1. Introduction

The displays of the black-headed gull (*Larus ridibundus*) are well known examples of complex species-specific stereotyped motor patterns. They are also classical examples of postures, postulated to have derived in form during the course of evolution from behaviour patterns resulting from interactions of tendencies to attack and to flee (*Tinbergen*, 1952). Furthermore it has been often suggested that such displays are still under the control of these tendencies (*e.g.* *Moynihan*, 1955). The present study of the ontogeny of the displays was conducted because of the following reasons:

1. In comparison to locomotory patterns, the period it takes for the displays to develop into complete adult forms is considerably longer (*Moynihan*, 1959). In this period, agonistic interactions with conspecifics frequently occur. These, as well as other environmental influences could possibly affect the development of the displays. The relatively long developmental period offers good opportunities for studying experimentally the effect of such influences.

2. A causal ontogenic research on display behaviour can be expected to be suitable for the verification of the above mentioned conflict hypothesis. For this purpose I considered it important to investigate...
whether the agonistic tendencies shape the displays in young birds in a
proximate sense. Krutt (1964) found aggressive and fear behaviour of
young jungle fowl to change with age; the complexity in motivational
background of adult display seems to be gradually built up during
ontogeny. It might therefore also be possible to gain a better under-
standing of the motivational background of adult display, by studying the
ontogeny of these postures and calls.

Because of these considerations we may expect the ontogeny of
displays to be more complex than that of locomotory patterns. Studies on
the ontogeny of the latter have shown that before the adult motor pattern
is seen, variable or incomplete forms of it can often be recognized. These
incomplete patterns seem to develop gradually into more stereotyped
functional ones in which the separate elements (e.g. the movements of
separate limbs) become better coordinated, probably in a hierarchical
system (e.g. Bekoff, 1981; Fentress & McLeod, 1987; Thelen, 1985).

An important question concerns the possible function of these
incomplete forms: are they necessarily precursors, with a function in the
development of the adult pattern? In other words: is experience with the
effect of the performance of the incomplete pattern required for the com-
plete form to develop?

Although early (and often spontaneous) motor activity appears to have
an effect on the growth of joints, muscles and their innervations of the
C.N.S., (cited in Fentress & McLeod, 1987; Prechtl, 1984; Oppenheim,
1981), this does not seem to have an important behavioral effect
on the development of the complete adult pattern. Several studies
indicate that the gross coordination of the motor pattern lies within the
central nervous system (see Dawkins, 1983 for a review). This central
pattern generator often develops prior to the function it has and some-
times even before the behaviour pattern itself can be observed (Bekoff,
1981; Bekoff et al., 1979; Clark et al., 1988; Provine, 1981; Prechtl,
1984). Studies in which practice with early motor performance or
afferent feedback was manipulated indicate, that sensory feedback,
resulting from motor performance is not very important for the develop-
ment of the gross coordination of the adult pattern (Carmichael, 1926,
1927; Fentress, 1978; Grohman, 1939; Hamburger, 1973; Provine,
1981; Weiss, 1941). Feedback mainly seems to be necessary for finer
adjustments of the pattern to the environment. Functional experience
mainly influences the way in which the motor patterns become linked to
each other and to the appropriate stimuli (see Fentress & McLeod, 1987
for a review).
However, results of these studies are almost exclusively obtained from motor patterns involved in locomotion, such as walking, kicking, swimming, flying, and of hatching behaviour in chickens and grooming behaviour in mice. The question whether these results are also applicable to the development of more complex motor patterns is still unanswered. The ontogeny of stereotyped postures and calls that are displayed by many animals during social interactions are of special interest. The period in which incomplete forms are performed seems to be much longer for display development than for the development of the patterns just mentioned (see below for more details). This might suggest that in the case of display development experience with the performance of incomplete forms of motor output has a function in the development of the complete pattern. Because these displays act as social signals it is possible that social experience is involved in their ontogeny. Moreover, in the case of song development in some species of songbirds, both imitation and matching by means of (auditory) feedback are important factors and these may also be involved in the ontogeny of other displays. Displays are also particularly interesting because the development of motivational systems (e.g. those for aggression and fear in the case of threat displays) could have an important influence on the ontogeny of these motor patterns. Because of this latter point, studies on the ontogeny of display behaviour may give insight in the influence of internal factors on display behaviour in adults. The lack of ontogenetic studies on display behaviour is possibly due to the old definition of a Fixed Action Pattern, proposed by Lorenz. He claimed that these patterns are ‘‘innate’’, a term which tends to mask our lack of knowledge about the mechanisms by which the display develops as a result of interactions within the organism and between the organism and its surroundings.

The first question to be answered concerns the development of the species-specific form of the displays during ontogeny: do these postures and their accompanying vocalizations develop gradually or are they already completely present early in ontogeny?

With respect to display postures, many authors suggest that its form is more variable in the young animal than in the adult. Also, a gradual shift in their form during ontogeny, often from what is called ‘‘simple’’ to ‘‘more complex’’ has been suggested (e.g. van de Burg, 1976; Dane et al., 1964; Farris, 1967; Fischer, 1965; Fox, 1970; Henty, 1966; Kruijt, 1964; Moynihan, 1959; Platz, 1974; Wiley, 1973; Williams, 1972; Wyman & Ward, 1973). Such a relatively long period during which the display is still not completely performed suggests that the
development of the display is open for experiential influences during its ontogeny. However, most of these studies are not very detailed and lack quantitative data concerning the form of the postures. Moreover, except for some anecdotal reports on the outcome of social isolation experiments, no attempt has been made to systematically test hypotheses about the mechanism by which the displays develop during their ontogeny.

Other authors report more or less complete display patterns occasionally performed by very young animals e.g. the crowing posture and tidbitting in chickens: ANDREW (1966, 1969); strutting in turkey chickens: SCHLEIDT (1970); SCHULMAN (1970). ROGGENBRUCK (1986) and STAMPS (1978) studied the form development of displays in lizards in more detail and found adult-like displays in very young lizards. They also found ontogenetic changes in some details of the movements. Some of these changes took place during the first days after hatching (ROGGENBRUCK, 1986). Such early changes in the form of a motor pattern, already completely present early in ontogeny, were also found by HAILMAN (1962) in the ontogeny of bill pecking in gulls. These early changes may be due to maturation of the muscles. The early presence of complete display in ontogeny may be related to the function those patterns fulfill at that time (OPPENHEIM, 1981; STAMPS, 1978).

Many display postures are accompanied by species-specific vocalizations, which are of course equally interesting for ontogenetic studies. A gradual development in the form of vocalizations is well known for song in songbirds. Also, in many studies on the ontogeny of simpler calls, a gradual change in the morphology of these vocalizations has been found. Many authors report a change with age in pitch of various types of calls for various species (e.g. ANDREW, 1969; MEINERT, 1983; PLATZ, 1974; SCHLEIDT, 1973; THOMPSON, 1970; WÜRDINGER, 1970; ZANN, 1975). It is likely that these changes are related to changes in the anatomy of the syrinx (e.g. PLATZ, 1974; WÜRDINGER, 1970), but more complex ontogenetic changes in the vocalizations, like changes in frequency modulation and duration, as well as a gradual differentiation from one "precursor" to a more elaborated repertoire have often been reported (ANDREW, 1969; PLATZ, 1974; THOMPSON, 1970; WILKINSON, 1980; ZANN, 1975). The latter results are suggestive for ontogenetic changes in not just the effectors, the vocal apparatus, but also in the central nervous system, as is the case for song development.

On the basis of these data we can ask the following questions:
— At what age is the complete motor pattern present in the young animal?
— Why does the young animal perform complete patterns, if already present, so rarely?
— What kind of mechanism guides the development towards the species-specific form?
— To what kind of external influences is the development open and at what age?
— How does the completed motor pattern become fixed in the stereotyped adult form?

With the above mentioned questions in mind a study was carried out on the ontogeny of the species-specific displays in the black-headed gull. This species was chosen because adult birds have clearly recognizable stereotyped species-specific display postures and vocalizations which have already been studied and described in detail by others (Manley, 1960; Moynihan, 1955; Van Rhijn, 1981; Tinbergen, 1959). Black-headed gulls can easily be kept in captivity, in which they reproduce (Van Rhijn & Groothuis, 1985, 1987).

The results, presented in this paper, are given into two parts. The first part (part 3) consists of a detailed quantitative description of the form development of four displays. These displays consist of three of the four main displays of the adult birds of this species, which were performed frequently enough by the young for a detailed analysis: choking, oblique and forward. The fourth display consists of the begging display, typical for young gulls. These displays will be separately discussed in this sequence. In each of these four sub-parts first of all a description of the adult form of the display is given, in which several form elements will be distinguished (e.g. position of the bill, neck, body and carpal joints, as well as the accompanying vocalization). Thereafter the development of the display is described: first, the vocalization typical for the display; second, the frequency during ontogeny of those postures in which the main elements of the complete posture is present; third, the development of the different form elements of the posture and their combinations. Each of the four sub-parts ends with a separate discussion on the ontogeny of the display concerned. Part 3 ends with a general conclusion concerning normal display development in black-headed gulls.

In the second part of the results, part 4, the results of an experiment are discussed in which the normal course of display development was manipulated by raising young gulls in a situation lacking the normal context for display development. This experiment was carried out to gather some hints about the mechanisms underlying the form development found in the displays and as an introduction to further investigations.
The last part, part 5, consists of a general discussion in which on the basis of the main results from the descriptive- and experimental parts possible mechanisms are suggested, responsible for the form development found in the displays.

2. Material and methods

2.1. Description and procedure for the analysis of postures and calls.

In the display repertoire of adult black-headed gulls four main postures can be distinguished:

1. The oblique, an erect posture with an oblique neck and a horizontal or upwards directed bill or with a vertical neck and an upwards directed bill. This posture is always accompanied by the species specific long-call, a series of loud harsh sounding notes.
2. The upright; an erect posture with the bill held horizontally and the neck held vertically. This posture is performed without a vocalization.
3. The forward in which the neck is somewhat extended in forward direction and in which the bill is held horizontally or upwards. This posture is often performed immediately after the oblique and is in that case accompanied by the last notes of the long-call.
4. Choking in which the neck is held at an angle of less than 45 degrees with the horizontal and in which the bill points downward. This posture is accompanied with the choking call, a series of short notes in a fast rhythm.

This paper deals with the ontogeny of three of these postures and their calls. The upright was hardly seen in the young gulls. The paper also deals with the begging display of the young, which consists of a rapid up and down pumping movement of the head.

All postures, performed during social interactions, were classified in one of the four display categories, according to their form:

- Erect postures with long-call like vocalizations in the oblique-like category.
- Postures with the head held in front of the body and with a horizontal or vertical bill position were considered as forward-like postures.
- Postures with the bill held down and the neck held in an angle of less than 45 degrees with the horizontal were classified in the choking-like category.
- All pumping movements of the head were lumped as begging-like movements.

The form development within such a category was analyzed for five age classes according to the form criteria relevant for that particular category:

- The position of the bill (for choking-, oblique- and forward like postures), the neck (all postures), and the body (for choking-like postures) in the vertical plane;
- The degree of extension of the carpal joints (choking-, oblique- and forward-like postures);
- The duration of the postures (for oblique-like and pumping postures);
- The combination of separate form elements with each other (all postures) and of the posture with the typical call (all postures);
- Whether the posture was performed during sitting or hiding (only for choking-like postures).

The analyses of the vocalizations were done on four categories of calls (choking-like, long-call-like, begging- and alarm calls), which were distinguished on the basis of pitch and form of the main frequency bands (see 3.1.2). Rhythmical calls with short intervals between the notes were considered as choking-like vocalizations. If these rhythmical calls had higher pitched notes, these vocalizations were classified as long-call-like vocalizations. The quantitative analysis concern the duration of the notes and of the intervals between these notes.
The data concerning the development of the form of the displays are all derived from an analysis of video registration of the postures, except for the begging display. In this way, the postures could be analyzed in detail by means of slow motion and re-play of the video film although this had the disadvantage that the birds could not always be individually recognized, due to difficulties in identifying the colour bands. All motor patterns which stayed stationary for more than 0.2 sec were analyzed. Duration of postures was measured in .05 sec. All observations were made from a hide at a distance of maximally 4 meters from the observation cages.

The vocalizations of the birds were sampled from the groups which were hand-raised, and analyzed on an Uniscan I type 4500 Spectrum Analyser. The duration of notes and intervals between notes was measured in .05 sec.

2.2. Composition of the groups used for observation.

This study was started with observations made in the field. In this way information about the natural context of the displays performed by the young and about changes in frequency and form of these motor patterns was obtained. However, these field observations proved not to be suitable for a detailed quantitative analysis of the form of postures and calls. Therefore they were mainly used as a basis and as controls for the observations made on young held in captivity; both types of observations were always in close agreement with each other. Therefore, most of the data presented in this paper result from observations made on groups of gulls raised in pens in the laboratory yard.

Three types of observation groups were raised at the laboratory.

1. Semi-natural groups.

Data from these birds were used to describe: a. the development of absolute frequencies of behaviour patterns from hatching until the end of the first year; b. the development of the form of the forward; c. the development of the form of the begging display; d. the form of the oblique, forward and choking displays in adults. The observed birds in these groups were raised by adult gull pairs in a large aviary (see below for details).

2. Large groups with conspecifics of the same age.

Data from these groups were used to describe the form development of a. the choking display; b. the oblique display; c. the vocalizations. In these groups young chicks, sampled in the field, were raised from the 3rd day after hatching until they were more than 15 weeks old. Data concerning the form development of the oblique and choking could not be obtained from the semi-natural groups because in these groups the occurrence of these agonistic postures was too rare and too unpredictable for obtaining enough postures on video for a detailed form analysis. By raising large groups of conspecifics, the frequency of agonistic interactions could be considerably increased. This was due to the fact that the chicks formed already in the first week small subgroups within the large one, each defending their own part of the cage against the others. This resembles the field situation in which every sibling group defends its territory against intruders. In addition, agonistic interactions were initiated by placing an adult intruder in the cage once a week. In the indoor cages I used a stuffed adult gull that was slowly moved on the end of a stick and in the outdoor cages a live one was used.

3. Experimental groups.

Small groups of 3 conspecifics were raised from hatching until the age of one year, in visual isolation from other groups. These groups were composed in an attempt to manipulate the normal course of display development. This raising condition was chosen because observations in the field and under laboratory conditions had revealed that the agonistic displays were almost never performed spontaneously but almost always during
agonistic interactions with adults, other than the parents, or with non-sibling young. In contrast, the begging display was almost exclusively performed towards the own parents. Therefore, by raising young chicks from hatching on in small groups with conspecifics of the same age, an attempt was made to exclude the normal context for display development in a less drastic way than in an isolation experiment. At the age of 15 weeks, when normally raised birds frequently show completely forms of display (see below), the birds were confronted with unknown individuals to test their stage of development of display behaviour.

2.3. Housing conditions.
The birds in the semi-natural conditions were kept in an aviary of 10 by 6 m containing 13 adults and 4 nests with young. When eggs or young of less than three days old were robbed by other gulls in the cage, they were replaced by new eggs or hatching young, collected in the field. All birds were colour banded, but due to the vegetation in the aviary it was not always possible to recognize individuals.

The young from the large groups were collected in the field at an age of approximately 3 days and were kept until the age of four weeks in groups of 17 birds in indoor cages of 3.5 by 1 m. Thereafter they were placed in groups of 7 to 9 birds in outdoor aviaries measuring 3.6 by 1.8 m. When the large groups were split up, the social structure was taken into account in such a way that in every new group at least 3 subgroups were present. In the outdoor cages the subgroups also defended parts of the cage as well as, temporarily, the bathing pool.

The experimental birds were raised from hatching on in groups of 3 conspecifics of the same age in indoor cages of 1 by 1 m until they were 5 weeks old. Thereafter they were placed in outdoor cages of 2 by 2 m. The indoor as well as the outdoor cages had wooden walls except for the front part which consisted of wire. They were placed in such a way that the birds were visually isolated from other groups. In order to test the birds at an age of 15 weeks with unknown conspecifics, the outdoor cages were placed together in groups of two, in such a way that the partition in between the cages could easily be removed.

Eggs and young were collected in the field in the Lauwersmeer polder, in the northwestern part of the Netherlands. Hand-raised chicks were fed by a mixture of food pellets for mink farms, yeast, dried insects and water; they were stimulated to eat during the first week by holding some food in front of them on the top of a small stick (simulating the parental bill). Young of more than two weeks old were fed ad libitum with the above mentioned pellets. Chicks in the semi-natural condition were fed by their parents who got pellets ad libitum and two times a day the above mentioned pap and some fresh fish. Water was refreshed at least once a day; in the outdoor cages bathing pools were present, measuring 0.6 by 0.4 m.

In the indoor cages of the large groups, 3 to 4 shelters were placed, measuring 0.3 by 0.15 by 0.15 m which served as hiding places. In the outdoor aviaries, the young could hide in the vegetation.

2.4. The experiment.
Every week during the first 14 weeks of age each of the four small groups was observed 5 times during 1 hour. To increase the amount of social interactions, the bathing water was refreshed from the 6th week onwards, just before two of the five observation hours. In order to test whether the display frequencies in the small groups were different from those in the control groups, the frequencies during the first 10 weeks of age in the small groups were compared with those of 4 young raised under the semi-natural conditions. Because the latter birds could not be distinguished individually, the mean of these 4 animals was tested against the individual scores of the 12 experimental birds from the
four small groups. This was done with a two way Anova with repeated measurements: on one factor the effect of group (two levels), and on the other a repeated measurement of the weekly scores of the display frequencies (5 levels: week 2, 3, 4, 6, 8).

In order to test whether the form development of the displays in the small groups was different from that of normally raised birds, the scores for the oblique posture of the birds in the small groups were compared with those of the large groups raised with conspecifics of the same age. Data from the young in the semi-natural conditions concerning the oblique could not be used because no detailed video recordings were obtained from oblique-like postures, performed by these birds. To treat the data from the large group as controls was considered legitimate because the birds in these groups had at least as high a display frequency as those in the semi-natural conditions; moreover, scores made directly by hand of the different forms of the oblique in the semi-natural condition revealed essentially the same results as were obtained from video analysis for the large groups; 77% complete oblique postures during the 10th-12th week, against 83% in the large group during the same period.

In order to test whether the low frequencies of display performance and the low percentage of complete displays in the small groups could be regarded as a long term retardation of display development, and not just as the momentary effect of lack of stimulation in those small groups, the birds in one group were confronted with the birds in the other adjacent cage at the age of 15 weeks. In this way, two groups of six individuals were made from four groups of three. Observations were made during the first three days after the removal of the partition, 8 hours in total for each group of 6 individuals.

2.5. Statistical treatment.

Data concerning differences in duration of some call-types, interval between notes, the oblique-like postures and pumping bouts were statistically assessed with a one way analysis of variance. However, because these data were collected from groups of birds in which single birds often contributed more than once to the same group of data, the data are not fully independent of each other. On the other hand, an Anova with repeated measurements could not be done because the birds were not always individually recognizable. Because the groups were often quite large, and because results of a normal Anova often match those from an Anova with repeated measurements, a normal Anova was carried out to give an indication of the statistical significance of the results.

3. Development of displays under normal conditions

3.1. Development of choking.

3.1.1. The adult posture and call.

In the adult choking display seven major elements can be distinguished:
1. bill held down;
2. bill closed;
3. fast rhythmical head movements towards the ground with a small amplitude;
4. neck somewhat extended at an angle of less than 45 degrees with the horizontal;
5. body tilted to the ground;
6. carpal joints raised;
7. choking call: a typical rhythmic vocalization, stifled and with low fre-
quencies (Figs 1j and 2g). All these elements are not always present, but the positions of neck and bill are seen as characteristic for choking; postures containing these two elements (1 and 4) will be called choking-like postures (see Manley, 1960; Mynihan, 1955; van Rhijn, 1981; Tinbergen, 1959). The morphogenesis of choking was studied according to these characteristics.

3.1.2. Development of the choking-call.

The rhythmical call is the first developing element. In young black-headed gull chicks three distinctive types of vocalization can be distinguished (all names after Impekoven, 1971):

1. Pee-calls (Pee) having the most pronounced harmonic around 4 kHz and sounding as high pitched peeps (Figs 1a and b);
2. Chatter-calls (Cha), often much lower in pitch and in which the frequency bands have a more or less zigzag form (Fig. 1c-f);
3. Harsh sounding calls (Ha) with the main frequency band around 2 kHz (Fig. 1g-i).

The mean duration of the note intervals for these three different call types were not the same: (one-way anova: $F = 33.27; p < .001$). Pee and Cha did not differ significantly from each other, but Ha had significantly shorter note intervals than the other two (Newman-Keuls test: $p < .01$). These short intervals in Ha-bouts give this type of vocalization its choking-like fast rhythm. In fact, the duration of intervals of Ha did not differ significantly from that of adult choking (t-test, $p < .5$) (Fig. 4, first half).

Comparison of the durations of note intervals of Ha and those of the other choking-like calls for several age classes revealed, that the short note interval gradually developed with age: Ha-calls produced before the fourth day of age had significantly longer intervals than Ha-or choking-like calls produced by older gulls, (one-way anova: $F = 40.28, P < .001$; Newman-Keuls test for comparing early Ha with the others $p < .01$) (Fig. 4).

The form of the notes also changed with age: from a note with clearly distinguishable harmonics towards a more harsh sounding note that became lower in pitch and more stifled by the time the birds keep their bill closed during choking (see below) (Fig. 1g-j).

3.1.3. Frequency.

The frequency during ontogeny of choking-like postures is given in Fig. 3. It increased during the first two weeks of age and decreased at the time
Fig. 1. Sonograms of the main vocalization types of black-headed gulls of different ages. A = Pee-call day 1; B = Pee-call day 29; C = Chatter-call day 1 with modification of the Pee-call; D = Chatter-call day 1 with modification of the Harsh-call; E = Chatter-call day 3; F = Chatter-call day 25; G = Harsh-call day 1; H = Harsh-call day 5; I = Harsh-call day 19; J = Choking-call during choking with bill closed, day 26; K = vocalization made at the moment an adult gull is going to sit; L = Landing-call week 12; M = Mew or Luring call week 10; N = Mew or Luring call adult; O = Long-call like vocalization day 30; P = Long-call like vocalization week 10; Q = juvenile Long-call in first spring; R = adult Long-call.
the young were able to fly and no longer territorial; in the field young of this age normally leave the colony.

3.1.4. Development of the posture.

a. Bill position.

Fig. 5a presents for 5 age classes the relative frequency of 3 bill positions (horizontal, downward-oblique and downward-vertical) in postures accompanied by choking-like vocalizations (see 3.1.3) and in which the neck was held less than 45 degrees above the horizontal. It shows that when choking-like calls were given, postures with horizontal bills were most frequent in chicks under three weeks old. The relative frequency of these postures considerably decreased in older young, in favour of postures with a bill pointed extremely downward.

Reversely, choking-like postures were nearly always accompanied by choking-like vocalizations, for every age class in more than 90% of the
Fig. 3. The mean frequency per individual per hour of 4 displays in 10 different age classes in semi-natural condition. "obl" = all oblique-like postures. "cho" = all choking-like postures. "fw" = all forward-like postures. Pump = all pumping bouts. See text.

Fig. 4. Duration (mean and s.e.m.) in sec. of note intervals for different call-types. 1 = Pee-call; 2 = Chatter-call; 3 and 6 = Harsh-call after day 5 of age; 4 and 8 = adult Choking-call (with closed bill); 5 = Harsh-call before 4th day of age; 7 = Choking-call during week 10-12 (with closed bill).
observed cases. Apparently, the connection between the choking-like calls and the choking posture strengthened during the first weeks of age.

The percentage of choking-like postures in which the bill was closed was less than 10 in gulls which were under ten weeks old, but increased gradually to 100 in adults (Fig. 5b).

b. Head movements and the position of carpal joints and body.

As can be seen in Fig. 5c, the typical head movements gradually increased from 0% in less than 3 weeks old chicks to 62% in adults. The raising of the carpal joints also gradually increased from less than 20% to almost 100% (Fig. 5d). And finally, the tilting of the front part of the body gradually increased from almost 0% to more than 80% (Fig. 5e).

c. Hiding and standing while choking.

The early choking-like postures were often performed while the young gull was trying to hide: the birds moved to the shelters or tried to move under other chicks in the corner of the cages where they crouched. As can be seen in Fig. 5f, the relative frequency of choking-like postures neither performed in the shelter nor in a group of other young increased considerably with age. The percentage of choking-like postures performed while standing (in contrast to sitting), also increased with age (Fig. 5g). Consequently, young black-headed gulls, growing older, more and more perform choking postures on their own while standing openly in front of the opponent.

d. Combinations of form elements.

Fig. 5h gives for the 5 age classes the percentage of all choking-like postures in which all form criteria for the complete form of choking are fulfilled. This complete form was hardly seen in gulls younger than 10 weeks; in adults the choking-like postures consisted for almost two thirds of complete choking postures.

To investigate whether the performance of the different form elements of the complete choking postures become more coordinated during

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Fig. 5. The percentage of choking-like postures in which a specific form element of the complete adult posture is present, for five age classes of black-headed gulls. A: bill position; B: closed bill; C: head movements; D: extended carpal joints; E: tilted body; F: non-hiding; G: standing; H: complete postures containing the next elements: bill down, bill closed, head movements, extended carpal joints and tilted body.
ontogeny, I traced for each age class whether a combination of two form elements typical for the complete choking display, occurred more or less frequently than should be expected in case those elements occurred independently of each other. Due to the gradual development of the posture, not every age class yielded enough data for the test, but as can be seen in Table 1, most of the combinations occurred much more frequently than should be expected. There seem to be no differences between the age classes in this respect: positive correlations during the last two age classes were already seen in earlier ones. Only head movements were performed significantly less during standing compared with sitting, while other combinations with standing gave almost no significant results. Therefore there are no indications that the occurrence of the different elements become more coordinated during ontogeny.

3.1.4. Development of choking: discussion.

From the fact that in choking-like postures the incidence of form elements typical for the adult form of choking gradually increased, it is concluded that the complete form of choking gradually develops during ontogeny.

The typical choking-call also gradually develops. During the first week, its basis, the harsh notes, are more and more placed in a stereotyped rhythm and become harsher and more stifled with age.

The typical rhythmical structure of the ha-call was also found in the landing-call, the copulation-call and the long-call of juvenile and adult birds (Fig. 11, 1o-1r). Moreover, the former two are, like the choking-call, performed on a particular spot (resp. the territory and the female), in a choking-like posture. Therefore I would like to suggest that these calls also develop from the harsh-call (the developmental origin of the long-call will be discussed in more detail below).

It is possible that also the luring- or mew call, by which the adult male tries to attract a nearby female, is related to the Ha-call. Although this vocalization lacks the typical rhythm of the other vocalizations, it consists of harsh sounding notes with low frequencies like the choking-like vocalizations, which seemed to become gradually longer in ontogeny (Fig. 2m, 2n). Secondly, this call is also performed at a particular spot, e.g. the nest site, and it is given in a choking-like position, as is the case for the other calls just mentioned.

The Ha-call of young chicks was often performed during a posture in which the bill is held horizontally; such a bill position occurred very often in freezing, during which the young chick sat motionless on the ground
Table 1. Results of chi-square tests on the frequencies of combinations of two form elements, characteristic for the complete choking posture, which were scored from choking-like postures in five age classes of black-headed gulls

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<th>Bil down (BD)</th>
<th>Bill closed (BC)</th>
<th>Head movement (HM)</th>
<th>Body tilt (BT)</th>
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— = not enough data available for testing; 1 = 0-2 weeks old gulls; 2 = 3 w; 3 = 4-6 w; 4 = 10-12 w; 5 = adult gulls. N.S. = not significant (p > 0.05); * = p < 0.05; ** = p < 0.01; *** = p < 0.001.
in a resting posture while the bird remained silent. This freezing was almost always performed in a hiding place, after the chick moved away from the stimulus: this was also often the case for incomplete forms of choking. I therefore conclude that the incomplete forms of choking develop gradually from freezing.

The interpretation of the gradual development of the form of complete choking is depicted in Fig. 2b-g and is in line with remarks made by other authors about the development of choking in several gull species (Delius, 1973; Henty, 1966; Moynihan, 1959). The posture develops gradually towards a more pronounced form through the simultaneous occurrence of more form elements. Because these elements had a tendency to occur together with other form elements already in the beginning of the development (Table 1), there is no ground to suppose that the different form elements of the posture first occur relatively independent of each other, to become more rigidly coordinated in older gulls.

3.2. Development of oblique and long-call.

3.2.1. The adult posture and call.

The complete adult oblique posture consists of an erect posture in which the following form elements are present:
1. Neck held obliquely to vertically;
2. Bill held horizontally (only if the neck is held obliquely) or upwards inclined;
3. Carpal joints raised.

The oblique posture is always performed together with the long-call. The adult long-call consists of a series of loud and harsh sounding notes in rapid succession; the first notes are louder, higher in pitch and longer in duration than the last ones. These last notes can be performed during the forward, a posture in which the head is held in front of the body, and which often follows the oblique (Manley, 1960; Moynihan, 1955; van Rhijn, 1981; Tinbergen, 1959) (see Fig. 2k).

3.2.2. Development of the long-call.

The most frequent vocalization of chicks up to 2 weeks old during agonistic interactions was the Ha-call. However, from the third week on more and more Ha-call bouts were heard in which one or more notes sounded higher than the other notes, just as in the long-call. This happened especially when the bird performed an erect posture following choking (Fig. 1i and 1o). These special notes became longer by the time
the young were ten weeks old at which time the call sounded much clearer and higher (Fig. 1p). In the next spring, juvenile black-headed gulls produced very hoarse long-call like vocalizations (Fig. 1q), which became again louder after the birds were more than 10 months old; by that time they were undistinguishable from the adult long-call (Fig. 1r).

Quantitative data also indicate that the long-call develops from the Ha-call. The similarity in the duration of note intervals between the Ha-call and the long-call (like) vocalizations is shown in Fig. 6a. These were

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**Fig. 6.** The development of the long-call and its association with the oblique: A: Note intervals (mean and st.err. in seconds) of four different call types of young and adult black-headed gulls. B: Note duration (mean and st.err. in seconds) of six vocalization types. C: The relative frequency in five age classes of three call types during oblique-like postures performed in agonistic encounters. Ha = harsh-call; L-call-like = long-call-like vocalizations; juv. L-call = long-calls of young gulls older than 10 weeks; ad. L-call = long-calls of adult black-headed gulls; juv. cho = choking calls of gulls older than 10 weeks; ad. cho = choking calls of adult black-headed gulls. See text.
almost the same for Ha-calls, Ha-calls with higher pitched notes (which will be called long-call like vocalizations), juvenile long-calls and adult long-calls (one way anova: $F = 1.11$, $P = .347$: no significant difference between the four groups). The duration of the longest note of the high pitched notes in the call bouts, (Fig. 6b) suggests that the Ha-call develops in one direction in the choking vocalization and in the other in the oblique vocalization. There is a steady increase of note duration from Ha-calls to Ha-calls with a high pitched note and further to the juvenile and to the adult long-call (one way anova: $F = 61.4$, $p < .001$. Stars mark significant differences according to the Newman-Keuls test). Conversely, from the Ha-call to the choking-call the note duration decreases (one way anova: $F = 33.02$, $P = .043$).

Fig. 6c gives for five age classes the relative frequency of three types of vocalization: Ha-calls, long-call-like vocalizations and chatter-calls, during the occurrence of erect postures in agonistic interactions. It shows that during the first two weeks of age, the chicks performed the erect postures most often with the Ha-call. But from then on, the birds performed more and more long-call like vocalizations during these postures, whereas other call types were hardly given. So, erect postures performed during agonistic encounters were more and more performed together with long-call-like vocalizations.

3.2.3. Frequency.

The changes in frequency during ontogeny of oblique-like postures (postures in which the neck is erect more than 45 degrees above the horizontal and which are accompanied by Ha-calls or long-call like vocalizations) can be read from Fig. 3. These postures appeared during the second week of age, increased gradually in frequency up to an age of 4 weeks, and they decreased in frequency, together with choking-like postures, by the time the young became independent and non-territorial. They increased again in frequency after the birds were more than nine weeks old. From that time on the oblique was the most frequently performed display; it was used in all kinds of interaction between conspecifics, agonistic as well as sexual ones (see Groothuis, 1989b).

3.2.4. Bill- and neck position.

As can be seen in Fig. 7a, the relative frequency of oblique-like postures in which the bill clearly points downward was relatively high in birds younger than 4 weeks. However, this form decreased during ontogeny
Fig. 7. Percentage of oblique-like postures in which one or more particular form element was present, for five age classes: A: with different bill positions; B: with a particular bill-neck position (bill horizontal, neck vertical); C: with normal adult bill and neck positions (bill not down, and bill not horizontal when neck vertical).

and gradually disappeared almost completely in birds older than ten weeks. During these periods, first the horizontal position, and later the upward position of the bill increased in frequency.

The combination of a vertical neck and a horizontal bill (the upright posture), is hardly seen in adults giving the long-call, but often in young birds performing long-call-like vocalizations. Fig. 7b shows the relative frequency of postures with a horizontal bill and a vertical neck, (upright-like postures), calculated for those oblique-like postures which were accompanied by long-call like vocalizations in which the bill was not held down. As can be seen, the frequency of these upright-like postures decreased considerably during ontogeny, which led to an increase of normal oblique postures, with horizontal bill and the neck oblique, or with the bill held upwards and the neck oblique or vertical. The increase in
the relative frequency of complete, adult-like oblique postures is given in Fig. 7c. It can be concluded that the normal adult-like bill - and neck position of the oblique develops gradually during ontogeny.

3.2.5. Duration.
The mean duration of oblique-like postures increased with age, especially between the third and fourth age class (Fig. 8: \( r = .414, p < .0001 \)). No significant difference was found between the last two age classes (student t-test: \( t = 1.82, p = .833 \)). Significant differences in duration were found between the different forms of the posture: within the first four age classes, the oblique with bill up had the longest duration, which is significant for the 2nd, 3rd, and 4th age class. In adults however, this extreme form of the oblique had a shorter duration than the form with horizontal bill. This is in line with van Rijn’s (1981) findings in adult black-headed gulls.
3.2.6. Sequence.

In adult gulls, the oblique posture is very often immediately followed by the forward; in fact so often that this sequence of two contrasting postures might be regarded as one display. Fig. 9 shows that this sequence gradually developed during ontogeny. The increase in frequency of this sequence is not due to changes in the relative frequency of forward-like postures. As can be seen in Fig. 3, forward-like postures, in which the head is held in front of the body, were very frequently performed during all ages and showed a peak in the third age class. The relative decrease after this peak went together with the increase of the oblique-forward sequence as shown in Fig. 9.

![Graph showing percentage of oblique-like postures followed by forward-like postures for five age classes.](image)

Fig. 9. The percentage of oblique-like postures which are immediately followed by forward-like postures, for five age classes.

Different modifications of the oblique-like posture had a different probability of being followed by other postures. For the second and third age classes (for which a sufficient number of data could be collected) the bill down posture was followed by choking twice as much as the other forms of the oblique (for the second age class: 63% versus 38%: $\chi^2 = 11.99$, $P < .001$; for the third age class: 33 versus 14%: $\chi^2 = 7.61$, $P = .006$).

3.2.7. Discussion.

From the similarities in the form of the note and the length of the intervals between the notes, as well as from the gradual increase of the dur-
tion of the long note in the bout, I conclude that during ontogeny the long-call gradually develops from the Ha-call. One interesting point has to be mentioned. A closer look at Fig. 10 reveals two harmonics in the high pitched notes which do not have the same shape. It is as if the Ha-note (Fig. 1i) is combined with another note, namely one in which the harmonics have the same form as in the pee-call (Fig. 1a-b). The last notes of the long-call in young birds indeed sounded rather similar to this Pee-call. This phenomenon of two groups of harmonics each with a different form, but present in the same note, often appeared on our sonograms of long-call like vocalizations. It is known, that passerine birds have a neural lateralization in the control of vocal production, by which the left and right membranes of the syrinx can produce different sounds at the same time (e.g. Nottebohm, 1972). One might think that in such a way it would be possible that one membrane produces the Ha-call while at the same time the other produces a pee-like call. An interpretation of the ontogeny of vocalization in terms of a shift in activity between the left and right syrinx membranes has earlier been suggested by Nottebohm (1972) and Wilkinson (1980). The contribution of two independent sound producing mechanisms in the long-call is relevant for understanding the ambivalent structure underlying this kind of calls. Such a structure was also found for example by Veen (1987) in the long-call of the little gull and two tern species.

From the findings that:
1. The first oblique-like postures were mainly performed with the Ha-call, which is typical for choking-like postures;
2. The first oblique-like postures were often performed with the bill held down, as in choking-like postures;
3. This oblique form was often followed by choking;
4. Both choking-like and oblique-like postures were performed almost exclusively in an agonistic context,

I conclude that the oblique display gradually develops from the early incomplete forms of the choking display. The suggestion of Moynihan (1959) that the oblique has its developmental origin in the begging display will be discussed in 3.4.6. As is the case for choking, during ontogeny the oblique changed towards a more pronounced form, in which the bill points higher and the posture is longer maintained (Fig. 2h-k). Duration and bill position were already correlated from the beginning. Because in every age class the carpal joints were almost always extended, no increase was found in the tendency of the birds to extend their carpal joints during ontogeny while performing oblique-like postures.
**Van Rhijn** (1981) interpreted his finding that in adults the most extreme form of the oblique (the one in which the bill points upwards), has a shorter duration than the other forms, as evidence for the fact that this extreme form is relatively difficult to perform. However, this explanation is not likely because young gulls at an age of ten weeks tend to maintain these postures longer than adults, while the less extreme forms in young gulls had shorter durations than the extreme forms. The shift in duration during ontogeny between these two forms is probably due to a shift in context: the extreme forms become more selectively involved in obvious agonistic interactions, during which they are likely to end by attacks of either the performer or the opponent, whereas the normal form becomes more and more restricted to non-agonistic interactions (Groothuis, 1989b).

The oblique-like posture with horizontal bill and vertical neck has the same form as the adult upright posture. Both displays differ only in the accompanying vocalization: the upright posture is never accompanied by long-call like vocalizations, whereas the oblique-like posture is always accompanied by such a call. Thus, it seems plausible that the upright develops from the oblique-like postures, although sufficient data concerning the development of the upright posture are lacking.

3.3. Development of the forward.

3.3.1. The adult posture.

The main form element in the adult forward posture is the position of the head, which is held in front of the body. The bill is held horizontally or upward (this last form is called the forward 3 by Manley, 1960, and the low-up by Van Rhijn, 1981). The neck is clearly, but not maximally extended, and can be held obliquely down, especially in the low-up. The carpal joints are almost always extended (Fig. 2t-u). The forward can be performed without accompanying vocalizations, but especially when the forward follows the oblique, it may be combined with the last notes of the long-call (Moynihan, 1955; Manley, 1960; Van Rhijn, 1981; Tinbergen, 1959).

3.3.2. Frequency.

In Fig. 3 the frequency during ontogeny of all forward-like postures is given. These postures consist of motor patterns in which the head is held in front of the body (in contrast to the oblique-like postures) and in which the bill is not held down (in contrast to choking-like postures). Forward-
like postures gradually increased in frequency during the first four weeks of age. During this period they were more frequently performed than the other categories of postures. They decreased in frequency when the young became independent. The incomplete forms of the forward were frequently performed during begging ceremonies directed towards the parents. However, they were also performed during agonistic interactions which remain the main context of the display in juvenile gulls. Adults use the complete form of this display in interactions with opponents as well as with partners.

3.3.3. Vocalization.

Young birds between the age of one and six weeks often performed the forward-like postures without vocalizations (58%, n = 383). If calls were made during these postures, pee-calls were most frequently performed (87%). These notes could already be heard in the egg. During ontogeny they hardly changed; they only became louder and more stable in form (Fig. 1a-b). Pee-calls gradually disappeared when the birds became sexually mature.

Gulls older than six weeks more frequently produced calls when performing forward-like postures (75%, n = 238). At this age most of the calls produced during this posture consisted of the short notes of long-call like vocalizations (70%). This change marks the shift in context of this posture during ontogeny: from begging to a more clearly agonistic context.

3.3.4. Bill position.

Despite the fact that postures in which the bill was held down were excluded in the analysis of the development of forward postures (see above), it was evident that the chicks often performed forward-like postures with the bill pointed just below the horizontal (Fig. 10a). After the third week of age the relative frequency of this bill position during forward-like postures gradually decreased from 80% to 10%, while the horizontal position increased, as did, from the age of 12 weeks onwards, the upward position. As for the development of the oblique, a gradual development towards a higher bill position was found.

3.3.5. Position of the neck.

Four alternative neck positions were distinguished in forward-like postures: the head held against the body: "neck in"; neck half extended
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Fig. 10. Percentage of forward-like postures with a specific bill position (A), neck position (B), and carpal joint position (C), for five age classes. hor = horizontal; cp = carpal joints.

in forward direction: “neck half”; neck more clearly extended in forward direction: “neck out”; neck extended obliquely downwards: “neck deep”. This last position could occur during the former categories. Fig. 10b gives the relative frequencies of these neck positions during ontogeny. The “neck in” position decreased with age from almost 70% to approximately 20%. Postures in which the neck was only slightly extended remained roughly constant in their relative frequencies, while postures in which the neck was clearly extended gradually increased in relative frequency from 0 to 50%. The “neck deep” position was almost exclusively performed by adults.

3.3.6. Position of the carpal joints.

As can be seen in Fig. 10c, very young gulls rarely performed forward-like postures with extended carpal joints. The relative frequency of this
form element increased from almost 0 to 90% in the last age class. The amount of extension also increased, especially by the time the birds became adult.

3.3.7. Combinations of form elements.

If the complete form of the forward is defined as a posture in which the bill is held horizontally or upwards, the neck clearly extended forwards or downwards, and with the carpal joints raised, then the relative frequency of this posture increased during ontogeny from 0% during the first 8 weeks of life, via 30% in the age class of 10-15 weeks, to 60% in adults. The extreme form of the forward, the low up, in which the bill points upward and in which the neck is often bent to the ground, was almost exclusively performed by adult gulls.

Similarly as for choking, I tested for the five age classes separately whether combinations of two different form elements characteristic for the complete forward, tended to occur together. The results, comprised in Table 2, show that in adults all combinations occurred significantly more frequently than expected on the basis of a random distribution, whereas in the younger birds this was only the case for some combinations. The data suggest that the different form elements may occur as independent units in young birds, while in older birds they are very often combined. This seems to be in contrast with the results presented for choking and the oblique. However, it might be possible that the non significant results for the young birds are due to the low frequencies of some form elements in the first age classes. For instance, the combinations in which the bill positions were involved were significantly correlated with other form elements in adults because of the high incidence in this age class of the bill up position, which was almost lacking in young birds.

3.3.8. Discussion.

The present data clearly indicate that the complete forward posture gradually develops during ontogeny. Bill position, neck position and the position of the carpal joints are more and more carried out in the way adult birds do in the course of ontogeny. Thereby the posture becomes more conspicuous; it develops from a posture which is often called the "hunched", in which the neck is less extended (e.g. MOYNIHAN, 1955), towards the forward and the low up. The hunched is still present in
TABLE 2. Results of chi-square tests on the frequency of some combinations of two form elements, characteristic for the complete forward posture, which were scored from forward-like postures in five age classes

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For abbreviations see Table 1.

adults, especially when begging to the mate. It seems likely to me that the pee-call of young gulls, often performed during the hunched, develops into the adult hoarse begging call, but I do not have data to support this hypothesis. The adult call is performed by the female when she is begging for food to the male, and by the male just before copulation. It seemed to have approximately the same note duration as the pee-call.

In Fig. 2q-u a pictorial survey of the morphogenesis of the forward is given. The hunched is drawn as if it develops from the resting posture. However, it can also be thought to develop from freezing. Both the hunched and freezing were often performed during fearful situations. The chick mostly tried to escape in the hunched, and subsequently froze in a hide (see also GROOTHUIS, 1989a). Both postures further resemble each other because the head is withdrawn to the body and because the hunched is often performed silently in young chicks, which is always the case for freezing.
3.4. The development of pumping.

3.4.1. The posture.

The pumping display is typical for begging in young gulls. It consists of a rapid up and down movement of the head, accompanied with a call during every downward movement. The mean speed of these movements is approximately 1 per sec. The display is given in almost every encounter of the young with its parents, and is often followed by pecking at the parents bill. Adults also perform begging movements. Pumping is only shown by the male just before copulation. The display in adults is less conspicuous than in young gulls: the head is moved up and down by stretching the neck along a vertical line, which will be called high pumping. Adults beg for food in a hunched posture; during every begging call the head is tossed up in backward direction (Moynihan, 1955).

3.4.2. Frequency.

The frequency during ontogeny of pumping bouts (burst of pumping movements separated by intervals shorter than 3 seconds) are shown in Fig. 3. The display was observed as early as the second half of the first week. It increased rapidly during the first three weeks. During the first week the parents often regurgitate food spontaneously, whereas older young almost never get food without pumping. The frequency of pumping decreased by the time the young became independent of their parents.

3.4.3. Form development.

Four forms of pumping were distinguished, depending on the place of the head in the lowest position during the movement (Fig. 2m-p):

1. High pumping, in which the head is held above the body;
2. High-low pumping in which the head is held obliquely in front of and against the body;
3. Low-in pumping in which the head is held in front of and against the body in a hunched position;
4. Low pumping in which the head is held in front of the body, but with the neck extended as in the forward.

For every pumping bout, the most frequent pumping form was scored, and the relative frequencies of these forms during ontogeny are given in Fig. 11. The first form which appeared was high pumping; during the first week its relative frequency was very high, almost 80% but it decreased in frequency to 0% in the last age class. High-low pumping
had its frequency peak in the second week of age: in the period when the two forms of low pumping started to rise. These two became the most important ones in the fourth age class. In the last age class, at the time the total frequency of pumping had already become reduced (Fig. 3), high-low pumping again increased in relative frequency while low-in pumping is more frequent than low pumping.

3.4.4. Vocalization

The main vocalization type during pumping was the pee-call which has already been discussed. Almost the only other call given during pumping was the chatter-call (see 3.1.3.). Like the pee- and the Ha-call, this call could be heard already on the first day after hatching and it seems to be a modification of the two former calls (resp. Figs 1c and 1d). During the first weeks of age, the frequency modulation on the sonograms looks like a zigzag, but in older gulls the note is almost split up in several very short low pitched notes (Fig. 1f). This so called rattle-call was the only call given during the alert posture, assumed in situations with important changes in the surrounding of the gull (e.g. the appearance of one of the parents when a chick was hungry, the appearance of a predator or other disturbances). The pee-call was not only given during pumping, but also very frequently during forward-like postures (see above). Both the pee-call and the rattle-call were often given during pumping, and in pump-
ing, both a forward or horizontal component and an alert or vertical component may be present. Table 3 shows that both calls had a different distribution over the different pumping forms. Two forms of pumping were distinguished: one in which the vertical component of the movement dominates, (high-low pumping and low pumping in which the upward movement was very pronounced), and one in which the horizontal element dominates (normal low(-in) pumping). In addition, the distribution of the calls during the alert- and forward like postures, (respectively the vertical- and horizontal component separately), is given.

Table 3. The percentual distribution (based on the total frequencies of the postures) of several call types over some display forms: two pumping types and two postures related to pumping

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<thead>
<tr>
<th></th>
<th>Alert</th>
<th>&quot;High&quot; pump</th>
<th>&quot;Low&quot; pump</th>
<th>Low posture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chatter</td>
<td>100</td>
<td>83</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Pee</td>
<td>0</td>
<td>17</td>
<td>83</td>
<td>89</td>
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<tr>
<td>Other</td>
<td>0</td>
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<td>0</td>
<td>4</td>
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<td>N</td>
<td>100</td>
<td>90</td>
<td>120</td>
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Data from young black-headed gulls between the age of 2 and 6 weeks. Field observations. See text.

These data were collected in the field because of the low incidence of low pumping with a pronounced vertical component in the semi-natural condition. This was due to the fact that this pumping form was often performed as a reaction to the parent flying above the young, which was not possible in the cage condition.

From these data it is clear that the pee-call and the chatter- or rattle-call were almost the only vocalizations given during pumping. Moreover, the relative frequency of these calls shifted to a higher proportion of the pee-call from the alert posture, in which the vertical component is the only component present, via pumping with a pronounced vertical component, to low pumping and the forward, in which the horizontal component is the most pronounced one.

3.4.5. Duration.

As a measurement for the duration of the pumping bouts the amount of pumping movements per bout is taken. The mean speed of one up-and-down movement of the head was .99 per second and did not change with
age. In Fig. 12 the bout lengths for the four pumping types are given for 5 age classes. The mean bout length of all pumping types increased during ontogeny (R = 0.292, P < 0.0001). In every age class there was also a tendency for larger bout lengths in pumping bouts with a more pronounced horizontal component in the movement. A one-way anova revealed significant differences within the second and fourth age class in this respect.

3.4.6. Discussion.

The form of the pumping display developed from high pumping, in which only a vertical component is present, to low pumping, in which also a horizontal component is conspicuous; the last one also had longer bout-lengths. Besides, I had the impression that the amplitude of the pumping movement increased with age. In these ways the display became more conspicuous during its ontogeny. Its frequency increased by the time the young needed to have a strong signal to persuade the parents to regurgitate and the frequency decreased by the time the young became independent. It is interesting that by that time the form of the display became less conspicuous again. This suggest that the “intensity” as well as the frequency of pumping are controlled by a same internal factor.
The pumping display seems to originate from the alert posture and to develop through an integration of incomplete forms of the forward display. This suggestion is supported by the following data. Pumping, especially those forms with a dominating vertical component, were accompanied by the chatter- or rattle-call, typical for the alert posture. In contrast, pumping forms with a dominating horizontal component were accompanied by the pee-call, the typical call for the incomplete forms of the forward posture. Indeed, the first high pumping movements were difficult to distinguish from alert postures with a very short duration: they only differed by the occurrence of a call during the downward movement of pumping. Moreover, the alert posture occurred most often during the first week in which high pumping developed. Thereafter, in the course of ontogeny, incomplete forms of the forward became integrated in the pumping movement as soon as they developed. In this way the form of the display changed from high pumping to low pumping.

Moynihan (1959), in his study on the ontogeny of display behaviour in two related gull species, suggests that the begging display develops into the oblique-forward display after a time of "internal reorganization" during the first winter. His suggestion is based on a resemblance between the displays mentioned (both consist of a sequence of an erect and a low posture) while he does not report incomplete, oblique-like displays in young gulls. My data do not support his interpretation. They show a gradual development of the oblique and forward display, separated from each other. Secondly, the oblique-forward display is accompanied by a vocalization which is completely different from that of the pumping display: namely a series of long-call like notes instead of one rattle or pee note. Thirdly, the duration of one pumping movement was at least three times shorter than the duration of the oblique-forward display, but the duration of the pumping movement did not change with age in the direction of the other display and we never saw transitional movements with elements of both displays. Fourthly, the erect part of the pumping display was rarely combined with extended carpal joints and never seen with a thickened neck in contrast to the oblique-like postures. Fifthly, a sequence of pumping and the oblique-forward display was only very rarely seen. Both displays were performed in a different context: the pumping display and also thepee-call are performed during begging, and the oblique-forward display during agonistic interactions (Groothuis, 1989). Sixthly, although young of several species of gulls show the same pumping display (Groothuis, Veen & Vodegel, unpubl. obs.), these species differ strongly in their oblique postures.
3.5. Normal display development: general conclusion.
The form development of three agonistic displays and of the begging
display have already been discussed separately. Their frequencies
gradually increased during ontogeny. Moreover, the form of the displays
became more and more pronounced, due to the fact that more different
form elements gradually became present in the postures and calls, and the
connection between the call and the posture became stronger. Some
displays had their origin in incomplete forms of other displays or were
combined with others which had developed separately.

On the other hand, complete adult-like postures may be observed
already in the first two weeks of age. For oblique postures and pumping
this can be deduced from the data presented above (Fig. 7c, resp. Fig.
11). As far as the forward is concerned, three times a complete low up
posture was seen, just after an experiment during which a stuffed black
headed gull was introduced in the cage. These early complete postures
often had a short duration and may be interpreted as a "coincidence"
of the right combination of several form elements. But these observations
do show, that the young chick is fully capable of performing the complete
posture. This seems not to be the case for the vocalizations, possibly due
to limitations of the not yet fully matured syrinx (GROOTHUIS, 1989a). I
will return to these early complete postures later.

4. Form development in the small groups

4.1. Results.

In Fig. 13a the mean frequency per hour over the first 8 weeks of age
is given for the three agonistic displays, the pumping display and the
aggressive peck, for both the small- and the control groups. The frequen-
cies were lower in the four small groups than in the control group (the
four birds in the semi-natural condition) and these differences were
statistically significant for all displays (p < .01). In fact, the estimated
total score over the first 8 weeks of age for each of the displays of the con-
trol group was even higher than the estimated total score over the first
14 weeks of the experimental groups.

Fig. 13a also shows that during the test in the 15th week of age, during
which the birds in the small groups were confronted with unknown con-
specifics of the same age, the frequencies of oblique-, choking- and
forward-like postures, as well as of aggressive pecks were higher than in
Fig. 13. Comparison of the frequencies (means per hour per individual) (13a) and the form (13b) of four displays and of the frequencies of aggressive pecks (13a) between normal raised control birds (scores for the first 8 weeks of life) and birds raised in small groups (scores of the first 8 weeks of life and of the test during week 15). OBL = complete oblique postures regardless of carpal joint position. OBL-out = oblique-like postures with extended carpal joints; %OBL-low = percentage of oblique-like postures which are followed by forward-like postures; FW = complete forward postures; LP = low (in) pumping. See text.
the weeks before. Pumping was not seen anymore during the test. This increase in frequencies was statistically tested by comparing the behavioural scores of the 12 individuals during the test in the 15th week with the scores of these individuals just before the test during the 13th and 14th week of age; these differences were statistically significant (Wilcoxon matched pairs test: \( p < .01 \) for the differences in oblique and choking-like postures; \( p < .05 \) for the forward like postures).

To assess the influence of raising conditions of the form development of the displays, the form of the three most frequently performed displays, the oblique like-, forward like- and pumping displays were analyzed in more detail, and compared with data obtained from the control groups (see 2). In Fig. 13b, the relative frequencies of some modifications of these displays are compared for three conditions: for the small groups under two conditions: during the 13th-14th week when the birds were still in their small groups and during the test in the 15th week of age; and for the controls during the 10th-12th week. The relative frequency of the normal oblique postures (oblique-like postures excluding those with the bill down or with neck vertical and bill horizontal; see part I, 3.2.), without regard to the carpal joint position, was considerably lower in the small groups than in the controls. The same result was found for the relative frequency of oblique-like postures in which the carpal joints were extended, for the percentage of the oblique-like postures which are followed by forward-like postures, for the percentage of complete forward postures and for the percentage of low pumping. During the test in the 15th week of age, these low scores of the small groups still remained below those of the controls. The differences between the controls and the small groups are difficult to test statistically due to the lack of individual data in the controls. However, the fact that 11 of the 12 scores (for the normal oblique posture) or 12 of the 12 scores (for the other form measurements) obtained from the small groups were all lower than the mean of the controls suggests quite a strong effect of group condition. Moreover, although the duration of the postures was not measured, I had the strong impression that the birds in the small groups performed displays with a much shorter duration than those of the control birds. Six of the birds raised in a little group were followed longer in their behavioural development. Normal display behaviour was not seen before they were 30 weeks old (four individuals); by that time it was winter, a period in which normally raised young hardly show any display behaviour.
4.2. Conclusion.
Raising black-headed gulls in small groups, in which the normal context for display performance is lacking, resulted in a very low frequency of these displays and of aggressive behaviour, and in a relatively low percentage of complete display patterns. During the test in the 15th week of age in which the birds were confronted with visually unknown conspecifics, the frequency of agonistic displays increased considerably. However, the form of the motor patterns did not improve. So, it can be concluded that the low frequency of complete displays during the test was not due to a lack of stimulation to perform these displays: apparently the birds were strongly stimulated to perform displays, but they were not able to perform frequently the complete patterns, in contrast to normally raised birds of the same age.

This suggest that raising young gulls in an abnormal situation, may retard their form development of displays.

5. General discussion
The central questions in this paper are:
1. Do the species-specific displays develop gradually or are they already completely present in the beginning of ontogeny?
2. How do the displays develop if the birds are deprived from the context in which these motor patterns normally develop?
3. Which possible mechanisms can explain the findings concerning the normal and manipulated display development?

From the conclusions presented above it is clear that the frequency of complete adult postures gradually increases during ontogeny, while the proportion of incomplete forms decreases, and that this development was retarded by withholding the normal context for the occurrence of the displays. Based on these conclusions and some additional data, several possible mechanisms will be discussed that may be responsible for the form development found in the displays of the black-headed gull.

It needs to be stressed that these mechanisms are not mutually exclusive.

One of the central questions in studies of motor development is whether feedback resulting from performance plays an important role in shaping the motor pattern into its final form. One possibility is that the young animal matches its output to information already present in the animal concerning the correct form of the display. If such a mechanism is responsible for the gradual development found in the displays, the
question has to be solved how this information or “template” develops during ontogeny.

The possibility that this information is gained by imitation, as is the case for song development in some species of songbirds, seems not very likely for the development of postures. Imitation of such motor patterns means that from seeing the complete adult display the watching bird adjusts the form of its own posture to that shown by the tutor. Because the bird cannot see the form of the motor pattern performed by itself, the input via the visual system (seeing the tutor’s display) must be compared with proprioceptive feedback resulting from its own performance. This process needs two different modes of information, and is therefore more complicated than imitation of song, where only one sensory modality (hearing) seems to be involved. At present, there is no evidence that such a complex mechanism exists. Moreover, because the birds raised in small groups never saw any displays of adult conspecifics (in contrast to the birds in the control groups), but yet sometimes performed correct complete displays, imitation cannot be indispensable for the complete form to develop.

Another source of information that can be conceived to be involved in matching developing displays are the reactions of conspecífics to the display performed. It is conceivable that conspecifics (and possibly in particular experienced adult gulls) to which the display is addressed, may react consistently differently to various modifications of a display executed by a young gull. For example, a more complete form of a display might have a stronger intimidating effect on the opponent and therefore cause the latter to retreat more often. Then, the young gull may match its display form to the reaction of the opponent, perhaps through operant conditioning. This possibility and the possible influence of imitation will be extensively discussed elsewhere on the basis of experimental data (see also Groothuis, 1989a).

In addition to these forms of matching against input from the environment, we should also consider the possibility that the bird reaches the adult forms of display because it is programmed, by as yet unknown mechanism, to receive a particular pattern of proprioceptive feedback, resulting from display performance. Such a matching mechanism might be responsible for the gradual development, and is suggested by the fact that the birds in the small groups, which showed a retardation in the development of the form of the displays, also showed a very low frequency of total display behaviour during their first 14 weeks of age. This means that these birds hardly had the opportunity to shape their display.
on the basis of such a matching process and this would make the retardation of their form development understandable. Moreover, in small groups there appeared to be a strong positive correlation between the total frequency with which a bird performed oblique-like postures, during the first 14 weeks and the percentage of complete obliques during the test in the 15th week of age (N = 12, r = .74, p = .013).

Regardless of the type of matching involved, the complete posture or call becomes more or less stereotyped in form in the course of ontogeny. This form fixation might be caused by repeated performance of the same posture after the period of shaping. Such a mechanism is suggested by several authors (Andrew, 1963; Baerends van Roon & Baerends, 1978; Hinde, 1969; Wiley, 1973). This process has similarities to the mechanism by which stereotyped motor patterns of animals, kept in captivity, develop from conflict behaviour or intention movements, and become fixed in form after some time (for a review see Dantzer, 1986). However, there are some findings which do not fit well with the matching-hypotheses just discussed. If a motor pattern develops by comparing the performance of the motor output against a template, it will develop just by trial and error. In that case one would expect that in young birds the form of a display might show a much greater variation than in adults, and that this variation might consist of more or less random combinations of separate form elements in the beginning of its development. Both expectations do not seem to apply. The gradual development observed does not involve more variable postures in young than in adults, in contrast to what is often suggested in the literature. It is true that young black-headed gulls show several different forms of the same incomplete display within one age class, but during the first two weeks of age the variability in form elements like bill position or carpal joint position is not greater than in adults, only different (see e.g. Figs 5a, 6c, 7a, and the N values for the different forms in different age classes in 8a, 10a, 10b, 10c, 11a). The gradual development also showed a consistent series of incomplete forms (e.g. Fig. 2) in which one form dominated after another less conspicuous form had had its peak. This is not in line with the expectation that the early incomplete forms would consist of relatively random combinations of form elements. Moreover, I got the impression that, despite the gradual development, discontinuities existed in the ontogeny of the behaviour, found also by other authors (e.g. Plooy (1980) for the development of behaviour in the chimpanzee). For example, certain birds during the fourth week of age suddenly seemed to show many more oblique-like postures in which the bill
was held horizontally instead of downwards, than they did the week before. Moreover, data concerning the occurrence of combinations of several form elements in the same type of posture during ontogeny did not show a gradual development from random combinations to more stereotyped ones.

As far as the stereotyped form of the displays is concerned, even in adults this stereotypy is not very strong, as was also found by van Rhijn (1981) for this species (see also Stamps & Barlow, 1973, for data on the bobbing display in lizards). Although the early incomplete forms of choking are rarely seen in adults, the complete form of choking is performed by adults in only 60% of the cases observed. The complete adult form of the oblique can be distinguished in three sub-forms, depending on bill- and neck position. The hunched posture, a typical incomplete form of the forward, is still seen in adults, while the complete display can have several forms, depending on bill and neck position. The fact that each display in adults consists of several subforms, each probably having its own message, is important for the study of animal communication (Beer, 1980). The fact that adults may still show incomplete forms of display suggests that during ontogeny the form of the display does not completely fixate.

The fact that motor patterns occurring early in ontogeny do not disappear completely is even true for motor patterns that under normal circumstances are never seen later in life. For example, freezing, which is never seen in adult birds was seen in an adult from which the flight-feathers were cut off and which was placed in a group of very aggressive young gulls. Low pumping was seen in one adult, raised in a very small group. Apparently the neural circuits for performing these motor patterns were still existing, and activated by an unusual situation. This is similar to the results found by Bekoff, 1979, for the hatching movements of already hatched chickens.

As was pointed out in the introduction of this paper, a gradual development of motivational factors could be responsible for the gradual development found in the display. Gull displays are a classical example of postures that developed during their evolution from intention movements of aggression and fear. It is possible that the displays in young gulls are still (partly) under the control of internal factors controlling aggression and fear (as seems to be the case for the displays in cichlid fish, extensively studied by Baerends (1984) and Vodegel (1978). Moreover, some authors (e.g. Kruijt, 1964) found interesting relationships between the development of aggression and fear and of display behaviour during
ontogeny. In this light it is of interest that the birds in the small groups, showing a retardation of display development, also showed little overt aggression towards each other, as compared with the controls. Retarda-
tion of the development of aggression and fear (although the last one has not been quantified in the small groups) may also be responsible for the retardation of the begging display, because in this display the clearly agonistic forward-like postures are involved. The relationship between the development of aggression, fear and display behaviour will be exten-
sively analyzed elsewhere (Groothuis, 1989b).

A positive relationship between frequency and form of a display and aggressive behaviour may be physiologically explained by an influence of testosterone. It is well known that this hormone influences the frequency of display- and agonistic behaviour in many species. Not much is known about the influence of this hormone on the form of the display, but some data suggest a positive relation between the level of testosterone produc-
tion and the completeness of the display form (Van de Burg, 1976). As was concluded in the discussion, already in the beginning of ontogeny the different form elements of a display are not performed independently of each other and the completeness of the posture may be controlled by one factor, a gradual rise in the blood level of testosterone. The delay in display development in the small groups may then be due to a lack of nor-
mal agonistic interactions, if these are necessary to stimulate the testosterone production in the birds. There is increasing evidence about the influence of social experience on the production of testosterone (for the influence of agonistic interactions on testosterone levels in birds see Wingfield (1984, 1985), and classical examples can be found in the work of Lehrman and his collaborators (e.g. Cheng, 1979). The possible influ-
ence of testosterone on the display behaviour of young black-headed gulls is supported by the following data. The colour of the head feathers is, at least for adults, known to be dependent on testosterone (Van Oordt, 1931, 1933). In small groups a positive correlation was found between the darkness of the plumage of the head at week 16 and the frequency with which the birds performed oblique-like postures during weeks eleven and fourteen. This positive correlation was significant for the six birds in one group (rs = .89, p < .01). The increase in frequency of the extreme form of the forward (the low up), and of the upright in spring, at the time the production of sexual hormones is expected to be relatively high, is also in favour of this hypothesis.

A possible consequence of the influence of motivational factors on the display development is that functional experience with incomplete forms
of display is not important for the development of the complete form. It is possible that the species-specific complete form is already present in the bird at an early stage of ontogeny, pre-functionally (Hogan, 1987), as seems to be the case for more simple motor patterns. In that case the display is just waiting for the appropriate stimulus to occur (see also Fen-tress (1978) for early grooming and locomotion patterns). The early performance of complete display patterns which are occasionally seen in young of several species could then be caused by an extraordinary stimulus, strong enough to trigger the most “intensive” form. Indeed, most reports on early complete display performance suggest the presence of such an extraordinary stimulus: for example the introduction of an imprinting object or conspecifics after a period in which the young bird was raised apart from this stimulus (Klopmann, 1961; Kruijt, 1964; Schulman, 1970). If this interpretation is correct, the question is not only how the neural coordination for the correct species-specific form develops during early ontogeny, but also what kind of ontogenetic changes causes the complete display to occur more frequently after its development. It is possible that the complete form increases in frequency as a consequence of a development in motivational factors, after which it becomes fixed in form as a consequence of repeated performance, or a temporarily high blood level of testosterone.

The influence of testosterone on the development of display behaviour, as well as the possible influence of a kind of matching process as discussed under 2, will be analyzed in other reports (see also Groothuis, 1989a).

Summary
The central question in this paper concerns the mechanism by which displays develop their species-specific stereotyped form. To this end the ontogeny of display behaviour in the black-headed gull was studied in birds kept and raised in aviaries. First it was analyzed whether the complete adult form of the display is present early in the chick, or whether it develops gradually over a longer period. Second, to answer the question whether experience with incomplete forms of display is necessary to develop the complete form, the normal display development was manipulated.

The descriptive part of the results deals with a detailed quantitative description of the form development in 3 agonistic displays: choking, oblique and forward, and with the development of the begging display. Data are presented concerning: ontogenetic changes in frequency of several form elements of postures and vocalizations, changes in their combinations, changes in duration of displays and changes in the context and sequences of displays.

The development of these displays is summarized in Fig. 2. Choking develops from crouching via incomplete forms of choking. First a choking-like vocalization develops in which the notes are more and more placed in a stereotyped rhythm. This call is performed by young chicks first during crouching, but later almost exclusively during
choking-like postures in which the bill points downwards. During ontogeny, these bill-down postures are increasingly performed with extended carpal joints, with a tilted body, with head movements, and while standing and not hiding, in this order.

From the age of two weeks on, the young regularly extend the neck upwards while choking. These postures are increasingly performed with a particular modification of the choking-like vocalization, which gradually develops to the adult long-call, typical for the adult oblique display. Two independent sound sources in the vocal apparatus of the gull seem to be involved in the development of the long-call. Early oblique-like postures are often performed with the bill held down, as in choking. Older young perform oblique-like postures more often with bill positions typical for adults, but with the neck held vertically. Young older than 10 weeks often perform normal adult oblique postures. By this time the duration of the postures has increased considerably. The sequence of the oblique with the forward, which is typical for adults, is also regularly seen from this time onwards.

Begging consists of a rapid up-and-down movement of the head; during every downward movement a specific call is uttered. In very young chicks, this display is hardly distinguishable from the alert posture. During ontogeny, the duration of the pumping bouts increases, while the form changes. This change in form is due to the fact that the incomplete form of the forward becomes integrated in the begging display, while this posture also changes in form. This integration of the alert and the incomplete form of the forward is reflected by the fact that in the begging display both the call typical for the alert posture, and the call typical for the incomplete forward posture, is given.

The forward develops by a gradual lowering of the head and a more pronounced extension of the neck, while the carpal joints are increasingly raised. Adult gulls often perform the posture with an upward pointed bill and a bent in the neck.

In accord with data from the literature it was found that under special conditions the young chick is capable of performing adult display. As a rule, however, before the tenth week of age, young gulls show incomplete forms of display. All species-specific adult displays, postures as well as vocalizations, develop gradually towards a more complete and pronounced form. This process takes place by addition of new form elements to already existing combinations, and by changes in the form of some elements. A display can also be built upon elements of another display. Nevertheless, the development of the form of the displays cannot be attributed to an increasing amount of coordination of the different elements; only the expression of the complete pattern increases with age. For the occurrence of one form element of an adult display in the precursor display of the chick is positively correlated with the occurrence of other such elements in that incomplete display. This already is the case early in ontogeny, before the complete form is regularly performed. The adult displays are not completely fixed in their form, and the variability in some displays of adults is of the same order as in the chick.

The second part of this paper deals with an experiment in which the normal course of the development of display behaviour was manipulated. Since the displays seem to develop during social interactions with parents (the begging display) or with intruders on the territory (the agonistic displays), young birds are raised in small groups with conspecifics of the same age. Agonistic- and begging interactions in these groups are rare an the development of display behaviour, both in frequency and in form, is retarded. Based on the frequency of overt aggression and on the plumage of the birds, it is likely that in these birds also the development of agonistic behaviour and the testosterone production is retarded. At the age of 15 weeks, these birds are confronted with unknown conspecifics. Although the frequency of the displays increases during the test, the form of the postures still appears to be incomplete; the birds do not seem to be able to perform complete display postures at an age at which normally raised birds perform complete display very often.

Based on the data of both the descriptive study as well as the experiment, possible mechanisms for the development of display behaviour are discussed. The main items are:
"imitation"; "matching" on the basis of feedback of the performed display via reactions of conspecifics or proprioceptive information and development of motivational factors including testosterone. This discussion lays the basis for a series of experiments which will be reported separately.

References

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Zusammenfassung


Von drei agonistischen Ausdruckshandlungen: das 'Choking' (= Stößeln), das 'Oblique' (= Schrägstellung) und das 'Forward' (= Vorwärtsstellung), sowie vom Bettelgehabe, wurden die während der Entwicklungszeit durchlaufenen Formänderungen qualitativ und quantitativ beschrieben. Diese Daten umfassen (zum Beispiel) den Frequenzverlauf der unterschiedlichen Formkomponenten und Lautäußerungen, die Änderungen in der Reihenfolge des Auftretens von beiden und in ihrem Zusammenhang, sowie auch in der Dauer des Anhaltens und in den Begleitumständen.
