svalbard barnacle goose *Branta leucopsis*. *Nord. Polarinst. Skr.* **181**, 37–47.

Owen, M. & Black, J. M. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. *J. Anim. Ecol.*, **58**, 603–617.

Owen, M., Black, J. M. & Liber, H. 1988. Pair bond duration and timing of its formation in barnacle geese (*Branta leucopsis*). In: *Waterfowl in Winter* (Ed. by M. W. Weller), pp. 23–38. Minneapolis: Univeristy of Minnesota Press.

Owen, M. & Ogilvie, M. 1979. Wing moult and weights of barnacle geese in Spitsbergen. *Condor*, **81**, 42–52.

Parker, G. A. 1982. Phenotype-limited evolutionary stable strategies. In: *Current Problems in Sociobiology* (Ed. by King's College Sociobiology Group), pp. 173–201. Cambridge: Cambridge University Press.

Parker, G. A. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–166. Cambridge: Cambridge University Press.

Petrie, M., Halliday, T. & Sanders, C. 1991. Peahens prefer peacocks with elaborate trains. *Anim. Behav.*, **41**, 323–331.

Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.*, **136**, 376–405.

Rising, J. D. & Somers, K. M. 1989. The measurement of overall body size in birds. *Auk*, **106**, 666–674.

Sedinger, J. S. & Raveling, D. G. 1990. Parental behaviour of cackling Canada geese during brood rearing: division of labour within pairs. *Condor*, **92**, 174–181.

Sullivan, M. S. 1990. Assessing female choice for mates when the males' characters vary during the sampling period. *Anim. Behav.*, **40**, 780–782.

Teunissen, W., Spaans, B. & Drent, R. H. 1985. Breeding success in brent geese in relation to individual feeding opportunities during spring in the Wadden sea. *Ardea* **73**, 109–119.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Wittenberger, J. F. 1983. Tactics of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 435–447. Cambridge: Cambridge University Press.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Mechanisms of female choice in red jungle fowl. *Evolution*, **44**, 477–485.