

AGE ASYMMETRIES IN THE AERIAL DISPLAY OF LITTLE GULLS *LARUS MINUTUS*

LEEFTIJDSVERSCHILLEN IN DE LUCHTBALTS VAN DWERGMEEUWEN *LARUS MINUTUS*

THEUNIS PIERSMA

Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel;
and Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box
14, 9750 AA Haren, The Netherlands. E-mail: theunis @nioz.nl

Aspects of age differences in the aerial display of Little Gulls Larus minutus are described based on fieldwork carried out in May 1983 in the Lauwersmeer area, The Netherlands. Aerial displays occur when an initiator or 'sender' approaches a 'receiving' individual. The sender initially makes (individually identifiable) kay notes, followed by several ke-kèh repeats. Once the sender has approached the receiver to within a few meters, it increases flight speed, jerks up the head to almost a vertical position whilst starting to call a repeated ke-kòo. The head-up part of the display is rounded off with a short glide over the receiver, but often the display is aborted somewhere along the sequence. This is especially the case when immatures are the initiators. Immatures seem particularly keen to exercise the display, and when doing so preferentially act towards adults. During display flights between adults, receivers tended to respond with their own display flights. However, in aerial interactions initiated by immatures the receivers tended to either flee or to retaliate by attack. I suggest that the aerial display presents a compound quality signal (possibly derived from aerial mosquito-catching movements), that requires much physical and social practising, even during the immature stages of life.

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INTRODUCTION

Little Gulls *Larus minutus* are amazingly attractive little gulls. Whether on the hunt for flying insects above the marshes and the lakes, or interacting with each other in the air near their cryptic colonies, their elegance, the pink shine of their breeding dress, and the clear and almost song-like calls, are a pleasure to the human senses. I shared the breeding season of 1983 with Little Gulls, whilst working on an undergraduate project with Jan Veen, then of the Ethology-group of Professor Gerard Baerends at the University of Groningen. We studied several aspects of the communication of the gulls (see Veen & Piersma 1986, Piersma & Veen 1988), and also the gulls' aerial display (unpublished).

More than 15 years later, much of the data collected on the Little Gulls, which themselves have disappeared from the study areas in Lauwersmeer since

then (Koks 1998), remain hidden on old video and computer tapes and, in partially analysed form, in dark boxes. Having realised how preciously little new information on this species has seen the light of day since the 1980's (e.g. Burger & Gochfeld 1996), I have assembled my observations on the aerial display of Little Gulls, and discuss the striking age differences in behaviour.

STUDY AREA AND METHODS

The study was carried out in the central parts of Lauwersmeer, an estuary of the Wadden Sea that became embanked and that was turned into a freshwater wetland in 1969. On some of the former tidal flats, in areas with short grassy vegetation, small colonies of Little Gulls got established for the first time in 1972, often in the vicinity of much larger colonies of Black-headed Gulls *Larus ridibundus* (Veen 1980; Koks 1998). Observations on aerial display were carried out from 18 to 31 May 1983. The areas of observation consisted of mosaics of shallow water, reedbed and rough pasture. The areas where Little Gulls showed intense aerial display were often quite close to small colonies that became established in the latter half of May.

Observations were either carried out by a single observer, or simultaneously by two observers, in which case one spoke a running commentary in a cassette-recorder whereas the other recorded the sounds made by the Little Gulls by a Sennheiser directional microphone (MKH 405) on Uher tape-recorder. Single observer observations yielded information on group sizes, frequencies of aerial display, and the sorts of interactions going on in the air, whereas the observations made by pairs of observers made it possible to link up sounds and visual features of the behaviour. In all cases we tried to document: the age of the approaching (the 'sender') and the approached individual (the 'receiver'), the total number of birds in flocks in which the aerial display was recorded, the type of sounds and the movements that were made (see next paragraphs), and the minimal distance between the approaching and the approached individual. In a few cases we managed to get complete counts of the total number of adults and immatures in the general area of a few hectares over which the aerial displays were recorded for a certain length of time.

Immature birds (birds in their second calendar year) and adults (birds in their third calendar year and more) are easy to tell apart, especially in the air, as the former have dark zigzag markings on their back and upper wings, as well as a dark band at the end of an otherwise white tail, features that are absent in adults (see Fig. 1, based on Veen 1980). The head of immatures is usually not as dark as it is in adults, and they lack the pinkly shine of the white contour feathers characteristic of sexually mature individuals during the mating season (Cramp & Simmons 1983). Whereas the adults tended to arrive in Lauwersmeer

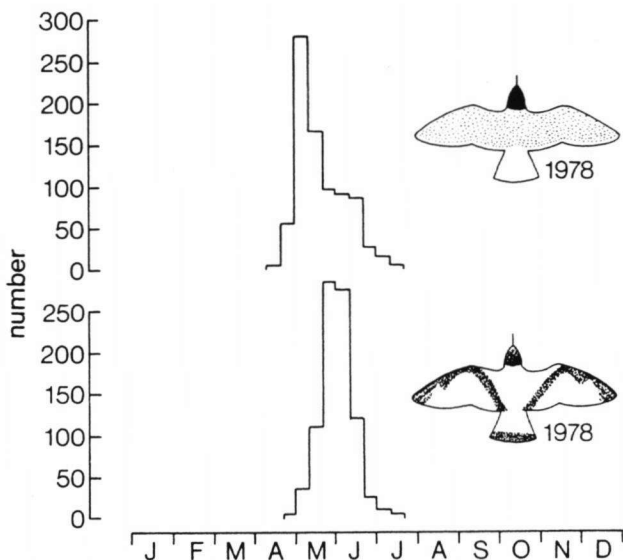


Figure 1. Maximum number of adult (top) and immature (bottom) Little Gulls recorded per 10-day period in Lauwermeer in 1978 (modified from Veen 1980).

Figuur 1. Maximale aantallen in het Lauwermeer waargenomen oude (bovenste paneel) en jonge (onderste paneel) Dwergmeeuwen per decade in 1978 (veranderd uit Veen 1980).

in early May (Fig. 1), the majority of immatures only arrived in the course of that month. Even though the immatures actively participate in the aerial display that we recorded in May 1983, they have not been found to breed at this age (Veen 1980).

All detailed recordings were examined on a Uniscan 4500 Spectrum analyser (range 0-10 000 Hz), which shows frequency/time and frequency/amplitude sound spectrograms on a monitor. Hardy copy sonographs were produced on a Kay SonaGraph model 6061B, using a wide band (300 Hz) filter setting (see Veen 1985).

A DESCRIPTION OF THE AERIAL SONG AND DISPLAY

The general outline of an aerial display sequence, or 'ceremony' is as follows (see also Cramp & Simmons 1983). An initiator approaches another individual

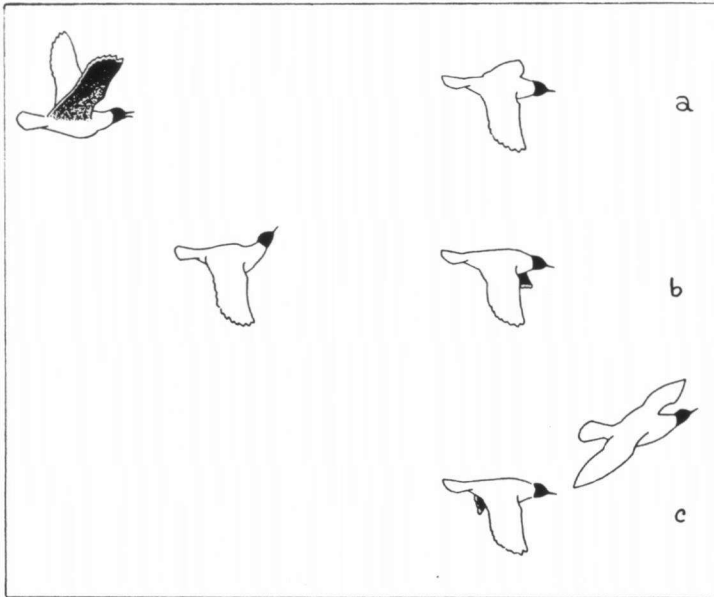


Figure 2. Scheme of a complete aerial display ceremony by two adult Little Gulls: (a) the far-range approach, the approaching bird calling *kay* and a repeated *ke-kèh*, (b) the close approach, the approaching bird changing from a repeated *ke-kèh* in a repeated *ke-kòo* when it turns the head up, and (c) final episode of the complete interaction as the approaching bird passes the approached individual very closely with a slightly upturned head keeping its wings still for a few seconds and being silent. After drawings by Jan Veen; see also Cramp & Simmons (1983:p. 735).

Figuur 2. Schema van een volledige luchtbalts-ceremonie van twee volwassen Dwergmeeuwen, waarbij in (a) een Dwergmeeuw al *kay* en *ke-kèh* roepend een soortgenoot nadert, en (b) dichtbij gekomen z'n kop omhoog gooit en van een herhaald *ke-kèh* overgaat in een herhaald *ke-kòo*, en dan (c) zonder geluid, met iets opgeheven kop en vleugels die een paar seconden stijf gehouden worden in een soort zweefvluchtje over de benaderde vogel heen vliegt. De tekeningen zijn gemaakt door Jan Veen, en in iets andere vorm eerder gepubliceerd door Cramp & Simmons (1983:p. 735).

from quite afar (Fig. 2a), initially making *kay* sounds (Fig. 3, and see discussion of notes below) and then calling a repeated *ke-kèh*. Upon close approach (a few meters), the approaching bird changes sound from a repeated *ke-kèh* towards a repeated *ke-kôo*. As it changes to *ke-kôo* it turns the head up and accelerates its speed with stiff and rapid wing beats (Fig. 2b). In a complete sequence this is immediately followed by the approaching bird passing closely ('gliding') over the receiving individual, the silent sender keeping its wings still for a few seconds with the head still turned up (Fig. 2c). The complete sequence of calls, as well as the upward thrust of the head when starting to call the repeated *ke-kôo*, is similar to the display behaviour on the ground, the sequence of notes being called the 'long call' (Cramp & Simmons 1983; Veen 1985). The receiver can respond to a display ceremony accompanied by ignoring, accepting or actively resisting the display, as will be detailed below.

The notes made during aerial display as part of the long call thus consist of the following notes (Fig. 3; naming following Veen 1985): (1) the short *ke* (as in the Spanish question ¿*Que?*), (2) the similarly sounding but slightly longer *kèh*, (3) the *kay*-note (as in the English word 'gay') that, on the basis of the large interindividual variation and results of playback-experiments (Veen 1985), is thought to convey individual identity, (4) the longer wailing sound *kôo* (as in the English word 'claw'), and (5) the *kwèh* note that on the sonograph look like a hybrid between *kay* and *kôo* notes, but sounds more like an intermediate between *kèh* and *kôo* notes.

The sequence of the notes in long calls of immature and adult Little Gulls during aerial display, even upon visual inspection (Fig. 4), shows clear patterning. *Kay*'s come first, and are often followed by one or sometimes two *kwèh* 's, before being followed by repeated *ke-kèh* and/or *ke-kôo* series. An analysis of transition probabilities supports this brief poetic description in statistical terms. Furthermore, it is apparent that long calls of adults contain more *kay*-notes than those of immatures, and that the *ke-kèh* series of immatures tend to be longer than those of adults, and the *ke-kôo* series shorter. A big difference between the aerial displays with and without *ke-kôo* series relates to the nearest approaching distance between sender and receiver (Fig. 6 in Veen 1985). In aerial displays/long calls with *ke-kôo* the nearest approaching distances are much shorter (mainly 1-2 m) than those without *ke-kôo* (5-50 m). In a detailed study on the long calls of Little Gulls, including those made on the ground and on or near the nest, Veen (1985) suggested that *ke-kèh* notes signal the intention of the sender to approach, whereas *ke-kôo* indicates the intention to approach peacefully at very close range.






sonogram	name of note	symbol
— = 0.25 sec		
	KÈ	
	KEE	■
	KAY	▲
	KWE	▴
	KOO	▴

Figure 3. Sonograms, names en symbols for the different notes uttered by Little Gulls during aerial display. The sonograms give the sound intensities in the 5 kHz range (see Cramp & Simmons 1983:p. 737 and Veen 1985:p.66 for comparison). The symbols on the right are the ones used to present full sequences in Fig. 4.

Figuur 3. Sonogrammen, namen en symbolen voor de noten die Dwergmeeuwen tijdens de luchtbalts gebruiken. De sonogrammen geven veranderingen in geluidintensiteit weer over een variatiebreedte van 5 kilohertz (bekijk ter vergelijking eventueel ook Cramp & Simmons 1983:p. 737 en Veen 1985:p.66). De grafische symbolen die in de rechter kolom staan worden gebruikt om in Fig. 4 de volledige roepen weer te geven.

DIFFERENTIAL PARTICIPATION OF THE AGE CLASSES

More important than the composition in terms of different notes of the long calls of immature and adult Little Gulls, was the relative intensity with which the different age categories approached each other in the air with intense display (i.e. long calls including *ke-kôo*). A few times I scored the occurrence of such display as they were initiated by immatures and adults and directed at each other (Table 1). In all three cases the occurrence of displays among interaction-categories was significantly different from the predictions based on the numerical presence of the two age classes. Immatures were much more likely to direct aerial displays to adults than to immatures, and almost all displays by adults were directed towards adults; there was only one exception where an adult approached an immature. Thus, adults are the preferred receivers, both when adult birds and when immature birds initiate the aerial interaction.

Another important difference in the occurrence of aerial displays of immatures and adults concerns the sizes of the groups in which the displays are carried out. Interactions involving adult senders consist of groups sizes of two (i.e. a pair) in 90% of the cases ($n = 136$). Interactions with immature senders consist of pairs in only 35% of the cases ($n = 196$), displays sometimes taking place in groups as large as 10 birds.

ASYMMETRIC INTERACTIONS IN THE AIR

When a Little Gull in flight finds itself approached at close range by a displaying conspecific that has its head up, calls *ke-kôo* a few times, and soars for a few seconds, it can accept the approach and respond 'in gratitude' by answering the display with a display flight of its own directed at the original sender (either or not including the vertical head and *ke-kôo* notes). However, it can also 'actively resist' the approach by evading the sender by fast flight or by quickly turning away, and it can even retaliate by an attack on the sender. Of course, a receiver can also simply fly on, and behave as if nothing has happened.

Table 1. Comparison of the occurrence of aerial displays containing ke-kôo notes (and the vertical head posture accompanying these notes) between immature (Imm) and adult (Ad) Little Gulls in relation to the prediction of the frequencies of their occurrence based on relative numbers of both age categories at the time of observation. In the expected/observed columns the age category mentioned first is the 'sender', the age category mentioned second the 'receiver'. The Chi-square (χ^2) values ($df = 3$) are all very significantly different from zero ($P < 0.001$).

Tabel 1. Het voorkomen van baltsvluchten met ke-kôo's (inclusief de verticale kopstand) tussen jonge (Imm) en oude (Ad) Dwergmeeuwen in verhouding tot de verwachte aantallen op grond van de relatieve aantallen aanwezige oude en jonge vogels. Bij het berekenen van de verwachtingswaarden werd ervan uitgegaan dat de kans dat bijvoorbeeld een volwassen vogel een jonge benadert met een baltsvlucht (Ad - Imm) even groot is als het omgekeerde (Imm - Ad). De toetsingrrootheid χ^2 is steeds significant groter dan nul (P -waarden kleiner dan 0.001).

Date	Time of day	Imm. present	Adults present	Numbers Expected/observed				χ^2
				Imm-Imm	Imm-Ad	Ad-Imm	Ad-Ad	
21 May	14.00-16.00	65	15	61/21	14/50	14/0	3/21	241
29 May	17.00-18.00	100	15	82/15	12/79	12/1	2/13	499
31 May	18.00-18.20	50	10	17/2	4/21	4/0	1/3	93

The way in which the Little Gulls tended to respond depended strongly on the age of the sender (Table 2). Immatures approaching an adult with aerial display were usually treated by avoidance or by attack, and the situation was not much different when the receiver was an immature. In contrast, the adults that were observed during aerial interactions accepted each other's display flights in the majority of cases.

DISCUSSION

The long calls of Little Gulls, whether made in ground or aerial display, are nice compound signals (Veen 1985). The first notes, the *kay*'s, reveal the identity of the sender, the *ke-kêh* series indicate the intention to approach from afar, whereas the vertical head accompanied with *ke-kôo* notes indicates the additional willingness to come in close and friendly contact. The longer *ke-kêh* series of immatures may thus be interpreted as their failure to establish close enough contact to continue with the *ke-kôo* part of the long call. Aerial display occurs predominantly in the early part of the breeding season, and is obviously related to the establishment and maintenance of pair bonds. That aerial display and long calls fulfil the latter role is suggested by the observation that once the birds are incubating, such display only occurs after serious disturbances of the small colonies. It was as if the birds wanted to appease each other on such

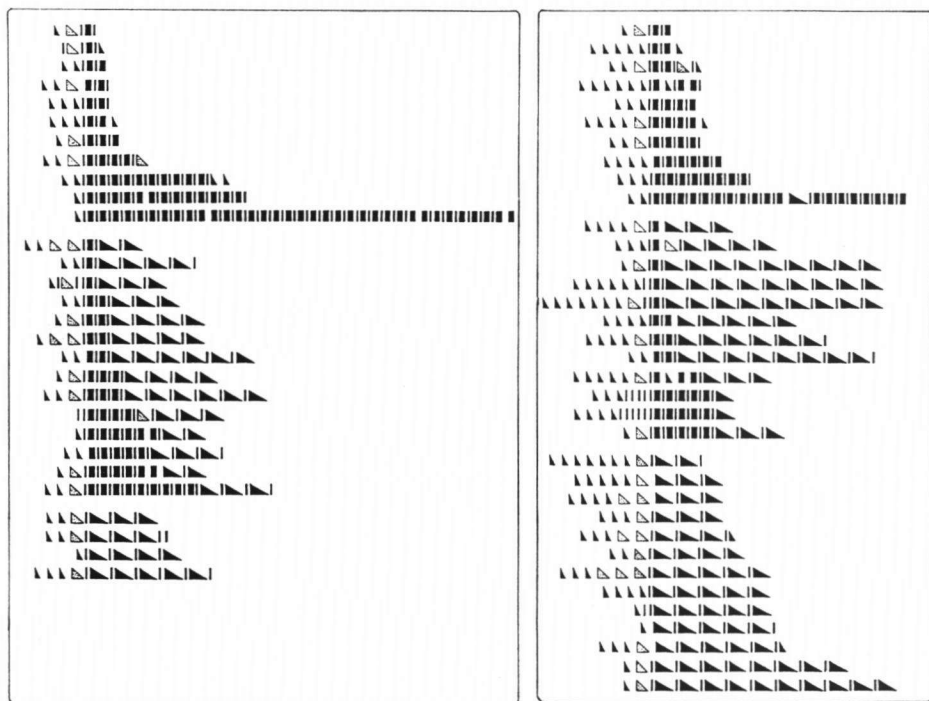


Figure 4. Composition and sequences of complete 'long calls' during aerial display of immature (left) and adult (right) Little Gulls in Lauwersmeer in May 1983. These observations are based on complete sonographic analyses, backed up by running comments.

Figuur 4. Samenstelling van de volledige roepen (de zogenaamde 'long calls') tijdens luchtbalts van jonge (links) en volwassen (rechts) Dwergmeeuwen in het Lauwersmeer in mei 1983, gebaseerd op nauwkeurige sonografische analyses.

Table 2. Response on the part of the receivers of approaches with aerial displays containing ke-kôo notes (and the vertical head posture accompanying these notes) by senders of different age.

Tabel 2. De manier waarop baltsvluchtjes met ke-kôo's (inclusief de verticale kopstand) werden beantwoord door de ontvanger ('receiver') als functie van de leeftijd van de initiator ('sender').

Age of		Displays (n)	Reaction of receiver		
sender	receiver		Acceptance	Refusal	No reaction
Immature	Immature	27	11%	71%	18%
Immature	Adult	156	3%	86%	11%
Adult	Adult	70	74%	10%	16%

occasions, even though the lack of individual marking did not allow us to establish whom was directing its aerial display at whom.

The apparent urge with which immatures in pre-breeding flocks try to direct aerial display at adults and fellow immatures is striking. Are they exercising a practice that is very important to them, perhaps later in life? Are they 'testing the waters' by performing at unwilling adults, learning the details of differential responses? Nuptial displays such as the aerial performances of Little Gulls are commonly interpreted as 'quality indicators' nowadays (Gould & Gould 1996; Zahavi & Zahavi 1997). Could it be possible that flying fast with a head up *and* calling at the same time, rounding this off with an elegant glide, is a difficult game, one that needs much practise as well as stamina? Does this particular display reflect the sender's capability to perform fast mosquito-snapping movements, often with the head up? Is the last part of the aerial display (vertical head and *ke-kôo*) a kind of ritualised feeding sequence that honestly reflects aspects of health, vigour and 'quality' of these small insectivorous gulls?

ACKNOWLEDGEMENTS

I dedicate this paper to Jan Veen, my inspiring mentor in ethology with whom I spent the field season of 1983, in the hope that reduced managerial responsibilities will allow him to re-open his true treasure-trove of observations on communication in gulls, and share them with the world. I thank Kees Camphuysen for giving me an incentive to write this note, and for editing a draft.

SAMENVATTING

Dwergmeeuwen Larus minutus onderscheiden zich van de grotere meeuwen door een tamelijk melodieuze en elegante luchtbalts. Op grond van in mei 1983 verzamelde waarnemingen in het centrale gedeelte van het Lauwersmeergebied, wordt een algemene beschrijving van deze luchtbalts gegeven, en worden enkele nieuwe aspecten beschreven met betrekking tot verschillen in luchtbalts tussen jonge en oude vogels. De luchtbalts bestaat uit een geritualiseerd 'vluchtje' waarbij een

aantal verschillende en uitermate goed herkenbare geluiden worden gemaakt. Een vogel (de 'zender') nadert een andere (de 'ontvanger'), en roept in eerste instantie een aantal keren kay (deze noten zijn waarschijnlijk karakteristiek voor individuen, en dus voor andere Dwergmeeuwen herkenbaar), en vervolgens een aantal keren ke-kèh. Als de zender de ontvanger tot op een paar meter is genaderd trekt ie z'n kop omhoog, gaat met een stijve snelle vleugelslag wat sneller vliegen terwijl ke-kèh overgaat in ke-kôo. Daarna volgt zonder geluid een glijvluchtje zo dicht mogelijk over of langs de ontvanger. Deze ontvanger kan zo'n baltsvlucht beantwoorden met een eigen baltsvlucht; dat zie je vooral tussen volwassen vogels. Als een jonge vogel probeert een baltsvlucht uit te voeren, wordt dat erg vaak beantwoord met een aanval; haast nooit wordt zo'n vluchtje 'geaccepteerd'. Regelmatig moet een baltsvluchtje worden afgebroken. Niettemin proberen jonge vogels wel steeds te baltsen; als het even kan, gericht op volwassen vogels die er dus geen boodschap aan hebben. Mogelijk fungeert de luchtbalts als een kwaliteitssignaal dat een rol speelt bij de vorming en het 'onderhoud' van de paarband en dat is ontstaan uit de jacht op vliegjes in de lucht (waarbij tijdens de vlucht de kop ook omhoog wordt bewogen). Jonge vogels moeten kennelijk goed oefenen om één of meer jaren later een partner te kunnen veroveren.

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