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BLACK-HEADED GULL OR BLACK-HEADED GIRL? ON THE ADVANTAGE OF CONCEALING SEX BY GULLS AND OTHER COLONIAL BIRDS

by

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SUMMARY

Mechanisms for sex-recognition in the Black-headed Gull, *Larus ridibundus*, were analysed in order to understand the occurrence of homo-sexual male pairs among captive members of this species. No discontinuities between males and females could be detected in either external characteristics or behaviour. Although most individuals select a mate of the opposite sex, there is no evidence that individuals which do not belong to the same pair are able to determine each other's sex. The adaptiveness of concealing sex for colonial monogamous species is discussed. Its significance was tested in a group of captive gulls. Small female-like males appeared to be most successful in reproduction. The development of polygynous mating systems seems to be opposed by a preference of females for caring males.

INTRODUCTION

Veen (this volume) suggested that gulls are able to broadcast signals containing both information about identity and a message about the desire for a close encounter with another individual. I wish to proceed with these close encounters, particularly those in which the participants are searching for mates. In order to select a suitable mate from available conspecifics, sex and quality must be determined. This paper deals with questions around sex-recognition by gulls and other birds breeding in colonies.

It seems to be self-evident that natural selection contributes to the development of properties permitting individuals to determine sex of nearby conspecifics without ambiguity. Individuals which select a partner without paying attention to sex will be penalized in evolution because, on average, they will obtain less offspring than individuals which always select a partner of the opposite sex. Nevertheless, both sexes of Black-headed Gulls, *Larus ridibundus*, look very similar. I had many problems in identifying the sex of these birds in the gullery. Even in our experimental breeding groups in cages the sexes of some individuals remained doubtful until their fourth year of life. For the gulls themselves sex-recognition seems to be difficult too. In the experimental groups I observed 7 homosexual male-pairs out of a total of

38 pairbonds. Moreover, in natural populations of at least 3 species of gulls homosexual female-breeding-pairs seem to occur rather commonly (HUNT, 1980). Surprisingly, reliable sex-recognition by gulls is not so selfevident.

SEXUAL CHARACTERISTICS

To pose the problem more precisely, I want to consider first which clues are available for Black-headed Gulls to determine the sex of conspecifics. Consequently the differences between males and females must be described in detail. Most data collected on this subject refer to the experimental groups of Black-headed Gulls in captivity.

Among the external morphological characteristics only body-size seems to be different for males and females. Body-weights of 13 males and 11 females were determined in 3 successive years (1980-1982) at the end of October. The average weight of males was 273.5 g (s.d. = 22.6) and of females 235.0 g (s.d = 25.9). There was considerable overlap between male and female data, as can be deduced from the large standard deviations. None of the other measures I determined in relation to body-size could be used for separating sexes without ambiguity. Head *plus* bill length gave the best prediction of sex. For the 13 males the average length was 85.1 mm (s.d. = 2.2), and for the 11 females 77.8 mm (s.d. = 1.2).

Egg-laying provides certainty about the sex of an individual, but unfortunately it cannot be seen very often. Besides, reliable identification of sex can be obtained by direct inspection of the gonads by means of laparotomy (HUNT & HUNT, 1977). There are no indications that sex of gulls can be determined on the basis of hormone levels in blood samples. In the Western Gull, *Larus occidentalis wymani*, WINGFIELD *et al.* (1982) found very few differences in circulating levels of the luteinizing hormone and androgens among breeding males and females. In some cases, however, females did show elevated levels of estrogens.

Sex-determination of birds can sometimes be based on the behaviour. Copulation gives a good prediction of the sexes of both participants, but occasionally homosexual or even reversed copulations may occur. Furthermore, members of some pairs never seem to copulate during the observer's attendance. For these reasons two other behaviour patterns from the gull's repertoire will be considered, namely 'begging' and 'luring' which have been interpreted by earlier fieldworkers (MOYNIHAN, 1955; TINBERGEN, 1959, 1965; MANLEY, 1960) as respectively typical feminine and masculine elements.

In spring 1981 the behaviour of 10 males and 10 females was studied in detail under weekly changing experimental conditions (fig. 1). For

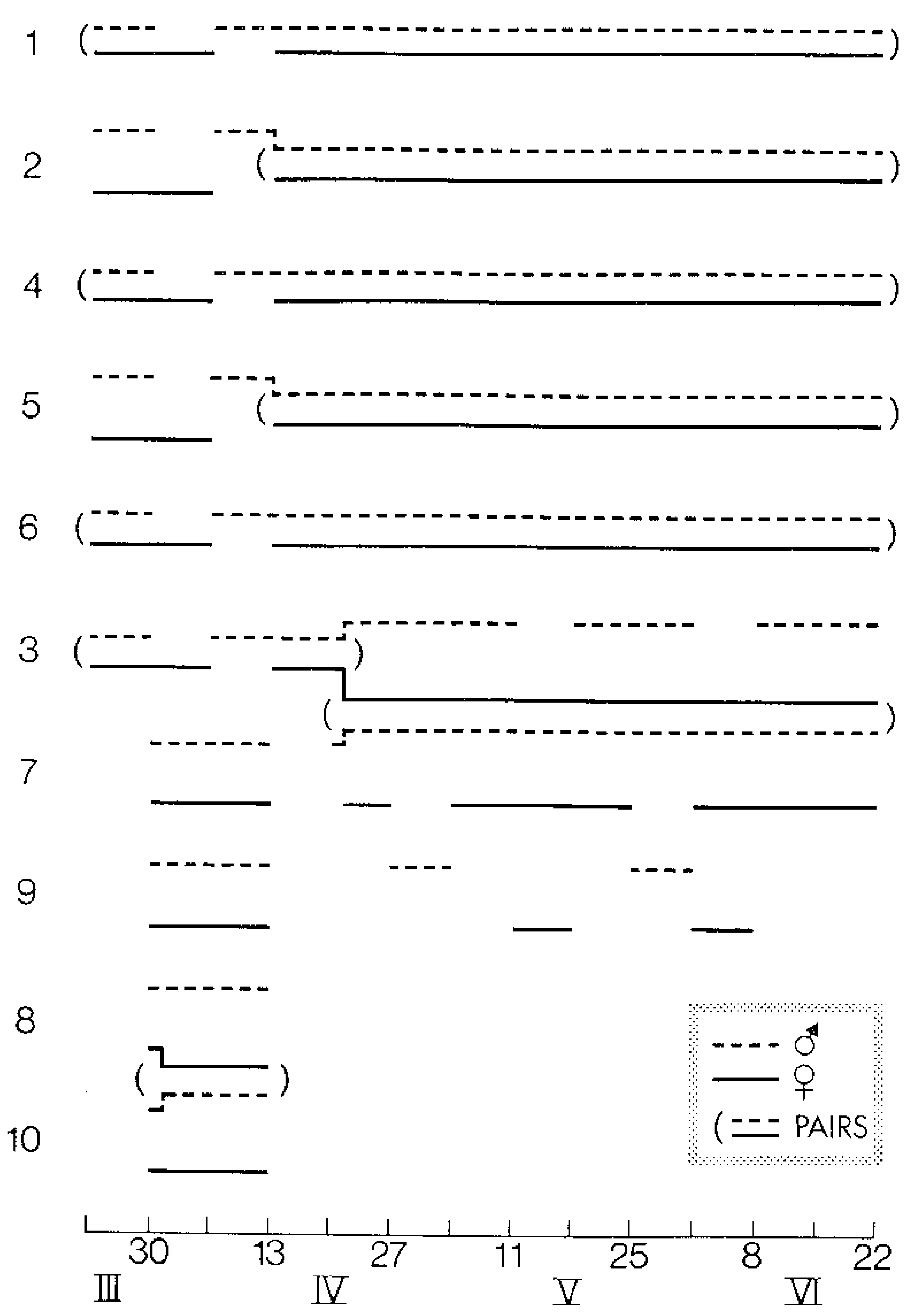

Fig. 1. Presence of 10 male and 10 female gulls in the experimental cage from 23 March up to 22 June 1981. The lines symbolizing members of the same pair are drawn close together. The periods during which the different pair-bonds were observed are enclosed in brackets.

the 14 individuals which were present most of the time in the experimental cage frequencies of both begging and luring were plotted per week (fig. 2). Data for members of the same pair are indicated in the same graph. Both begging and luring are shown by males and females. On average females beg more often than males, but there is considerable overlap. This cannot be explained by a tendency of females to beg mainly for food in the long period between pairformation and egg-laying and a tendency of males to beg mainly for copulation in the last weeks before egg-laying. Namely in the first weeks of observation some males were begging more often already than part of the females. It further seems that begging is associated with a state of being mated with another individual, because unmated birds rarely beg. On average males lure more often than females. Nevertheless, females may perform luring behaviour, even before hatching of the chicks. Luring behaviour may be shown by unmated individuals.

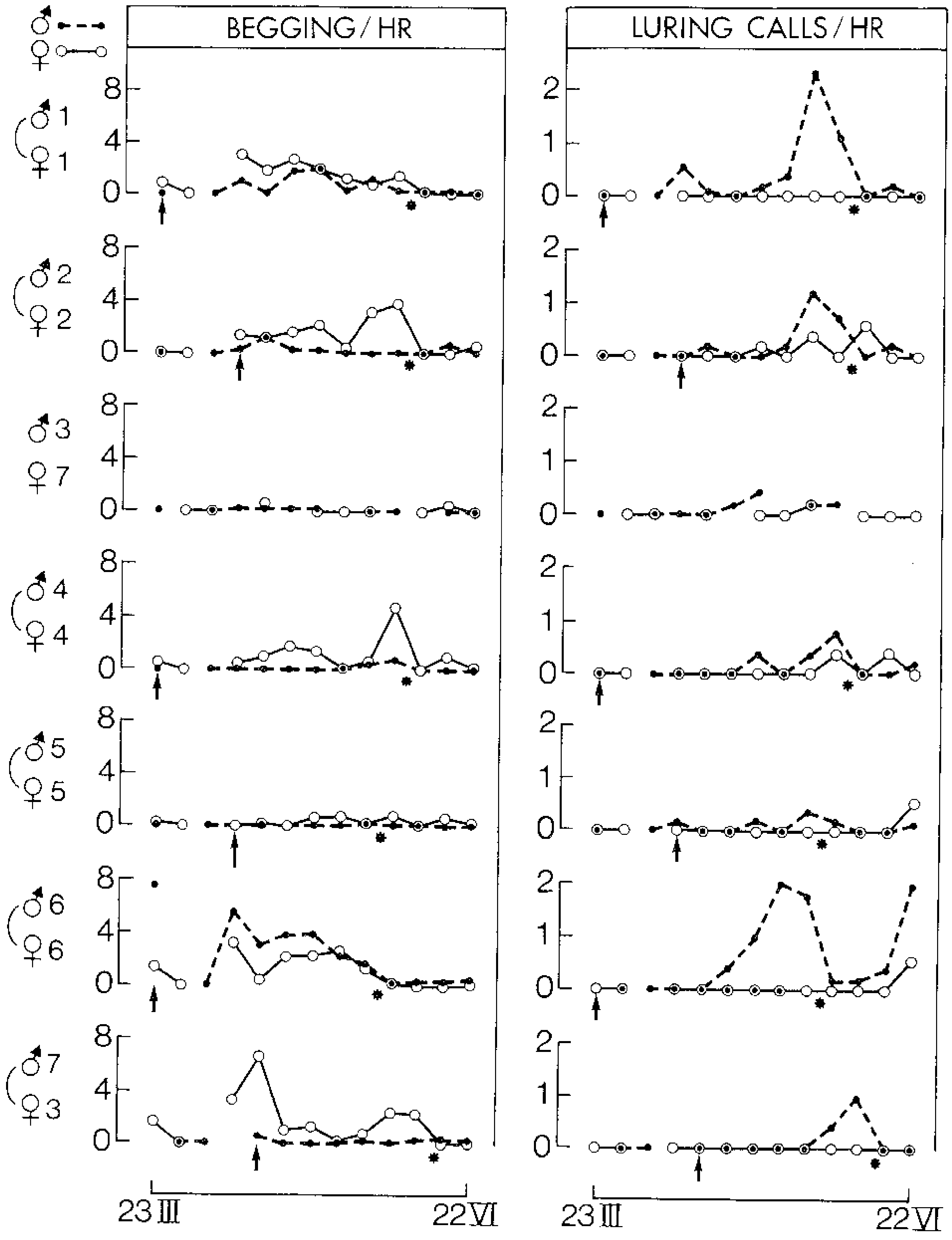

Fig. 2. Average frequency per hour of begging and luring calls by 7 male and 7 female gulls in the 13 weeks between 23 March and 22 June 1981. Members of the same pair are given in the same graph. The establishment of the pair-bonds are indicated with arrows, the first eggs by asterisks.

However, its occurrence seems to be restricted to the period when most pair-bonds are settled. Thus, in spite of overlaps between sexes, begging and luring seem to provide fairly reliable information about sex, but, in view of the status of the birds which display this behaviour, it remains very doubtful whether this information is available before and during pairformation.

CEREMONIAL ENCOUNTERS

To understand how potential partners recognize each other's sex during the early part of pair-formation, the analysis must be concentrated on close encounters between individuals searching for mates. During these encounters displays are mostly shown in a typical sequence (*e.g.* MANLEY, 1960) and both participants seem to become synchronized during at least part of this sequence (VAN RHIJN, 1981). Encounters with display will be indicated as 'ceremonial encounters'. They include a sequence of three postures: 'oblique', 'forward' and 'upright' (MOYNIHAN, 1955), of which the first two may be replaced by 'straight-up' and 'low-up' (VAN RHIJN, 1981) and may be repeated several times (MANLEY, 1960) during high intensity encounters. The oblique and straight-up are mostly accompanied by the long note of the 'long-call'. The upright is often accompanied by 'head-flagging', which can be described as facing away from the other participant. Ceremonial meetings may be followed by begging.

Changes in the constitution of the experimental cage (fig. 1) caused a large number of social interactions associated with some sudden changes in social relations. In order to gain more insight into male and female roles, I want to consider four examples of those sudden changes: pair-formation, reunion of old breeding pairs, partner change, and formation followed by disruption of homosexual male-bonds.

The frequency of ceremonial encounters (fig. 3) increased immediately after pair-formation between female 8 and male 10. A few days later it decreased again. After reunion of old breeding pairs, as exemplified by pair 6, a similar change in the frequency of ceremonial encounters could be observed. Ceremonial encounters were extremely common after female 3 changed to another mate, male 7. Before this, the frequency of encounters with her former mate, male 3, was very low.

Male-male relationships need to be explained somewhat further. From 30 March - 6 April males 1 and 2 were housed in a cage containing only males, in which a mutual bond between both individuals arose. This bond continued to exist in the next week (6-13 April), when both males were back in the experimental cage, but without their former breeding mates, females 1 and 2. The bond was not very strong, as can be deduced from the low frequency of ceremonial encounters by male 2. In the same period a new bond developed between males 1 and 9 with a large number of ceremonial meetings. In the next two weeks (13-27 April) female 1 was together again with her former breeding mate, male 1, and male 9 was housed in another cage. Most ceremonies were seen between male 1 and female 1, and a small number continued to occur between male 1 and male 2. After this period male 9 was introduced again, which resulted in an extremely high number of ceremonial encounters between male 1 and male 9 during the first four hours, a large number between male 1 and female

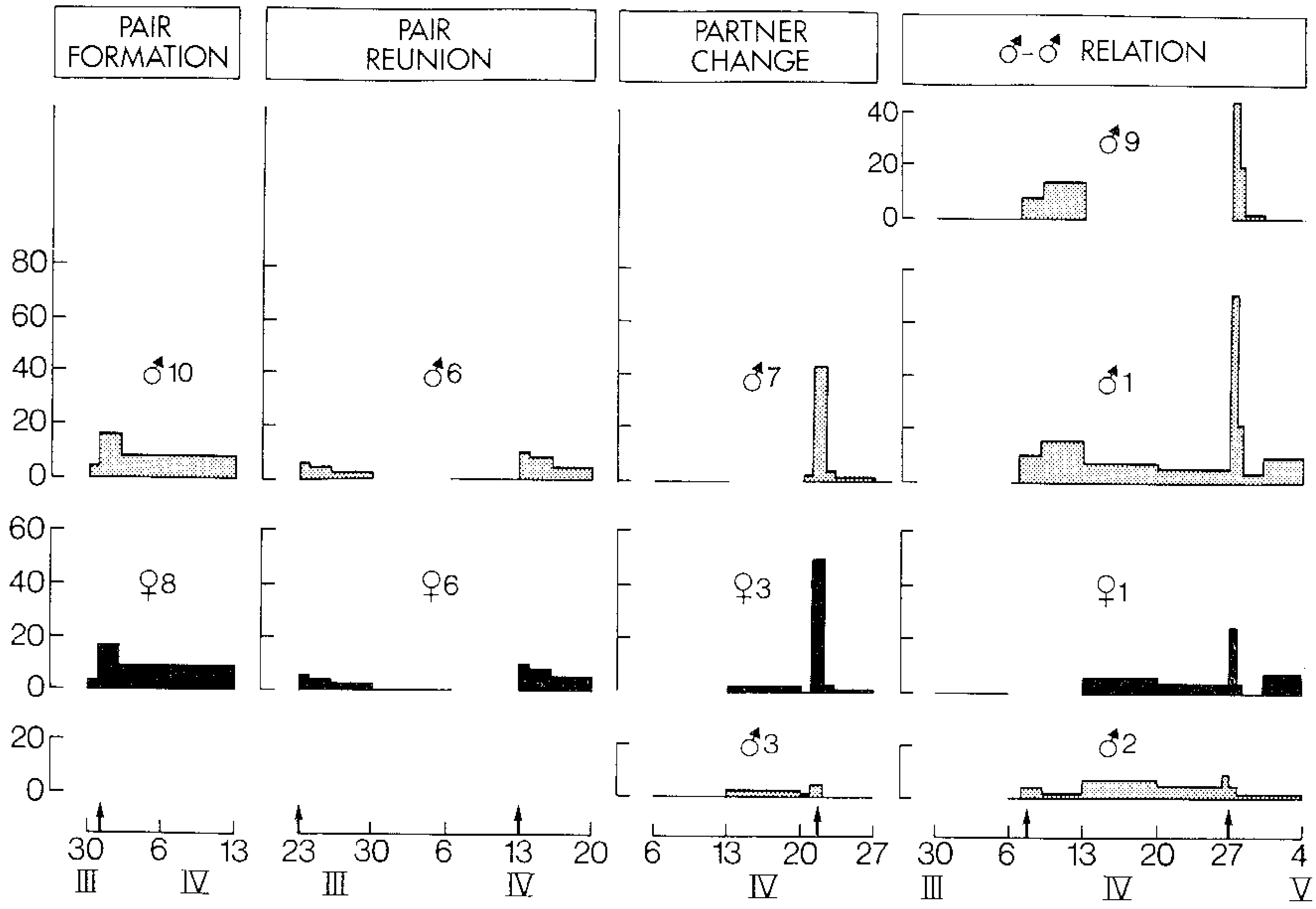

Fig. 3. Average frequency per hour of taking part in ceremonial encounters by several individuals in four examples referring to different processes. Further explanation in the text.

1, and even a considerable number between males 1 and 2. After this period of high activity, male 1 chased male 9 away and ceremonies between these two individuals were not seen anymore.

Peaks in the frequencies of long-calls (fig. 4) were shown by male 10 just before pair-formation, by female 3 and male 7 just after partner change, and by male 9 after he was reintroduced into the experimental cage with his former mate, male 1 (27 April). It is striking that long-call frequency did not suddenly rise to a high value after reunion of old breeding pairs, as in pair 6. It must be noted, however, that these data do not only refer to ceremonial encounters, since long-calls may occur in a large number of other situations.

Head-flagging (fig. 5) was often shown by male 9, female 8, male 6, female 3, and extremely often by male 7 after settling a pair-bond with female 3. These data do not suggest that in heterosexual encounters head-flagging is shown in particular by one of both sexes.

Begging (fig. 6) was on the average most often shown by females, as for instance by female 3 after partner change. In some cases begging frequencies were almost similar for male and female, as for male 10

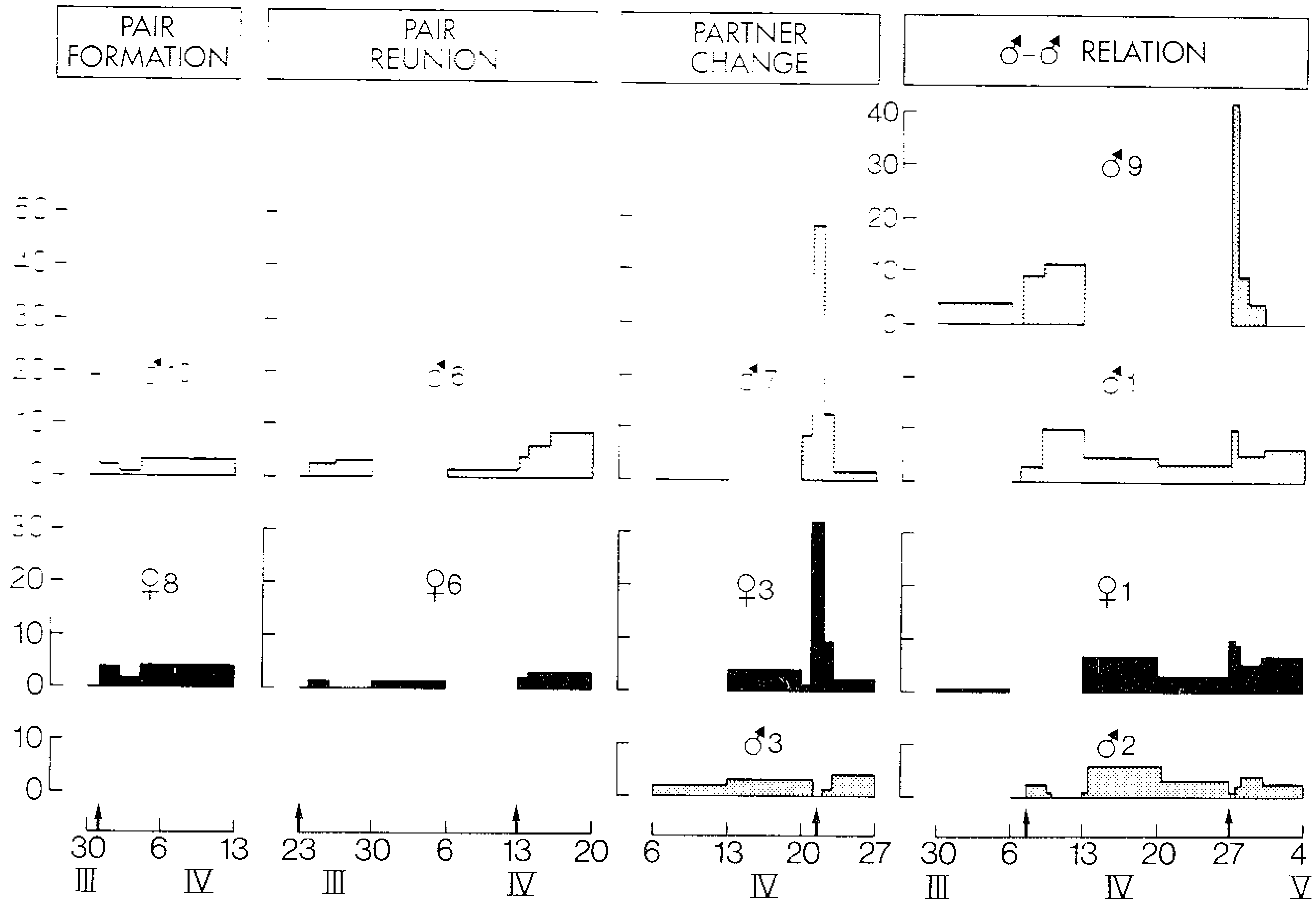

Fig. 4. Average frequency per hour of long-calling by several individuals in the same examples as in fig. 3.

and female 8 and for pair 1. In a few cases begging frequencies for males exceeded those of their female mates, as for pair 6.

It may be concluded that during changes in the social relations between individual gulls explosions of activity are rather common. Evidence for role differentiation between males and females during these explosions is extremely poor. Thus, it remains doubtful whether the behaviour during the first encounters provides a reliable clue about the sex of potential males. Perhaps the absence of reliable clues offers an explanation for the high incidence of homosexual pair-bonds in the experimental groups.

SEX RECOGNITION BETWEEN GULLS

In spite of the lack of reliable clues about sex, most pair-bonds which were settled in the experimental groups were heterosexual bonds. Apparently most partners finally succeed in recognizing each other's sex. It may be questioned now to what extent sex-recognition occurs between individuals which do not belong to the same pairs. To solve this question, the aggressive encounters between such individuals have been examined. The analysis refers to the period from 20 April to 22

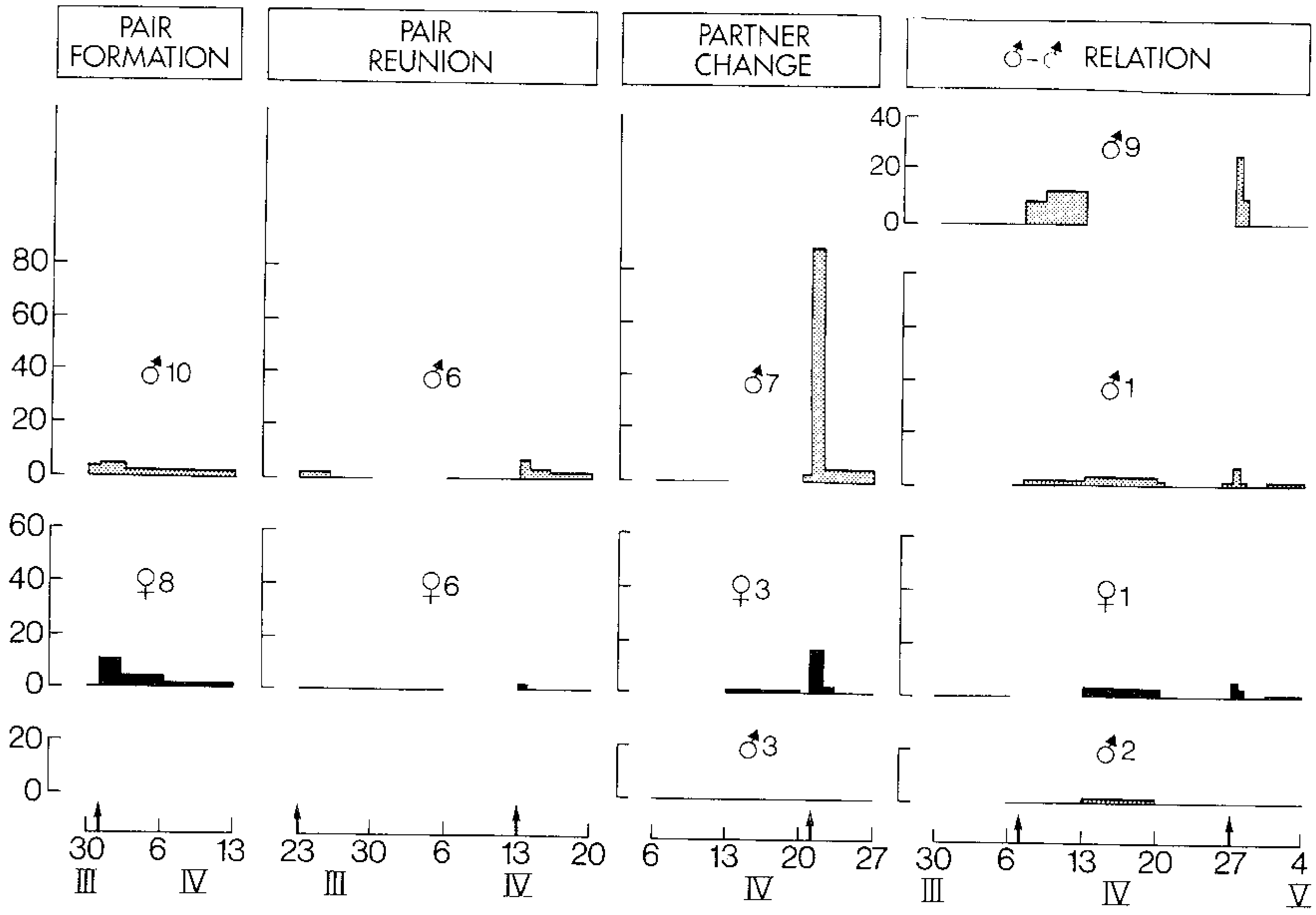

Fig. 5. Average frequency per hour of head-flagging by several individuals in the same examples as in fig. 3.

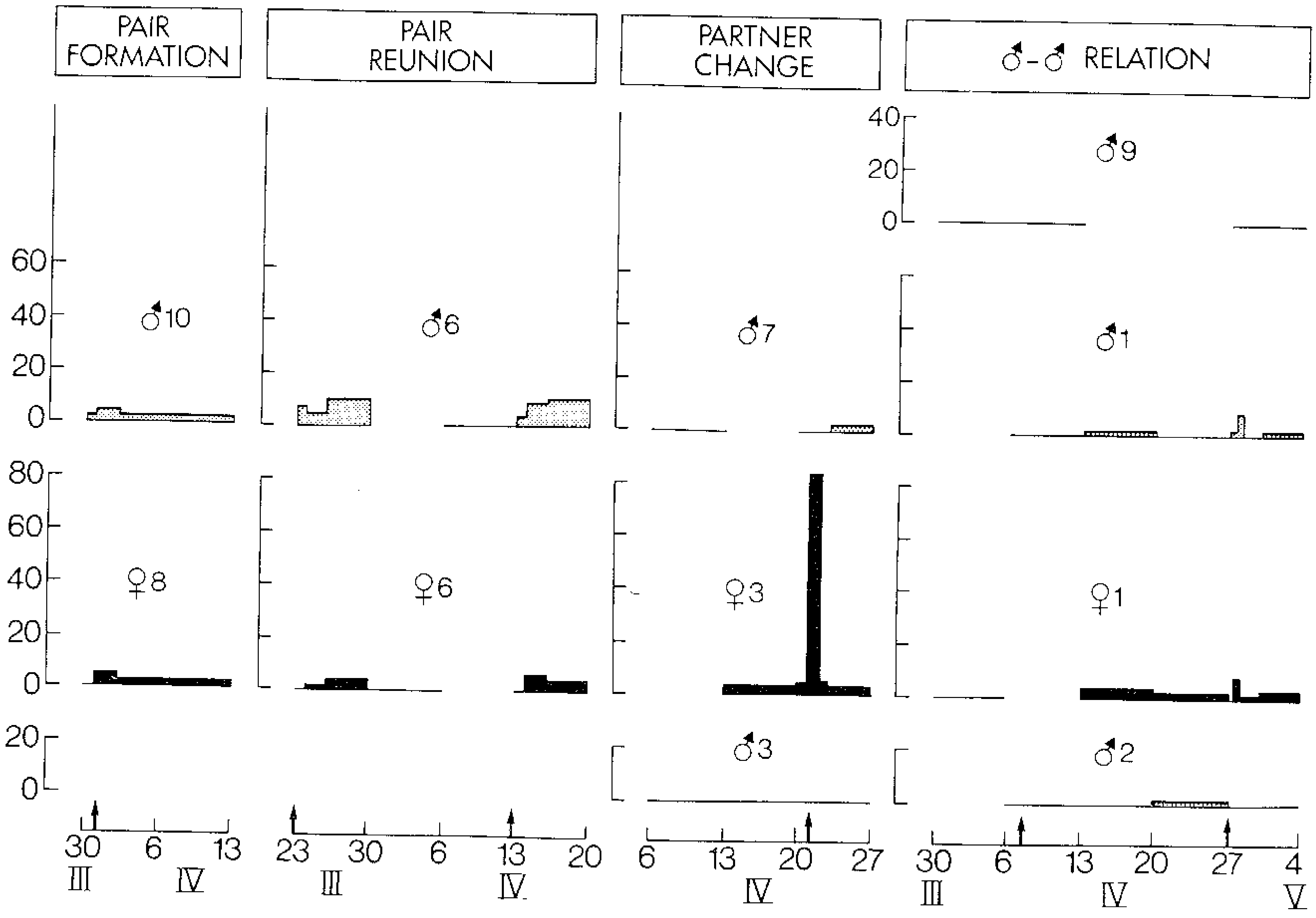

Fig. 6. Average frequency per hour of begging by several individuals in the same examples as in fig. 3.

TABLE I

Aggressive encounters between 12 paired and 4 unpaired gulls.

		RECIPIENT UNPAIRED				
		male		*female*		*totals*
	male	133		85		218 (68%)
		exp.	127.8	exp.	90.2	
ACTOR	*female*	54		47		101 (32%)
PAIRED		exp.	59.2	exp.	41.8	
	totals	187	(59%)	132	(41%)	319
						X^2 = 1.62
						non significant

		RECIPIENT PAIRED				
		male		*female*		*totals*
	male	70		25		95 (64%)
		exp.	73.2	exp.	21.8	
ACTOR	*female*	44		9		53 (36%)
UNPAIRED		exp.	40.8	exp.	12.2	
	totals	114	(77%)	34	(23%)	148
						X^2 = 1.70
						non significant

June (fig. 1) when all members of the final 6 breeding pairs were together in the experimental cage.

There are at least two reasons to expect that aggressive encounters mainly occur between members of the same sex. *Firstly*, each member of the same sex is a potential competitor, while each member of the opposite sex is a potential mate. *Secondly*, there is a difference between the average male and female body-weight, which might be associated with differences in the average fighting strengths. It is conceivable that only matched birds engaged in aggressive encounters.

In the encounters between the 12 mated gulls and 4 unpaired individuals (males 3 and 9, and females 7 and 9), both mated and unpaired males initiated and received more aggressive actions than females (table I). Both phenomena might be connected with a high level of activity in most males. The distribution of aggressive actions over the four combinations of sexes, however, was completely random. Consequently, these data do not provide evidence about sex-recognition. In the aggressive encounters between individuals belonging to the same breeding group, but without adjacent nests (table II),

TABLE II

Aggressive encounters between paired gulls belonging to the same breeding group, but without adjacent nests.

		RECIPIENT				
		male		*female*		*totals*
ACTOR	*male*	303		105		408 (60%)
		exp.	302.4	exp.	105.6	
	female	198		70		268 (40%)
		exp.	198.6	exp.	69.4	
	totals	501	(74%)	175	(26%)	676 $X^2 = 0.01$ non significant

TABLE III

Aggressive encounters between paired gulls with adjacent nests.

		RECIPIENT				
		male		*female*		*totals*
ACTOR	*male*	270		166		436 (48%)
		exp.	281.1	exp.	154.9	
	female	320		159		479 (52%)
		exp.	308.9	exp.	170.1	
	totals	590	(64%)	325	(36%)	915 $X^2 = 2.36$ non significant

again males initiated and received more often than females, and again the distribution over the combinations of sexes was random. Finally, even between individuals on adjacent nests (table III) the distribution over the four combinations was random. Thus, even for neighbours there is no evidence that individuals recognize each other's sex. On the contrary the finding that males and females initiate aggressive actions about equally often against neighbours (table III) might be interpreted as an extra effort by the gulls to conceal their sexes.

ADVANTAGES OF CONCEALING SEX

The finding that even between neighbours sex-recognition seemed to be absent was unexpected. One may argue that under normal conditions mechanisms for the identification of sex will be perfected by natural selection. Nevertheless it is conceivable that under particular circumstances natural selection does contribute to the development of sexual indistinguishability with respect to conspecifics.

In a number of polygynous and promiscuous species only the larger and stronger males are able to monopolize one or more mates. Small males do not gain by advertizing their sex. On the contrary, in some species small males are able to reproduce by mimicking a female while approaching a receptive female or an unfertilized clutch of eggs (*e.g.* Gadgil, 1972; Dominey, 1980). Small males which advertize their sex are unable to perform these actions.

Gulls are predominantly monogamous. It has been suggested by Burley (1981) that strong sexual competition in monogamous species is also an important factor in the evolution of sexual indistinguishability. She provided convincing support for the prediction that colonial birds would be monomorphic, against both territorial and solitary birds being mainly dimorphic.

Strictly Monogamous Mating Systems

In strictly monogamous species sexual competition may be expressed in two different ways. *Firstly*, it may occur during the process of finding a mate of the opposite sex. Competition may be strong if the sex-ratio is unequal. *Secondly*, competition may be expected during the process of winning the best partner. Competition may be strong when there are large differences in the qualities of potential mates.

Competition is expensive for all participants. Therefore it must be advantageous for an individual to avoid competition as much as possible. This may be attained by advertizing sex and quality only to the preferred future mate. However, it is almost impossible to select a mate when all individuals of a species try to conceal sex and quality. The only possibility of avoiding most competition is to hold back part of the information about sex and quality from the majority of conspecifics, and to advertize a small bit of information which arouses the interest of a limited number of equivalent conspecifics, from which a suitable mate can be selected.

The next question therefore concerns the kind of information which is suitable for a first selection among conspecifics. For a Black-headed Gull this implies: how to attract attention of a small group of equivalent conspecifics from the huge group of colony members. By advertizing sex the attention of a very large subgroup may be attracted. Furthermore, information about sex gives no definite answer to the question whether the individual is interesting for future encounters. It only tells about the individual's possible role in future encounters: partner or competitor. Information about quality, however, may be very suitable for attracting the attention of a small group of equivalent birds. It is therefore plausible 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.

Predominantly Monogamous Mating Systems

It may be questioned whether gulls and other colonial birds are strictly monogamous. In a large number of apparently monogamous colonial bird-species forced extra-pair copulations are fairly common (GLADSTONE, 1979). In addition, in a number of species low frequencies of polygamous mating systems can be found (*e.g.* SHUGART & SOUTHERN, 1977; RÖELL, 1979; GREEN, 1980). Finally, in several colonial species members of a pair may be assisted with parental care by one or more helpers (*e.g.* PIEROTTI, 1980; EMLEN, 1981).

In the experimental groups of Black-headed Gulls all deviations mentioned above could be observed. Forced extra-pair copulations were seen 6 times, in at least 4 cases a male was paired with two egg-laying females, and one time an extra female assisted two parents with incubation and feeding a chick. All these deviations from monogamy enlarge the chances for sexual competition. It may therefore be questioned whether they could have induced the evolution of sexual indistinguishability.

Successful forced extra-pair copulations enlarge reproductive success of the male concerned. In the evolutionary sense, his regular mate will not experience disadvantages from this action, unless the male invests in extra-marital bonds. Again in the evolutionary sense the raped female will not always meet disadvantages, because her copulation partner's quality is not necessarily worse than her regular mate's quality. In fact the sons of both females may inherit a high fitness if variability in the tendency to perform extra-pair copulations is connected with genetical factors. The only real victim of the extra-pair copulation is the raped female's regular mate. This male has to invest in parental care for non-related chicks. A male could lower the chance of being deceived, however, by selecting a regular mate without clear feminine characteristics. Thus, protection against extra-pair copulations may initiate the evolution of sexual indistinghuishability because males are expected to prefer male-resembling female mates.

Consequences of polygamy and cooperative breeding systems will be considered together, because some of their transitions occurred in my experimental groups. The system in which one male was mated with two females which layed their eggs in separate (but adjacent) nests, seemed to be purely polygynous. On the other hand, the system of two parents with an extra female incubating and feeding the chick seemed to be purely cooperative. The system of the last trio in the subsequent season, however, when both females layed their eggs in the same nest, seemed to be a transitional stage.

I want to confine myself to systems with one male and two or more females, because in the experimental groups only males exhibited the tendency of maintaining several bonds at the same time. For these systems costs and benefits for the different participants will be considered again in order to understand evolution of sexual indistinguishability.

Males with two mates will, on average, obtain more offspring than males with only one mate. Females, however, which have to share one mate will, on the average, be less successful than females with a monogamous mate, because the male's parental investments must be shared too. In the evolutionary sense, a polygynous system offers advantages for males, but disadvantages for females (*e.g.* ORIANS, 1969). It could be questioned then, why some females invest in a bond with a paired male. The answer could be that it is the best choice she can make under the given circumstances, because all males are mated already, or the remaining unmated males have bad qualities. Thus, it is possible to argue that the second female makes a good choice. The first female, however, meets several disadvantages as soon as her mate initiates a bond with a second female, unless that second female is only helping.

When males, as in most gull species, perform a similar role in parental care as females, unmated females searching for a mate should prefer unmated males which are not attractive for a second female. Female-resembling males with good properties for parental care seem to fulfill this condition. Thus, protection against polygyny may also initiate the evolution of sexual indistinguishability because females are expected to prefer female-resembling male mates.

A TEST FOR SELECTION FOR SEXUAL INDISTINGUISHABILITY

When individuals really profit by concealing their sex, it must be possible to demonstrate selective forces for sexual indistinguishability. I therefore tried to correlate reproductive success of my experimental birds with body-size, measured by head plus bill length. An almost equal number of large and small females observed during about the same number of seasons (table IV) were engaged in a similar number

TABLE IV

Reproductive success of the experimental females in relation to size.

head + bill length	*number of females*	*number of seasons*	*long lasting hetero-sexual bonds*	*short lasting hetero-sexual bonds*	*number of eggs*
large (> 77 mm)	8	22	13	7	34
small (≤ 77 mm)	7	21	15	5	36

TABLE V

Reproductive success of the experimental males in relation to size.

head + bill length	*number of males*	*number of seasons*	*long lasting hetero-sexual bonds*	*short lasting hetero-sexual bonds*	*homo-sexual bonds*	*number of egss*
large (≥ 86 mm)	4	14	6	5	3	13
intermediate	5	15	8	3	1	20
small (≤ 84 mm)	5	15	14	4	4	37

of pair-bonds and produced a similar number of eggs. Consequently, there is no evidence for selection on female size. Success for males, however, seemed to be strongly related to body-size (table V). Small males fathered about three times the number of eggs as large males. These data strongly suggest that selection works in favour of female-resembling small males.

On the basis of these results it is possible to speculate about the nature of the selective forces for sexual indistinguishability in Black-headed Gulls. No selection for male-resembling females suggests that protection against forced extra-pair copulations is not very important. The evidence for selection for female-resembling males, however, suggests that protection against polygyny could be the most important factor in the evolution of sexual indistinghuishability. I suspect that polygynous systems may easily arise in Black-headed Gull populations when food is abundantly present. This can be deduced from the large number of bigamous males in the experimental groups where food was always present. A predisposition for polygyny can also be concluded from the contents of Black-headed Gull nests in the field. During the first season I was working in a Black-headed Gull colony in spring 1974, Gerard Baerends already pointed out to me that many nests contained eggs from different females!

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I am greatly indebted to Gerard Baerends for giving free play to my scientific creativity. This was essential for the present study. I realize that my use of this freedom could have provoked some conflicts, particularly when I wandered too far away from his own interests. Nevertheless he really stimulated my work: sometimes by convincing me to consider another side of the story, sometimes by arousing my obstinate attempts to prove the correctness of my view. Both kinds of stimulation turned out to be fruitful.

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