

---

# The social and communication behaviour of the Great Black-headed Gull

*Evgeniy N. Panov*



MTE.09  
Martin Elliott

**ABSTRACT** The social behaviour and vocalisations of the Great Black-headed Gull *Larus ichthyaetus* were studied at breeding colonies in northern Kazakhstan and in Turkmenistan, along the southeast shore of the Caspian Sea. These are described in this paper, and related to the unusual social organisation at breeding colonies, where intraspecific predation and infanticide are widespread. Aspects of signalling behaviour are also discussed in relation to the taxonomic position of the species.

This paper describes the social and communication behaviour of the Great Black-headed Gull *Larus ichthyaetus* at breeding colonies, with particular reference to the rather peculiar social organisation of the species. For example, the typically high density of birds at breeding colonies leads to a consid-

erable reduction in breeding success owing to a number of density-dependent factors such as intraspecific predation and infanticide (Panov *et al.* 1980; Kostina & Panov 1982; Panov & Zykova 1982, 1987, 2001; Zykova & Panov 1988). The suggested phylogenetic affinities of the species are also examined.

*Study areas and methods*

Data were collected in spring (between late March and early June) in the years 1978-80, 1983-84 and 1986-87 at Lake Tengiz (northern Kazakhstan) and in the southeast Caspian Sea area (Kara-Bogaz-Gol Bay and Ogurchinskiy Island, Turkmenistan). In parallel with other studies, ethological data were gathered to

describe the signalling behaviour and communication systems of the species. Observations were conducted and photographs taken from a hide overlooking breeding colonies. A portable tape recorder was used to record both observations and acoustic signals. Some adults in the study colonies were individually marked, and many of the chicks were colour-ringed at these colonies too. In total, 185 hours of observation time was accumulated. Sonograms made from tape recordings were analysed at the Laboratory of Comparative Ethology and Biocommunication of the Severtsov Institute of Ecology and Evolution, using the software A-PC Avisoft-Sonograph. A catalogue of the birds' behavioural repertoire was created using the photographs obtained. All mean values are given with their standard deviations.

*General breeding ecology* The Great Black-headed Gull is one of the world's largest gulls, with a mean weight of c. 1,600 g for males and c. 1,220 g for females. Nesting colonies are almost invariably situated on islands, in flat, bare areas, often only slightly above the water level and sometimes in flooded areas. Nests are distributed unevenly within colonies, the size of which varies greatly, from 20-30 up to 600-700 pairs. Densely populated sections (subcolonies) within large colonies usually occupy slightly elevated places and may number from several nests to many dozens. A negative correlation between the number of nests in a subcolony and the mean minimum distance between them is apparent; in subcolonies with 100 or more nests, the distance between nests is 0.4-0.5 m, while in small clusters of <10 nests it is 1.4-3.2 m (Panov &



Evgeniy Panov

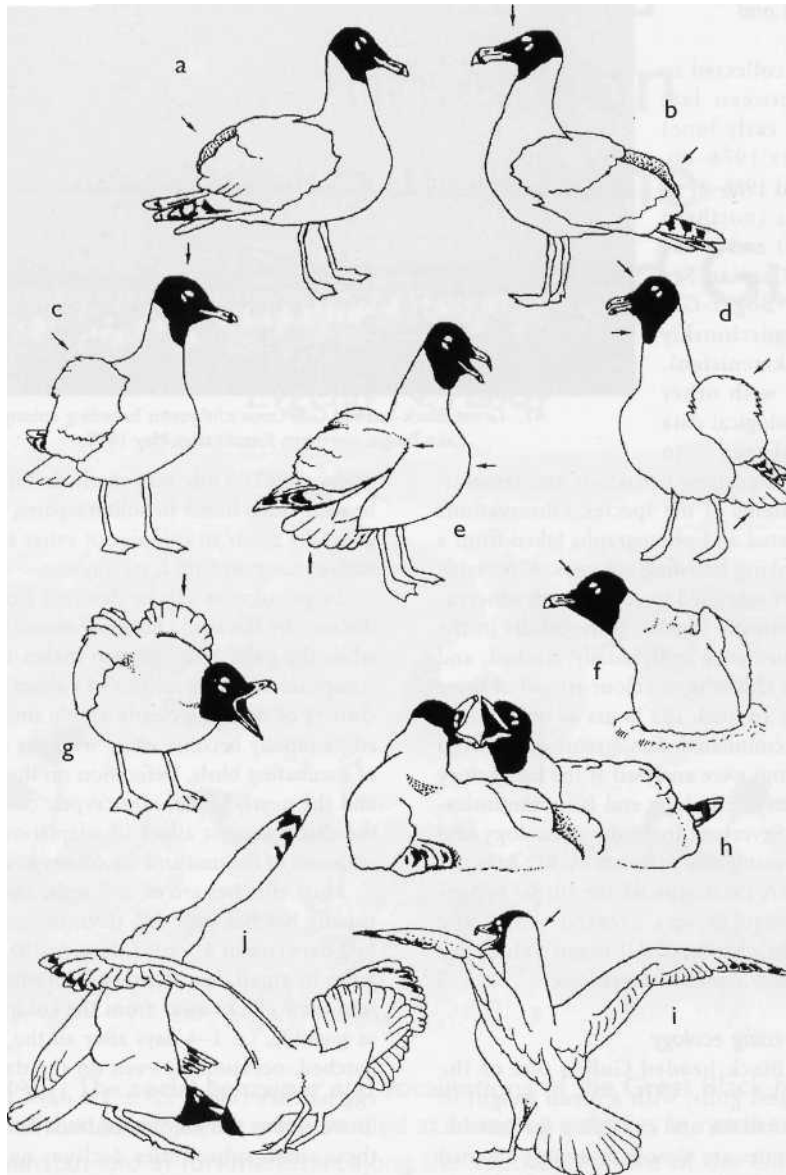
47. Great Black-headed Gull *Larus ichthyaetus* breeding colony, Lake Tengiz, northern Kazakhstan, May 1978.

Zykova 1982). Only very rarely do Great Black-headed Gulls breed in solitary pairs, and these generally occur in colonies of other large gulls, such as Caspian Gull *I. cachinnans*.

Large colonies can be detected from a great distance by the loud chorus of sound produced, while the gulls' plumage also makes the colony conspicuous at long range. On a closer approach, clusters of nests are clearly visible since the nest edges rapidly become white with the droppings of incubating birds. Defecation on the nest edge and the nearly white, non-cryptic coloration of the chicks suggest a lack of adaptation for concealment of the nest and the colony as a whole.

Most clutches are of 2-3 eggs, and a clutch usually hatches over 4-5 days, occasionally up to 7 days (mean  $4.3 \pm 0.5$  days,  $n=15$ ). Breeding pairs in small, less dense subcolonies tend to lead their chicks away from the colony as soon as possible, i.e. 1-4 days after all the eggs have hatched, occasionally even on the day the last egg hatches (mean  $2.3 \pm 1.4$  days,  $n=13$ ). As broods leave, the number of birds remaining in these small subcolonies declines quickly and these groups cease to exist 1-2 weeks after hatching begins. Families from small subcolonies usually move to larger and denser subcolonies, swelling the density of both adults and chicks at the latter. An increase in abundance and density, together with the growing mobility of resident and immigrant broods, leads to a higher rate of aggressive interactions among adults and to a gradual breakdown of social organisation.

When family broods disintegrate and the chicks intermingle, a so-called creche may form in large subcolonies, often near the centre. Several adults surround the dense group of



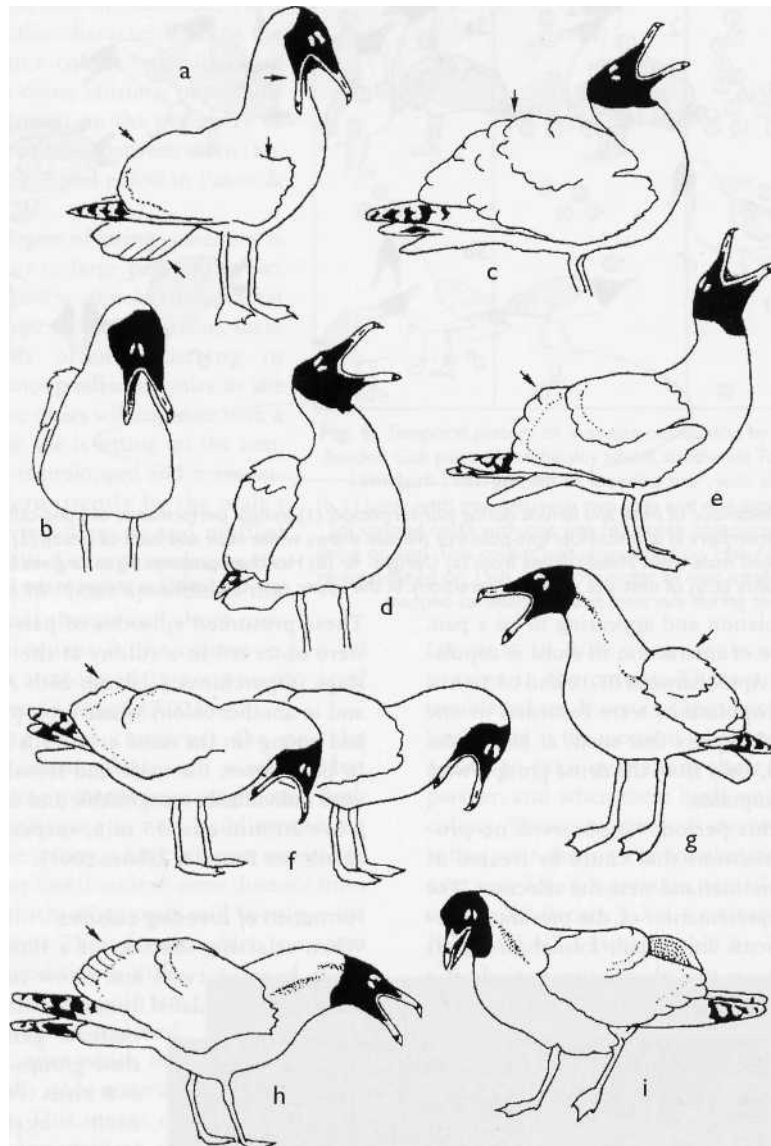
**Fig. 1.** Motor components of the signalling behaviour of Great Black-headed Gull; (a-d) Upright-posture ((a) female, (b) male); (c-e) increasing aggressive motivation; (f) transition to Jabbing (g); (h) mutual threat-behaviour of two incubating birds in adjacent nests; (i) threat with raised wings; (j) fighting (one of the two rivals holds its opponent by the bill). Arrows indicate typical features of display-postures ([variable] ruffling or raising of feathers, etc.).

chicks at these sites, although there is regular interchange of such adults. In due course, such creches may start to move slowly towards shallow-water areas, and the chicks will enter the water in an emergency. Broods from different subcolonies may join the creche as the juveniles grow older. Creches, like breeding colonies themselves, are characterised by a high density of birds and a large number of antagonistic contacts (Kostina & Panov 1982).

Great Black-headed Gulls thus tend to remain in compact aggregations throughout the breeding cycle. This constant high density governs the social climate, which itself provides the background for communication in breeding colonies.

*The mating stage of the breeding cycle*

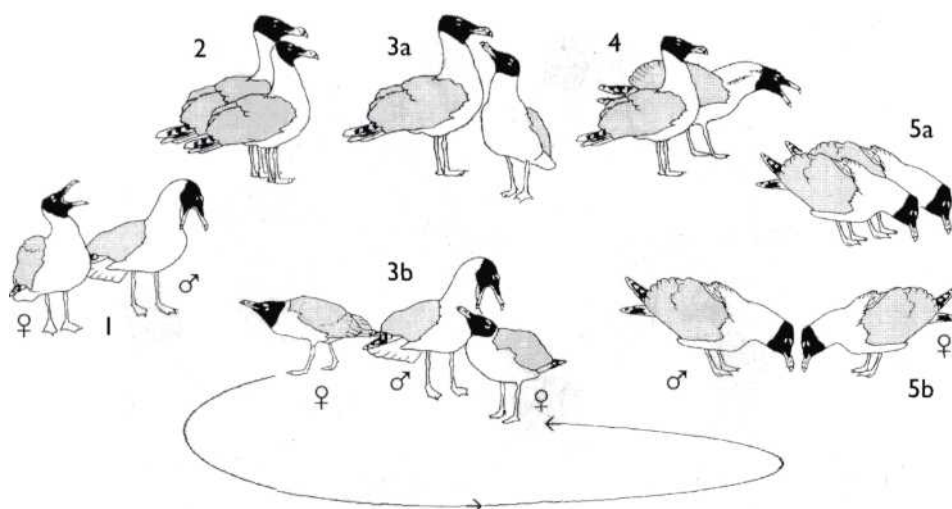
Great Black-headed Gulls are often already paired when they arrive at spring 'club' (pre-



**Fig. 2.** Motor components of Long-call and Mew-call displays in Great Black-headed Gull: (a, b) first phase during typical Long-call; (c, d) second phase; (e) third phase; (f) untypical variant of Long-call display with elements of Mew-call (given simultaneously by a male (in background) and a female (in foreground)); (g) Mew-call with body in vertical position; (h, i) typical Mew-call. Arrows indicate typical features of display-postures, as fig. 1.

breeding) sites, before moving to the breeding colony proper, so it can be assumed that pair-formation begins in late winter. In 1980, between 22nd March and 6th April, compact groups of 10-20 individuals and loose aggregations of up to 150 gulls were observed in Kara-Bogaz-Gol Bay. A few single birds were also observed in clubs of Caspian Gulls. Birds in a compact aggregation often maintained the Upright-posture (fig. 1) for long periods. Con-

stantly given Long-calls (fig. 2) sometimes merged into a continuous chorus resembling a loud roar, which could be heard in the evenings, even in complete darkness. Passing conflicts often arose between group members and followed in series as a chain reaction. The successful attacker occupied the place of the victim, the latter moving within the group and thus provoking another conflict. Attempts at aggression are sometimes observed in birds



**Fig. 3.** Behaviour of male and female during pair-formation: (1) mutual performance of Long-call display; (2) pair-members in identical Upright-postures (female shows white nape and back of head); (3) female walks around male while Head-tossing from (a) Upright- or (b) Hunched-posture; (4) male gives Mew-call; (5) two variants (a, b) of nest-site selection ceremony. In the upper row the female is always in the foreground.

sitting in isolation and appearing to be a pair. Another type of interaction in clubs is copulation. On 6th April, between 07.10 and 08.10 hrs, at least 15 copulations were recorded in one club. Those few pairs that spent at least some time isolated, away from the dense groups, were also seen to copulate.

During this period, we observed no prolonged interactions that could be treated as mating ceremonies and nest-site selection. The schematic representation of the presumed succession of events during pair-formation (fig. 3) is deduced from two observation periods at a more advanced stage of the breeding cycle.

These presumed episodes of pair-formation were observed in a colony at the incubation stage (Ogurchinskiy Island, 26th April 1984) and in another colony where most pairs already had young (in the same area, 19th May 1983). In both cases, the male and female involved were individually recognisable and observed for 2 hrs 20 min and 55 min, respectively (for details, see Panov & Zyкова 2001).

**Formation of breeding colonies** When selecting the site for a future colony, birds keep in twos and show no signs of wanting to be isolated from other similar 'pairs', instead gathering in close groups of perhaps 6-8 birds. For birds in such aggregations, Upright-postures and interactions including synchronous Ground-touching with the bill by two birds are characteristic (fig. 3: 5a, 5b). During such a ceremony, a third gull, or more individuals, will try to join the main participants. This causes constant conflicts, which are unpredictable and chaotic. The aforementioned displays are prob-



Evgeniy Panov

48. Great Black-headed Gull *Larus ichthyaetus* breeding colony, Kara-Bogaz-Gol, northwest Turkmenistan, May 1979.

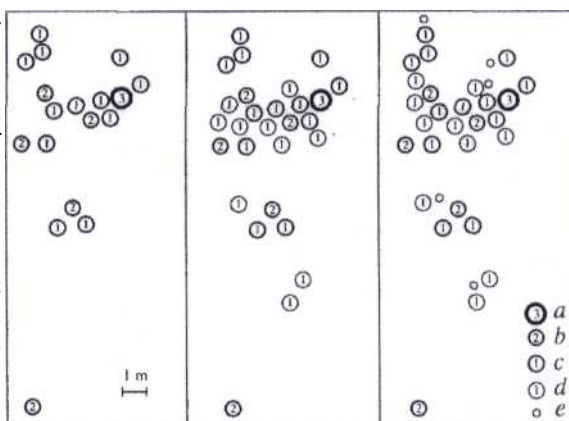
ably aimed at nest-site selection. Their quasi-collective character leads to the first nests in a colony typically being grouped in dense clusters; nests built later are situated on the periphery of such clusters and/or between them (fig. 4; see also fig. 2 and p. 890 in Panov & Zykova 1987).

A high degree of laying synchrony is probably due in large part to the fact that copulation is stimulated in several pairs in a type of chain reaction, these interactions often occurring in sequence among adjacent pairs in the colony. Some males will copulate with a female while she is sitting on the nest. Copulation is prolonged and is accompanied intermittently by the male's energetic wing-flapping and muffled rhythmic calls. During copulation, the female jerks her head upwards. At this stage, mutual threats and short conflicts are frequent in the colony (e.g. c. 30 episodes in a colony of 25 nests on 6th April 1979 between 15.00 and 17.00 hrs).

Breeding pairs construct the nest by bringing in aquatic plants such as seaweed but also by stealing material from neighbours. Both partners participate in nest-building and, on arrival at the colony, a bird will pass seaweed to its partner or toss it aside at some distance from the nest, which other pairs will then use for their own nests. Those females which come into breeding condition a little later than others will lay their eggs in an unlined depression, after which the pair gradually adds material to the nest. This means of adjusting laying date to match the timing of breeding of pioneer pairs enhances breeding synchronisation in a dense cluster of nests.

#### Incubation and hatching

In those clusters of nests where breeding is highly synchronised, the general social situation stabilises with the onset of incubation. Typically, only a small proportion of off-duty birds



**Fig. 4.** Temporal pattern of nest-site occupation by Great Black-headed Gull pairs, Ogurchinskiy Island, southwest Turkmenistan, 15th April 1987: (a) nest of 'founding pair', with three eggs; (b, c) nests with material, with two eggs and one egg, respectively; (d) unlined nests with one egg; (e) empty nest-scrapes with no lining or eggs. This colony was abandoned on 14th April 1987, and re-established on 15th, when the order of nest establishment was mapped carefully at three intervals during the day.

(at most 10-20% of those incubating) are present in the colony. These are potential troublemakers, however. Open conflicts usually begin only at the moment when incoming gulls arrive to take over from their incubating partner, and when these birds walk across the colony. These changeovers are comparatively infrequent during the incubation phase; on average, 3.0-3.7 arrivals per 10 minutes in colony N5 (large), 1.3-1.4 arrivals in colonies N7.2 and N7.3 (small; table 1). When a gull



49. Great Black-headed Gull *Larus ichthyaetus* breeding colony, Ogurchinskiy Island, southwest Turkmenistan, May 1984.

Evgeniy Panov

walks past close to the nests of others, the owners will threaten it by attacking with open bill (Jabbing; fig. 1). Non-incubating birds may attack a newcomer and so provoke short fights (fig. 1j). These bursts of aggression are usually accompanied by Long-calls from several birds, both participants in the conflict and others. The behaviour varies during changeovers at the nest. The most typical variant is the following: the incoming partner approaches the nest in the Upright-posture - both birds give a Long-call - the male adopts the Mew-call posture - the female starts Head-tossing. Subsequently, the partner that has arrived may regurgitate. If the

female is begging, tossing her head and walking around the male in the Hunched-posture, she may try to take the food directly from the male's throat just when he regurgitates.

The rate of Long-call performances in a colony may be an indicator of the level of social tension in the group and of the intensity of the communication process. If the dynamic density is high, practically all members of a particular sector in the colony participate in the process. Counting Long-calls at different stages of the breeding cycle in colonies with different structural characteristics provides support for this suggestion (table 1, based on 28 hours of

**Table 1.** Rate of aggressive encounters and Long-calls in Great Black-headed Gull *Larus ichthyaeetus* colonies of different size and density; Kara-Bogaz-Gol, Turkmenistan, 1979.

No. <sup>1</sup> and type of colony	Number of nests	Mean minimum distance between nests (m)	Stage of breeding cycle <sup>2</sup>	Overt aggression <sup>3</sup> (mean ± SD and range)	Long-calls <sup>4</sup> (mean ± SD and range)
N5 Dense	102	0.44	Incubation (n=19)	3.4 ± 2.0 (0-9)	6.8 ± 4.4 (0-15) **
			Onset of hatching (n=12)	2.0 ± 1.3 (0-4)	13.3 ± 6.9 (3-22)
			Mass hatching (n=18)	1.9 ± 1.2 (0-6)	27.9 ± 13.6 (9-55)
N1B Dense	63	0.45	Incubation (n=12)	2.4 ± 1.9 (0-6)	8.3 ± 4.1 (3-17)
			Onset of hatching (n=6)	5.0 ± 5.0 (0-13)	3.7 ± 1.8 (2-7)
			Mass hatching (n=6)	9.7 ± 2.5 (5-12)	38.5 ± 11.3 (21-51)
N7.2 Dense	26	0.49	Incubation (n=34)	0.5 ± 0.7 (0-3)	4.7 ± 3.7 (0-14) ***
			Onset of hatching (n=12)	2.5 ± 2.5 (0-8)	15.7 ± 11.6 (2-39)
			Mass hatching (n=9)	–	3.1 ± 3.3 (0-7)
N7.3 Dispersed	31	0.61-1.46 (in different subcolonies)	Incubation (n=27)	0.3 ± 0.5 (0-2)	0.8 ± 1.0 (0-3)
			Onset of hatching (n=6)	0.5 ± 0.8 (0-2)	1.2 ± 1.9 (0-5)
			Mass hatching (n=9)	0.7 ± 2.0 (0-6)	0.9 ± 1.6 (0-5)

Notes:  
<sup>1</sup> See Panov & Zykova (1982) for more details.  
<sup>2</sup> Figures in parentheses are number of 10-minute observation periods.  
<sup>3</sup> Aggressive encounters measured as attacks by off-duty birds on other colony members.  
<sup>4</sup> \* P<0.5; \*\* P<0.1; \*\*\* P<0.001 (Mann-Whitney U-Test).

observations); general trends are clear, even though not all the differences are statistically significant. In dense colonies, the rate of Long-call performances increases from incubation to hatching, whereas in loose breeding groups it does not vary with time. The increasing rate of Long-call performances in dense colonies is caused by more frequent arrivals of gulls bringing food for their chicks (e.g. 4.3 arrivals in 10 minutes in colony N7.2 cf. 1.9 arrivals during incubation), and by the increasing aggression of parents striving to maintain the integrity of their brood, both by defending their chicks from neighbouring adults and by preventing unrelated chicks from joining their family group.

#### Broods in the colony

The brood stage is characterised by a high rate of interactions, not infrequently with the participation of more than two individuals. In general, the social situation in dense colonies is unstable, with a high level of destructive behaviour. The latter becomes apparent in the high frequency of mutual threats with open bill (mean 11.4 but up to 25 episodes of such Jabbing in 10 minutes, in colony N5), and by attacks, usually on strange chicks, but sometimes on the attacker's own offspring (see Panov *et al.* 1980 and Kostina & Panov 1982 for more detail). In loose, less dense colonies, similar instances of growing social tension and disorganisation are recorded only locally, for example in sectors

where intruding Great Black-headed Gulls appear temporarily (such as birds leading their young to a creche). The key components of infanticide behaviour are the same as those constituting the standard antagonistic behaviour (Upright-posture with ruffled head and 'back' feathers, and lunges with wide-open bill). The posture of a gull attacking a nestling suggests a high level of aggressive motivation. This aggression is often.

intermingled with actions from the repertoire of sexual, nest-building and parental-behaviour patterns. Of 40 documented cases of attacks on chicks, seven were accompanied by a Long-call given just before or after the aggression (i.e. in 4% of 174 situations in which the context of the Long-call was ascertained reliably).

Apart from spontaneous attacks on strange chicks, systematic attacks on a juvenile by the adults tending it were observed frequently. Many such attacks resulted in the death of the chick; in rare cases, it survived (for further details, see Kostina & Panov 1982). The chick may have been either a stranger adopted by the pair or the adults' own offspring. Even though in such situations adults will brood the chick and feed it from time to time equally with other brood members, there are instances when this parental behaviour suddenly becomes aggressive. A typical sequence of the aggressor's actions in such cases is as follows: Stare-down - incipient pecking movement - touching the chick's head with closed bill (all these are analogues of movements during nest-site selection) - seizing the chick's head in the open bill - shaking the chick and throwing it in the air (as in cases of open, spontaneous aggression against young mentioned above). Sometimes, having pecked at the chick's head, the attacker unexpectedly follows this by performing movements that normally precede the feeding of a nestling. For further discussion of this 'mosaic structure' of parental and aggressive behaviour in



Evgeniy Panov

50. Great Black-headed Gull *Larus ichthyaetus* chicks with unhatched egg, Ogurchinskiy Island, southwest Turkmenistan, May 1984. Note the uniformly light plumage of the downy chicks, which is a distinctive character of this species. A similar appearance is found only in Ross's Gull *Rhodostethia rosea*, kittiwakes *Rissa*, and Relict Gull *L. relictus*.





51. Adult Great Black-headed Gull *Larus ichthyaetus* feeding chicks, Ogurchinskiy Island, southwest Turkmenistan, May 1984.



52. Adult Great Black-headed Gull *Larus ichthyaetus* killing small chick, Ogurchinskiy Island, southwest Turkmenistan, May 1984. Note dead chick lying to the right of the chick being attacked.



53. Great Black-headed Gulls *Larus ichthyaetus* jabbing, Ogurchinskiy Island, southwest Turkmenistan, May 1984. Note two dead chicks lying in the foreground.



54. Great Black-headed Gull *Larus ichthyaetus* creche, Ogurchinskiy Island, southwest Turkmenistan, May 1984. Note that some chicks are marked with dye for research observations.

Great Black-headed Gulls towards their own offspring, see Kostina & Panov(1982, p. 1535 and fig. 4). Aggression of adults towards the young may be combined with 'altruistic' acts, for example when an adult attempts to protect a neighbour's chicks from aggression and thus leaves its own brood unguarded. Such behaviour frequently causes chaotic conflicts, with the participation of four or five adults; such encounters proceed as a chain reaction.

*The creche*

At the creche stage, the rate of antagonistic encounters increases still further (Kostina & Panov 1982). Whereas at the brood stage the number of conflicts between adults was 1.9-9.7 per 10 minutes (table 1) in the densest colonies, up to several dozen aggressive acts were recorded in creches during the same time interval. For example, in a group comprising seven juveniles and varying numbers (13-26) of adults, the rate of confrontations among the latter varied between 18 and 69 per 10 minutes (mean 37.6 ± 15.6, n=9). Attacks on chicks by adults were even more unevenly distributed: in four 10-minute intervals such attacks were absent, in five others they varied between 2 and 29 (mean 6.3 ± 10.0 over the

whole observation period). A prolonged outbreak of aggression towards the young (55 attacks in 40 minutes) coincided with the maximum number of adults in the group, as well as with an increased number of confrontations among them (197 episodes during the same period).

The reason for this high level of aggressive contacts is the generally unpredictable situation in creches. As the control of adults over their juveniles weakens, the latter tend to gather in compact, temporary groups, with juveniles of other broods. Then, when a parent/guardian tries to regain control of its brood, confrontations with guardians of other chicks prevent the parent from approaching the creche. Such conflicts often cause redirected aggression towards young birds, both strange chicks and the aggressor's own offspring. Precisely the same

outcomes arise from competition among adults for the role of guardians. Birds that have lost clutches or broods will try to take chicks from genuine parents or foster-parents (Panov & Zykova 1981).

The break-up of family units, the links of which become progressively weaker from the moment when creches are formed, is an important cause of disorganisation. The colony as a conglomerate of families, each one keeping its integrity and relative autonomy owing to those familial ties, evolves into an amorphous group with rather anonymous composition at the creche stage. It then consists of a constantly changing contingent of adults and a great number of juveniles which gradually gain independence from their guardians.

The repertoire of signals used in parental and antagonistic behaviour patterns does not change significantly compared with the previous stage, when the broods remain in the colony. In a creche, adults often maintain the

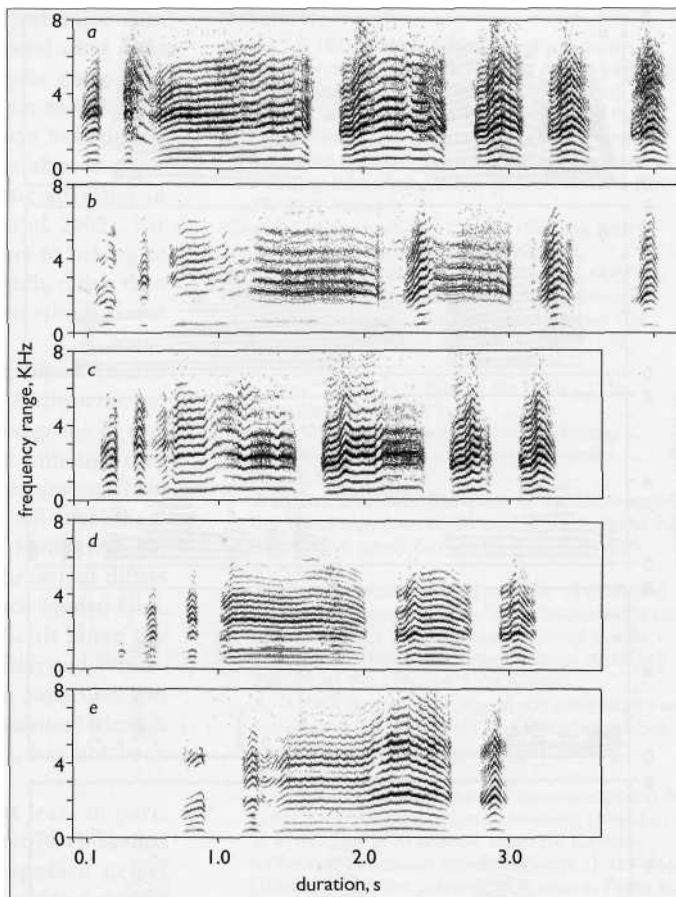
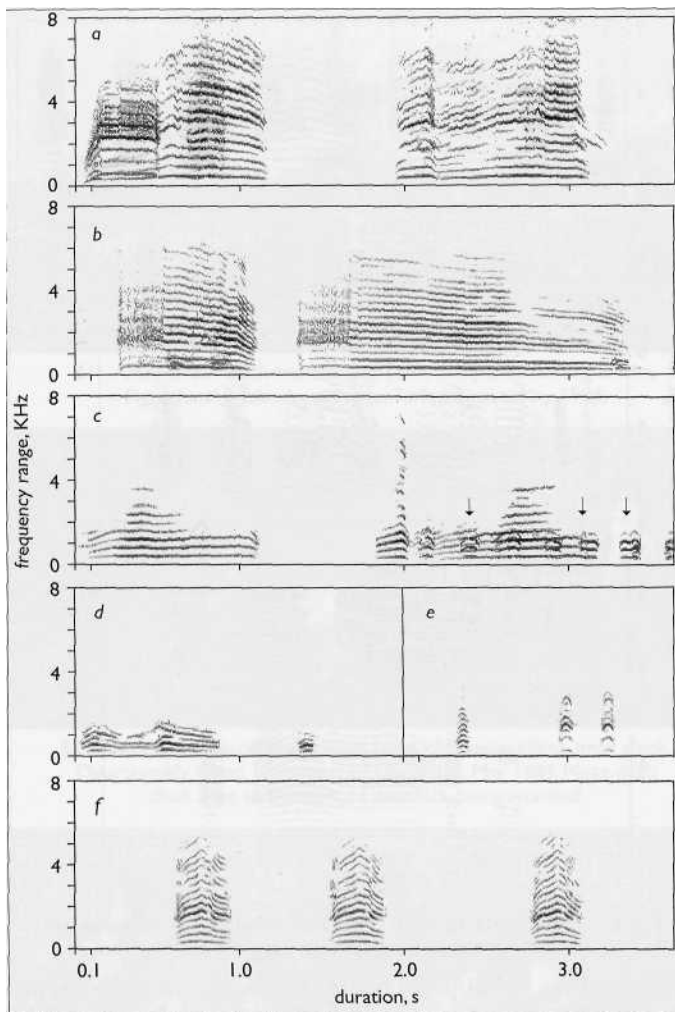


Fig. 5. Variation in Long-call of Great Black-headed Gull. Sonogram (e) shows variant intermediate between Long-call and Mew-call.

Upright-posture for a long time and often give Long-calls. Conflicts between juveniles of the same 'brood' may be seen for the first time when adults are feeding them.

#### *The signalling behaviour of the Great Black-headed Gull as an indicator of taxonomic position*

In general terms, the signalling behaviour of the Great Black-headed Gull is essentially similar to that of other, ethologically well-studied gull species, such as those of the 'large white-headed gull' group. This basic similarity is true of the configuration of most display-postures and the vocal components of most principal displays, such as Long-call and Mew-call. However, among the most characteristic features of the Great Black-headed Gull's signalling behaviour is the absence of Choking (found in the vast majority of gulls whose behaviour has been well studied; see Cramp & Simmons 1983, fig. G and



**Fig. 6.** Components of vocal repertoire of Great Black-headed Gull. (a-e) different variants of Mew-call ((d) 'bass' variant); (c) simultaneously with Mew-call of one individual, another bird gives a rhythmic 'gouh' call (shown by arrows); (e) alarm-call; (f) common (everyday) call.

full description in Herring Gull *L. argentatus* account, p. 826). There is also no Head-flagging, which is present in more-or-less pronounced form in a number of so-called 'hooded gulls' (although note that actions reminiscent of the classical Choking and Head-flagging occurred in the antagonistic behaviour of a two-year-old Great Black-headed Gull raised in semi-natural conditions).

There are other unusual features of the signalling behaviour of this species. The components of the Long-call display (fig. 2, a-e) are characterised by a lack of the 'Throw-forward', with head jerked down to the level of the breast or lower (Cramp & Simmons 1983; see fig. D in

Herring Gull account, p. 825); these movements are typical of most gull species. During virtually all the antagonistic displays of the Great Black-headed Gull, the back plumage is raised, whereas the carpal joints are not held away from the body. Tinbergen (1953) believed that that part of the display when the carpal joints are held away from the body showed a high level of aggressive motivation in the Herring Gull. This cannot be true of the Great Black-headed Gull, because in this species, even in the most aggressive encounters, rivals keep their wings pressed to the body, with carpal joints hidden under the body feathers (fig. 3). As for vocalisations, the typical feature is a high level of variation in the Long-call of the Great Black-headed Gull (fig. 5). Data on the behaviour of an immature bird (see Panov & Zykova 2001) suggest that such variation may be a result of the long maturation of this reaction as the young bird

develops, so that individually acquired components modify the species-specific hereditary matrix to a considerable extent. Other components of the Great Black-headed Gull's vocal repertoire are shown in fig. 6.

Only three other species included in Moynihan's 'primitive hooded gulls' group (Moynihan 1959) have been well studied in ethological terms: Laughing Gull *L. atricilla*, Mediterranean Gull *L. melanocephalus* and Relict Gull *L. relictus* (Beer 1975; Zubakin 1979; Buzun & Mierauskas 1987). Similarities with the signalling behaviour of Great Black-headed Gull can be found in only one of these, Relict Gull.

It is interesting to measure these comparative ethological findings against a recent study

on gull phylogeny based on molecular data (Pons *et al.* 2005). This concluded that Moynihan's 'primitive hooded gulls' group is an artificial category, based more on morphological and plumage characters than behavioural data (and plumage characters are often an unreliable indicator of phylogenetic affinities in birds; e.g. Panov 2005, Pons *et al.* 2005). For example, Laughing Gull appears to belong to another clade, that of 'hooded' gulls, rather than to the 'black-headed' clade to which Great Black-headed Gull is assigned.

Wolters (1975) placed Great Black-headed Gull in the monotypic genus *Ichthyæetus* but Pons *et al.* proposed a polytypic genus of that name incorporating six species, although they admitted that 'the relationships among these "black-headed" species are not well established'. In particular, the position of Mediterranean Gull is in doubt, given that its behaviour differs sharply from that of Great Black-headed Gull. Other comparisons are difficult since the behaviour of Sooty *L. hemprichii* and White-eyed Gulls *L. leucophthalmus* in particular, and also that of Audouin's Gull *L. audouinii* (though see Cramp & Simmons 1983), has not been fully documented.

In conclusion, my data, at least in part, support distinguishing the Great Black-headed Gull as a member of a separate genus *Ichthyæetus* within the family Laridae. I predict that future studies, both ethological and molecular, will point to a subdivision of the rather large 'black-headed' gull group, to show a closer relationship between the two species showing the greatest similarity of signalling behaviour, Great Black-headed and Relict Gulls.

#### Acknowledgments

It is a pleasure to express my gratitude to N. N. Andrusenko (then researcher at the Kurgal'dzhinskii [Qorghalzhyn] Nature Reserve, Kazakhstan) for help with the organisation of my field studies at Lake Tengiz, and to M. E. Gauzer and the late V. I. Vasiliev for invaluable support and assistance over a number of years which enabled me to collect data on the breeding biology of the Great Black-headed Gull on islands in the south-eastern part of the Caspian Sea. I also thank Mike Wilson, who corresponded with the Editor about publication of this paper in *British Birds* and worked hard on the manuscript, improving my English, translating some late additions from Russian and making a number of valuable suggestions for changes to the text. The study was supported by the Russian Foundation for Basic Research (grant no. 98-04-48310).

*Prof. E. N. Panov, Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskiy Prospect 33, 117071 Moscow, Russia*

#### References

- Been C. G. 1975. Multiple functions and gull displays. In: Baerends, G., Beer, C. & Manning, A. (eds.), *Function and Evolution in Behaviour*, 16—54. OUP Oxford.
- Buzun, V. A., & Mierauskas, R. 1987. [Behaviour of the Mediterranean Gull (*Larus melanocephalus* Temm.) in the period of colony formation and at early stages of breeding]. *Byull. Mosk. Obshch. Ispyt. Prir. Otd. Biol.* 92 (3): 27-36. (In Russian)
- Cramp, S., & Simmons, K. E. L. (eds.) 1983. *The birds of the Western Palearctic*. Vol. 3. OUP Oxford.
- Kostina, G. N., & Panov, E. N. 1982. [Mortality of downy chicks and the nature of personal bonds between chicks and parents in the Great Black-headed Gull *Larus ichthyæetus*]. *Zool. Zh.* 61(10): 1531-1542. (In Russian)
- Moynihan, M. 1959. A revision of the family Laridae. *Amer. Mus. Novit.* 1928: 1-42.
- Panov, E. N. 2005. *Wheatears of Palearctic. Ecology, behaviour and evolution of the genus Oenanthe*. Pensoft, Sofia-Moscow.
- & Zykova, L. Yu. 1981. [Behaviour of the Yellow-legged Gull (*Larus argentotus cachinnans*) at late stages of the reproductive cycle]. *Zool. Zh.* 60 (11): 1658-1669. (In Russian)
- & — 1982. [Socially induced mortality of chicks and cannibalism in colonies of the Great Black-headed Gull *Larus ichthyæetus*. 2. Dynamics and scale of juvenile mortality in colonies with different spatial structure]. *Zool. Zh.* 61 (9): 1396-1412. (In Russian)
- & — 1987. [Impact of ecological and social factors on reproductive success in the Great Black-headed Gull *Larus ichthyæetus*]. *Zool. Zh.* 66 (6): 883-894. (In Russian)
- & — 2001. Signal behaviour and communication in the Great Black-headed Gull *Larus ichthyæetus* (Aves, Lari) as an indicator of its position within the Larinae subfamily. *Entomological Review* 81 (Suppl. 1): 161-166. [This paper was first published in Russian as Panov & Zykova 2001. *Zool. Zh.* 80 (7): 839-855.]
- , —, Kostina, G. N., & Andrusenko, N. N. 1980. [Socially induced mortality of chicks and cannibalism in colonies of the Great Black-headed Gull *Larus ichthyæetus*. 1. Scale and causes of juvenile mortality]. *Zool. Zh.* 59 (11): 1694-1705. (In Russian)
- Pons, J.-M., Hassanin, A., & Crochet, R.-A. 2005. Phylogenetic relationships within the Laridae (Charadriiformes: Aves) inferred from mitochondrial markers. *Molecular Phylogenetics and Evolution* 37: 686-699.
- Tinbergen, N. 1953. *The Herring Gull's World*. Collins, London.
- Wolters, H. E. 1975. *Die Vogelarten der Erde*. Lfg. 1. Paul Parey, Hamburg and Berlin.
- Zubakin, V. A. 1979. [Display and breeding behaviour of the Relict Gull (*Larus relictus* Loennb.) at Lake Baruntorey]. *Byull. Mosk. Obshch. Ispyt. Prir. Otd. Zool.* 84 (2): 15-20. (In Russian)
- Zykova, L. Yu., & Panov, E. N. 1988. [Hatching asynchrony as the main cause of differential juvenile mortality in the Great Black-headed Gull (*Larus ichthyæetus*)]. *Zool. Zh.* 67 (12): 1865-1877. (In Russian)