ISSN 1062-3590, Biology Bulletin, 2015, Vol. 42, No. 9, pp. 808–820. © Pleiades Publishing, Inc., 2015.
Original Russian Text © A.V. Druzyaka, M.A. Minina, Z.V. Chasovskikh, 2015, published in Zoologicheskii Zhurnal, 2015, Vol. 94, No. 1, pp. 76–89.

The Early Development of Aggressive Behavior and Rapid Growth of Chicks in the Black-Headed Gull (*Larus ridibundus*) in Conditions of Diffused Nesting

A. V. Druzyaka, M. A. Minina, and Z. V. Chasovskikh

Institute of Animal Systematics and Ecology, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 630091 Russia
e-mail: decartez@gmail.com

Received October 9, 2013

Abstract—The effect of low nesting density caused by the fragmentation of nesting biotopes due to seasonal flooding on the development of aggressive behavior and on growth of black-headed gull chicks was investigated. An analysis of the behavior of birds nesting with different densities showed that contacts with neighboring broods were less frequent in chicks from more sparsely distributed nests, while aggressive behavior could be observed in these broods earlier and more often than in their peers from the nests located in more densely populated areas. By testing the parent birds using a standard stimulus of territorial behavior—a remotely controlled stuffed gull—we found that the hosts of widely spaced nests reacted more aggressively but left the clutches less frequently than their neighbors that nested more densely. On average, the chicks from the sparsely distributed broods grew faster and the daily increment of the skull size of the chicks correlated inversely with the frequency of parental visits. We suppose that in the case of the seasonal decrease of nesting grounds, the offspring of more aggressive young couples nesting in the most sparsely populated areas had an advantage in the development probably due to the maternal influence on the composition of the eggs. According to our data, in the conditions of low-density nesting, the parental influence on the growth of chicks and development of their aggressive behavior prevailed over the possible developing effect of the social experience.

Keywords: colonial nesting, Laridae, behavior development, social relations, maternal effect, breeding density

DOI: 10.1134/S1062359015090034

INTRODUCTION

Chicks of colonial gulls grow and develop, constantly communicating with the nearest neighbors in the colony. The negative consequences of such contacts are well known: chicks from neighboring nests can steal food from the brood and adult birds can eat chicks, particularly in the larger species of gulls (Hunt, G.L. and Hunt, M.W., 1975; Butler and Janes-Butler, 1982; Zykova and Panov, 1983). On the other hand, experiments in captivity have shown that regular contact with neighbors and participation in territorial conflicts can be important for the formation of the social behavior of chick (Groothuis, 1992). In particular, during a conflict, a short-term elevation in the concentration of testosterone occurs in the blood, which, in turn, reinforces the behavioral response (the "challenge" hypothesis, Wingfield et al., 1990). In black-headed gull chicks, regular conflicts cause the hormonal elevation to become less pronounced and the response, on the contrary, stronger (Ros et al., 2002). In addition, in this species, the experience of social contact indirectly, through a long-term increase in the concentration of testosterone, accelerates the replacement of direct aggression with developing territorial demonstrations (Groothuis and Meeuwissen, 1992). For the chicks in their natural environment, it was shown that high levels of yolk testosterone increases their mobility and aggressiveness in territorial confrontations (Muller et al., 2009), but it is unclear whether contacts between the chicks from different nests influence the development of their aggressive demonstrations.

Chicks more often come into contact with neighbors in densely populated areas of the nesting colony (Hunt, G.L. and Hunt, M.W., 1976), and a protected nesting territory reduces the risk for the chicks to be crippled or robbed because their parents guard it from invasions and teach their nearest neighbors to adhere to the boundaries of their nesting sites (Burger, 1984). It can be assumed that the aggressive behavior of chicks is stimulated or launched by contacts between them, in which case, it must develop faster in densely populated parts of the colony in the nests with a small protected area.

Regardless of the influence the neighborhood, an increase in the concentration of testosterone in the egg yolks promotes aggressive demonstrations in the chicks of black-headed gulls (Muller et al., 2009). In the yolks of eggs from sparsely distributed nests, testosterone levels are higher and the clutches are lighter, indicating a younger age of the females (Groothuis and Schwabl, 2002). As a result, the aggressive behavior of chicks can develop sooner due to the maternal hormonal investments of the more aggressive females. If such a maternal influence on the development of the behavior of chicks takes place in nature, it is more pronounced in the diffuse parts of the colony inhabited by aggressive parents.

Therefore, to clarify the issue of the impact of social contacts on the development of aggressive demonstrations, it is necessary to compare the behavior of chicks growing in different nesting density conditions.

For the black-headed gull, there is no direct evidence regarding the quantity of testosterone in the clutches of densely populated plots of the colonies. The work cited above does not include such nests. In the conditions of elevated nesting density, gulls are often more aggressive, as they are forced to spend more energy to protect their nesting territories (Bukacinska and Bukacinski, 1993). This probably affects the state of the mother during egg-laying, although the issue has not been fully clarified (Coulson et al., 1982; Becker and Erdelen, 1988; Verboven et al., 2005). It cannot be excluded that frequent conflicts over the territory observed in gulls in conditions of high nesting density contribute to laying testosterone-rich eggs—as has been shown for other species of birds (Whittingham and Schwabl, 2002). At the same time, these broods make contact with their neighbors more often than in other parts of the colony, so the contacts between the broods and the maternal investments will have an equal impact on the development of chicks. Consequently, testing of the assumptions about the effect of social contacts on the development of chicks is hardly possible in the conditions of high nesting density.

For this work, we chose a colony of the black-headed gull that formed under unusually rare conditions for the studied area with few suitable places for nests. The mosaic, with little or no local clusters, distribution of such sites significantly restricted the nesting density (examples of colony sites in 2010 and in the typical 2009 in Figs. 1a and 1b, respectively). By comparing the developmental behavior of chicks from different broods, we tried to ascertain what effect the nesting density of the closest neighbors contributes to the early manifestation of aggression in chicks. The territorial behavior of parents and their care for the broods were observed in order to explain the reasons for the differences in the development of the behavior of the chicks, and monitoring of the growth of the chicks allowed us to show the total value of nesting with varying densities in this colony.

MATERIALS AND METHODS

Studies were conducted in a long-term colony of black-headed gulls (*Larus ridibundus*) on a floodplain site of a freshwater lake in southern West Siberia (53.751° N, 77.975° E) in 2010. Two groups of 93 and 110 nests were selected from the colony of approximately 1000 pairs. Owing to the high level of the spring flood in 2010, only clumps of vegetation from the previous year were above the water level, which served as the only possible places for nests. Compared with the preceding years, these clumps were located sparsely and relatively rarely but uniformly and did not hide the neighboring nests from each other (Figs. 1a, 1b).

The nests were mapped using a TD-10 theodolite; on the basis of the map, the average distance from the center of the nesting tray to the centers of nests of the closest neighbors (R_3) was calculated. In the colony studied, this value ranged from 0.40 to 4.05 m, with an average of 1.56 m. According to our data, in the studied area, R_3 varied from 0.25 to 4.62 m. The minimum distances between the nests were observed in the clumps of nesting substrate, up to several meters in size (e.g., muskrat (*Ondatra zibethicus*) last year den). In the years with a high water level and sparse places suitable for nesting, this parameter is, on average, 2.40 ± 0.01 m (80 nests, 2002–2003); in the normal years, it is 1.28 ± 0.09 m (414 nests, 2004–2007 and 2009). In the European part of the species' range, the optimum distance between the nearest nests is 60–90 cm (Glutz v. Blotzheim and Bauer, 1982). On the basis of these data, we considered the average $R_3 = 1.56$ m as an adequate border that conventionally divides the nests into sparse ones ($R_3 > 1.56$ m) and modal ones, i.e., arranged with a density that is modal for the species ($R_3 \leq 1.56$ m).

The nests with the surrounding area were enclosed with floating fences made of wood-fiber board and Styrofoam, in groups of 5–8 nests, which allowed us to observe the life of chicks at their nesting sites and their interaction with the neighbors.

The time of egg-laying was established directly, by registering the appearance of eggs in repeated visits to the colony, or by the date of hatching of the chicks, or, if neither of these methods could be used, by the so-called water sample based on the change in buoyancy of eggs during incubation (Mikhel'son et al., 1963). At the same time, a certain stage of egg buoyancy was timed to a certain stage of incubation. The maximum number of eggs observed in the nest was considered as the clutch size. A clutch was considered incomplete if 1 or 2 eggs were registered in it for three days after the laying of the first egg. If a clutch consisting of one or two eggs was found later, the data on its size were excluded from the analysis, as one of the eggs could have been lost (stolen or rolled out from the nest) and was not replaced by the female because of her start of incubation.

Fig. 1. Fragments of colonies of the black-headed gull in the years with various levels of flood water: (a) fragment of a black-headed gull colony that is typical for the studied area; the water level is low, the vegetation is dense and hides the nests. The gulls in the nests and nest marks are indicated with white arrows. (b) Fragment of a black-headed gull colony studied in 2010; the water level is high, the lack of sites suitable for nesting is evident, as is the deficiency of above-water vegetation, which serves as the material for making the nests, compared with the colony in Fig. 1a.

The fate of each chick was monitored by means of banding and repeat registrations of chicks every two days. The size characteristic of a chick was the traditional distance from the tip of the beak to the nape. As the size parameter of the chick we used traditional distance from the rear of skull to the tip of bill (head length, Becker and Erdelen, 1986), which was measured on the day of hatching and then every four days, and on day 15 after hatching.

Observations of the Behavior of Gulls

The territorial behavior of adult birds in the incubation period was studied by observing their reaction

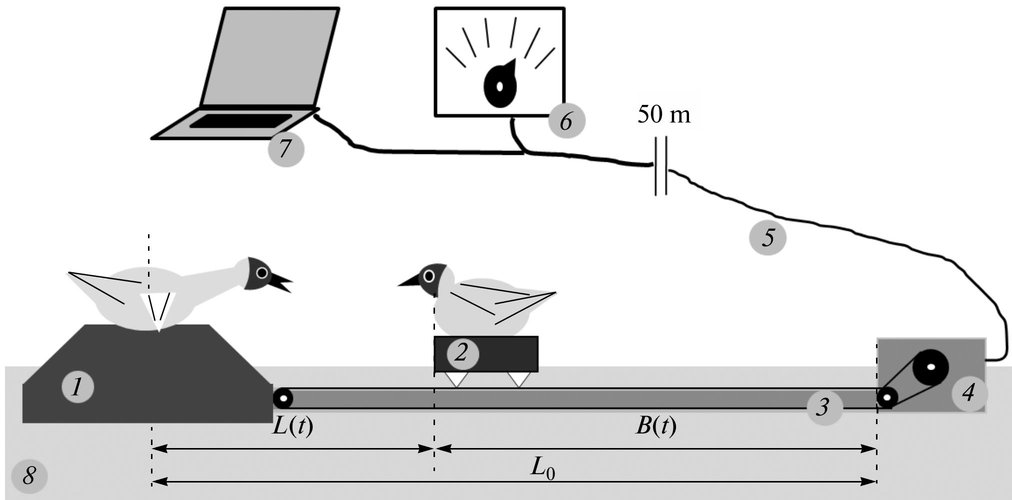

Fig. 2. Layout of the structure of a remote-controlled stuffed bird (“Intruder” installation): (*1*) nest of a black-headed gull with an incubating bird; (*2*) shifted float with the stuffed black-headed gull; (*3*) guideline of the float movements with a cable stretched on the rollers along the whole guideline; (*4*) base (the block that sets the dummy in motion and measures the distance that it passed); (*5*) transmitting cable (UTP, twisted pair) with a length of 50 m; (*6*) remote control for the dummy; (*7*) computer (laptop) registering the distance passed by the dummy; (L_0) distance from the chest of the dummy to the center of the nesting hollow; (t) time from the beginning of movement of the dummy; ($B(t)$) distance passed by the dummy from the initial point over the time t; ($L(t)$) distance between the chest of the dummy and the center of the nesting hollow at the moment of time t calculated by the formula $L(t) = L_0 - B(t)$.

to a remote-controlled, stuffed, male black-headed gull at the nesting territory; the installation was called the “Intruder” (Druzyaka and Zotov, 2006; Ryabko et al., 2013).

The method of presentation of a stuffed gull or conspecific individual is widely used for investigating the social behavior among various groups of animals (fish: Tinbergen, 1953; Faria et al., 2010; birds: Ryabitsev, 1993; Patricelli and Krakauer, 2010; mammals: Broadbooks, 1965), and especially in studying the breeding and territorial behavior of birds (Lack, 1940; Stout and Brass, 1969; Groothuis, 1989; Bright and Vaas, 2002; and many others). The unquestionable advantage of this method is the ability to manipulate the conditions: the time and place of presenting the stuffed bird and its posture and signals, including vocalizations (Bright and Vaas, 2002). Experiments with presentation of a stuffed animal or dummy usually allow researchers to distinguish the role of a certain releaser (De Schutter et al., 2001). A prominent disadvantage of the method is the lack of an adequate response from the stuffed bird or dummy.

The structure of the nesting area of the black-headed gull was studied in detail by Kharitonov (1982, and other the works of the author) by moving a neighboring nest into the protected zone around the nest of the bird being studied. A method that is similar in essence is attracting neighbors on roost sites within the protected area of the studied nest (Verboven et al., 2005). An analogue that is extensively applied in captivity to identify the particular features of the aggressive repertoire of the host of the territory is paired encounters of animals on the territory of one of them, which helps identify the aggressive repertoire of each, assess the degree of persistence in the defense of the territory, etc. (Koolhaas et al., 2013). However, to solve the task of comparing the behavior and structure of territories in different individuals, the method of moving the neighboring nest does not seem to be completely adequate in view of the following circumstance: gulls are characterized by the personification of contacts with the neighbors (Patterson, 1965; Pierotti and Annett, 1994; and others), and the response to the movement of the adjacent nest may largely reflect the personal relations of the studied bird with the neighbor, rather than the structure of the nesting territory protected from the rest of the population of the colony. Using a dummy or stuffed bird provides a standardized reaction to the same stimulus by different individuals. The latter induced us to choose the generally accepted method of a dummy presentation instead of moving the adjacent nest or observing the contacts with the neighbors in the colony. The particularities of the reaction to the stuffed bird versus a live bird are discussed at the end of the paper.

The function of the “Intruder” installation consists in the controlled movement of the stuffed gull or other object toward the floating nest of a black-headed gull and back, and measuring the distance between the dummy and the nest in the real-time mode. The installation consists of the following components: a base, a guideline, the float with the dummy, a 50-meter transmission cable, and a remote control (Fig. 2). The installation was connected with a computer to fix the distance traveled by the dummy. The remote control and computer were located at the observation post (OP), which had the form of a shelter on a floating tower with a height of 4 m at a distance of 30–45 m from the nest. The main part of the installation is the so-called base, which includes an electric motor and a reduction gear, a block controlling the direction and engine speed, a device measuring the number of rotations of the engine, a unit disconnecting the motor at extreme positions of the float, and a power supply (an accumulator with a rated voltage of 12 V and a capacity of 2.1 A h). The base is connected by the cable (UTP, twisted pair) to the remote control and the computer at the OP. The guideline has a length of 180 cm and is equipped with a movable cable stretched between the rollers at its ends; the rear roller is connected to the output shaft of the base reduction gear by a chain drive. The float covered with a reed mat is connected to the cable. On this mat, simulating a nest, a stuffed gull was placed. By means of the cable and the engine controlling block, the remote control allowed the observer from the OP to set the frequency and direction of rotation of the motor and thereby move the stuffed bird along the guideline at the correct speed. For the duration of the experiment, the front end of the guideline was secured close to the nest under the water surface, and the entire device was oriented so that the stuffed bird moved exactly to the center of the nesting hollow and from it. In the initial position (the rear edge of the float leaning against the base), the distance between the chest of the dummy and the edge of the nest was 150 cm. The system of floats and loads attached to the base and on the guideline hides the lower part of the base together with the chain gear under the surface of the water, as well as the guideline, cable, and rollers, masking the work of the installation. The device measuring the number of revolutions made by the motor was constructed on the basis of a ball computer mouse (Genius Mouse Dear V1.2) board, connecting the motor shaft to the shaft of one of the optical encoders of the mouse. The signal from the board was transmitted by the cable to the computer at the observation point. To process this signal and calculate the distance traveled by the dummy, the authors created the datchik 2.0 computer program. The result of operation of the program is a protocol of the dummy movements: a table of time values t from the beginning of the experiment and the distance values between the base and breast of the stuffed bird with the accuracy $B(t)$ up to 1 ms and 1 mm, respectively. Knowing the initial distance between the dummy and the center of the nesting hollow L_0, we calculated the distance between the dummy and the nesting hollow center, where the brooding bird is usually sitting, according to the formula $L(t) = L_0 - B(t)$. The behavior of the gulls during the experiment was recorded on a video camera. During the subsequent processing with the datchik 2.0 program, the protocol of movements of the dummy and the video recording were combined, thereby obtaining the distance between the dummy and the nest host at the moment of demonstration of a certain behavior.

Prior to the experiment, the dummy was set in the initial position and the behavior of the gulls was observed for five minutes. In all the experiments, the gull incubated the clutch calmly, without reacting to the stuffed bird, but manifested aggression or fear later on, when the dummy approached to a certain distance. On the basis of this behavior, we drew the conclusion that in all the experiments, when the stuffed bird was in the initial position, it was outside the boundaries of the protected territory. The experiment consisted in leading the dummy up to the nest and bringing it back to the original point. The reaction of the incubating gull was recorded using a Sony DCR SR45 video camera with a variable zoom up to 16×. At the same time, the second observer was watching through binoculars with a 12-fold zoom and recorded a commentary on the behavior of the bird and its neighbors, which were outside the field of vision of the video camera. The state and behavior of the incubating bird can vary depending on the visits of other gulls to its territory, the background sounds in the colony, the wind speed, and other quick successions of events. To reduce the impact of external circumstances on the behavior of the gulls, the stuffed bird was presented three times, alternating with pauses of three minutes.

To monitor the contacts between the chicks and neighbors, as well as to assess the parental care for the brood, the nest and the nesting territory were shot by a video camera next to them (Sony DCR SR45) without zooming for 90 min. To distinguish the chicks from different broods, before the start of the experiment, marks were applied to their beaks, which were made of a mixture of BF-6 medical adhesive and the following dyes: a solution of brilliant green (green), methylene blue (blue), or azure-eosin (red). This mixture hardens within one or two minutes as a thin colored film, which is easily removed at the end of the experiment without leaving traces on the beak. To register the age-related dynamics of the behavior of the chicks, we repeated the recording at the age of 2–4 days, 6–8 days, and 12–14 days.

Behavior Analysis

For adult birds, we used the generally accepted classification of intraspecific aggressive demonstrations of gulls (Moynihan, 1955; Tinbergen, 1960). We assessed the duration of the demonstrations, and, for short vocalizations (screeches), leaving of the nest, and attacking the dummy, and the number of demonstrations and the distance at which they were first manifested. For all demonstrations, their proportion of the entire time of dummy presentation was calculated. For screeches, we also calculated the intensity as the ratio of the number of vocalizations per one presentation to its time.

The boundary of the area registered using the "Intruder" was considered to be the distance of the first aggressive display or the distance of leaving the nest. The distance from the center of the nesting hollow to that point was called the reaction distance, and it was considered to be an approximate estimate of half of the medium cross size of the incubating bird's territory. For each parameter, the average value for the three presentations was calculated, which was then used as a characteristic of the territorial behavior of the bird. To evaluate the fearfulness of gulls in the territorial conflicts, we used the total number of nest leavings over the three presentations of the dummy. The inclination of birds to direct aggression was estimated by the total number of attacks on the dummy.

For the growing chicks, we recorded the visits to the nest and the area around it by neighboring broods, visits to the neighboring nests, arrivals and leaving of the nesting site or nest by the adult birds, and the beginning and end of feeding of chicks by parents. A contact with the neighbors was considered to be a meeting with a chick or an adult near the neighbor's nest. Aggressive manifestations, which were called attacks and included direct aggression and elements of aggressive demonstrations characteristic of this age, were registered in the behavior of the chicks during the contacts with the neighbors (Groothuis, 1989). The duration of such attacks was usually less than 1 s, so the quantitative characteristic of the aggressiveness of a chick was the number of attacks on neighbors over 1 hour of observations, on average. To evaluate the intensity of contacts of the brood with the neighbors, the average number of visits of all the chicks in the brood to the inhabited nests of neighbors in 1 h was counted, summing it with the number of visits to the brood by the neighbors.

To evaluate the parental care for the brood, we calculated the share of time of their presence at the nesting site to the total time of observation and the average number of feedings of chicks per hour of observation (feeding frequency), separately for the modal and sparse groups of nests.

Statistical Analyses

Data analysis was performed for relatively small samples, less than 30 trials in one group, which did not allow us to investigate them for compliance with the normal distribution. Therefore, the hypotheses about the differences in the parameter values of the behavior of adult birds and chicks between the modal and sparse groups was verified using the Mann–Whitney test ($U_{n,m}$, where U is the criterion value and n and m are the number of elements in the groups). Similarly, the same criterion was used to verify the hypothesis about the differences of reproductive parameters, the group samples of which were not normally distributed, such as the clutch size and the starting time of breeding of the couple (the time distribution peaks are usually shifted to the left). The hypothesis of the existence of an association between the variables, measured in the continuous or ordinal scale, were checked for a sampling combined for both groups, calculating the Spearman's correlation coefficient (S_n, where S is the criterion value and n is the volume of sample tested). The critical level of significance of the null hypothesis was considered the common threshold of 5% (Borovikov, 2003).

The Volume of Material

A total of 203 nests were mapped. The growth of 61 broods was followed, which contained 138 chicks, 24 nests were presented with the "Intruder," and the behavior of 18 broods (46 chicks) was recorded on a camera near their nests: 8 broods at the age of 2–4 days (19 chicks), 12 broods at 6–8 days old (21 chicks), and 15 broods at the age of 12–14 days (30 chicks).

RESULTS

The Territorial Behavior of Adult Birds

In the reactions of the gulls to the "Intruder," we observed the following: screeching at the stuffed bird, aggressive upright posture accompanied by screaming and without it, aggressive oblique posture accompanied by a long call and without it, leaving the nest, and direct attack of the dummy. Other demonstrations characteristic of land territorial conflicts of black-headed gulls, such as choking, forward position, pecking grass-pulling, and facing-away were not observed. The first demonstration addressed to the approaching dummy was always screeching if the bird had not left the nest before. The reaction distance was, on average, 0.82 ± 0.07 m (for 24 nests), and did not differ between the modal and sparse groups (Table 1). At the same time, the proportion of time spent on screeching and the intensity of screeching were greater in the sparse group of nests.

An analysis of the combined sample of nests (modal and sparse groups) showed that inhabitants of more crowded nests were more fearful and more often left the nest at the approach of the stuffed bird ($S_{24} = -0.44$, $P < 0.05$). The birds that did not leave the clutch or flew away only once (usually, at the first presentation of the dummy), nestled with different density, while the birds that left the clutches more than once inhabited only the modal group nests (Fig. 3).

Caring for the Young in Adult Gulls at Different Densities of Nesting

During the observation of a brood, one of the parents spent a relatively long time in or near the nest, keeping visual and audio contact with the brood (adult

Table 1. Differences in the reactions of gulls nesting with different densities to the "Intruder"

Parameter	Group of nests		Differences, Mann–Whitney test; level of significance
	modal, 14 nests	sparse, 10 nests	
Intensity of screeching (number of acts per 1 s)	0.34; 0.13, 0.67	0.84; 0.78, 0.94	2.37; $P = 0.02$
Percentage of screeching time, %	6.87; 2.70, 13.89	17.07; 15.56, 19.51	2.34; $P = 0.02$
Distance of the first screech, cm	73.5; 64.0, 96.0	78.5; 61.7, 126.7	0.14; $P = 0.88$

The median, upper, and lower quartiles are given.

gulls often sat on fences located 1–2 meters from the nest, which gave them an excellent view of both their own and neighboring territories). Both parents simultaneously were near the nest very rarely and for no longer than a few seconds. On average, one bird was present near the nest or in it 33.6 ± 4.5 min over the 90-minute period of observations. The duration of their presence decreased with the age of the chicks ($S_{35} = -0.44$, $P < 0.05$, Fig. 4). With two- to four-day-old chicks, the parent spent 69.2% of the entire time of its presence in the field of view of the camera in the nest, warming the brood. For 6- to 8- and 12- to 14-day-old chicks, this figure decreased to 13.0 and 8.5%, respectively, and this time was spent mostly on feeding the brood. When in the nest or close to it, the parent usually attacked the neighbors that trespassed into the nesting site. Neither the frequency of feeding the brood nor the time of the presence of parents in the nest differed between the modal and sparse groups of nests, independently of the age of the chicks.

Age Dynamics of the Social Behavior of Chicks, Depending on the Density of Nesting

The contact of chicks with neighbors, as well as aggressive skirmishes between them, were rare events in the life of chicks. In 46% of observations, no such contacts were registered at all, in 23%, only one contact occurred, and in the remaining 31%, meetings with neighbors took place several times during the observation. Aggressive encounters among neighbors occurred in 29% of observations, of which 86% were fights between the chicks, and only 14% were adult attacks on chicks. As the chicks grew older, their contacts with neighbors and aggression toward them became more frequent, both among the sparsely nesting gulls and among the modal group (Figs. 5a, 5b). Nesting with the modal density promoted a greater frequency of meeting of chicks from neighboring broods: they started earlier than in the broods from the sparse group (Fig. 5a). On the other hand, chicks from the nests located sparsely more often engaged in

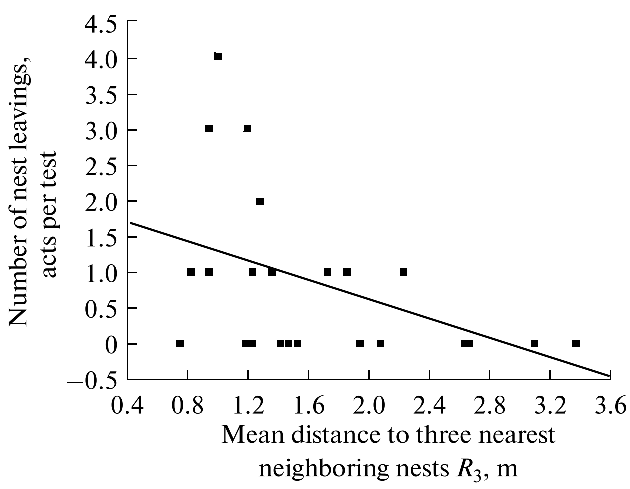

Fig. 3. Correlation between the number of nest leavings by the gull during the movements of the "Intruder" and the mean distance to three nearest neighboring nests.

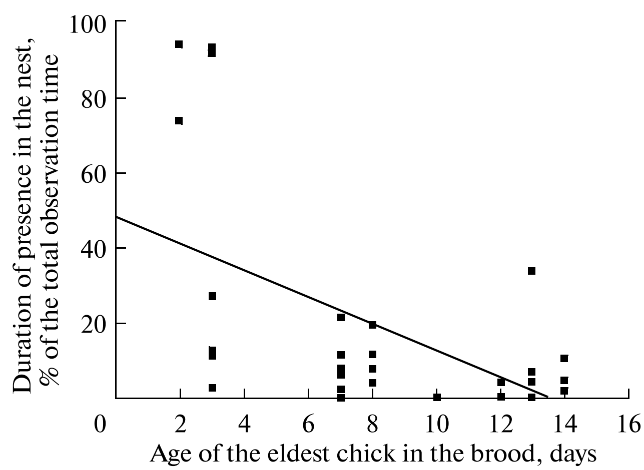

Fig. 4. Correlation between the duration of parental presence in the nest and the age of the chicks.

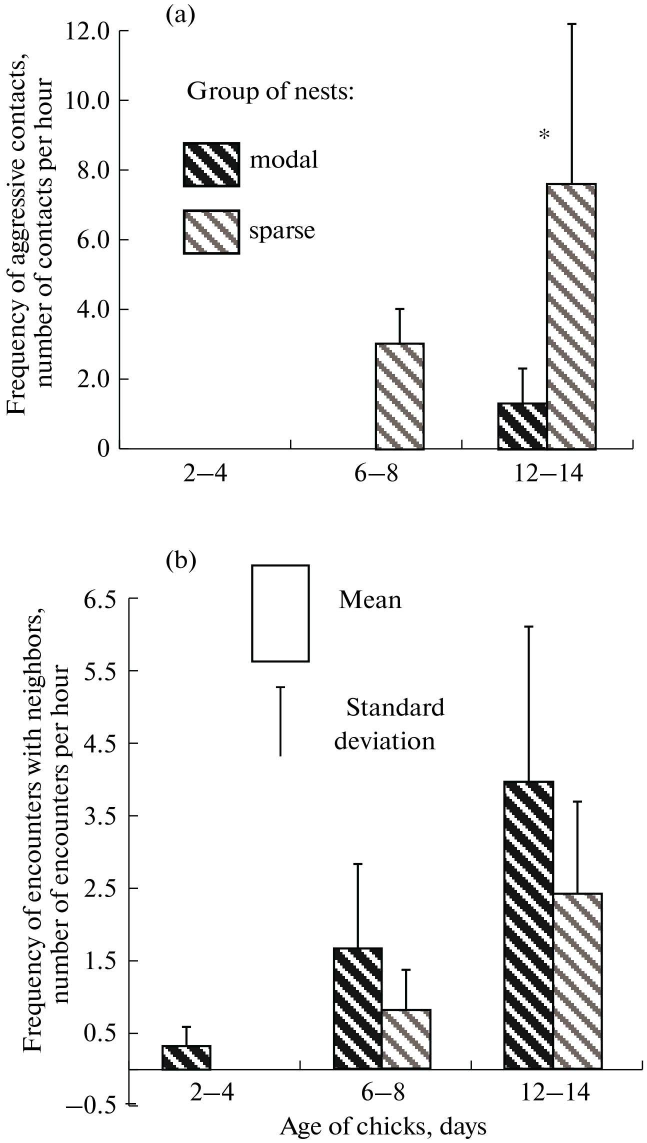

Fig. 5. Age dynamics of the behavior of chicks: (a) frequency of aggressive contacts, (b) frequency of encounters with neighbors; (*) reliable differences between the groups.

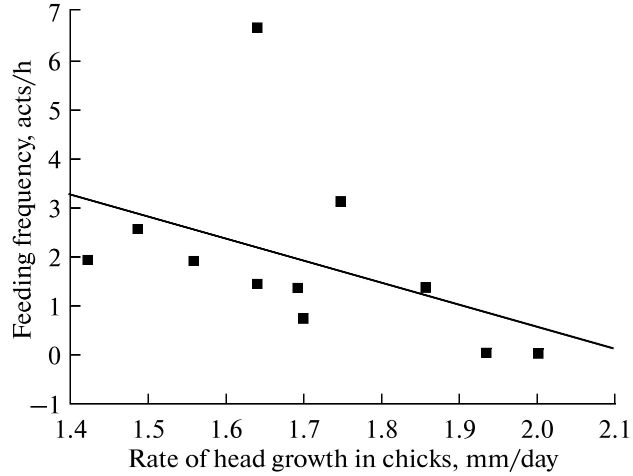

Fig. 6. Association between the frequency of feeding of 6- to 8-day-old chicks by parents and the average brood rate of head growth.

aggressive interactions with the neighbors, beginning to do so at 6–8 days of age, whereas in the modal group, fights between the chicks started only at 12–14 days of age and occurred less frequently than in the sparse group ($U_{4,\,8} = 4$, $P < 0.05$; Fig. 5b).

Influence of Parental Care and Nesting Density of the Neighbors on the Breeding Output

The clutches in which at least one chick grew to the start of observations were predominantly complete (three clutches of two eggs were registered in the nests attributed to the modal group and no incomplete clutches were found in the sparse group). The starting date of the egg-laying in these nests did not differ between experimental groups either ($U_{9,\,11} = 0.91$, $P = 0.36$). In general, among all the investigated nests, neither the starting date of egg-laying nor the size of the clutch showed any reliably differences between the modal and sparse groups (Table 2).

The dynamics of the head growth in the black-headed gull in the first 8–9 days after hatching corresponds to the linear law, and the average daily growth at this time is maximum (Druzyaka et al., 2005). In 6- to 8-day-old chicks, the increase in the head length was inversely related to the frequency of their feeding ($S_{12} = -0.66$, $P < 0.05$, Fig. 6).

By the 15th day of their life, the growth conditions associated with the nesting density had a significant impact on the growth of the skeleton: at this age, the length of the head in the older chicks of the brood correlated directly with the average distance to the next three neighboring nests ($S_{19} = 0.47$, $P < 0.05$, Fig. 7). This dependence was observed owing to the broods that were complete (3 chicks) by the time of hatching ($S_{12} = 0.65$, $P < 0.05$), whereas the contribution of the incomplete (1 and 2 chicks) broods was not significant ($S_7 = 0.18$, n.s.), possibly due to the small number of the latter (7 broods).

DISCUSSION

The reactions of gulls to the presentation of a remotely controlled stuffed bird consisted of a limited number of demonstrations, compared with the repertoire of territorial conflicts described in the literature. The “dialogues” of the gulls with the dummy did not contain the forms of behavior that gulls use to demonstrate their attitude to the demonstrations of the opponent—choking and facing-away (demonstration of appeasement (Tinbergen, 1960)). Apparently, the gulls

Table 2. Differences in the terms of egg-laying and clutch sizes in the modal and sparse groups of nests

Parameter	Group of nests		Differences, Mann–Whitney test; level of significance
	modal, 68 clutches	sparse, 48 clutches	
Date of the start of egg-laying	7.05; 11 [8, 14]	7.05; 11 [9, 13]	0.09; $P = 0.93$
Clutch size ($x \pm s_x$)	2.8 ± 0.1	2.7 ± 0.1	1.39; $P = 0.32$

For the date of the start of egg-laying, the calendar date (median) is given; the number of days from the date of laying of the first egg in the colony (median [upper, lower quartiles]).
(x) Mean and (s_x) standard error of mean.

did not demonstrate grass-pulling (simulated fights (ib.)), as only their nests could serve as a source of vegetation for this demonstration, destroying which in the conditions of lack of materials would be very costly. The forward posture usually follows the oblique posture in conflicts with live birds (Groothuis, 1992); in our observations, the oblique posture was common, whereas the forward one was absent. This is not easily explained by the existing data, but supposedly, the finished sequence of the oblique–forward posture requires a high level of irritation of the gull, which was not reached by the stimulation with the stuffed bird. The reaction of almost half of the birds to the dummy ended in one or several leavings of the nest and, in a large part of the rest, in attacks and attempts to throw

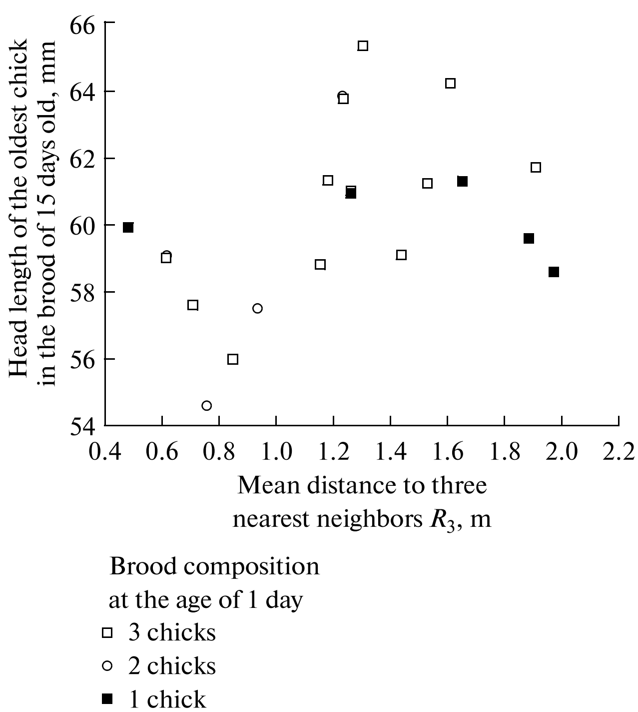

Fig. 7. Association between the head length of 15-day-old chicks and the distance to three nearest neighboring nests.

the stuffed bird from the float. A stuffed bird differs from a live one primarily in that it does not alter its behavior in response to the demonstration of the nest's owner. This and other details (immobile part of the stuffed bird, movement of parts of the installation) appear to have induced some gulls to perceive the dummy as an alien and possibly dangerous thing, in response to which they flew from the clutch. However, the stuffed bird possessed the characteristic gull looks—the breeding attire, including the complex "white ring of periorbital feathers—red fleshy periorbital ring—brown iris—black pupil," the second and third components of which are a contact sign of an individual of its own species in gulls (Smith, 1966). Apparently, these two groups of signs of the stuffed bird induced two different motivations in the gulls: the characteristic features of the appearance of an adult gull encouraged the birds to respond with stereotypical territorial demonstrations, while the signs of an inanimate object caused a reaction of fear and escape. It is likely that the choice in favor of escape indicates the extensive experience of conflicts with live gulls, while the stubborn demonstrative behavior shows a high level of aggression and absence of such experience. According to our data, adult inhabitants of widely spaced nests behaved more aggressively toward the dummy, screeching at it longer and more intensely. As the stuffed gull moved, the gulls accumulated experience of observing it, which could be compared with the experience of real territorial conflicts, and the signs that distinguish the stuffed bird from a live one had to become more prominent. However, the birds from the sparse group screeched more intensely at the stuffed bird as it approached. The escape reaction was less common in them. The high aggressiveness of sparsely nesting gulls is usually explained by their young age and lack of nesting experience, which entails excessive efforts in the defense of the nesting sites (Burger, 1984; Becker and Erdelen, 1986; Bukacinska and Bukacinski, 1993); however, the age of the gulls in the latter paper was determined indirectly, by the size of the eggs and clutches, and only in a small number of birds was it determined directly, by the presence of elements of juvenile attire. It was shown for the European herring gull that sparse nesting is not always a sign of young individuals; large breeding territories or even sparse nesting can be characteristic of the oldest and most experienced birds (Burger and Lesser, 1980; Becker and Erdelen, 1986). In another large gull, the great black-backed gull (*Larus marinus*), no connection was found between the age and the density of nesting (Butler and Trivelpiece, 1981). In the black-headed gull, there is no unambiguous connection between the nesting density and the age, as during the formation of a colony, young birds can take either the most preferred sites, increasing the density of nesting to the limit values, or remote sites, less preferred by older birds, where the density is low (Kharitonov, 1983). In most birds, including the gulls, young females typically nest later (Coulson and White, 1960; Viksne, 1968; Parsons, 1975; Hatchwell, 1991), mainly due to the lack of experience and age-related immaturity of the reproductive system (Moreno, 1998; Gonzalez-Solis et al., 2004), and often lay an incomplete clutch (Coulson and Porter, 1985; Becker and Erdelen, 1986; and others). However, we found no differences between the terms of reproduction and the clutch size in the sparse and modal groups that could attest to the selective nesting of young birds with a lower nesting density. It is likely that this was partly due to the formation of colonies in the conditions of a high spring flood, as in this period, flooding and destruction of nests by the wind were frequent. This could have caused intense migration of gulls between parts of the colony, in particular, the movement of older birds into the areas occupied by the younger ones and vice versa.

As a result, sparsely nesting birds were characterized by greater territorial aggressiveness and lower fearfulness, but data on the number and timing of laying of their eggs do not allow us to consider these differences in behavior age-specific. Sparse nesting owing directly to the high aggressiveness was not confirmed by our data either: there was no difference in the distances of response to the "Intruder" between the groups. However, during the formation of the colony, the differences in territorial aggression could be more pronounced. It is also possible that the simultaneous sparse nesting, high aggressiveness, and inability to distinguish the dummy from a live gull is the result of more insufficient nesting experience, which may not be closely correlated with age, for example, due to the refusal of some of the birds to reproduce. A similar picture was shown for the common tern, in which the mass of the laid eggs, the rate of growth, and survival of chicks were more closely associated with the individual number of reproductive seasons (experience) of the parents, rather than the calendar age (Wendeln and Becker, 1999). Evidently, in our case, a more detailed study of the link between the territorial behavior, nesting density, and individual traits of birds, which was touched upon in this paper, is required.

On average, during the feeding of the chicks, one of the gulls was present near the nest or in it for about a third of the entire observation period. At 2–4 days of age, the duration of the presence of a parent was the highest, and for most of it, the bird was in the nest and warmed up the brood. By the 7th day, thermoregulation in the chicks of charadriiformes improves, while the yolk bag resources end (Galbraith, 1988), so the major form of parental care for the offspring becomes supplying them with food. However, at the same age, chicks begin to leave the nest and enter into conflicts with neighbors. Protection against the negative consequences of such conflicts requires the presence of a parent near the nest. According to our data, in the chicks of the parents that were near the nest more often during the entire period of observation of the week-old chicks, the average daily growth of the head length was lower. For seabirds, primarily fish-eating ones, both the duration and the frequency of flights for food are indicators of parental care, as they are closely related to the amount of food procured and the growth of the chicks (Chaurand and Weimerskirch, 1994; Castillo-Guerrero and Mellink, 2011; Dänhardt et al., 2011), but the correlation between the frequency of foraging flights and the quantity of food procured was not confirmed for the terns nesting near internal water bodies (Sirdevan and Quinn, 1997; Paillison et al., 2007). In the conditions of the researched colony, the smaller frequency of visits to brood by the parents was accompanied by their longer absence. This, probably, had a positive impact on the length of foraging and, ultimately, on the amount of food brought to the brood, which, in turn, could be important for the growth of chicks more than a week old. Therefore, the lengthy and frequent presence of parents with broods older than one week is not an indication of the quality of parental care, as it is not accompanied by a proportional increase in the growth rate of the chicks. The chicks from the nests distributed more sparsely grew larger, especially in the couples that had complete clutches and were, according to the literature, older and more experienced parents (Coulson and Porter, 1985; Gonzalez-Solis et al., 2004). Apparently, sparse nesting allowed the more experienced parents to spend less effort on defending the brood from neighbors, and to procure food instead, as the chicks of such gulls rarely had contact with other broods and did not need to be protected from them so often. In the colony studied, this behavior of parents proved to be more effective.

Aggressive behavior of the chicks from the sparse group of nests was manifested earlier than in the ones from the modal group, already at one week of age, and when growing up, the former entered into conflict significantly more often than their peers from the modal group. At the same time, contacts with the chicks from neighboring broods were consistently more common in the modal group, apparently due to the smaller distance between the nests. In the conditions of an aviary, it was shown that, in the black-headed gull, direct aggression precedes the maturation of antagonistic demonstrations and is manifested precisely at one week of age (Groothuis, 1989). The antagonistic demonstrations in the broods isolated from their neighbors at a later age developed faster and more fully when the chicks were surrounded by a larger number of other chicks, or in contact with more developed gulls, brought over from the group of broods that constantly communicated with each other (Groothuis and van Mulekom, 1991). But, unlike the cages of the aviary, where all the chicks have contact with each other with approximately identical frequency, in natural conditions, for the chick to enter into conflict, it has to get to the neighboring territory or nest, i.e., contacts with neighbors with a frequency that is at least equal to the frequency of contacts in the aviary should be a mandatory condition for developing the effect. Since contacts among the quickly developing chicks were less frequent, their direct contribution to the manifestation of aggression is unlikely. In all probability, in the conditions of low or normal nesting density, episodic interbrood contacts at the early stages of development of chicks are insufficient to launch a program of maturation of aggressive behavior according to the principle of behavioral "challenge." Early and intense development of aggressive behavior in the chicks from the sparse group of nests inhabited by more aggressive adult birds testify in favor of the dominant role of the maternal effect. Figuring out the real contribution of maternal hormonal investments to the formation of aggressive reactions in the offspring is a matter for future research, but it is already possible to suggest that the early development of aggression in chicks liberates the parental resources for effective provision of food, without distracting them for the defense of the brood from the neighbors. It is considered that laying testosterone-rich eggs in the colonial gulls is one way to compensate for the unfavorable living conditions of the brood or a single chick by the mother's organism (Eising et al., 2001). The positive effect of yolk steroids is not always observed; some experimentation showed a negative impact of a high testosterone content in the yolk (Rubbolini et al., 2006) or blood of the chick (Ros, 1999). Nonetheless, according to our data, if in nature maternal hormonal investments take place, in the conditions of the shortage of nesting shelters and low nesting density, they can create substantial benefits for the offspring at the early stages of development through adaptive changes of behavior.

On the whole, we can assumed that, in nature, the early development of aggressive behavior skills in the black-headed gull chicks creates significant advantages over more passive peers in the extreme conditions of nesting. Despite the developed system of social relations in the gull colonies, in the conditions of relatively rare contacts between broods, the main role in the development of behavior is played by parental investments. Additional experiments are required to understand the role of interbrood relationships in this species in the formation of stereotypical behavioral demonstrations in the conditions of breeding colonies.

ACKNOWLEDGMENTS

The authors thank A.Yu. Zotov for the thorough assistance in the field collection of the material, D.A. Weiner and A.Yu. Generozov for help in designing and developing the "Intruder" installation, Zh.I. Reznikova for valuable comments and editing of the manuscript, and S.P. Kharitonov for valuable advice in understanding the results obtained.

The study was supported by the Russian Science Foundation (grant 14-14-00603) through the Institute of Systematics and Ecology of Animals SibRAS.

REFERENCES

Becker, P.H. and Erdelen, M., Egg size in Herring Gulls (*Larus argentatus*) on Mellum Island, North Sea, West Germany: the influence of nest vegetation, nest density, and colony development, *Colonial Waterbirds*, 1986, vol. 9, pp. 68–80.

Borovikov, V.P., *Statistica. Iskusstvo analiza dannykh na komp'yutere* (STATISTICA: The Art of Computer Data Analysis), St. Petersburg: Piter, 2003.

Bright, A. and Vaas, J.R., Effects of bill pigmentation and UV reflectance during territory establishment in Blackbirds, *Anim. Behav.*, 2002, vol. 64, pp. 207–213.

Broadbooks, H., Ecology and distribution of the pikas of the Washington and Alaska, *Am. Midl. Nat.*, 1965, vol. 73, no. 2, pp. 299–335.

Bukacinska, M. and Bukacinski, D., The effect of habitat structure and density of nests on territory size and territorial behaviour in the Black-headed Gull (*Larus ridibundus* L.), *Ethology*, 1993, vol. 94, pp. 306–316.

Burger, J., Pattern, mechanism, and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*), *Ornithol. Monogr.*, 1984, vol. 34, pp. 1–106.

Burger, J. and Lesser, F., Nest site selection in expanding population of Herring Gull, *Larus argentatus, J. Field Ornithol.*, 1980, vol. 45, pp. 270–280.

Butler, R.G. and Janes-Butler, S., Territoriality and behavioral correlates of reproductive success of Great Black-backed Gulls, *Auk*, 1982, vol. 99, pp. 58–66.

Butler, R.G. and Trivelpiece, W., Nest spacing, reproductive success, and behavior of the great Black-backed Gull (*Larus marinus*), *Auk*, 1981, vol. 98, pp. 99–107.

Castillo-Guerrero, J.A. and Mellink, E., Occasional intersex differences in diet and foraging behavior of the Blue-footed Booby: maximizing chick rearing in a variable environment?, *J. Ornithol.*, 2011, vol. 152, pp. 269–277.

Chaurand, T. and Weimerskirch, H., The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird, *J. Anim. Ecol.*, 1994, vol. 63, pp. 275–282.

Coulson, J.C. and Porter, J.M., Reproductive strategies of the Kittywake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality, *Ibis*, 1985, vol. 127, pp. 450–466.

Coulson, J.C. and White, E., The effect of age and nest density on the time of breeding of the Kittiwake, *Ibis*, 1960, vol. 102, pp. 71–84.

Coulson, J.C., Duncan, N., and Thomas, C., Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in the size and density of the colony, *J. Anim. Ecol.*, 1982, vol. 51, pp. 346–349.

Dänhardt, A., Fresemann, T., and Becker, P.H., To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea, *J. Ornithol.*, 2011, vol. 152, pp. 347–357.

De Schutter, G., Theraulaz, G., and Deneubourg, J.-L., Animal–robots collective intelligence, *Ann. Math. Artif. Intell.*, 2001, vol. 31, pp. 223–238.

Druzyaka, A.V. and Zotov, A.Yu., Coloniality in birds: new method of territory size measurement enables to enrich concept of its biological functions, in *The 11th International Behavioural Ecology Congress: Book of Abstracts*, Tours (France): CNRS, 2006, p. 183.

Druzyaka, A.V., Vainer, D.A., Zotov, A.Yu., Potapov, M.A., and Evsikov, V.I., The choice of parental strategy in larids depends on the success in territorial competition, *Dokl. Biol. Sci.*, 2005, vol. 404, no. 6, pp. 846–849.

Eising, C.M., Eikenaar, C., Schwabl, H., and Groothuis, T.G.G., Maternal androgens in Black-headed Gull (*Larus ridibundus*) eggs: consequences for chick development, *Proc. Roy. Soc. London B*, 2001, vol. 268, pp. 839–846.

Faria, J.J., Dyer, J.R.G., Clément, R.O., Couzin, I.D., Holt, N., et al., A novel method for investigating the collective behaviour of fish: introducing "Robofish," *Behav. Ecol. Sociobiol.*, 2010, vol. 64, pp. 1211–1218.

Galbraith, H., Effects of egg size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks, *J. Zool.* (London), 1988, vol. 214, pp. 383–398.

Glutz von Blotzheimm, U.N. and Bauer, K.M., *Handbuch der Vögel Mitteleuropas*, vol. 8/I: *Charadriiformes III*, Wiesbaden: Akademische Verlagsgesellschaft, 1982.

González-Solís, J., Becker, P.H., Jover, L., and Ruiz, X., Individual changes underlie age-specific pattern of laying date and egg-size in female Common Tern (*Sterna hirundo*), *J. Ornithol.*, 2004, vol. 145, pp. 129–136.

Groothuis, T.G.G., On the ontogeny of display behaviour in the Black-headed Gull: 1. The gradual emergence of the adult forms, *Behaviour*, 1989, vol. 109, pp. 76–123.

Groothuis, T.G.G., The influence of social experience on the development and fixation of the form of displays in the Black-headed Gull, *Anim. Behav.*, 1992, vol. 43, pp. 1–14.

Groothuis, T.G.G. and Meeuwissen, G., The influence of testosterone on the development and fixation of the form of displays in two age classes of young Black-headed Gulls, *Anim. Behav.*, 1992, vol. 43, pp. 189–208.

Groothuis, T.G.G. and Schwabl, H., Determinants of within- and among-clutch variation in levels of maternal hormones in Black-headed Gull eggs, *Funct. Ecol.*, 2002, vol. 16, pp. 281–289.

Groothuis, T.G.G. and van Mulecom, L., The influence of social experience on the ontogenetic change in the relation between aggression, fear and display behaviour in Black-headed Gulls, *Anim. Behav.*, 1991, vol. 42, pp. 873–881.

Hatchwell, B.J., An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*), *J. Anim. Ecol.*, 1991, vol. 60, pp. 721–736.

Hunt, G.L. and Hunt, M.W., Aspects of the reproductive ecology of the Western Gull, *Larus occidentalis*: the importance of nest-spacing, *Auk*, 1975, vol. 92, pp. 270–279.

Hunt, G.L. and Hunt, M.W., Gull chick survival: the significance of growth rates, timing of breeding and territory size, *Ecology*, 1976, vol. 57 pp. 62–75.

Kharitonov, S.P., Colony structure and migration dynamics of Black-headed Gulls (*Larus ridibundus*) during the nesting season, *Zool. Zh.*, 1983, vol. 62, no. 7, pp. 1066–1076.

Kharitonov, S.P., Regulation of nesting density in the Black-headed Gull colonies, *Biol. Nauki*, 1982, no. 10, pp. 28–34.

Koolhaas, J.M., Coppens, C.M., de Boer, S.F., Buwalda, B., Meerlo, P., and Timmermans, P.J.A., The resident–intruder paradigm: a standardized test for aggression, violence and social stress, *J. Visual. Exp.*, 2013, vol. 77, pp. 43–67.

Lack, D., Pair-formation in birds, *The Condor*, 1940, vol. 42, pp. 269–287.

Mikhelson, Kh.A., Leinsh, G.T., Klimpinsh, V.A., and Liepa, V.K., Analysis of population dynamic of some ducks in Latvia using total ringing of incubating females and ducklings, *Ornitologiya*, 1963, no. 6, pp. 280–292.

Moreno, J., The determination of seasonal declines in breeding success in seabirds, *Etología*, 1998, vol. 6, pp. 17–31.

Moynihan, M., Some aspects of reproductive behaviour in the Black-headed Gull (*Larus ridibundus ridibundus* L.) and related species, *Behaviour*, 1955, Suppl. 4, pp. 1–201.

Muller, W., Dijkstra, C., and Groothuis, T.G., Maternal yolk androgens stimulate territorial behaviour in Black-headed Gull chicks, *Biol. Lett.*, 2009, vol. 5, pp. 586–588.

Paillison, J., Reeber, S., Carpentier, A., and Marion, L., Reproductive parameters in relation to food supply in the Whiskered Tern (*Chlidonias hybrida*), *J. Ornithol.*, 2007, vol. 148, pp. 69–77.

Parsons, J., Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success, *J. Anim. Ecol.*, 1975, vol. 44, no. 2, pp. 553–573.

Patricelli, G.L. and Krakauer, A.H., Tactical allocation of display effort reduces trade-offs among multiple sexual signals in Greater Sage-Grouse: an experiment with a robotic female, *Behav. Ecol.*, 2010, vol. 21, pp. 97–106.

Patterson, I.J., Timing and spacing of broods of Black-headed Gull (*Larus ridibundus*), *Ibis*, 1965, vol. 107, pp. 433–460.

Pierotti, R. and Annett, C., Patterns of aggression in gulls: asymmetries and tactics in different social categories, *The Condor*, 1994, vol. 96, pp. 590–599.

Ros, A.F.H., Effects of testosterone on growth, plumage pigmentation, and mortality in Black-headed Gull chicks, *Ibis*, 1999, vol. 141, pp. 451–459.

Ros, A.F.H., Dieleman, S.J., and Groothuis, T.G.G., Social stimuli, testosterone and aggression in gull chicks: support for the challenge hypothesis, *Hormones and Behavior,* 2002, vol. 41, pp. 334–342.

Rubbolini, D., Romano, M., Martinelli, R., and Saino, N., Effects of elevated yolk testosterone levels on survival, growth and immunity of male and female Yellow-legged

Gull chicks, *Behav. Ecol. Sociobiol.*, 2006, vol. 59, pp. 344–352.

Ryabitsev, V.K., *Territorial'nye otnosheniya i dinamika soobshchestv ptits v Subarktike* (Territorial Relationships and Community Dynamics of Birds in the Subarctic), Yekaterinburg: Nauka, 1993.

Ryabko, B., Reznikova, Z., Druzyaka, A., and Panteleeva, S., Using Kolmogorov complexity for studying biological texts, *Theor. Comput. Syst.*, 2013, vol. 52, no. 1, pp. 133–147.

Sirdevan, J.E. and Quinn, J.S., Foraging patterns of Caspian Terns (*Sterna caspia*) determined using radio-telemetry, *Colonial Waterbirds*, 1997, vol. 20, pp. 429–435.

Smith, N.G., Evolution of some Arctic Gulls (*Larus*): an experimental study of isolating mechanisms, *Ornithol. Monogr.*, 1966, no. 4, pp. 1–99.

Stout, J.F. and Brass, M.E., Aggressive communication by *Larus glaucescens*: 2. Visual communication, *Behaviour*, 1969, vol. 34, pp. 42–54.

Tinbergen, N., *Social Behaviour in Animals, with Special Reference to Vertebrates*, Oxford, England: Wiley, 1953.

Tinbergen, N., The evolution of behaviour in Gulls, *Sci. Am.*, 1960, vol. 203, no. 6, pp. 118–130.

Verboven, N., Evans, N.P., D'Alba, L., Nager, R.G., Blount, J.D., et al., Intra-specific interactions influence egg composition in the Lesser Black-backed Gull (*Larus fuscus*), *Behav. Ecol. Sociobiol.*, 2005, vol. 57, pp. 357–365.

Viksne, Ya.A., Nesting site fidelity, dispersal of the young, and formation of new colonies in the Back-headed Gull, in *Migratsii zhivotnykh* (Animal Migrations), Leningrad: Nauka, no. 5, pp. 116–133.

Wendeln, H. and Becker, P.H., Effects of parental quality and effort on the reproduction of Common Terns, *J. Anim. Ecol.*, 1999, vol. 68, pp. 205–214.

Whittingham, L.A. and Schwabl, H., Maternal testosterone in tree swallow eggs varies with female aggression, *Anim. Behav.*, 2002, vol. 63, pp. 63–67.

Wingfield, J.C., Hegne, R.E., Dufty, A.M., and Ball, G.F., The challenge hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies, *Am. Nat.*, 1990, vol. 136, pp. 829–846.

Zykova, L.Yu. and Panov, E.N., Effect of nesting population size and density on breeding success in the Caspian Gull, *Larus argentatus cachinnans, Zool. Zh.*, 1983, vol. 52, no. 10, pp. 1533–1540.

Translated by N. Smolina