Spatial and temporal dynamics of wader numbers in the delta complexes of the northern subarctic Y.Yu. Blokhin

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Wader counts were carried out in the summers of 1984, 1985 and 1987 on a 960 km route in the central part of the Lena river delta, north-western Yakutia. Fifteen breeding wader species were recorded, 40% of the total number of breeding species present. Of these, Calidrid sandpipers dominated (40%). The most abundant breeding wader almost everywhere was Grey Phalarope Phalaropus fulicarius, with co-dominants, depending on habitat, being Little Stint Calidris minuta, Pectoral Sandpiper C. melanotos, Temminck's Stint C. temminckii and Ruff Philomachus pugnax. In the first half of the breeding season wader densities were high (266-418 birds km-2) and comparatively stable. During this time, the number of different species present and the overall numbers of waders are characterised by sharp within-season changes, with a peak during the breeding period. The total population of breeding waders during three seasons (15 June to 15 July) varied annually up to two-fold. For individual species such as Little Stint, Temminck's Stint, Ruff, Turnstone Arenaria interpres and Snipe Gallinago gallinago, the size of the fluctuations were, however, more pronounced and mainly influenced by weather conditions. Species breeding on the banks and in the river valley were also noticeably influenced by spring floods. Only two species, Grey Plover Pluvialis squatarola and Dunlin Calidris alpina, had relatively stable populations. A few Red-necked Phalaropes Phalaropus lobatus, which here are at the edge of their range, breed in some years.

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Учеты численности куликов были проведены летом 1984, 1985 и 1987 гг. на маршруте протяженностью 960 км в центральной части дельты р. Лена, в северо-западной Якутии. Были зарегистрированы 15 видов гнездящихся куликов, что составляло 40% общего числа гнездящихся там видов птиц. Среди них преобладали песочники рода Calidris (40%). Самым многочисленным видом гнездящихся куликов почти везде являлся плосконосый плавунчик Phalaropus fulicarius, в зависимости от биотопа кодоминантами были кулик-воробей Calidris minuta. AVTЫШ C. melanotos, белохвостый песочник C. temminckii и турухтан Philomachus ридпах. В первой половине гнездового сезона плотность куликов была высокой (266-418 особей на 1 км²) и сравнительно стабильной. В этот же период количество различных видов и общая численность куликов характеризируются резкими внутрисезонными изменениями с пиком в гнездовой период. Общая численность популяции гнездящихся куликов в течение трех сезонов (с 15 июня по 15 июля) варьировала между годами до двух раз. Однако, для таких отдельных видов, как кулик-воробей, белохвостый песочник, турухтан, камнешарка Arenaria interpres и обыкновенный бекас Gallinago gallinago, размер колебаний был выражен более резко и зависел преимущественно от погодных условий. Гнездящиеся на берегах и в поиме реки виды также заметно подвергались влиянию весеннего половодья. Лишь у двух видов, а именно у тулеса Pluvialis squatarola и чернозобика Calidris alpina, популяции была относительно стабильными. Единичные круглоносые плавунчики Phalaropus lobatus, которые здесь находятся на краю их гнездового ареала, гнездятся в отдельные годы.

Introduction

A simple structure and a pronounced seasonal rhythm are characteristic of arctic and subarctic habitats. However, even at such high latitudes, flood-plains and particularly river deltas differ from other habitats in their high productivity. This is due to a constant nutrient influx from the large riverbasin areas. High biodiversity is also maintained by the warming effect of the large, northern Eurasian rivers, which flow into them from the south. Tundra landscapes are extremely wet and swampy, particularly in the delta areas. An abundance of different types of water body and a variety of trophic conditions lead to flourishing wetland animal communities. Anseriform and Charadriiform birds are the main terrestrial vertebrates of these northern subarctic wetlands.

The bird populations of the delta areas of northeastern Asia are poorly studied. Few quantitative data exist in the literature and the delta of the Lena River is no exception (Blokhin 1988), even though quantitative data usually provide the only opportunity to understand the spatial and temporal organization of bird communities. The largest delta in the Eastern Hemisphere (covering c. 30,000 km²), the Lena river delta is a heterogeneous geological formation and consists of a true delta, formed by alluvial sediments, and the remains of coastal lowland, formed by Quaternary deposits. In this paper, the fluctuations in wader numbers at the Lena river delta are presented and discussed. We suggest that these data can be extrapolated to other subarctic delta bird communities.

Study Area and Method

At the high latitudes (72-74°N) of this region the recent landscapes are cryogenic in origin and this is reflected in the current relief and flora. Characteristics of the climate include a short frostfree period (40-60 days) and low average July temperatures (+4°C in the north and +8°C in the south). Between-year variation in some environmental features of the regions summers is shown in Figure 1. Two-thirds of the area is covered by northern subarctic (typical) tundra, the rest lies in the southern arctic tundra subzone. Tetragonal and polygonal moss-sedge bogs occupy up to 80% of the area. On the whole, in spite of certain peculiarities, the Lena delta is typical of the northern subarctic and can be considered as holding typical studies of delta bird communities.

Standard survey methods, widely used in zoological research in Russia, were used. Random censuses were carried out using the same methods as Ravkin (1967). All birds which were seen on a transect were counted. The density of each species (birds km⁻²) was calculated later according to the average estimated distance at which it was seen. These data are not the real densities of breeding birds (they only approximately reflect breeding densities) and should be treated only as "density indices". Censuses were conducted on foot and census routes totalling 960 km were covered. Most of them were carried out in the first half of summer (from 15 June to 15 July) during the breeding period of the majority of birds and when most were settled on territories, but in 1984 censuses continued until the end of August. Data collected in 1984-1987 were used for yearly comparisons. The population size, distribution and numerical changes of all species present were analysed separately for three habitats: lower flood-plain (flooded annually), upper floodplain (not flooded every year), and river terraces above the flood-plains, in order to describe the spatial and temporal variations of summer wader communities.



Figure 1. Climatic characteristics for 1980-1987 according to data from the Sagyllakh and Stolb meteorological stations in the Lena river delta.

Estimates of relative wader abundance were made according to definitions used by Kuzyakin (1962): "extremely abundant" - 100 or more individuals km⁻², "abundant" - 10-99 ind km⁻², "common" - 1-9 ind.km⁻², "rare" - <1 ind.km⁻². Species representing 10% or more of the total wader population were called the "dominant" or "co-dominant" species.

Results

A total of 15 breeding wader species were recorded at the Lena delta, approximately one-third of the list of breeding birds of the region. In addition, Dotterel Charadrius morinellus, Wood Sandpiper Tringa glareola, Spotted Redshank T. erythropus, Sharp-tailed Sandpiper Calidris acuminata and Pintail Snipe Gallinago stenura were observed sporadically during the summer. Several other waders were considered as vagrants or appeared only during seasonal movements. Waders form the basis of the bird population in the whole Lena delta and in the northern part are the dominant taxonomic group. In almost all habitats Grey Phalarope Phalaropus fulicarius are dominant, the codominants most often being Little Stint Calidris minuta and Pectoral Sandpiper C. melanotos.



Figure 2. The role of dominant species in the wader population of the lower flood-plain in different parts of the Lena delta during the first half of summer in 1984-1987 (% of total density; absolute total densities are shown in lower left corner): Delta areas: S - southern, W - western, E - eastern.

Altitudinal variation in distributions of wader species and populations resulting from typological differences between flood-plain and terrace habitats are characteristic of the region. Bird numbers are heavily influenced by the close proximity of the lower and upper delta habitats. The existence of unflooded areas with moss, herb, and shrub vegetation greatly increases the wader populations in such areas.

The wader population in the lower flood-plain of the delta is rather poor as a result of regular prolonged floods which occur every year. No more than three species were dominant; up to seven species were abundant. The average total density of waders in the lower flood-plain in the first half of the summer over all years was 94 ind.km⁻². The populations vary between the different areas studied. In the southern part of the delta, the total abundance of waders is about ten times higher than in more northerly coastal areas (229 and 21 ind.km⁻² respectively) (Figure 2) and the number of species is two to three and a half times higher (seven and two species respectively). Pectoral Sandpiper, Ruff Philomachus pugnax and Ringed Plover Charadrius hiaticula, which are common in the southern part of the lower flood-plain, gradually become less common further north; Turnstone Arenaria interpres and Little Stint were the only species in the lower

flood-plain which remained abundant in the northern part of the delta. As expected, the proportion of the arctic species Grey Phalarope (11-16 ind.km⁻²) increased with latitude (from 6-76% of the total wader density), while the subarctic species Temmincks Stint *Calidris temmincki* was more numerous in the southern delta area (116 ind.km⁻²).

The upper flood-plain of the northern subarctic occupies large areas of the Lena delta, especially in its eastern and southern part. Species diversity (14 species) and mean density of waders (227 ind.km⁻²) in the first half of summer are almost twice as high in the upper flood-plain as the lower one (Figure 3). The dominant species is Grey Phalarope (79 ind. km⁻²) and in the northern delta the co-dominant is Little Stint. Among other numerous species recorded in the upper flood-plain of the northern subarctic were Pectoral Sandpiper, Ruff, Curlew Sandpiper C. ferruginea, Dunlin C. alpina, Temminck's Stint, Grey Plover Pluvialis squatarola, and Turnstone. In different parts of the Lena delta their contribution to the total wader population varies considerably but in any particular location there are usually only four to eight of these abundant species, and three to five dominant species.

Abundant species formed between 71-100% of the



Figure 3. The role of dominant species in the wader population of the upper flood-plain in different parts of the Lena delta (northern subarctic tundra) during the first half of summer in 1984-1987 (% of total density; absolute total densities are shown in lower left corner): Delta areas: S - southern, C - central, N - northern, W - western, E - eastern.

wader population in the upper and lower floodplain habitats. Densities of waders were highest in the central part of the Lena delta and lowest in its western part. The latitudinal differences described above for the lower flood-plain delta areas are also true of the upper flood-plains. Longitudinal changes (of c. 5°E) in wader species composition and especially in species' densities are also found in the subarctic tundra subzone. Little Stint, the second most abundant species in terms of density in the eastern part of the Lena delta, were present in much lower densites in the western part and was not one of the group of abundant species found there. The same trend is observed in the Grey Plover. On the other hand Ruff, which are common in the western part of the delta, are rare in the east. These features of wader assemblages in the upper flood-plains are probably connected with differences in soil and vegetation characteristics in the two areas, which in turn determine the birds feeding and reproductive conditions.

The wader population in the upper flood-plains of the southern arctic tundra subzone has many characteristics which are similar to those in the northern subarctic subzone. The dominant wader species in both subzones are Grey Phalarope and Little Stint and four to five abundant species in populations of these subzones accounted for 92-96% of the total wader density (Figure 4). Average

estimates of total wader densities in the first half of summer in the southern arctic and northern subarctic subzones are also similar (227 and 238 ind.km² respectively). However, there are several subtle differences which highlight the difference between bird avian communities of the upper floodplains and those of the northern tundra subzone. For example, Pectoral Sandpiper is a co-dominant species in the northern subarctic tundra of the eastern delta, whereas in the southern arctic tundra it is not, although it is still an abundant species. The proportion of Grey Phalarope and Turnstone in the total wader population is higher and that of Little Stint and Dotterel is lower in the southern arctic subzone than in the northern subarctic. The total number of dominant species in the southern arctic tundras is lower than in the northern subarctic (two to three compared with three to four), but they form a higher proportion of the overall wader population than in northern subarctic habitats. Several species, such as Red-necked Phalarope and Dunlin, which were breeding in the subarctic tundras of the Lena delta were not recorded in southern arctic tundra.

Fluvial terraces (10-50 m above sea level) occupy approximately half the Lena delta. Their bird populations, especially close to the edges, represent an improverished variant of the upper flood-plain community. In the first half of the summer, 13 wader species with an average density of 126



Figure 4. The role of dominant species in the wader population in the upper flood-plain in different parts of the Lena delta (southern arctic tundra) during the first half of summer in 1984-1987 (% of total density; absolute total densities are shown in lower left corner). Delta area: N - northern, E - eastern.

ind.km² were recorded in the fluvial terraces of the northern subarctic tundra terraces (Figure 5). Similar species are dominant here, but their contribution to the total wader population differs noticeably. The highest densities in the central delta are observed in Grey Phalarope, both on the upper flood-plain (176 ind.km⁻²) and on the fluvial terraces (52 ind.km⁻²). The list of abundant species for the terraces is rather variable: Dunlin, Grey Plover and Ruff drop out of this group in different places. There are between four and six abundant species and between three and five dominant species, depending on the area of the delta in question.

Studies carried out in 1985 and 1987 suggest that, during the first half of the breeding season, wader numbers in the Lena delta are rather high and stable (Figure 6c). In several wader species, for example Grey Plover and Dunlin, fluctuations in breeding numbers during three reproductive seasons (1984, 1985 and 1987) did not vary more than two-fold. In several abundant species, these fluctuations in

Table 1.	Ranges of variation in wader densities (ind.km ⁻²) in different habitats of the upper flood-plain of the central par	t of
the Lena	delta during the first half of summer.	

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Phalaropus fulicarius	94-412	143-149	158-198
Calidris minuta	12-89	14-53	61-80
Calidris temminckii	3-70	0-5	0-19
Philomachus pugnax	14-92	16-129	28-54
Calidris melanotos	15-65	76-96	90-111
Calidris alpina	11-30	24-36	15-30
Calidris ferruginea	8-27	3-32	13-48
Pluvialis squatarola	10-29	11-16	7-12
Pluvialis fulva	-	-	0-1
Gallinago gallinago	2-3	3-13	13-17
Limnodromus scolopaceus	0-3	0-1	-
Phalaropus lobatus	0-11	3–35	0-26
Arenaria interpres	0-5	1-11	1-2



Figure 5. The role of dominant species in the wader population of the fluvial terraces in different parts of the Lena delta (northern subarctic tundra) during the first half of summer in 1984-1987 (% of total density; absolute total densities are shown in lower left corner): Delta areas: S - southern, C - central, W - western.



Figure 6. Changes in wader population densities in the Lena river delta:

A - average estimates of spatial wader distribution for the altitudinal delta profile during the first half of summer; B - seasonal changes in wader densities in the flood-plain and on fluvial terraces;

C - seasonal and annual changes in wader densities in the upper flood-plain (for the first and second halves of each month).

numbers were clearly due to changes in weather conditions: there was a three-fold difference in Grey Phalarope density, a four to six-fold difference in Ruff, a two to four-fold difference in Little Stint, a three to nine-fold difference in Curlew Sandpiper, a three-fold difference in Pectoral Sandpiper and a two to five-fold difference in Common Snipe *Gallinago gallinago*. The densities of waders either breeding close to the limits of their range (*e.g.* Red-





Figure 7. Changes of the role of abundant (A) and common (B) species in wader population of the upper flood-plain habitats of the Lena delta during summer 1984 (for the first and second halves of each month).

necked Phalarope) or with a localised distribution (e.g. Pacific Golden Plover Pluvialis fulva, Longbilled Dowitcher Limnodromus scolopaceus, Turnstone) were the most variable throughout the study. Temminck's Stint, which tended to breed on river banks, suffered in some years (e.g. 1987) from prolonged spring floods (Table 1).

Sharp seasonal fluctuations in numbers (two to four-

fold or more) were typical, both for the total wader population and for separate species, with maximum density levels during the breeding season. Wader species composition became poorer everywhere in July-August compared with the beginning of summer. Quantitative changes in wader populations are more pronounced in the flood-plain habitats than on the fluvial terraces (Figure 6b). The total number of waders present gradually declines in the second half of the summer, as the adults which will take no further part in incubation or brood-rearing depart (e.g. Grey Phalarope, Ruff, Pectoral Sandpiper) (Figure 7a). In some common species, such as Grey Phalarope, their relative abundance increases because the numbers of several other species (e.g. Ruff, Little Stint, Temminck's Stint, Curlew Sandpiper), which are abundant at the beginning of the summer, decrease by July-August (Figure 7b). Waders which are at the limit of their range in the Lena delta breed irregularly and do not significantly influence the total wader population densities.

Discussion

Latitudinal and altitudinal differences in the composition of wader populations results in variations in the diversity and densities observed in the study area throughout the breeding and postbreeding periods. The high productivity of delta habitats is reflected in the abundance and species diversity of the waders. It is most obvious in the upper flood-plain habitats which are not flooded every year. Habitats above flood-plain level, in terms of the conditions for waders and other birds, are rather similar to upland habitats. However, the bird population of the fluvial terraces, especially at their edges and in areas with lakes, represents only the impoverished type of upper flood-plain avian community. The latter is explained by the rather high water supply (though lower than in the floodplain) and broken relief, which leads to a mosaiclike structure of soil and vegetation.

Wader populations both on the flood-plain and on the fluvial terraces are characterised by a polydominant structure, which is strengthened by the super-dominance of single species. This phenomenon is typical for high latitudes. The super-dominant species (100-120 ind.km⁻²) in the upper flood-plains of the northern and eastern delta is Grey Phalarope, while in the lower flood-plain of the southern delta it is Temminck's Stint. Superdominance is not observed on the fluvial terraces of the Lena delta. The group of abundant species, usually accounting for more than 85% of the total species density and more than 50% of the species diversity is also characteristic of these areas.

Continuous qualitative and quantitative changes in bird fauna occur during the whole summer due to seasonal movements of waders. The specific pattern of seasonal dynamics in wader populations, as well as in some other birds, with the peak in numbers during the breeding season, is considered an adaptation to the extreme arctic environment (Kistchinski 1988). The fluctuations in numbers of different bird populations is evidently the result of the complex interaction of many factors. For many bird groups, particularly for waders, pronounced numerical fluctuations, due to redistribution within the breeding range, migration and other movements, are typical and they are most often observed in arctic regions. Taking into account the fact that the northern subarctic landscapes are sparsely inhabited by people and have experienced little damage from human activities, it can be assumed that seasonal and annual fluctuations in numbers of waders in particular, are determined mainly by natural environmental factors.

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