BIPARENTAL CARE AND THE BASIS FOR ALTERNATIVE BOND-TYPES AMONG GULLS, WITH SPECIAL REFERENCE TO BLACK-HEADED GULLS

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1. INTRODUCTION

The occurrence of different types of reproductive behaviour in the same population may be explained by three mechanisms, which do not exclude each other:

Firstly, different types of behaviour may be the consequence of genotypical variation within the population. This explanation has been advocated for the alternative reproductive strategies in male Ruffs *Philomachus pugnax* (*e.g.* Van Rhijn 1983). A satisfactory proof for this hypothesis was given by Cade (1981) with respect to the case of alternative reproductive strategies in male Field Crickets *Gryllus integer*.

Secondly, each individual may have the disposal of a set of reproductive strategies as adaptive responses to the various ecological conditions which are normally met by the species. Consequently, the different types of behaviour are the result of different conditions for individuals. This explanation seems to be valid for the occurrence of alternative strategies in a variety of animal species, such as calling or non-calling in Bullfrogs *Rana catesbiana* (Howard 1978), and territory establishment or helping in the Pied Kingfisher *Ceryle rudis* (Reyer 1980).

Thirdly, each individual may show the same adaptive reproductive strategy if exposed to ecological conditions which are usually met by the species. Non-adaptive types of reproductive behaviour may arise when individuals are exposed to unusual conditions, since, in the course of evolution, the proximate mechanism underlying reproductive behaviour was insufficiently subjected to a selection for adaptive responses to these situations. An example of this phenomenon is provided by the parental behaviour of several songbird species towards eggs and young of the Cuckoo *Cuculus canorus*. Especially in animals held under experimental conditions apparently non-adaptive reproductive patterns are frequently shown. In most cases such reproductive variants have been considered to be abnormalities, which do not deserve any further study. It may be argued, however, that such 'abnormality' is a normal response of the organism to the particular conditions to which it was exposed, and thus may give information about the causal processes within the organism.

Within the gull-family (*Laridae*) the care by two adults is essential for the survival of eggs and young chicks. A gull or tern, which mostly breeds at exposed sites in a colony, cannot leave its nest unguarded without running a high risk that the broods are chilled, overheated, or robbed. Yet, such birds have to spend much time away from their nests for food-collection. Thus, single individuals are unable to raise a family, unless their chicks are large enough to stay alone for some time (Nisbet *et al.* 1978). The most common parental care system in the *Laridae* is based on a stable monogamous pair-bond between the two parents: one female and one male (*e.g.* Coulson 1972, 1980, Glutz & Bauer 1982, Cramp & Simmons 1983). In fact, such a system is also the most parsimonious so-

lution which could be designed by natural selection for care by two adults: each individual should only invest in its own offspring (*e.g.* Trivers 1972, Van Rhijn 1984). Yet, within the gull-family there are several exceptions to the rule of care by the two parents.

In this paper we present the data on experimental groups of Black- headed Gulls *Larus ridibundus* kept in aviaries. The results will be compared with the variety of reproductive patterns described for several gull species in the field. A number of data on Black-headed Gulls under natural conditions will be added. Our final goal is to consider this heterogeneous set of results in the light of the three explanations mentioned above.

2. SUBJECTS AND METHODS

The data on captive birds refer to 57 mating units between gulls which led to nest-building and/or egg-laying. These units arose among 122 second calendar year or older individuals, altogether observed during 301 bird seasons. Definitions of the units are given in Table 1. All birds were reared in or near the laboratory ever since hatching or a few days after. The population was established in 1977 with two groups of nine birds each, originating from eggs and young chicks collected in a colony of wild gulls. In the succeeding years varying numbers of young chicks from the field were added. In most cases these individuals were kept in separate groups during the first months. After that period they were usually transferred to groups composed of different age-classes.

The observations up to and including 1980 mainly refer to the birds kept in two aviaries measuring 3.6 × 3 m each, and 2 m high. In 1981 a third cage was used for observation. This cage was 6 × 4 m and 2 m high. In 1983 all three cages were connected to one another (Fig. 1). The birds were kept at densities of at most one individual per m^2. Dry commercial food pellets for trout farms in the beginning, and for mink farms in later years, were always available to the birds. Other food was not given, except in periods when the eggs were hatching. Then small fish were added to the diet and for the young chicks we prepared a pap from the food pellets plus extra calcium, yeast, and dried insects with water. Water for drinking and bathing was always available and refreshed every two or three days in the first years, but it percolated continuously from the autumn of 1981 onwards. We further provided straw for nest construction during the springs.

Table 1. Definitions

mating unit
an association, established for one season, comprising two or more individuals, which maintain mutual pair-bonds in such a way that all individuals are directly or indirectly connected with each other.
bond-type
class of mating units, such as:
monogamy
one male — one female bonds
polygyny
one male maintaining bonds with two or more females
(our data only refer to bonds with two females)
homosexual pairs
male — male bonds or female — female bonds
(our data on Black-headed Gulls refer to male-male pairs)

All birds were colour-banded in order to be recognizable for the observer. The social situation for each gull was experimentally controlled. For instance, a few individuals were reared without conspecifics during their first year of life, and several birds were kept without members of the opposite sex during periods of a few weeks. In most years we strongly changed the composition of the groups. In one year it was done for a large number of times. All changes in group compositions were well-considered moves in a game aimed at the aquisition of a maximum amount of information about the social behaviour of our birds. Throughout the year we observed social behaviour and social preferences, especially during the reproductive seasons. 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 emerging eggs from the field. Many of them were successfully raised by the foster-parents.

The data on wild Black-headed Gulls refer to scattered observations from blinds during pair-formation, egg-laying, incubation, and care for chicks in a number of colonies in the north of The Netherlands (Lauwersmeer). Additional information was obtained by the inspection of 277 nests in 1974 and 118 in 1983, altogether with 568 and 302 eggs. On the basis of the number of eggs per nest (Hunt & Hunt 1977) and the variability of groundcolours of eggs within nests (for details see Baerends & Van Rhijn 1975, Baerends & Hogan-Warburg 1982) we tried to obtain some indications

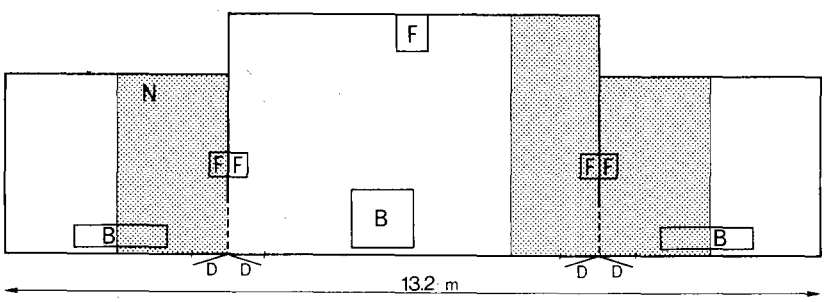

Fig. 1. Arrangement of observation cages in 1983 and 1984. Connections between cages are indicated by dotted lines and closed roofs by shaded areas. B = bathing pool, F = food container, D = door, and N = main nesting area in both years.

about the number of females laying in the same nest. Additionally, inter-nest distance was measured to get information about the existence of polygynous associations (Shugart & Southern 1977).

3. RESULTS

3.1. BONDS BETWEEN CAPTIVE GULLS

In the experimental groups we observed three bond-types which could lead to nest-building and/or egg-laying: monogamous, polygynous, and homosexual (Table 2). Monogamous pairs predominated nearly every year. Polygynous pairs, which invariably were made up of one male and two females, were less-numerous. In the summer of 1982, however, the number of polygynous associations was higher than the number of monogamous pairs, although the sex-ratios were perfectly balanced in all groups. Possibly this very unusual situation was caused by a very extensive reorganization in the preceding autumn of the composition of the groups, through which the members of most monogamous pairs were separated. Homosexual pairs were also rare. These were always made up of two males, and hence never led to egg-laying. For unknown reasons the frequency of homosexual pairs was relatively high in 1984.

The different bonds of both individual males and females did not necessarily belong to the same type (Table 3). Almost half of the birds, which were at least two times a member of a mating unit, only participated in monogamous pairs. Most other birds engaged in two or more mating units were seen to participate in different bond-types. The rare bond-types (polygynous and homosexual) were usually combined with the common monogamous pair-bond. Males in which only the first bond-type was observed, were rarely polygynous, but frequently homosexual. Females in which only the first bond-type was seen were a member of a polygynous trio in half of the cases.

3.2. BIPARENTAL CARE

We now want to consider how the normal bond-type functioned under the experimental conditions, and whether failures of these mating units may be attributed to particular properties of the environment. In the majority of these monogamous pairs nest construction was initiated before egg-laying. A few pairs started nest-building after the first egg was laid. From that time onwards the adults sat for almost 100% of the time on the eggs, which were laid with intervals of 1.5 — 2.5 days. Incubation did start before the last egg was laid but was not as efficient

Table 2. Frequency per season of the different bond-types among captive Black-headed Gulls

	1979	80	81	82	83	84	Totals
Monogamous	3	6	8	3	12	11	43
Polygynous	0	0	1	5	1	1	8
Homosexual	1	0	0	0	1	4	6
Totals	4	6	9	8	14	16	57

Table 3. Frequency of the various combinations of bond-types for males and females in relation with the number of times they were a member of a mating unit

	Number of times that an individual was a member of a mating unit					
	Males			Females		
	1	2/3	>3	1	2/3	>3
Only Monogamous	6	4	2	3	4	3
Only Polygynous	1	0	0	3	0	0
Only Homosexual	5	1	0	—	—	—
Mono + Poly	—	1	3	—	3	5
Mono + Homo	—	2	1	—	—	—
Poly + Homo	—	0	0	—	—	—
Mono + Poly + Homo	—	0	1	—	—	—
Totals	12	8	7	6	7	8

as later on in the cycle. This could be deduced from the finding that the eggs hatched in the order in which they were laid but with shorter intervals.

Usually the male spends slightly more than 50% of the time on the eggs. In some pairs incubation was mainly performed by the male, in other pairs mainly by the female. The latter pairs usually failed to produce hatching eggs (Fig. 2). According to Ytreberg (1956) the division of incubation between males and females was less variable under field conditions. The deviations with respect to the average proportion of incubation performed by males were significantly smaller in the field-sample than in the sample of experimental birds (Mann-Whitney U test, $P < 0.01$).

The average duration of incubation shifts seemed to be longer in birds living in the field than in the experimentals (Fig. 2), although the difference was not statistically significant (Mann-Whitney U test, $P > 0.05$). These short shifts were probably caused by a strong competition for sitting on the eggs in most pairs. This competition could be inferred from the high nest attendance by the non-incubating partner (Fig. 3: visits) resulting in prolonged nestbuilding and stealing of nest materials. Although we do not have quantitative data from the field, our impression is that similar frequencies do not occur among wild gulls, but that this behaviour may

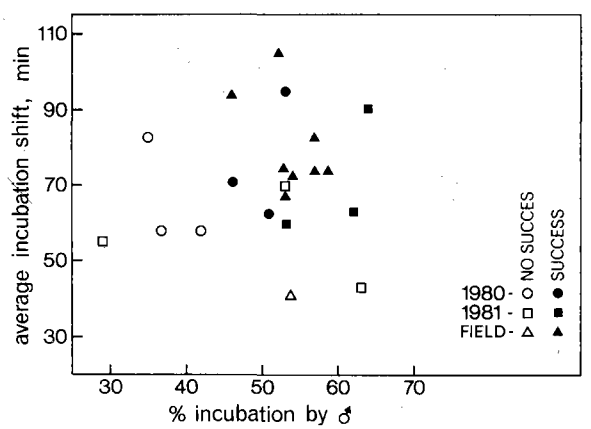

Fig. 2. Distribution of incubation between male and female and its relation with average duration of incubation-shifts. Open symbols refer to nests without hatching eggs, solid symbols to nests with chicks. The field data are derived from Ytreberg (1956).

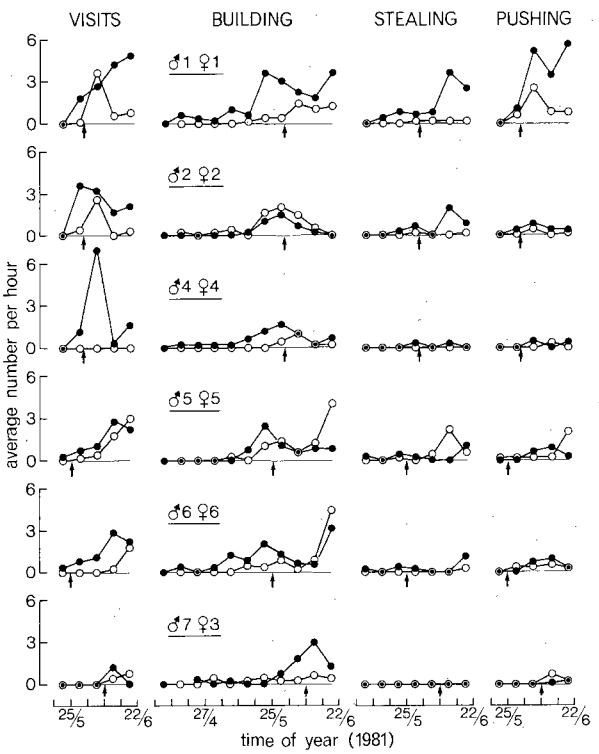

Fig. 3. Average frequency of visits to nest, building sequences, stealing actions of nesting materials, and pushing against mate on eggs by the males (solid dots) and the females (open circles) of six monogamous pairs. Arrows indicate the day the first egg was laid.

appear at lower frequencies when food is exceptionally abundant. The strong competition for sitting on the eggs could also be concluded from the regular occurrence of pushing against the incubating partner before shifts took place (Fig.3). This behaviour was only rarely observed among wild gulls. We assume that the strong competition for incubation was caused by the ad-lib food conditions in our aviaries. It is possible that, as a result of the continuous tussle between mates, the temperature regulation of the of eggs was insufficient. This may be the reason why hatching success was low.

Survival of the young chicks was also low. Most or all pairs failed to feed their chicks. These died after two or three days having lost weight considerably. The sole chicks surviving came from nests supplied with special food which was only eaten by them when their parents pecked in it. Parents falling short of doing so, were unable to keep their offspring alive.

The surviving chicks fed in the same way as the chicks in the field. Wild parents regurgitate food and then vigorously peck in the material, at least when their chicks are still very small. We suspect that the parents in our groups did not regurgitate at the right moment.

3.3. FORCED EXTRA-PAIR COPULATIONS

Gladstone (1979) focussed the attention on the high incidence of forced extra-pair copulations in monogamous colonial birds, including gulls. In most cases females and males strongly resist being subjected to a copulation attempt by a strange male (MacRoberts 1973). In a few gull-species, however, males have been observed to copulate successfully with gulls, not being their mate (Hunt & Hunt 1977, Pierotti 1981). Thus, as a result of extra-pair copulations some males may be induced to care for unrelated offspring.

In wild Black-headed Gulls we observed several attempts to such forced extra-pair copulations. These attempts were always characterized by a hovering gull apparently trying to land on the back of its victim, in a fashion identical to that in fixed pairs. Forced extra-pair copulation-attempts could be preceded by begging of the initiator, but never by meeting ceremonies (Van Rhijn 1984b). The victims were always seen to peck and thrust with their bills in the direction of their waylayers. Moreover, they tried to avoid all contacts with their waylayer's feet. We probably never observed successful forced extra-pair copulations. In many cases nothing was known about the participants. In a few cases we knew some details about the victim. These birds, which could be of either sex, were always in the phase of egg production. Their waylayers probably were males. In the two cases in which some clarity could be obtained about the identity of these waylayers, they were seen to nestle in the close vicinity of the victim. This is in accordance with MacRoberts' data (1973) on Lesser Black-backed Gulls.

In the experimental groups of Black-headed Gulls we observed on four different occasions nine forced extra-pair copulation-attempts. The data about victims and waylayers were in agreement with the ideas obtained in the field.

On the first occasion (25 May 1981) a mated male (♂1) with a nest, but still without eggs, tried to copulate two times in succession with the same mated female (♀5), which was nesting at a distance of 2.5 m. The copulation-attempts were initiated by the approach of the male, which was followed by threat and attack by the female, begging by the male, mutual choking (Van Rhijn 1981), and finally hovering by the male. The victim's mate (♂5) was present, but initially non-aggressive. During the second copulation-attempt ♂5 started to attack ♂1, and finally succeeded to chase him away. One day earlier ♀5 laid her first egg of that season. At the time of these copulation-attempts she walked with drooping wings, apparently expecting her second egg, but also creating the impression of a female which is ready to allow a copulation. ♂1 and ♀5 never formed a pair-bond with each other (see also Fig. 5). Both male and female were nesting for the third time. Their first breeding attempts were two years earlier, when they were housed in the same cage. During their second breeding attempts they were in different cages.

On the second occasion, one day after the first, ♂1 returned to ♀5 after she had laid her second egg, but just before ♂1's mate (♀1) laid her first egg of that season. ♀5 was again frequently seen with the drooping-wing posture. This copulation-attempt was preceded by head-bobbing by ♂1. ♀5's mate (♂5) was present and immediately started to attack ♂1, which was driven away within a few minutes.

On the third occasion, a week after the first, ♂1 approached an other victim (♀2), about 10 min before she laid her final egg. ♂1's mate had finished her clutch one day earlier. ♀1 was nesting at a distance of 1.4 m. On this occasion ♂1 tried to copulate five times, the first, third, and fifth time with the female, and the second and fourth time with her mate (♂2), which immediately started to behave aggressively towards ♂1. Because ♀2 was straining in a very pronounced drooping-wing posture for the birth of the egg, she was unable to resist strongly to ♂1. This might be the reason why the sequence lasted very long. These copulation-attempts were not preceded by begging or head-bobbing by ♂1. However, having been chased away after the fifth copulation attempt, he returned with begging calls, but did not manage to perform more copulation-attempts. It cannot be excluded that during the attempts with ♀2 cloacal contact was made and sperm-transfer was achieved. However, since ♀2 was laying her last egg, and because fertilization of the ovum occurs about 24 h before parturition (Lake 1975), the possibility of sperm-transfer in this case was not associated with fertilization. ♂1 and ♀2 never had a pair-bond with each other, but ♂1 and ♂2 established a homosexual bond in the early spring of the same year. ♂1, ♀1, ♂2, and ♀2 were almost continuously housed in the same cage. ♂2 and ♀2 were breeding for the second time.

The fourth occasion was three years later (14 May 1984). The initiator was a new male which played the male role in a homosexual pair without a nest. The victim was again ♀2, four days before she laid her first egg of that season, but precisely on the day she adopted an egg of another pair (♀5 and ♂11, section 3.7). On the same day three copulations were observed between ♀2 and her mate (♂10, see also Fig. 4). The first copulation was seen several hours before the extra-pair copulation-attempt, the second and third respectively 20 and 50 min after that attempt. ♀2 was not seen in a drooping-wing posture that day. However, another fe-

male (♀5), which was nearby at the time of the copulation-attempt, had a very pronounced drooping-wing posture and laid her second egg of that season (which was adopted by ♀2 and ♂10) 20 min later. It could be suggested that ♀2's drooping-wing posture released this copulation attempt, which was preceded by a begging and feeding ceremony between the males of the homosexual pair. In this case the initiating male had no breeding or social experience with its victim (♀2) and the possible target of his action (♀5).

3.4. HELPING

No reports exist on incubating female gulls with a step-father for their offspring after the loss of their original mate. But Pierotti (1980) describes how incubating male Western Gulls *Larus occidentalis* remated within two days after the loss of their first partner, which laid the eggs. A few cases are known of gull pairs which were assisted by an extra female during incubation and feeding of chicks (Pierotti 1980). Here it turned out that the extra female established some kind of a pair-bond with the male. She could participate in copulations and, in the following season, succeed in laying eggs with the same male. Trios of one reproducing pair with an extra female may therefore develop into polygynous associations in which both females reproduce.

Some of the mating units in the experimental groups contained more than two adult individuals. Once a mating unit was formed in which a male and a female (♂10 and ♀8; Fig. 4 and section 3.5) reproduced and a second female (♀10) participated in incubation and care for the surviving chick. This unit arose after the establishment of a stable pair-bond between ♂10 and ♀8.

Whilst ♂10 and ♀8 completed their nest and clutch the second female started to display meeting sequences towards ♂10, which now and then responded. Gradually the meeting ceremonies became more frequent, and in some instances ♂10 even took the initiative. In the mean time ♀10 started to approach the male when he was sitting on the eggs. This was associated by some nestbuilding activities by ♀10 near to the nest with the incubating ♂10. In the course of the first week of incubation she edged up until she was sitting against the nest when occupied by the male. When ♀8 was sitting on the nest, however, ♀10 was never tolerated in the neighbourhood. From the second week onwards ♀10 succeeded to perform incubation shifts with ♂10. Shifts between ♂10 and ♀8 were also observed, but shifts between the two females were never seen. On the contrary, the relations between them appeared to be strongly competitive, as was reflected by a number of serious fights between them. The relation between ♂10 and ♀10 resembled a pair-bond of a reproducing pair, in which only the phase of egg-laying was omitted. In the second week of incubation mutual begging, luring, regurgitation. and a copulation was seen between these birds, and immediately after hatching ♀10 was fully prepared to care for the chick.

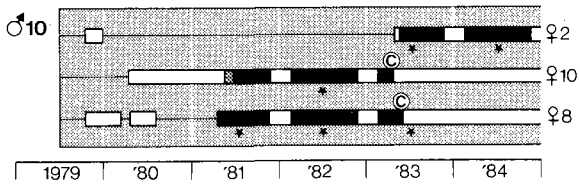

Fig. 4. Social preferences displayed by ♂10. Time of birth is indicated by the left limitation of the diagram. Each line represents one partner, which sex and identity are given on the right side. Black bars on these lines refer to periods with strong social preferences of the subject (♂10), grey bars to periods with weak social preferences, white bars to no discernable preference although both birds were in the same cage during that period, and interruptions of the bars refer to periods when both birds were not in the same cage. Nesting and breeding attempts are indicated by asterisks and partner changes by mates are marked with C.

3.5. POLYGYNY

Polygynous mating units have been observed in several wild populations of a number of larid species (Nethersole-Thompson & Nethersole-Thompson 1942, Shugart & Southern 1977, Fitch & Shugart 1984).

We have not been able to demonstrate polygynous breeding in wild Black-headed Gulls. During the phase of pair-formation (in the middle of April), however, one male was observed to court on four consecutive days for several hours with at least two females. In the same area Veen (pers.comm.) observed two cases of polygyny in Little Gulls *Larus minutus*.

In one case the two females (among which one second calendar year female) laid altogether 5 eggs in the same nest. Incubation was performed by all three parents. Incubation shifts were usually effected between the male and one of the females. The relation between the two females appeared to be very strained. At least some of the eggs of this super-clutch hatched.

In the other case the two females (among which probably again a second calendar year female) laid complete clutches in two different nests 0.6 m apart. This inter-nest distance was exceptionally small for the Little Gulls in that population (Veen 1980). In this case the male was only participating in the care for the nest of the oldest female. The young female incubated on her own and abandoned the nest after a dozen days.

In the course of our study several males in the cage have been observed which were simultaneously mated with two reproducing females. The trio described in the previous section (♂10

and ♀8 with ♀10; Fig. 4) arose in spring 1981. The same trio was formed in the next year, 1982, but then the relationships already became clear before the eggs were laid. In that season again the relations between ♀8 and ♀10 seemed to be strongly competitive. Nevertheless, they both laid their eggs in the same nest.

The first clutch, which was initiated on 11 May, contained 3 eggs of ♀8 and 2 eggs from ♀10. The second clutch, initiated on 15 June, contained 2 eggs of ♀10 and 1 egg from ♀8. Both clutches failed because the eggs disappeared.

Only one other case has been observed in which two females, which were paired with the same male, laid their eggs in a communal nest. Here the relations between both females were also competitive. For the three communal clutches in the two trios we further found that the laying dates of the first eggs of the two females were never farther than 5 days apart (1, 4, and 5 days).

We observed four other cases in which eggs were laid by two females, which were mated with the same male at the same time, but not in one communal nest. In all cases the intervals between the first egg of the two females was much longer (11, 13, 15, and 31 days) than of the females nesting communally.

In one case the second female built a nest at the slope of the large nest hill occupied by her mate. During the first week after the second clutch was laid, the male only sat on the first clutch. However, this clutch started to smell and it turned out that all eggs were rotting. Then the male moved towards the second clutch, of which two eggs hatched after two weeks.

In another case the second female laid her eggs without making a nest, rather close to the nest with the male she preferred. That female failed to incubate, while the male ignored her and the eggs.

In a third case the second female (♀12) produced an egg in the nest of a male (♂7) and his main female-mate (♀3), but before that main female started to lay. Nevertheless ♀12 was not tolerated on the nest to incubate her egg and two previously dumped eggs originating from another pair (♀5 and ♂5; section 3.7). Incubation was only performed by the bigamous male (♂7) with his main female-mate (♀ 3), who finally started to lay 9 days after all these other eggs had disappeared.

The final case involved a second female (♀2) who started to lay immediately after the clutch of the first female (♀8; Fig. 4; 1983) was destroyed by a polecat.

3.6. HOMOSEXUAL PAIRING

One could suggest that polygyny is an initial step in the establishment of another bond-type, the female-female pair, which is currently very much in the limelight (Hunt & Hunt 1977, Ryder & Somppi 1979, Kovacs & Ryder 1981, Conover 1983, Hunt *et al.* 1984). The occurrence of both bond-types in a large number of populations of different species (Conover *et al.* 1979, Shugart 1980, Lagrenade & Mousseau 1983, Kovacs & Ryder 1983) might be considered as positive evidence for this idea. However, direct observations in the field on the behaviour of female-female pairs, polygynous trios, and monogamous pairs (Pierotti 1981, Fitch & Shugart 1984, Hunt *et al.* 1984) do not support the idea that female-female pairs arise after desertion of the male in a polygynous trio. No males have been found to be associated with the territory of female-female pairs at any stage of the breeding cycle. Furthermore, copulations of females belonging to female-female pairs seem to occur with males which defend another territory and which are paired with another mate. And finally, females of polygynous trios seem to be very competitive which contrasts with the females in female-female pairs. It is more likely that polygyny and female-female pairing are two alternative responses to a sex-ratio which is skewed towards females and which might be rather common among the *Laridae* (Coulson & Wooller 1976, Hunt *et al.* 1980, Burger & Gochfeld 1981, but see also Nisbet & Drury 1984). There is some evidence that recently this sex-ratio has become more and more unbalanced because of DDT induced feminization of gull embryos (Fry & Toone 1981).

Male-male pairing among gulls has not yet been reported from wild populations. This does not necessarily imply that it never occurs under field conditions. It may be very difficult to detect this phenomenon in the field, because it is not associated with egg-laying and rarely with full nest construction. Among Black-headed Gulls held in captivity, however, male-male bonds occurred rather commonly (Van Rhijn 1985b). In this situation such a mating unit may result in nest construction, and even proceed with incubation and feeding of chicks after fertile eggs have been offered. Thus, theoretically, male-male pairing may result in the care for unrelated offspring by males. The only requirement is that females occasionally dump an egg in an empty nest occupied by other gulls (see section 3.7).

Nestbuilding was observed in 6 different pairs of male gulls. In 5 of these cases both members were seen to contribute to the construction of the nest. In the remaining case building was only performed by one member, which displayed a strong social preference for a male having a pair-bond with a female with nest and eggs.

In one of the former 5 cases one of the males also displayed a strong social preference for another male; in one other of those 5 cases one of the males displayed a strong social preference for a female too; in the remaining three cases the males entertained no other bonds.

Since the birds were sitting for long periods on their (empty) nests, we tried to supply two of the pairs with wooden egg-dummies and after a few days with fertile eggs. Most eggs were faithfully incubated and they hatched, but the males failed to keep these chicks alive. One of these two male-male pairs, however, was then supplied with peeping eggs and special food. These two eggs hatched, and in this case the chicks were successfully raised.

3.7. BROOD-PARASITISM

Some evidence for egg-dumping in wild populations has been obtained for the Ring-billed Gull *Larus delawarensis* (Conover *et al.* 1979).

In contrast to the large majority of the pairs kept in aviaries, the members of one couple (♂11 and ♀5; Fig. 5) failed during two successive seasons (1983, 1984) to sit on their eggs for a long time. Additionally, the female of this couple was not strongly attached to a particular spot, her intervals between laying were larger and more irregular than in other females, and she produced a relatively large number of big eggs. A considerable proportion of these eggs was adopted by other gulls who started incubating them.

We do not believe that these eggs were actually laid in the nests of the foster-parents. It is more plausible that they were retrieved by the other gulls. It is salient that these eggs were larger than those produced by the other females, and that they had a more greenish colour than most other eggs. These properties have been shown to be extremely effective for eliciting incubation (Baerends & Van Rhijn 1975, Baerends & Drent 1982).

The behaviour of this pair at the time of egg-laying could have facilitated adoption. The sites chosen for egg- laying were near to other nests, sometimes claimed by these pairs, and often somewhat elevated. The laying of one egg was directly observed. It occurred on a spot which was claimed by a pair without a nest or eggs (♂10 and ♀2). ♂11 and ♀5 abandoned the egg within an hour. Then it was taken over by the other two birds, who moved the egg towards their preferred spot, built a nest around it, and laid one additional egg after precisely 4 days. During spring 1982, which preceded the two years mentioned above, the female was mated to another male (♂5; Fig. 5). The first two eggs she laid in that season were adopted by another pair (♂7 and

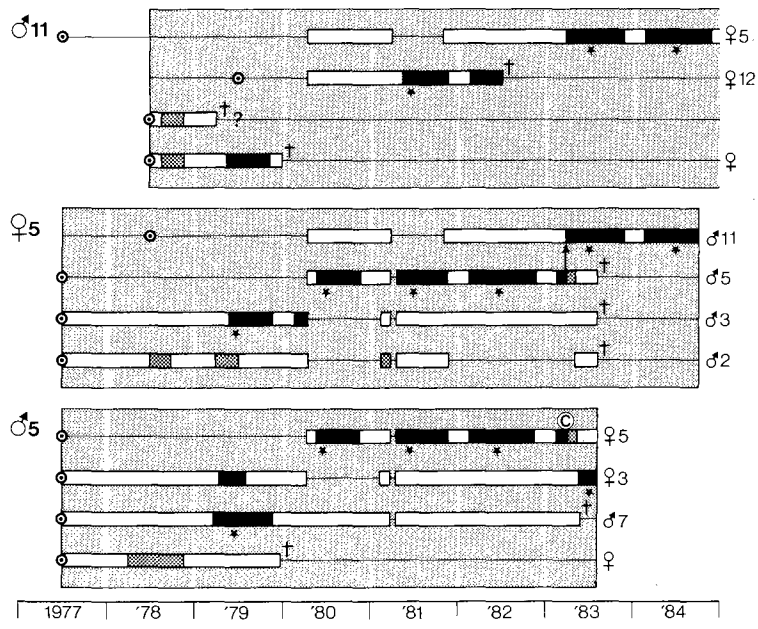

Fig. 5. Social preferences displayed by ♂5, ♀5, and ♂11. For a further explanation see also Fig. 4. Time of death of a subject is indicated by the right limitation of its diagram, time of birth of a partner is indicated by a circle on its line, time of its death by a cross, and finally, partner-change by a subject by an arrow.

♀3), but her mate (♂5) tried to regain the eggs at that time. In 1980 and 1981 she was also paired with ♂5. In both years they built a nest and incubated their own eggs. The male partner from 1983 and 1984 (♂11) was likewise able to care normally for a clutch of eggs as he demonstrated in 1981 with another female.

3.8. ADOPTION

Unrelated offspring may be adopted by adults of either sex. Pierotti (1980) emphasized that in some species of gulls chick recognition develops at a much later age than in most other bird species with semi-nidifugous offspring. This may be the cause of the high adoption rate, and of the occurrence of creching, in which a few adults protect any chick in the flock, regardless of its parentage.

Acceptance of eggs in wild Black-headed Gulls was shown by egg retrieval experiments (Baerends & Van Rhijn 1975). Both egg dummies and strange eggs were easily retrieved, although some birds seemed to display a slight preference for their own eggs. This preference became more pronounced when a choice was given between complete clutches. Thus, Black-headed Gulls seem to be able to distinguish their own eggs.

We were unable to observe clear cases of adoption of young Black- headed Gulls in the field. It was obvious, that in a few families the number of chicks was not absolutely constant when these chicks were less than one week old. These changes in number could not be due to overlooking them or to mortality. It must be concluded that young chicks are to a certain extent able to move between nests. Nevertheless we did observe that even very young chicks could be heavily attacked by adults. It is possible, however, that adults with peeping eggs or young chicks are fairly tolerant towards strange chicks of similar age. We never saw such changes in family size when chicks were over one week old. Strange chicks of that age were always attacked, particularly when running. Aggression was not only shown by the adults in these cases, but also by the young which remained near the nest.

Our captive birds were seen to accept eggs, egg-dummies, peeping eggs, and young chicks. We replaced clutches altogether 4 times by normal eggs, 3 times by wooden egg-dummies, 2 times by peeping eggs, and 5 times by young chicks. All these replacements were accepted by the owners of the nest. Further we supplied two empty nests with egg-dummies which were accepted by the gulls. Finally, in one case we added an extra egg to a clutch of two eggs, which had been incubated for about two weeks. This third egg was not accepted. On two occasions it was found outside the nest, and after it had been laid back for the second time, the birds started to destroy their nest.

On 5 different occasions a chick less than 4 days old moved towards another nest, where it was accepted. In all these cases the other nest contained chicks of similar age or peeping eggs (one nest). Sometimes the arriving chicks were softly pecked at by the foster-parents. In a few cases the approaching young chicks were threatened by the nest-owners. Older chicks were always chased away. Threatened chicks usually returned directly to their original nests. It was obvious that young chicks were not always treated in a friendly way by strange adults. We found at least four dead chicks with clear indications of pecks by adults. On one occasion we observed such an attack by a strange adult, which finally resulted in the death of the chick.

3.9. CLUTCHES OF WILD BLACK-HEADED GULLS

Inspection of nests in the field may give some idea about the occurrence of different bond-types among wild gulls (Hunt 1980). For this reason a few data on the clutches of wild Black-headed Gulls will be presented. In 1974 we measured the groundcolour of eggs in a big sample of 90 one-egg, 83 two-egg, and 104 three-egg clutches. Nine years later (1983) additional information was obtained on the groundcolour of eggs and minimal inter-nest distance in a random sample of 112 clutches (one, two, three, and four eggs), supplemented by 6 four-egg clutches.

The groundcolour of an egg was determined through comparison of the egg with an Ostwald colour scale (Baerends & Hogan-Warburg 1982). The variability between groundcolours of the eggs in the same nest was studied on the basis of the two samples of three-egg clutches. For all these clutches the scores of the three eggs were compared with eachother. In this way it

could be established how often two eggs in the same clutch 1) got the same score, 2) differed one degree only with respect to the scale of pure colours, 3) differed one degree only with respect to black or white content, 4) differed one degree with respect to black and white content, but in a complementary way (lighter or darker), and differed in other respects (Table 4). We also calculated how often such combinations would occur if the eggs of these samples were randomly distributed over all clutches (expected values). Observed values for the frequencies of the different combinations were only higher than the expected ones when the eggs 1) got the same score, 2) differed one degree on the pure colour-scale only, or 3) differed one degree in black and white content in a complementary way. The term 'similar eggs', which will be used below, remains restricted to these three combinations of groundcolours.

Homogeneousness amongst the eggs in the same nest is mainly caused by individual specific features of the laying apparatus of the female (Baerends & Hogan-Warburg 1982). It may therefore be expected that variability within clutches established by two females is higher than within one-female clutches. To investigate whether large clutch-sizes could be produced by more than one female, we compared the proportion of 'similar' pairs of eggs for the different clutch-sizes (Table 5). Indeed, our 1983 sample did show that the proportion of similar pairs of eggs was higher in two-egg and three-egg clutches than in four-egg clutches ($\chi^2 = 20.57$, df = 1, $P < 0.001$).

Statistical differences in the proportion of similar pairs of eggs could not be demonstrated between the two-egg and three-egg clutches of the same sample ($\chi^2 = 0.69$). In our 1974 sample, however, two-egg clutches seemed to contain a lower proportion of similar pairs of eggs than three-egg clutches ($\chi^2 = 9.02$, df = 1, $P < 0.01$). This unexpected difference may be caused by various factors, such as proportionally strong differences between the first and the second egg in cases in which the two-egg clutches were not yet completed (this factor is not likely in view of the data on the Herring Gull *Larus argentatus* eggs: Baerends & Hogan-Warburg 1982), or in the case of nest-robbery by a proportionally high risk for the first egg in a nest.

It may be concluded from the data above that

Table 4. Differences between the scores of groundcolours of all combinations of two eggs within three-egg clutches. Expected values are based on a random distribution of eggs over the nests. Asterisks refer to significant differences (χ^2 tests, 1 df, $P < 0.05$)

	1974			1983		
	Observed		Expected	Observed		Expected
Similar combinations:						
Same score	172	*	42.1	79	*	23.0
One degree on pure colour scale	39	*	25.0	27		18.8
Lighter or darker	25		32.5	45	*	27.1
Dissimilar combinations:						
One degree on black or white scale	0	*	5.9	6		7.5
Other differences	76	*	206.5	47	*	127.6
Total number of:						
Combinations of eggs		312			204	
Three-egg clutches		104			68	

Table 5. Frequencies of similar and dissimilar combinations of eggs in clutches of various size

Clutch size	1974		1983	
	Similar	Dissimilar	Similar	Dissimilar
Two eggs	49	34	18	9
Three eggs	236	76	151	53
Four eggs			16	26

statistical analysis:
1974: two eggs versus three eggs $\chi^2 = 9.02$, 1 df, $P < 0.01$
1983: two eggs versus three eggs $\chi^2 = 0.69$, 1 df, $P > 0.05$
two and three eggs versus four eggs $\chi^2 = 20.57$, 1 df, $P < 0.001$

four-egg clutches seem to be founded more often by two females than two-egg and three-egg clutches. This does not mean, however, that clutches by two females are common in the field. Among our randomly chosen 1983-sample of 112 nests we only found one four-egg clutch. Moreover the method of counting superclutches and extremely heterogeneous clutches gives little information about bond-types. Such clutches may be the result of polygyny, female-female pairing, or egg-dumping. Even four-egg clutches with dissimilar pairs of similar eggs do not necessarily originate from polygynous associations or female-female pairs, since the observations on captive birds suggest that the same female may parasitize the same nest on successive occasions.

Some indications for the underlying breeding association may be obtained from direct observation of suspected nests. We kept an eye on two nests during 5.5 h. The first nest initially contained two dissimilar pairs of similar eggs. At the time of observation, 11 days later, three chicks had just emerged and the fourth egg had little cracks. The second nest initially contained three eggs. Two of these eggs were similar and the third deviated strongly. At the time of observation one egg was left. Both nests were visited by two adults only, most likely a male and a female, during that observation period.

Additional information about the existence of polygynous mating units might be obtained from nest-site distribution. The distribution of minimal inter-nest distances in a sample of 112 randomly chosen nests is given in Fig. 6. Almost all nests lay more than 50 cm from their nearest neighbour. Six nests, however, were closer together: two at 20 cm and four at 40 cm. Possibly these nests belonged to polygynous mating units. If so 3 out of 109 males must have been paired with two females on neighbouring nests. There was no opportunity, however, to verify this supposition by direct observations.

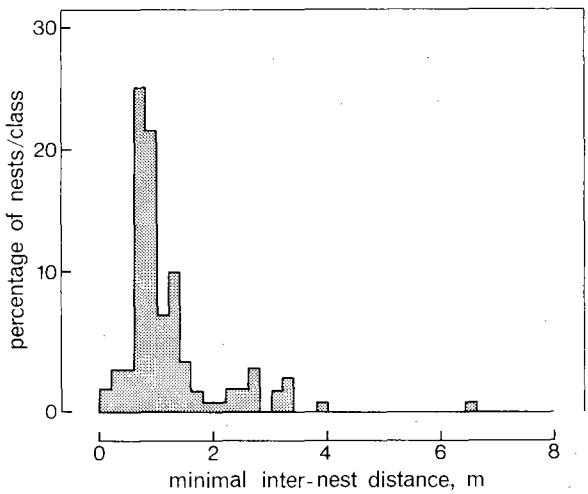

Fig. 6. Distribution of minimal inter-nest distances in a sample of 112 randomly chosen nests with at least one egg in a Black-headed Gull colony.

4. DISCUSSION

4.1. CONSTRAINTS OF PROXIMATE MECHANISMS

A comparison between the two sets of data presented in sections 3.1 and 3.9 demonstrates that unusual bond-types were much more common under the experimental conditions than in the field. Further, it could be shown that hatching and fledging success of the usual monogamous bond-type was much lower in our cages than in wild populations. These two findings might lead to the suggestion that the appearance of unusual bond-types was an adaptive response to the conditions met by the experimental birds. If this suggestion was correct, one would expect that the birds which participated in monogamous mating units produced less offspring than those which formed other mating units. This expectation did not hold. One would further expect that the unusual bond-types were better suited for the special cage environment. An important distinction between life in our cages and life in the field concerns the time needed for food-collection. Our birds were able to spend much more time for other purposes than the wild gulls. In fact, our gulls would have the time and energy resources to double their reproductive efforts. Under such conditions double clutching, such as found in a few wader species (Hildén 1975, Van Rhijn 1984, 1985a) in which both male and female care for a whole clutch of eggs on their own, would certainly yield much more offspring for both parents. This option, however, is probably not available to the gulls. Utilization of the extra time for parental care could neither be shown for the opti-

ons which were practised by our birds. For instance, this would imply that females of polygynous trios should not lay in the same nest, and should always be prepared to care on their own. None of these predictions was supported by the data.

It must be concluded that evolutionary reasoning does not offer a satisfying explanation for the occurrence of the various patterns of parental care observed under the experimental conditions. This means that the high incidence of unusual bond-types or other patterns of reproductive behaviour among Black-headed Gulls held in captivity must be ascribed to the constraints of the proximate mechanism for the formation of the normal monogamous pair-bond. For instance, the phenomenon of starvation of most very young chicks might be due to a disturbance of the normal chain of causal processes by the *ad-lib* food situation in our cages. The following elements may be relevant for that chain. During pair-formation females frequently beg and males may regurgitate in response to begging. In wild gulls the extra food is greedily consumed by the females. Our satiated females in cages, however, mostly rejected the food. This may be brought in relation with the frequency of regurgitation of males during pair-formation, shortly before egg-laying, and after hatching of the eggs, which was much lower in our experimental birds than in wild gulls. Therefore, one could suggest that the male's frequency of regurgitation for chicks depends on feed-backs from the female in an earlier phase of the reproductive cycle. Another example of a proximate explanation for unusual reproductive activities refers to the forced extra-pair copulations. Such copulation attempts might simply be released by the drooping-wing posture, because that posture is so similar to the one adopted by a female just before she accepts a copulation with her mate.

The proximate machinery must be constructed in such a way that all the different options observed are possible. To solve the question why many of these options have not yet been eliminated by natural selection, two topics need further consideration. First, the functioning of this proximate mechanism must be explained in more detail. This cannot be done within the scope of this article and will be presented in another paper. Second, the possibility that these options involve adaptive components for particular situations, which will be discussed in the following section.

4.2. ADAPTIVE COMPONENTS

In comparison with the normal biparental care system, the other patterns of parental care described in this paper may be classified in three categories on the basis of effects on reproductive success.

The first group of patterns might be associated with an increase of fitness. This group comprises mated males which additionally perform forced extra-pair copulations, polygynous males, and monogamous pairs which employ the method of brood-parasitism. The readiness of a very small number of females to accept extra-pair copulations might also be associated with such an increase of fitness, because the copulating male may have superior genes, or because their sons will become more fertile by the inherited tendency to perform extra-pair copulations (Gladstone 1979, McKinney *et al.* 1983, Van Rhijn 1985b). The scarce data available from wild gull populations of these effects on fitness only refer to polygynous males. These data, however, do not support the idea that male success is increased by polygyny (Kovacks & Ryder 1983, Lagrenade & Mousseau 1983, Fitch & Shugart 1984).

The second group of patterns must be associated with a decrease of fitness in comparison with biparental care, but all these patterns might be aimed at making the best of a worsening situation. This group comprises the participants of female-female pairs, and the female partners of polygynous males. Data on wild gulls support that reproductive success in all these types of females is low (Hunt & Hunt 1977, Kovacks & Ryder 1983, Lagrenade & Mousseau 1983, Fitch & Shugart 1984).

The third group of patterns is associated with an absence of any success during the same season, but all these patterns might be aimed at an increase of future reproductive success. This group comprises helping females, the participants of male-male pairs, and the birds caring for adopted eggs or chicks. There are no data

available of future effects on reproductive success of birds displaying these patterns.

One may come to the conclusion that the selective forces, maintaining the unusual bond-types listed in this paper cannot be very strong. Yet, certain aspects of these bond-types might be very useful for the birds. In fact, some of these aspects might have been moulded already by natural selection. On the other hand, the occurrence of useful components offer a broad substrate for future evolution. To examine these possibilities, some more details about the different bond-types must be evaluated.

Forced extra-pair copulations appeared to be directed to birds in the close vicinity, usually females, which were mostly in the phase of egg-laying. This suggests that the behaviour has been subjected to natural selection, resulting in a higher pay-off than in the case of forced extra-pair copulations being randomly directed towards other gulls. It is likely that males first try to determine sex and reproductive phase of potential victims, before actual attempts for copulations are made.

The only case of helping we observed, finally resulted in the establishment of a pair-bond. This may be comparable with cases described for Pied Kingfishers (Reyer 1980) and for White-fronted Bee-eaters *Merops bullockoides* (Emlen 1981), in which helpers really seemed to increase their future reproductive success. Helping might pay when suitable mates are not available but may be acquired in the future as a consequence of this relationship.

Polygynous males were mostly older and usually obtained their nuptial plumages earlier in the season than males with monogamous bonds (Van Rhijn & Groothuis in press). One might therefore suggest that polygynous males possess high qualities. It may therefore pay for a female to select such a male as a mate. The establishment of a polygynous trio, however, is always associated with certain risks for the participants. When the two females succeed in laying full clutches in the same nest, hatching success will probably be very low, because such a large number of eggs cannot be warmed optimally by one individual. When the two females lay in adjacent nests only one of them can be assisted sufficiently by her mate. Thus, if the formation of polygynous associations has been influenced by natural selection, one may expect that 1) females of the same mate strongly compete with each other, 2) males tend to care for only one nest, and 3) males tend to limit the amount of eggs in communal clutches. Indeed, strong competition between females could be observed in all polygynous associations. Similarly, males with two females with separate nests always assisted only one of them, except in the case that the first clutch turned out to be infertile and the male switched towards the second nest. Limitation of the amount of eggs in communal clutches was not observed in our experimental birds. However, such a mechanism might explain why clutches with 5 or 6 eggs of various gull species in the wild always belong to female-female pairs (Hunt 1980).

Homosexual pairing among females may be adaptive if males are of the rare sex and if these females succeed to copulate with fertile males. Both conditions seem to be met within populations in which female-female pairing has been observed (Hunt & Hunt 1977). Homosexual pairing among males does not seem to be adaptive at first sight. Considering that this phenomenon mostly occurs among young males and when females are of the rare sex (Van Rhijn & Groothuis in press), it may be suggested that homosexual pairing among males increases future reproductive success by the experience acquired in these relationships.

Brood-parasitism may be adaptive when it is likely that the eggs will be adopted by the foster-parents selected. There are at least two arguments for the hypothesis that this behaviour has been subjected to natural selection. Firstly, the only female which was seen to display this behaviour produced eggs which were extremely attractive as incubation objects. Secondly, the eggs were always deposited in or near the nests of birds which were in or close to the phase of egg-production.

Thus, all unusual bond-types seem to contain adaptive components. Yet, it is unlikely that, under the normal range of ecological conditions met by the species, these bond-types cause an increase of fitness for the participants in comparison with the situation in which both biological parents tend their joint offspring together.

4.3. GENETIC DIVERSITY BETWEEN INDIVIDUALS

One may finally question whether all birds had the disposal of a complete set of bond-types, or whether some bond-types could only be shown by particular individuals. This latter possibility might be ascribed to genetical determinants for bond-type diversity.

The various data presented in this paper demonstrate that most gulls displayed a number of bond-types during their life. On the basis of the life-histories of our experimental birds we could deduce that in most cases the gulls participating in the unusual polygynous and homosexual bond-types were seen in other seasons to form monogamous pair-bonds. Concomitantly, unusual parental care patterns, such as helping and brood-parasitism, where shown by individuals which had also been observed to display the usual pattern of parental care.

Our data do not exclude, of course, that the probabilities of the adoption of the various bond-types differ between individuals. This idea is supported by the fact that we observed many birds which were engaged in monogamous bond-types only, whilst, on the other hand, several males were seen to maintain polygynous bonds during a number of seasons (*e.g.* ♂10 in Fig. 4) and other were seen to maintain homosexual bonds during more than one season. Additionally, the few males which were seen to perform extra-pair copulations and the only female which was seen to dump eggs close to other nests, mostly showed this behaviour on several occasions.

On the basis of observational data only, we cannot conclude that the differences between individuals were caused by genetical factors. The effects of environmental factors can certainly not be excluded. It must be remarked, however, that the differences were not very strong. This indicates that genetical differences between individuals only provide part of the explanation for alternative bond-types, and most likely a minor part.

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6. SUMMARY

Unusual breeding bond-types, such as polygyny and male-male pairing were very common among Black-headed Gulls held in aviaries. Such associations seemed to be rare among Black-headed Gulls in the field (3.9).

To investigate the factors responsible for the occurrence of the different bond-types, we analysed all variants of parental care which could be observed. Most individuals participating in unusual bond-types also appeared to participate in the normal monogamous bond-type during other seasons (3.1). Yet, the usual bond-type was not very successful amongst the experimental gulls. Forced extra-pair copulations occurred between birds breeding in each other's vicinity, and were directed to females which were in the phase of egg-laying (3.3). The only case of a female helping a monogamous pair resulted in a polygynous association in the following season (3.4). The strongly competing females in polygynous mating units laid in the same nest or in different, but adjacent ones. Polygynous males only cared for one nest (3.5). Female-female pairing was not observed. Male-male pairing could lead to nest-building and even to incubation and care for chicks when the nest was supplied with fertile eggs (3.6). Brood-parasitism was shown by one female, which also appeared to lay 'attractive' eggs for incubation (3.7). Adoption of eggs was easily accomplished. Adoption of chicks was feasible too, but only when they were still young. It was repeatedly observed between families on neighbouring nests (3.8). These different phenomena, and those observed among various species of wild gulls, cannot sufficiently be explained by assuming that all bond-types are adaptive strategies which have been perfected by natural selection. Neither the idea that particular bond-types are bound to particular genotypes, nor that each individual has the disposal of a set of adaptive responses to various ecological conditions, offers a satisfactory solution. Consequently, the explanation must mainly bear upon constraints of proximate mechanisms for the formation of monogamous pair-bonds.

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8. SAMENVATTING

Centraal in dit artikel staan een aantal experimentele groepen Kokmeeuwen die in volières gehuisvest waren en waarvan de individuen vanaf de eerste zomer gedurende een verschillend aantal jaren werden waargenomen. Binnen deze groepen ontstonden een groot aantal ongewone sociale relaties, zoals mannen met twee vrouwen (polygynie) en man-man (homosexuele) paarbanden. Uit een nader onderzoek aan nesten in het Lauwersmeergebied kon niet worden geconcludeerd dat dergelijke ongewone sociale verbanden veel voorkomen in een natuurlijke situatie (3.9).

Om te begrijpen welke factoren ten grondslag kunnen liggen aan het verschijnen van de verschillende sociale verbanden, onderzochten we alle details van de relaties die wij tussen individuen zagen. Vrijwel alle individuen die betrokken waren bij ongewone banden bleken gedurende andere seizoenen ook in staat te zijn om de gebruikelijke monogame paarband te vormen (3.1). Deze gebruikelijke band leidde echter zelden tot voortplantingssucces bij de experimentele meeuwen. Soms vonden copulatie-pogingen plaats door mannen ten opzichte van dieren waarmee geen paarband onderhouden werd. Meestal betrof het hier vrouwen die een nest hadden in de buurt van hun belager, en die gedurende dezelfde periode ook eieren legden (3.3). Hulp bieden bij de ouderzorg aan een monogaam paar werd één maal waargenomen, en wel door een wijfje dat in het daaropvolgende seizoen samen met de eerste vrouw eieren legde bij dezelfde man (3.4). De vrouwen binnen polygyne verbanden bleken tamelijk vijandig tegenover elkaar te staan. Toch slaagden zij er soms in om hun eieren in hetzelfde nest te leggen. In de andere gevallen werden naburige nesten gebruikt. De polygyne man zorgde in die gevallen voor slechts één van de nesten (3.5). Paarbanden tussen wijfjes werden door ons niet gezien, hoewel het bestaan van dergelijke banden bij een aantal meeuwesoorten suggereert dat ook bij de Kokmeeuw de vrouw-vrouw paarband tot de mogelijkheden behoort. Paarbanden tussen mannen werden echter veelvuldig waargenomen. Dergelijke banden konden tot nestbouw leiden, en in de gevallen waarin wij zorgden voor eieren werd er met succes gebroed. In één geval werden er zelfs jongen groot gebracht (3.6). Broed-parasitisme werd toegepast door slechts één wijfje. Het was opmerkelijk dat dit wijfje eieren legde die, meer dan de eieren van andere wijfjes, zeer attractief waren als broedobject (3.7). Het vervangen van eigen eieren door vreemde eieren werd bijna altijd aanvaard door de experimentele dieren. Het vervangen van afgestorven eieren door jonge kuikens was ook mogelijk. Bovendien werd een aantal malen adoptie waargenomen van jonge kuikens die uit het nest van buren waren gelopen (3.8).

Deze en de resultaten die betrekking hebben op een aantal wilde meeuwenpopulaties kunnen slechts voor een gering deel verklaard worden door de aanname dat het deelnemen aan elk van de sociale verbanden opgevat kan worden als een door natuurlijke selectie geperfectioneerde 'aangepaste' strategie. De diversiteit van sociale verbanden had in dat geval tot stand moeten komen door 1) genetische verschillen tussen individuen, of 2) voor ieder individue het bezit van een breed scala van strategieën als aanpassingen voor diverse situaties. Het verschijnen van ongewone banden zal daarom moeten worden beschouwd als een gevolg van de bouw van de 'machinerie' die onder (voor de Kokmeeuw) normale omstandigheden leidt tot de vorming van een monogame paarband. De analyse van de werking van die machinerie vereist een speciaal onderzoek.