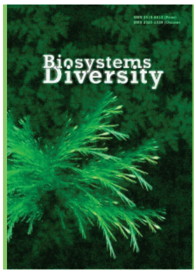

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Ecology of Laridae under conditions of unstable hydrological regime: colony sizes and synchronization of reproduction

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The problem of criteria for distinguishing colonies from similar socio-demographic structures (mainly in terms of nesting density) is highly relevant and has remained in the focus of attention of ornithologists for a long time. The synchronization of reproduction in a colony is one of the criteria which require special development. Based on particular works (1972–2005), I present synchronization of the reproduction of gulls in colonies of different sizes. In contrast to previous studies, this paper uses a specially developed Index of Synchronization of Bird Breeding (I_{sr}) to study this phenomenon, making it relatively easy to determine its level. The index distinguishes between different species of birds of this group: 75.7% (white-winged black tern) and 97.6% (black-headed gull) of the total variability of synchronization of breeding birds in colonies. Frequent failure of nesting attempts often causes repeated (compensatory) reproduction, which in the case of a mass manifestation significantly reduces the synchronization of the nesting period in colonies and thus significantly reduces this indicator. It is proved that a higher synchronization of reproduction characterizes small colonies (up to 50 nests). In all species of gulls, the beginning of reproduction in different colonies differs in terms of the appearance of the first eggs by 1–10 days and at the beginning of mass egg-laying – by 1–18 days. To the same extent, they differ in the timing of the hatching of eggs. In small colonies, the total egg-laying period is shorter by 34.9–49.7% compared to larger colonies. My observations show that large colonies are formed by the nesting of several small colonies on one plot. This phenomenon is noticeable during periods of mass re-nesting of birds after a high loss of nests (up to 69.5% or more) because of severe flooding. Differences in the breeding periods of colonies that differ in size appear when several small colonies with different breeding periods of birds are combined into one larger colony. This phenomenon is well detected in the formation of several sub-colonies and in the differences in the timing of reproduction of different parts of a large colony.

Keywords: coastal birds; water level; size of nesting groups; nesting density; egg-laying in groups.

Introduction

For shorebirds and waterfowl of the mountainous regions and adjacent territories of Eastern Siberia, the dynamics of hydrological regime during the nesting period is of great importance. This is mainly due to the pronounced mountain-floodplain water regime of a significant part of this region. It is characterized by high but short spring floods and several intense summer floods (from two to seven), sometimes reaching a catastrophic scale. The main reasons for this phenomenon are the intense melting of snowfields in the mountains, combined with heavy precipitation in summer. Also, a similar result is caused by prolonged (up to three or four days) or heavy rainfall (after two or three hours, a monthly or more precipitation rate falls) covering a large area (Melnikov, 2019). In large lake systems, overtaking phenomena also play a critical role, when the water level rises by 20 cm or more from the windward side (Fialkov, 1983; Imethenov, 1994; Melnikov, 2019).

Severe and frequent rises in the water level during the breeding season, leading to a large loss of nests, determine many ecological features of species that use the biotopes of river floodplains for breeding. This applies primarily to colonial bird species that form large nesting clusters in small areas. In the case of an unsuccessful choice of habitat, the entire colony often fails, which can significantly affect the reproductive success of the nesting group (population) of birds in this area. The failure of the breeing attempt reaches 69.7% or more (Melnikov, 1983). Finding out the level of adaptation of birds to exist in such extreme conditions is an essential task of population and evolutionary ecology (Schwartz, 1969; Georgievsky, 1989; Dinevich et al., 2003; Chaplygina et al., 2019).

Previously, it was shown that the synchronization of reproduction of colonial birds is an evolutionary acquisition that contributes to the complete realization of the reproductive potential of the population (Darling, 1938; Nelson, 1967; Emlen & Demong, 1975; Parsons, 1975; Viksne & Janaus, 1980). However, this problem has not yet been completely solved. Some works criticize this position (Orians, 1961). Besides, the formation of reproduction synchronization remains undisclosed since the high concentration of individuals within a limited space is the trigger of this process (Darling, 1938), which does not stand up to reasoned criticism (Orians, 1961). In the late 20th – early 21st centuries, new hypotheses and proofs emerged, revealing the essence of this phenomenon (Melnikov, 2003). These theories require the intensification of research on the ecology of colonial bird species in this direction. The solution to these problems is complicated, since, for a long time, there were no methods for accurately estimating the level of synchronization of reproduction in birds of different species. Today, a special index (I_{SR}) has been developed to determine its magnitude in any bird colony (Melnikov, 2020). Therefore, we can proceed to a more detailed study of this phenomenon of colonial birds. Our paper is devoted to examining this issue with the example of Laridae, as one of the principal families of truly colonial species (Panov, 1983).

Material and methods

The work was carried out in the Selenga River Delta (1972–2005) and covers two 11-year climatic cycles, which differ in the level of water content in this area. The lowest water level is typical for 1972–1982, and at this time, the delta flooding returned to the state which was typical for it before the construction of the Irkutsk hydroelectric power station and the regulation of runoff from Lake Baikal. During this period, new biotopes developed for birds that had not previously been recorded there or were very rare. This allowed us to obtain unique and very useful materials revealing the features of adaptation of birds to existence in dynamic environmental conditions (Melnikov, 2014). The material collected is shown in Table 1.

Table 1
The material used in the work to determine the level of reproduction synchronization in colonies of gulls and terns

Species	Number of colonies
Mew gull *Larus canus* Linnaeus, 1758	41
Mongolian gull *Larus mongolicus (vegae)* Sushkin, 1925	26
Black-headed gull *Larus ridibundus* Linnaeus, 1766	42
Little gull *Larus minutus* Pallas, 1776	41
Caspian tern *Sterna caspia,* Pallas, 1770	34
Common tern *Sterna hirundo* Linnaeus, 1758	18
Whiskered tern *Chlidonias hybrida hybrida* (Pallas, 1811)	39
White-winged black tern *Chlidonias leucopterus* (Temminck, 1815)	28

Using both water motor vehicles and rowing boats, I examined the entire Selenga River Delta. Its relatively small size (1120 km^2) allowed me to calculate the colonies and the number of gulls in a relatively short period of 12–15 days. Depending on the weather conditions that determine the nesting dates of birds every year, I carried out calculations from May 25 to June 25 and considered the phenological breeding cycles of birds of different species. During the work, I revealed the ratio of colonies in size for eight gull and tern species and examined more than 1300 colonies, of which 269 were investigated in detail (Table 1). I found that birds inhabit the lowest part of the delta. Only some colonies are located in its upper part. The border of their distribution in the Selenga River Delta passes through slightly swampy islands. Gulls appear there at high water levels at the beginning of each new 11-year flood irrigation cycle. I performed the studies at all major levels of Selenga Delta flooding characteristic of the 11-year climate cycle (high, medium, and low levels) (Melnikov, 2014).

I found colonies of gulls and terns using 12 x magnification binoculars as a result of a detailed examination of the area and observations of the behaviour of birds. In addition, I determined the size of the colonies and the number of birds in them based on a direct count of nests. Given the high nest mortality in colonies (sharp fluctuations in water level), accompanied by mass compensatory reproduction, I also examined the remaining and newly emerging colonies. Studying the colonies, I found out the ratio of nests with different clutch sizes and the minimum distance between neighboring nests (Zubakin, 1975). In the colonies selected for detailed study, I identified the degree of egg incubation (flotation method) (Westerskov, 1950; Onno, 1975). Using the simplest measurements on the ground, I mapped the nests (Ganshin, 1983). Later, this approach allowed me to restore the course of reproduction of birds in each colony.

Based on these materials, I used the graphical method proposed for studying bird migrations (Keskpike, 1989) to determine the main phenological parameters of their reproduction accurately. This step allowed me to calculate the breeding synchronization index, which I developed during special studies of the ecology of colonial and group breeding of non-colonial bird species (Melnikov, 2020). The breeding synchronization index was calculated by the following formula:

$$I_{sr}= \sqrt[2]{(n/l)/N}$$

where *n* is the number of clutches started during the period of mass laying, in pieces; *l* is the duration of mass egg laying, in days (up to tenths); *N* is the size of the colony, aggregation, or total number of clutches in the population (number of nests or pairs).

This index, calculated both for individual clusters of nests, colonies, and for the entire group of species studied, allowed them to be compared. Thus, I managed to quantify the proportion of birds that started nesting during the period of mass reproduction (egg-laying). This period is much shorter in real colonial species, although it is characterized by great variability. When the proportion of nesting birds during the mass breeding period increases, the synchronization of nesting in clusters of nests of any type or the entire population increases. This index ranges from 0 to 1, facilitating its use and interpretation. Its upper limit tends to 1 and reaches it in some cases, when all birds of the colony begin to nest on the same day. The situation is rare, but it is continuously found in colonial species in very small colonies (from 5–10 to 30 nests). The lower limit of the synchronization index tends to 0, but does not reach it even in large colonies and nesting clusters of birds.

The collected materials were processed by statistical methods (Sachs, 1976). Besides, I calculated the generally accepted statistical indicators. However, to determine the level of the multiple determination coefficient (R^2), which shows the proportion of the resulting feature (in this case, playback synchronization) selected by the variables that make up this indicator, I used the multiple linear regression function (Sachs, 1976). The names of the species and the order of their description are given in accordance with the latest Russian ornithological reports and the world's birds summary (Howard & Moore, 2003; Koblik et al., 2006; Ryabitsev, 2014).

Results

The first detailed studies of colonization in birds confirmed that the maximum synchronization of reproduction is more typical for small colonies. In this regard, this issue requires more particular and detailed consideration. In the practice of scientific research, the approach associated with the predominant use for the study of large colonies prevails. This approach facilitates the rapid production of mass material but prevents the survey from covering the full diversity of this phenomenon. Therefore, it is logical to start studying colonization features among Laridae by determining the ratio of colonies of different sizes. The analysis of scholarship shows that in different regions, the ratio of colonies in size in many species of this group of birds differs significantly. However, this issue is unfairly given too little attention. In the Selenga River Delta, which is characterized by a distinctive dynamic hydrological regime, most gull and tern species nest in colonies of small size (up to 50) nests. Only the black-headed gull *Larus ridibundus* has a higher proportion of large colonies than small ones. Compared to other species of gulls and terns, it has an exceptionally high proportion of colonies over 100 nests (26.9%, Fig. 1).

At the beginning of our research, I mentioned that shorebirds and waterfowl clusters almost always form close to areas with abundant food. If there are no places suitable for nesting in their feeding areas, gulls and terns settle in the nearest convenient places (sometimes at several kilometers' distance). The variety of foods taken by this group of birds in the nesting period is wide. However, in the Selenga River Delta, it is essential for the common black-headed gull to have sandbanks in the colonial areas, where clusters of small species of mollusks are formed, during the hatching period and the beginning of feeding of chicks (with mollusks). This fact is evidenced by the large number of mollusk shells in the nests with hatched chicks. Mollusk shells were absent from the nests of birds with an unsuccessful breeding season. Besides, the study of the patterns of distribution of Laridae in this area of Lake Baikal showed that all large colonies of common black-headed gulls or their clusters were located near large river banks, often in the mouths of second-and third-order canals.

The materials collected in this region allowed me to study the synchronization of the reproduction of colonial species of Laridae and its relationship with the size of colonies. During the fieldwork, I selected the colonies for a more detailed study in accordance with their typical size ratio for this area. The analysis of the level of reproduction synchronization in colonies of different species, based on the new synchronization index, showed its high variability. The range of variation covered almost the entire range of their possible variability (0.23–1.00). However, the average level of synchronization of reproduction in colonies of different species was quite close (0.47–0.60, Table 2), due to the fact that all these birds belong to the facultative colonial species.

The average bird breeding synchronization index does not show any differences between large and small colonies of gulls on this basis. In this regard, it is necessary to compare colonies of different sizes. Analysis of the materials shows that the synchronization of reproduction is higher in small colonies (up to 50 nests, Table 3). The index of reproduction synchronization in colonies of different sizes significantly overlaps, but the differences in the average values of this feature are quite significant (Table 3). The only exception is the Common Tern. I examined only three large colonies similar in size to small colonies (55, 60, and 76 nests). The existence of this pattern is indisputable. However, I emphasize that the variability of this feature is very high, which requires additional discussion of the collected materials. Simultaneously, the lowest levels of synchronization of reproduction were characteristic of very large colonies, for which duration of reproduction corresponded to the breeding period of the entire breeding group of any particular species in a given region.

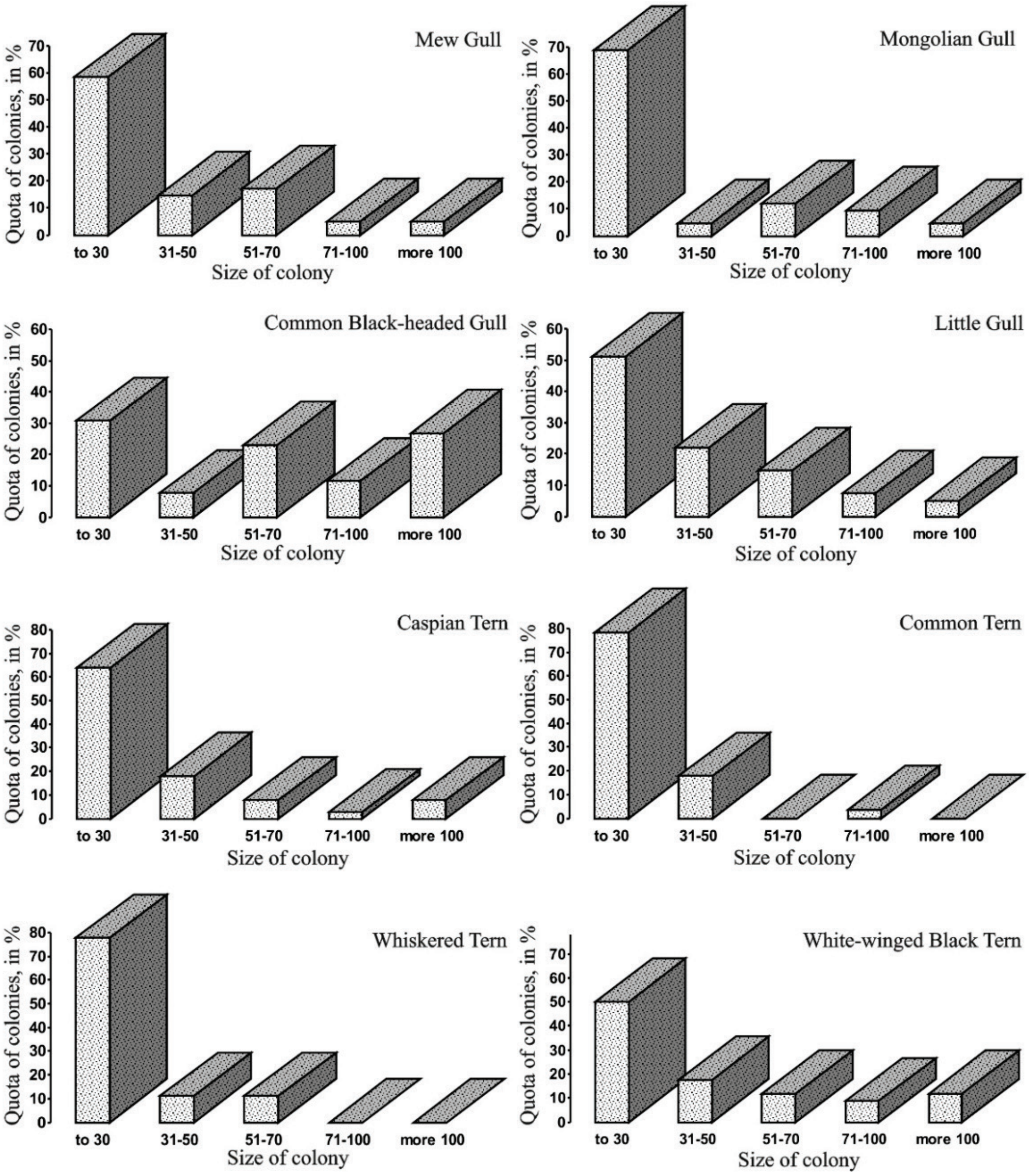

Fig. 1. The ratio of colonies of different sizes in gulls and terns of the Selenga River Delta in 1977–1982 (Lake Baikal, Eastern Siberia)

Table 2
General index of reproduction synchronization in colonies of gulls and terns in the Selenga River Delta (Lake Baikal, Eastern Siberia)

Species	Number of colonies	Index breeding synchronization		R^2
		x ± SD	index value limits	
Larus canus	41	0.50 ± 0.02	0.31–0.79	0.87
L. mongolicus (vegae)	42	0.51 ± 0.02	0.23–0.83	0.85
L. ridibundus	26	0.49 ± 0.03	0.28–0.74	0.98
L. minutus	41	0.50 ± 0.02	0.25–0.79	0.83
Sterna caspia	39	0.56 ± 0.03	0.30–1.00	0.86
S. hirundo	28	0.52 ± 0.03	0.30–0.76	0.91
Chlidonias hybrida	18	0.47 ± 0.04	0.24–0.71	0.81
Ch. leucopterus	34	0.60 ± 0.03	0.32–1.00	0.76

Note: R^2 is a multiple coefficient of determination indicating the proportion of the resulting feature selected by the variables that make up this multiple linear regression function (Sachs, 1976).

To address this question, I further analyzed the relationship between colony size and the level of reproduction synchronization (based on a special index – I_{sr}) using multiple regression analysis (Sachs, 1976) (Fig. 2). The multiple determination coefficient (R^2), which shows the degree to which the input variables determine the resulting feature (the tendency to change the level of communication between the features), is reliable in all cases (Fig. 2). The lowest rate of connection was found in the common black-headed gull – $R^2 = 0.29$; like in other species, it is highly reliable (Fisher criterion, $F = 9.8 > 7.6$; $P < 0.01$). In other species of gulls and terns, its reliability is significantly higher ($P < 0.001$). The relationship of these colony features is indisputable and reliable in all studied species of gulls and terns. Therefore, there is no doubt that with the increase in the size of the colony, the level of synchronization of the reproduction of birds significantly decreases (Fig. 2).

Observations on the common black-headed gull well illustrate this conclusion. It has the highest proportion of large colonies (Table 2). In the large colony of this species that I studied in detail (875 nests), the reproduction synchronization was close to the average level of 0.41. Simultaneously, in several species in small colonies, it was significantly lower (0.29–0.31). It is very characteristic that this trend was observed in colonies of all species of terns. At the same time, one should keep in mind that terns occupy the most unstable habitats for nesting, exposed to the constant and strong influence of changes in the water level (its increase is more likely to affect birds adversely). Some pairs may settle in colonies with repeated (compensatory) breeding, where nesting is already over. This significantly increases the reproductive period of colonies and dramatically reduces the level of nesting synchronization of birds. To a lesser extent, this phenomenon is observed in colonies of gulls. Therefore, it is necessary to conduct an additional and more detailed analysis of the factors determining the reproductive processes of gulls.

Table 3
Index of reproduction synchronization in colonies of gulls and terns of different sizes in the Selenga River Delta (Lake Baikal, East Siberia)

Species	Index of reproduction synchronization in colonies of different size					
	up to 50 nests			more than 50 nests		
	n	x ± SD	index value limits	n	x ± SD	index value limits
Larus canus	30	0.54 ± 0.03	0.32–0.79	11	0.41 ± 0.03	0.31-0.51
L. mongolicus (vagae)	31	0.56 ± 0.03	0.38–0.83	11	0.36 ± 0.03	0.23–0.51
L. ridibundus	10	0.60 ± 0.04	0.43–0.74	16	0.39 ± 0.03	0.28–0.55
L. minutus	28	0.55 ± 0.03	0.30–0.79	13	0.39 ± 0.03	0.25–0.51
Sterna caspia	32	0.59 ± 0.02	0.31–1.00	7	0.38 ± 0.04	0.30–0.44
S. hirundo	25	0.53 ± 0.03	0.30–0.76	3	0.39 ± 0.06	0.34–0.42
Chlidonias hybrida	15	0.50 ± 0.05	0.31–0.71	3	0.29 ± 0.06	0.24–0.36
Ch. leucopterus	23	0.68 ± 0.03	0.34–1.00	11	0.43 ± 0.03	0.32–0.52

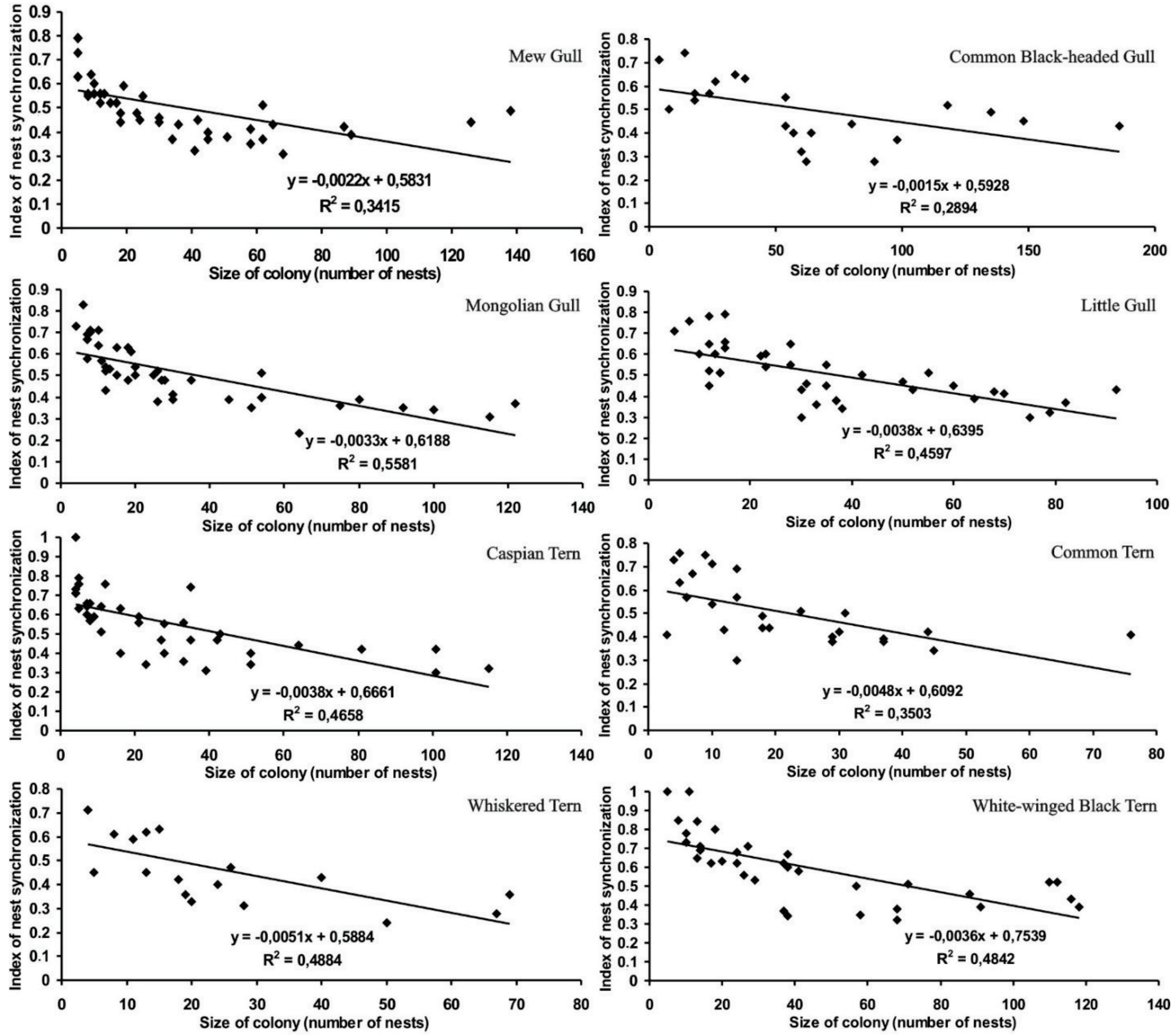

Fig. 2. The level of correlation between the reproduction synchronization index and the size of colonies of various species of gulls and terns in the dynamic conditions of the mountain-floodplain water regime of the Selenga River Delta

The only exception to these species is the Caspian Tern. This species is characterized by the formation of a day nursery for chicks, which is typical for obligate colonial bird species. Although this species belongs to this group, it, as a younger group at the initial stages of transition to another group, has its mixed characteristics at the present stage of evolution. The most striking feature that characterizes the transition of the Caspian Tern to the group of obligate colonial bird species is its use of nesting biotopes. This group of birds is characterized by a very high nesting density and the use of open habitats (sandy islands, often near the seacoast). In the Selenga River Delta, the Caspian Tern, at high water levels, can occupy grassy islands, but the vegetation on them is usually represented by a pioneer species of new shallows – the knotgrass (*Hippuris vulgaris*).

The nesting density of this species is much higher than that of other colonial gull species. The nesting density index of the Caspian Tern averages 0.23 (maximum 0.4). In other species, it ranges from 0.012 to 0.070 (maximum 0.25). In sporadic cases (twice in 25 years of research) in colonies of White-winged Black Terns located on very small lakes in the open steppe, it reached a higher indicator (0.41). Also, the Caspian Tern during the period of rising water levels (as a result of driving surges) is characterized by the completion of nests using vegetation collected in the surf zone, which is typical mainly for the former group of birds. This phenomenon is sporadic. The use of sufficiently specific habitats, along with the formation of nurseries and high average nesting density, indicates a clear modern evolution and a gradual transition of this species to the group of obligate colonial bird species. This transition is also facilitated by the specific feeding of the Caspian tern, a classic ichthyophage.

Discussion

In previous studies, I focused mainly on the high synchronization of reproduction of birds in large colonies, which, according to various scientists, dramatically increased their reproductive performance. There was an opinion that the high density of nesting and large number of birds in the colony stimulated their earlier and mass entry into breeding and increased reproductive success (Darling, 1938; Nelson, 1967; Parsons, 1975; Viksne & Janaus, 1980). However, no one has yet received a clear and unambiguous confirmation of this based on mass materials. Indeed, sometimes one can find relatively large colonies with highly compressed (synchronized) breeding periods. Such results in the Selenga River Delta were obtained from the common black-headed gull (a colony of more than 1000 nests) (Gilevich, 1977). Subsequently, I found large colonies with synchronous reproduction in all species of gulls. Nevertheless, all these cases can be attributed to exceptions. It is not every year that such a colony can be found in any species (and no more than 2–3). In most cases, the breeding of birds in exceptionally large colonies is extended, and, often, its duration corresponds to the nesting of birds of the entire regional population of a particular species. It is due to this aspect of the problem that Oriens (1961) concluded that the larger the group of nesting birds, the less synchronized its reproduction. Undoubtedly, synchronized breeding effects are more typical for small groups of nesting birds (Nelson, 1966; Davis & Dunn, 1976; Beecher & Beecher, 1979).

The total duration of egg-laying in colonies of gulls in the Selenga River Delta ranges from 35 to 44, or even 55 days. In the largest colonies (from several hundred to several thousand birds) the duration of this phase of the reproductive cycle also reaches this value. In small colonies (up to 50 nests), these periods are unstable, from 1 to 24 days. Very often, in small colonies (20–30 nests), egg-laying lasts up to 18 days. The main reason for this tendency is that many compensatory (repeated) clutches formed among birds after the failure of the first nests. Moreover, under extremely unstable hydrological conditions, birds that have lost their first clutches in the first half of incubation can resume them up to five times (Melnikov, 1983; Melnikov, 2019). In the polders of the Netherlands, which are characterized by overintensive agricultural production, the Lapwing *Vanellus vanellus* resumes lost clutches up to eight times (Beintema & Müskens, 1987). Single repeated clutches significantly extend the reproductive period of small colonies. Usually, birds that begin to reproduce again form independent colonies after a truly short courtship process, join existing colonies, and sometimes single pairs with preserved nests. Far less often, they occupy a new nesting site, searching for which they explore the delta.

Special investigation of such colonies (the latest in the season) showed that the synchronization index of their reproduction does not differ from the first (earliest) colonies or is very close to them. Therefore, the mechanism of their formation is the same, and environmental factors have little effect on the manifestation of this feature. Only mass repeated (compensatory) nesting of birds, when some of them are attached to existing colonies and even single nests and small groups of them are preserved, can dramatically reduce the synchronization of reproduction in different colonies. For the egg-laying period of colonial birds, the distribution of repeats (positive excess) is very characteristic, in which the period of mass nesting occurs in a short period (sometimes 2–3 days), and at least 50% of the birds of the colony participate in it. Sedentary birds of repeated and even third nesting attempts significantly distort this picture. This colonization has a powerful effect on small colonies, where the proportion of nesting birds during the mass egg-laying period decreases sharply, and the total number of nests increases (sometimes significantly). This trend leads to a noticeable decrease in the level of synchronization of breeding birds in small colonies but usually has little effect on large colonies, whose breeding periods are initially relatively long.

The difference in the timing of egg-laying in colonies is an essential factor. The usual differences in the timing of the first eggs in different colonies are 1–10 days; however, sometimes they reach 15–18 days, and in the case of repeated colonies – up to 40 days. This is due to the fact that with late breeding, combined with high mortality of nests, repeated colonies appear only in the second half of July. The general extension of the egg-laying period is an adaptation of the population that ensures the successful nesting of birds in all conditions. As mentioned above, this process is complicated by multiple breeding of birds. A significant reduction in laying time accompanies a low level of nest mortality. It usually ends in the second half of June for all species of gulls and terns. However, the high death rate of nests and repeated reproduction lead to the late egg-laying. During some seasons, the last colonies are formed in the second half of July, and individual pairs can lay eggs even in early August.

The productivity of late breeding is lower than that of birds that have previously started nesting. This is due to the fact that at the end of the season, young birds are starting to breed for the first time. Even the size of the clutches is much smaller (clutches with two eggs predominate). In addition, birds of this age group have many abandoned nests with one egg (often up to 80.0%); that is, they make a nest, lay one egg, but do not begin to incubate the clutch. The same trend was observed in the American White Pelican *Pelecanus erythrorhynchos* in different parts of the colony. In the central part of the colony, the number of remaining clutches was considerably less than in its periphery (Knopf, 1979). All such colonies are formed at the end of the usual nesting cycle of birds (usually before relaying). The situation is aggravated by (compensatory) repeated reproduction. This can be demonstrated with the example of the White-winged Black Tern, which has a higher proportion of repeated nesting than other Laridae species (it inhabits the most unstable habitats).

The size of the first clutches in this species averages 2.78 ± 0.05 eggs ($n = 278$). The proportion of nests with three eggs among them is always at least 83.3%. The average size of repeated clutches decreases to 2.56 ± 0.06 eggs ($n = 158$), and the proportion of nests with three eggs in them decreases to 69.0%. In the case of the mass appearance of third clutches, their average size decreases to 1.47 ± 0.10 eggs ($n = 105$), and they consist mainly of one egg (63.2%). The differences between the average clutch sizes of different bird breeding cycles are substantial ($P < 0.01$).

The same differences in the average size of clutches of different breeding cycles are observed in all other species of gulls and terns studied. Therefore, regardless of the level of synchronization of reproduction, the productivity of early and late colonies will always differ greatly. It is much higher in colonies formed at the beginning of the breeding season, when experienced adult birds begin to nest. Other authors also emphasize this fact (Gauser, 1981a; Gauser, 1981b; Panov & Zykova, 1982). In large colonies, different sites differ significantly in the timing of nesting and the level of synchronization. Most often, synchronization is higher in the central parts of colonies. Nevertheless, if there are sub-colonies that stand out well in the area, it can be much higher in them than in the main colony, which is also confirmed by the research of other authors (Patterson, 1965; Nelson, 1966; Kharitonov, 2006; Kharitonov, 2007). The most common effect of such differences is observed in the central and peripheral zones of large colonies (differences in reproduction between the center and periphery).

High synchronization of reproduction in dense colonies can have a double effect. According to numerous observations, this phenomenon increases the survival success of downy chicks, as their behaviour changes with age. In colonies with high synchronization of reproduction, the activity of all hatched chicks increases almost simultaneously, which contributes to their rapid movement by their parents to areas of the colony that are convenient for their rearing. On large lakes of the Selenga River Delta, open water windows can be found among dense horsetail thickets on the outskirts of the colony, located on higher and usually dry sections of the coast or islands. As a result, there is a decrease in the death of downy chicks from unmotivated aggression of birds still incubating clutches (Viksne & Janaus, 1980). Such mortality can be relatively high, which is well shown in the common black-headed gull (Gilevich, 1977) and other species of colonial birds (Knopf, 1979; Melnikov, 2019). With long-term incubation of chicks in neighboring nests, downy chicks are exposed to aggression from birds of neighbouring nests for a more extended period, especially during transfer of chicks to other parts of the colony, which increases their overall mortality.

However, it is possible that the mass hatching of chicks in groups with synchronous nesting of birds may also cause intense arousal of adult gulls and an increase in their aggressiveness (Panov, 1983). The authors who studied the hatching of chicks in colonies of different gull species came to the same conclusion (Davis & Dunn, 1976; Gauser, 1981b; Panov & Zykova, 1982). At the same time, our observations show that the reason for the increased aggressiveness towards hatched birds is the movements of more active grown-up chicks in the colony. This is especially evident when chicks hatch from neighbouring pairs at different times (Gilevich, 1977; Melnikov, 2019). Consequently, high nesting synchronization can, to some extent, reduce the overall death of chicks among gulls, which was previously well shown in common black-headed gulls (Viksne & Janaus, 1980).

A separate issue is the relationship between the synchronization of reproduction in colonies of different sizes and nesting density. This issue is quite complex and requires the analysis of a large amount of material on the formation of colonies in various environmental conditions. There is no doubt that the choice of colony location often determines the nesting density of birds. In small, convenient areas, the nesting density is always higher, and in extreme conditions, the nesting density of optional colonial species of gulls reaches the level of obligate colonial species. The equal distribution of nests was observed on the flat islands of Sora of the Selenga Delta, covered with sparse thickets of the knotgrass (*Hippuris vulgaris*). They are formed from large spots of intense sedimentation in the mouths of second-and third-order canals when the water level changes from high to low, which is typical for 11-year hydrological cycles of widespread flooding of the territory. The distance between the nests ranged from 40 to 50 cm; the shape of the colonies was oval, close to a regular circle. This arrangement of nests is most characteristic of black-headed and little gulls. The common (mew) and Mongolian gulls, as well as the common tern and Caspian tern, even under such conditions, formed micro-aggregations that are clearly distinguishable on the ground.

Large colonies of Mongolian and mew gulls (up to 70–100 nests), formed on very small islands in the spring (high water level), have a very high density of nests – the density index of V. A. Zubakin is up to 0.1–0.2. As a result, a significant part of the nesting birds remain until the chicks hatch. This fact means that the reproductive success of such nests is low. Other authors also noted a negative relationship between high nesting density and reproductive success (Burger, 1979; Zykova & Panov, 1983). It is characteristic that small species of gulls avoid nesting on such islands. However, they willingly occupy the same area of hummocky horsetail lakes in the steppe. Based on the fact that nutrition determines the choice of the location of the colony in the adjacent territory, such a distribution of birds of different species can be related to the timing of their nesting. Large gulls occupy colonies and begin to breed somewhat earlier than small species.

All species of gulls and terns are characterized by nesting in hummocky areas of lakes and swamps. In such cases, the location of nests is often determined by the distance between the nearest hummocks since such hummocks are always flooded with water. This is especially true for small species of gulls and terns. With a sparse arrangement of bumps, even small colonies can occupy large areas. First of all, this is true for white-winged black terns; second – for whiskered terns. However, the Common Tern avoids such biotopes and nests in such conditions only at very high water levels when the area suitable for nesting is sharply reduced. With a dense arrangement of bumps, small colonies are often formed, rarely found in other conditions.

Regardless of the density of nesting, the synchronization of reproduction in such areas follows a general pattern, decreasing as the size of the colonies increases. Nesting density has little to do with this factor. The synchronization of nesting in small colonies, regardless of the density of nests, was the same. However, large colonies in this situation usually consist of many sub-colonies (usually 3–4, and sometimes up to 7–10) that stand out well on the ground. The synchronizing of reproduction in each sub-colony was high, while for the entire colony it was significantly lower. However, there were cases when the timing and level of synchronization of reproduction almost coincided in clearly distinguishable sub-colonies. The differences between them in these reproductive parameters of birds were no more than 2–3 days. This fact indicates that colonies are formed before the nesting site is occupied, and in nesting places located within the area occupied by the colony, only the formation of individual pairs of the colony is observed. At the same time, the number of birds and the density of their nesting cannot determine the level of synchronization of reproduction in the colony.

A separate special issue is the nesting of single pairs of colonial bird species. This is undoubtedly due to their synchronization of reproduction since this phenomenon implies the participation of at least several pairs of colonial species in forming a colony. Single gull nests are rare in years with high water levels. This situation is due to the limited area suitable for nesting birds. As the water level decreases, the number of such nests gradually increases. The largest number of nests is typical for large species of gulls (Mongolian and mew gulls, up to 21%). However, in this case, the allocation of single nests is often rather tricky. Some of the single isolated nests could belong to sparse colonies, the distance to the nearest nests of which exceeded 200 m. They were found on sandbanks and vast swampy meadows completely dried up because of falling water levels. Among small species of gulls and terns, single nests were also noted, but rarely. Nevertheless, as the water level decreased, they could be met more often – up to 1.0–1.5%. These species are more characterized by nesting of single pairs in mixed colonies of several species of gulls and terns. Simultaneously, the nesting of several pairs among the Caspian terns was observed only once in a mixed colony of large gulls, and I never saw isolated nests.

Previously, it was shown that single pairs are usually found on the northern border of the ranges of accommodating species of colonial birds (Bergman, 1980). In this situation, they are observed even in obligate colonial species. Currently, in Eastern Siberia, there is a strong northward expansion of the range in almost all species of shorebirds, waterfowl, and gulls associated with sharp warming of the climate. The habitats of all common and abundant species of gulls and terns have significantly shifted to the north, and in the Selenga River Delta, there were cases of the appearance of the following southern species:

1) great black-headed gull *Larus ichthyaetus* Pallas, 1773;
2) relict gull *Larus relictus* Lönnberg, 1931;
3) slender-billed gull *Larus genei* Breme, 1839;
4) black tern *Chlidonias niger* (Linnaeus, 1758);
5) whiskered tern *Chlidonias hybrida* (Pallas, 1811);
6) gull-billed tern *Sterna nilotica* J. F. Gmelin, 1789;
7) little tern *Sterna albifrons* Pallas, 1764.

The appearance of the following single birds and small groups of northern gull species is even more impressive:

1) pomarine skua *Stercorarius pomarinus* (Temminck, 1815);
2) parasitic jaeger *Stercorarius parasiticus* (Linnaeus, 1758);
3) long-tailed jaeger *Stercorarius longicaudus* Vieillot, 1819;
4) glaucous gull *Larus hyperboreus* Gunnerus, 1767;
5) great black-backed gull *Larus marinus* Linnaeus, 1758;
6) black-legged kittiwake *Rissa tridactyla* (Linnaeus, 1758);
7) ivory gull *Pagophila eburnea* (Phipps, 1774);
8) arctic tern *Sterna paradisaea* Pontoppidan, 1763.

In general, their emergence is not surprising. Currently, it is common for cold Arctic air masses to invade the territory of Eastern Siberia, with which they are brought to Lake Baikal. There are no nesting cases among these northern species, and episodic nesting of single and mixed pairs with closely related species was observed in southern species (Melnikov & Gagina-Skalon, 2016). Consequently, the single emergence and, in some cases, nesting of colonial gull species and their movement away from the main areas, are determined by the specific ecological situation in the areas of the main nesting sites and migration routes. Climate warming leads to the expansion of their main ranges far to the north (Baikal species are recorded nesting within the Central Yakut Lowland) (Melnikov & Gagina-Skalon, 2016).

Various aspects of the relationship between the high synchronization of breeding of colonial birds and the size of their colonies underline the multi-faceted nature of this problem. Under different nesting conditions, the same factor can be evaluated differently (Shilov, 1977). In particular, when nesting in stable environmental conditions and low nest mortality, synchronous reproduction can play a critical role in increasing the reproductive success of birds. In such cases, the duration of the breeding season is sharply reduced, and increased reproductive success is always accompanied by early nesting. Besides, such situations are accompanied by a very high correlation between the main reproductive parameters of birds:

(1) synchronous and early reproduction, (2) colony size, (3) large average clutch size, and (4) high reproductive success due to low nest mortality.

Similar situations are observed with nesting colonial birds in extremely unstable (dynamic) environmental conditions. However, here they are fixed as an exception in specific periods of the breeding season or even in certain seasons that are most favourable for breeding birds. In all cases, the earliest formed colonies located in areas with a low probability of flooding (high river terraces) are characterized by the highest reproductive indicators and a high correlation. In such conditions, there are many exceptions to the general rules identified when observing the nesting of birds in relatively stable environmental conditions (MacRoberts & MacRoberts, 1972; Knopf, 1979; Melnikov, 1983). Working in colonies located in different regions that differ sharply in the timing of nesting birds, one can come to controversial conclusions.

The issue of differences in the level of synchronization of reproduction in colonies of different sizes is related to the solution to the ways of its development. Moreover, the high concentration of birds in a limited area, which leads to an increase in the density of nesting birds, is associated with an increased loss of clutches and often with a decrease in their average size. Therefore, it is unlikely that this factor could dominate in the formation of high synchronization of breeding birds in the colony. This phenomenon requires further study.

Conclusion

As a result of special long-term studies, it was proved that the highest indicators of the synchronization index of colonial birds are characteristic of small colonies (up to 50 nests). In large colonies (more than 50 nests), it is significantly lower. Simultaneously, there are cases of the formation of extensive colonies characterized by high indicators of this feature. As a rule, they are formed in stable ecological conditions, when constraining environmental factors are limited, and their socio-demographic parameters determine the colonies' functioning entirely. Despite an extended study of this phenomenon, its adaptive significance was not clarified. Formal studies of the ecology of colonial birds are usually conducted in large colonies, which allows one to quickly collect the field material necessary to obtain answers to many interesting questions. Ignoring small colonies distorts the essence of the birds' response to dynamic environmental conditions. For the correct solution to the problem, it is necessary to conduct a proportional study of colonies of different sizes. The analysis of materials should consider all limiting factors and the degree of their impact on the colony. Only in this case, can this problem be solved entirely.

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References

Beecher, M. D., & Beecher, I. M. (1979). Sociobiology of bank swallows: Reproductive strategy of the male. Science, 205(4412), 1282–1285.

Beintema, A. J., & Müskens, G. J. D. M. (1987). Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology, 24, 743–758.

Bergman, G. (1980). Single-breeding versus colonial breeding in the Caspian tern, *Hydroprogne caspia*, the common tern *Sterna hirundo* and the Arctic tern, *Sterna paradise*. Ornis Fennica, 57(4), 141–152.

Burger, J. (1979). Colony size: A test for breeding synchrony in herring gull *Larus argentatus* colonies. The Auk, 96(4), 694–703.

Chaplygina, A. B., Pakhomov, O. Y., & Brygadyrenko, V. V. (2019). Trophic links of the song thrush (*Turdus philomelos*) in transformed forest ecosystems of North-Eastern Ukraine. Biosystems Diversity, 27(1), 51–55.

Darling, F. F. (1938). Bird flocks and the breeding cycle: A contribution to the study of avian sociality. Cambridge University Press, Cambridge.

Davis, J. W. F., & Dunn, E. K. (1976). Intraspecific predation and colonial breeding in lesser black-backed gulls *Larus fuscus*. Ibis, 118(1), 65–77.

Degtyarev, A. G. (1990). Prostranstvennaya struktura naseleniya kolonial'nykh okolovodnykh ptits vysokikh shirot: Adaptivnye osobennosti i mekhanizmy ustoychivosti [The spatial structure of the population of colonial near-water birds of high latitudes: Adaptive features and stability mechanism]. In: Chernichko, I. I. (Ed.). Sovremennyye problemy izucheniya kolonial'nosti ptits [Modern problems of the study of coloniality in birds]. Sonat, Simferopol, Melitopol. Pp. 59–61 (in Russian).

Dickinson, E. C. (Ed.). (2003). The Howard and Moore complete checklist of the birds of the word. 3rd Edition. Christopher Helm, London.

Dinevich, L., Matsyura, A., & Leshem, Y. (2003). Temporal characteristics of night bird migration above Central Israel – A radar study. Acta Ornithologica, 38(2), 103–110.

Emlen, S. T., & Demong, N. J. (1975). Adaptive significance of synchronized breeding in a colonial bird: A new hypothesis. Science, 188(4192), 1029–1031.

Fialkov, V. A. (1983). Techeniya pribrezhnoy zony ozera Baykal [Currents of the coastal zone of Lake Baikal]. Nauka, Novosibirsk (in Russian).

Ganshin, V. N. (1983). Prosteyshiye izmereniya na mestnosti [The simplest measurements on the ground]. Nedra, Moscow (in Russian).

Gauser, M. E. (1981a). Sotsial'no obuslovlennaya smertnost' ptentsov v koloniyakh pestronosoy krachki *Thalasseus sandvicensis* Lath. (Laridae) na ostrovakh Krasnovodskogo zaliva. 1. Obshchaya kharakteristika yuvenil'noy smertnosti i yeye vozmozhnyye prichiny [Socially determined mortality of chicks in the colonies of the Sandwich tern *Thalasseus sandvicensis* Lath. (Laridae) on the islands of the Krasnovodsk Bay. I. General characteristics of juvenile mortality and its possible causes]. Zoologichesky Zhurnal, 60(4), 530–539 (in Russian).

Gauser, M. E. (1981b). Sotsial'no obuslovlennaya smertnost' ptentsov v koloniyakh pestronosoy krachki *Thalasseus sandvicensis* (Laridae) na ostrovakh Krasnovodskogo zaliva. 2. Rol' struktury i organizatsii kolonii [Socially determined mortality of chicks in the colonies of the Sandwich tern *Thalasseus sandvicensis* Lath. (Laridae) on the islands of the Krasnovodsk Bay. II. The effect of the structure and organization of the colony on the socially determined mortality of chicks]. Zoologichesky Zhurnal, 60(6), 879–886 (in Russian).

Georgievsky, A. B. (1989). Evolyutsiya adaptatsiy: Istoriko-metodologicheskoye issledovaniye [The evolution of adaptations. Historical and methodological research]. Nauka, Leningrad (in Russian).

Gilevich, A. L. (1977). Razmnozheniye chernogolovoy chayki v del'te reki Selengi na ozere Baykal [Breeding of black-headed gull in the Selenga River Delta at Lake Baikal]. In: Skrjabine, N. G. (Ed.). Ekologiya ptits Vostochnoy Sibiri [Ecology of birds of Eastern Siberia]. Irkutsk State University, Irkutsk. Pp. 37–58 (in Russian).

Imethenov, A. B. (1994). Katastroficheskiye yavleniya v beregovoy zone Baykala [Catastrophic events in the coastal zone of Baikal]. Buryat State Pedagogical Institute, Ulan-Ude (in Russian).

Keskpike, Y. E. (1989). Izuchenie migratsii [The study of migration]. In: Neufeldt, I. A., & Keskpike, Y. E. (Eds.). Metodicheskiye rekomendatsii po izucheniyu zhuravley [Methodological recommendations for the study of cranes]. Academy of Sciences of the Estonian Soviet Socialist Republic, Tartu. Pp. 36–58 (in Russian).

Kharitonov, S. P. (2006). Prostranstvenno-etologicheskaya struktura koloniy okolovodnykh ptits [Spatial and etiological structure of colonies of shorebirds]. Moscow State University, Moscow (in Russian).

Kharitonov, S. P. (2007). Izucheniye struktury koloniy okolovodnykh ptits [Studying the structure of colonies of shorebirds]. In: Lebedeva, N. V. (Ed.). Metody i teoreticheskiye aspekty issledovaniya morskikh ptits [Methods and theoretical aspects of seabird research]. Southern Scientific Centre of the Russian Academy of Science, Rostov-on-Don. Pp. 122–147 (in Russian).

Knopf, F. L. (1979). Spatial and temporal aspects of colonial nesting of white pelicans. The Condor, 81(4), 353–363.

Koblik, E. A., Redkin, Y. A., & Arkhipov, V. Y. (2006). Spisok ptits Rossiyskoy Federatsii [The list of the birds of the Russian Federation]. KMK Scientific Press Ltd, Moscow (in Russian).

MacRoberts, B. R., & MacRoberts, M. H. (1972). Social stimulation of reproduction in herring and lesser black-backed gulls. Ibis, 114(4), 495–506.

Melnikov, Y. I. (1983). Opredelennyye prisposobleniya u pribrezhnykh ptits [Certain adaptations in coastal birds]. The Soviet Journal of Ecology, 13(2), 134–139 (in Russian).

Melnikov, Y. I. (1985). Adaptivnyye osobennosti kolonial'nogo gnezdovaniya v izmenchivykh usloviyakh sredy [Adaptive features of colonial nesting under fluctuating environmental conditions]. In: Collins, B. A. (Ed.). Acta XYIII Congressus Internationalis Ornithologicus. Nauka, Moscow. P. 355 (in Russian).

Melnikov, Y. I. (2003). Sinkhronizatsiya razmnozheniya i yeye rol' v evolyutsii kolonial'nosti u ptits [Reproduction synchronization and its role in the evolution of coloniality in birds]. In: Maksimova, N. B. (Ed.). Biologicheskaya nauka i obrazovaniye v pedagogicheskikh vuzakh [Biological science and education in pedagogical universities]. Novosibirsk State Pedagogical Institute, Novosibirsk. Pp. 105–112 (in Russian).

Melnikov, Y. I. (2014). Dinamika prostranstvennoy struktury chaykovykh ptits v 11-letnem klimaticheskom tsikle (del'ta r. Selengi, Yuzhnyy Baykal) [Dynamics of the spatial distribution pattern of larid birds during an 11-year climate cycle (the

Selenga River Delta, Southern Lake Baikal)]. Russian Journal of Ecology, 45(1), 54–61 (in Russian).

Melnikov, Y. I. (2019). Limitiruyushchiye faktory i uspeshnost' razmnozheniya okolovodnykh i vodoplavayushchikh ptits v usloviyakh gorno-poymennogo vodnogo rezhima v del'te r. Selengi (Vostochnaya Sibir') [Limiting factors and the success of breeding shorebirds and waterfowl in the conditions of mountain-floodplain water regime in the Selenga River Delta (Eastern Siberia)]. Nature of Inner Asia, 4(13), 7–34 (in Russian).

Melnikov, Y. I. (2020). Synchronization of reproduction in birds colonies and populations and determination of its level. In: Khismatullin, D. R. (Ed.). Science. Education. Practice: Materials of the International University Science Forum. Infinity Publishing, Toronto. Pp. 135–146.

Melnikov, Y. I., & Gagina-Skalon, T. N. (2016). Ptitsy ozera Baykal (s kontsa XIX po nachalo XXI stoletiya): Vidovoy sostav, raspredeleniye i kharakter prebyvaniya [Birds of Lake Baikal (from the end of the 19th to the beginning of the 21st century): The species structure, distribution, and character of stay]. Bulletin of Moscow Society of Naturalists, Biological Series, 121(2), 13–32 (in Russian).

Molodovsky, A. V., Bakka, S. V., & Kulikova, E. V. (1990). Struktura i organizatsiya kolonial'nykh poseleniy ptits na torfyanykh kar'yerakh [The structure and organization of colonial bird settlements in peat quarries]. In: Chernichko, I. I. (Ed.). Sovremennyye problemy izucheniya kolonial'nosti ptits [Modern problems of the study of coloniality in birds]. Sonat, Simferopol, Melitopol. Pp. 87–94 (in Russian).

Nelson, J. B. (1966). The breeding biology of the gannet *Sula bassana* on the Bass Rock, Scotland. Ibis, 108(4), 194–231.

Nelson, J. B. (1967). The breeding behavior of the white booby *Sula dactylatra*. Ibis, 109(2), 194–231.

Onno, S. (1975). Vremya gnezdovaniya u vodoplavayushchikh i pribrezhnykh ptits v Matsaluskom zapovednike [Nesting time of waterfowl and shorebirds in the Matsalu National Park]. In: Onno, S. (Ed.). Transactions of the Baltic Commission for the Study of Bird Migration. Zinatne, Riga. Vol. 8. Pp. 107–155 (in Russian).

Orians, G. H. (1961). Social stimulation within blackbird colonies. The Condor, 63(4), 330–337.

Panov, E. N. (1983). Povedeniye zhivotnykh i etologicheskaya struktura populyatsiy [Animal behavior and etiological structure of populations]. Nauka, Moscow (in Russian).

Panov, E. N., & Zykova, L. Y. (1982). Sotsial'no obuslovlennaya smertnost' ptentsov u morskogo golubka (*Larus genei*, Laridae). 2. Prichiny i razmakh yuvenil'noy smertnosti v gnezdovykh koloniyakh razlichnoy chislennosti i plotnosti [Socially conditioned mortality in the colonies of Slender-billed gull *Larus genei*. II. Dynamics and range of juvenile mortality in colonies with different spatial structure]. Journal of Zoology, 61(9), 1396–1412 (in Russian).

Parsons, J. (1975). Seasonal variation in the breeding success of the herring gull: An experimental approach to pre-fledging success. The Journal of Animal Ecology, 44(2), 553–573.

Patterson, I. J. (1965). Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis, 107(4), 433–459.

Ryabitsev, V. K. (2014). Ptitsy Sibiri: Spravochnik-opredelitel' v dvukh tomakh [Birds of Siberia: Handbook-identification guide in two volumes]. Cabinet Scientist, Moscow, Yekaterinburg (in Russian).

Sachs, L. (1976). Statisticheskoye otsenivaniye [Statistical evaluation]. Statistika, Moscow (in Russian).

Schwartz, S. S. (1969). Evolyutsionnaya ekologiya zhivotnykh. Ekologicheskiye mekhanizmy evolyutsionnogo protsessa [Evolutionary ecology of animals. Ecological mechanisms of the evolutionary process]. Ural Branch of the Academy of Sciences of the USSR, Sverdlovsk (in Russian).

Scryabin, N. G., & Razmakhnina, O. V. (1978). Pitaniye chayek i krachek Baykala [Nutrition of gulls and terns of Lake Baikal]. In: Skrjabine, N. G. (Ed.). Rol' v biotsenozakh ptits Vostochnoy Sibiri [Role of birds in the biocenoses of Eastern Siberia]. Irkutsk State University, Irkutsk. Pp. 4–52 (in Russian).

Shilov, I. A. (1977). Ekologo-fiziologicheskiye osnovy populyatsionnykh otnosheniy u zhivotnykh [Ecological and physiological bases of population relationships in animals]. Moscow State University, Moscow (in Russian).

Viksne, J., & Janaus, M. (1980). Breeding success of the black-headed gull *Larus ridibundus* in relation to the nesting time. Ornis Fennica, 57, 1–10.

Westerskov, K. (1950). Methods for determining the age of game birds eggs. The Journal of Wildlife Management, 14(1), 56–67.

Zubakin, V. A. (1975). Indeks plotnosti gnezdovaniya nekotorykh vidov chaykovykh ptits i sposob yego vychisleniya [Nesting density index of some species of gulls and terns and the method of its calculation]. Journal of Zoology, 54(9), 1386–1389 (in Russian).

Zykova, L. Y. (1983). Rol' sotsial'nykh faktorov v reproduktivnom povedenii serebristoy chayki (*Larus argentatus* Pontopp.) [The role of social factors in the reproductive behavior of the herring gull (*Larus argentatus* Pontopp.)]. In: Mozgovoiy, D. P. (Ed.). Kolonial'nost' u ptits: Struktura, funktsii, evolyutsiya [Coloniality in birds: Structure, functions, evolution]. Kuibyshev State University, Kuibyshev. Pp. 143–157 (in Russian).

Zykova, L. Y., & Panov, E. N. (1983). Vliyaniye chislennosti i plotnosti gnezdovykh poseleniy na uspekh razmnozheniya khokhotun'i (*Larus argentatus cachinnans*) [Influence of the number and density of nesting settlements on the reproductive success in the Yellow-legged gull (*Larus argentatus cachinnans*)]. Journal of Zoology, 62(10), 1533–1540 (in Russian).