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THE PHENOMENON OF SYNCHRONOUS TAKE-OFFS IN GULL-BILLED TERNS

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Abstract. The phenomenon of synchronous takes-off displayed by Gull-billed Terns was studied during the pre-nesting period on Lakes Shalkar and Ayke, in southern Russia in 2000, 2003 and 2004. Synchronous take-offs of Gull-billed Terns are prominent phenomena observed during the pre-nesting period, and they could be considered as a component of pre-nesting aerial and ground behavior in this species. The intensity and dynamics of synchronous take-offs are influenced by a number of factors, among the more prominent ones being the time of the day, number of birds and weather conditions. The maximum number of synchronous take-offs was recorded in the morning and evening hours when the most birds were present at the gathering and roosting site. With the arrival of new parties of birds to the site the number of synchronous upflights increases, then reaches the maximum and stops rising when the mean number of birds is approximately 70 individuals per hour. The high intensity of synchronous take-offs is thought to be attributed to the abrupt change in the bird number per time unit, which occurs in the evening particularly from 19^{00} to 20^{30}. Air temperature and wind speed also have impacts on the intensity of synchronous take-offs, especially at their extreme values: strong wind in conjunction with low temperatures lowers the intensity of synchronous take-offs and vice versa. Synchronous take-offs are strongly suspected to be an adaptive mechanism permitting synchronous egg-laying and thus reducing overall duration of maximal reproductive stages, which is very important when nesting in unstable habitats.

Key words: Gull-billed Tern, *Gelochelidon nilotica*, behavior, courtship display, number of birds.

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Феномен синхронных взлетов у чайконосых крачек. - Е.В. Барбазюк. - Беркут. 15 (1-2). 2006. - Синхронные взлеты у чайконосых крачек представляют собой ярко выраженное явление, наблюдаемое в предгнездовой период, и могут рассматриваться как часть брачного поведения этого вида. На интенсивность и динамику синхронных взлетов влияет ряд факторов, наиболее заметными из которых являются время суток, численность птиц, участвующих во взлетах, и погодные условия. Максимальные значения синхронных взлетов наблюдались в утреннее и вечернее время, когда на месте ночевки присутствовала большая часть птиц. Число синхронных взлетов увеличивается по мере прибытия новых партий птиц на место постоянного сбора и ночевки, становится максимальным и перестает расти при средней численности примерно 70 птиц за час. Предполагается, что высокая интенсивность синхронных взлетов связана с резким скачками численности птиц за единицу времени, что происходит в вечернее время, особенно с 19^{00} до 20^{30}. Температура воздуха и ветер могут также оказывать влияние на интенсивность синхронных взлетов, особенно существенное при своих экстремальных значениях. Сильный ветер в сочетании с низкими температурами снижает интенсивность взлетов и наоборот. Предполагается, что синхронные взлеты являются приспособительным механизмом, позволяющим синхронизировать процесс откладки яиц и сократить таким образом максимально процесс размножения, что крайне важно при гнездовании в нестабильных биотопах.

Introduction

This study addresses an interesting phenomenon exhibited by Gull-billed Terns (*Gelochelidon nilotica*) early in the season, during pre-nesting phase – collective upflights (Lind, 1963b), or rising up high in the air of the whole bird flock.

The question of the collective flights in the pre-nesting period, their dynamics, intensity and determining factors have virtually not been studied previously. Scanty literature on Gull-billed Terns behavior provides no reference to synchronous upflight display in this species. Cramp's comprehensive review on the Gull-billed Tern (1985) says nothing about this notable pattern of social behavior. Collective flights, or the rising up of the whole flock into the air, are described by Lind (1963b) for the Sandwich Tern (*Sterna sandvicensis*). He suggested that such communal flights might exert positive influence on the sexual behavior of the birds (Lind, 1963b). Meanwhile, my observations have shown, synchronous upflights

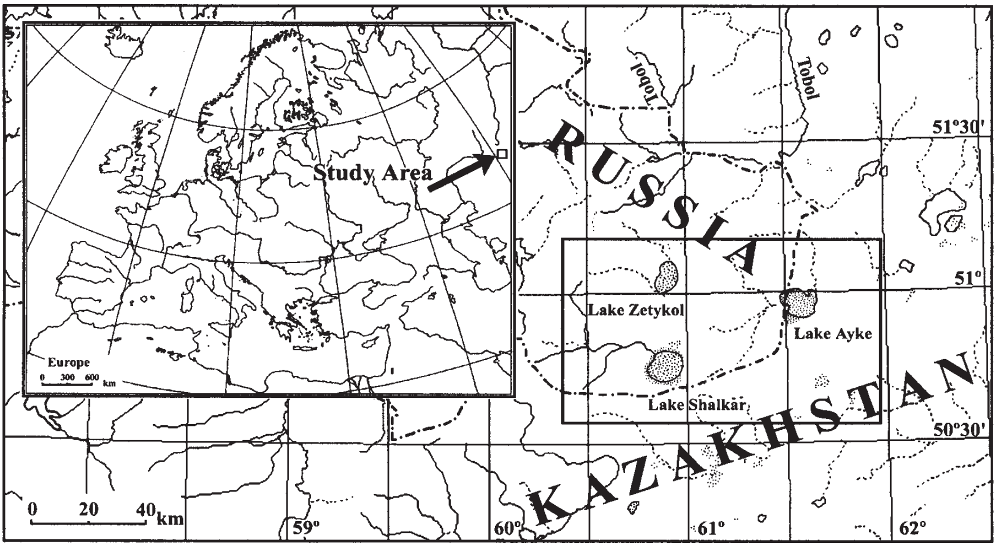

Fig. 1. Study Area. Рис. 1. Район исследований.

are a prominent and important constituent in tern behavior during courtship and pair-formation.

The Gull-billed Tern belongs to a group of Laridae, forming nesting settlements, known as the "second type". Type II species colonize areas for short periods initially with high nesting in great densities. It is thought that normally later in nesting cycles territories diminish in size only imperceptively, and distances between nests are nearly constant throughout incubation in undisturbed colonies. The settlement process of nesting is highly synchronous in this communally nesting species 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 (McNichol, 1975; Møller, 1982; Kharitonov, Siegel-Causey, 1988), such as those in the study area (see the Study Area section).

Thus, detailed study of the primary causes and determining factors underlying synchronous upflights during the pre-nesting stage could make clear a number of important biological features of type II species obvious during early egg-laying and incubation phases, such as causes for highly synchronous breeding, and the rate and manner of nesting settlement formation.

Study Area

The study was conducted in Gull-billed Tern colonies on Lakes Shalkar (50º47´N 60º55´E) and Ayke (50º58´N 61º30´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 –17ºC, in July – +21ºC.

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 for their full depth. Roughly 70 % of the lake's surface may be covered with Common Reed (*Phragmites communis*), Bulrush (*Scirpus lacustris*), and Narrow-leaved Cattail (*Typha angustifolia*). 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, which makes plant cover a heterogeneous mosaic (Ryabinina et al., 1996; Davygora, 2000; Sviridova, 2000).

Methods

The studies were conducted on Lakes Shalkar and Ayke in May–June, 2000, 2003, and 2004. Overall observation time viewing Gull-billed Tern synchronous upflights totaled no less than 130 hrs (23 days) under varied weather conditions (with the exception of prolonged widespread rain), and 109 hrs of the total were used in the analysis. Consequently, any one day contained several hour-long observations (e.g. 17^{00}–18^{00}, 18^{00}–19^{00} hrs and so on) that were rated as independent cases. The bulk of the work was done on Lake Ayke from 24 April to 10 May 2003 and 2004, primarily in the evening and late daylight hours. For the convenience of the data presentation, this

Table 1

Some Characteristics of Periods

Некоторые характеристики периодов

Parameters / Periods	Time Limits, hours	Independent Number of Hours-observations for 3 Years	Number of Synchronous Upflights per Hour			Mean Number of Birds per Hour, birds			Temperature per Hour, °C			Wind Speed per Hour, m/s		
			min.	max.	mean ±SE	min.*	max.	mean ±SE	min.	max.	mean ±SE	min.	max.	mean ±SE
Morning	$5^{00}-10^{00}$	16	1	12	5.25 ±0.73	12.32	145.12	57.88 ±8.04	+1.40	+13.00	+8.85 ±1.03	1.50	9.00	4.10 ±0.42
Daytime	$11^{00}-17^{00}$	44	0	5	2.50 ±0.24	4.15	65.62	27.45 ±2.08	+9.60	+20.00	+14.55 ±0.51	1.50	10.10	5.49 ±0.43
Evening	$17^{00}-21^{00}$	49	0	11	4.35 ±0.29	14.43	411.89	86.78 ±11.62	+6.20	+22.70	+14.84 ±0.58	1.30	11.10	5.86 ±0.36
Combined Daytime and Evening Periods	$11^{00}-21^{00}$	93	0	11	3.47 ±0.21	4.15	411.89	58.71 ±6.90	+6.20	+22.70	+14.70 ±0.39	1.30	11.10	5.68 ±0.28

* To ease data representation the standard error is not given for the minimum and maximum values of the mean number of birds per hour. The same holds for Tables 2 and 3.

paper uses local time, which differs from Greenwich Time by six hours (local time minus 6 hrs).

Watching courtship behavior and counting birds and synchronous upflights were made at a distance of 25 (in the hide) to 60 m and more through 8^x binoculars. The number of birds was estimated by counting all individuals during a synchronous upflight when the whole flock was rising high up in the air, but also counts were made when the birds were sitting on the ground, within the roost site. The mean number of birds per hour was derived from four counts of birds during this hour, approximately once every 15 minutes (for the sake of more reliability, in evening hours between 20^{00} and 21^{00}, birds were counted more than four times per hr during each synchronous upflight when it was possible). To estimate the total number of individuals in the observation area on any one day, the terns were always counted on the roost site in the evening hours, at which time all the birds were present and reaching their maximum numerical values. It was assumed that before 6^{00} and after 21^{00} hrs (closely corresponding to sunrise and sunset in late April – early May in the study site) the number of birds in a roost remained permanent and maximum possible.

Meteorological data was taken from a state meteorological station, located in the village of Ozernyy on the northern shore of Lake Zetykol, some 44 km north-west of the study site (Fig. 1). At the station the air temperature and wind speed are recorded only eight times during 24 hrs, once every three hours. Extrapolation, assuming a proportional change of the air temperature and wind speed during every 3-hours interval, was used to estimate missing data for each hour.

Thus, operating with customary hour limits was convenient, and each independent case (1 case = 1 hour-long observation, or 1 hour-observation) in the analysis was characterized by the maximum number of synchronous upflights, mean number of birds (consisting of four bird counts), air temperature per hour and wind speed per hour. In a few isolated instances the maximum number of birds per hour and mean number of synchronous upflights per hour were used in the calculations.

To examine the influence of varied factors on synchronous upflights, it has generally been considered sufficient realistic to split the day into three periods: Morning, Daytime and Evening since different periods play an unequal role in the lives of birds. This fact needed to be considered in the interpretation of analysis results; and also combined Daytime and Evening periods were used in the calculations (Table 1). Most of the data obtained is associated with Daytime and Evening periods, while the number of Morning cases included in the analysis totals only 16 hrs (Table 1). For this reason only Daytime and Evening periods were used in the analysis whereas a small amount of Morning period data is documented at the end of the Results section. The following scale measuring the intensity of synchronous upflights was adopted: 1) 1–3, 2) 4, and 3) 5 and more synchronous upflights per hour – low, medium, and high intensity of synchronous upflights, respectively.

Running a statistical analysis of the data, the parametric methods implemented in the software package STATISTICA 6.0 (StatSoft, Inc. 1984–2001) were predominantly used. Though the distribution for some characteristics deviated somewhat from the normal distribution pattern in several cases, the sample size justified the use of the parametrics.

Results

The Phenomenon of Synchronous Take-offs

This phenomenon marks the pre-nesting period of Gull-billed Terns – from appearance of the first birds at the breeding grounds up to the first week of egg-laying. On arrival terns get attached to a selected site (typically within a section of a sandy island) that initially serves as the “club” (Tinbergen, 1956) and roost, and afterwards as the breeding site. The pre-nesting period (from the arrival of the first birds at the breeding grounds to the clutch-initiation) lasts 16 to 38 days and possibly even more. In the daytime, most birds feed in the steppe, and by the evening they assemble on a communal site near the prospective nesting territories reaching their maximum numbers around 21^{00} hrs local time. For the first few days of their arrival, terns are extremely vulnerable to human disturbance. Visitation to their roosts and gathering spots, especially in the evening, can cause birds to shift the site or even completely abandon the area.

When engaged in ground displays, Gull-billed Terns exhibit what has been defined above as synchronous upflights that could be considered an element of pair formation behavior early in the breeding season. Performing a synchronous take-off the entire flock rises 30 m or more from the ground level and makes a large, wide circling pattern over the gathering site. The mass of birds forms a swirling vortex while circling in the air that is characteristic of the synchronous upflight display. The vortex rapidly breaks up, and a proportion of birds lands immediately on the ground while the remainder splits into pairs or small groups of 3–5 birds that follow each other in a chasing fashion high in the air. Thereafter, during 3–8 minutes, all the birds alight gradually on the original site. In a while the synchronous upflight occurs again. A synchronous upflight is preceded by distinct increased levels of visible and audible activity among birds in the “club” (gathering spot) on the ground: the birds are engaged in ground displays performing various courtship postures. The hum from the birds uttering Advertising- (Lind 1963a) and other diverse cackling calls rises progressively, and at some point the birds’ excitement builds to a climax. Then one or more birds whirl sharply off up into the air, and the entire flock of birds – growing by seconds – follows them and the synchronous upflight ensues.

A synchronous upflight can be distinguished from ordinary sudden scattering of birds into the air when a small group is involved in a bout of ground courtship display. In this latter case the flying vortex is not formed, and the terns rapidly return to the ground. This synchronous upflight recognition based on the presence of the vortex display is especially important during daytime when the birds are present in small numbers.

Synchronous upflights occur throughout daylight time with a marked intensification during morning and evening hours, which generally coincides with largest numbers of birds present in similar periods (Fig. 2).

Morning, Daytime and Evening Periods

Characteristic features defining the Morning period are sunrise, minimum day temperatures, birds’ waking up, and their rapid decline in numbers as the birds leave the roost for foraging purposes. The defining characteristics of the Daytime period are maximum day temperatures, minimum bird numbers at the gathering and roosting site. The Evening period is characterized by rapid increase in bird numbers as they return from feeding on the steppes. In late April early May, the sun in the study area is setting about 21^{30}–21^{40} hrs local time, and with heavy cloud cover typical for this time of year it gets dark by 22^{00} hrs. Bird numbers were highest by about 21^{00} hrs at the roosting site. Daytime and Evening period data were significantly different from each other with respect to the frequency of synchronous upflights ($t_{91} = 4.91$; $P < 0.01$) and the total number of birds present ($t_{91} = 4.77$; $P < 0.01$) (Table 1).

Factors that Influence the Mean Number of Synchronous Take-offs/hour

In studying the synchronous upflights, three factors were examined whose impact was evident even during my first observations of Gull-billed Tern flock behavior. These factors are the number of birds present, air temperature and wind speed.

The Effects of Bird Numbers on Dynamics and Rates of Synchronous Take-offs

The minimum number of birds required to perform a typical synchronous upflight in my

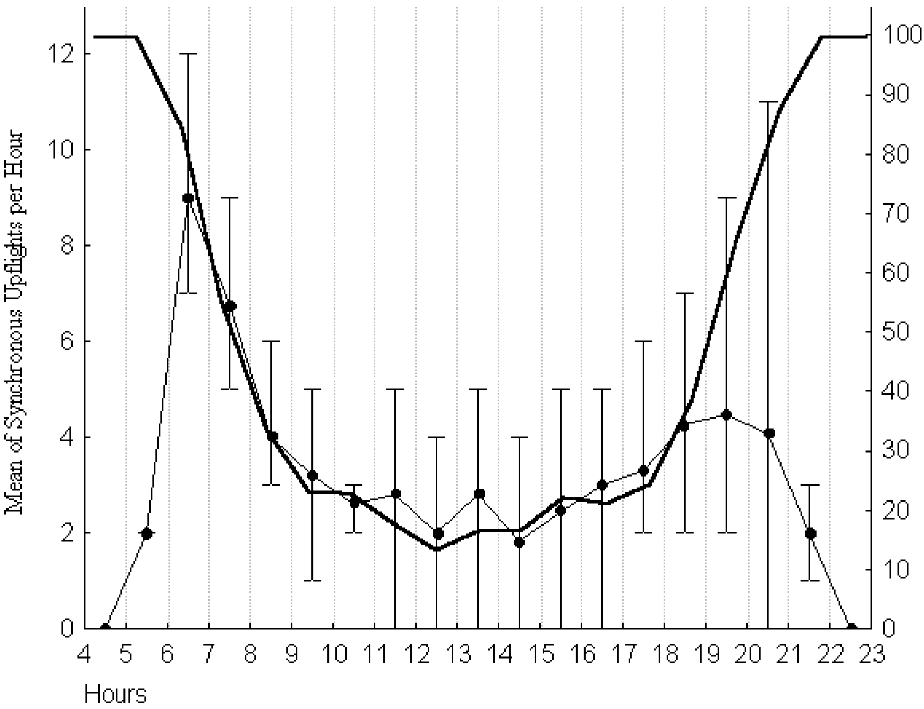

Fig. 2. Changes in the number of birds and dynamics of synchronous upflights during daylight time of the day.

—	Synchronous upflights	Синхронные взлеты
—	Bird numbers	Численность птиц

The mean number of birds per hour t was calculated as follows:

1. The mean number of birds per hour t was determined for <u>each</u> day of the observations (by four counts of birds, see Methods).
2. The obtained mean number of birds per hour t was expressed as a percent of the maximum number of birds present on this day at 21^{00} hours. The largest number of birds recorded between 20^{45} and 21^{15} was chosen to be 100 %.
3. The mean number of birds (%) per hour t was determined for <u>all</u> of the days of the observations.

The mean number of synchronous upflights (without percent conversion) was calculated analogously.

Рис. 2. Динамика численности и синхронных взлетов за светлую часть суток

Средняя численность птиц за час t рассчитывалась следующим образом:

1. Определялось среднее число птиц за час t для <u>каждого</u> дня наблюдений (по 4 подсчетам численности, см. Методы).
2. Среднее число птиц в час t выражалось в процентах от максимальной численности птиц в этот день, в 21^{00} вечера. Из нескольких подсчетов численности с 20^{45} до 21^{15} выбиралась максимальная, которая и принималась за сто процентов.
3. Определялось среднее число птиц (%) за час t за <u>все</u> дни наблюдений.

Аналогичным образом (без перевода в проценты) рассчитывалось среднее число синхронных взлетов.

study was 14 individuals. With a mean number of 23.15 birds per hr, the terns performed as many as five synchronous upflights per hr (Fig. 3). Nevertheless, the maximum values of synchronous upflights (more than five per hour) were recorded in the evening hours, with

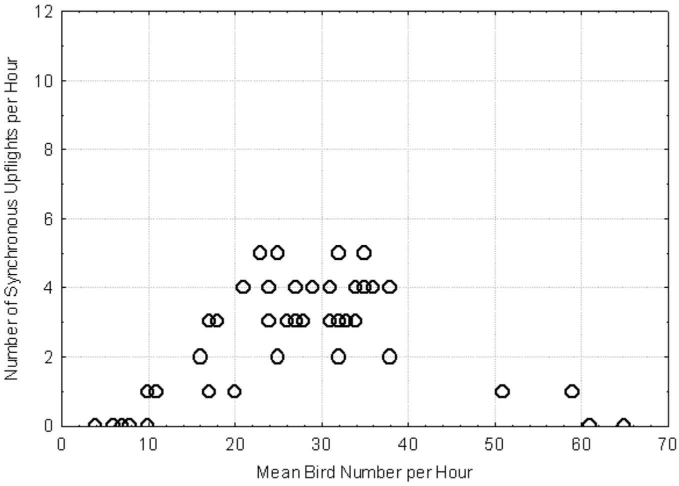

Fig. 3. The relation between the number of synchronous upflights and number of birds in daytime period.

Рис. 3. Зависимость числа синхронных взлетов от численности птиц в дневной период.

on the landing of even just one bird, a bout of display occurred as a result of this occasion. Following the mass bird arrival to the gathering and roosting site the degree of display activity sharply heightened. This was evident from the continuous movement of the birds in the flock on the ground while the hum of calls uttered during courtship display became increasingly louder. In calm weather, it could be heard a few hundred meters from the gathering site.

After about 20^{30} it was getting dark, the numbers present stopped increasing as dramatically, since the bulk of birds were present on the roosting site. Tern activity diminished and the number of synchronous upflights rapidly declined even though the number of birds present was close to the maximum daily value. After 21^{30} no synchronous

a record of 11 synchronous upflights per hr with a mean of 152.22 birds present per hour (Fig. 4), and the absolute maximum number of birds present that same hour being 184 birds. Further, as the flock continues increasing, the number of synchronous upflights per hour (intensity) becomes stabilized at this level, and the number of birds seems to be no longer of large significance in the intensity of synchronous take-offs. For example, two flocks with means of 23.15 and 241.39 birds per hr are able to perform the similar high number of synchronous upflights – five (Table 2). On the contrary, high numbers might account for their decline (Fig. 5). Progressively rising correlation coefficients between the mean number of birds present and number of synchronous upflights observed, as the cases (hour-

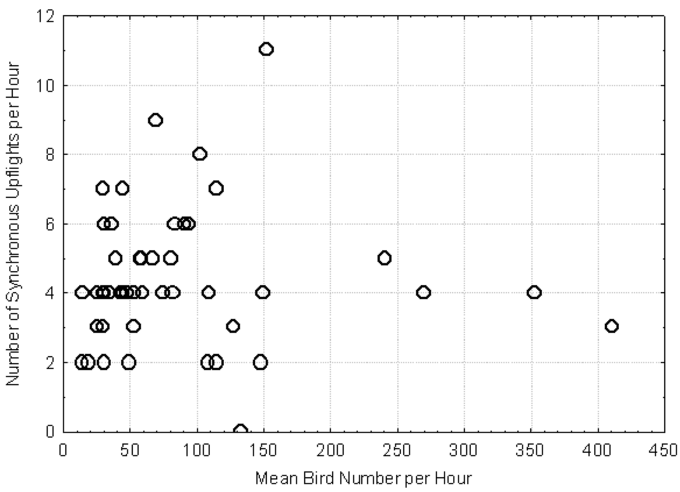

Fig. 4. The relation between the number of synchronous upflights and number of birds in evening period.

Рис. 4. Зависимость числа синхронных взлетов от численности птиц в вечерний период.

Table 2

Meteorological Parameters (Air Temperature and Wind Speed) and Number of Birds at Which a High Intensity (5 and greater) of Synchronous Upflights was Recorded

Значения метеорологических показателей (температура воздуха и скорость ветра) и численности птиц, при которых наблюдалась высокая интенсивность (5 и более за час) синхронных взлетов

Number of Synchronous Upflights per Hour	Frequency	Temperature per hour, °C			Wind Speed per Hour, m/s			Mean Number of Birds per Hour, ind.		
		min.	max.	mean ± SE	min.	max.	mean ± SE	min.	max.	mean ± SE
5	12	+ 9.30	+22.70	16.25 ± 1.10	1.50	8.50	4.00 ± 0.62	23.15	241.39	69.00 ± 17.04
6	5	+15.50	+20.00	17.98 ± 0.84	3.00	9.20	5.60 ± 1.23	31.87	94.21	67.40 ± 13.76
7	3	+10.40	+16.90	13.20 ± 1.93	4.00	6.70	5.40 ± 0.78	30.28	115.12	63.33 ± 26.19
8	1	+17.80			5.00			102.18		
9	1	+16.20			6.00			70.42		
11	1	+17.10			5.00			152.89		

long observations) are artificially excluded from the analysis for those periods with the greatest total number of birds, suggest that the number of synchronous upflights rises to a maximum level with a mean of roughly up to 100 birds present per hour (Table 3). The mean number of birds present during periods showing the high rates of synchronous upflights totaled 73.21 ± 10.33 (N = 23) varying between 23.15 and 241.39 birds per hr (Table 2).

The minimum number of birds was observed on the roost site in midday between 12.00 and 13.00. The numbers steadily grew from 17^{30} onwards, the bulk of the birds arriving during a peak between 19^{00} and 20^{00}, during which the number of birds increased by 26.99 % (Fig. 1). By 21^{00} nearly all the birds assembled for roosting.

The lowest observed mean number of synchronous upflights was recorded at mid-day between 14^{00} and 15^{00} (1.83 per hr). Synchronous upflights increased in frequency of occurrence from then until 19^{00}–20^{00} hr reaching 4.47 per hr. The minimum observed values of synchronous upflights between 17^{00} and 20^{00} were never less than two per hour. They declined thereafter. After 21^{30} no synchronous upflights were observed (Fig. 1). Thus, a timing interval of 19^{00}–20^{00} was notable for a coincident maximum growth in the mean number of birds per hour (26.99 %) and maximum growth in rates of synchronous upflights observed per hour (4.47) (Table 4).

A bird, briefly after alighting near another in the “club”, facing it, adopted “Erect-posture” with “Head-turning”, in which its head rotated rapidly from side to side with its bill pointing almost vertically upwards; or performed one of the other “Erect-posture’s variations” (Lind, 1963a). Ceremonial displays followed during which the two birds paraded around each other performing varied postures (e.g. “Down-erect”, “Forward-erect”), which occasionally ended with formation of the whole clusters of birds up to six individuals, participating in courtship ground display. Often an alighting bird was approached by neighbors from nearby, and in this case again lively ground activity followed. Thus, upflights were recorded (Fig. 2, Table 4). Shortly thereafter, the sun was down and dark came quickly.

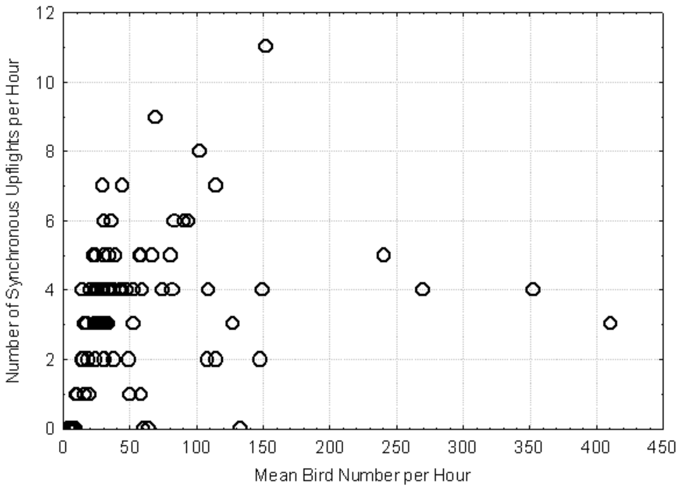

Fig. 5. The Relation between the Number of Synchronous Upflights and Number of Birds in Combined Period: Daytime and Evening.

Рис. 5. Зависимость числа синхронных взлетов от численности птиц в объединенный период – дневной и вечерний.

The Effects of Weather Conditions on Dynamics and Rates of Synchronous Take-offs

My observations indicated, weather conditions may play a considerable role in the variation of rates of observed synchronous upflights.

In the daytime the correlation between air temperature and number of synchronous upflights totaled 0.4 (Table 5), but even at high temperatures the number of synchronous upflights did not exceed 4–5 per hour (Fig. 6). In the Evening period the highest values of synchronous upflights (5 and more) were recorded at temperatures above +14.0°C, the correlation totaled 0.3 (Fig. 7, Table 5).

Though no significant correlation between the number of synchronous upflights and wind speed was found (Table 5), the wind in conjunction with the other elements occasionally had immediate impacts on the dynamics of synchronous take-offs. During the day a maximum of synchronous upflights was recorded at a wind speed of no more than 5.5 m/s (Fig. 8). In the evening the maximum synchronous upflights were observed at wind speeds up to 9.2 m/s, though most of the maximum observed values occurred at or below wind speeds of 6.0 m/s (Fig. 9).

A separate and isolated examination of the cases where the maximum values of synchronous upflights per hour occurred has shown that their

Table 3

The Correlations (Pearson’s and Partial) between the Number of Birds and Number of Synchronous Upflights

Корреляции числа синхронных взлетов и численности птиц

Daytime Period			Evening Period			Combined Daytime and Evening Periods		
r, P	r partial, P	N	r, P	r partial, P	N	r, P	r partial, P	N
Maximum Number (65.62 Birds)			Maximum Number (411.89 Birds)			Maximum Number (411.89 Birds)		
0.14 P = 0.36	0.01 P = 0.96	44	–0.00 P = 0.97	0.02 P = 0.92	49	0.21 P < 0.05	0.23 P < 0.05	93
Up to 50 Birds			Up to 150 Birds			Up to 150 Birds		
0.73 P < 0.01	0.63 P < 0.01	40	–0.04 P = 0.81	0.14 P = 0.38	44	0.26 P < 0.05	0.37 P < 0.01	88
			Up to 100 Birds			Up to 100 Birds		
			0.42 P < 0.05	0.39 P < 0.05	35	0.48 P < 0.01	0.46 P < 0.01	79
			Up to 70 Birds			Up to 50 Birds		
			0.38 P < 0.05	0.34 P = 0.09	29	0.59 P < 0.01	0.52 P < 0.01	61

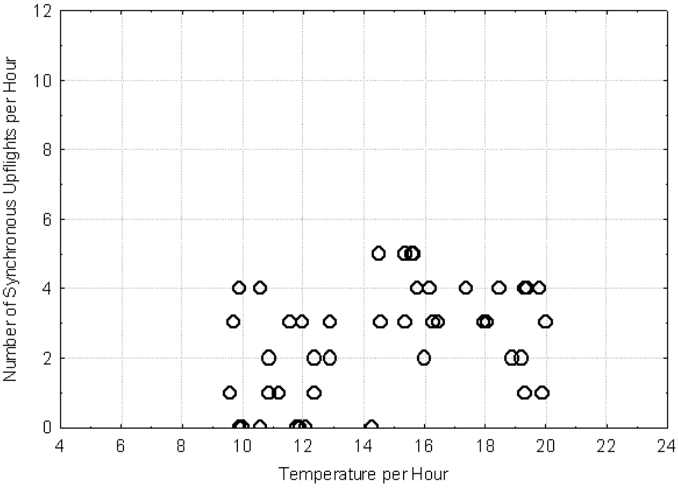

Fig. 6. The Relation between the Number of Synchronous Upflights and Air Temperature in Daytime Period.
Рис. 6. Зависимость числа синхронных взлетов от температуры воздуха в дневной период.

highest observed rates did not occur below a mean temperature of +13°C and at a mean wind speed of less than 6.0 m/s (Table 2). This indicates there is a tendency of Gull-billed Terns to perform higher numbers of synchronous upflights in relatively warm and calm weather, rather than in cool or windy conditions.

In cold and cloudy weather distinct depression in tern activity was observed, particularly at low temperatures coupled with strong, steady wind (e.g. +6.2°C and 9.0 m/s; +8.6°C and 9.0 m/s). In these conditions, wind ruffled birds were observed to be silent, sitting in a tight flock, bills turned towards the wind. Although birds were present in considerable numbers (e.g. on average 133 birds per hour), synchronous upflights were not recorded at all (Fig. 2: Evening period, 20^{00}–21^{00}). Occasionally a high number of synchronous upflights was recorded at a temperature not higher than +14.5°C but with a light wind (e.g. five synchronous upflights at +14.4°C and 1.7 m/s; seven at +12.3°C and 4.0 m/s; and five even at +9.3°C and 5.8 m/s). Thus, the wind definitely increased the “weather hardness” and it was a strong wind that had the most adverse effect on the intensity of synchronous upflights in combination with low temperatures.

Steady rain may also adversely affect the intensity of synchronous take-offs and pairing behavior in general. In this context, a good example could be set. It was the only case when the observations were made during continuous steady rain. Despite being present in considerable numbers (approximately 60 birds) in the daytime

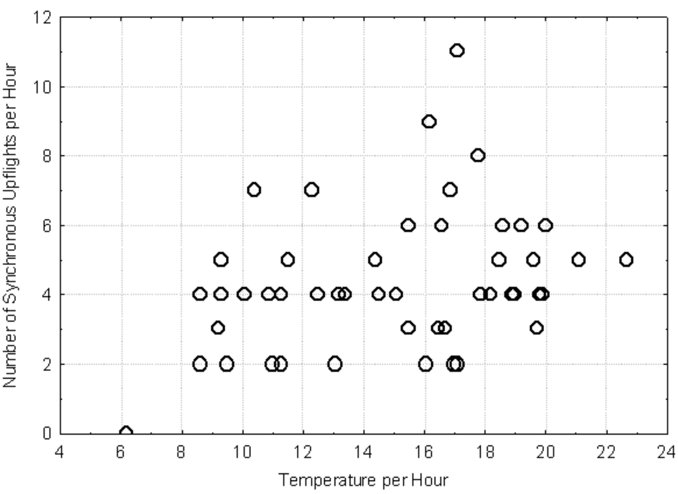

Fig. 7. The Relation between the Number of Synchronous Upflights and Air Temperature in Evening Period.
Рис. 7. Зависимость числа синхронных взлетов от температуры воздуха в вечерний период.

Table 4

Changes in the Means of Birds and Synchronous Upflights per Hour during Daylight Time of the Day
Изменение средней численности птиц и среднего числа синхронных взлетов за час за светлую часть суток

Timing Intervals	Mean Number of Birds per Hour*, %, M ± SE (N)	Changes in Mean Number of Birds per Hour in Comparison with Previous Interval, %	Mean Number of Synchronous Upflights per Hour, M ± SE (N)
4^{00}–5^{00}	100.00 ± 0.00 (1)	0.00	0.00 ± 0.00 (1)
5^{00}–6^{00}	100.00 ± 0.00 (1)	0.00	2.00 ± 0.00 (1)
6^{00}–7^{00}	86.02 ± 2.87 (2)	–13.98	9.00 ± 1.53 (3)
7^{00}–8^{00}	58.28 ± 13.81 (3)	–27.74	6.75 ± 0.85 (4)
8^{00}–9^{00}	34.44 ± 3.21 (4)	–23.84	4.00 ± 1.00 (3)
9^{00}–10^{00}	24.56 ± 3.75 (5)	–9.88	3.20 ± 0.80 (5)
10^{00}–11^{00}	23.37 ± 2.62 (6)	–1.19	2.60 ± 0.24 (5)
11^{00}–12^{00}	18.63 ± 2.97 (5)	–4.74	2.80 ± 0.86 (5)
12^{00}–13^{00}	16.34 ± 2.58 (8)	–2.29	2.00 ± 0.62 (7)
13^{00}–14^{00}	17.70 ± 7.12 (6)	1.36	2.80 ± 0.97 (5)
14^{00}–15^{00}	17.81 ± 3.76 (7)	0.11	1.83 ± 0.60 (6)
15^{00}–16^{00}	21.55 ± 2.58 (7)	3.74	2.43 ± 0.65 (7)
16^{00}–17^{00}	21.27 ± 3.49 (11)	–0.28	3.00 ± 0.53 (9)
17^{00}–18^{00}	25.09 ± 2.81 (12)	3.82	3.30 ± 0.42 (10)
18^{00}–19^{00}	40.07 ± 3.15 (15)	14.98	4.25 ± 0.32 (16)
19^{00}–20^{00}	67.06 ± 3.50 (15)	26.99	4.47 ± 0.54 (17)
20^{00}–21^{00}	88.54 ± 1.60 (15)	21.48	4.06 ± 0.62 (16)
21^{00}–22^{00}	100.00 ± 0.00 (5)	11.46	2.00 ± 0.45 (5)
22^{00}–23^{00}	100.00 ± 0.00 (4)	0.00	0.00 ± 0.00 (4)

* For the calculations of the mean number of birds per hour see the footnote for Figure 2.
* Для расчета средней численности птиц за час см. сноску к рисунку 2.

hours the birds sat ruffled up, occasionally shaking their wings and performing no more than one synchronous take-off per hour. The situation was further complicated by the fact that terns arriving with small and medium-sized lizards (food-carrying by advertising males is considered to be an element of courtship display – Cramp, 1985) were attacked by immature Yellow-legged Gulls (*Larus cachinnans*) as a breeding colony of this species was located nearby. They made dive-attacks towards the flock of the terns and forced them to fly up and drop the food (Fig. 3: four right-hand cases in the plot). Elimination of these four cases from the analysis yields a high correlation between synchronous upflights and mean birds present per hour (Table 3).

"Initiative Group". Some External Factors Eliciting Synchronous Take-offs

There were always birds in the flock that were more noticeable in aerial and ground activities. Typically, it was as many as the whole group (3–14 birds) or several groups of birds that alighted in the flock together and often

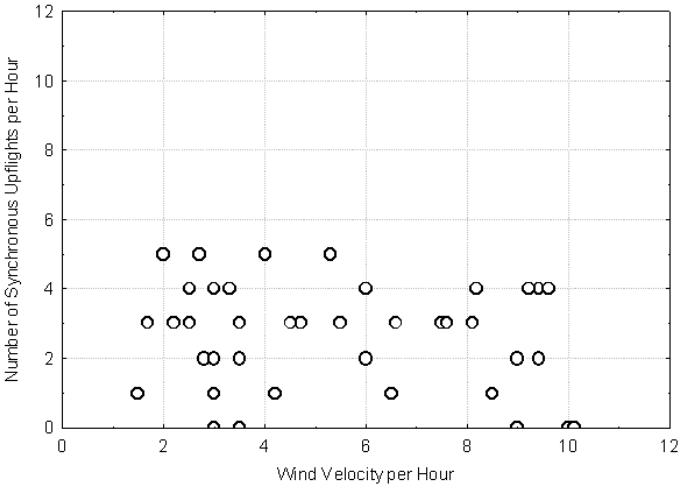

Fig. 8. The Relation between the Number of Synchronous Upflights and Wind Speed in Daytime Period.
Рис. 8. Зависимость числа синхронных взлетов от скорости ветра в дневной период.

flew up together after a short bout of ground display. They were called the "initiative group" from their prominent extra active behavior compared to the bulk of birds. While composition and stability of these groups is unclear, they were significant in the initiation of synchronous upflights since they served as a catalyst for the entire flock engaged in ground display. It often was these active birds suddenly flushing up from the ground that attracted all the other birds to follow, thereby initiating a synchronous upflight.

By day, high rates of synchronous upflights could be maintained exclusively by the "initiative group" activities of active birds at the gathering site. In a number of cases only active birds at the gathering site were present, that is the "initiative group." Viewing separate active individuals has shown that much of their time was spent in the air chasing each other back and forth or simply circling high in the sky over the gathering site, thus acting as if in a prolonged synchronous take-off, and not willing to land immediately. Despite an energetic ground display of the active birds, synchronous upflights did not occur more frequently than in the evening time. After increased strong excitement during ground courtship a sudden and sharp take-off of the whole "initiative group" ensued. The birds described a short and low circle over the ground, and then immediately returned, often to the same spot, to display. Occasionally a portion of the birds did not come back to the display site at all. Thus, when high rates of these

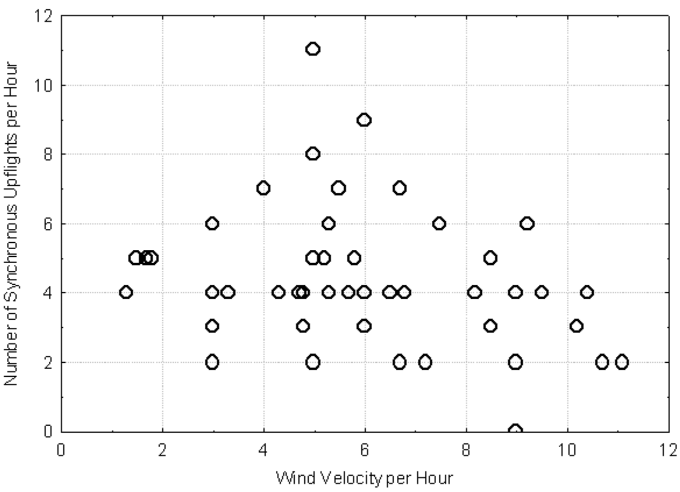

Fig. 9. The Relation between the Number of Synchronous Upflights and Wind Speed in Evening Period.
Рис. 9. Зависимость числа синхронных взлетов от скорости ветра в вечерний период.

brief scatterings were observed (up to 18 per hour), the maximum rate of real synchronous upflights (with vortex) did not exceed 4–5 per hr.

In the evening, return of bird parties from feeding grounds appeared to increase frequency of synchronous upflights observed. Even, in this case, influence of "initiative groups" in the initiation of synchronous take-offs was evident. Occasionally a few birds flying in line or a few small groups of birds alighting in the main flock, appeared to stimulate synchronous upflights. However, it was rather difficult to document this effect statistically. As described for daytime observations the activity increased inside the "initiative group" displaying on the ground, and its sudden scattering in the air developed into a powerful synchronous upflight during which all the remaining birds, rapidly joined this group. Despite provocative actions from the "initiative groups," they were not always successful in getting the entire flock to rise into the air. The flock often ignored sudden and sharp upflights of separate birds. The sustained rate of synchronous upflights remained on average four per hr (Table 1).

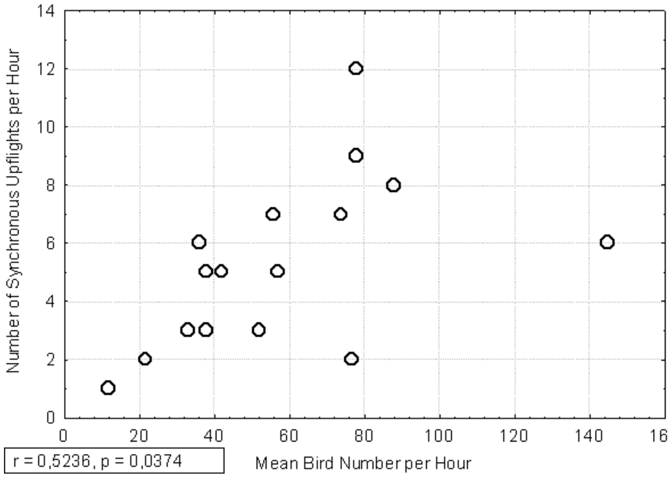

Fig. 10. The Relation between the Number of Synchronous Upflights and Number of Birds in Morning Period.
Рис. 10. Зависимость числа синхронных взлетов от численности птиц в утренний период.

Other causes of synchronous upflights observed included flying attacks of immature *L. cachinnans*, attempting to rob the terns of lizards. Several cold days of late April, when food

Table 5

The Correlations (Pearson's and Partial) between the Number of Synchronous Upflights and Values of Meteorological Factors (Air Temperature and Wind Speed)
Корреляция числа синхронных взлетов и метеорологических факторов (температуры воздуха и скорости ветра)

	Daytime Period			Evening Period			Combined Daytime and Evening Periods		
	r, P	r partial, P	N	r, P	r partial, P	N	r, P	r partial, P	N
Number of Synchronous Upflights & Air Temperature	0.39 P < 0.01	0.38 P < 0.05	44	0.32 P < 0.05	0.33 P < 0.05	49	0.33 P < 0.01	0.34 P < 0.01	93
Number of Synchronous Upflights & Wind Speed	–0.25 P = 0.10	–0.19 P = 0.23	44	–0.26 P = 0.07	–0.28 P = 0.06	49	–0.19 P = 0.06	–0.19 P = 0.08	93

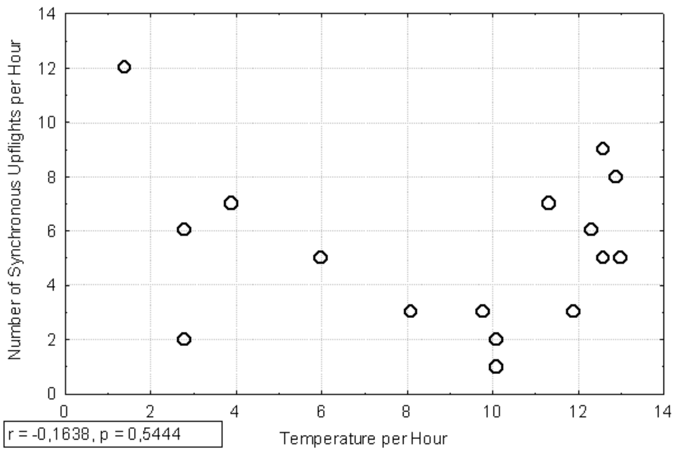

Fig. 11. The Relation between the Number of Synchronous Upflights and Air Temperature in Morning Period.
Рис. 11. Зависимость числа синхронных взлетов от температуры воздуха в утренний период.

resources were apparently lacking, contained multiple observation periods that included repeated aggressive swoops of these gulls. This data was eliminated from analysis for it was felt the continuous upflight activity triggered by the swoops distorted a real picture of synchronous upflight dynamics shown by the terns when undisturbed. Bursts of flight of Ruff (*Philomachus pugnax*) flocks foraging on the ground nearby, low passages over the "club" by the Mute Swan (*Cygnus olor*), human approach or an aerial predator approaching the colony, and possibly other causes could occasionally elicit a synchronous upflight of the terns.

Synchronous Breeding of Gull-billed Terns and Habitat Instability in Study Area

Observations of laying and hatching processes have shown that Gull-billed Terns demonstrate highly synchronous breeding: egg-laying and hatching periods take only 7–8 days, with the egg-laying peak occurring within only 3–5 days (five examined breeding settlements, data in preparation).

The lakes in the study area are characterized by very unstable hydrological regime. The basins occupied shallow depressions subject to considerable fluctuations in water level during frost-free seasons. Rapid snow melt in spring filled the lake bowls with melt water, rapidly lost to evaporation, due to the combined effect of high temperatures and strong winds. Therefore, availability of small islands and islets suitable for the Gull-billed Tern breeding changed almost weekly. During rapid drying of the basin lakes, the islands and sand-banks with the tern breeding colonies may rejoin the mainland, thus permitting easy access for quadruped predators and cattle. In addition, wet sand-banks which occasionally create attractive nest sites for Gull-billed Terns are subject to sporadic floods caused by heavy wind and rains. Thus, nesting habitat using by terns in the study area may be characterized as extremely unstable.

Extinction of Synchronous Take-offs

Synchronous upflights diminish quickly during the first week of incubation as the following example made clear.

In 2003, two colonies of terns originally existed at Lake Ayke: the first on a low, wet sand-bank in a shallow bay (approximately 370 nests, May 23 estimate) and another on a large sandy island some two kilometers away from the first. In the second colony all 143 nests were staked during early incubation. The first colony on the wet islet was destroyed by flooding on May 27. By May 29 the number of nests in the second colony on the large dry island jumped to 214, and on June 1 it totaled 292 nests. New nests may have been constructed by either or both birds from the destroyed

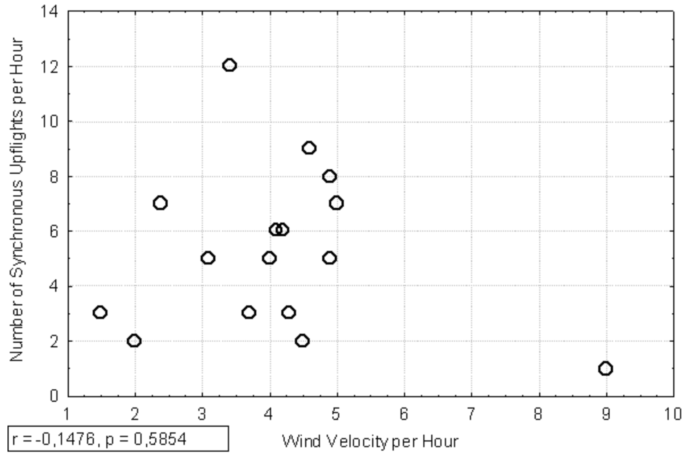

Fig. 12. The Relation between the Number of Synchronous Upflights and Wind Speed in Morning Period.
Рис. 12. Зависимость числа синхронных взлетов от скорости ветра в утренний период.

colony and/or late comers from the southern areas. What was important, all the new nests were arranged compactly on one edge of the original colony thus extending it 20–30 meters on that side. After May 31 synchronous upflights recommenced in the larger colony, and were only observed to be performed only by the recently settled birds within the newly added section of the colony. Birds within this colony, on nests marked earlier and predating the storm, ignored synchronous upflights of the new comers and continued to incubate. Only in exceptional cases did the entire flock fly up, apparently prompted by gregarious instinct. Synchronous upflights gradually diminished and ceased altogether by 6 June. Hatching data revealed that the final colony consisted of several subcolonies, each of them occupying discrete areas within the colony and having different dates of formation and highly synchronous hatching of eggs within each subcolony area.

During late incubation and early hatching phases, massive upflights of the entire flock were caused by occasional external factors, but occasional upflights could be in no way considered as normal display inspired synchronous upflights of the early breeding and pair formation period.

Morning Period

Despite a paucity of the morning observation data (Table 1), several specific differences of Morning period appeared to distinguish it from the rest of daylight observations.

The highest numbers of synchronous upflights, 12 /hour, were recorded in the morning (Fig. 2, 10, Table 1). Synchronous upflights were most strongly correlated with the mean number of birds present per hour within the colony (Spearman's rank correlation coefficient: R = 0.69, N = 16, P < 0.01). During this time period, no significant relationship between synchronous upflights and air temperature (Spearman's rank correlation coefficient: R = 0.09, N = 16, P = 0.73); (Fig. 11), or wind speed was recorded (Spearman's rank correlation coefficient: R = 0.07, N = 16, P = 0.78) (Fig. 12).

Discussion

Type II colony formation was said before to have a high selective advantage for species nesting in unstable habitats (See Introduction). Consequently, breeding initiation and synchrony demonstrated by Gull-billed Terns is considered vital to successful breeding in unstable environments where an additional two-week delay at a certain nesting location may result in total loss for the entire colony.

Some researchers believe that social stimulation synchronizes physiological processes in birds with synchronous egg-laying as a direct consequence of this synchronization (Vermeer, 1973; Burger, 1979). Synchronous take-off displays by Gull-billed Terns in the pre-nesting period appear to provide mutual stimulation of birds, and may be the mechanism, or adaptation permitting maximum synchronization of clutch initiation. Such synchrony would shorten laying, incubation, and early chick phases as much as possible, which is very important in unstable habitats where probability of breeding success rapidly declines over time. The prominence of synchronous upflights exclusively at the early reproductive stage, and their rapid extinction during the first week of incubation is evident from the fact that incubating birds become behaviorally unresponsive to synchronous upflights of those conspecifics beginning nesting later in the season for any reason (the case described above).

It might be supposed that upon their arrival to the breeding grounds, Gull-billed Terns exhibit varied physiological readiness for breeding. By accumulating in potentially suitable nest sites, participating in courtship display and in synchronous upflights birds might thereby increasingly become a physiologically homogenous group collectively ready to start breeding. Very active birds form “initiative groups” and appear to contribute much to this reproductive synchrony. Apparently they do not need to forage throughout the entire daylight unlike the bulk of birds, and can afford to spend more time on the gathering site courting, displaying, and vigorously provoking the entire flock to participate in synchronous upflights.

To be sure, the number of individuals stimulates bird activity only to a certain limit. In the late evening, largest numbers of birds evidenced a lower frequency of synchronous upflights/hour, than earlier observations. This could be due to a greater proportion of passive and inert birds in the flock as they ready for sleep. It was shown that earlier in the evening the highest intensity of synchronous upflights and the largest increase in the mean number of birds per hour were recorded. These facts as well as visual observations of ground behavior displayed by Gull-billed Terns suggest that rather than being due to the numbers itself, the high intensity of synchronous upflights can be accounted for by the rapid changes in the number of terns from lower to higher values, or greater levels of overall activity among the birds present. The larger the increase in bird numbers per hour the higher the increase in frequency of synchronous upflights is likely to be per the same hour. To understand why this occurs, the patterns of ground display behavior of Gull-billed Terns must be remembered. Even one bird alighting in the “club” precipitates a burst of increased calling and activity among neighbors. During the mass evening return to the roost and gathering site this increased calling and activity is multiplied many times, and is apparent to birds and observers from the increasing movement and hum produced by cackling birds in the “club”. Consequently, the probability of the entire flock being able to fly up in the air after a single bird or “initiative group” suddenly flushing up, increased largely as well. Furthermore, the total number of “originally” excited and active birds, i.e. “initiative groups”, assembling by the evening for roosting seemed to increase, too. This could be account for the fact that synchronous upflights were performed much more regularly in the evening, when a mass arrival of birds occurred, and their intensity was higher than in the daytime, even during inclement weather. Therefore, the jumps in numbers of birds and provocative behavior of the “initiative groups” affecting the entire flock could be identified as essential mechanisms affecting dynamics of synchronous upflights.

High air temperature is thought to accelerate physiological processes and intensify bird social stimulation through which the efficient synchronous egg-laying occurs. Observed high frequency of synchronous upflights early in the morning at the lowest daily temperatures close to the freezing point suggests that synchronous upflights in the morning may serve the complementary function of limbering and warming-up birds, after prolonged inactivity on cold ground within the roosting site for the night.

In summary, data suggest conditions under which the highest intensity of synchronous up-flights is likely to occur. The maximum number of synchronous upflights will be observing in the evening notably within 19^{00}–20^{30} when the maximum growth of the number of birds occurs, and with the mean number of birds estimating roughly to be 70 individuals per hr. The auspicious weather conditions are also required: relatively warm or hot (from +14°C and higher), windless or lightly windy (to 4–6 m per second), dry weather. Only under these conditions is there a strong probability of expecting a high intensity of synchronous upflights.

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