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Reviewed work(s):
Source: *Behaviour*, Vol. 100, No. 1/4 (Feb., 1987), pp. 134-169
Published by: BRILL
Stable URL: http://www.jstor.org/stable/4534580
Accessed: 22/02/2013 07:16

ON THE MECHANISM OF MATE SELECTION IN BLACK-HEADED GULLS

by

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(With 10 Figures)

(Acc. 20-IV-1986)

1. Introduction

The purpose of this paper is to identify proximate mechanisms for mate selection in black-headed gulls (*Larus ridibundus*). Little is known about how pair-bonds between gulls are established, which roles are played by the two sexes, and which criteria are used in mate selection. Yet, such information is important, and even indispensible for the ultimate goal of understanding which messages are exchanged between individuals during courtship ceremonies (MOYNIHAN, 1955; MANLEY, 1960; VAN RHIJN, 1981). Such information can only be obtained by a very careful analysis of pair-formation between known individuals.

For kittiwakes (*Rissa tridactyla*) part of the required data could be obtained under ideal field conditions (COULSON, 1972, 1980). In wild black-headed gulls the situation is more complex, since courtship and nesting are rarely tied to the same location. Their way of life offers almost no opportunities for tracking individuals over the different phases of their reproductive cycle. We were convinced that we would circumvent this difficulty by taking captive birds as subjects for the analysis of the causal

[1]) We are greatly indebted to Gerard BAERENDS for taking the initiative for this study, for the encouragements and his constructive guidance. We wish to express our gratitude to Jan VEEN for his support with field data, his continuous interest and critical reading of drafts of this paper. We further wish to thank Marian HULSCHER-EMEIS for suggesting many improvements after a very careful review of the manuscript, Ab BULT, Hans GROLLE, Herman GROOTERS, Dick van HOFFEN, Rob MANTEL, Hein MASSELING, Rob MINKELS, Gerry MUG, Leo van MULLEKOM, Marcel van der POL, Leo POSTHUMA, Wim RUITERKAMP, Gera SCHMIDT, Janny SWAVING, Ron VODEGEL, Henk de VRIES, and Eddy van der ZEE, for their help in collecting the data, Dick VISSER for drawing the figures, Hil LOCHORN-HULSEBOS for typing the manuscript, and Auke MEINEMA for saving the life of many gulls by removing a dangerous predator.

mechanisms underlying pair-formation and parental care. We do realize that the behaviour of these birds is not a very precise reflection of the events in the field, but that is not necessarily unfavourable for the present approach.

The results will be presented and discussed under two different headings. The first, 'Dynamics of social relationships', specifies a number of aspects of pair-bonding, including the tactics applied by males and females for establishing a bond, and the second, 'Factors affecting the formation of social relationships', enumerates the effects on pair-bonding of age, reproductive state, physical condition, social experience, and social environment. In a final discussion, 'Possible factors leading to the formation of unusual associations', some ideas about the establishment of polygynous, male-male, and female-female associations will be developed.

2. Methods

2.1. *Subjects.*

The present data refer to in total 168 black-headed gulls kept in experimental groups in aviaries. Altogether these gulls were observed during 469 bird seasons. All the gulls were reared in or near to the laboratory ever since hatching or a few days after. Details about rearing conditions, housing, and food are given in another paper (VAN RHIJN & GROOTHUIS, 1985).

All birds were colour-banded in order to be recognizable for the observer. Head plus bill measurements were taken for sexing (VAN RHIJN, 1985). Weights were determined on several occasions to obtain information about sex and condition. Hood colouration was checked every week during the late winter and early spring as a measure of the reproductive state.

The social situation for each gull was controlled experimentally. For instance, some individuals were kept without conspecifics during their first year of life, others without members of the opposite sex during periods of a few weeks. All changes in group compositions were aimed at the acquisition of a maximum amount of information about the social behaviour of our birds. In most years we changed the social situations for the gulls by transferring birds from one group to another. In one year several successive rearrangements of the groups were performed. By these procedures several gulls became separated from previous mates and got the opportunity to establish new social preferences.

Throughout the year we observed social behaviour and social preferences, especially focussing upon the reproductive season. The first pair-bond was established in 1978, the first eggs were laid in 1979, and the first offspring from captive parents was raised in 1980. Because hatching success was very low in the aviaries, we replaced a number of clutches which did not hatch by peeping eggs from the field. Many of the hatched chicks were raised successfully by the foster-parents.

2.2. *Defining strong and weak social preferences.*

Pair-bonds which finally resulted in reproduction were the most stable social relationships. All these pair-bonds were characterized by a period of several weeks during early spring in which the two members mutually perform many meeting ceremonies. Such ceremonies contain the same behavioural elements as displayed in certain agonistic interactions, but the ceremonies are rarely followed by overt agonistic behaviour. Both partners are seen to take the initiative for the ceremonies. In the early parts of the season (Fig. 1) the ceremonies contain synchronized repetitions of a Straight Up with Long-Call followed by a Low Up, which are concluded by an Upright Out with Head-Flagging (MOYNIHAN, 1955; TINBERGEN, 1959; MANLEY, 1960; FJELDSÅ, 1978; VAN RHIJN, 1981). In the later stages the number of repetitions decreases (MANLEY, 1960), the Straight Up is replaced by the Oblique Out, and the Low Up by the Forward (VAN RHIJN, 1981). Finally the whole sequence tends to be reduced to an Upright with Head-Flagging (MANLEY, 1960). In these reproducing pairs the meeting ceremonies are frequently followed by Begging by the female, Luring and Regurgitation by the male, and in several instances by Begging by the female combined with Head-Bobbing by the male which often leads to Copulation.

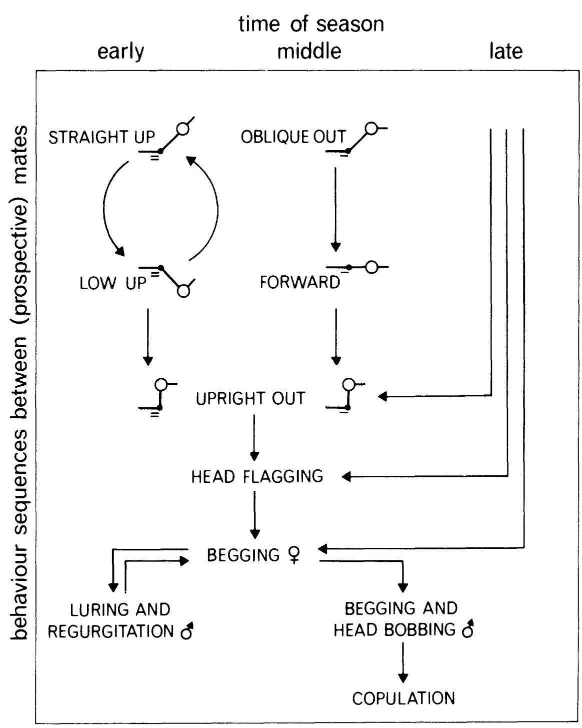

Fig. 1. Main sequences of behaviour initiated by meeting ceremonies in different parts of the pre-laying season. The diagrams of the postures show the angles of body-axis, neck and bill, and the extension of the carpal joints (–: slightly extended; =: strongly extended). See also text.

All members of these successful pairs were considered to have *strong* social preferences for their mates. In non-successful combinations of individuals both members were also considered to have *strong* social preferences for each other if their meeting ceremonies were marked by the same phenomena as in successful pairs and had been shown for at least one week.

In a few non-successful combinations of individuals meeting ceremonies were always initiated by one particular member, while the other was hardly responding. In this case the initiator was defined to have a *strong* social preference for the other bird if complete meeting sequences (Straight Up or Oblique Out followed by Low Up or Forward and concluded by Upright Out with Head-Flagging) were given for at least one week. In the remaining cases the initiator was defined to have a *weak* social preference. A *weak* social preference for the initiator was attributed to the other bird if it was seen to participate in the meetings only now and then, and *no* social preference for the initiator if the display was ignored or responded to by avoidance or aggression. In all combinations of individuals between which recognizable relationships existed, but which were not reflected by the occurrence of complete meeting sequences during at least one week, both members were considered to have *weak* social preferences for each other.

3. Dynamics of social relationships

3.1. The establishment of bonds.

Apart from parent-offspring connections, the first bonds during life in our experimental chicks were observed when they were a few weeks old. Frequently, particular combinations of individuals, usually the members of a small groups raised in the same cage, tended to sit, eat, and bathe together with no signs of aggression or fear. Mutual begging was often observed in these combinations. Meeting ceremonies did not occur between these birds. In contrast some other combinations of chicks were highly competitive. Among the wild black-headed gulls early bonds arise between nest companions.

In sub-adult birds (second calendar year) early bonds were sometimes re-established after the first winter, but new bonds were also formed. Every association between individuals of that age was initiated by meeting ceremonies. Usually bonds between sub-adults were formed after the majority of the adults had paired (see below). Nuptial moult was late in sub-adults and only a very small proportion developed a fully dark head.

During the late winter and early spring, the adults were rarely seen to display social preferences. All birds seemed to move randomly amongst each other. On several occasions they were seen to sit in dense groups, but no clear patterns of associations between particular individuals could be detected. Interactions between gulls were mainly seen when both participants were attracted by the same food or water. At the various food-containers and bathing pools different social-dominance hierarchies were established.

The first meeting ceremonies of the season, in which two or more birds performed synchronized display sequences and Long-Calls, appeared at the end of March. This coincided with the first meeting ceremonies we observed between the wild gulls wintering in the same area, and with the time that we saw black-headed gulls returning to the colony sites in the northern part of the Netherlands. The first complete nuptial plumages (chocolate-brown head with red eye-rings, bill, and legs) appeared at the end of February, just as is the case in the wild gulls in the region. At the time of the first meeting ceremonies approximately 50% of the adult birds (from their third calendar year onwards) possessed fully dark heads. Completion of nuptial plumages in adult birds was spaced out until the beginning of May.

At the end of March only a small proportion of the adult birds took initiatives for meeting ceremonies. This proportion gradually increased during April. After the middle of May the formation of new pair-bonds ceased.

3.2. Social preferences of males and females.

The majority of the bonds arose between a male and a female. Female-female bonds were not found among the captive black-headed gulls, male-male bonds were frequently observed.

Several parameters of social preferences occurring during 173 male and 137 female seasons are represented in Fig. 2. This diagram also presents the effect of age for the two sexes (see also section 4.1.). The average number of social preferences per bird per season was higher in males than in females (A), but the proportion of strong social preferences remained lower in males (B); this was particularly true for the older age classes. In males this proportion of strong social preferences was fairly constant from their second calendar year onwards (roughly 65%), but in females this proportion increased with age (Spearman's rank-correlation) and approximated 100% in the older age classes.

All social preferences of females were directed to males. Although most of the social preferences of males were directed to females, a considerable number of their preferences were towards other males (C). We were unable to identify the sex of all individuals preferred by males, but the proportion of preferences for evident males was negatively, and the proportion of preferences for evident females was positively correlated with age (Spearman's rank-correlation). Males of the older age classes mostly directed their social preferences to females, but even then some of their preferences (roughly 20%) were to males. This was partly due to the fact that, infrequently, a male, during its later life, continued to display homosexual social preferences only.

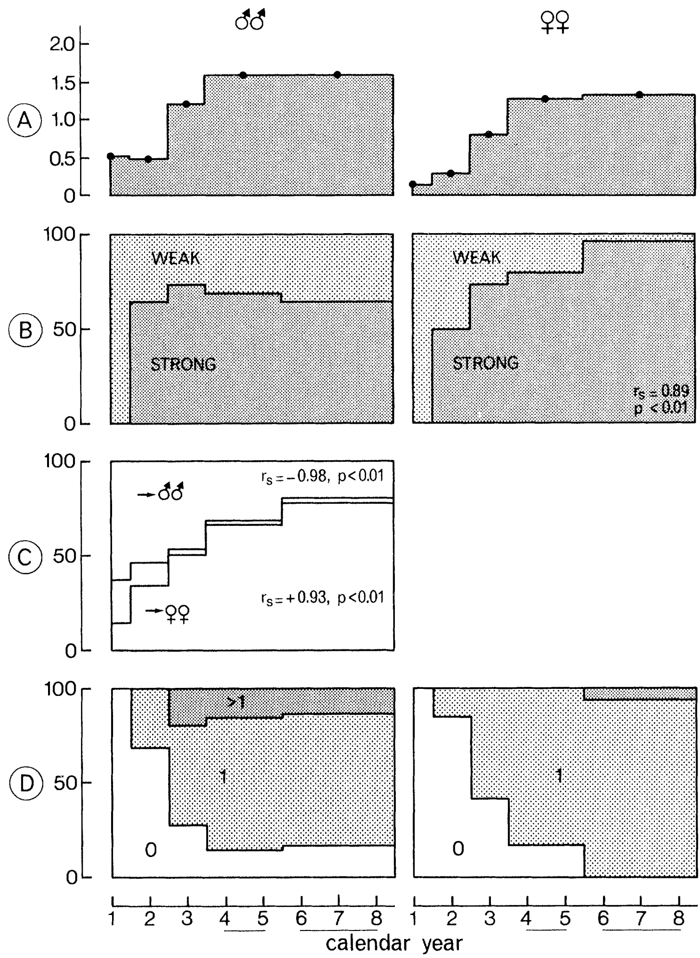

Fig. 2. Social preferences in relation to sex and age. A = average number of social preferences per bird per season, B = percentage of weak and strong social preferences, C = percentage of social preferences of males directed to each of the sexes, and D = percentage of birds without strong social preferences, with one at the same time, or with more strong social preferences at the same time.

Another difference between males and females refers to the frequency of birds without strong social preferences, birds with one preference at the same time and birds with more strong preferences at the same time. (D). Young females were rarely seen to display any strong social preference. The probability to display such preferences increased to 100% in females of the older age classes, but only a very small proportion

TABLE 1. Proportion of birds maintaining additional strong preferences when they established new social preferences (except for their first strong one) or definitely terminated old ones (except when caused by own death)

All kinds of social preferences by males and females:

A. establishment			B. termination	
males	females		males	females
52	36	no additional bonds	41	31
15	2	additional bonds	12	2
$\chi^2 = 5.35$, one sided test $P<0.01$.			$\chi^2 = 4.16$, one sided test $P<0.05$.	

Homosexual and heterosexual social preferences by males:

C. establishment			D. termination	
homosexual	heterosexual		homosexual	heterosexual
19	33	no additional bonds	11	30
6	9	additional bonds	4	8
$\chi^2 = 0.06$; n.s.			$\chi^2 = 0.19$; n.s.	

displayed two strong social preferences simultaneously. In males the probability to display strong social preferences never reached 100%. Yet, a fairly constant proportion (about 15%) displayed two or more of such preferences at the same time. Thus, at least some male black-headed gulls tend to show polygamous behaviour, while females appear to behave mainly monogamously.

The tendency for polygamy in males is further illustrated by a high probability to maintain additional social preferences when they establish new social preferences, or when they terminate existing social preferences (Table 1). During establishment (A) and termination (B) of bonds males more often maintain additional social prefernces than females. This proportion of additional strong social preferences does not differ between males establishing (C) a bond with a member of the other and of their own sex. Similarly, additional strong social preferences are equally common in mates terminating a homosexual as in those terminating a heterosexual bond (D). Thus, for male gulls, establishment and termination of homosexual social preferences occur, with regard to additional

TABLE 2. Proportion of birds continuing social preferences for two consecutive seasons

Strong and weak social preferences by the two sexes:

A. strength before winter[1])			B. strength after winter[2])	
strong	weak		strong	weak
50	36	not continued	53	52
62	17	continued	57	13
$\chi^2 = 7.86$, one sided test $P<0.01$.			$\chi^2 = 17.23$, one sided test $P<0.01$.	

Homosexual and heterosexual strong social preferences by males:

C. strong preferences[1]) before winter			D. strong preferences[2]) after winter	
homosexual	heterosexual		homosexual	heterosexual
7	23	not continued	9	24
3	29	continued	0	29
Fisher exact probability test, $P = 0.125$.			Fisher exact probability test, $P = 0.002$.	

[1]) Based on subjects which stayed alive until next spring.
[2]) Based on subjects which displayed at least one strong social preference in a previous year.

bonds, under similar conditions as in the case of heterosexual preferences.

3.3. Continuation of bonds.

The first meeting ceremonies of each season were often shown among individuals which were paired in the preceding summer. Generally, the frequency of their encounters increased within a few days and in these cases the birds rarely selected another mate for that reproductive period. Out of 52 birds which stayed in the same cage as the bird with which they performed a breeding attempt in the previous year 69% succeeded to continue nesting with the same mate. It further turned out (Table 2) that strong social preferences more often led to continuation (weak or strong) after the winter than weak ones (A). Similarly, these strong ones were more often the result of a continuation of a weak or strong social preference in the previous year than the weak ones (B). Thus, the strength of the preference for a particular bird seems to be one of the causes of the prolongation of that preference. Strong homosexual social preferences by males were less often associated with continuations than strong heterosexual ones (C and D). Thus, after a season of thorough experience with a particular bird, males seem to be less inclined to proceed with the same individuals when these are males than when these are members of the appropriate sex for reproduction. For the heterosexual pairs we were unable to demonstrate a statistically significant effect of reproductive success on the probability of continuation, such as found by COULSON (1980) for the Kittiwake.

The average number of eggs in 25 pairs which were re-established in the following season, was 1.88 against 2.29 in 7 pairs which did not continue after the winter, but did have the opportunity to do so. The average number of hatched eggs was 0.84 and 0.43 respectively.

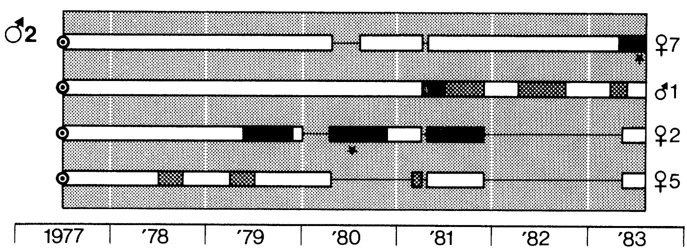

Fig. 3. Social preferences displayed by ♂2. Time of birth and death of the subject is indicated by the left and right limitation of the diagram. Each line represents one partner, whose sex and identity are given on the right side. Black bars on these lines refer to periods with strong social preferences of the subject (in this case ♂2) for the partners concerned, grey bars to periods with weak social preferences, white bars to no discernable preferences although both birds were in the same cage during that period. Interruptions of the bars refer to the periods when both birds were separated. Time of birth of partners is indicated by small circles, nesting and breeding attempts are marked by stars.

Social preferences for previous mates did not easily fade. Even after long periods of separation, which in some cases led to the establishment of new bonds, we saw that previous bonds could be restored.

The following examples illustrate this phenomenon:

In spring 1979 we observed strong social preferences between ♂2 and ♀2 for the first time (Fig. 3). In the beginning of January 1980 the two individuals were accommodated in separate cages. When they were brought together again in the end of April, they immediately started to court one another, and the pair-bond was re-established within a few days.

In the beginning of April 1980 we observed for the first time strong social preferences between ♂7 and ♀3 (Fig. 4). At the end of the same month ♀3 was transferred to another cage to be paired with ♂3, whose mate (♀5) was at the same time transferred to again another cage. Our match-making was successful and the new pair-bond between♂3 and ♀3 was even continued in spring 1981. However, when on 20 April ♂7 was put into the cage with ♂3 and ♀3, the 'new' bond between ♂3 and ♀3 was terminated, while the original bond between ♂7 and ♀3 was re-established.

During one week in spring 1981 strong social preferences were formed between ♂1 and ♂9 (Fig. 5) when ♂1's mate (♀1) was temporarily accomodated in another cage. This bonds was supplementary to an already existing bond between ♂1 and ♂2 (see also: VAN RHIJN, 1985). After that week ♂9 was transferred to another cage, while ♀1 was brought back to her mate. The latter pair-bond was immediately re-established. When, after two weeks, ♂9 was brought back in the cage with ♂1 and ♀1, he started to initiate many meeting ceremonies towards ♂1 from the first minute of reunion onwards.

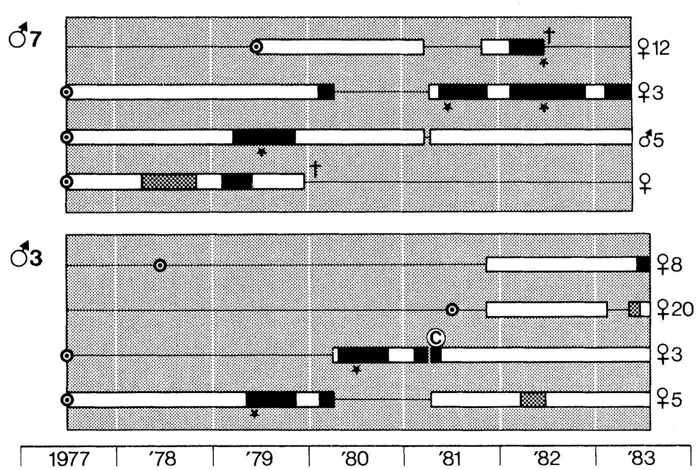

Fig. 4. Social preferences by ♂3 and ♂7. For a further explanation see also Fig. 3. Additionally, time of death of partner is indicated by a cross, and the termination of a bond by a change of mates by the partner by C.

3.4. Maintenance of bonds.

During the initial phase of pair-formation when meeting ceremonies predominated, a gradual rise of the frequency of Begging was observed. This behaviour was mainly performed by females, but Begging by males was certainly not negligible (VAN RHIJN, 1985). Begging by the female of a pair sometimes elicited Luring and Regurgitation by the male. Regurgitation mainly occurred in the early phase of pair-formation. Among wild black-headed gulls it was most often seen just before and during the period of egg-laying, when females seemed to be very much

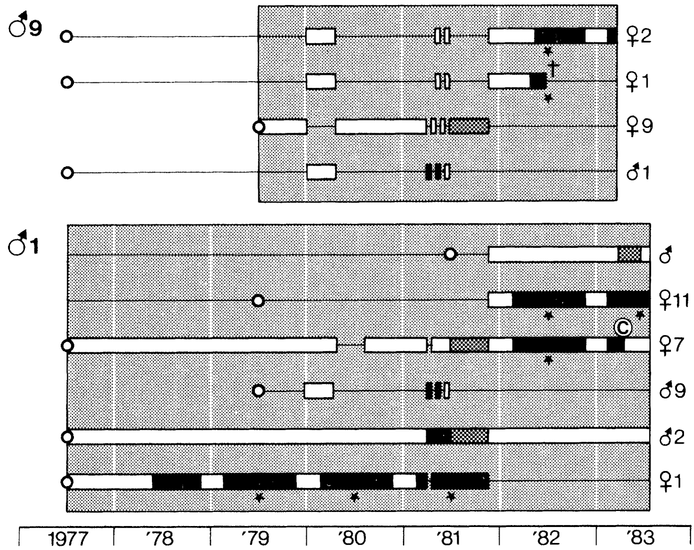

Fig. 5. Social preferences by ♂1 and ♂9. For a further explanation see also Figs 3 and 4.

interested in eating the food. The decrease of the incidence of Regurgitation in our groups might be caused by the fact that these females were mostly reluctant to eat the food, possibly due to the ad-lib food conditions.

Quite often, Begging of one member of a pair elicited Begging in the other member. Such Begging in males frequently changed into Head-Bobbing, which was followed by Copulation Attempts in many cases. In those pairs which were still in the beginning phase of pair-formation, Copulation Attempts usually failed, because the male partner was unable to maintain its equilibrium on its mate's back. For instance, out of 25 copulation attempts, which contained (for each pair in 1981) the first 50% of all attempts, 78% failed. In the experienced pairs both partners were seen to cooperate in achieving a series of cloacal contacts during each single mount, which could last for several minutes. Out of the remaining 25 copulation attempts, occurring later on in the cycles of the pairs in 1981, only 22% failed. In heterosexual pairs the female was never seen to mount the male. In a few male-male pairs both members were seen to mount each other, but in most homosexual pairs only one male was observed to mount. In the majority of male-male pairs the homosexual Copulation Attempts were not seen to lead to cloacal contacts. Two male-male pairs formed exceptions. In one of them the number of cloacal contacts was extremely high. One member performed all the mounts, although a few intentions for mounting by the other were observed.

Before the eggs were laid, a few birds were seen to preen their mates. In one pair (♂6 and ♀6) it was regularly observed: exclusively the female partner preened her mate, mostly during periods when both partners were sitting quietly together. The preening movements were always directed towards the neck region close to the border of the white and dark feathers. In another pair one case was documented in which preening was performed by the female just before Copulation and directed to the same region. Another observation of social preening in a third pair involved the male who was preening his mate one day before we found her first egg of the season. In view of the low incidence of social preening we think that this behaviour plays an insignificant role in most relationships for the maintenance of the pair-bond.

Several weeks after the establishment of the pair-bond, the pair-members were often seen to start nestbuilding at one or more locations. After egg-laying and during incubation the frequency of meeting ceremonies, Begging, and Luring was generally low, and social preening was never seen. If a brood failed the display frequency rose again, and copulation activity was observed to resume in several pairs. Many of such pairs laid a second clutch.

After incubation, but still during the care for chicks a new peak in display activities could be observed. Meeting ceremonies were very common, and Begging, Luring, and even Copulations occurred on many occasions. This new period with social interactions, which can also be seen among wild gulls in the vicinity of their feeding areas, often lasted until the beginning of the winter. Almost all these interactions came to pass between members of established pairs, or they were initiated by birds which were kept in isolation up to the beginning of that summer. We do not have indications that new pairs were formed during this period. The sudden rise of display activity during the summer is surprising, because it coincides with the beginning of moult, resulting in the loss of the dark head in the beginning of August.

3.5. Shifts of relationships.

The establishment of new social preferences often occurred after the death of the previous partner or after artificial separation. In the pre-laying, and particularly in the laying and in the early incubation phase, many of the individuals having become single established new preferences within a very short period, sometimes within one day. Later, during summer or autumn, we found no indications that such rematings occurred after the death or the separation of a partner.

The following examples illustrate this seasonal influence on the tendency to remate: In the beginning of April 1981 the sexes were separated for two weeks. Within this period at least two male-male pairs were established.

In the end of April 1980 ♂3 and ♀3 (Fig. 4), originating from different groups, were separated from their respective mates and brought together in a cage with two other pairs. After two weeks ♂3 and ♀3 frequently had meeting ceremonies with each other. After three weeks they started nesting, and after five weeks the first egg was laid. One of the former mates also remated within a short period, the other one remained single. In the end of May 1983 two gulls (♂7 and ♀6; Figs 4 and 6) were killed by a polecat, which had managed to penetrate into the cage. Both the widow (♀3) and widower (♂6) remated in about one day. The widower (♂6) did not reproduce afterwards during the same season (Fig. 6). The widow (♀3), however, produced two eggs with her new mate (♂5), about three weeks later.

The same polecat (just before it was caught and removed from the area) killed seven other gulls in the end of July 1983. The five birds that consequently lost their mates did not remate that summer.

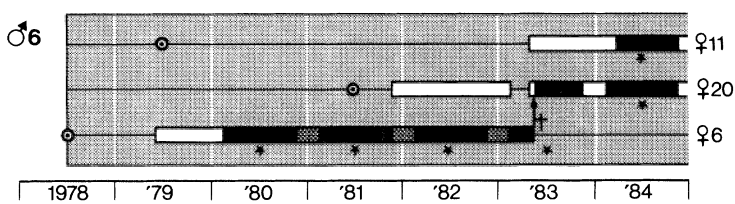

Fig. 6. Social preferences by ♂6. For a further explanation see also Figs 3 and 4. Additionally, a change of mates by the subject is indicated by an arrow.

In a number of cases the establishment of new social relationships was associated with the active termination of the previous relationship (Table 3B and C). Initiatives for the termination of bonds were more often taken by females than by males (A). The occurrence of such shifts was also restricted to the pre-laying, laying, and possibly the early incubation phase.

The most fascinating case concerned ♀3 (Fig. 4). In the end of March 1981 her pair-bond with ♂3 was re-established. The male, however, did not seem to be very active. Perhaps because of this, the female started to approach other individuals in the middle of April, and initiated meeting ceremonies. She still spent most of her time together with ♂3 and initiated meeting ceremonies with him. Several times, however, she approached the male from which she had been separated in the early spring 1980 (♂7), and which had remained single since then. At first ♂7 did not react upon her advances, but after a few days he participated in the meeting ceremonies, and then the female changed mates definitively. From that moment onwards and during the next few days she was almost continuously at the side of ♂7, while both were engaged in many meeting ceremonies together, ♂3 was never approached again (see also: VAN RHIJN, 1985). In this case the abandoned ♂3 did not try to approach his former mate (♀3) very often. If he did, however, she simply ignored him.

TABLE 3. Proportion of birds clearly taking the initiative for leaving former mate during the termination of old social preferences (termination by own death not included) and during the establishment of new ones (establishment of first strong social preference not included)

All kinds of social preferences by males and females:

A. Termination			B. Establishment	
males	females		males	females
3	10	own decision to leave	0	7
50	23	other cases	67	31

Fisher exact probability test, $P = 0.0028$. (A)

Fisher exact probability test, $P = 0.0006$. (B)

Heterosexual social preferences by males and females:

		C. Establishment	
		males	females
Former bond terminated by:	own decision to leave	0	7
	other cause	3	3
No former bonds or no former bonds terminated		39	28

In many cases gulls continued to initiate meeting ceremonies with their previous partners after these had changed their social preferences. In those cases these initiators were often strongly attacked. Even so, some of these unidirectional social preferences have been observed to last several weeks.

3.6. Termination of bonds.

In the course of November and December the frequency of meeting ceremonies and other behaviour patterns associated with social preferences were seen to decrease to a very low level. Almost all birds which were paired in the preceding summer started to move independently of their mates. In January no indications for the existence of individual recognition between former pair-members could be observed any longer, except in one pair (♂6 and ♀9; Fig. 6), in which both members remained in contact during the whole winter period by means of begging calls. The latter pair was the one which regularly performed social preening in the pre-laying period (section 3.4.). This pair was exceptional in the sense that both members had been kept in visual isolation from other gulls up to the summer of their second calendar year.

3.7. Role differentiation between the sexes.

It has been suggested that 'during pair-formation gulls first try to investigate each other's qualities, and if both individuals appear to be sufficiently equivalent, they subsequently may exchange information about sex' (VAN RHIJN, 1985). The present data can test the validity of this suggestion. Moreover, they can also reveal a detailed picture of the behaviour of prospective mates and of the roles played by the two sexes.

The results of the data on pair-formation show several differences between males and females in the establishment of social relationships. Females were seen to direct social preferences to males only. Additionally, they almost never exhibited more than one social preference at the same time. In contrast, males were seen to direct social preferences towards females and males, and to maintain several of these at the same time (Fig. 2C and D). Such data suggest that female black-headed gulls are very selective with respect to sex during the process of pair-formation, whilst male gulls are far less so. Females must have made very precise judgements about the sex of potential mates before they display any interest. Consequently, the suggestion cited above (VAN RHIJN, 1985) does not seem to fit in with the behaviour of females.

Additional evidence for a tendency of females to be highly selective during mate-choice arises from observations on changing mates. Ten cases were seen in which the establishment of a new social preference by a female was associated by the termination of her old bond (Table 3C). In seven of these cases it was clear that the female took the initiative for termination by actively leaving her mate. Only three cases were seen in which the establishment of a new heterosexual social preference by a male was associated with the termination of his old bond. In none of these cases it could be deduced that the male took the initiative for termination. Because of these differences almost all adult females become paired with one mate at a time during the reproductive period (Fig. 2D). Some adult males, however, are forced to remain single for a shorter or longer period of time, other maintain but one strong social preference for a female or a male, and again others achieve a higher number of social preferences (Fig. 2D).

If both male and female could take the initiative for pair-formation, the greater number of heterosexual social preferences in males in comparison with homosexual social preferences might be a consequence of female initiatives, and not necessarily by an active preference of males for females. An indication for the existence of a higher preference by males for the opposite sex than for the own sex is the low probability of continuation of strong homosexual social preferences (Table 2C and D). Since the probability of continuation of weak homosexual social preferences was at least as high as of weak heterosexual social preferences, it may be suggested that only after thorough experience with a particular mate, male gulls are able to decide whether the relation is worth continuing.

It may be concluded that the mechanism for the establishment of social preferences in black-headed gulls seems to be based upon two different strategies in males and females. Our data strongly suggest that unmated males start to advertize mainly by means of the Long-Call, without directing their activities to particular individuals. Unmated females, however, do not seem to advertize at random, but they direct their Long-Calls and other activities to particular individuals. These targets of female interest can be advertizing unmated males, as well as mated males which are seen to display frequently towards their partners. Our suggestion is that most or all heterosexual bonds are initiated by these directed activities by females. This does not mean that all directed activities by females lead to social bonds in the end. Some females persistently court a particular male, which does not react to these pair-formation attempts, in spite of the fact that such males may be unpaired. Apparently, the final decision for the establishment of a social bond involves the agreement of the male.

Unmated males which fail to arouse the interest of females may change their behaviour from undirected towards directed activities and then thus behave like unmated females. Thus, the targets of interest of these males are also either advertizing unmated males, or active mated males. As a result of this, in some cases homosexual bonds may be established. It is plausible that the establishment of such homosexual bonds can be cut short by the final decision of the approached male.

Mated males seem to direct their courtship activities only to birds displaying interest in them. Extramarital Copulation Attempts by such males have never been observed to be preceded by courtship. In contrast, mated females have been seen to direct some courtship activities towards males, other than their mates. After the termination of a bond males may persist for some time in displaying directed courtship towards former mates. Females very rarely have been seen to display their previous preferences after changing mates.

In spite of their predominantly monogamous mating system and their equally shared parental care system, males and females in the black-headed gull seem to display strongly differing roles in mate selection. Such differentiation is plausible for species in which females invest much more in their offspring than males (TRIVERS, 1972). The explanation for role differentiation in internally fertilizing species with equally investing sexes might be caused on some fundamental differences between females and males (VAN RHIJN, 1984). For an indispensable condition for the evolution of parental care by the male is a property to establish a kind of pair-bond during the period from copulation to parturition. However, under certain conditions the relative success of the males with this property is inversely related with the proportion of such males in the population. One might therefore conceive that males maintained alternative methods for reproduction, including mate desertion after copulation. In contrast, the success of caring females is independent of the proportion of such females in the population. Thus, in those species in which the care of the two parents is needed for a proper development of the offspring, the probability of future care by the male at the time of copulation is never higher than the probability of care by the female, but mostly lower. It is therefore plausible that females developed a tendency to be very selective during mate-choice.

4. Factors affecting the formation of social relationships

4.1. Age.

The most important effects of age have been mentioned before (Fig. 2). The average number of social preferences per bird per season tended to increase with age (A). Age and total number of social preferences per bird from the second calendar year onwards were clearly correlated ($r = .50$, $N = 266$, $p < 0.001$). The actual figures for birds in their first calendar year (the year they were hatched) are probably higher than those given in the diagram, because we hardly investigated social preferences in young gulls.

In the very young birds (first calendar year) all social preferences observed were weak according to the criteria mentioned in section 2.2 (Fig. 2, B). In the older birds roughly 70% of the social preferences were strong. Although in the young age categories a considerable proportion of the birds could not reliably be sexed, it was very clear that the proportion of homosexual social preferences decreased, and the proportion of heterosexual social preferences increased with age (C). The proportion of birds without strong social preferences appeared to decrease considerably with age (D). The differences between the various age classes were all statistically significant, except between calendar year 4/5 and 6/8 (χ^2 tests, one sided, $P<0.05$). Gulls with strong social preferences at the same time for more than one bird were at least in their third calendar year. The proportion of these birds was fairly low, but seemed to remain constant from that third calendar year onwards (about 10%).

We also considered the interrelations between age and reproductive performance. The percentage of birds with eggs (males and females) was seen to increase strongly with age (Table 4). The differences between the various age classes were all statistically significant, except between calendar year 1 with 2, and 4/5 with 6/8 (χ^2 tests, one sided, $P<0.05$). For those birds producing eggs, the total number of eggs also seemed to increase with age, but only the difference between calendar year 3 and 6/8 was statistically significant (Mann-Whitney U test, one sided, $P<0.05$).

TABLE 4. Reproductive performance and age

Calendar year	1	2	3	4/5	6/8
Total number of bird seasons	132	87	69	69	41
Percentage of birds with eggs	0	1	20	70	73
Average number of eggs per egg producing bird	—	2.0	2.4	2.8	3.3

4.2. Reproductive state.

The probability and the timing of reproduction is basically determined by the state of the gonads. We did not try to measure size and activity of the reproductive organs of our birds directly, but we consider the date upon which the darkening of the head was completed to be an indirect measure of gonad development. The rationale of this supposition bears on the finding that the amount of circulating sexsteroids and the probability of development of a dark head are interrelated (VAN OORDT & JUNGE, 1933; GROOTHUIS, in prep.).

The second calendar year gulls rarely obtained a fully dark head. If they did, however, it occurred much later in the season than in their third calendar year (Fig. 7; Sign test, one sided, $P<0.01$). From the third calendar year onwards all gulls acquired a complete nuptial plumage.

The date they became fully dark in their fourth calendar year was again somewhat earlier than in their third ($P < 0.01$). Although the graph (Fig. 7) might suggest that after the fourth calendar year a retardation in the development of darkening of the head occurred, statistically significant differences between these age classes could not be established (Sign tests, one sided, $P > 0.05$). Third calendar year females seemed to start later with egg-laying than in their following season (Fig. 7). The number of cases, however, was too small for a statistical verification. From the fourth calendar year onwards the timing of the first egg seems to coincide with that in older age classes (Sign tests, two sided, $P > 0.05$).

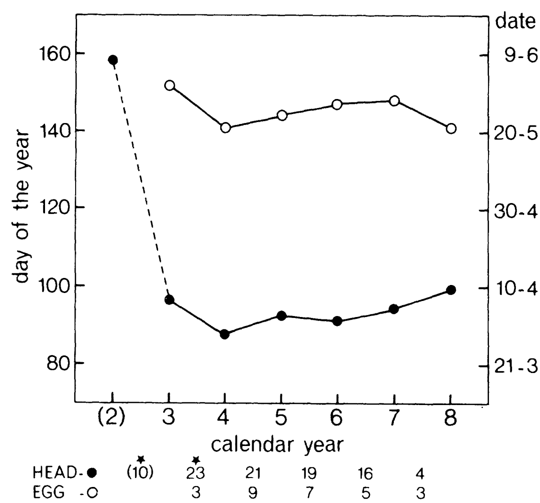

Fig. 7. Relation between age and timing of the end of nuptial moult of the head (black dots) or between age and timing of the first egg (open circles). Statistical comparisons were made between groups of individuals of which data for two successive years were available. Group sizes are indicated below the diagrams. Statistical significant differences are marked with stars.

The relation between reproductive state and head colouration in females clearly follows from the statistically significant correlation between timing of the change to a dark head and timing of the first egg ($r = .41$, $N = 43$, $P < 0.01$). For the calculation of this and many other correlation-coefficients Julian dates were used (day of the year: Fig. 7). The number of eggs per season laid by the females was also correlated with the timing of the appearance of the dark hoods ($r = -.43$, $N = 60$, $P < 0.01$). The number of eggs per season sired by the males appeared to be correlated with the timing of the darkening of the head-feathers too ($r = -.26$, $N = 70$, $P < 0.05$). Thus, the earlier the moult of a gull's head proceeds, the higher its number of eggs will be.

The correlation between timing of moult and reproductive success is highly interesting because timing of moult is fairly constant for each individual (Fig. 8). The correlation between successive years in the timing of the appearance of the dark hood in the same individual (from its fourth calendar year onwards) was statistically significant for both males ($r = .78$, $N = 45$, $P < 0.01$) and females ($r = .67$, $N = 38$, $P < 0.01$). The correlation between successive years in the timing of the first egg by females of the same age classes was likewise statistically significant too ($r = .65$, $n = 27$, $P < 0.01$). These correlations suggest that early moulting individuals have a higher fitness than individuals which moult later in the season.

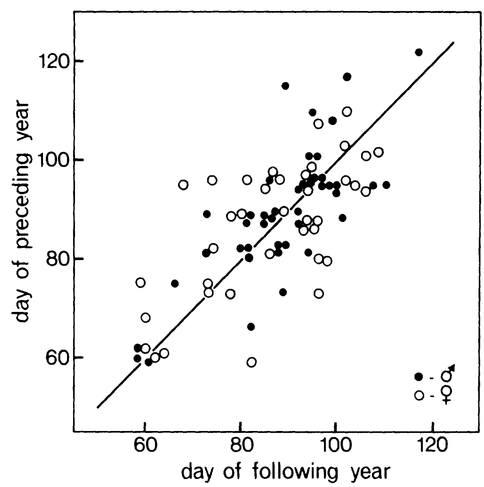

Fig. 8. Timing of the end of moult of the head in successive years from the fourth calendar year onwards.

A strong social preference is a prerequisite for egg production. Thus, the large average number of eggs of the early moulting gulls could be the result of a higher incidence of strong social preferences among birds of this group. The following data support this supposition.

Moult occurred latest in gulls which did not develop social preferences during the same season, it occurred somewhat earlier in the gulls which only developed weak social preferences, still earlier in gulls establishing

TABLE 5. Day of the year (Julian date) of obtaining a fully dark head in connection with the incidence of social preferences per bird season

	Males		Females	
	average	N	average	N
No social preferences	107.4	5	88.3	3
Only weak social preferences	89.8	8	101.5	4
One strong social preference at the same time	88.8	46	88.8	52
More strong social preferences at the same time	80.8	11	73.0	1

one strong social preference at the same time, and earliest in gulls establishing several strong social preferences at the same time (Table 5). All these differences, except the one between 'only weak' and 'one strong' social preference, were statistically significant in males (Mann-Whitney U tests, one sided, $P<0.05$). In females the difference between 'only weak' and 'one strong' social preference was the sole one being statistically significant (same test, $P<0.05$).

While Table 5 summarizes data at the level of individuals, a further analysis at the level of separate relationships was done. For various kinds of relationships Table 6 gives (1) the average Julian dates that the participants acquired fully dark heads (day of year), (2) the average difference between the dates of males and females (♂-♀), and (3) the average of the absolute differences between dates within the pairs (synchrony). The table shows that in males moulting time was not related with the strength of the social preferences, the probabilities that these preferences would be continued in succeeding years, the reproductive success, or the probabilities that these preferences would be directed towards the same sex. In females, however, both the strength of the social preferences and the probabilities that these preferences would be continued in succeeding years appeared to be related with moulting time (Mann-Whitney U tests, one sided, $P<0.05$).

There was no clear pattern in the order of moult in male and female of the same pair, except in the group of egg-producing pairs. Females with hatching eggs were earlier in comparison to their mates than females of which the eggs did not hatch (same test, $P<0.05$). The absolute differences between the moulting times of the members of a pair (synchrony) were of the order of 14 days on average. This measure for synchrony was not related with strength of the social preference, with the probability of continuation of the preference in succeeding years, with

TABLE 6. Days of the year (Julian dates) that the two pair-members obtained a fully dark head in connection with the types of relationships between gulls

	N	Day of year males	Day of year females	♂ - ♀	Synchrony
Heterosexual relationships					
All	75	86.4	88.3	-1.9	14.2
Weak social preferences of at least one of the participants	15	86.5	94.3	-7.9	14.5
Strong social preferences of both participants	60	86.4	86.8	-0.4	14.1
Strong social preferences maintained for one season	12	89.2	93.4	-4.3	14.4
Strong social preferences maintained for more seasons	48	85.7	85.2	+0.5	14.0
Strong social preference but no eggs	19	88.7	86.7	+0.2	11.6
Strong social preferences with eggs, but no hatching	27	84.0	89.0	-5.0	16.9
Strong social preferences with hatching eggs	14	87.9	82.8	+5.1	12.1
Homosexual relationships					
All	14	84.9			11.0
Weak social preferences of at least one of the participants	8	83.4			13.1
Strong social preferences of both participants	6	86.8			8.2

reproductive success, and with the combination of sexes (same tests, $P > 0.05$).

Our quantitative data of fourth calendar year and older gulls give no evidence whatsoever for a synchrony of nuptial moult among members of the strong heterosexual pairs ($r = -.17$, $N = 49$). Nevertheless, some observations suggest that synchrony plays a role. For example in 1981 we observed a group of 6 males and 6 females, derived from 6 heterosexual pairs in the preceding summer. One male (♂2) and one female (♀5) were seen to moult very early in the season. Their former mates (♀2 and ♂5) were very late, and the other birds moulted somewhere between these extremes. The first social preferences of that season developed between the early birds ♂2 and ♀5. This is in accordance with the idea of synchrony, although it must be mentioned that both preferences were weak. When ♀2 and ♂5 started to moult after a few weeks, the early couple was dissolved and both individuals returned to their former mates (Fig. 3).

One may conclude from the data given above, that:
(1) the main factor causing the early moulting males to sire more eggs than the males moulting later was their higher probability of maintaining several strong social relationships at the same time (Table 5);
(2) the main factor causing the early moulting females to lay more eggs than the females moulting later was their higher probability of establishing strong social relationships (Table 5 and 6);
(3) strong social relationships of both early moulting males and early moulting females did not lead to more offspring than those of the individuals moulting later, and
(4) synchrony of moult between prospective mates did not seem to be very important.

4.3. Physical condition.

The theory of natural selection predicts that animals should select healthy mates for reproduction. Consequently the chances for ill and defective gulls to find a mate should be low.

This expectation seemed to be correct under field conditions. In 1979 pair-formation and territory establishment was observed in a colony in the northern part of the Netherlands. In order to identify as many birds as possible all striking features of the individuals were recorded. In the course of the early season, together with the increase of the number of established pairs, a considerable increase of the proportion of crippled individuals was observed among the birds which were still trying to find a mate. In our aviaries ill and lame birds likewise seemed to be less often engaged in social bonds than healthy individuals. An example of the low incidence of pair-formation among lame birds was shown in 1980, when we could not use enough closed cages to house all our gulls. We clipped the wings of 19 individuals and accommodated them in a large fenced area. Among these birds only 6 social preferences (2 strong and 4 weak ones) were observed. On the basis of the age distribution of these gulls and the data underlying Fig. 2, a total number of 13.63 social preferences had to be expected, which is considerably higher ($\chi^2 = 4.27$, 1 df, one sided, $P<0.05$).

We were unable to quantify 'healthiness' in our caged birds, but we did measure two other parameters of the bird's physical condition, namely body-weight in winter (November, December or January: before any courtship activity was shown) and head plus bill length (which was thought to be related with body-size).

Our body-weight data indicate that males are heavier than females (Fig. 9). In addition, birds of both sexes were seen to reach their highest body-weight during their first winter. This suggests that there is no strong interdependence between fat-reserves and reproductive performance in these birds, since second calendar year birds rarely participate

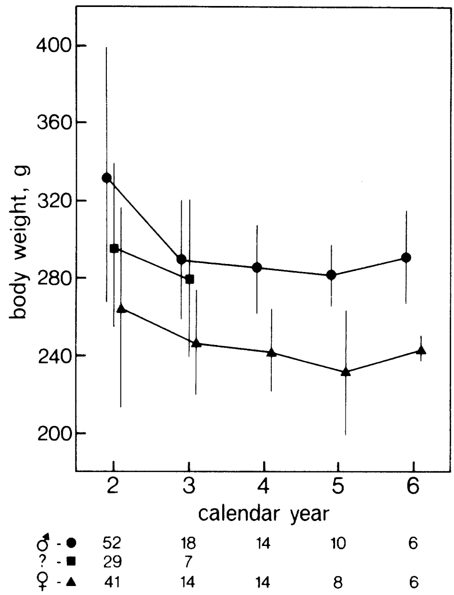

Fig. 9. Average and standard deviation of body-weight in males, females and young birds of unknown sex in relation to age. Sample sizes are given below the diagram.

in reproduction. We observed only one such individual, a female which laid 2 eggs, out of 87 potential cases of that age. The lack of a strong interdependence between fat-reserves and reproductive performance is also suggested by the data on mate selection. We could not show that body-weight is important for the establishment of pair-bonds or for the success of a pair-bond. In addition, we could not find statistically significant indications for the existence of matching of weights between partners ($r = -.22$, $N = 37$) in our sample of strong heterosexual social preferences. We observed only one effect of body-weight which might influence mate selection, namely that heavy males (from the fourth calendar year onwards) were seen to develop their nuptial plumages earlier in the season than the light ones ($r = -.33$, $n = 29$, $P < 0.05$).

Intra-individual variation was small in our data on head plus bill length. Therefore, we assumed that this measure remains constant in each gull. We determined its value on the basis of the average of the available data. Head plus bill length was larger in males than in females (Table 7). Within the 4 different classes of individuals head plus bill length was not clearly correlated with body-weight. Only in adult males (from their third calendar year onwards) this correlation was statistically

TABLE 7. Correlation between body-weight (g) and head plus bill length (mm)

	Males		Females	
	Juveniles	Adults	Juveniles	Adults
Number of individuals	50	48	39	42
Average body-weight	334	287	266	242
Average head plus bill length	85.8	85.1	78.1	78.1
Correlation	$r = .04$	$r = .34$	$r = .20$	$r = .09$
Probability	n.s.	$p<0.01$	n.s.	n.s.

TABLE 8. Head plus bill length (mm) in connection with the incidence of social preferences per bird season

	Males		Females	
	Average	N	Average	N
No social preferences	85.0	9	78.7	10
Only weak social preference	86.1	9	78.3	6
One strong social preference at the same time	85.2	57	78.0	57
More strong social preferences at the same time	84.0	14	76.0	1

significant (Table 7). Assortative mating for this parameter could not be detected in our sample of strong heterosexual social preferences.

Gulls with large head plus bill measurements did not establish more or stronger social preferences than gulls with smaller ones (Table 8). In males we observed the reversed trend. Males maintaining only weak social preferences and males with one strong social preference were larger than those maintaining several strong social preferences (Mann-Whitney U tests, two sided, $P<0.05$ and $P=0.07$ respectively). The success of pair-bonds was not improved by large head plus bill measurements of the participants either (Table 9). On the contrary, the females participating in weak bonds were larger than those in strong bonds, and the females participating in bonds maintained for not more than one year were larger than those in bonds persisting over a longer period of time (Mann-Whitney U tests, two sided, $P=0.06$ and $P<0.05$ respectively). The males participating in strong heterosexual bonds with eggs that did not hatch, were smaller than those in strong heterosexual bonds with no eggs at all (Mann-Whitney U test, one sided, $P<0.05$). These reproductive

TABLE 9. Head plus bill lengths (mm) of the two pair-members in connection with the types of relationships between gulls

	Males		Females	
	Average	N	Average	N
Heterosexual relationships				
All	85.5	85	78.1	82
Weak social preferences of at least one of the participants	85.5	17	79.1	15
Strong social preferences of both participants	84.8	68	77.9	67
Strong social preferences maintained for one season	85.0	20	78.6	19
Strong social preferences maintained for more seasons	84.8	48	77.6	48
Strong social preferences but no egg	86.0	21	77.8	20
Strong social preferences with eggs, but no hatching	83.9	30	78.3	30
Strong social preferences with hatching eggs	84.9	17	77.3	17
Homosexual relationships				
All	85.0	42		
Weak social preferences of at least one of the participants	85.0	22		
Strong social preferences of both participants	85.0	20		

advantages for small gulls are also supported by negative correlations between head plus bill length and number of eggs produced or sired. This correlation, which was statistically significant in males ($r = -.38$, $N = 54$, $P < 0.01$) but not in females ($r = -.21$, $N = 46$), has been interpreted as a selection by females against sexual dimorphism (VAN RHIJN, 1985).

4.4. Early experience.

In connection with a study of the ontogeny of social behaviour in black-headed gulls (GROOTHUIS, in prep.), the early experience of the birds was manipulated in a number of ways. Six categories of social experience during their first year will be considered in the present paper: (1) birds without visual experience with conspecifics, (2) birds without visual experience with conspecifics during the later part of that first year of life, (3) birds with social experience with a small number (≤ 3) of conspecifics

TABLE 10. Social experience and the development of social preferences

	Experience during first year of life*)					
	iso	(iso)	<3	>3	ad	par
Number of birds	12	5	15	16	13	8
% with strong social preferences before 4th calendar year	58	20	60	63	92	75
Observed total social preferences	23	5	52	97	48	17
Expected	27.5	4.9	52.4	96.2	43.8	17.3
Observed weak	5	4	22	23	13	4
Expected	7.8	1.5	15.4	26.4	13.2	5.5
Observed strong	18	1	30	74	35	13
Expected	19.7	3.4	37.1	69.8	30.6	11.9
Observed homosexual	6	2	20	10	8	6
Expected	5.6	1.3	10.7	16.6	9.4	4.3
Observed heterosexual	17	2	27	87	40	11
Expected	19.9	3.1	37.6	73.8	30.7	11.3

*) iso: no conspecifics, (iso): no conspecifics during later part of year, <3: ≤3 conspecifics of same age, >3: >3 conspecifics of same age, ad: with adults, par: with (foster)parents.

of the same age, (4) birds with social experience with a large number (>3) of conspecifics of the same age, (5) birds with social experience with conspecifics of various ages, but not with parents, and (6) birds with social experience with conspecifics of various ages, including their (foster)parents. There were only small differences between these categories in the tendency of the birds to initiate their first social bonds. Table 10 shows that the proportion of birds which established the first strong social preference before their fourth calendar year, was low in birds without experience with adults (categories 1, 2, 3, 4) as compared with birds which had been able to interact with adults during their first year of life (categories 5 and 6; $\chi^2 = 5.58$, 1 df, one sided test, $P < 0.05$).

A further analysis of later social preferences of the six categories of birds was complicated by the fact that their age compositions were different. To cope with this problem, expected values for the number of social preferences were calculated on the basis of ages and the data for all birds in Fig. 2. These values turned out to be very similar to the observed number of social preferences (Table 10). The only clear effect we found, referred to the relatively high number of homosexual social preferences among the birds which were raised with a small number of conspecifics of the same age (category 3; $\chi^2 = 8.17$, 1 df, two sided test, $P<0.01$). This effect might be explained, however, by the sex-ratios in these small groups, which were skewed towards males in most cages.

Early experience with particular individuals could have a specific influence on later social preferences for those individuals. Many of the bonds between first calendar year gulls were continued during later life. A maximum of 14 (out of 41) social preferences could have been continued because both birds remained together in the same group. Actually, 12 of these preferences were continued in the second calendar year, and even 10 of them became strong. After that second calendar year only one combination of individuals (2 males) was kept in the same group, altogether for 5 consecutive seasons. During these seasons we observed once a strong and a reciprocal weak preference and four times a unidirectional weak homosexual social preference between these two birds. Since the bonds between first calendar year gulls arose in small groups raised in the same cage (laboratory conditions), or (field conditions) in groups of nest companions (see section 3.1.), members of the same family group might be serious candidates for later social preferences. We observed one other, peculiar case of later social preferences between family members.

This pair-formation attempt refers to ♂7 and his foster-daughter ♀12 (Fig. 4), which was tended by a male-male pair (♂7 and ♂5) in her early youth. This female stayed together with ♂7 until the early spring of her third calendar year (1981). After their separation ♀12 initiated a pair-bond with ♂11. In October 1981 ♀12 with her mate (♂11) were put in the same cage with ♂7. In spring 1982 ♂11 started to perform meeting ceremonies towards ♀12, but she did not participate. On the contrary, she started to perform meeting ceremonies towards the foster-father (♂7), which participated to some extent, but without abandoning his mate (♀3). Nevertheless, copulations between ♂7 and ♀12 were observed several times, followed by the laying of one egg by ♀12, that was incubated by ♂7 and ♀3.

4.5. Later social experience.

The influence of later social experience of two birds with one another on social relationships was quantified by the number of seasons that they were housed in the same cage from their second calendar year on to each season that both birds attempted to breed. With regard to the first breeding attempts this value turned out to be much higher in mates (Table 11) than in non-mates. This was partly due to the fact that the proportion of combinations of birds starting to breed in the same cage and the same season without preceding experience was significantly

TABLE 11. Experience with mates and non-mates breeding in the same cage

	Number of comparisons between individuals	Average number of seasons together	% with an experience of: 0	1	>1 season
Preceding to first breeding attempts					
Mates	33	1.30	24	48	27
Non-mates	296	0.55	59	28	13
Preceding to all breeding attempts					
Mates	55	1.73	15	36	49
Neighbours	240	1.33	24	38	38
Non-neighbours	222	0.80	53	25	22

lower among mates (Table 11: 24%) than among non-mates (59%; $\chi^2 = 15.07$, one sided test, $P < 0.001$). Thus, most pair-bonds were established between individuals which had been together for a relatively long period.

To investigate whether the kind of relationship among non-mates could also be influenced by later social experience, we separately analysed the data for neighbours and non-neighbours. Neighbours were defined as those non-mates nesting closer than 1.5 m from each other without other nests between them. Non-neighbours were defined as all other non-mates breeding in the same cage and the same season. With regard to all breeding attempts the value for the number of seasons together turned out to be much higher in neighbours than in non-neighbours (Table 11), but lower in neighbours than in mates. The difference between neighbours and non-neighbours was partly due to the fact that the proportion of combinations of birds breeding in the same cage and the same season without preceding experience was significantly lower among neighbours (Table 11: 24%) than among non-neighbours (53%: $\chi^2 = 41.02$, one sided test, $P < 0.001$), and to the fact that the proportion of combinations of birds breeding in the same cage and the same season with at least two seasons of preceding experience was significantly higher among neighbours than among non-neighbours ($\chi^2 = 13.86$, one sided test, $P < 0.001$). Thus, close nesting occurred mainly by individuals which had been together for a relatively long period.

The influence of social experience on preferences also follows from the high probability of pair-bonds to be continued in successive years (see section 3.3.). Besides, we observed several cases in which weak social preferences between individuals were, after some years without preferences, followed by the establishment of a real pair-bond. Additionally, we recorded some cases in which pair-formation occurred after the male participant maintained a social bond with the previous mate of the female participant. Thus, it may be suggested that social relationships other than pair-bonds may have an influence on future mate selection.

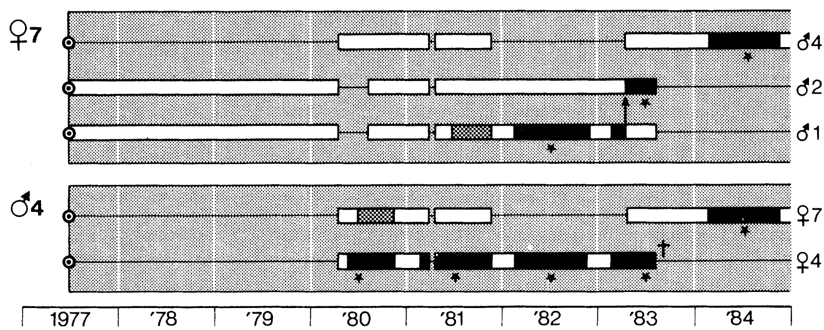

Fig. 10. Social preferences by ♂4 and ♀7. For a further explanation see also Figs 3, 4 and 6.

This suggestion may be illustrated by the following examples:

In spring 1980 ♂4 established a pair-bond with ♀4 (Fig. 10). In the mean time weak social preferences were observed between ♂4 and ♀7. The pair-bond was kept up the following 3 years, but the weak preferences between ♂4 and ♀7 could no longer be detected. In summer 1983 both ♂4 and ♀7 lost their mate. In spring 1984 a pair-bond between ♂4 and ♀7 was established although several other combinations were possible. Male 4 had not shown any other social preferences during his life, ♀7 had displayed social preferences for males which had died before 1984.

In spring 1981 strong social preferences were observed between ♂1 and ♂2. In the following two years social preferences between these individuals remained present, but were no longer strong. In 1982 ♀7 established a pair-bond with ♂1, which also established a pair-bond with ♀11. In the beginning of spring 1983 both ♂-♀ bonds seemed to be re-established, but somewhat later, probably because competition between the females was very strong, ♀7 left ♂1 to select for a new bond out of 8 unmated males ♂2, which had frequently been interacting with ♂1 before that time (Figs 3, 5 and 10).

In spring 1981 strong social preferences were also observed between ♂1 and ♂9 (section 3.3.). At that time ♂1 was paired with ♀1 and ♂2 (which also had a strong social preference for ♂1) with ♀2. In November 1981 both pairs were separated and the females were housed in the same cage as ♂9. In spring 1982 both females established a pair-bond with ♂9, although there were other males available (Figs 3 and 5).

4.6. Social environment.

The establishment of social preferences may be influenced by an animal's social environment. The incidence of male-male pairs suggests that males may form bonds with other males in the absence of suitable mates. The incidence of polygynous associations suggests that females may form bonds with mated males in the absence of suitable mates for them. Thus, both in small groups and in groups with an unbalanced sexratio, one might expect a high probability of the establishment of such unusual social preferences. These suggestions have been further investigated for the pair-bonds between adult birds. Table 12 shows that there was no relation between the number of adults present in the cage at the time of

TABLE 12. Group composition at the time of pair-formation

	Number of adult pairs	Average number of adults present in cage	Average % of ♂♂ among the adults with know sex
Homosexual bonds	12	13.7	65
Heterosexual bonds	71	13.7	54
Female initiates bond with unmated male (monogamy)	56	14.0	54
Female initiates bond with mated male (polygyny)	15	12.6	54

pair-formation (group-size), and the establishment of male-male pairs or of polygynous associations. The Table further shows that there was a relation between sex-ratio and unusual social preferences, but only for the establishment of male-male pairs (Mann-Whitney U test, one sided, $P < 0.001$).

The lack of a relation between polygynous pair-formation and group-size of sex-ratio suggests that the number of potential mates for a female is not simply given by the number of males in a group. Mate-selection by females might be so delicate, that its real nature remains completely masked by such crude measurements as group composition. Mate selection by males, however, might be based on relatively simple criteria. Males seem to establish as many bonds as possible, females seem to select the most suitable mate.

4.7. An evaluation of the different criteria for mate selection.

In monogamous species with equally shared parental care, such as in the black-headed gull, reproductive success of an individual is not only influenced by its mate's genetical properties which will be transferred to the offspring, but also by the parental abilities of its mate. Thus, the decision to select a particular mate may be very important for future reproductive success. Consequently, one may expect that mechanisms for mate selection have been perfected by natural selection.

The present data give some indications about the criteria for mate selection. (1) The positive correlation between age on the one hand, and number or strength of social preferences on the other (Fig. 2), suggests that old gulls are more attractive as a mate than young ones. This suggestion agrees with a strong positive correlation between age and reproductive success (Table 4). (2) The correlations between time of nuptial moult and number or strength of social preferences (Tables 5 and 6) suggest that early moulting gulls are most attractive as a mate. Attractiveness of males moulting early is concluded from a proportionally high frequency of multiple strong social relationships at the same time. Attractiveness of females moulting early appears from a proportionally high number of strong social preferences. (3) The correlations between head plus bill lengths and number or strength of social preferences (Tables 8 and 9) suggest that small gulls (both males and females) are most attractive as a mate. (4) Finally, the amount of experience with each other seems to be the most important factor investigated for mate choice (Tables 2 and 11).

One would expect that some other criteria are important for mate selection too. (1) We failed, however, to demonstrate an effect of body weight, which was thought to reflect nutritional state, and thus health. Yet, it cannot be excluded that this factor is important, because its effect could be masked in the present data by the preference for small gulls as a mate, and by the *ad-lib* food conditions which probably did not lead to considerable differences in nutritional states. (2) We also failed to demonstrate any tendency for assortative mating. Early moulting males did not seem to mate more often with early moulting females than with females moulting later. Moreover, the correlations between the body-weights of partners and the correlations between their head plus bill lengths even tended to be negative. Yet, we do not believe that matching of mates is unimportant. For instance, matching for timing of moult and for nutritional state might promote the synchronization of reproductive efforts between mates. This is very important for reproductive success. Our inability to demonstrate these factors might be associated with the small number of options for an individual searching for a mate in our aviaries.

It may be elucidating to discuss the adaptive significance of the various criteria, which did turn out to be important. The attractiveness of older gulls may be associated with fitness, because age reflects an ability to survive. The attractiveness of early moulting gulls may be associated with direct reproductive success, because early moult leads to early breeding with a high probability of a repeat clutch in case the first fails. The attractiveness of small gulls, especially of small males, has been interpreted as a selection against polygynous males (VAN RHIJN, 1985). The advantages for small females, however, cannot be understood easily within the framework of that hypothesis. Hence, it might be possible that the earlier interpretation was incorrect and has to be replaced by a general preference for small mates. The adaptive significance of such a preference is not very clear. If genetical variance for size is still present in a population, such mating preference should lead to a gradual decrease of body-size, unless large-sized individuals benefit by other processes, such as competition. The attractiveness of known birds and previous partners was certainly the most obvious criterion used by our gulls for mate choice. Its preponderance could have obscured the roles of many other criteria. Its adaptive significance is probably related to considerable investments of prospective mates in the assessment of each other's qualities and sex (VAN RHIJN, 1985). Additionally, long-lasting pair-bonds may lead to a better synchronization of reproductive activities between mates, and thus to an increase of reproductive success. We were unable to demonstrate such effects, but the data collected on wild kittiwakes, *Rissa tridactyla* (Coulson, 1972, 1980), do suggest that these phenomena may occur.

5. Possible factors leading to the formation of unusual associations

One may finally question why, considering the above developed model, gulls in the field normally achieve to establish the typical heterosexual monogamous social preference. This requires some reflection about the factors leading to the establishment of polygynous associations, and those leading to the different kinds of homosexual bonds.

Polygynous associations were thought to be the result of females directing their courtship activities to mated males, which finally accepted these females as a second mate (see section 3.7.). Observations on captive birds supported this theory (VAN RHIJN & GROOTHUIS, 1985). The circumstances leading to polygynous associations did not become very clear in the present study (Table 12). We suspect, however, that polygynous males have on the average a better quality than monogamous and unpaired males. This might be deduced from the high frequency of multiple bonds in gulls of the older age classes (Fig. 2) and from the early nuptial moult of males maintaining several strong social preferences at the same time (Table 5). We further suspect that females only select mated males when quality or sex of the available unmated males is doubtful, but we do not have very clear indications for this idea. Some support, however, is provided by our experience that a number of females terminated bonds with polygynous males when new unmated males were introduced into the group, or when more experience with other unmated males was acquired by these females. If these ideas are correct, the incidence of polygyny under natural conditions is bound to be low. In most moderate or large-sized colonies or clubs we would namely expect a fair number of unmated males during the main part of the period of pair-formation. Only those females arriving near the end of that period would sometimes be forced to select a mated male. The low frequency of polygyny observed in the field (VAN RHIJN & GROOTHUIS, 1985) supports these ideas.

Homosexual bonds among males were thought to be caused by males which did not succeed to interest females by undirected advertisement, and subsequently changed their behaviour to directed advertisement towards active birds, usually males (section 3.7.). The majority of the homosexual bonds have been observed among (1) young males (Fig. 2), (2) males which had only experience with a small number of conspecifics during their first year of life (Table 10), and (3) males which established social relationships while living in groups with a low proportion of females (Table 12). Homosexual bonds among young males may also occur in the field, but they are difficult to recognize because they rarely lead to full nest construction. It is unlikely that condition (2) and (3) arise very often among wild gulls, which often roost and forage in enormous groups and breed in large colonies.

The fenomenon of female-female pairing observed in several wild larid species (reviewed by VAN RHIJN & GROOTHUIS, 1985) does not follow from the female strategy for partner choice (section 3.7.). We are inclined to ascribe such female-female pairing to the tendency of gulls to associate with family members. It has pointed out that during the first calendar year members of the same family group tend to develop mutual social preferences (section 4.4.). In almost all cases in which the participants of such relationships were kept in the same aviary, these early social preferences were continued in the second calendar year, and mostly developed into strong social preferences. Thus, it seems plausible that an early bond between two sisters may develop into an association of two females laying in the same nest. Our failure to demonstrate the existence of early bonds between females may be due to the low number of opportunities in which such bonds could be formed. If we accept this idea, the low incidence of female-female pairing among wild gulls suggests that family members are only chosen when no other suitable mate can be found.

Summary

Processes leading to the establishment of social relationships are the main topic of the present study, which is based on observations of black-headed gulls kept in experimental groups in aviaries. Among these birds various kinds of social relationships were established, such as heterosexual monogamous pair-bonds, polygynous associations, and male-male relationships. Some of the factors which give rise to the formation of such relationships could be studied, because it was possible to watch all individuals during their whole life, and during all stages of their reproductive cycle.

Quantitative data were collected on the influence of sex, age, reproductive state, physical condition, and various social factors on the incidence of social relationships. On the basis of these data it could be concluded that males and females play strongly differing roles. Unmated males advertize randomly. Unmated females direct their courtship to particular individuals, belonging to the category of advertizing unmated males, or of the active mated males. The final decision for pair-formation involves an acceptance by the approached male. Unsuccessful unmated males may adopt the female strategy, and thus establish homosexual social relationships. Mated males do not initiate courtship towards other females, but they may be courted by them. Mated females sometimes display social interest for other males.

The main criteria for mate choice were advanced age, early nuptial moult, small body-size, and, in particular, social experience with one another. In contrast to our expectation, body weight and matching of nuptial moult and physical condition between partners were not important in our birds. The significance of the criteria age and moult may be directly related to fitness. The preference for small males had earlier (van Rhijn, 1985) been interpreted as a mechanism preventing polygyny, but additional data provide some inconsistencies with that idea. Finally, the significance of social experience with each other has been related with considerable investments of prospective mates before establishing a pair-bond, and with an increase of synchronization between mates as a result of long-lasting pair-bonds. Female-female pairing among some wild larids has been interpreted as a continuation of early bonds between nest companions.

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