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EXPERIMENTAL STUDY OF TERRITORIAL STRUCTURE IN THE GULL-BILLED TERN

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Abstract. The nest territory structure and territorial behavior of the Gull-billed Tern was studied at Lakes Shalkar and Ayke (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 neighboring nest. The area surrounding a Gull-billed Tern nest was shown to consist of at least three territorial units, 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 a more aggressive Inner Layer directly bordering the Core Zone, and a less aggressive Outer Layer. The hostility of the both birds increased as the distance between the nests lessened. In the Core Area tern aggression was maximal, and was expressed by absolute intolerance of other individuals.

Key words: Gull-billed Tern, *Gelochelidon nilotica*, territorial behaviour, colony, nest territory structure.

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Экспериментальное изучение структуры территории у чайконосой крачки. - Е.В. Барбазюк. - Беркут. 14 (1). 2005. - Работа проводилась весной и летом в 2000, 2001 и 2003 гг. на востоке Оренбургской области, на озерах Шалкар-Ега-Кара (50°47´ с. ш., 60°55´ в. д.) и Айке (50°58´ с. ш., 61°30´ в. д.). Использовался метод полевого эксперимента. В каждом опыте проводилось поэтапное передвижение одного гнезда к ближайшему соседнему неподвижному. Один отрезок передвижения составлял 5–20 см. После каждого передвижения птицам передвигаемого и неподвижного гнезд предоставлялась возможность вернуться к гнезду и посидеть на нем 10–15 мин. По окончании опыта гнездо возвращалось на место. При проведении экспериментов, во время которых подопытное гнездо постепенно перемещалось к неподвижному гнезду, хозяин неподвижного гнезда по-разному воспринимал пододвигаемого соседа, в зависимости от степени удаленности гнезд друг от друга. Выяснилось, что у чайконосых крачек пространство вокруг гнезда состоит из трех элементов, или субъединиц, не видимых путем обычных наблюдений, но хорошо различающихся между собой по степени выраженности и проявлению агрессивности и по наличию или отсутствию некоторых элементов поведения, наблюдавшихся во время опытов. Чайконосая крачка демонстрирует довольно сложную территориальную структуру, элементы которой могут быть выявлены только экспериментальным путем. В ней происходит нарастание агрессивности крачек и усиление дискомфортного поведения в направлении от периферии к гнезду по схеме: полное отсутствие дискомфорта, агрессии → первый слой зоны конфликтов → второй слой зоны конфликтов → абсолютно охраняемая зона. В абсолютно охраняемой зоне агрессивность крачек максимальна, что проявляется в их нетерпимости к другим особям. Абсолютно охраняемая зона является самой стабильной единицей территории и, видимо, обусловливает наличие двух других территориальных структур – первого и второго слоя зоны конфликтов, в которых крачка выражает свое отношение, степень терпимости к другим особям, находящихся на разных расстояниях от ее гнезда. Предположительно, абсолютно охраняемая зона совпадает с индивидуальной дистанцией птицы.

1. Introduction

The question of territorial behavior 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. The territorial factor in colonial waterbirds is not by itself a sufficient condition for regulation of population density through territorial behavior, because the size of a territory may vary greatly even in the course of one reproductive season – for example, it may decrease under pressure from new intruders settling among existing nests in a colony (Tinbergen, 1956; Kharitonov, 1998; Panov, Zykova, 2002), which appears to suppress its regulatory function. To understand how the factor of territory prevents overcrowding, it is necessary to take a closer look at what the territory is, i.e., examine in detail its internal structure. Several recent experimen-

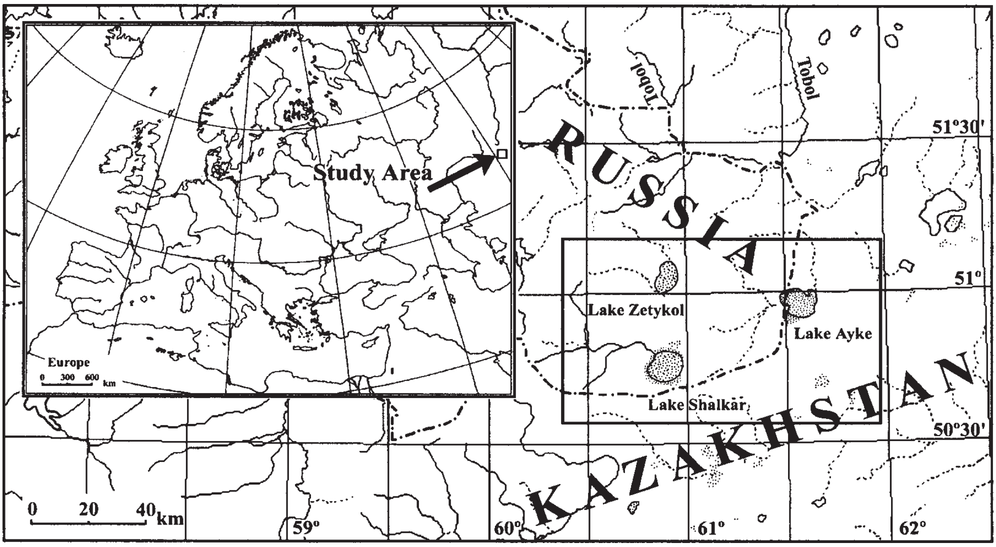

Fig. 1. Study area. Рис. 1. Район исследований.

tal studies were conducted in which the nest-territory structure of the Black-headed Gull (*Larus ridibundus*) and Pacific Black Brant (*Branta bernicla nigricans*) was examined. The territorial structure of those species was found to have a quite complex pattern, and certain 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. In contrast to the Core Area, the greater portion of nesting territory is not defended vigorously, varies greatly depending on conditions, and functions as a buffer zone (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 (*Gelochelidon nilotica*), which generally nests in colonies and displays distinct territorial behavior (Cramp, 1985; Zubakin, 1988). In 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.

This study investigates in detail the nest-territory structure and certain aspects of the territorial behavior of this species. As regards the role of territorial structure and territorial behavior in nest density regulation in Gull-billed Tern colonies, this question will be examined separately in another paper.

2. Study area and methods

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, in 2000, 2001 and 2003 (Fig. 1). 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, at times as many as 700 pairs (Barbazyuk, 2003).

Each pair of terns guards a small area around the nest. To study this area in detail, field experiments were conducted using a special technique. Sergei P. Kharitonov applied this technique to studies of the nest-territory structure of the Black-headed Gull and Pacific Black Brant (Kharitionov, 1978, 1982, Kharitonov, Kharitonova, 1995).

The method can be described as follows. Observations were made from a small portable booth covered with camouflage fabric with several observation slits. The experiments consisted of moving one nest step-by-step towards the nearest neighboring nest. The nest was moved a distance of 5–20 cm from its original position toward the fixed neighbor nest. After that, all the birds were permitted to incubate eggs for 10–15 min. The nest was then again moved a certain distance, and so on. The measured distances were between the centers of the nests. The territorial interactions of the occupants of both nests (moveable and stationary) were recorded. Usually the host of the stationary nest permitted the "intruding" pair to come closer to its nest than the initial distance between these nests. However, when the moveable nest reached a certain area around the stationary one, the host of the latter kicked the "intruding" pair out of their own nest. It did so despite resistance from the occupants of the moveable nest. More often, however, the moveable nest's tern stopped following its nest. As a result of these experiments it was sometimes possible to determine the size of the most defended area immediately surrounding a nest. This area was called the Core Area or Core Zone (Kharitonov, Kharitonova, 1995). The distance between the centers of the nests during the last steps of the experiment reflects the Core Area radius (Fig. 2). The Core Zone cannot be seen by means of direct observation and could be detected only by experiments.

Since the birds were largely vulnerable to human disturbance during early incubation, 34 experiments remained uncompleted. Their main purpose was only to determine the initial aggressive reaction of the birds. Overall observation time (including that spent carrying out the experiments) totaled 231 hrs, 25 minutes over three years; the number of experiments was 232 (Table 1).

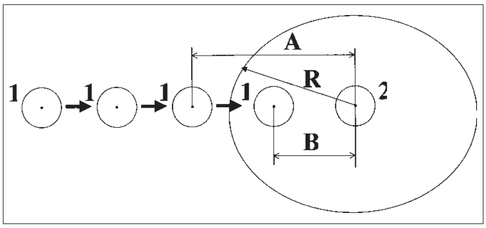

Fig. 2. Determination of the Core Area (Core Zone) Radius (Kharitonov, Kharitonova, 1995): 1 – moveable nest, 2 – stationary nest; A – distance at which Bird 1 is still sitting on its nest, B – distance at which Bird 2 drives away Bird 1, R – Core Zone radius A ≥ R ≥ B.
Рис. 2. Определение радиуса абсолютно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

Tern behavior was recorded during the first 10–15 minutes after each nest movement. Then the overall behavior flow was split up into a number of patterns (Hinde, 1970). Later, in processing data, a 10 cm-interval scale was devised (from 0 to 160 cm), and all numerical values of each pattern superimposed on it. An aggregate table of pattern frequencies was formulated, and for each 10-cm segment the numerical value of a particular pattern was counted only once (including zero values).

Table 1

Number of experiments performed in 2000, 2001 and 2003
(L – initial distance between nests)
Количество экспериментов, проведенных в 2000, 2001 и 2003 гг.

L, cm	Completed experiments	Uncompleted experiments	"Abnormal" experiments	Row totals
50–80	41	11	4	56
80–110	82	14	6	102
110–140	42	8	5	55
>140	18	1	0	19
Column totals	183	34	15	232

Table 2

Frequency of occurrence of patterns in experiments
Частота встречаемости паттернов в экспериментах
1 – 50–80 cm, 2 – 80–110 cm, 3 – 110–140 cm, 4 – >140 cm

1

Patterns \ L,cm	160-150	150-140	140-130	130-120	120-110	110-100	100-90	90-80	80-70	70-60	60-50	50-40	40-30	30-20	20-10	10-0	Experiment number in which pattern occurred	Total number of experiments	Percent of total
I. Occupation of Nest in Comfort[1]									1	6	9	7	3				26	52	50,0
II. Discomfort Behavior[2]										7	13	15	20	10			35	41	85,4
III. Aggression S: R(A) M: R(A)										5 2	7(2) 6	15 5(1)	22(5) 14(3)	23(11) 11(6)	2 1		39 27	41	95,1 65,9
IV. Bird Stops Getting on Nest S: M:											 1	 4	 13	2 19	1 1		3 38	41	7,3 92,7
V. Moveable Bird Looks for Original Nest Site										3	5	16	17	13			29	41	70,7
VI. Neighbor Nest Seizure														3	2		5	41	12,2
VII. Disappearance S: M:											 1	 6	1 2	2 4			3 10	41	7,3 24,4

2

Patterns \ L,cm	160-150	150-140	140-130	130-120	120-110	110-100	100-90	90-80	80-70	70-60	60-50	50-40	40-30	30-20	20-10	10-0	Experiment number in which pattern occurred	Total number of experiments	Percent of total
I. Occupation of Nest in Comfort							3	11	21	17	8	4					64	96	66,7
II. Discomfort Behavior							1	10	17	31	45	36	32	16			78	82	95,1
III. Aggression S: R(A) M: R(A)							1	9 1	13 5	31(2) 9	46 8	35(4) 14(4)	48(6) 17(3)	21(10) 6(4)	1		78 38	82	95,1 46,3
IV. Bird Stops Getting on Nest S: M:									 1	 2	 5	 8	3 33	2 25	 3		5 77	82	6,1 93,9
V. Moveable Bird Looks for Original Nest Site							2	6	7	19	23	20	35	17			62	82	75,6
VI. Neighbor Nest Seizure													2	1	1		4	82	4,9
VII. Disappearance S: M:									2 2	1 3	3 3	4 2	7 8	4 5	 1		20 21	82	24,4 25,6

3

Patterns \ L,cm	160-150	150-140	140-130	130-120	120-110	110-100	100-90	90-80	80-70	70-60	60-50	50-40	40-30	30-20	20-10	10-0	Experiment number in which pattern occurred	Total number of experiments	Percent of total
I. Occupation of Nest in Comfort					1	4	12	9	10	3	3	2					44	50	88,0
II. Discomfort Behavior						2	6	4	12	17	22	12	19	1			35	42	83,3
III. Aggression S: R(A) M: R(A)						1 1	4 2	3 1	9(1) 3	10 6	21(2) 3	13(2) 2(2)	26(6) 8(3)	4(3) 3(1)			36 17	42	85,7 40,5
IV. Bird Stops Getting on Nest S: M:										 4	 3	 4	 21	1 8	 1		1 41	42	2,4 97,6
V. Moveable Bird Looks for Original Nest Site					3	4	8	6	8	7	14	11	18	4			34	42	81,0
VI. Neighbor Nest Seizure													2	3	1		5	42	11,9
VII. Disappearance S: M:					 1	1 	 1	2 1	 2	 2	 4	 2	 4				3 13	42	7,2 31,0

End of the Table 2

4

Patterns \ L,cm	160-150	150-140	140-130	130-120	120-110	110-100	100-90	90-80	80-70	70-60	60-50	50-40	40-30	30-20	20-10	10-0	Experiment number in which pattern occurred	Total number of experiments	Percent of total
I. Occupation of Nest in Comfort	1				1	3	3	3	4	3	1						19	19	100,0
II. Discomfort Behavior					2	1	3	3	5	9	9	6	7	1			18	18	100,0
III. Aggression S: R(A)						1	2	2	3	7	7	6(2)	9(1)	1(1)			18	18	100,0
M: R(A)					2		1	1	2	1(1)	3	3	3	1			11		61,1
IV. Bird Stops Getting on Nest S:																	0	18	0,0
M:										1	1	4	9	3			18		100,0
V. Moveable Bird Looks for Original Nest Site			2	1	3	3	4	4	3	7	5	5	7	2			14	18	77,8
VI. Neighbor Nest Seizure													1				1	18	5,6
VII. Disappearance S:										1		1					2	18	11,1
M:										2	1	1	3				5		27,8

Comments. R – aggressive rattle, A – attack, S – bird occupying stationary nest, M – bird occupying movable nest; first gray stripe (left) – boundary of the first layer of the Conflict Zone (Outer Layer), second one (right) – boundary of the second layer of the Conflict Zone (Inner Layer).

[1] To prevent overloading the table, only the final point at which terns still "occupy the nest in comfort" is shown for Pattern I in each experiment. For example, the numbers "1," "6," etc., mean that only one case was recorded where a tern still "occupied the nest in comfort" within the 80–70 cm segment; six cases were recorded in the 70–60 cm segment, etc. In this way, each separate experiment could only have one last "comfort" nest occupation. The numerical values of the pattern in experiments are equal to the number of experiments. The same holds for Pattern IV.

[2] In each experiment any pattern could be identified and recorded several times, within the various 10-cm segments – for example, within the 70–60 cm segment, 50–40 cm, 40–30 cm, etc. Consequently, the numerical values of the pattern in the experiments are larger than the total number of these experiments. The same holds for Patterns III, V, VI, and VII.

Thus, a series of movements over distances shorter than 10 cm was eliminated by the scale.

In 74 experiments conducted in 2003, tern behavior was recorded at strict 10-minute intervals from the first appearance of their occupants at the moveable and stationary nests, and sequential moving of the nest carried out in more uniform segments of 10–15 cm. Resulting tables were compiled analyzing patterns labeled "Aggression" and "Moveable Nest's Bird Looks for Original Nest Site".

During experiments so-called "alarm"–upflights" or "dreads" (Lind, 1963a, 1963b – review in: Cramp, 1985; Sears, 1981) were observed in which the entire flock flew up in fear of the observation booth. However, this occurred when the observer was sitting inside the booth. I had, therefore, to register several aggressive reactions, for example, instead of one. However, since this factor was continuously present throughout all the studies and occurred at comparatively regular time intervals, it was considered not to have influenced the overall picture of pattern distribution.

Performing a statistical analysis of the data, I used the distribution-free Wilcoxon test for comparing two independent groups (Hollander, Wolfe, 1973). Because in several cases the sample size was not large, conclusions were drawn by comparing the observed values (calculated in the software package STADIA 6.0) with the critical values found in the tables (Hollander, Wolfe, 1973). I used STATISTICA 6.0 (StatSoft, Inc. 1984–2001) for all other statistical analyses.

3. Results and discussion

For identifying structural units of a territory, the seven patterns which occurred most frequently in the experiments were used. On that basis an aggregate table of pattern frequencies was devised in which the initial distances between nests were subdivided into four classes (Table 2).

Pattern I. "Occupation of Nest in Comfort". Both the moveable and stationary nest's birds are present, sit on their nests, and pay no discernible and visible (for the observer!) attention to each other. There is no aggression and hesitation while getting on the nests. The order in which birds occupied their nests was disregarded. Whenever aggression and hesitation were recorded as early as the first nest-moving stage of the experiment, it was considered to have no Pattern I and was not included in the corresponding column of the table. Data for the uncompleted experiments were included in Table 2.

Pattern II. "Discomfort Behavior". Both birds get on their nests and continue nesting, but already display signs of discomfort (mainly aggressive reaction; also hesitation, fright, and searching for the nest at its original site).

Pattern III. "Aggression". This pattern includes: a) aggressive rattles ("Ack-, Chip-, Rattle-calls"– Lind, 1963a; Sears, 1981), plus exhibiting the open bill with a bright red oral cavity to the opponent; and b) attack (ground and aerial).

Pattern IV. "Bird Stops Getting on Nest". Due to an increasing feeling of discomfort one of the two birds stops getting on its nest (> 15–20 min). In most cases, this occurred when the two nests were only 30–40 cm apart. In cases where, having sat on its nest for a certain period of time, a bird arose and then sat no more, such behavior was considered simultaneously as both "Discomfort Behavior" and "Bird Stops Getting on Nest," and recorded in both patterns. 32 cases with the Core Area revealed were included in Table 2 as Pattern IV.

Pattern V. "Moveable Nest's Bird Looks for Original Nest Site". The moveable nest's tern gets up from it and walks towards its original nest site. The tern scratches around there searching for its eggs. After futile searches, it turns back. The passage of a bird from its moveable nest toward the original nest site and back was considered to be one complete unit of this pattern.

Pattern VI. "Seizure of Neighboring Nest/Passive Moving onto Neighbor's Nest". The difference between seizure of the moveable nest and passive crossing over to the moveable nest by the stationary nest's bird during near nest approach was disregarded in both cases. This pattern often occurred in the "abnormal experiments," when the movable and stationary nests were only 15–25 cm apart (see below). The "abnormal experiments" were not included in the table of pattern frequencies, but rather examined separately. In all other cases the pattern was included in the table.

Pattern VII. "Disappearance". "Disappearance" is defined as a 5–15 min delay in getting on the nest after the whole flock has landed. If a bird under observation disappeared for > 20 min, the experiment was halted and excluded from analysis in this study.

Thus, at each moving stage in the course of a single experiment a tern might display several patterns, for example "Bird Stops Getting on Nest," "Moveable Nest's Bird Looks for Original Nest Site," "Disappearance," and "Aggression."

As concerns "Domination", dominant birds are considered to be those displaying a greater number of aggressive rattles and attacks. At the conclusion of the experiment the dominant bird often remained in its nest incubating. The leading (dominant) position could change during the experiment (especially after nest-relief).

As the moveable and stationary nests approached each other, the stationary nest's occupant responded in various ways to the intruder, depending on the distance between the two nests. It turns out that the space surrounding a Gull-billed Tern nest consists of three elements, or units, which are invisible through direct observations, but differ significantly in level of aggressiveness and absence or presence of certain behavior patterns.

The very small area directly surrounding the nest is known as the Core Area (the Core Zone), which is encircled by a larger Conflict Zone (terms suggested by Kharitonov, 1978). The Conflict Zone, in turn, is divided into a lesser conflict Outer Layer and a greater conflict Inner Layer adjacent to the Core Area.

3.1. Conflict Zone

At a certain point in the moving stage, the moveable nest first enters this territorial unit. The Conflict Zone is a space around the nest in which one of the terns elicits an aggressive reaction from its neighbor. Within the Conflict Zone, two components could easily be discerned – Outer Layer and Inner Layer.

3.1.1. Outer Layer

The main indication that the Outer Layer has been breached is the first aggressive reaction a tern displays to its neighbor. However, it is rather weak and in most cases non-obligatory within a certain moving stage. The nest's owners often preferred "to take no notice" of its neighbor's approach.

The order of priority in which birds took their nests was important. If the moveable nest's occupant managed to get on its nest sooner, the stationary nest's tern then took its seat silently, without aggressive signs, despite its antagonistic behavior the previous time when getting on first (as mentioned earlier, there were several attempts to get on the nest during a moving stage because of the "dreads"). This circumstance should be taken into account; otherwise, the distance value of the first aggression could be significantly underestimated.

Thus, during the step-by-step moving of the moveable nest towards the stationary nest, on a certain piece of space known as the Outer Layer, there are both "Sitting on Nest in Comfort" and "Discomfort Behavior" (Table 2 – Patterns I, II). These patterns could be combined in one experiment or occurred separately in different experiments, during one or several step-by-step movings. The number of attacks is not significant (Table 2 – Pattern III). Despite the appearance of threat, the moveable nest's terns followed their nests rather well and in most cases did not abandon them (Table 2 – Pattern IV).

Due to a weak aggressive reaction in this layer, its external boundary varied greatly. The external boundary was most discernible in experiments with 1- to 10-day-old clutches in low-density areas deprived of vegetation. As the initial distance between nests increased, the external boundary of the Conflict Zone (the Outer Layer) increased as well (Table 2).

3.1.2. Inner Layer

In general, this layer is characterized by an increase in the aggressiveness level, firstly for the stationary nest's occupant. In this layer, relations between the birds became increasingly tense. At the outer boundary of the Inner Layer the last "Comfort Sittings" ended (Table 2 – Pattern I). There was exclusively "Discomfort Behavior" (Table 2 – Pattern II). After that, the number of moveable nest birds ceasing to follow and get on their nests increased sharply, as compared with the Outer Layer (Table 2 – Pattern IV – distribution-free Wilcoxon test for comparing two independent groups, 50–80 cm: $W_{obser.} = 34 > W_{crit.}(6, 4) = 31$, N = 10, P = 0,033; 80–110 cm: $W_{obser.} = 81 > W_{crit.}(10, 6) = 68$, N = 16, P = 0,036; 110–140 cm: $W_{obser.} = 23,5 > W_{crit.}(6, 3) = 22$, N = 18, P = 0,048; >140 cm: $W_{obser.} = 33,5 > W_{crit.}(6, 4) = 31$, N = 20, P = 0,033). In antagonistic behavior, the share of attacks magnified (Table 2 – pattern III) – one of the birds, fearing for its nest, at-

Table 3

Mean changes ($\bar{X}$) in the “aggression” pattern (attacks and aggressive rattles) at 10-min intervals as one nest is steadily moved toward the other during experiments
Средние изменения в паттерне “агрессия” (атаки и агрессивное стрекотание) по 10-минутным интервалам, пока одно гнездо приближалось к другому в ходе эксперимента
1 – 50–80 cm (14 experiments*), 2 – 80–110 cm (30), 3 – 110–140 cm (19), 4 – >140 cm (11)

1

L, cm	$\bar{x}_1 \pm SE$: S→M**	$\bar{x}_2 \pm SE$: M→S	$\bar{X} \pm SE$
80–70	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
70–60	3,1 ± 1,9	0,3 ± 0,3	3,4 ± 1,9
60–50	4,1 ± 1,7	1,0 ± 0,8	5,1 ± 1,8
50–40	6,4 ± 2,7	0,3 ± 0,3	6,7 ± 2,7
40–30	4,7 ± 1,9	1,4 ± 0,5	6,1 ± 1,9

2

L, cm	$\bar{x}_1 \pm SE$: S→M	$\bar{x}_2 \pm SE$: M→S	$\bar{X} \pm SE$
110–100	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
100–90	0,0 ± 0,0	0,6 ± 0,6	0,6 ± 0,6
90–80	1,5 ± 0,8	0,0 ± 0,0	1,5 ± 0,8
80–70	2,8 ± 0,9	0,1 ± 0,1	2,8 ± 0,9
70–60	4,2 ± 1,2	0,6 ± 0,4	4,9 ± 1,3
60–50	5,0 ± 0,9	1,1 ± 0,6	6,1 ± 1,1
50–40	6,1 ± 1,8	2,9 ± 1,2	8,9 ± 1,9
40–30	8,4 ± 1,2	3,7 ± 1,6	12,1 ± 2,2

3

L, cm	$\bar{x}_1 \pm SE$: S→M	$\bar{x}_2 \pm SE$: M→S	$\bar{X} \pm SE$
140–130	0,00 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
130–120	0,00 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
120–110	0,00 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
110–100	0,20 ± 0,2	0,4 ± 0,4	0,6 ± 0,4
100–90	0,22 ± 0,2	0,1 ± 0,1	0,3 ± 0,2
90–80	0,63 ± 0,4	0,0 ± 0,0	0,6 ± 0,4
80–70	1,00 ± 0,4	0,1 ± 0,1	1,1 ± 0,4
70–60	2,56 ± 0,8	0,3 ± 0,2	2,9 ± 0,7
60–50	3,58 ± 0,9	0,0 ± 0,0	3,6 ± 0,9
50–40	6,60 ± 1,2	0,2 ± 0,2	6,8 ± 1,3
40–30	6,00 ± 1,6	1,6 ± 0,8	7,6 ± 2,0

tacked its neighbor who had approached the short distance (distribution-free Wilcoxon test for comparing two independent groups, 50-80 cm: $W_{obser.} = 34 > W_{crit.} (6, 4) = 31$, N = 10, P = 0,033; 80–110 cm: $W_{observ.} = 81 > W_{crit.} (10, 6) = 68$, N = 16, P = 0,036; 110–140 cm: $W_{obser.} = 24 > W_{crit.} (6, 3) = 22$, N = 18, P = 0,048). For distance group > 140 cm, the difference in numbers of attacks between the two layers of the Conflict Zone is insignificant, owing to insufficient data. However, when general turmoil calmed down, for example, following an “alarm”-upflight,”, and all the neighbors gradually reoccupied their nests, the attacked tern approached its nest stealthily and got on it quietly, thereby attempting to elicit no strong aggressive reaction from its neighbor. Both birds continued incubating, as before.

Within the entire Conflict Zone, the terns of the moveable nests tried to find their nests at the original nest site (Table 2 – Pattern V).

Tables 3 and 4 show the mean change of the “Aggression” and “Moveable Nest’s Bird Looks for Original Nest Site” patterns during 10-minute intervals when moving the moveable nest towards the stationary one up to the Core Area. One can see that the level of aggressiveness of both birds rises when their nests approach each other (Spearman’s rank correlation coefficient, 50–80 cm: R = – 0,3, N = 43, P < 0,05; 80–110 cm: R = –0,6, N = 113, P < 0,001; 110–140 cm: R = –0,75, N = 84, P < 0,001; > 140 cm:

R = –0,6, N = 61, P < 0,001), while the increase in the number of times a tern searches for its original nest site is less, depending on the nest-distance decrease (Spearman's rank correlation coefficient, 50–80 cm: R = – 0,5, N = 30, P < 0,05; 80–110 cm: R = –0,5, N = 110, P < 0,001; 110–140 cm: R = –0,4, N = 76, P < 0,01; >140 cm: R = –0,44, N = 72, P < 0,001) (Table 3 and 4).

Seizure of the neighbor's nest or passive occupation of it was a quite infrequent phenomenon and observed at the boundary of the Conflict and Core Zones, or directly in the Core Zone (Table 2 – Pattern VI).

End of the Table 3

4

L, cm	$\overline{x}_1$ ± SE: S→M	$\overline{x}_2$ ± SE: M→S	$\overline{X}$ ± SE
160–150	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
150–140	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
140–130	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
130–120	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
120–110	0,0 ± 0,0	0,2 ± 0,2	0,2 ± 0,1
110–100	0,4 ± 0,4	0,0 ± 0,0	0,4 ± 0,4
100–90	0,5 ± 0,5	0,0 ± 0,0	0,5 ± 0,5
90–80	0,3 ± 0,3	0,3 ± 0,3	0,5 ± 0,3
80–70	0,3 ± 0,2	0,3 ± 0,3	0,7 ± 0,3
70–60	1,5 ± 0,9	0,5 ± 0,3	2,0 ± 0,9
60–50	1,4 ± 0,4	0,0 ± 0,0	1,4 ± 0,4
50–40	4,4 ± 1,8	0,3 ± 0,3	4,7 ± 1,8
40–30	2,0 ± 0,5	0,7 ± 0,6	2,7 ± 0,8

* Each experiment consists of several observations: one observation in each 10-cm segment of 10-min intervals.
** The occupant of the stationary nest reacts aggressively to its moveable neighbor; the third column is the reverse.

In the experiments with an initial distance of 110–140 cm between nests, the moveable nest's terns were absent more frequently than the terns in the stationary nest ($\chi^2 = 6,3$, df = 1, P < 0,05). In other experiments (with initial distances of 50–80 cm, 80–110 cm and > 140 cm between nests), differences are insignificant, likely owing to insufficient data (Table 2 – Pattern VII).

It may be seen clearly that the number of experiments containing Pattern I ("Occupation of Nest in Comfort") increases as the initial distance between nests increases (Table 2, the last column "Percent of Total"). In the experiments with closely arranged nests (50–80 cm), Pattern I may be found only in half of all the experiments, whereas in experiments with an initial distance of approximately 1,5 m between nests, the pattern occurs in each experiment (50–80 cm and 80–110 cm: $\chi^2 = 3,3$, df = 1, P < 0,05; 50–80 cm and 110–140 cm: $\chi^2 = 15,4$, df = 1, P < 0,001; 50–80 cm and >140 cm: $\chi^2 = 12,91$, df = 1, P < 0,001, one-tailed). This fact indicates that closely arranged tern nests are located within the Conflict Zone initially – i.e. the Conflict Zones of neighboring nests are subject to overlap. This is also confirmed by direct observations. In a number of cases in dense colony plots, aggressive rattling of neighboring terns was registered when they were getting onto their nests. The distance between those nests did not exceed 70–80 cm. The reduced negative correlation (–0,3) between the distance and aggressiveness in the experiments with an initial distance of 50-80 cm, as compared to correlations for the other initial nest-distance groups (Table 3), also supports this presupposition.

3.1.3. Domination

In most experiments, the terns of moveable nests, affected by an increasing sense of discomfort, stopped following and getting onto their nests; only infrequent instances of the opposite situation were recorded (Table 2 – Pattern IV). In the latter case, females were usually the occupants of stationary nests who were afraid to sit on the nest because of aggressive males sitting close by on their move-

Table 4

Mean changes ($\overline{X}$) in the "Moveable Nest's Bird Looks for Original Nest Site" Pattern at 10-min intervals as one nest is steadily moved towards the other during experiments
Средние изменения в паттерне "поиск гнезда на старом месте" по 10-минутным интервалам, пока одно гнездо приближалось к другому в ходе эксперимента

L, cm	$\overline{X} \pm SE$, 50–80 cm (12 experiments*)	$\overline{X} \pm SE$, 80–110 cm (29 experiments)	$\overline{X} \pm SE$, 110–140 cm (17 experiments)	$\overline{X} \pm SE$, > 140 cm (12 experiments)
160–150				0,0 ± 0,0
150–140				0,0 ± 0,0
140–130			0,0 ± 0,0	1,0 ± 0,7
130–120			0,0 ± 0,0	0,3 ± 0,3
120–110			1,3 ± 0,7	0,9 ± 0,7
110–100		0,0 ± 0,0	1,0 ± 0,4	0,8 ± 0,8
100–90		0,5 ± 0,5	0,7 ± 0,3	0,4 ± 0,2
90–80		0,5 ± 0,3	1,0 ± 0,6	1,0 ± 0,5
80–70	0,0 ± 0,0	0,5 ± 0,3	1,2 ± 0,7	0,6 ± 0,4
70–60	0,7 ± 0,3	1,3 ± 0,4	1,9 ± 1,0	0,7 ± 0,2
60–50	0,4 ± 0,3	1,0 ± 0,2	2,2 ± 0,6	1,6 ± 0,5
50–40	2,2 ± 1,3	1,2 ± 0,3	2,6 ± 1,1	4,8 ± 1,9
40–30	2,9 ± 0,7	3,0 ± 0,4	2,7 ± 0,5	2,0 ± 0,5

* Each experiment consists of several observations: one observation in each 10-cm segment of 10-min intervals.

able nests. Generally, the occupants of stationary nests behaved more aggressively than those of moveable ones (Table 3) (distribution-free Wilcoxon matched pairs test, 50–80 cm: Z = 3,2, N = 29, P < 0,01; 80–110 cm: Z = 5,5, N = 85, P < 0,001; 110–140 cm: Z = 5,3, N = 48, P < 0,001; >140 cm: Z = 3,2, N = 25; P < 0,01) and dominated throughout the experiments (Table 5).

3.2. Core Zone

This is the small area around the nest into which no intruder is permitted. In the Core Zone, a stationary nest's occupant attacks its moveable neighbor whenever the latter attempts to get onto its moveable nest; therefore each attempt of the moveable bird to sit on its nest results in failure.

In spite of considerable difficulty in revealing it (most of the moveable nest's terns gave up trying to follow their nest somewhere on the approach to this territorial unit – Table 2, Pattern IV), the Core Zone really exists. In 32 cases, its radius (R) was determined. The minimum radius of the Core Zone was $20 \leq R \leq 23$ cm; the maximum radius was $32 \leq R \leq 49$ cm; the mean radius was $26{,}13 \pm 0{,}48 \leq \overline{R} \leq 33{,}81 \pm 0{,}96$ cm (N = 32).

To examine the Conflict Zone and the Core Zone boundary changes as the initial distance between nests increases (i.e., as colony density changes), the growth rate index has been used (Table 6). It is clearly seen that the very first layer of the Conflict Zone is subject to the largest variation, and that the Core Zone is the most stable unit of the three. As the distance between nests increases by 92 %, the

Table 5

Dominant position of Gull-billed Terns during experiments
(L = Initial distance between nests)
Доминирование у чайконосых крачек во время экспериментов

L, cm	Dominant Position (number of experiments)		
	S	M	S↔M*
50–80	32	3	6
80–110	72	2	8
110–140	36	1	5
> 140	15	1	2
Total	155	7	21

* The dominant position changes during the experiment

Core Zone mean radius ($\overline{R}$) increases by 10,6 % (U = 20,5, P < 0,05, Mann-Whitney U test), while the first and second layers of the Conflict Zone increase by 61,5 % and 28,6 %, respectively. The value of the Core Zone mean radius for the distance interval of > 140 cm is in single digits (Table 6).

In most cases when determining the Core Zone, both nests were drawn together until the occupant of the stationary nest, sitting in it, could reach for its neighbor's bill and snap at it. In some experiments, unsuccessful tern attempts to lunge at its opponent were recorded; however, the distance between nests was not close enough to attack, and the bird preferred simply to sit tensely on the nest and show 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, their individual distance is identified and associated with that spot.

3.3. "Abnormal experiments"

Here, the "abnormal experiments" should be noted (Table 1). In these experiments, lowered aggressiveness or its complete absence in the occupants of both nests (moveable and stationary) was recorded and, eventually, it was possible to move two nests very close to each other with no space in between. Extensive additional observations of such nests indicated that this occurred when there were females in both nests at the last moving stages. In contrast, males in "abnormal experiments" were "normal" and occasionally even extra aggressive. Later on, as the male relieved the female

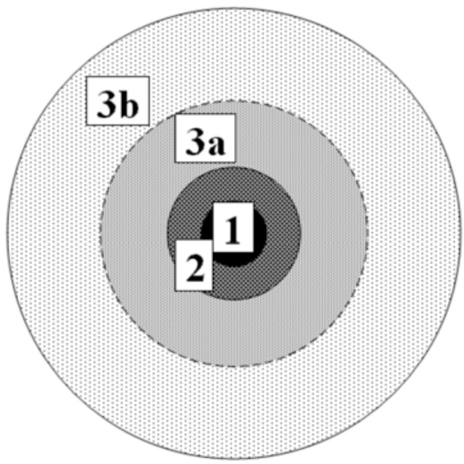

Fig. 3. Diagrammatic representation of the territorial structure of the Gull-billed Tern.
Рис. 3. Схематическое представление территориальной структуры у чайконосой крачки.
1 – nest; 2 – Core Area (Core Zone); 3 – Conflict Zone: 3a – Inner Layer, 3b – Outer Layer.

Table 6

Dynamics of three territorial units: Outer Layer, Inner Layer and Core Zone, as the distance between nests changes
Динамика трех территориальных единиц: первый и второй слой зоны конфликтов и абсолютно охраняемая зона

L, cm	Boundary of Outer Layer in Conflict Zone, cm (N)*	Growth rate index, %		Boundary of Inner Layer in Conflict Zone, cm (N)	Growth rate index, %		Radius, cm $\overline{R} \pm SE$ (N)	Growth rate index, %	
		in comparison with previous level	in comparison with base level (50–80 cm)		in comparison with previous level	in comparison with base level (50–80 cm)		in comparison with previous level	in comparison with base level (50–80 cm)
50–80	60–70 (7)	–	–	30–40 (3)	–	–	28,5 ± 0,9 (14)	–	–
80–110	90–100 (1)	46,2	46,2	40–50 (4)	28,6	28,6	31,0 ± 1,05 (10)	8,6	8,6
110–140	100–110 (2)	10,5	<u>61,5</u>	40–50 (2)	0,0	<u>28,6</u>	31,6 ± 1,8 (7)	1,8	<u>10,6</u>
> 140	110–120 (2)	9,5	76,9	50–60 (1)	22,2	57,1	28,5 ± 0,0 (1)	-9,7	-0,1

* The length of the layer radius is given (measured from the center of the nest). For example, 60–70 (7) means that the radius length is 60–70 cm, and the Outer Layer boundary was determined by seven marginal numerical values of Pattern II “Discomfort Behavior” (see Table 2, 50–80 cm), and so on. The boundary of the Inner Layer was determined by marginal numerical values of Pattern I “Occupation of Nest in Comfort” (see Table 2).

at the nest, the "abnormal" situation turned into the "normal" one. Such behavior is evidence that birds recognize their neighbors by sex, and that females are apparently less aggressive than males, at least in some parts of the colony. They are able only to maintain and adhere to the territorial boundary line established by males (Lind, 1963a) and not always even that, as experiments have indicated. In this way, the expression "abnormal experiments" merely emphasizes specific features of certain individuals and the distinction in aggressiveness of the partners, or more correctly, lowered female aggressiveness in certain experiments compared with the general level of aggressiveness in most experiments.

3.4. Conclusion

Thus, the Gull-billed Tern demonstrates a multilayer spatial structure (Fig. 3). In this structure, a marked increase in the level of aggressiveness occurs in an inward direction from the periphery toward the nest according to the following pattern: complete absence of discomfort behavior and aggression → the first layer of the Conflict Zone → the second layer of the Conflict Zone → the Core Zone (the Core Area). In the Core Zone terns' aggressiveness reaches its highest point, and is expressed in their intolerance towards other individuals. The Core Zone is the most stable unit of the three and seems to determine the existence of the two Conflict Zone layers, in which a tern expresses its attitude and tolerance towards other individuals depending on their distance from its nest.

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