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FEEDING ECOLOGY AND TIME BUDGETS OF CURLEW SANDPIPER AND DUNLIN DURING SPRING STOPOVER IN THE SIVASH, UKRAINE

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Кормовая экология и бюджеты времени краснозобика и чернозобика во время весенних миграционных остановок на Сиваше, Украина. Хоменко С.В., Гармаш Б.А., Азово-Черноморская орнитологическая станция; Метцнер Й., Никел М. Institut fur Vogelforschung «Vogelwarte Helgoland» (Germany)
Параллельными учетами и наблюдениями за поведением птиц в период с 1 по 27 мая 1996 г. были охвачены район Джанкойского залива и полуостров у с. Целинное (рис. 1). Анализировалось распределение птиц в пределах контрольных площадок, динамика численности в ходе миграции и сравнивалась доля времени, затраченная птицами на дневное кормление в условиях опресненного залива (SE-41, рис. 1) на Восточном Сиваше (SE) и гиперсоленых угодий Центральной части (SC) водоема (SC-20 и 22, рис. 1). В последнем случае фиксировалась интенсивность потребления основного корма - артемии. Показана сильная избирательность краснозобиков в отношении гиперсоленых участков, как и меньшая, но достоверная, в отношении опресненных у чернозобиков. Сроки достижения максимальной численности чернозобиком (табл. 1) опережали таковые у краснозобика на 4-5 дней: 1 волна - 3-4 мая (у краснозобика 8-9 мая), вторая волна 18 мая (у краснозобика 22 мая). Затраты времени на кормление у краснозобика были достоверно большими на SC (79.4±22.3) по сравнению с SE (74.5±23.8). Еще большие различия обнаружены у чернозобика (SC - 75.5±24.9; SE - 47.1±36.0). Этот показатель не различался между видами на SC, но резко контрастировал на SE, что связано с возможностью ночного кормления чернозобиков нереисом в опресненном заливе. При прочих равных условиях оба вида демонстрировали предпочтение дневного кормления (рис. 2). Затраты времени на кормление на SC хорошо согласуются с общей динамикой пролета каждого вида куликов, njulf rfr d ckexft краснозобиков на SE они больше соответствуют срокам пролета чернозобиков (табл. 4, рис. 5). Скорость потребления артемии на SC зависела от ее обилия. Усредненная частота клевков была выше у краснозобика, особенно в условиях сравнительно невысокой

численности артемии. Этим куликам была свойственна тенденция интенсифицировать кормление в течении светового дня, что не было отмечено для чернозобика. В связи с перераспределением артемии наблюдалась высокая мобильность скоплений песочников на SC. При постоянстве мест ночевок, происходило ежедневное перемещение птиц вдоль побережья в поисках оптимальных условий для кормления (рис. 3). Сравнение расходной (1.8-1.9 BMR) и приходной (3.2-3.3 BMR) статей энергетического бюджета птиц при кормлении артемией (табл. 6) показало потенциальную способность птиц наращивать массу тела со скоростью от 3.6 до 5.6 г/день (краснозобик - 4.3±1.1 г/день, чернозобик - 3.8±0.4 г/день). С учетом продолжительности остановок (5-6 дней) это дает возможность краснозобикам накапливать массу достаточную для «броска» порядка 2-2.5 тыс. км. Ожидается, что для чернозобика это расстояние больше, но за отсутствием оценки продолжительности периода остановки это нуждается в дополнительных исследованиях. Во время остановок на Сиваше большинство краснозобиков полагается на артемию, массовый, но непредсказуемый источник корма, доступность которого ограничена дневным временем. Поэтому они скапливаются здесь в первой половине мая, останавливаясь ненадолго. При благоприятных условиях они используют весь световой день для кормления и после этого могут достичь следующего района остановок. При неблагоприятных кормовых условиях у них остается время для того, чтобы откорректировать маршрут, назначение и сроки миграции. Чернозобики демонстрируют большую лабильность в отношении кормовых условий. Они способны использовать как планктонные, так и бентосные корма, кормиться днем и ночью. В зависимости от ветра они скапливаются в опресненных или соленых заливах, что приводит к частому перераспределению по Сивашу. Поэтому период остановок чернозобика дольше, и высока вероятность того, что майские мигранты стартуют отсюда прямо к местам гнездования.

Introduction

The Sivash, one of the most extensive wetland complexes in the Azov-Black Sea area, is situated in the northern part of the Crimean peninsula, Ukraine (Fig. 1). Its area spreads for 160 km from E to W, and 115 km from N to S making a total of 2,453 km^2. Highly indented coastline (3,100 km) provides variety of waterfowl habitats throughout the year. Up to now relatively sufficient data sets on wader numbers and distribution patterns were collected in the area (Chernichko et al. 1991; Have van der, 1993, Distribution ..., 1999), but little is known about the ways most waders use it. This mainly concerns their feeding strategies, rates of body mass gain, and duration of stay.

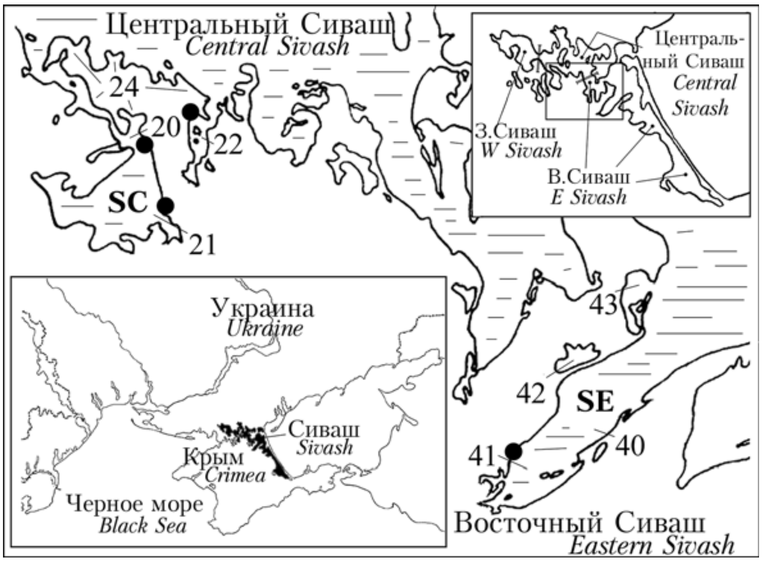

Fig. 1. *Location of the study area (insets) and study localities (filled circles) at the Central (SC) and Eastern Sivash (SE).*

Рис. 1. *Расположение района работ (вставки) и стационары (заполненные кружки) на Центральном (SC) и Восточном (SE) Сиваше.*

The Sivash is an internationally important staging area for Curlew Sandpiper (Calidris ferruginea). In spring this species makes large concentrations (33000-66000 ind.) in the area, which constitute up to 4-9%% of the total flyway population (Dyadicheva, Khomenko et al. 1999, see in this volume). Another numerous spring migrant is Dunlin (Calidris alpina), which numbers are estimated in the range of 170000-254000 ind. (Chernichko et al. 1991). Some studies into the feeding ecology of these waders were conducted in the area in 1993 (Verkuil et al. 1993). Then, basic ideas were outlined on the foraging conditions for these sandpipers in the hypersaline Central and brackish Eastern parts of the waterbody. More research was suggested, especially on the role of Brine Shrimps (Artemia salina) as a main prey. The two closely related species of arctic sandpipers were chosen to carry out a comparative study of their feeding ecology and time budgets. Given the fact that both species feed mainly on terrestrial fauna during breeding season and are related to marine and often tidal habitats during winter and on migrations, comparison of their adaptations to the hypersaline and non-tidal conditions of the Sivash can contribute to a better understanding of their migration ecology in general. The collected material also brings more light on the significance of the Sivash in the migration systems of long distance arctic migrants. Along with some rough energetic evaluations and flight range estimates these data allowed to formulate the species specific staging strategies the waders demonstrate in the area during spring stopover.

Study area

The study localities were chosen to have sufficient numbers of both species for conducting regular behavioural observations. These were Dzhankoi Bay in the Eastern (fig. 1, SE-40, 41, 42, 43) and a peninsula near v. Tselinnoe in the Central (fig. 1, SC-20, 21, 22) Sivash. They both make about 15% of the total Sivash area and had been shown to hold majority of spring migrants of both species (Have et al. 1993, Dyadicheva at. al. 1999). Most of wader habitats in the study area are wind flats, which are flooded and exposed regularly. Dependent on the wind speed and direction, this has a strong influence on the wader distribution and activity, which are subjects to sharp and somewhat opposite changes at these localities. Moreover, the two sites are good examples of brackish (Eastern) and hypersaline (Central) lagoons and are quite representative of the main wader habitats found in the area. While the first (Dzhankoi Bay) provides a variety of benthos food, at the second locality food choice of waders is restricted to Brine Shrimps (Verkuil et al. 1993; Chernichko & Kirikova 1999). This allowed to study redistribution of birds, compare their activity patterns, time-budgets and feeding tactics simultaneously, that helped to better understand advantages and disadvantages of these areas for waders.

Material and methods

The expedition lasted from 1 to 27 May 1996, almost totally covering the migration period of Curlew Sandpier (Dyadicheva et al. 1999), whereas only the second part of Dunlin passage was observed. Counts of waders were simultaneously carried out by two groups every 4th day since 6 May. Between consequent surveys activity scanning took place (beginning from 2 May). To characterise activity patterns of the species during each study period up to 50-60 activity scans were taken with interval of 15 minutes throughout day-time. The samples generally ranged around 100 randomly selected birds. To increase representativeness of the data, in the large concentrations all birds were scanned (counted by tens). The activities distinguished included «foraging», «preening», «standing», «resting,» «running» and «flying». Some statistics on the data collected are presented in table 1.

Table 1. *Characteristics of data set used to evaluate the time-budgets, activity patterns and energetics of Curlew Sandpiper and Dunlin during spring migration 1996.*

Таблица 1. *Характеристика объема данных использованных для расчетов бюджетов времени и энергии и динамики активности краснозобика и чернозобика во время весенней миграции 1996 г.*

Statistics Показатель	Calidris ferruginea		Calidris alpina	
	Central Sivash Центральный Сиваш	Eastern Sivash Восточный Сиваш	Central Sivash Центральный Сиваш	Eastern Sivash Восточный Сиваш
Complete observaion days Число полных дней наблюдений	8	5	8	5
Total duration (h) Общая продолжительность (ч)	120	75	135	74
Birds scanned at a time (mean+SD) Просмотрено птиц за один раз (средняя + SD)	117±250	28±27	87±109	165±229
Birds scanned at a time (min-max) Просмотрено птиц за один раз (min-max)	23-5000	12-100	17-900	52-1000

In addition to that, pecking rates of birds foraging on Artemia were collected in the Central Sivash by counting number of pecks of an individual during 2-3 min. Total numbers of pecking rate measurements make 518 and 603 for Curlew Sandpiper and Dunlin respectively.

Twenty four Artemia samples (a 22 cm square sieve, inserted into the water, was moved to make a half circle 5 times) were taken at the feeding sites of waders. Brine Shrimps were counted per sample. Daily movements of wader flocks (consisting mostly of Dunlin, Curlew Sandpiper and Little Stint (Calidris minuta)) were recorded every morning and evening at the Central location from May 1 to May 16 These watches resulted in the sketch map showing morning and evening movements of birds between the roosts and feeding sites. This strongly helped to interpret the results of activity scanning and get a complete picture of the birds' behaviour.

The basal metabolic rate of waders was calculated according to the formula: $BMR\ [J/sec] = 5{,}06 * mass\ [kg]^{0{,}729}$ (Kersten & Piersma, 1987). After V.R.Dolnik (1982) activity costs were considered as: «foraging»=1.5*BMR, «preening»=2.2*BMR, «running»=1.5*BMR, «resting» = 1,25*BMR, «flying» =12*BMR, «standing» = 1.35*BMR. Night-time expenditures were presumed to be equal to «resting». Thermostatic costs were ignored (mean daily temperature = 25.4 °C), as well as costs of moult, because majority of both waders were shown to have summer plumage in May (Khomenko, Dydicheva 1999). Time budgets were calculated per observation period and further used for estimates of energy expenditure. In the same way correspondent values of the feeding time were included into the evaluation of food and energy intake. Waders feeding on Artemia were presumed to have 100% success (Verkuil et al. 1993). Winter body mass was considered to be only the minimum with which birds arrive to the area as well as to the next stopover area. The below assumptions and constants were used in the calculations:

Daily energy expenditure (DEE)	= sum of the % of the 6 activities each multiplied with BMR and activity costs (Dolnik, 1982)
Net energy intake rate (NEI)	= pecking rate * caloric value of prey * assimilation efficiency (Verkuil et al., 1993)
Daily energy intake (DEI)	= NEI * length working day * % foraging activity
Assimilation efficiency	= 80% (Verkuil et al., 1993)
Caloric value Artemia	= 23.86 kJ AFDM $(g)^{-1}$ (Verkuil et al., 1993)
Length of the daytime	= 900 min
Length of the night-time	= 540 min
Winter body mass of Curlew Sandpiper	= 52 g (Zwarts, Ens at al. 1990)
Winter body mass of Dunlin	= 48 g (Zwarts, Ens at al. 1990)
Energy needed to gain 1 g of fat	= 34.2 kJ (Verkuil et al. 1993)

Results of activity scanning were transformed into per cent of the total number of birds scanned at an instant and each used as a separate data point. Statistical tests were performed in the «Basic Statistics» and «Non-parametric distribution» modules of the STATISTICA 4.3 for Windows software package. The maximum flight range (MFR) of waders in the air still conditions was estimated according to formulae of V.V.Gavrilov (1992): $MFR\ [km]=95.447*V(M_1^{0.302}-M_2^{0.302})$, where V is the flight speed (65 km/h, Zwartz, Ens et al. 1990), $M_1[g]$ is the estimated departure body mass, $M_2[g]$ is the presumed arrival mass (=winter body mass, 52 g according to Zwarts, Ens et al., 1990).

Results

Distribution and migration phenology. Results of the counts are presented in table 2. The Central locality held on average 5.7 times higher numbers of both species. Given this ratio, Curlew Sandpiper show strong preference of the hypergalinic lagoons, 14.5 times overnumbering the expected figure if both species were evenly distributed. The same calculation revealed some preference of the brackish conditions for Dunlin, which occurred in the Eastern Sivash in 1.7 times higher numbers than expected.

Table 2. *Numbers of Dunlin and Curlew Sandpiper in the Eastern (SE) and Central (SC) Sivash in May 1996.*

Таблица 2. *Численность чернозобика и краснозобика на Восточном (SE) и Центральном (SC) Сиваше в мае 1996 г.*

Species, locality Вид, место	Date of count – Дата учета					
	6.V	10.V	14.V	18.V	22.V	26.V
C.alpina, SE	5030	2700	3697	10690	3510	977
C.alpina, SC	17772	18419	4844	2108	5935	3780
C.ferruginea, SE	42	120	90	1880	425	110
C.ferruginea, SC	9531	28448	1729	370	6151	727

The distribution in numbers between the habitats changed only for a short period around 18 May. On the days before count the SE wind exposed extensive mudflats in Dzhankoi Bay and flooded lagoons at the Central locality. This had resulted in increase of bird numbers in the Eastern Sivash, although four days later the situation turned back to the «normal» state with majority sandpipers found again in the Central Sivash. Overall numbers of Curlew Sandpipers peaked on 10 May, with a smaller increase recorded on 22 May. Until 14 May numbers of Dunlin were decreasing after they had peaked on 6 May. The second wave reached maximum on 18 May.

Time-budgets and patterns of feeding activity. The averaged time spent foraging by Curlew Sandpipers in the Central Sivash was significantly higher (Mann-Whitney test, $U=41298$, $Z=2.4$, $p<0.05$) than that in the Eastern Sivash. But even a more striking difference (Mann-Whitney test, $U=24990$, $Z=9.3$, $p=0.00$) in feeding activity was found between these localities for Dunlin: Central Sivash - 75.5%, Eastern Sivash - 47.1% out of the total observation time. Feeding time of Dunlins in the Central Sivash did not differ significantly from that of Curlew Sandpipers (Mann-Whitney test, $U=72990$, $Z=1.6$, $p=0.1$), but the time spent resting was notably higher (Mann-Whitney test, $U=43598$, $Z=10.7$, $p=0.00$). Time budgets of Dunlin in the Central Sivash and Curlew Sandpiper in the Eastern Sivash were essentially identical, with no significant differences between all activities confirmed.

Day-time patterns of foraging activity also differed between species and study locations (fig. 2). Thus, Curlew Sandpipers in the Central Sivash were tending to reduce foraging by the end of the day, whereas in the Eastern Sivash they had the period of highest feeding activity from 10.00 to 14.00 o'clock. Contrary to this, Dunlins in the Central Sivash had a period of resting in the mid day. By 19.00 o'clock they started intensive foraging again with a tendency to decrease it later till the end of the day. In the Eastern Sivash Dunlins tended to be foraging only for 40% of the time for the most part of the day and obviously relayed on nocturnal foraging. For this reason the data were excluded from the further analysis.

Table 3. *Averaged time-budgets (% ±SD) of Curlew Sandpiper and Dunlin in the Central (SC) and Eastern (SE) parts of the Sivash in May 1996.*

Таблица 3. *Усредненные бюджеты времени (%±SD) краснозобика и чернозобика в Центральной (SC) Восточной (SE) части Сиваша в мае 1996 г.*

Activities Вид активности	C.ferruginea		C.alpina**	
	SE (62:30 h)*	SC (93:15 h)	SE (52:30)	SC (100:30)
Foraging Кормение	74.5±23.8	79.4±22.3	47.1±36.0	75.5±24.9
Preening Чистка	14.2±16.6	14.5±19.1	11.2±13.6	11.2±14.4
Standing Стояние	2.1±4.5	2.4±4.9	6.0±17.3	1.3±3.2
Resting Отдых	6.9±12.0	0.2±0.5	33.7±33.8	10.0±19.5
Flying Полет	0.6±2.3	1.5±3.8	0.7±2.3	0.6±2.2
Running Бег	1.7±4.9	2.0±4.4	1.3±3.2	1.4±2.6
Total Всего	100	100	100	100

Notes: * Number of observation hours are given in parentheses.
** A time budget of Dunlin with extremely low per cent of feeding taken on 23 May in the Central Sivash is excluded from the analysis.

Примечания: *Количество птиц приводится в скобках.
**Бюджет времени чернозобика 23 мая на Центральном Сиваше с крайне низкой долей кормления исключен из анализа

Feeding activity at the Central and Eastern Sivash by observation periods. In case of Curlew Sandpiper the difference between study localities appeared to be significant on 7-9 May and 19-21 May (table 4) that does fit the two waves of arrival to the Central Sivash, whereas in the Eastern Sivash no increase of feeding time related to the increase of numbers was apparent. On the days before and after the peak of numbers the feeding time even decreased compared to the first half of May, when the numbers were much lower (table 2).

In the same way the feeding activity of Curlew Sandpipers and Dunlins in the Central Sivash was compared (table 4). Percentage of foraging birds differed between the localities by periods in 4 cases out of 6, although the means for the whole study period did not (table 3). Indicative is the absence of difference between Curlew Sandpipers in the Eastern Sivash and Dunlins in the Central Sivash.

Pecking rates and food intake. The highest abundance of Artemia was found in the samples taken at the study sites SC-22 (469±1128 ind., n=6) and SC-20 (1911±928 ind., n=8) which were characterised by the highest salinity too (Nickel, 1997). According to this (table 5) pecking rates of birds were significantly lower at SC-22 than at SC-20 for both species (Mann-Whitney U-test; U=12716.0, Z=9.5 for Curlew Sandpiper and U=12121, Z=14.8 for Dunlin; p=0.00). The averaged pecking rates for both localities were higher in Curlew Sandpipers (Mann-Whitney U-test; U=133012.0, Z=4.3, p=0.00). This difference was due to significantly higher pecking rate of this species at SC-22 (Mann-Whitney U-test; U=11513, Z=5.5, p=0.00) compared to Dunlin, while at SC-20 the means were apparently equal (Mann-Whitney U-test; U=67746, Z=0.18, p=0.86).

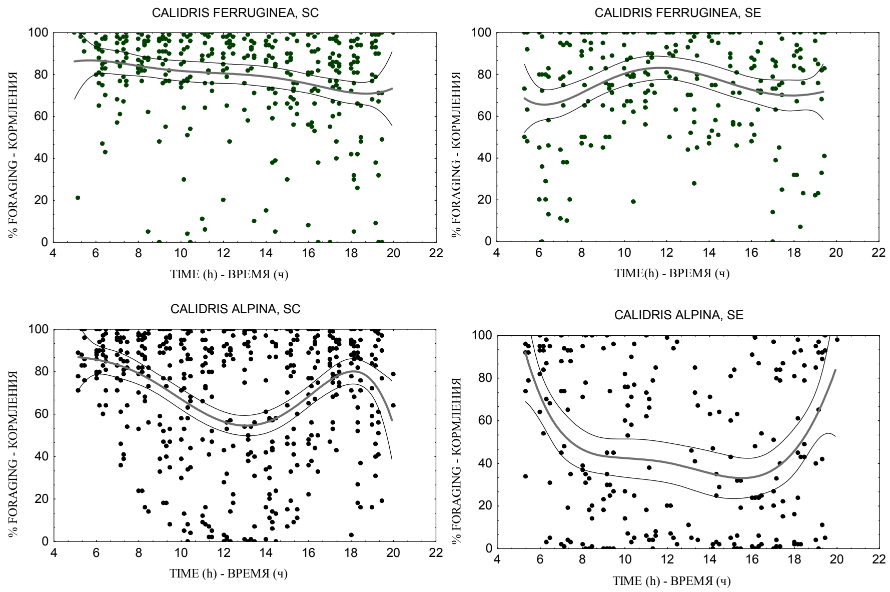

Fig. 2. *Day-time patterns of feeding activity of Curlew Sandpiper and Dunlin in the Central and Eastern Sivash in May 1996. Each dot represents results of one activity scanning. Data points are fitted by a solid line (polinomial fit), dotted lines indicate 95% confidence intervals. Time of sunrise decreased from 05:34 h on May 1 to 04:58 h on May 27. Time of sunset incresed from 20:18 h on May 1 to 20:53 h on May 27.*

Рис. 2. *Динамика кормовой активности краснозобика и чернозобика на Центральном (слева) и Восточном (справа) Сиваше в мае 1996 г. Каждая точка - результаты одного просмотра стаи. Тенденции описаны с помощью полиномиальной кривой (сплошная линия), пунктиром обозначен 95% доверительный интервал. Время рассвета уменьшалось от 05:34 ч 1 мая до 04:58 ч 27 мая. Время заката увеличивалось от 20:18 ч 1 мая до 20:53ч 27 мая.*

The pecking rates turned up to be time dependent (table 5). When plotted against the time of day they revealed overall increase of Artemia consumption in case of Curlew Sandpiper, whereas Dunlins apparently did not show such a trend. Under the conditions of lower prey availability (SC-22) both species decreased pecking rates, though this was more pronounced in Curlew Sandpipers. Higher prey abundance at SC-20 resulted in sharp increase of pecking frequency through the day in the first species, while that was insignificant for Dunlin.

Table 4. *Comparison of the percentage of time spent foraging by Curlew Sandpiper and Dunlin in the Central Sivash, that for Curlew Sandpipers in the Eastern Sivash and results of Mann-Whitey U-test per observation period.*

Таблица 4*. Сравнение процента времени затраченного на кормление краснозобиком и чернозобиком на Центральном Сиваше, то же для краснозобика на Восточном Сиваше и резульаты U-теста Манна Уитни по периодам наблюдений.*

Periods Периоды	Central Sivash Центральный Сиваш				Eastern Sivash Восточный Сиваш		Mann-Whitey U-test, Significance* U- тест Мана Уитни, достоверность*		
	C.ferruginea		*C.alpina*		*C.ferruginea*				
	n, h n, ч	Feeding, % Кормление	n, h n, ч	Feeding, % Кормление	n, h n, ч	Feeding, % Кормление	p1	p2	p3
3-5.V	48	84.2±9.5	46	72.3±28.8	52	80.4±22.5	0.58	0.16	0.44
7-9.V	116	88.9±11.6	43	66.3±24.8	54	59.6±28.0	**0.00**	0.25	**0.00**
11-13.V	55	82.8±19.6	103	81.3±17.7	50	83.6±22.3	0.33	0.10	0.42
15-17.V	75	70.0±23.7	157	76.8±27.0	57	75.2±19.3	**0.00**	0.12	0.27
19-21.V	30	85.1±17.4	71	72.1±24.7	37	74.3±16.6	**0.01**	0.88	**0.01**
23-26.V	48	58.6±34.0	50	32.2±29.7	-	-	**0.00**		-

Notes:* p_1 - between C.ferruginea and C.alpina at the Central Sivash; p_2 - between C.alpina at the Central Sivash and C.ferruginea at the Eastern Sivash; p_3 - between Central and Eastern Sivash for C.ferruginea. Significant at p<=0.01 are highlighted.

Примечания: * p_1 - между C.ferruginea и C.alpina на Центральном Сиваше; p_2 - между C.alpina на Центральном и C.ferruginea на Восточном Сиваше; p_3 – между Центральным и Восточным Сивашом для C.ferruginea. Достоверные различия (p<=0.01) выделены жирным шрифтом.

Table 5. *Pecking rates and co-relation between pecking frequency and time of day (R) for Curlew Sandpiper and Dunlin foraging on Artemia at two study sites in the Central Sivash.*

Таблица 5. *Частота клевков и ее зависимость от времени суток (R) для краснозобиков и чернозобиков кормящихся артемией в двух разных местах на Центральном Сиваше.*

	SC-22		SC-20		Average Средняя	
	C.ferruginea	*C.alpina*	*C.ferruginea*	*C.alpina*	*C.ferruginea*	*C.alpina*
Pecks/min Клевков/мин.	68.6±21.4	56.2±20.4	98.2±31.9	97.7±33.0	89.7±32.2	81.6±35.1
R (time) R (время)	- 0.37	-0.15	0.5	-0.028*	0.26	0.01*
n birds n птиц	148	234	370	369	517	603

Note: * non-significant (at p<0.05).

Примечание: недостоверны (при p<0.05).

Movements of waders within the staging area

While in the Eastern Sivash no specific usage of the sites was noted, in the Central Sivash birds (both sandpipers and Little Stints) demonstrated a particular daily redistribution pattern (fig. 3). From 5.00 to 6.30 a.m. wader flocks of 20-100 individuals started from the roosts in the vast inner shallows of SC 21 and SC 21a and moved along the narrow strait of SC-20. Up to 30% of them flew directly to SC-22. They gradually distributed all over the suitable feeding sites along the coast. In the afternoon the day-time roosts formed in the most isolated shallow areas. Backwards movements of these flocks was observed between 6.00 and 8.00 p.m. By the sun-set they concentrated in the main roost of SC-21 and to a lesser extent at SC-21a, returning along the same strait. A part of birds flew directly across the peninsula. As a result, all birds concentrated in large roosts far from the main coast of the Sivash. Up to 10% of birds flew eastwards, where probably another roost was located. Later, large numbers of waders started migration flight from the above-mentioned roosting sites. They were seen leaving the area in the evening between 13-16 May. These flights were undoubtedly targeted on finding Artemia concentrations along the shore, which were daily redistributed by the wind. They point out that the feeding conditions at the Central Sivash are very changeable, and birds are forced to have additional expenditures in search of sufficient prey density.

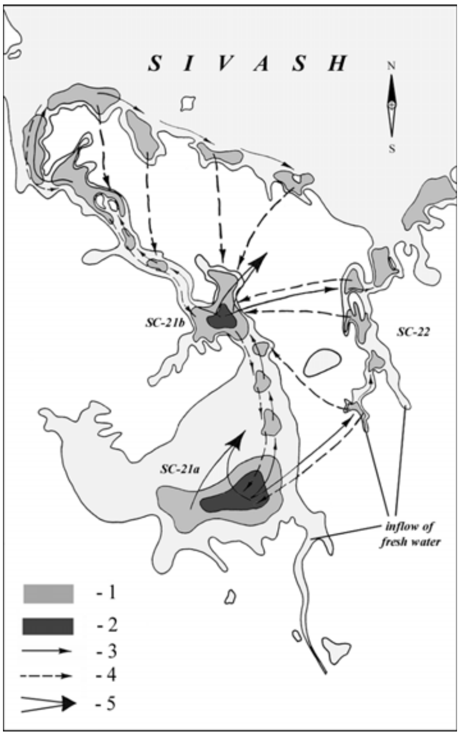

Fig. 3. *Morning and evening movements of waders foraging on Artemia in the Central Sivash: 1 - night roosts, 2 - foraging sites, 3 - routes of morning flights, 4 - routes of evening movements, 5 - sites from where migration started.*

Рис. 3. *Утренние и вечерние перемещения куликов кормящихся артемией на Центральном Сиваше: 1 - места ночевок, 2 - кормовые участки, 3 - маршруты утреннего разлета, 4 - маршруты вечерних перемещений, 5 - места миграционного старта.*

Discussion

The preference of the hypersaline part of the Sivash by Curlew Sandpiper indicates that staging conditions there are generally more favourable for this species. As the time-budgets suggest, birds tend to use up most of the day-time to forage on Artemia.

Pecking rates of Curlew Sandpiper feeding on Artemia indicate that under the lower prey availability these waders feed more intensively than Dunlins do. Intake rates become equal when availability increases to the upper limit of possible consumption. This fact, along with the general increase of Artemia consuption during the day, indicates that Curlew Sandpipers relay more on this kind of food and look for large concentrations where there are more opportunities to intensify feeding. This may be due to some morphological advantages of the first species (Yudin, 1965) as well as to a certain feeding specialisation. Further inland Curlew Sandpipers are likely to find mostly saline waterbodies (e.g. in the Caspian region, South of the W Siberia) which are rich mainly in plankton (Formozov, 1981).

Behaviour of Dunlin seems to be more variable. They also occurred in the Eastern Sivash, where their diet consists of Nereis deversicolor, the most abundant species of macrozoobenthoth (Metzner 1997, Chernichko, Kirikova 1999). Its availability was likely to increase at night as followed from their time budgets and activity patterns at the Eastern locality. Indeed, during the study period most of the mudflats in Dzhankoi Bay were flooded because of the N-E winds. Only in the evenings did wind drop a little, generally resulting in the decrease of water level. Thus, at night birds were likely to find more opportunities to feed on benthos by probing. Probably activity patterns of Nereis, affected both by darkness and fluctuations of water level, contribute to the feeding success of Dunlins as well.

The means of the feeding time of Curlew Sandpiper in the Central Sivash plotted by periods (fig. 4) do correspond to the migration pattern of the species at the same locality (see also tables 1, 4 and 5). Peaks in both the numbers and feeding time of Dunlin are correspondent too, but about 1 week earlier. Interestingly enough, the feeding time of Curlew Sandpipers in the Eastern Sivash seemed to fit more the overall migration pattern of Dunlin as well as the feeding activity of this species in the Central Sivash (actual feeding time of Dunlins in Dzhankoi Bay remains unknown). Due to low number of cases these observations can not be tested statistically, but they indicate that occurrence of Curlew Sandpiper in the Eastern Sivash is mostly occasional. Moreover, these birds can merely join flocks or concentrations of Dunlins by chance, probably even at the previous staging areas.

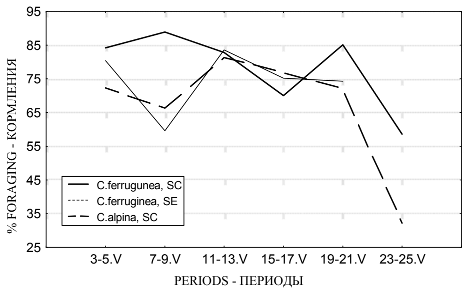

Fig. 4. *Mean feeding time (%) of Curlew Sandpipers at the Eastern and Central Sivash and Dunlin at Central Sivash by periods of observations.*

Рис. 4. *Усредненное время кормления (%) краснозобика на Восточном и Центральном Сиваше и чернозобика на Центральном по периодам наблюдений.*

The data set collected at the Central Sivash permits some energetic calculations. The DEE was estimated according to standard procedure described by Dolnik (1982) and expressed as a BMR multiplier (table 6).

Total daily energy expenditure appeared to be lower than 2.5*BMR used in earlier study by Verkuil et al. (1993). The DEE of both species varied in the range from 1.7 to 2.1 in relation to the basal metabolic rate. Curlew Sandpiper and

Dunlin had close DEE/BMR rates (1.9±0.15 and 1.8±0.03) (Mann-Whitney test, U=16, Z=1.0, p=0.3).

Table 6. *Daily energy expenditure in relation to basal metabolic rate (DEE/BMR), energy intake, energy surplus and resultant estimate of body mass increase of Curlew Sandpiper and Dunlin foraging on Artemia.*

Таблица 6. *Суточный расход энергии по отношению к уровню базального метаболизма (DEE/BMR), ее приход, общий профицит бюджета энерии и расчетное значение суточного прирости массы тела краснозобика и чернозобика при кормлении артемией.*

Period Период	DEE/BMR	Energy intake, kJ/day Приход энергии кДж/день	Energy surplus, kJ/day Профицит бюджета энергии, кДж/день	Mass gain, g/day Прирост массы, г/день
		C. ferruginea		
3-5.V	1.8	259.5	169.2	4.9
7-9.V	1.7	273.8	185.5	5.4
11-13.V	2.0	255.2	153.1	4.5
15-17.V	1.8	215.9	122.4	3.6
19-21.V	1.8	262.5	171.9	5.0
23-26.V	2.1	180.8	72.1	2.1
Average Средняя	1.9±0.15	241.8±32.5	146.3±38.4	4.3±1.1
		C.alpina		
3-5.V	1.8	202.7	126.2	3.7
7-9.V	1.8	186.1	108.5	3.2
11-13.V	1.8	227.8	148.5	4.3
15-17.V	1.7	215.4	140.0	4.1
19-21.V	1.8	202.2	124.3	3.6
23-26.V	2.0	90.3	1.5	0.04
Average Средняя	1.8±0.03	207.6±14.2	130.4±13.9	3.8±0.4

According to Verkuil et al. (1993) the average AFDM of individual Artemia is known to increase during May from 0.11 mg in the first half of the month to 0.29 mg in the second. Lacking original data for our study period, we used the average (0.20 mg AFDM) of these values in our calculations.

Though income of energy (kJ/day) is higher in Curlew Sandpipers, Dunlins manage to keep it less variable. Both species turn up to have equal energy surplus in relation to BMR (3.2+1.1 and 3.3+0.8 respectively; Mann-Whitney U-test, U=13.5, Z=0.27, p=0.78). Its upper limit is considered to be 3.9 times the BMR (Zwartz et al. 1990), so the given surplus estimates are not beyond their potential abilities.

On most days (table 6) both species were potentially able to gain from 3.6 to 5.6 g/day. These rates are rather high, but comparable to the individual ones given for Curlew Sandpipers in Baharan (5.5 g/day, Herchfield 1992). Ability to quickly gain body mass is common for most waders and this species in particular (Cramp & Simmons 1983) . We did not find in the literature values over 1.9 g/day (Zwartz, Ens et al. 1990) in case of Dunlin. Unless some part of birds is not very successful in picking up Artemia, the benefit of this food is likely to be similar to the previous species. This may be true in a way, given the preference of some Dunlins for the brackish lagoons. Van der Have et al. (1993) reported on possible sex separation of Dunlins with more males likely to be found in the Central Sivash and vice versa. Generally smaller males may have some advantages because of lower energy expenditure and smaller bill. Larger and longer billed females therefore tend to concentrate in the brackish lagoons of the Eastern Sivash. To confirm this observation, careful examination of the Dunlin morphometrics at both study sites is needed.

In spite of considerable data on the time budgets and pecking rates, the above calculations may suffer from various errors. At first, the expenditure could have been higher because of the underestimated ratio of flying. At second, the income could have been underestimated: a) because the pecking rates of both species at certain places can reach average of 97-98 (or even 150) pecks/min; b) individual mass of Artemia may be over the average which we used, especially later in May; c) it is not known how effective the daily search for Artemia is, what are the chances to find enough Artemia and cover the flight costs. All this means that at times and locally birds can potentially reach consumption of food twice as higher as the given average. It seems however, that advantages of feeding on Artemia are higher and birds did ensure sufficient prey consumption. Otherwise hardly tens of thousands of sandpipers would concentrate in the Central Sivash.

The period between dates on which the 50% of the maximum numbers of Curlew Sandpipers arrived and 50% departed makes only 5 days. Dependent on the arrival body mass (winter mass of 52 g or actual 55.6 g, according to trapping data (Khomenko, Dyadicheva 1999), the departure mass can be estimated given the averaged rates of mass gain (table 6). The flight range of these Curlew Sandpipers, departing after 5 days' staging period, is about 2000-2500 km . Thus, they are not likely to flight directly to the Taimyr (Wilson et al. 1980) especially taking into account early departure from the Sivash (before mid May). The Caspian region and, even more likely, the South of the Western Siberia, seem to be the next destination staging area in spring.

Unfortunately, there is even less ground to make flight range estimates for Dunlin. But the following points seem to indicate that they do start off from the Sivash to arrive directly to the breeding grounds. First, according to the migration pattern, the stay duration of birds is likely to be longer. Second, if feeding only on Artemia, the birds would be able to build enough fat reserves. Third, the birds which start form the Sivash later in the third decade of May, hardly have enough time to stop over elsewhere more. Because of the nocturnal feeding, it is difficult to say how profitable is to forage on Nereis. However, contrary to Curlew Sandpiper, Dunlins apparently have three options: to relay on Artemia or Nereis or both. That accounts for lager numbers of Dunlin found in the area (Chernichko et al, 1991). These reasons are also true for the second (smaller) wave of Curlew Sandpiper migration. A group of birds as heavy as 92 g were captured in the Sivash only late in May in 1999 (I.I.Chernichko, pers. com.), while earlier hardly even single individuals reach that weight (Khomenko, Dyadicheva 1999 in press). The wind rose in the late May is known to change more towards predominance of southern winds. This may also increase opportunities for Curlew Sandpipers to forage on Nereis at day, that was actually observed in the Dzhankoi Bay around 18 May.

The following conclusions on the staging strategies of the sandpipers (which on certain conditions apparently overlap to some extent) can be formulated. Majority of

Curlew Sandpipers relay on Artemia - abundant, but unforecastable source of food, availability of which is restricted to the day-time. For this reason they pass the area in the first half of May staging here for a short time. During this period the waders use up the best of the time to build up fat reserves to fly about 2,500 km to the next staging area. In case they face unfavourable feeding conditions, birds would still have time to correct their route, destination and time-scheme of migration.

Dunlins have a variable strategy in respect to the feeding options available in the area. They utilise both kinds of food, can forage both at day and night with probably sex related preferences of each option. Dependent on wind conditions these waders are able to make use of brackish and saline lagoons, but this results in higher redistribution. Because of that Dunlins tend to have a longer stop-over period and are likely to depart directly to the breeding grounds late in May.

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