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POSSIBLE MECHANISM OF NEST DENSITY REGULATION IN GULL-BILLED TERN COLONIES

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Abstract. Nesting territory structure and territorial behaviour of the Gull-billed Tern was studied at Shalkar and Ayke Lakes (southern Russia) in 2000, 2001 and 2003. To examine the defended area around nests, field experiments were conducted during which one nest was moved gradually toward the nearest neighbouring nest. The area surrounding a Gull-billed Tern nest was shown to consist of at least three territorial units, which are not visible by direct observation. Immediately surrounding the nest is a small area designated as the Core Area; the Core Area is surrounded by a larger area called the Conflict Zone, consisting of an aggressively defended Inner Layer directly bordering the Core Zone, and a less aggressively defended Outer Layer. Agonistic interactions between birds increased as the distance between the nests was reduced. In the Core Area aggression was greatest, as expressed by absolute intolerance of other individuals. The Core Area is thought to play the prime role in nest density regulation in Gull-billed Tern colonies. Analysis of the distribution of nearest-neighbour distances in colonies in the study area as well as literature sources support this hypothesis. The size of the Core Area is suspected to correspond to that of the individual distance maintained by each bird around itself throughout the year.

Key words: Gull-billed Tern, *Gelochelidon nilotica*, behaviour, nesting territory, colony, aggression.

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Возможный механизм регуляции плотности гнездования в колониях чайконосых крачек. - Е.В. Барбазюк. - Беркут. 16 (1). 2007. - Структура гнездовой территории и территориальное поведение чайконосых крачек изучалось на озерах Шалкар и Айке (крайний восток Оренбургской области) в 2000, 2001 и 2003 гг. С целью изучения охраняемой территории вокруг гнезда проводились полевые эксперименты, во время которых одно гнездо поэтапно передвигалось к ближайшему соседнему гнезду. Было выяснено, что пространство, окружающее гнездо чайконосых крачек, состоит, по крайней мере, из трех территориальных единиц, которые не видны путем прямых наблюдений – абсолютно охраняемой зоны, расположенной непосредственно вокруг гнезда, и двух слоев (с большей и меньшей степенью агрессии) зоны конфликтов. Агрессивное поведение между двумя крачками усиливалось, по мере того как расстояние между гнездами сокращалось, и достигало максимального уровня в абсолютно охраняемой зоне, что выражалось в полной нетерпимости птиц друг к другу. Предполагается, что абсолютно охраняемая зона играет ключевую роль в регуляции плотности гнездования в колониях чайконосых крачек. Анализ распределения минимальных расстояний до ближайшего соседа в ряде колоний этого вида, а также литературные источники подтверждают это предположение. Предполагается также, что размер абсолютно охраняемой зоны совпадает с индивидуальной дистанцией, которая поддерживает вокруг себя каждая птица на протяжении всего года.

Introduction

The question of territorial behaviour and the role territory plays in the lives of birds is extremely complex. Despite considerable research, the structure and functions of bird territory as a dispersal mechanism remain insufficiently studied. Some research testifies to a dispersal function of territorial behaviour (Kluyver, Tinbergen, 1953; Mihelison et al., 1957). Alternatively, there are indications of changes in nest density and size of defended nest-area in territorial bird species during one breeding season after new individuals settle into the given area (Lack, 1955; Kharitonov, Siegel-Causey, 1988; Ryabitsev, 1993; Panov, Zykova, 2002). Thus, it remains unclear with regards to many species how the factor of territory and territorial behaviour prevents overcrowding, to what extent a territory is subjected to shrinkage and if such behaviour should be generally considered as a constraint.

Several recent experimental studies were conducted in which the nest-territory structure of the Black-headed Gull (*Larus ridibundus*) and the Pacific Black Brant (*Branta bernicla nigricans*) were examined. The territorial factor in this species was found not to be in itself

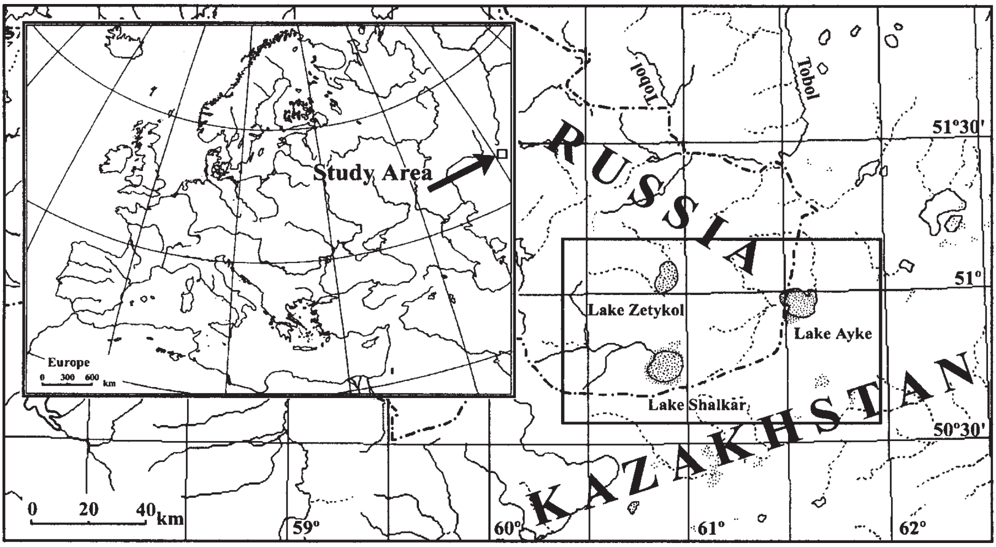

Fig. 1. Study Area. Рис. 1. Район исследований.

a sufficient condition for regulation of population density through territorial behaviour. The territorial structure of those species was shown to have a quite complex pattern, and a certain number of its elements were not visible by direct observation. Immediately surrounding the nest is a small area known as the Core Area, which can be considered as the main regulator of nest density for those species (Kharitonov, 1978, 1982; Kharitonov, Kharitonova, 1995). I have carried out experiments somewhat similar to those of Kharitonov. As a research subject I chose the rare and poorly studied (for Eastern Europe) Gull-billed Tern which generally nests in colonies and displays distinct territorial behaviour (Cramp, 1985; Zubakin, 1988).

In 2000, 2001 and 2003, the Gull-billed Tern was one of the most numerous colonial waterbirds in the study area and nested with high density, which enabled the necessary experimental research to be conducted, with the major task of investigating the role of nest-area (territory) in the regulation of nest density in colonies of this species.

The present study is a continuation of the research investigating in detail the nest-territory structure and certain aspects of the territorial behaviour of Gull-billed Terns under experimental conditions (Barbazyuk, 2005). Here, the emphasis is placed on internal population mechanisms accounting for density regulation in colonies of this species.

Study Area

The study was conducted in Gull-billed Tern colonies on Lakes Shalkar (50°47´N 60°55´E) and Ayke (50°58´N 61°30´E) in southern Russia, near the Kazakhstan border (Fig. 1). The lakes are located approximately 50 km apart, in the grassland (steppe) region with a dry, continental climate, in the northern middle-latitude zone. The average annual precipitation totals 250 mm. The average air temperature in January is –17°C, in July – +21°C.

The northern limit of the present-day breeding range of the Gull-billed Tern is to be found here (Ryabitsev, 2002), while most of the breeding range on the territory of the former USSR lies southward – in Kazakhstan and Turkmenistan (partially also in Ukraine, Black Sea) where the arid and semiarid climates are still hotter in summer (Zubakin, 1988).

The lakes studied are brackish water occurring in large shallow basins, with a surface area of more than 70 km^2, and prevailing depth 0.8–1.5 m and occupy bowl-like depressions in relief. Since the lakes lack streams offering constant water flow, their level varies greatly seasonally and from year to year. About once in every ten years, the lakes dry up completely and every 3–5 years they freeze to the lake bed. Their prevailing depth is 0.8–1.5 m. Roughly 70 % of the lake's surface may be covered with Common Reed (*Phragmites communis*), Bulrush (*Scirpus lacustris*), and Narrow-leaved Cattail (*Typha angustifolia*). Water in the reservoirs is brackish. The lakes are surrounded by semiarid steppe grasslands including combinations of Fescue (*Festuca sulcata*), feather grass (*Stipa* spp.) and wormwoods (*Artemisia* spp.). In lowland areas, typical halophytes are very common – *Salicornia europaea*, *Halocnemum strobilaceum*, *Kochia prostrata* and other species growing in clay-based and alkaline soils, creating a heterogeneous mosaic plant cover (Ryabinina et al., 1996; Davygora, 2000; Sviridova, 2000).

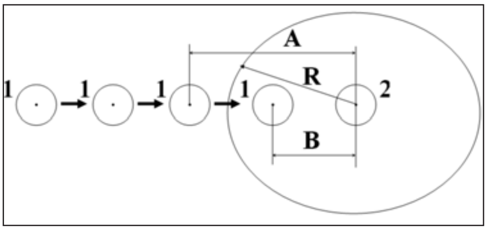

Fig. 2. Determination of the Core Area (Core Zone) Radius (Kharitonov, Kharitonova, 1995): 1 – moveable nest, 2 – stationary nest; A – distance at which Bird 1 is still sitting on its nest, B – distance at which Bird 2 drives away Bird 1, R – Core Zone radius A ≥ R ≥ B.
Рис. 2. Определение радиуса абсолютно охраняемой зоны (по: Kharitonov, Kharitonova, 1995).

Methods

On the lakes in the study area Gull-billed Terns preferred to nest together with other colonial *Laridae*, usually on small sandy alluvial islands in shallow water, with the annual population during this three year period fluctuating from approximately 80 to 700 nesting pairs on each colony (Barbazyuk, 2000, 2001, 2003).

Each pair of terns defends a small area immediately around the nest. To study this area in detail, field experiments were conducted using a special technique. Kharitonov applied this technique to studies of the nest-territory structure of the Black-headed Gull and Pacific black Brant (Kharitonov, 1978, 1982, Kharitonov, Kharitonova, 1995). The method can be described as follows. Observations were made from a small portable hide covered with camouflage fabric with several observation slits. Experimental protocol consisted of moving one nest step-by-step towards the nearest neighbouring nest. The nest was moved a distance of 5–20 cm from its original position toward the fixed neighbour nest. Subsequently, all birds were permitted to incubate eggs for 10–15 minutes. The nest was then again moved a certain distance, and so on. After the experiment completion, the movable nest was placed back at its original location. The experiments were conducted in the open sections of colonies without obstructive vegetation. In the experiments clutches of one week on older age were used, in several exceptional cases the clutches with piping eggs were used. Distances between nests in the experiments were measured between their centres with a tape measure. When possible, the sex of birds was identified, which was easier to do when both members of pair were present at the nest differing by the exterior and behaviour.

Each experimental manipulation was considered complete if one of the following cases took place: 1) one of the terns attacked (from the air or ground) and did not permit its neighbour to approach closer to sit on the nest – revealing so called the Core Area; 2) the moved nest's occupant stopped following its nest and stood on the original nest spot more 15 minutes or disappeared. If the occupant of the more often stationary nest kicked the moved nest's occupant out of its own nest and then did not allow it closer, the moveable nest was considered to breach the Core Area of stationary nest's occupant. The border of the Core Area certainly lies somewhere between the two last positions (A and B) of the moveable nest where the tern of the moveable nest was still able to sit on its nest during next to last movement but at the last nest-moving stage it is driven out by the occupant of the stationary nest (Fig. 2).

The initial distances between experimental nests ranged between 46 and 159 cm. The N of of completed manipulations was 183. Overall observation time (including that spent carrying out the experiments) totalled 231 hrs, 25 minutes over three years.

To examine nearest-neighbour distances in colonies of Gull-billed Terns, two small colonies and one segment of a colony with different nest density were plotted on the map; all the nest distances were measured between centres of nests. In this study STATISTICA 6.0 (StatSoft, Inc. 1984–2001) was used for data processing and plotting.

Results

During experiments, as the moveable and stationary nests approached each other, the stationary nest's occupant responded in one of several ways to the intruder, depending on the distance between the two nests. In general outline during each manipulation followed a similar sequence of behaviour: At the first nest-moving stages the occupant of the stationary nest showed no obvious response to the occupant of the moveable nest, which sat on its moveable nest easily and continued incubating. During the further moving of the moveable nest closer towards the stationary nest, the stationary nest's occupant suddenly "took notice" of the closely settled neighbour which was evident from his aggressive rattles and attacks while the moveable neighbour showed signs of agitation judging from his delay in getting on the nest, hesitation, increasingly long searches for the nest on the original site. Such birds became increasingly reluctant to return to their nests and resume incubation activity.

If nests were moved still closer in proximity, two primary scenarios were possible: (1) The moveable nest's occupant (or, in several experiments conversely) responded to increasing aggressiveness from the stationary nest's occupant (increase in number of aggressive rattles and attacks per time unit) by simply ceasing to occupy its own nest, standing away in a "gloomy" manner not daring to approach any closer. In 127 experiments of a total of 183 one of the two experimental birds stopped following and getting onto its nest when the distance between the centres of the two neighbouring nests was only 20–50 cm. (2) In 32 manipulations the moved nest's occupants risked following their nests even when they were moved closer despite the prominent aggressive respond from the stationary nest's ones. Finally they were driven out of their nests by the occupants of the stationary nests and afterwards were not allowed to return to them. In these last cases the moved nest was considered to be located within the Core Area (Barbazyuk, 2005).

Thus, the Core Area may be defined as a small, unmarked area around the nest into which no intruder is permitted. In the Core Area, a stationary nest's occupant attacks its moveable neighbour whenever the latter attempts to get onto its moveable nest; therefore each attempt by the latter to sit on its nest results in failure. The primary indicator of the Core Area is the impossibility for the both birds to sit together in their nests and incubate as a result of straining bird relations and strong discomfort. Outside of the Core Area the simultaneous incubation is still possible. During the experiments attacks occasionally were recorded when one of the birds attempted to frighten its neighbour away while 40–60 cm remained between the two nest centres, i.e. on the approach to the Core Area. After several minutes attacked terns approached their nests stealthily and got on it quietly, thereby eliciting no strong aggressive reaction from its neighbour. Both birds continued incubating, as before.

Core Areas were quite difficult to identify because most birds associated with moved nest's suddenly gave up trying to follow their nest, and refused to sit onto it somewhere on the approach to this territorial unit. This suggests great tensions between the two closely positioned birds and discomfort especially since the Gull-billed Tern is a species with distinct territorial behaviour and a high degree of aggressiveness (Cramp, 1985). In 32 experiments though the Core Area radius was determined quite precisely. The minimum radius of the Core Area was $20 \le R \le 23$ cm; the maximum radius was $32 \le R \le 49$ cm; the mean radius ($\overline{R}$) was $26.13 \pm 0.48 \le R \le 33.81 \pm 0.96$ cm, the mean radius class midpoint ($\overline{R}$ mid) was 29.97 ± 0.68 cm (N = 32).

High levels of aggression displayed by the stationary nest's occupant combined with absolute intolerance of the intruder suggested that the presence of a Core Area could prevent neighbouring pairs from building their nests closer during the colonization of a certain habitats, suggesting the prominence of the Core Area in nest density regulation for Gull-billed Terns.

To confirm this idea we might consider Core Area radius as a function of the distance between nests, i.e. colony density. For this purpose all distances recorded during manipulations during which Core Area radius values were obtained were subdivided into 10 classes. The length of each distance interval, or class is specified to be equal to 10 cm. The initial distances between nests in manipulations which successful revealed Core Areas showed initial internest radii ranging from 46–142 cm. For each distance class (L) the Core Area mean radius ($\overline{R}$) was calculated. Core Area radius changes imperceptively in relation to initial internest distance. As the distance between nests increases by 92%, the Core Area mean radius increases by 10.62 % (Table 1).

Core Area radius appears to be weakly dependent of the colony density, I consider the ratio change of the Core Area radius (R) to half the nest distance (L/2) as this nest distance changes. For calculation the midpoint of a distance interval (L mid) and the mean radius class midpoint ($\overline{R}$ mid) for each class, or distance interval (L) were used:

$$\overline{R}\text{ mid}/L\text{ mid}/2 = 2\,\overline{R}\text{ mid}/L\text{ mid}$$

For simplicity I shall henceforth refer to $2\,\overline{R}$ mid/L mid as 2R/L. Figure 3 illustrates the 2R/L change as the distance between two nests reduces. For 2R/L = 1 the Core Areas of two nests start being in contact with each other, with the distance (L) between the nests equal to the

Table 1

The change of the Core Area radius (R) as the initial distance between nests (L) increases in Gull-billed Tern colonies
Изменение радиуса абсолютно охраняемой зоны (R) с увеличением первоначального расстояния между гнездами (L) в колониях чайконосых крачек

L, cm	Mean Radius, $\overline{R} \pm$ SE , cm	Mean Radius Class Midpoint, $\overline{R}$ midpoint ±SE , cm	Number of Experiments	$\frac{2R}{L}$
45 – 55	24.75 ± 0.48 = $\overline{R}$ = 31.25 ± 1.44	28.00 ± 0.84	4	1.12
55 – 65	24.50 ± 1.55 = $\overline{R}$ = 30.75 ± 3.09	27.63 ± 2.29	4	0.92
65 – 75	24.66 ± 0.88 = $\overline{R}$ = 32.00 ± 1.53	28.33 ± 0.60	3	0.80
75 – 85	27.17 ± 1.58 = $\overline{R}$ = 36.50 ± 2.73	31.83 ± 2.06	6	0.80
85 – 95	25.75 ± 1.25 = $\overline{R}$ = 33.00 ± 1.91	29.38 ± 1.26	4	0.65
95 – 105	27.00 ± 0.00 = $\overline{R}$ = 32.00 ± 0.00	29.50 ± 0.00	1	0.59
105 – 115	26.33 ± 0.67 = $\overline{R}$ = 35.67 ± 1.76	31.00 ± 1.15	3	0.56
115 – 125	27.00 ± 1.00 = $\overline{R}$ = 32.00 ± 0,58	29.50 ± 0.58	3	0.49
125 – 135	32.00 ± 0.00 = $\overline{R}$ = 49.00 ± 0.00	40.50 ± 0.00	1	0.62
135 – 145	26.66 ± 1.67 = $\overline{R}$ = 34.33 ± 3.93	30.50 ± 2.78	3	0.44

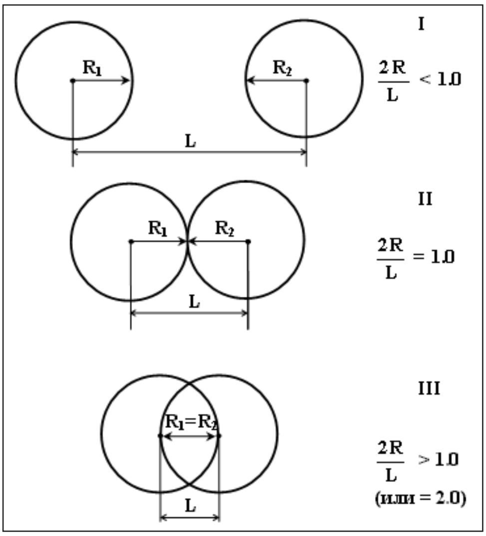

Fig. 3. The 2R/L change as two Core Areas are being drawn together when the distance between the nests reduces. Comments see in the text.

Рис. 3. Схема изменения величины 2R/L по мере сближения двух абсолютно охраняемых зон при сокращении расстояния между первым и вторым гнездами. Комментарии в тексте.

sum of two Core Area radiuses (R_1 and R_2). For the case 2R/L < 1 the distance between the nests greater the sum of two Core Area radiuses and for 2R/L > 1 the Core Areas start to overlap up to the position when the distance between the two nests does not exceed the length of the common radius for two Core Areas – 2R/L = 2 (Fig. 3).

In the data resulting from manipulations possible variation in the relative Core Area radius (2R/L) was 1.12–0.44. As the distance between nests is reduced the relative Core Area radius increases and in the 60–50 cm segment 2R/L becomes more than unity (Table 1), i.e. the Core Areas of moved and stationary nests partially overlap. Theoretically it is possible for both neighbouring nests to show 2R/L = 2. In this case the distance between the nests is equal to the radius (Fig. 3) and tension between the terns should become excessive. During experiments this situation was not found to occur.

Within the Core Area, tern aggression is at a maximum, as expressed by absolute intolerance of other conspecifics. Greater tensions between neighbours might be expected in dense colony plots (2R/L = 1, L = 50–60 cm) when compared to areas of low density (2R/L < 1) because in the former case the distances between neighbouring Core Areas are very small. As Core Areas partially overlap (2R/L > 1), in denser colony areas relations between neighbouring terns seem to become even more tense, which probably prevents the nests from being packed in more densely. Growing tensions between neighbouring terns is evident as well from an increase in the aggressiveness level of experimental birds (the significant increase in the number of attacks and aggressive rattles per time unit) when their nests approach each other (Barbazyuk, 2005).

To test this assumption that tension and discomfort displayed in birds with near overlap between their Core Areas are efficient deterrents to increasing nest density, nearest-neighbour distances in three colonies with different nest densities were analyzed (Fig. 4–6, Table 2).

The densest colony of Gull-billed Terns existed on Shalkar in 2001. In that location slightly more than 600 nests were arranged on an islet, with a nesting habitat consisting primarily of sandy-shingle dunes overgrown with *Tournefortia sibirica*. Figure 5 shows the distribution of nearest-neighbour nest distances in a typical section of this colony (nests are charted on one of the several flat sandy dunes). During nest-building and early egg-laying (on 20–30 May) shoots of Tournefortia sibirica appeared from the sand, and appeared to only slightly reduce visibility between nests. By mid June *Tournefortia* heavily covered the dunes and entirely hid the nests and nesting birds. Thus, each nest was now surrounded by dense and obstructive vegetation. Based on personal observations over the period 1999–2004 and data from literature, that colony was one of the densest colonies ever recorded.

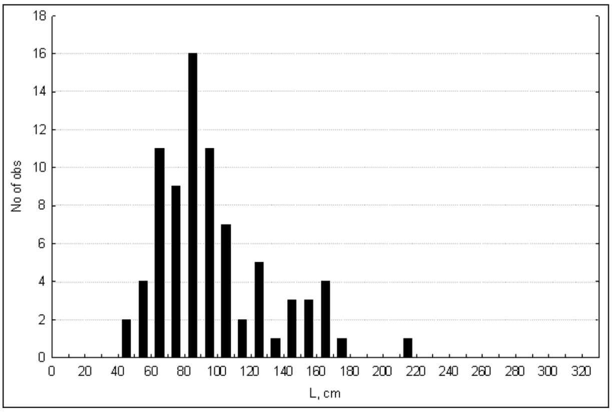

Fig. 4. The distribution of nearest-neighbour distances in a colony on Lake Shalkar in 2000 (N = 81).
Рис. 4. Распределение минимальных расстояний в колонии на оз. Шалкар в 2000 г. (N = 81)

Figure 6 displays the distribution of nearest-neighbour nest distances in one of the least dense colonies recorded over six years – Lake Ayke in 2003. There terns nested on a wet and practically bare islet. At the highest elevation of the islet (15–25 cm above the water surface) patches of low wetland vegetation was found, which was actually the site where minimum nearest-neighbour nest distances were found – more than 70 cm.

One tern colony on Lake Shalkar in 2000 was located on a sandy islet that by late June was connected with the mainland by an isthmus, forming a spit. The nests were both on and around small and sloping sandy dunes covered with *Tournefortia*, all over the islet in the open and semi-open, on wet lowland patches carpeted with *Salicornia europaea*, 5–10 cm in height (Fig.. 4).

The histograms demonstrate that as the colony nest density increases accumulation and concentration of nearest-neighbour distances at a limit of 50–60 cm occurs (Fig. 4–6). Even in the densest colony the bulk of nearest-neighbour distances lie within 50–80 cm (Fig. 5). In less dense colonies, the nearest-neighbour distance peak is skewed even more to the right, i.e. within 60–110 cm (Fig. 4) and 70–120 cm (Fig. 6). Thus, even in dense sections of colonies most nearest-neighbour distances are not less than 40 cm between nest centres, which also supports the idea that the neighbour Core Areas keep the nests from approaching closer.

Figure 7 displays the distribution of nearest-neighbour distances in percentage terms for the three colonies. As it was shown above, the 50–60 cm segment appears to be the critical

Table 2

Some parameters for three colonies with different nest densities at Lakes Shalkar and Ayke in 2000, 2001 and 2003
Некоторые показатели, характеризующие плотность колоний чайконосых крачек на озерах Шалкар и Айке в 2000, 2001 и 2003 гг.

Parameters	Colony on Lake Shalkar in 2000 (81 nests)	Colony part on Lake Shalkar in 2001 (113 nests)	Colony on Lake Ayke in 2003 (158 nests)
Mean nearest-neighbour distance, cm, $\overline{X} \pm SE$ (N)	97.55 ± 3.85 (81)	70.56 ± 2.18 (113)	111.18 ± 3.10 (158)
Minimum nearest-neighbour distance, cm	48.00	38.00	35.00
Maximum nearest-neighbour distance, cm	210.00	152.00	324.00

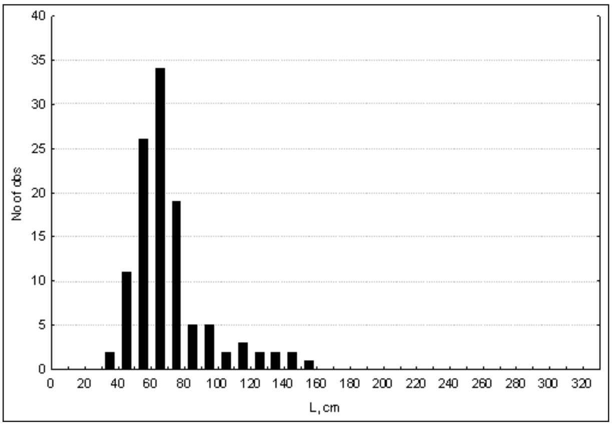

Fig. 5. The distribution of nearest-neighbour distances in the part of a colony on Lake Shalkar in 2001 (N = 113).
Рис. 5. Распределение минимальных расстояний в части колонии на оз. Шалкар в 2001 г. (N = 113).

distance between nests of Gull-billed Terns. Any closer than this and terns appears to avoid settling because their Core Areas start touching or partially overlapping (2R/L ≥ 1, Table 1). In the densest colony the nearest-neighbour distance peak lies within 50–80 cm and 2R/L equals unity within this peak (Fig. 7). It is therefore highly likely that the Core Area is a main factor in determining nest density in Gull-billed Tern colonies.

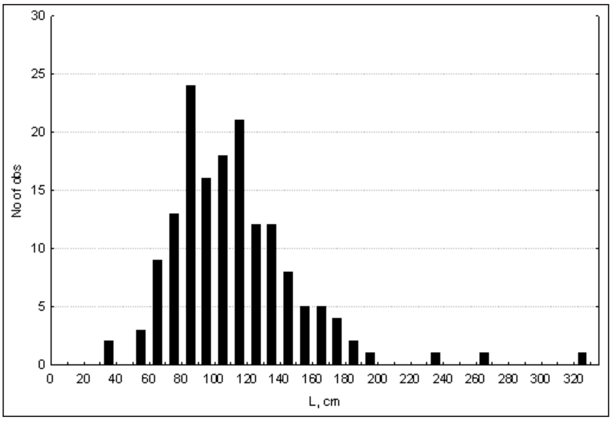

Fig. 6. The distribution of nearest-neighbour distances in a colony on Lake Ayke in 2003 (N = 158).
Рис. 6. Распределение минимальных расстояний в колонии на оз. Айке в 2003 г. (N = 158).

Records of the minimum nearest-neighbour distances between proved active nests having been built <u>in the open</u> totalled 51 and 53 cm between nest centres and these records were found in short *Salicornia europaea* in the dense colony, Lake Shalkar, 2001. In other rare instances where the nearest-neighbour distances ranged from 35 to 49 cm including those shown in the histograms, the nests were constructed in vegetation and the closer nests were arranged the more impenetrable for bird visibility the plant barrier was between them, or one of the two closely arranged nests contained nothing, was abandoned or depredated.

In two cases the Core Area radius was obtained as follows. The movable experimental nests were moved from the initial distances 75 and 97 cm and then left on the approach to the stationary nests (46 cm and 57 cm in each experiment respectively). In a few days the experiments were finished. In this case the terns did not leave their nests either. The distances 46 and 57 cm were taken as the initial ones since the birds were assumed to acclimate to close cohabitation over several days. In a number of experiments with nests having initial distances up to 70–80 cm terns displayed mutual aggressive rattling when we moved their nests, even before the experiments were started.

Core Area radii were primarily obtained when both nests were moved closer until the occupant of the stationary nest, sitting in it, could reach for its neighbour’s bill and snap at it. In some experiments, unsuccessful attempts by terns to lunge at opponents were recorded; however, the distance between nests was not close enough to attack, and the bird remained sitting tensely on the nest and showing its bill to the opponent, rather than attack. It may be that the size of the Core Zone corresponds to that of the individual distance maintained by each bird around itself throughout the year (Conder, 1949). During nest-building, egg-laying and incubation stages, when birds commit themselves to a particular spot (the nest), individual distance may be identified and associated with that area.

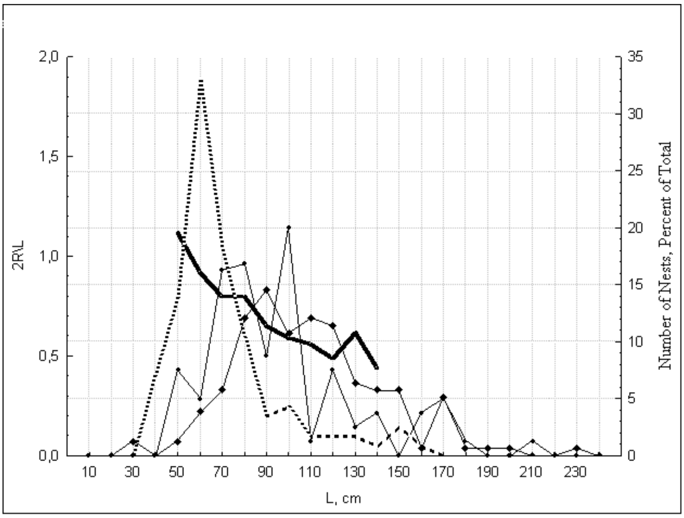

Fig. 7. The 2R\L change and the distribution of nearest-neighbour distances in the colonies on Lakes Ayke and Shalkar.

A dense plot of the colony in thick vegetation, Lake Shalkar, 2001;
The colony on a sparsely vegetated islet, Lake Shalkar, 2000;
The colony on an islet almost free of vegetation, Lake Ayke, 2003;
2R\L.

Рис. 7. Изменение относительного значения радиуса абсолютно охраняемой зоны (2R/L) и распределение минимальных расстояний между гнездами в колониях на озерах Шалкар и Айке.

Discussion

The Gull-billed Tern is a colonial species with pronounced territorial behaviour. Before egg-laying males establish nest-area territories, which are later defended by the pair (Møller, 1975). This species seems to belong to a group of *Laridae*, forming nesting settlements, known as the “second type” (Kharitonov, Siegel-Causey, 1988). Type II species colonize areas for short periods initially with high nesting great densities. It is thought that normally later on territories diminish in size only imperceptively, and distances between nests are nearly constant throughout incubation in undisturbed colonies. The settlement process is synchronous and spatially organized into groups or subcolonies, at times as large as several thousand pairs. This type of colony formation has a high selective advantage for species nesting in unstable habitats, such as those in the study area (see the Study Area section). This definition of the “second type” implies therefore that later arrivals do not move into the inner parts of the original settlement; hence, territory crowding through reduced defense of areas of the earlier breeders does not occur, e.g. Black-headed Gull (the “first type” – Kharitonov, Siegel-Causey, 1988). However, Gull-billed Tern colonies which differ in size are characterized initially not by identical nest densities, which may be associated with birds starting to breed in different numbers, nest site restrictions, relief features for the colony to settle etc. Consequently, variation in territory size, occasionally considerable, may occur, e.g. size of defended areas can be only 50 cm in diameter or range from 3 to 8 m^2 (Cramp, 1985).

During manipulations, especially in colony segments with nests situated 60–80 cm apart, off-duty males beside their nests repeatedly chased intruders within 1.5–2 m from the nests whereas strange birds passing by the other side from the nests even more closely were left unnoticed. It seemed as if the territory in dense plots at least in some pairs has a long peculiar extension, or “offshoot” mostly stretching towards one of the sparsest and nest-free sides.

Along that branch the male was running actively and chasing intruders considerable distances from the nest while evidently avoided doing so in the direction of the closely arranged neighbouring nests. Irregular-shaped and elongated territories extending in the direction of the least local density have been identified, for example, for the Black-headed Gull (Kharitonov, 1978), the Western Gull (*Larus occidentalis*) (Hunt, Hunt, 1975) and for a number of other species.

Thus it appears that regulation of density on the colony is difficult to explain simply through territorial behaviour because the nest territory, varies in size and configuration and is more likely fit to the existing environment (active density, numbers, relief, vegetation and etc.) rather than conforming to a predetermined social environment, i.e. the territory is an effect, not a cause. To explain density regulation mechanism properly the Core Area, which may be associated with the bird's individual distance, must be brought in. Conder (1949) found that the individual distance of Black-headed Gulls in flocks was one extended body-length around a bird. Within that distance no birds were allowed. There were two ways of maintaining individual distance – avoiding movements and threats. In the former case when the another bird landed too close the gull moved at least a body-length away, while in the latter situation, the gull threatened with the open bill and the second bird drew back. According to Conder, all types of the territory including the nest territory are a modified individual distance that gradually starts being associated with select sites. He provides an example of Canada Geese (*Branta canadensis*) and Snow Geese (*Anser caerulescens*). The winter movable distance in these species increased in size, acquired precise limits and functioned as a standard territory. According to Conder, the individual distance is a smaller unit, in distinction from the territory, and it is not bound to ground surface (Conder, 1949). Evidence for the individual distance as described by Conder agrees very well with the obtained experimental data. The stationary experimental birds were assumed to have no other choice but to attack the closely positioned movable neighbours that stubbornly kept following their nests. They did so to keep a safe individual distance, or to maintain the Core Area which is equal on average to bird length (35–38 cm, Cramp, 1985).

On the one hand, if conditions permit, birds may nest as close together as possible. In dense nesting conditions, mutual social stimulation leads to more synchronous breeding and, in theory, higher reproductive success for individuals (Darling, 1938; Vermeer, 1973 and others). On the other hand, owing to particular spatial and ethological factors, co-existence in tightly-packed groups does not allow the population to reach its maximum reproductive potential. It is known that intraspecific aggression is one of the main factors contributing to the lowered breeding success of larids. Chicks suffer the highest rates of mortality during hatching and fledging periods. In dense colonies, chick mortality may be very high compared to low-density ones (Hunt, Hunt, 1975). The presence of the Core Area well explains how these two tendencies can balance each other out. Despite the tendency to nest densely, which is displayed by all larid species, by showing nest distances less than 50 cm, Gull-billed Tern settlement is a rare event (and in this case the presence of vegetation is obligatory) since the neighbouring Core Areas start overlapping, and the terns experience strong discomfort as a result of more and more strained relations. Thus, equilibrium is attained – social instinct is satisfied, and the Core Area guards birds from further detrimental effect of overcrowding.

It needs to be emphasized that a barrier of 50–60 cm is not an optimal distance between nests but rather a critical one. This is proven by literature sources and personal direct observations over a period of 1999–2004 (during this time there were 11 records of Gull-billed Tern breeding colonies). Dense colonies such as that existing on Lake Shalkar in 2001 are rather an exception than the regular pattern. Normally, birds preferred to be much more dispersed and colonies with lower densities as those on Lakes Shalkar in 2000 and

Ayke in 2003 seem to be more typical for the study area. Numerous other reports also support this. For example, in North Carolina, USA, nest distances ranged from 2 to 114 m, on average 21 ± 19.3 m, N = 50 (Sears, 1978). In Denmark the mean distance between nests recorded at one colony was 1.5 m (Lind, 1963). At Chernomorski (Ukraine, former USSR) nests generally 1–2 m apart, mean 21 m, with the minimum of 83 cm (Borodulina, 1960) which is considered as "very close" (Cramp, 1985). One Spain colony reached 1000 breeding pairs with the nest distances up to 0.25–0.30 m (Vargas et al., 1978).

Any explaining particulars in the latter case are not available but even under the assumption of bird breeding in the open those minimal nest distances correspond to the mean radius class midpoint ($\overline{R}$ midpoint) of the Core Area (29.97 ± 0.68) obtained experimentally. Given that in most of the experiments performed the terns kept incubating up to 30–40 cm between the nest centres despite the complexity of their mutual relations such tightly-packed co-existence can be seen as an exception.

To sum up, the obtained results covered by this paper suggest that nest density regulation through the Core Area, which is highly likely to control the territorial defence in the Gull-billed Tern species, appears to be a permanent and reliable internal mechanism of population homeostasis, which is weakly dependant on the external conditions.

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Замітки	**Беркут**	**16**	**Вип. 1**	**2007**	**130**

НАБЛЮДЕНИЕ ОСЕННЕГО СКОПЛЕНИЯ ЧЕРНЫХ АИСТОВ НА СУМЩИНЕ

Observation of an autumn accumulation of Black Storks in Sumy region. - N.P. Knysh, N.M. Tverdokhleb. - Berkut. 16 (1). 2007. - 30 birds were found on a meadow on 15.09.2007. This flock has appeared here on 1.09 and did not change its location. [Russian].

Как известно, черные аисты (*Ciconia nigra*) иногда объединяются в большие осенние стаи, которые в Украине отмечались в Прикарпатье и Карпатах, а также южнее – в Черновицкой области и Молдавии (Смогоржевський, 1979; Горбань, 1992). В том числе в сентябре 1983 г. на рыбных прудах в Ивано-Франковской области наблюдалось самое большое их скопление – до 200 особей (Горбань, 1992). По различным данным, на северо-востоке Украины мигрирующие черные аисты как правило встречаются поодиночке, иногда небольшими группами до 5 особей (1 наблюдение). Впервые скопление черных аистов численностью до 30 особей нам удалось наблюдать 15.09.2007 г. в луговой пойме в месте слияния речек Павловка и Крыга (бассейн р. Сейм) – между селами Мороча и Марьяновка Белопольского р-на Сумской обл. Птицы вразброд кормились и отдыхали на лугу. По свидетельству местных охотников, эта стая была впервые замечена здесь 1.09 и все последующие дни не меняла дислокации. Сроки отлета стаи нами не прослежены. Несомненно, появление у нас на Сумщине такого относительно большого осеннего скопления черных аистов связано с ростом общей численности восточноевропейской популяции вида.

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